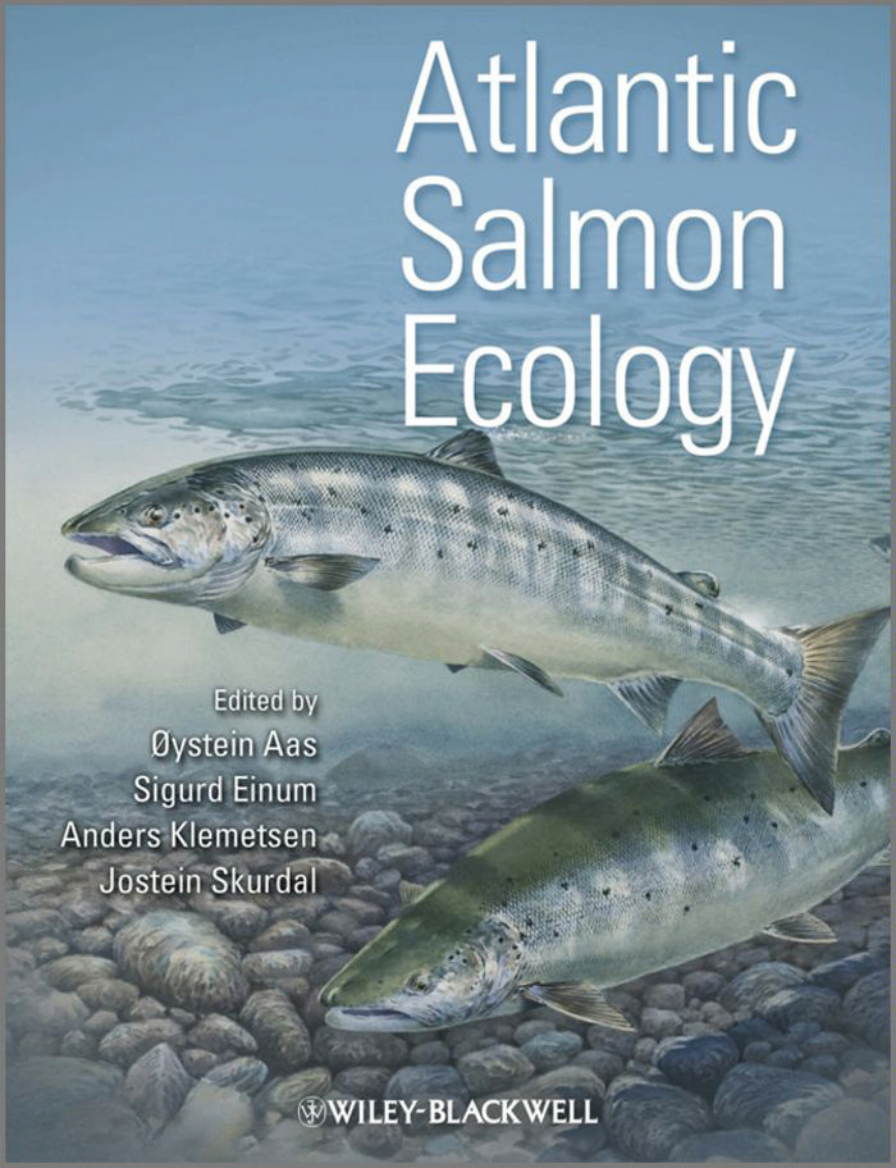


Atlantic Salmon Ecology

The background of the cover is a photograph of two Atlantic salmon swimming in clear water. One salmon is in the upper half of the frame, swimming towards the left, with its mouth slightly open. The other salmon is in the lower half, also swimming towards the left, just above a bed of dark, rounded river stones. The water is a light blue-grey color with some ripples.

Edited by
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Atlantic Salmon Ecology

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Foreword

The Atlantic salmon is an amazing creature which captures the human imagination. Its birth and growth in streams and rivers from the Atlantic coast of the Iberian Peninsula to northern Russia and from New England to Ungava Bay in Canada; its transformation from a freshwater fish to a seawater fish with all the physiological changes that are involved; its migration across thousands of miles of ocean and its accurate return to the river where it was born; sometimes leaping giant obstacles, so as to breed and re-start its life cycle – all these attributes fill us with admiration.

Each successful salmon shows a remarkable tenacity and strength in its life and an unfathomable skill in navigation across trackless seas to find its feeding grounds and then, even more remarkably, to get back to where it was born. Perhaps for these reasons socio-economic studies show that people who will never catch a salmon or perhaps never even see one, care very much about its survival. It is also, in a sense, a symbol or an icon for humankind. If the wild salmon are in our rivers and in our oceans and going about their migrations, then all is well in our world.

But all is not well in the salmon's world. All the North Atlantic governments with salmon interests have taken strong conservation measures, all have cooperated internationally through NASCO to ensure that salmon originating in one country are rarely intercepted in fisheries in another country. International agreements have also been adopted guiding management of salmon fisheries, protecting and restoring salmon habitat and interactions from salmon farming, introductions and transfers and transgenic salmon.

All of these actions can only greatly benefit the wild stocks but, in spite of this, the wild salmon have not returned in their former abundance. In fact over the last 30 years survival of salmon at sea has halved. It seems that large factors beyond our control may be influencing survival. That is why the research focus now includes much more work on the marine phase in addition to the efforts to further understand the freshwater stage where management actions aim to maximise smolt production.

To understand such a complex fish needs many scientific inputs from many specialists, on migratory behaviour, reproduction, habitat, feed in the river and in the oceans, predators, parasites, impacts of forestry, hydropower, aquaculture and pollution as well as the impacts of climate change. All these are covered here.

For all these reasons I am delighted that this book, *Atlantic Salmon Ecology*, has been produced. It is timely and I congratulate the Norwegian Research Council and other sponsors who facilitated its production, and all who contributed to it. It puts together a complex jigsaw of all the myriad elements which comprise and affect *Salmo salar*. Such a synthesis will undoubtedly help us all, scientists, managers, administrators and interested members of

the public to understand the issues and factors which surround the salmon's life cycle. If knowledge is the key to successful management, and I am sure that it is, this book should strengthen the hand of all of us who work for the conservation and restored abundance of this remarkable species.

Dr Malcolm Windsor
Secretary of NASCO
Edinburgh
October 2009

Preface and acknowledgments

Another salmon book? Is there really a need for another book on Atlantic salmon? We think the answer to this is an emphatic ‘yes’. Although other books have treated conservation, genetics and evolution of salmonids, or even the ecology of other salmonid fish species, none of these focus on the ecology of Atlantic salmon or cover this topic in a comprehensive way. Furthermore, the scientific understanding of Atlantic salmon ecology has grown immensely during the past few decades, and many of the issues that have turned out to be important for this species are likely to be of importance for others as well. Thus, there is a lot to be learnt about general ecology by using this species as a model organism. Finally, there has been a recent, and alarming, decline in many Atlantic salmon populations across its entire range, and understanding the ecology is the key for appropriate management response.

The main aim of this book is therefore to give a comprehensive treatise on Atlantic salmon ecology. To achieve this, we cover migration, reproduction, habitat, feeding, growth, competition, predation, parasitism, population dynamics and landscape use. Some of these chapters touch upon problems faced by Atlantic salmon due to anthropogenic disturbance (e.g. alteration of in-stream habitat, the spread of parasites in fresh water including *Gyrodactylus salaris*, fishing mortality). In addition, five of the chapters deal explicitly with obvious ecological threats caused by human activity (sea-lice problems associated with aquaculture activities, landscape use, hydropower development, pollution and climate change). Some might ask why the current challenges related to genetical and ecological impacts from escaped farmed salmon is not covered in a separate chapter. While some of these challenges are discussed for instance in Chapter 2 and Chapter 7, we would direct the reader specifically interested in these topics to the recent book “*Atlantic Salmon. Genetics, Conservation and Management*” edited by Verspoor et al. (2007).

When we started discussing the framework, aims and focus of the book, some decisions had to be made. Should we ask for detailed literature reviews of all aspects of Atlantic salmon ecology, or should the focus be on the very recent research placed within conceptual structures? After some discussion, we decided to let this vary between chapters because, in some fields, it is feasible to give a rather comprehensive review while in other fields it would be better to draw attention to the most recent developments at the expense of a full literature coverage, especially of the older literature. We also wanted to give the authors more leeway in their approach to the field we asked them to cover. We think this decision has made the book more interesting, while, at the same time, the primary goal of presenting state-of-the-art knowledge on the ecology of the Atlantic salmon is not lost.

A second issue was to what extent information from other salmonid species should be included. Although many salmonids, and perhaps particularly brown trout, are similar to

Atlantic salmon in many respects, it is not always obvious whether information from these species is directly transferable. Differences among species are often just as obvious as are the similarities. We therefore decided that the focus as far as possible should be on the Atlantic salmon.

We also knew that a book on Atlantic salmon ecology would have the potential to attract readers from different disciplines and professions. We wanted to produce a book that can be of use for managers, scientists, students and general naturalists. Thus, we try to avoid extensive use of scientific jargon (or else explain scientific terms either in the text or the accompanying glossary). However, scientific style is sometimes required for a full understanding or for applying particular theories or techniques in one's own work. Thus, technical and/or theoretical issues that are not required for a more general understanding are placed in boxes to enhance readability for non-specialists.

Finally, this book should deal with ecology. Yet, there is a fine line between ecology and evolution; the ecology of a species will influence its evolution and vice versa. Our philosophy with regard to this was to invite authors that we knew had their main interest biased towards the ecology, and to let the authors themselves to a large extent define the focus of the chapters within the given topics. We are very happy with the way this worked out, and believe that we have successfully avoided significant overlap with previous books on salmonid evolutionary ecology and genetics.

To cover the vast area of Atlantic salmon ecology is no minor task. To accomplish that, we wanted active Atlantic salmon ecologists as authors, be they basic, applied or management scientists. We deliberately encouraged a mixture of well established and younger scientists in the writing teams. Parts of the book reflect the effort that the Norwegian Research Council initiated by running a research programme on the Atlantic salmon during 2001–2007. This boosted publication and, very importantly, national and international cooperation among salmon ecologists. This cooperation is apparent in most of the writing teams. We are pleased to say that few of the authors we contacted declined to take part in producing the book, and those who did had very good reasons to do so. We are also pleased to say that all authors have delivered with enthusiasm; there would have been no book without their whole-hearted effort and cooperation.

The financial sponsors of the project have of course been instrumental in its completion; we thank wholeheartedly the Norwegian Research Council, the Norwegian Directorate for Nature Management, the Atlantic Salmon Centre and the Norwegian Institute for Nature Research for their support. To work with our publisher Wiley-Blackwell and their team lead by Nigel J. Balmforth and supported by Kate Nuttall and Tiffany Feist, has – as always – been a great pleasure! We also acknowledge NASCO and Dr. Malcolm Windsor for an inspiring Foreword. Finally, we would like to thank our reviewers. Two or more reviews were provided for each chapter. The review reports were highly valuable and the comments have contributed immensely to the quality of the different chapters and the book as a whole. To acknowledge the high importance of the review process we present an alphabetic list of all referees following the Introduction. Thank you, all of you!

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Glossary

- 1SW salmon** an Atlantic salmon which has spent one winter at sea before returning to fresh water to spawn; see also **grilse**
- 2SW salmon** an Atlantic salmon which has spent two winters at sea before returning to fresh water to spawn
- ad libitum*** in excess, typically referring to feeding regimes
- alevin** juvenile salmon that still relies (at least partly) on yolk as energy source
- allometry** the relation between the size of an organism and the size of different body parts or its performance (e.g. growth rate)
- allopatric** occurring alone within a geographic area, i.e. non-overlapping distribution with other species in question
- anadromous** having a life-history which involves a migration to salt water and a return migration to fresh water to reproduce
- anthropogenic** human influence on nature
- aquatic** living in water
- bedrock** solid rock underlying surface materials
- benthos** organisms living on the substratum or bottom of water bodies
- Beverton-Holt model** see **stock-recruitment models**
- biological reference point** a calculable quantity against which a comparison of population size yields a description of a population's status
- Bottom-up control** refers to ecosystems in which the nutrient supply and productivity and type of primary producers (plants and phytoplankton) control the ecosystem structure
- carnivorous** feeding on animal tissue
- cascade effects** in ecology, secondary (or higher order) effects caused by the change in population status of one species
- caudal fin** tail fin
- chinook salmon** *Oncorhynchus tshawytscha*, species of **Pacific salmon**
- chum salmon** *Oncorhynchus keta*, species of **Pacific salmon**
- circumpolar** distributed around the North or South Pole
- cline** gradual spatial variation of a character, often paralleling variation in a climatic or other environmental gradient
- coho salmon** *Oncorhynchus kisutch*, species of **Pacific salmon**
- cohort** a group of individuals having a factor in common; in fish ecology often age-class
- common garden experiment** an experiment in which the performance of two different groups of organisms are compared in the same environment to control for the effect of environment on monitored differences

- compensatory growth** enhanced growth compensating for mass or energy losses after periods of slow growth due to food deprivation or cold temperatures
- confidence interval** interval of values within which the estimated mean value can be said to lie with a certain confidence (typically given as 95%)
- conservation limit** demarcation of undesirable population size levels
- conspecific** belonging to the same species
- consumption rate** the rate at which food is ingested
- cortisol** sharp increases in a stress hormone
- countergradient variation** used in relation to genetically based variation in performance among populations along a geographical gradient. Can cause populations that inhabit habitats with poor growth conditions to outgrow other populations when reared in a common environment.
- Cushing model** see **stock-recruitment models**
- degree days** the product of the daily temperature multiplicity the number of days summed over a given period of time
- deme** a local population of potentially interbreeding individuals
- diadromous** fish species that undertake migrations between fresh and salt water
- diel** throughout the day-night cycle
- diet selectivity** the non-proportional ingestion of some prey types over others relative to their availability
- diurnal** active during the daytime
- dorsal fin** fin located on the back
- drift** material carried downstream in running water; in ecology often used for drifting invertebrates
- ectotherms** organisms whose body temperature is primarily determined by that of their environment cold-trading
- emergence** for salmon, the transition from living as an **alevin** in nests to the active life in the water column
- endemic** native to a particular area
- epipelagic zone** the layer in the oceans with enough sunlight for photosynthesis, normally from the surface down to 200 m
- epizootics** sharp increases in the incidence of a disease within a population
- estuary** a water passage where the tide meets a river current
- eurythermal** an organism that tolerates a wide range of temperatures
- exploitation rates** the rate at which individuals are removed from a population for human use
- exploitative competition** reduction in per capita resource availability that is not due to direct interactions among individuals
- fecundity** the potential reproductive capacity of a female salmon measured by the potential number of viable eggs it produces
- fitness** the ability of an individual, in a given environment to survive and produce offspring so as to pass genes on to the next generation(s)
- fluvial** aquatic habitats with running water
- foresight management** decision making regarding a population that is based on predictions regarding the status of the population in the future
- fry** the first stage of the free-living period of a salmon juvenile (i.e. between **alevin** and **parr**); usually used during their first summer

- functional response** the change in feeding rates with changing abundance of prey
- gamete** a mature sperm or egg containing a single chromosome set
- genotype** the genetic constitution of an individual
- glacial deposit** unconsolidated material produced and laid down by a glacier
- grilse** a small adult salmon after one sea-winter found in river or coastal marine area; in practice often defined by size (e.g. <3 kg)
- handling time** the time spent by the predator handling the prey
- homing** the return to a place formerly occupied instead of to other equally probable places, e.g. return to spawning grounds
- hydrology** the movement, distribution, and quality of water
- hyporheos** interstitial spaces between or under stones and gravel
- hyposaline** water with salinity greater than fresh water
- hypoxia** water with reduced oxygen concentration
- immunology** the study of immunity, the chemical response to an infection, used to work out relationships between species based on similar responses
- infestation intensity** the number of parasites per host individual
- interference competition** reduction in per capita resource availability due to direct interactions among individuals
- interspecific** among species
- intraspecific** within a species
- iteroparous** breeding more than once
- kelt** an anadromous salmon that has completed spawning but has not yet returned to the sea
- lacustrine** aquatic habitats without running water, usually lakes
- landlocked salmon** salmon that have lost access to the sea and therefore complete their life cycle in fresh water
- local adaptation** evolutionary adjustments of the characteristics of a population which increases fitness in its local environment
- log-normal distribution** a probability distribution of a random variable whose logarithm is normally distributed
- management target** a desirable stock level, which may be used as an aiming (or reference) point to achieve management objectives
- maternal effect** a non-heritable influence of the phenotype or genotype of the female parent on the development or growth of its offspring
- maximum sustainable yield (MSY)** the largest average annual catch that may be taken from a stock continuously without affecting the catch in future years
- meristic characters** body traits that can be counted (e.g. number of vertebrae, fin rays)
- mesohabitat** hydromorphological classification of habitat types into a categorical framework (e.g. pools, riffles, glides, rapids)
- metapopulation** a group of spatially separated populations of the same species which experience significant amounts of dispersal of individuals among themselves
- microhabitat** habitat over small spatial scales which are relevant for a given individual at a given time
- mixed-stock fishery** a fishery that simultaneously exploits two or more separate populations
- Monogenea** small ectoparasitic flatworms mainly found on skin or gills of fish; the genus *Gyrodactylus* is one of five genera

- morphology** the appearance, form and structure of an organism, especially based on external characters
- mucus** a protective secretion that covers and protects fish skin
- multi-sea-winter (MSW)** a salmon which has spent two or more winters at sea
- natural selection** the systematic difference in survival and/or reproduction among genotypes/phenotypes
- niche** the resources (in a broad sense) utilised by a population or a species
- nocturnal** active during night-time
- North Atlantic Oscillation** a climatic phenomenon in the North Atlantic Ocean of fluctuations in the difference of atmospheric pressure at sea level between the Icelandic Low and the Azores High
- ontogeny** the life history of an individual
- opportunistic feeder** an animal that feeds on all possible food types; its diet reflects food availability
- optimal egg density** the egg density that maximises the recruitment in the next generation
- optimal foraging** foraging which maximises fitness, usually measured as energy intake per unit time
- optimality models** models for how animals are expected to behave to maximise fitness or some trait correlated with fitness
- osmoregulation** *see* **osmotic balance**
- osmotic balance** a balance between the concentration of the body fluids and that of the surrounding water
- ouananiche** landlocked salmon found in eastern Canada
- ovary** female reproductive organ
- overyearling** having spent at least one winter in the stream
- ovulate** to produce eggs or release them from an ovary
- ovum** female **gamete**
- Pacific salmon** salmon species in the genus *Oncorhynchus* native to rivers draining into the Pacific Ocean
- parapatric** geographically adjacent but not, or only marginally, overlapping
- parr** juvenile salmon after the fry stage, named for the characteristic black ‘parr’ marks on the sides of their bodies
- phenology** the seasonal timing of biological development
- phenotype** the traits belonging to an individual (or population/species)
- phenotypic plasticity** the capacity to alter the **phenotype** arising from a given **genotype** in response to variation in environmental conditions
- phototactic** behavioural movement response to light
- pink salmon** *Oncorhynchus gorbuscha*, species of **Pacific salmon**
- piscivorous** feeding on fish
- population** group of individuals that share habitat and gene pool, and that is sufficiently different from other such groups to be treated as a self-reproducing system
- post-smolt** young **anadromous** salmon in the sea, at stage from leaving river until middle of first sea-winter
- precocious** early ripening; sexual maturation in a morphologically juvenile stage
- pre-fishery abundance (PFA)** population size of a cohort prior to any exploitation

- predator** animal that feeds on other animals by ingesting whole or significant parts of individuals
- prevalence** the proportion of a host population that is infected by a given parasite
- prey profitability** the energetic benefit provided by a prey item for a predator while considering both its energetic content and energetic costs associated with locating, capturing and ingesting the prey
- pycnocline** a layer of water where salinity changes with depth
- recruitment** the origin of new individuals to a population through reproduction, in fisheries often defined at the time when the fish become available for exploitation
- regime shifts** when the ecosystem ‘flips over’ from one apparently stable state to another (see also **cascade effects**)
- regression model** a statistical model that describes the relationship between two variables
- rainbow trout** *Oncorhynchus mykiss*, species of Pacific trout
- relative fitness** the relative ability of an individual, **genotype** or **phenotype**, to survive and contribute genetically to the subsequent generation(s); see also **fitness**
- replacement line** a line that describes how population size for a cohort at the reproductive stage (**stock**) depends on its size at the recruitment stage within a cohort
- reproductive isolation** the inability to interbreed, usually used in the context of species but also applicable to isolated populations
- resident** not migrating; stationary
- residual** the deviation between a single observed relation between two variables and the model that describes the overall relationship between the two
- ricker model** see **Stock-recruitment models**
- riparian** located on the bank of a watercourse
- Salmoninae** sub-family of Salmonidae (the salmon family); the main genera are *Salmo* (Atlantic trouts and salmon), *Oncorhynchus* (Pacific trouts and salmon) and *Salvelinus* (charrs)
- scale circuli** rings made in the scale of fish due to temporal variation in growth rates
- sea age** the number of winters that a salmon has remained at sea before returning to spawn
- searching time** the time spent by a predator in finding the prey
- semelparous** breeding only once before dying
- Shepherd model** see **Stock-recruitment models**
- size-selective fishery** a systematic effect of body size on exploitation rate
- smolt** fully silvered juvenile salmon migrating or about to migrate to sea
- smolt age** the number of winters in fresh water prior to emigration as a **smolt**
- smoltification** the physiological and behavioural adaptation to sea water by juvenile salmon
- Sockeye salmon** *Oncorhynchus keta*, species of Pacific salmon
- spawning target** see **Management target**
- spermatophore** a capsule or mass created by males containing sperm
- spermatozoon** male gamete
- spring salmon** salmon which return to fresh water early in the year, generally before May
- standardized mass-specific growth rate (Ω)** a measure of growth which controls for allometric relationships, allowing comparison of growth for fish of different sizes

stochasticity non-deterministic or random process

stock a group of individuals of a species defined on management criteria, such as river of origin, area of capture, or time of capture, which may encompass part of, all of or more than one **population**. This term is generally used to describe salmon either originating from or occurring in a particular area

stock-recruitment model a type of model that describes the relationship between the population size in the parental generation (**stock**) and that of the resulting next generation (**recruitment**); different types exist (e.g. Beverton-Holt, Cushing, Ricker, Shepherd)

straying the movement of, and reproduction by, individuals from one population to another one

swim-up see **Emergence**

sympatric occurring together with another species within the same geographical area

terrestrial living on land

territory a location with a given spatial extent that is defended by one individual against other individuals

top-down control refers to when a top predator controls the structure/population dynamics of the ecosystem

topography the configuration of a landscape including its relief and the position of its natural and man-made features

trade-off a situation that involves losing one quality or aspect of something in return for gaining another quality or aspect

tributary a stream feeding a larger stream or a lake

trophic level the position an organism occupies in a food chain or food web

von Bertalanffy growth model describes the change in growth with body size, usually applied at the mean population level

1

Aquatic Nomads: The Life and Migrations of the Atlantic Salmon

Eva B. Thorstad, Fred Whoriskey, Audun H. Rikardsen & Kim Aarestrup

Abstract

The Atlantic salmon *Salmo salar* L. is native to the temperate and subarctic regions of the North Atlantic Ocean. The species has a complex and diverse array of life-histories, but most forms are anadromous with a juvenile phase in fresh water, followed by smoltification and a long migration to the ocean for feeding and growth, and a return migration to fresh water to spawn. Atlantic salmon return with a high precision to their home river, and typically only a small percentage of a population strays to other rivers. Precise homing may generate and maintain local adaptations through natural selection, and salmon populations in different rivers differ both ecologically and genetically. Individuals of some populations complete their entire life cycle in fresh water, while others may undertake only short migrations to brackish water in estuaries, or stay within marine areas close to the home river. Factors affecting spawning and feeding migrations may impact the reproductive success and survival of individual fish. Migration studies identify pathways, and critical habitats like feeding and spawning areas, and hence are essential for the protection of Atlantic salmon populations. In this chapter, we synthesise information on patterns and mechanisms of movement during Atlantic salmon migrations, covering the freshwater, estuary and marine phases. An overview of the Atlantic salmon life cycle and geographical distribution is also given.

Key words

Life-history, upstream migration, downstream migration, marine migration

1.1 Introduction

The Atlantic salmon (*Salmo salar*, Salmonidae) is native to the temperate and subarctic regions of the North Atlantic Ocean. Like many other salmonids, the species has the ability to move between fresh and salt water (termed anadromy or sea-run, Box 1.1, Fig. 1.1 and Fig. 1.2). In a typical Atlantic salmon population, juveniles will rear for a number of years



Figure 1.1 Humans have exploited fish during their migrations for several thousand years, and fish migrations have historically played an important role in the settlement of human populations (Lucas & Baras 2001). Today, many migrating species have a high economic value, including the Atlantic salmon. Photo: Eva B. Thorstad.

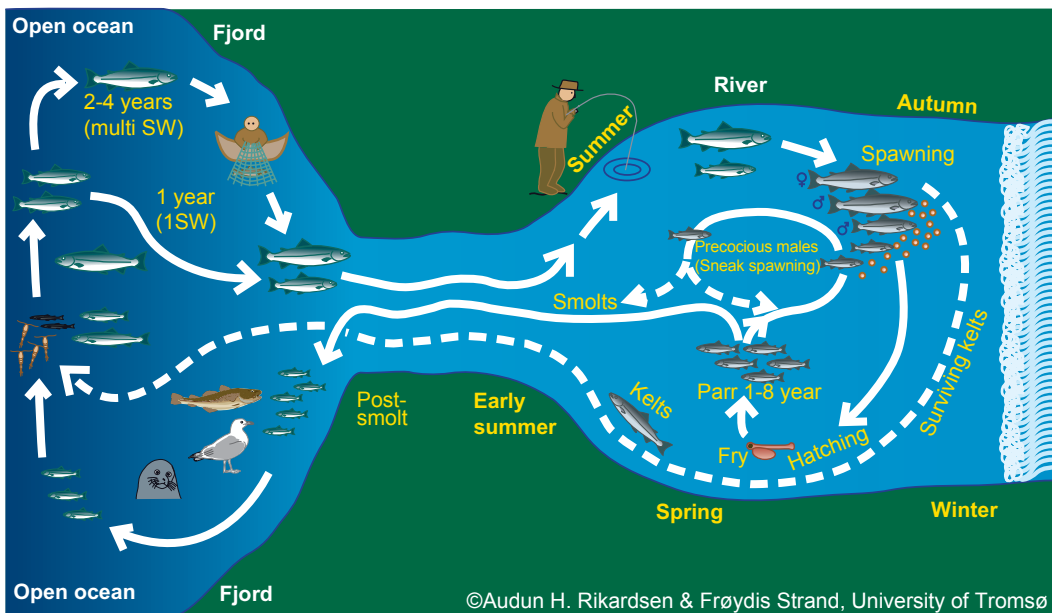


Figure 1.2 Schematic outline of the anadromous Atlantic salmon life cycle, with the different life stages spent in fresh water and at sea.

Box 1.1 Animal migration

Many animals restrict their movements to a well-defined region or space, termed a home range (Burt 1943). Longer-range exploratory movements and dispersal processes may help an animal discover better habitat and resources. Migrations differ from local movements and dispersal, but different authors define migrations differently. Many definitions agree that migrations are synchronised movements that are large relative to the average home range for the species, occur at specific, predictable stages of the life cycle and involve a large proportion of the population (Lucas & Baras 2001).

Migrations may be cyclic movements among reproductive, feeding and/or seasonal refuge habitats, with individuals increasing their fitness by utilising the best habitats during different stages of the life cycle (Northcote 1978, 1984). Lucas & Baras (2001) pointed out that migrations may occur vertically in the water column, or among areas differing in water velocity, water temperature and oxygen gradients. Thus a migration is not necessarily over a long distance.

Box 1.2 The oceanic stage – the least understood period of the Atlantic salmon life-history

Our knowledge of the migration and oceanic distribution of Atlantic salmon comes largely from the capture of fish in marine fisheries, and especially from the capture of individuals marked with external tags. However, the recaptures of externally tagged fish cannot provide definitive information on the migration pattern between the sites of mark and recapture. New tag technologies are beginning to make it possible to document ocean movements of Atlantic salmon in much greater detail, although no technology is yet suitable for all purposes and size groups of fish. Archival tags (also known as data storage tags, DSTs) can provide approximate fish positions and relatively long-term records of environmental data such as depth, temperature, light or salinity. Some of these tags are now small enough to be attached to large salmon smolts; however, they are expensive and the fish have to be recaptured for the stored data to be retrieved. Recently, DST technology has been combined with satellite technology, and these 'pop-up' tags can be programmed to be released from the fish at a set time, and send the logged DST data directly to satellites. Presently, such satellite tags are very costly and too large to place on fish smaller than adult salmon, which has limited their use. Sonic 'pinger' tags (acoustic tags) send a coded sound signal that can be recorded by fixed or movable acoustic receivers. Such tags are used for tagging fish as small as smolts. Course tracks for fish tagged with sonic tags are determined by placing lines of acoustic receivers across the migration routes of fish. As they pass sequentially from one line to the other, information about dates of arrival and rates of travel can be calculated. Sonic tags can also be fitted with sensors that report information such as the depth (pressure) and salinity the fish are encountering at the time they pass a receiver. Limitations on the sonic tags include short battery lives for small fish, and the paucity of receiver units deployed in the ocean.

in fresh water, then move as smolts to the ocean on a long migration for feeding and growth. They subsequently return with a high degree of fidelity to home rivers (fresh water) for spawning (Box 1.1, Box 1.2, Fig 1.2).

While the ocean migration can bring large growth and fitness benefits (e.g. increased fecundity for females), it also carries great costs (Gross 1987). As it migrates, a smolt alters its behaviour from that of a freshwater, territorial, benthic individual to a pelagic, possibly shoaling fish at sea. In the ocean they are confronted with and must adapt to novel predator fields and food types. Their physiology undergoes a major and energetically costly overhaul, changing from a freshwater organism that had formerly struggled to maintain its internal salt content, to an ocean dweller inundated with dangerous quantities of salt that must be excreted (McCormick *et al.* 1998). Many of the smolts leaving home rivers fail to cope with

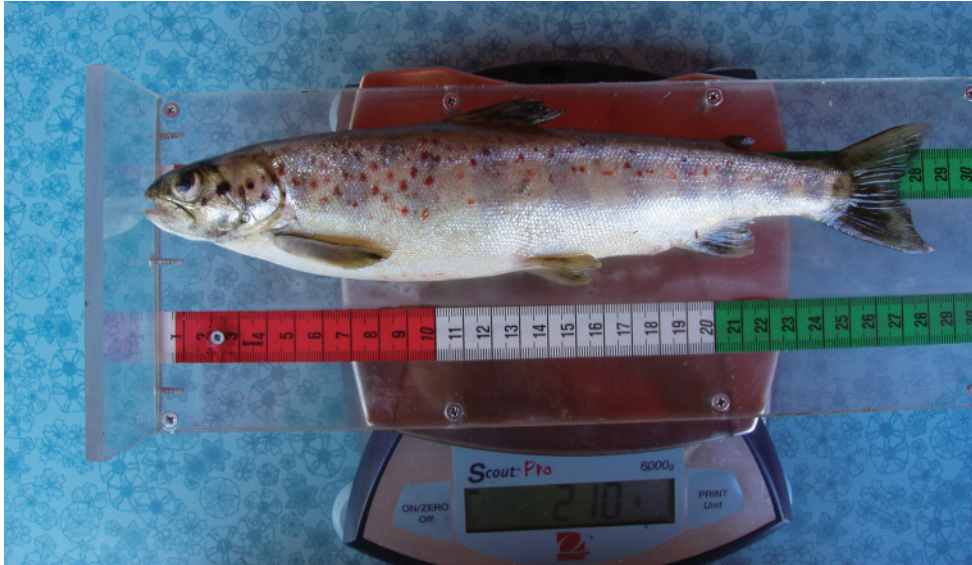


Figure 1.3 Some freshwater resident populations utilise lakes for feeding instead of the ocean, whereas only a few populations live their entire life in the riverine environment (Power 1958; Christie 1973; Berg 1985; Kazakov 1992). This is a salmon from a freshwater resident population in the River Namsen in Norway, which is one of the few populations of salmon spending their entire life in a river without migrating to sea or lakes (Berg 1953). Adult individuals larger than 250 g are rarely found in this population. Little information is available on the life-history and migrations of many freshwater resident populations (Webb *et al.* 2007). Photo: Eva B. Thorstad.

these challenges, and mortality of the migrants in salt water is typically high (90% to more than 99%, ICES 2008).

In nature, an astonishing diversity of migration patterns for Atlantic salmon is evident, ranging from exclusive residence in fresh water ('landlocked salmon', Fig. 1.3) to extensive, long-lasting movements to sea (Klemetsen *et al.* 2003; Webb *et al.* 2007). These patterns are linked to differing individual life-histories, and are presumed to be locally adaptive as they are persistent, widely distributed, and influenced by the environment. Atlantic salmon with very different migration and life-history patterns frequently co-occur at the same sites, suggesting that these characteristics are alternative solutions to optimising individual fitness.

This chapter reviews the life-history and migrations of Atlantic salmon. Our goal is to document the diversity of patterns present in nature, to show how such patterns are adaptive and interrelated, and illustrate why knowledge of them is important for the conservation of wild Atlantic salmon. Our focus is on Atlantic salmon migration to feeding areas in the ocean and return migration to rivers for spawning. Juvenile movements of this species are generally not considered to be migrations (McCormick *et al.* 1998), and are covered by Fleming & Einarsson 2011 [Chapter 2] and Finstad *et al.* 2011 [Chapter 3].

1.2 Atlantic salmon life cycle

Atlantic salmon have a complex and diverse array of life-histories, but most forms are anadromous with a juvenile phase in fresh water, followed by a long migration to the ocean for feeding and growth, and a return migration to fresh water to spawn (Box 1.1, Fig. 1.1



Figure 1.4 Small Atlantic salmon parr may be rather stationary, but large parr may not be as stationary as previously thought and utilise larger areas in the river. Movements over a 22–383 m-long river stretch have been recorded for individuals (mean home range 1300 m², Økland *et al.* 2004). Photo: Audun Rikardsen.

and 1.2). Although most Atlantic salmon undertake marine migrations, some populations complete their entire life cycle in fresh water (Fig. 1.3), while others may undertake only short migrations to brackish water in estuaries, or stay within geographical areas closer to the river such as in the Inner Bay of Fundy and the Baltic Sea (Klemetsen *et al.* 2003; Webb *et al.* 2007). There is also considerable diversity in the age of smolts at migration and first sexual maturation, both within and among populations. These life-history variations are partly under environmental control, since the strategy an individual fish adopts is strongly influenced by the conditions it experiences (Metcalf 1998). Abiotic and biotic factors that affect growth rate, body size and condition at earlier life stages influence subsequent life-history characteristics such as smolt age and age at maturation (Metcalf & Thorpe 1992; Einum *et al.* 2002; Jonsson & Jonsson 2007).

Generally, anadromous Atlantic salmon spawn in rivers from September to February, and the eggs hatch the following spring. Usually northern populations spawn earlier than southern populations, due to longer egg development times in colder water. During spawning, the females dig and deposit their eggs in one or more nests (sometimes termed redds). The eggs hatch in the spring, and the newly hatched fish (*alevins*, 15–25 mm long) utilise their yolk sac for nutrition during the first 3–8 weeks before they emerge from the gravel and start their first feeding as *fry*. The timing of gravel emergence is one of the major ‘bottlenecks’ in the salmon life-history, as an absence of suitable food at the time of emergence will lead to starvation. Therefore, the spawning time in each river is adjusted so that the fry will hatch at the most favourable time (Heggberget 1988).

After hatching, and depending on latitude, environmental conditions and genetics, the juveniles (*parr*) remain in fresh water for 1–8 years (Fig. 1.4), before they transform physiologically and morphologically into *smolts* (i.e. smoltify) and migrate to the sea for feeding (Fig. 1.5). The average total body length of wild smolts is usually 10–20 cm (minimum and

maximum values range from about 7 to 30 cm, respectively), and smolts may weigh from 10 to 80 g. After entering the sea these fish are termed *post-smolts*; this period is believed to be another major mortality ‘bottleneck’ for salmon as the fish struggle to cope with a salt onslaught, novel predators and learning to capture new food types (Klemetsen *et al.* 2003). Smolts leaving rivers seem to enter the open ocean quickly rather than pausing in areas of high predator densities, such as estuaries and fjords. They range over large areas in the North Atlantic Ocean before returning to home rivers to spawn after 1–5 years at sea. During the years at sea the salmon increase in weight from 50 g or less to 1–25 kg (45–135 cm total length), and some individuals may be larger than 30 kg when they return for spawning.

Atlantic salmon are iteroparous, which means that unlike most Pacific salmon species, they are not genetically programmed to die after a first spawning. Following a spawning season, individual Atlantic salmon may return, depending on the site, in the winter, spring or summer to the ocean for additional feeding and growth, and return in subsequent years to reproduce again. Not all individuals become repeat spawners, because many die during the spawning period because of predators, exhaustion of their energy reserves, and disease. Individuals may spawn seven or more times during their lifetime, but most individuals survive to spawn only once or twice (Fleming 1996).

Furthermore, some young males may, prior to migrating to sea for the first time, mature sexually as parr (‘precocious parr’). They produce viable sperm, but these small males are of little interest to large females and do not exhibit courtship behaviour. Instead, they ‘sneak spawn’ near pairs of large fish as the females release their eggs into their gravel nests. Previously mature male parr can either mature as precocious parr again or, if they reach the smolt stage, complete smoltification in spring and migrate to sea for feeding and spawn again when they return to fresh water (Fleming 1996). Thus, these fish are also multiple spawners.

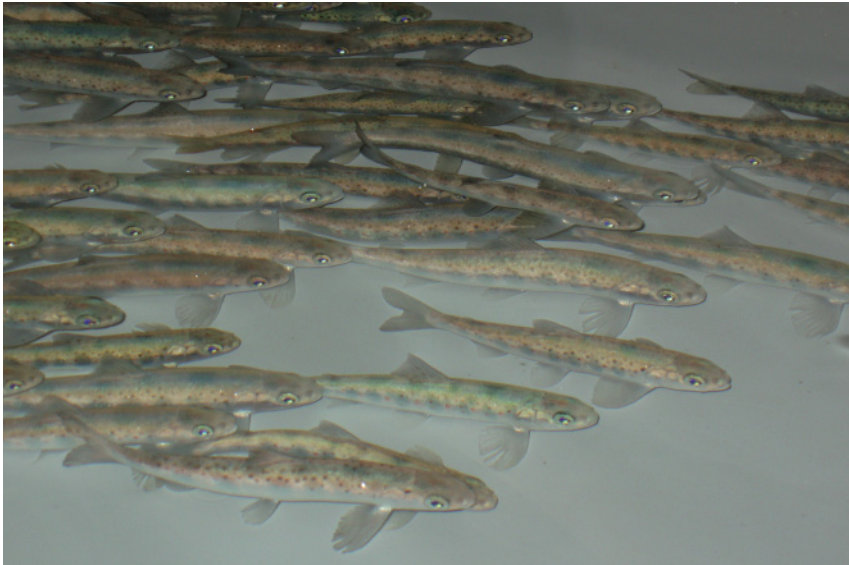


Figure 1.5 A synchronous smolt migration is expected if the optimal period for seawater entry is brief, but a synchronous migration may also reflect an anti-predator behaviour to increase survival (Finstad & Jonsson 2001). Photo: Eva B. Thorstad.

1.3 Geographic distribution

The Atlantic salmon is native to watersheds draining to the temperate and subarctic regions of the North Atlantic Ocean (Fig. 1.6, MacCrimmon & Gots 1979; Webb *et al.* 2007). In the northwest Atlantic Ocean, salmon historically occurred in rivers from New England in the United States to Ungava Bay, Canada. In the northeast Atlantic, salmon occur in watersheds from Portugal in the south to the Barents and White Sea areas of Russia in the northeast. Salmon populations are also found in rivers in the United Kingdom (UK), Iceland, Ireland and Greenland (only one river). The feeding areas in the sea cover large areas of the North Atlantic Ocean (Fig. 1.6; Rikardsen & Dempson 2011 [Chapter 5]).

Salmon populations where the entire life cycle is completed in fresh water (termed ‘fresh-water resident’) occur in both North America and Europe. In North America, they are common throughout the entire distribution range. In Europe, freshwater resident populations occur in rivers and lakes of Russia (Lakes Ladoga, Onega, Kuito and at least six other lakes), Finland (Lake Saimaa), Sweden (Lake Vänern) and Norway (River Namsen, Lake Byglandsfjord) (Kazakov 1992).

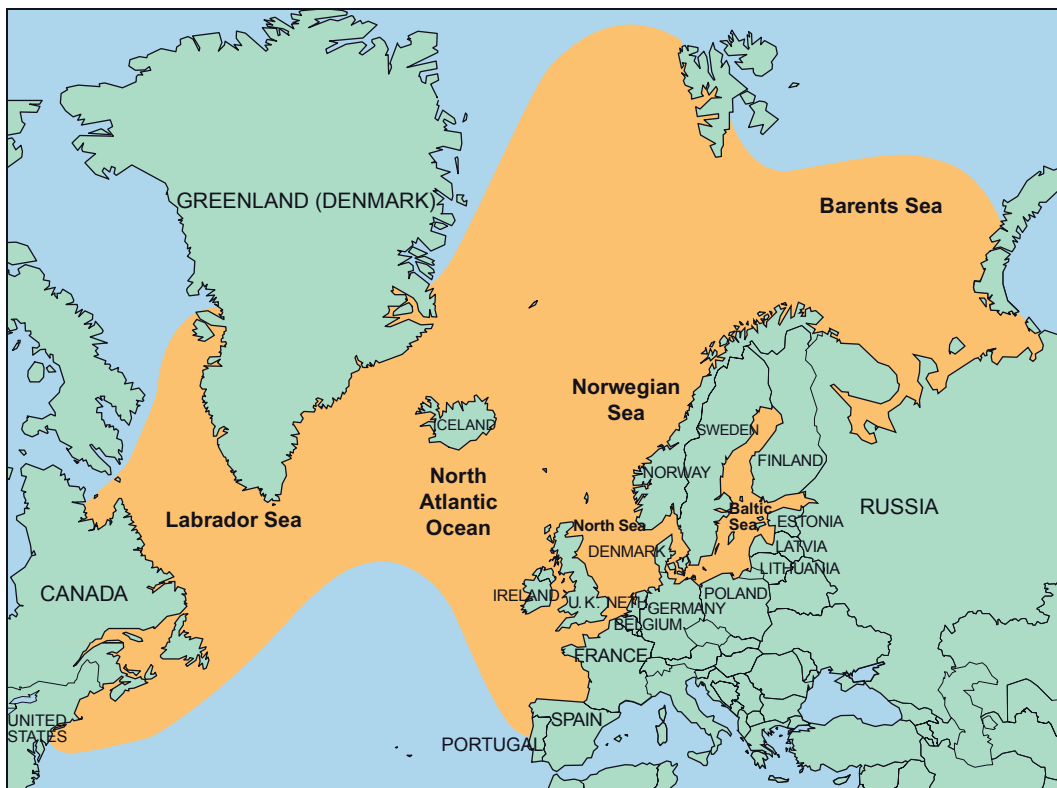


Figure 1.6 Assumed geographical marine distribution of the Atlantic salmon in the North Atlantic Ocean and the associated countries that hold natural spawning populations of Atlantic salmon (given with names). Atlantic salmon occur in watersheds both along the east coast of North America and the west coast of Europe, and feed over large areas of the North Atlantic Ocean. (Figure designed by Kari Sivertsen.)

Virtually all historical attempts to introduce anadromous populations of Atlantic salmon around the world have failed, indicating that the Atlantic salmon is a poor coloniser outside its native range compared to other salmonid species. No self-sustaining anadromous populations of Atlantic salmon have yet been established outside the natural range of the species, except in the Faroe Islands, although landlocked populations appear to have become established in the Southern Hemisphere in Argentina and New Zealand (MacCrimmon & Gots 1979; Lever 1996).

Historically, the Atlantic salmon was distributed in more than 2600 watersheds in the North Atlantic (WWF 2001). Many self-sustaining populations have disappeared or are endangered due to human impacts, and the species range has generally contracted and fragmented (WWF 2001; Webb *et al.* 2007). Nearly 90% of the known healthy populations are now found in four countries (Norway, Iceland, Scotland and Ireland; WWF 2001). In the remainder of the range, 85% of the populations are categorised as vulnerable, endangered or critical, and the species is on the brink of extinction in Portugal, Estonia, Poland, the United States and southern parts of Canada.

1.4 Smolt and post-smolt migration – from juvenile life in the river to feeding in the ocean

The Atlantic salmon smolt migration occurs in the spring and early summer. Before moving to the ocean, the fish undergo a smolting process involving a number of preparatory morphological, biochemical, physiological and behavioural changes that preadapt them for life in high-salinity water and for covering very long distances (Hoar 1988; Høgåsen 1998; Thorpe *et al.* 1998; Finstad & Jonsson 2001). The morphological changes include a slimmer body form, darkened fins and obliterative shading, with a dark back, white belly and silver sides helping to conceal the fish in the pelagic environment. Many of the changes are adaptive for the physiological challenges posed by seawater entry, especially the need to control body salt levels.

In late summer and autumn the year before a smolt potentially migrates, the growth rate and energetic status of the individual fish may determine if it should start its smolting process or delay it for one or more years, or alternatively mature in fresh water (Thorpe *et al.* 1998; Rikardsen *et al.* 2004). Overall, the smolting process is synchronised by photoperiod (increasing day length) and water temperature, and is initiated by environmental factors such as water temperature and water flow (McCormick & Saunders 1987; McCormick *et al.* 1998). Juveniles seem to need to reach a minimum size (typically about 10 cm, although rare smolts as small as 8 cm have been reported) before they smolt and migrate in response to these environmental cues.

1.4.1 Downriver smolt migration

Once the fish are physiologically prepared, the journey to the sea can begin. Usually, downstream movements require an environmental trigger (McCormick *et al.* 1998). The environmental factors cuing downstream migration are mainly water discharge and water temperature. However, each of these factors may be of varying importance, and they may stimulate migration in different ways in different populations (Carlsen *et al.* 2004; Davidsen

et al. 2005; Jutila *et al.* 2005; Antonsson & Gudjonsson 2002). For instance, increased water discharge during the spring spate may initiate the smolt migration in some rivers, whereas in other rivers the migration may be initiated solely by water temperature (Jonsson & Ruud-Hansen 1985; Hvidsten *et al.* 1995). Further, cumulative temperature experience by the smolts over time may initiate downstream migration (Zydlewski *et al.* 2005). Social cues, such as the presence of other migrants in the river, may also be important (Hansen & Jonsson 1985; Hvidsten *et al.* 1995).

The timing of the spring migration has an important role in determining smolt survival in the marine environment (McCormick *et al.* 1998; Rikardsen & Dempson 2011 [Chapter 5]). Within a given watershed, smolts from upper tributaries generally begin migration earlier than those from lower tributaries. This results in a synchronised sea entry for smolts from within the entire watershed (Stewart *et al.* 2006). It is believed that smolts use different environmental cues in the rivers that are predictably correlated with favourable ocean conditions to control movements so that they arrive at sea at an appropriate time (Hvidsten *et al.* 2009). This may account for the differences among populations in which environmental cues are the key triggers of downstream migration. For instance in Norway, smolts from rivers along the coast enter the sea at different times of the season (Rikardsen *et al.* 2004), and the downriver migration is triggered by different environmental factors, but all populations seem adapted to enter the sea when the sea temperature is 8°C or warmer (Hvidsten *et al.* 1998). This implies that smolts from south Norwegian populations start their migration earlier than the smolts from north Norwegian populations, where the salt water reaches the preferred temperature later in the season. This temperature preference could be explained by increased smolt mortality due to low salinity tolerance at low sea temperatures (Sigholt & Finstad 1990). Increased survival at increased temperatures may also be linked to increased prey availability, and perhaps also to increased swimming performance and predator avoidance at higher temperatures (Rikardsen *et al.* 2004; Hvidsten *et al.* 2009). In the southern part of the distribution range, such as in Spain, sea temperatures rarely fall below 11°C during the smolt migration (Javier Lobon Cervia pers. comm.).

The smolt migration usually extends over a 3–7 week period between April and July, with the earliest timing in southern populations (Stewart *et al.* 2006; McGinnity *et al.* 2007; Orell *et al.* 2007), and the majority of individuals within a population may migrate within a relatively short period (1–2 weeks). Smolts often migrate downstream in groups or ‘shoals’ (Hvidsten *et al.* 1995; Riley 2007), and it has even been suggested that smolts may migrate in kin-structured groups (Olsen *et al.* 2004). Shoaling may confer an anti-predator advantage.

Autumn smolt (sometimes termed pre-smolt) migrations are reported from both North American and European rivers (Riddell & Leggett 1981; Huntingford *et al.* 1992), but these fish may reside in fresh water or low salinity areas in the lower and tidal reaches of the river instead of migrating to sea. They seem not to be physiologically adapted to permanently enter the marine environment (Riley *et al.* 2008), and the drivers and reasons for such autumn migration are not presently understood. As downstream migration in the autumn has been studied in only a few rivers, this migration pattern may be more widespread than previously recognised.

Early researchers believed that smolts migrated downstream passively, moved by river currents, but active migration with smolts swimming also occurs (Fångstam 1993; Davidsen *et al.* 2005; Svendsen *et al.* 2007). Smolts may swim with their head pointing downstream,

or may turn against the current and orient their head upstream when, for instance, entering accelerating flow fields in riffles or at weirs (Hansen & Jonsson 1985; Haro *et al.* 1998; Davidsen *et al.* 2005). The net ground speed of downstream migration may vary considerably, with reported velocities from 0.2 to 28 km day⁻¹ (Ruggles 1980). Individual migration speeds may even reach 60 km day⁻¹ (Aarestrup *et al.* 2002). The speed of downstream migration appears slower in small streams than in large rivers (Ruggles 1980).

Downstream migrating smolts often utilise the middle part of the river channel with the highest water velocity, and they appear to move actively out into the main current of the river to avoid being caught in backwaters and sloughs (Hansen & Jonsson 1985; Davidsen *et al.* 2005; Svendsen *et al.* 2007). Smolts often migrate in near-surface waters, but sometimes they may occur in the deeper portions of the water column (Hesthagen & Garnås 1986; Hvidsten & Johnsen 1997; Davidsen *et al.* 2005; Svendsen *et al.* 2007). Differences in migration depth may be an adaptation to avoid local predators (predators hunting in near-surface waters versus those catching their prey close to the bottom), or an adaptation to use the part of the water channel with the highest water velocities (Davidsen *et al.* 2005). On average, the highest discharge in the deepest portion of the channel (the thalweg) occurs from the surface to approximately one-third of the depth, but this will vary with the shape of the river and fluid dynamics (Coutant & Whitney 2000). It has also been observed that smolts actively seek to avoid predators and typical predator habitats (Bakshanskiy *et al.* 1980). In many watersheds smolts encounter lakes and man-made reservoirs, which they actively swim through (Bourgeois & O'Connell 1988; Aarestrup *et al.* 1999).

Smolt migration usually takes place at night, but towards the end of the migration period it may take place both night and day (Hansen & Jonsson 1985; Hvidsten *et al.* 1995; Ibbotson *et al.* 2006). This diel migration pattern is likely to be linked to water temperature, with nocturnal migration occurring at temperatures up to approximately 12°C, and an increasing proportion of the population migrating during daytime at higher temperatures (Veselov *et al.* 1998; Ibbotson *et al.* 2006). Nocturnal migration at low temperatures is thought to be an adaptive behaviour to avoid visual predators. However, daytime migration using visual cues may be preferable for the smolts without considering the predation risk, and daytime migration may be safer at higher water temperatures when smolt escape responses are faster, and maybe also as the body silvers. At high latitudes with 24 hours of daylight, smolts may migrate at all times of the day (Davidsen *et al.* 2005).

If the Atlantic salmon smolts are exposed to contaminants in fresh water, this can have a significant impact on their physiology and migration behaviour. Exposure to sublethal concentrations of acid deposition, aluminium and pesticides can affect subsequent migration activity (Magee *et al.* 2001; Moore *et al.* 2007). Many contaminants, and acid precipitation and associated metal binding, can severely damage fish gills, compromising smolt osmoregulatory capacity (Kroglund *et al.* 2007). This can increase mortality of the fish when they enter salt water, and if the damage is severe enough could conceivably block sea water entry (see also Rosseland & Kroglund 2011 [Chapter 15]).

Hatchery-reared Atlantic salmon smolts from local strains have been released in many watercourses in an attempt to restore and enhance lost or reduced populations. However, survival rates of these cultivated smolts often are low (Finstad & Jonsson 2001). Even though these smolts are from the same strains as the wild smolts, they differ from wild smolts in physical condition and physiological status, and they have been protected from many of the selective factors in the wild (McCormick *et al.* 1998). Such differences may

affect migration timing and patterns of the hatchery-reared smolts, as well as their preparedness to survive in the wild (NRC 2004). The time and site of release also affect the homing abilities of the adult fish (Finstad & Jonsson 2001).

1.4.2 Marine post-smolt migration

The migration of Atlantic salmon smolts through estuaries, from fresh water to the sea, is characterised by active swimming and is a continuous movement, usually with no apparent period of acclimation to adjust to saltwater osmotic and ionic conditions (Moore *et al.* 1998; Lacroix *et al.* 2005). Smolts may not need a period of acclimatisation because they have previously, while still in fresh water, become modified physiologically to tolerate saline conditions (Hoar 1988). The migration of smolts through the estuaries occurs mainly at night and during ebb tides, with the smolts swimming close to the surface, which is often the fastest-moving section of the water column (Moore *et al.* 1995; Lacroix *et al.* 2004). Predation on seaward-migrating salmonid smolts can be significant (Hvidsten & Lund 1988; Jepsen *et al.* 2006; Ward & Hvidsten 2011 [Chapter 8]), and the fast and nocturnal migration through estuaries may serve to reduce the predation risk.

After they leave the river as smolts, Atlantic salmon are termed post-smolts. The migration patterns during the first phase of the coastal migration are complex, with some post-smolts taking a direct route through the coastal embayment and others moving in different directions over short spatial and temporal scales (Økland *et al.* 2006; Hedger *et al.* 2008). However, the migration is active, with an overall seaward vector. Hedger *et al.* (2008) found that swimming speed was greater during the daytime than at night, and suggested that this pattern was consistent with post-smolts migrating offshore nocturnally and using daytime for prey detection and predator avoidance. They also found that exposure to more saline waters increased swimming speeds.

Wild post-smolts in a Norwegian fjord spent on average 5.6 days passing the first 48 km of the marine migration, whereas hatchery-reared post-smolts spent 3.3 days covering the same distance (Thorstad *et al.* 2007b). The faster progression of the hatchery-reared fish was attributed to their larger body size, as their progression rates calculated as body length per second were similar (0.56 body lengths per second for hatchery-reared and 0.53 body lengths per second for wild post-smolts). Based on studies in different coastal areas (Finstad *et al.* 2005; Thorstad *et al.* 2007b; Davidsen *et al.* 2009; Økland *et al.* unpublished results), post-smolts may spend from less than one week and up to four weeks passing Norwegian fjord systems (which are up to 200 km long), before entering the open ocean. Similarly, wild and hatchery-reared post-smolts quickly moved through Passamaquoddy Bay in North America, with most negotiating a distance of 23–36 km in 2–6 days (maximum 12 days, Lacroix *et al.* 2004). However, individual variation in the post-smolt travel rates is generally large.

As post-smolts probably do not take the shortest possible route, progression rates calculated from straight-line transit times between distant points may not reflect true swimming speeds. Further, migration speeds relative to the ground through coastal areas depend not only on the active movement of the smolts, but also on the movements of the water currents, which are mainly forced by tides, winds and freshwater runoff (Thorstad *et al.* 2004). When corrected for the movement of the water, a true post-smolt swimming speed of 1.2 body lengths per second was calculated over 10-minute periods, further supporting the occurrence of active movement of the post-smolts during migration (Økland *et al.* 2006).

During the early marine migration, limited data suggest that post-smolts are usually swimming close to the surface (1–3 m depth), but make irregular dives down to 6.5 m depth (Davidsen *et al.* 2008). The reasons for these depth use patterns are not known, but factors such as predation risk, orientation mechanisms and feeding may singly or in combination affect depth choice. Smolts may also prefer to swim at depths providing the most efficient use of energy either for movements or physiological processes.

Once post-smolts leave the coastal areas, little is known of their detailed migration patterns to ocean feeding grounds (Box 1.2; Rikardsen & Dempson 2011 [Chapter 5]). Atlantic salmon are distributed over large areas of the Atlantic Ocean and undertake long sea migrations. They have been captured in the Norwegian Sea, north of the Faroe Islands, in the Labrador Sea and in the Arctic Ocean, including the North Greenland Sea and the Barents Sea (Hansen & Quinn 1998; Holm *et al.* 2000, 2003; Rikardsen *et al.* 2008). Fish from both North America and Europe may be found on some of the same feeding grounds, such as off the western coast of Greenland (Hansen & Quinn 1998), and it has been proposed that salmon in the North Atlantic Ocean could be classified as a single trans-Atlantic straddling stock (Spares *et al.* 2007). However, tagging experiments have shown that Atlantic salmon from North America remain mainly in the western North Atlantic (Ritter 1989), in contrast to fish from Europe which are believed to feed mostly in the Norwegian Sea and the northeast Atlantic Ocean (Holm *et al.* 2003). Recent tag recoveries have also indicated that some Atlantic salmon may feed in the Barents Sea and one tagged fish was recaptured as far north as 78°N at Spitsbergen (Rikardsen *et al.* 2008). These fish may mostly originate from northern European populations, although some fish from southern European populations may utilise this area as well. It is hypothesised that populations from the Kola Peninsula in Russia and northern Norway utilise the Barents Sea as feeding area, although few fish have been reported captured in these areas (Jensen *et al.* 1999; Rikardsen *et al.* 2008). One reason for this may be the lack of targeted fisheries for Atlantic salmon in these areas, in contrast to the extensive salmon fishing that had been carried out in the northern Norwegian Sea off the Faroe Islands. There is no systematic registration of salmon by-catches of salmon in the marine fisheries in the Barents Sea (Rikardsen *et al.* 2008).

Post-smolts can travel rapidly over long distances, as tagged individuals recaptured in the Faroe-Shetland Channel had covered 713–874 km during the 38–51 days after they were released in rivers as smolts, corresponding to a minimum progression rate of 7–30 km day⁻¹ (Shelton *et al.* 1997). Similar recapture data from the North Sea, the Norwegian Sea and the Barents Sea have shown minimum progression rates of between 6 and 26 km day⁻¹ (Holm *et al.* 2003). Multi-sea-winter salmon may move farther away from home than grilse (Hansen & Quinn 1998). However, it is not known to what extent individuals reside in the same ocean area during their time at sea, or whether they cover large areas.

1.5 Spawning migration – from feeding in the ocean to spawning in the river

1.5.1 Returning from ocean feeding grounds and entering the rivers

The sea age when Atlantic salmon first become sexually mature and return to their home river for spawning depends on genetics as well as on growing conditions at sea, but the

proximate factors initiating the homeward migration are unknown (Hansen & Quinn 1998). Atlantic salmon typically start entering coastal home waters and rivers up to many months before spawning, and the timing of the run is highly variable both within and among populations (Fleming 1996; Klemetsen *et al.* 2003). There appear to be two phases of the oceanic return migration, with a first phase with crude orientation from the feeding areas towards the coasts, and a second phase with more precise orientation in coastal and estuarine waters towards the home river (Hansen *et al.* 1993). The return migration is an active process, and the fish may move both with and against ocean currents, with an estimated migration speed relative to the ground of 50–100 km day⁻¹ in the open ocean (Hansen & Quinn 1998).

Travel rates slow down in near-coastal areas and estuaries, perhaps because the salmon require time to locate their natal rivers (Hansen & Quinn 1998). They may also wait for suitable conditions to enter the rivers, or within the rivers themselves (Potter 1988). Adult Atlantic salmon returning to coastal waters usually remain near the surface (1–5 m depth), but occasionally dive to greater depths. They may be sampling the water column for olfactory cues associated with thermal stratification, which they then use for orientation purposes (Westerberg 1982; Døving *et al.* 1985). When river conditions are favourable, most fish pass through estuaries from sea water to fresh water within a matter of a few hours (Solomon & Sambrook 2004; Thorstad *et al.* 1998). Hence, there appears to be no requirement for a period of physiological adjustment to the change in salinity at this stage, and it has been suggested that maturing Atlantic salmon preadapt to fresh water while still at sea (Høgåsen 1998).

Increased water discharge appears to be an important proximate factor stimulating adult Atlantic salmon to enter rivers from the sea, but may act in combination with other environmental factors such as water temperature, light, tides and water chemistry (Banks 1969; Jonsson 1991). The effects of different factors may also vary from place to place and with season (Banks 1969). Fluctuating water levels may have more pronounced effects in small than large rivers. The stimulating effect of increased water discharge is also found in many large rivers where water discharge seems not to be a limiting physical factor of further upstream migration. The role of discharge in these systems is more difficult to explain (Thorstad *et al.* 1998). However, it is possible that increased discharge is not important to stimulate the salmon to enter the river *per se*, but rather that increased freshwater supply to near-coastal areas may help the salmon to recognise and find their natal river, increasing the number of fish entering fresh water compared to low flow periods.

Most Atlantic salmon in Canada, Iceland and Norway enter the rivers from May to October, i.e. some weeks or a few months before spawning (Klemetsen *et al.* 2003). In Southern Europe, the salmon enter as early as February (Fontenelle *et al.* 1980). Generally, there is a tendency for large multi-sea-winter salmon to enter the rivers earlier in the season than smaller one-sea-winter fish (grilse) (Power 1981; Jonsson *et al.* 1990). In some rivers in Denmark, Scotland and other parts of the United Kingdom, salmon can enter the rivers in all months of the year, with some individuals entering more than a year prior to spawning (Johansen & Løfting 1919; Klemetsen *et al.* 2003). In certain Russian rivers, there is a summer run of salmon spawning the same year, and an autumn run of salmon that remains in the river until the spawning period the year after river entry (Berg 1935). In general, Russian rivers draining to the Barents Sea have few autumn run salmon (5–10%) compared to rivers draining to the White Sea, where autumn run salmon may constitute a larger proportion (up to 90–95%) of the total run (Berg 1948). The exception is the large Pechora River draining to

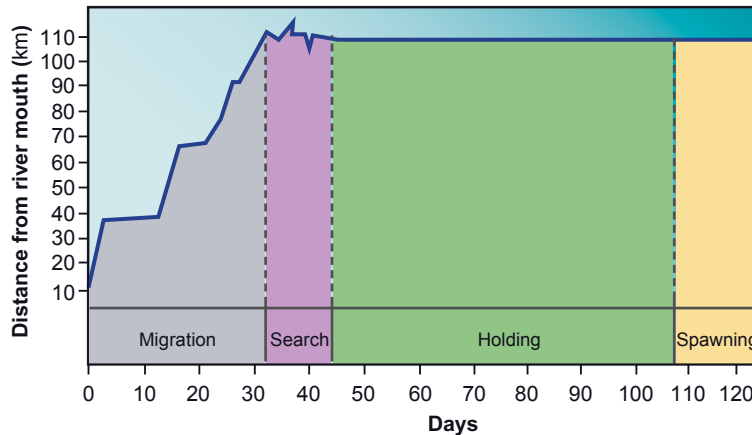


Figure 1.7 Typical upstream migration pattern by adult Atlantic salmon in rivers without large migration barriers (day 0 = entering the river from the sea). The migration pattern can be divided into a migration phase, a search phase and a holding phase (as described in Økland *et al.* 2001, figure designed by Kari Sivertsen, NINA).

the Barents Sea, where the majority of the salmon are autumn run salmon. Autumn run salmon have also been observed in some northern Norwegian rivers (Rikardsen *et al.* unpubl. data) and in the Saint John River in New Brunswick, Canada (Serpentine tributary fish, see Huntsman 1933; Saunders 1981), but why these fish leave the ocean so early instead of staying for one more season of feeding before spawning is not yet understood.

Run timing has been associated with several river characteristics including hydrological conditions, temperature regime, length and difficulty of ascent and sea age at maturity (Fleming 1996; Klemetsen *et al.* 2003). There is, however, no satisfactory adaptive explanation for the early entry time of Atlantic salmon, which results in lost feeding opportunities at sea, and thus reduced growth and potentially reduced reproductive success, especially for females who can carry fewer eggs (Fleming 1996). It has been argued that the early river entry should confer an advantage, because it is reasonable to expect that there would have been a relatively strong natural selection against early river entry if its benefits had not exceeded the disadvantages (Thorstad *et al.* 2008). However, there seems to be no universally valid explanation for early river entry that is applicable for all salmon populations.

1.5.2 Upstream river migration

In generally undisturbed systems, the riverine upstream migration of Atlantic salmon has been reported to take place in two or three successive phases: 1) a migration phase with steady progress upriver with periods of swimming alternating with stationary resting periods, 2) a search phase with movements both up- and downriver at or close to the position held at spawning, followed by 3) a long residence period, also termed the holding phase (Hawkins & Smith 1986; Baglinière *et al.* 1990; Økland *et al.* 2001; Fig. 1.7).

The migration phase may last from an average of a week to more than a month for individual fish, depending on migration distance (Økland *et al.* 2001; Finstad *et al.* 2005). The number of resting periods may increase with migratory distance (Økland *et al.* 2001). In

some UK rivers, where salmon may enter during any month of the year and therefore stay for longer periods in the river, resting periods may last many months, with fish leaving holding pools and migrating further upstream towards the spawning areas in the autumn (Hawkins 1989; Solomon *et al.* 1999). After the upstream migration, Atlantic salmon may have a residence period of one to several months with little or no movement until spawning (Thorstad *et al.* 2008).

A distinct ‘search phase’ after the migration phase has been observed in some studies (Økland *et al.* 2001; Jokikokko 2002; Finstad *et al.* 2005). This search phase may be important in order to select a spawning area, find potential mates or locate a position to hold in until spawning. The search phase may also be part of the orientation mechanism that helps Atlantic salmon to return to the same area of the river where they grew up. The generally observed migration pattern, with a relatively fast and steady upstream migration, seemingly to a particular site, followed by a long residence period, is consistent with the hypothesis that Atlantic salmon home to a site they ‘know’ in the river.

Mean net ground speeds recorded during upstream migration in different studies varied between 1.6 and 31 km per day (Thorstad *et al.* 2008; see also Box 1.3). However, the actual swimming speeds vary with the water velocity that the fish are swimming against, and has not been corrected for in any study that we are aware of.

It is well known among anglers that salmon can be delayed and congregate under large waterfalls and other natural migration barriers, but there are almost no studies documenting the magnitude of such delays, in contrast to the large number of studies on man-made migration barriers (Thorstad *et al.* 2008; Box 1.4). However, migration pauses of up to one month have been recorded under natural waterfalls (Johnsen *et al.* 1998). The fish may not necessarily remain stationary in the pool below the waterfall during this period, but may make local movements in river stretches below the waterfall.

In some river systems, salmon must pass through natural lakes before reaching the spawning grounds. There is little information on the migration pattern or speeds of Atlantic salmon through lakes.

Box 1.3 How fast can an adult Atlantic salmon swim and how high can it jump?

Maximum potential swimming speeds in fish depend on body length (Beamish 1978; Videler & Wardle 1991), among other factors. Maximum swimming speeds for Atlantic salmon grilse (50–60 cm body length) are at least 4 m s^{-1} , or 8 body lengths s^{-1} , according to laboratory studies over 18–20 m distances (Booth *et al.* 1996; Colavecchia 1998). Maximum swimming speeds of $4.3\text{--}6.0\text{ m s}^{-1}$, or $5.8\text{--}8.4$ body lengths s^{-1} , were reported for larger salmon (75–85 cm body length) by Beamish (1978). Maximum swimming speeds in nature are likely to be higher than those recorded under laboratory conditions. Bainbridge (1960) suggested that a 100 cm rainbow trout (*Oncorhynchus mykiss*) may be capable of swimming up to 9.5 m s^{-1} , and it is not unlikely that Atlantic salmon may also be able to obtain speeds up to 10 body lengths s^{-1} .

Little is known about how high Atlantic salmon can jump. Physical conditions such as water depth and velocity beneath the obstruction are important for the maximum leaping capability (Stuart 1962). It is particularly important that the pool beneath the obstacle where fish have to jump be deep enough to permit adequate acceleration. Beach (1984) gave an example of Atlantic salmon ascending a 3.65 m waterfall, which required a launch velocity of 8.46 m s^{-1} .

Box 1.4 Hydropower development and other river regulations affect downstream smolt migration and upstream spawning migration

Lost connectivity of watercourses and barred migration routes are two of the major threats to anadromous salmonid populations (see Johnsen *et al.* 2011 [Chapter 14] for more details). Power stations, dams, weirs and other river regulations may create major passage problems for downstream and upstream migrating Atlantic salmon.

Downstream smolt migration

River regulations may cause altered water discharge and temperature, which may affect both the smolting process and the timing of the downstream migration. If this results in a sub-optimal timing of the migration and entry to the sea, this may affect smolt survival. Smolts may also suffer considerable mortality when passing over spillways at dams, or if they are passing through power station turbines (Ruggles 1980; Hvidsten & Johnsen 1997). Causes of mortality may be mechanical damage, pressure-induced damage, shearing action damage due to passage through areas of extreme turbulence, and cavitation damage due to exposure to regions of particular volume (Ruggles 1980). Artificial reservoirs above dams may delay downstream migration and seriously increase predator exposure (Jepsen *et al.* 1998). Water can be diverted for uses other than for hydropower, and water extraction for fish farms has also been shown to cause mortality by diverting wild smolts into the fish farm instead of following the main river (Aarestrup & Koed 2003; Svendsen *et al.* 2010).

Upstream spawning migration

The high water discharges from power station tunnels frequently attract upstream migrating Atlantic salmon. Delays in such discharges may delay migration for up to several weeks (Rivinoja *et al.* 2001; Thorstad *et al.* 2005; Scruton *et al.* 2007). At some power stations, fish may be further delayed if they must pass an associated dam and fishway (Chanseau & Larinier 1998; Karppinen *et al.* 2002). River regulation sometimes reduces water discharge on certain river sections, for example downstream of power station or fish farm intakes, or downstream of interbasin water transfers. River sections with reduced water discharge may extend over many kilometres, and the reduction in water discharge may be considerable. Salmon may have problems finding and entering such river sections, and once they have entered, they may be further delayed in passing through them (Lundqvist *et al.* 2008; Thorstad *et al.* 2008). On many river sections with reduced water discharge, weirs are provided as mitigation. Such weirs and other artificial obstacles can also delay upstream migration. Rarely, they may completely block fish migration, causing the fish to abandon their home rivers and enter neighbouring ones (Solomon *et al.* 1999; Croze 2005). The length of the delay is hard to predict: fish may be considerably delayed at barriers that appear to humans to be easily passable, or they may quickly pass barriers that appear difficult.

1.5.3 Factors affecting the upstream river migration

Water discharge

River flow is the environmental factor most frequently reported to control upstream migration of Atlantic salmon. However, while numerous studies have shown that increased water discharge may stimulate Atlantic salmon to enter rivers from the sea, fewer studies have examined and documented the effect of water discharge on the general within-river spawning migration. The effects of changes in water discharge on migration seem generally limited in main stems of large rivers without major migration barriers (Hawkins & Smith 1986; Hawkins 1989; Karppinen *et al.* 2004), whereas changes in water discharge are likely to be



Figure 1.8 Fishways of various designs have been provided in many river systems to facilitate upstream passage of Atlantic salmon past power stations and other migration barriers. However, they may not always be successful in facilitating migration, and the fishway itself may act as an obstacle and delay upstream progress. Photo: Eva B. Thorstad.

more important in stimulating upstream migration in smaller rivers (Solomon *et al.* 1999) and past challenging migration barriers.

To allow a successful passage by Atlantic salmon past any particular riffle, waterfall or other migration barrier, water discharge often has to be within a site-specific range (Jensen *et al.* 1986; Rivinoja *et al.* 2001). Several studies have examined effects of water discharge on the upstream migration past fish counters installed in weirs and fishways, providing widely different conclusions (Thorstad *et al.* 2008). Many of these studies demonstrated the importance of water discharge in stimulating Atlantic salmon to pass obstacles, but we are far from understanding the complexity of how this mechanism works. Fish enumeration facilities (weirs, fishways) will in many cases act like a migration barrier (Fig. 1.8), with their own specific water discharge requirements. Results from studies at specific sites, therefore, may be valid only for that specific site. The lack of information about the presence and numbers of fish below the counting site prior to the change in discharge further limits the interpretation and value of such results (Trépanier *et al.* 1996).

We can conclude that the effects of water discharge on migration are complex – and that there is no particular median flow or flow pattern that is preferable for salmon in all rivers, at all sites and migration stages, for all years, or at all times of the year in a given river (Thorstad *et al.* 2008; see also Box 1.4). Responses of individual salmon to variations in water discharge also vary greatly at any given site and time. Water discharge seems to affect migration in a complex interaction with other factors. This complexity often makes it impossible to predict precisely the effects of water discharge on upstream migration, and to define threshold values (Thorstad *et al.* 2008), although wide experience in many places does allow for at least qualitative predictions.

Light conditions

Within-river migration on stretches without large barriers mainly takes place at night, but increased daytime activity may occur during spates or when the water is turbid (Hawkins & Smith 1986; Laughton 1991; Solomon *et al.* 1999). In northern rivers with 24 hours of daylight, migration may not be associated with any particular time of the day (Karppinen *et al.* 2004). The diel movement pattern at fish counting facilities seems site-specific, with conflicting results among studies (Thorstad *et al.* 2008). There may be a conflict between the need for light in order to see how to pass obstacles, and a preference to move in darkness or turbid water as an antipredator strategy (Banks 1969). The different results at different obstacles may, thus, be a result of differing conditions at the time the fish are negotiating their way past the obstruction.

Other environmental factors

Environmental factors other than water discharge, such as water and air temperature, turbidity, atmospheric pressure, cloud cover, and variations in concentrations of many dissolved ions, may affect the upstream migration of Atlantic salmon (Banks 1969). Many of these factors may covary with changes in water discharge. Banks (1969) concluded 40 years ago that such covariates have rarely been acknowledged in studies of upstream migration, and this conclusion still holds today. The principal environmental factor in addition to water discharge that has been studied and found to influence upstream migration is water temperature. Swimming capabilities are reduced at lower and higher water temperatures (Beamish 1978; Booth *et al.* 1996), so that physically demanding obstacles may be difficult to pass at low and high temperatures. Even small obstacles may be difficult to ascend at water temperatures below 5–6 °C (Jensen *et al.* 1986; Gowans *et al.* 1999). The lower and upper limits for fish activity are to some extent dependent on acclimatisation (Beamish 1978).

Water pollution

Sublethal exposure to environmental stressors, such as water pollution, may induce a behavioural response to avoid the stressor (Gray 1990). The ability to avoid physical and environmental stressors and find areas of more favourable conditions may have significant effects on fish survival rates. Avoidance behaviour of adult Atlantic salmon has only been demonstrated in a few cases; in relation to acidification events (high pH and labile aluminium), copper and zinc pollution and to non-toxic waste from decommissioned wood pulp industry facilities (Skogheim *et al.* 1984; Saunders & Sprague 1967; Thorstad *et al.* 2005). Confronted with these stressors, the fish showed avoidance behaviour, escaping to points either upstream

or downstream of the pollution source, and in some cases even leaving the river. However, when fish are not able to detect and avoid water pollution, survival and reproduction may be affected.

Intrinsic factors

Maturation stage, energy state, hormonal control and stress level may all be physiological factors influencing and in some instances controlling the upstream migration pattern. Such intrinsic factors are sometimes collectively referred to as 'motivation' for migration. Although intrinsic factors may be a key to understanding migration patterns, there are few studies of how these factors affect migration alone or interact with other factors. For example, a fish may not be motivated to pass a migration barrier before a certain internal state is reached, and the achievement of this state may or may not correspond with favourable timing of environmental characteristics that would permit the fish to negotiate the obstacle.

The motivation to migrate may increase as spawning time approaches. Early run fish tend to delay longer below fishways than later run individuals (Gowans *et al.* 1999; Laine *et al.* 2002), and Johnsen *et al.* (1998) noted that the motivation to pass a waterfall increased as the spawning season approached. However, both sustained and prolonged swimming performance of Atlantic salmon seem to be reduced as the spawning period approaches, probably due to a combination of decreased water temperatures, changes in body morphology due to maturation, and depletion of lipid levels (Booth 1998).

Previous experience

Several studies have shown that hatchery-reared and farmed fish deprived of natural juvenile river life differ from wild fish in their return migration pattern. Hatchery-reared salmon are released in many rivers to support populations. Farmed salmon occur in nature due to escapes from fish farms (Naylor *et al.* 2005). Common features of hatchery-reared and escaped farmed salmon seem to be a late river entry and an erratic within-river movement pattern compared to wild salmon, resulting in entry to spawning areas later in the season (Jonsson *et al.* 1990; Carr *et al.* 1997; Thorstad *et al.* 1998; Aarestrup *et al.* 2000). The altered migration behaviour is probably largely explained by a fish's previous experience and lack of river imprinting, but physiological, morphological and genetic differences may add to these differences.

Capture and handling of wild fish during the upstream migration may also affect the migration pattern. Catch-and-release angling may for instance cause unusual delays, downstream movements and erratic displacements (Mäkinen *et al.* 2000; Thorstad *et al.* 2007a; but see Whoriskey *et al.* 2000). The reasons for the altered migration behaviour are not known, but could signal stress effects. Downstream movements may also simply be an avoidance response in order to escape areas with 'unfavourable' conditions.

Consequences of altered migration patterns and delays

The upstream migration may be delayed up to many weeks at natural and artificial obstacles (Thorstad *et al.* 2008; Box 1.4). Prolonged delays that prevent timely arrival at suitable spawning areas may reduce individual reproductive success. However, the population consequences of the delayed arrival of significant numbers of salmon at spawning areas are not known. If the early river entry is associated with advantages at the spawning grounds, then delays may have disadvantages. The consequences of migration delays that do not extend

beyond the spawning period cannot be fully understood before we understand the reasons for, and possible advantages of, early river entry. In addition to population effects, migration delays may cause difficulties for sport fishery management, with increased catches in the lower parts of the rivers and decreased catches in the upper parts. Further, accumulation of fish below migration barriers may increase population vulnerability to disease outbreaks, such as from furunculosis (Johnsen & Jensen 1994).

Migration barriers, unusual migration patterns after stressful events or an avoidance response in an attempt to escape from unfavourable conditions may alter the distribution of the spawning population within the river. Salmon may, for instance, abandon their attempts to reach areas high in the watershed and instead spawn in lower reaches (Solomon *et al.* 1999; Box 1.4) or even leave the river. Juvenile survival is strongly density-dependent during the first months following emergence (Einum & Nislow 2005). Thus, the number of juveniles surviving through the first summer depends in part on the spatial distribution of utilised breeding habitats. A truncated or patchier distribution of spawners caused by migration barriers could result in localised and exceptionally high juvenile densities, which could reduce a river's total salmon production. Consequently, the maximum production potential of the river is not realised.

1.6 Kelt migration – after spawning and during outward migration

Atlantic salmon frequently survive spawning, return to the ocean, and can return to fresh water in future years for additional spawnings. The immediate post-spawn fish, termed kelts, are potentially a productive and economically important part of the population. Repeat spawners – especially females – can contribute many more eggs toward the production of the next generation than a first-time spawner, as they usually have a much larger average body size. Kelts either migrate to sea immediately after spawning, or remain in the river for weeks or months before returning to the sea (Webb *et al.* 2007). Little is known about this phase of the Atlantic salmon life cycle. Kelts from many rivers migrate to the sea during the spring or summer after spawning (Jonsson *et al.* 1991; Niemelä *et al.* 2000; Fig. 1.9). A high survival rate and fast progression of kelts throughout near-coastal areas may indicate that sea entry and early sea migration is not a critical phase for these fish, despite their presumed weakened condition due to the energetic drains of spawning and the absence of feeding during their sojourn in fresh water (Halttunen *et al.* 2009). In a study of salmon kelt migrations in a fjord, mean progression rates during the first 30 km after leaving the river was 1.6 km h^{-1} , and the fish generally stayed close to the surface (individual mean depth of 2 m, Halttunen *et al.* 2009). Kelts resume feeding in fresh water during their return to the sea. Survivors may remain at sea for as little as 3–5 months ('short absence', or 'consecutives') or more than a year ('long absence', or 'alternates'), before returning to repeat spawn (Webb *et al.* 2007).

1.7 Homing and orientation mechanisms

One of the most intriguing aspects of the Atlantic salmon life-history is their ability to leave their rivers to travel to distant ocean feeding areas, and then find their way back and rec-



Figure 1.9 Kelts potentially comprise a productive and economically important part of Atlantic salmon populations. It is important to facilitate downstream passage past dams and power station turbines for kelts as well as for smolts (Kraabøl *et al.* 2009). The challenges in providing downstream passage (avoiding turbines, finding a route through reservoirs where natural migration cues are lost) are different from those necessary for upstream movements. Photo: Eva B. Thorstad.

ognise their home river. Hasler's (1966) brilliant research documented the key role olfaction plays in fish homing. Atlantic salmon return with a high precision to their home river (Harden Jones 1968; Stasko *et al.* 1973), although a small percentage of the population strays to other rivers. Usually less than 3–6% of the mature wild salmon return to rivers other than the one they were hatched in (Stabell 1984; Jonsson *et al.* 2003). Precise homing may generate and maintain local adaptations through natural selection, and salmon populations in different rivers differ both ecologically and genetically (Taylor 1991; Verspoor *et al.* 2005; Garcia de Leaniz *et al.* 2007). Moreover, Atlantic salmon apparently return to the same area of the river where they spent their pre-smolt period, and ecological and genetic differences among subpopulations within rivers have been documented (Heggberget *et al.* 1986, 1988; Summers 1996; Verspoor *et al.* 2005).

There is limited experimental evidence regarding the sensory mechanisms and cues used in open-ocean migrations, but the stimuli guiding salmon in the open ocean most likely differ from those used in estuaries and rivers (Hansen & Quinn 1998). Oceanic migration can be fast and directional, and Atlantic salmon are able to hold general directions without the need for learning (Hansen *et al.* 1993; Hansen & Quinn 1998). The homing migrations cannot be described exclusively as passive and current-guided, or as random trial and error processes. A diverse array of cues used for homing has been proposed, including celestial and magnetic compasses and infrasound patterns in the ocean (Moore *et al.* 1990; Sand & Karlsen 2000), but the exact mechanisms are not known.

It is widely accepted that the final phase of the spawning migration is primarily governed by olfactory discrimination of home-stream waters. Nordeng (1977) proposed through his pheromone hypothesis that the homeward navigation was an inherited response to population-specific trails released from descending and outward migration smolts. However,

tagging and release experiments have shown that Atlantic salmon are able to return to the home river, or site they were released as smolts, regardless of the presence of outward migration smolts from the same population. Hence, the different river systems must have other olfactory characteristics that can also be recognised by the returning salmon.

Imprinting is thought to be the mechanism by which the young salmon, in a similar way to other fish species (e.g. Hasler 1966), learn the olfactory and other characteristics of their home site for recognition as returning adults (Harden Jones 1968). Hence, the homing of adult Atlantic salmon is likely to be based on sequential learning of cues gained as a smolt in a complex sequence during the downstream and outward migration (Hansen *et al.* 1993). The learning process during smolt migration to the sea seems to become fixed, and was not overridden by a new learning process at the post-spawning stage in a transplantation experiment (Hansen & Jonsson 1994).

1.8 Conclusion and future research needs

Accurate general outlines of the life cycle and migrations of the Atlantic salmon were described during the sixteenth century by Hector Boece and the priest Peder Claussøn Friis (summarised by Mills 1989). Despite this, there was a subsequent period of more than 150 years when many naturalists believed that the Atlantic salmon parr and the other life stages belonged to separate species. General agreement over the Atlantic salmon life cycle was finally reached during the 1860s (Mills 1989). Since then a large amount of scientific literature has been published providing new insights into the Atlantic salmon's life cycle and migrations. A search of the ISI Web of knowledge literature database on 'Atlantic salmon and life-history' resulted in a list of more than 700 published works (search made 2 June 2010). A second search on 'Atlantic salmon and migration' provided nearly 950 published works. These clearly demonstrate the considerable efforts made to understand the life and migrations of this species over the last few decades. Factors affecting feeding and spawning migrations may impact the reproductive success and survival of individual fish, with ensuing consequences for populations and the species as a whole. For the conservation and management of Atlantic salmon populations, knowledge of migration pathways and of critical habitats such as feeding and spawning grounds is, therefore, essential.

Although the Atlantic salmon is among the most studied fish species of the world, it still holds many secrets in both its freshwater and marine phases. One of the remaining mysteries is how this 'primitive' fish is able to migrate long distances in fresh water and at sea, and still be able to find its way back to its home river. Our understanding of the general mechanisms controlling the timing and patterns of Atlantic salmon migrations is lacking, especially for the return spawning migration. In rivers, certain factors (e.g. water temperature and discharge) affect migrations, yet we still cannot reliably predict when an upstream-migrating Atlantic salmon will pass a certain site or barrier. Additional factors such as maturation stage, physiological processes, energetic status and social factors probably modify responses to environmental cues, but presently we have a poor understanding of how this occurs. Further studies with a high resolution in time and space, incorporating more variables, and with large sample sizes, are needed. Controlled laboratory experimental studies, for example on swimming performances at different stages under different conditions, will help us to determine the limits of what the species can cope with at different points in its life. Not

surprisingly, many migration studies have been conducted in regulated rivers and at artificial migration barriers. The things we learn in these circumstances may not apply to the species in pristine rivers, but we have too few studies from undisturbed sites to know if this is the case.

For the riverine smolt migration, the triggers initiating the migration are better known, but the environmental factors that influence movements have largely river-specific effects. Hence, to provide mitigation measures for human disturbances (e.g. for hydropower installations), river-specific models will have to be developed. Many smolts in certain rivers are killed due to water abstractions, power stations and artificial barriers. There is an important need for new research on ways to assist the smolts to avoid these hazards during their migrations. Smolts are also vulnerable to contaminants, but our understanding of how different contaminants may affect the migration is lacking. Smolts within a river seem to synchronise their sea entry, perhaps to reduce predation risk through confusion effects and predator swamping. How different natural and anthropogenic factors may affect the synchronisation of sea entry and first part of the sea journey is also not well understood.

Kelts and multiple-spawners may be important components of Atlantic salmon populations. However, we have only just begun to investigate the migrations of these individuals.

A common problem for research at sea on all stages of Atlantic salmon has been a lack of capability to carry out the work. Advances in technology and molecular genetics during the last decade are beginning to provide this capability (Box 1.2). With the new methods, information on migrations of salmon in the open ocean is likely to increase in the coming years.

In conclusion, the life-history and migration strategies of Atlantic salmon are among the most plastic and variable in the animal kingdom. Individuals can complete their life cycle entirely in fresh water, or become anadromous. If they become anadromous, they can spend anything from a few months to more than five years at sea before returning to spawn. After spawning, they can return to sea, but spend much shorter or much longer periods there before returning to reproduce again compared to what they did in their previous spawning. The co-occurrence of these multiple strategies, frequently within the same site at the same time, indicates that there is more than one adaptive solution to an individual salmon's task of optimising its fitness. This variability has the potential to impart a remarkable resilience to this species. It provides a template upon which the species can adapt to both short- and long-term changes to its environment. As Darwin never said: 'It is not the strongest species that survive, nor the most intelligent, but the ones most responsive to change' (<http://www.guardian.co.uk/science/2008/feb/09/darwin.myths>).

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2 Reproductive Ecology: A Tale of Two Sexes

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Abstract

The reproductive ecology of Atlantic salmon involves the allocation of substantial amounts of resources, which need to be garnered throughout life, to the successful production of offspring. This investment of resources is devoted not only to the production of gametes, but also to breeding migration, competition for breeding resources and mates, courtship and mate choice, and the elaborate traits that underpin these behaviours. In this chapter, we explore the patterns and traits that comprise the reproductive ecology of Atlantic salmon, and their influences on the growth and survival of early life-stage juveniles. Both males and females invest approximately 60% of their total energy during reproduction, with females investing heavily in egg production and males in behavioural activity (e.g. mate competition). Intense male competition for access to mating opportunities has led to the evolution of elaborate secondary sexual characters (e.g. hooked snouts and gaudy breeding colouration) and alternative reproductive phenotypes, where some males mature in fresh water as parr at less than a hundredth the weight of their anadromous male counterparts. Rather than fight for access to spawning females, these mature parr attempt to ‘sneak’ fertilisations. In contrast to males, females direct much of their behaviour during reproduction towards activities that ensure oviposition success and offspring survival. There can be tight, direct links between maternal traits, such as egg size, spawning time and spawning location, and offspring success. Egg size largely determines the offspring’s resources until exogenous feeding several months after fertilisation, and spawning time and location the environmental conditions the offspring experiences prior to, and following emergence from the gravel nest.

Key words

Breeding system, reproductive success, alternative reproductive tactics, maternal effects, age at maturity, reproductive investment, breeding behaviour, egg size, spawning time, spawning location

2.1 Introduction

The differences in the way that the two sexes achieve reproductive success are fundamental to the biology of salmon. They can influence patterns throughout the life of a salmon, from

larval development to juvenile habitat, behaviour and growth to age and size at maturity. This is because sexual reproduction involves the allocation of substantial amounts of resources, which need to be garnered throughout life, to the successful production of offspring. This investment of resources is devoted not only to the production of gametes, but also to competition for breeding resources and mates, courtship and mate choice. And underpinning these behaviours are elaborate physical traits, such as diverse sizes at maturity, gaudy ornaments and formidable weapons. To Charles Darwin (1859), salmon were a prime example of his concept of sexual selection, which he introduced in *On the Origin of Species*:

How low on the scale of nature this law of battle descends, I know not; male alligators have been described as fighting, bellowing, and whirling round, like Indians in a wardance, for the possession of females; male salmons have been seen fighting all day long; male stag-beetles often bear wounds from the huge mandibles of other males. The war is, perhaps, severest between the males of polygamous animals, and these seem oftenest provided with special weapons. The males of carnivorous animals are already well armed; though to them and to others, special means of defence may be given through means of sexual selection, as the mane to the lion, the shoulder-pad to the boar, and the hooked jaw to the male salmon; for the shield may be as important for victory, as the sword or spear.

In this chapter, we explore the elaborate patterns and traits that comprise the reproductive ecology of Atlantic salmon, and their influences on the growth and survival of early life-stage juveniles.

The very nature of having two sexes affects the fundamental patterns of reproduction. That is, having one sex that produces large gametes for improved offspring survival (by definition females) and another sex that produces small gametes for increased fertilisation success (by definition males). As such, the large gametes, ova, evolve to a size that maximises the number of surviving offspring and the small gametes, sperm, to a size that maximises their ability to access ova and compete with other sperm for fertilisations (Parker 1984). This fundamental distinction between the sexes influences the patterns of sexual selection (i.e. selection for traits that enhance breeding opportunities) and the life-history and structural, physiological and behavioural traits the two sexes express. It also gives rise to the basic, though somewhat simplistic, paradigm that female breeding traits tend to be shaped mainly by selection for offspring production and survival, and those of males by selection for access to mates (Box 2.1).

Box 2.1 Operation of sexual selection

The investment in gametes and offspring survival decreases the potential rate of reproduction for females (Clutton-Brock & Parker 1992; Ahnesjö *et al.* 2001) and biases the numbers of receptive females to sexually active males at any one time (the operational sex ratio; Emlen & Oring 1977). This bias in the operational sex ratio is generally thought to lead to increased intrasexual competition, greater variance in breeding success and stronger selection for traits affecting competitive ability in males than in females. Simultaneously, females are favoured to be more selective in their choice of mating partner, generating selection for traits in males that display their quality as breeding partners. This framework provides a robust foundation upon which to understand breeding systems and the operation of sexual selection, even though other factors may play into the intensity of reproductive competition and expression of associated traits (Clutton-Brock 2007). Indeed, the framework is directly applicable to understanding the reproductive ecology of Atlantic salmon.

As in many other organisms, the differences in reproductive investment between the sexes of Atlantic salmon reflect the operational sex ratio (Box 2.1), which is typically male-biased. Male salmon require little ‘time out’ between periods of reproductive activity, unlike females, which are limited by egg production and the need to perform ancillary activities such as the making and covering of nests. Female salmon ovulate all their eggs for a breeding season simultaneously, and once they have ovulated they have a short time window (a few days) within which to deposit the eggs before they begin to overripen and become infertile (de Gaudemar & Beall 1998). This, in conjunction with the asynchronous nature of spawning among females, which may occur over eight or more weeks (Calderwood 1900; Heggberget 1988; Fleming *et al.* 1996, 1997), and the ability of males to remain sexually active for long periods and spawn repeatedly and frequently, can strongly bias the operational sex ratio. Thus, while differences in the sex ratio of adults returning to breed may amplify or reduce differences in the operational sex ratio, these will frequently be far outweighed by the disparity between males and females in potential rates of reproduction. Indeed, male-biased operational sex ratios are the norm in salmonid fishes (e.g. Schroder 1982; Fleming & Gross 1994; Quinn *et al.* 1996; Blanchfield & Ridgway 1997), even when the sex ratio of returning adults is female-biased (Fleming 1998). The strong male bias in the operational sex ratio and associated intensity of selection for access to mates, in conjunction with female competition for breeding resources, sets the stage for understanding the reproductive patterns of Atlantic salmon.

2.2 Reproductive strategies: age and size at maturity

Among the first reproductive ‘decisions’ a salmon will face is the age and size at which to mature. This decision is shaped by growth and the risk of mortality, as well as by potential reproductive success (i.e. number of offspring produced) as affected by the breeding environment. As we will see, potential reproductive success is shaped by the differing selective forces acting on the sexes that result in differing ages and sizes at maturity between the sexes.

2.2.1 Among populations

The variability in age and size at maturity that exists both among and within Atlantic salmon populations is matched by few vertebrates. In their review of Atlantic salmon life-histories, Hutchings & Jones (1998) reported age at maturity to range an order of magnitude, from 1 year for male parr in France to 10 years for some anadromous salmon in northern Quebec. Similarly, size at maturity can vary by more than two orders of magnitude, even within populations (Fleming 1996), from less than 10g for male parr to more than 20kg for anadromous salmon. There are clear regional patterns, with the youngest mean ages at maturity of anadromous salmon being found in the southern range of the species’ distribution (i.e. 3.21 years in the River Nivelle, France) and the oldest ages in the northern regions (i.e. 8.80 years in George River, Quebec) (Hutchings & Jones 1998). This to a large extent reflects a latitudinal decrease in growth during the freshwater life stage that affects the age at seaward migration (Metcalf & Thorpe 1990). By contrast, there is no clear latitudinal pattern in sea age at maturity, with United States (1.96 years), Norwegian (1.83 years) and southern European (1.81 years) salmon spending 60 to 70% more time at sea than those in



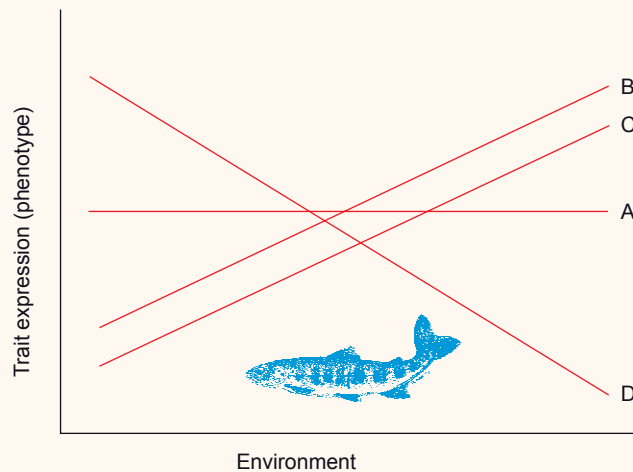
Figure 2.1 Rivers with discharges of less than $40 \text{ m}^3 \text{ s}^{-1}$, such as Gilbert River in Labrador, shown above, may select against large salmon due to low water flows that make successful ascent and breeding by large salmon risky and difficult. Photo: Ian Fleming.

Newfoundland (1.15 years) and Ireland (1.13 years). Even at a fine scale, such as neighbouring rivers or tributaries within river systems, there can be significant differentiation in sea age at maturity, with some populations or subpopulations being composed primarily of grilse (one-sea-winter fish) and others of multi-sea-winter fish (e.g. Vähä *et al.* 2007).

The above observation prompts the question: why does such variation in sea age, and thus size at sexual maturity exist among Atlantic salmon populations? Evidence from common garden and selection experiments with both wild (Jonasson 1996; Jonsson & Jonsson 2007) and domesticated salmon (Nævdal 1983; Glebe & Saunders 1986; Gjerde *et al.* 1994) indicates that there is likely to be some genetic basis to the variation. Such genetic effects appear to be expressed through differing reaction norms to environmental conditions (Box 2.2) and are indicative of adaptive differentiation among populations (Garcia de Leaniz *et al.* 2007). For example, river discharge may be important in shaping the mean sea age and size at sexual maturity of Atlantic salmon, particularly in rivers with discharges of less than $40 \text{ m}^3 \text{ s}^{-1}$ (Jonsson *et al.* 1991a). Jonsson *et al.* (1991a) argue that selection in such rivers may act against large salmon due to low water flows that make successful ascent and breeding by large salmon risky and difficult (Fig. 2.1), counteracting size advantages such as fecundity and competitive ability. This effect appears to be common for anadromous salmonids (reviewed by Fleming 1996), even within large rivers systems where large, multi-sea-winter fish predominate in main stem reaches and large tributaries and grilse in the smaller tributaries (e.g. Webb & McLay 1996; Vähä *et al.* 2007). In large rivers, however, the determinants of mean size and age at maturity are less clearly understood and factors such as length of the breeding migration (i.e. energetic requirements) may play a more important role (Schaffer & Elson 1975; Thorpe & Mitchell 1981; Scarnecchia 1983; Jonsson *et al.* 1991a).

Box 2.2 Reaction norms

Reaction norms describe how the expression of different genotypes varies across environments. They are indicative of: (1) the magnitude of plasticity in the trait of interest, (2) the extent to which its expression is affected by genotype-by-environment (GxE) interaction, and (3) how its additive genetic variance (V_A) may change across environments. For example, the figure below depicts the expression of four different salmon genotypes (A–D) across an environmental gradient. Line A is indicative of a salmon genotype where trait expression is independent of environment, i.e. there is no phenotypic plasticity and trait expression can be said to be purely genetic. Lines B and C show two salmon genotypes where trait expression changes with the environment in a similar way (i.e. the slopes are parallel and non-zero). These genotypes are plastic, but exhibit no GxE interaction relative to one another. By contrast, the salmon genotype depicted by line D does show GxE effects (i.e. crossing reaction norm) relative to genotypes B and C. The figure also indicates that if the genetic variation is additive, V_A will be greatest at the extremes and least near the centre of the environmental gradient (see Hutchings 2004 for detailed discussion of how reaction norms may apply to salmonid trait variation).



It is also clear that age and size at maturity in Atlantic salmon are phenotypically plastic, being shaped by environment, particularly as it affects growth (e.g. Reimers *et al.* 1993; Jonsson & Jonsson, 2004, 2007; L'Abée-Lund *et al.* 2004). Increases in sea age and size at maturity are associated with rapid growth during the first year at sea (Nicieza & Brana 1993; Jonsson *et al.* 2003; Jonsson & Jonsson 2007; but see Salminen 1997). This may relate to the expected fitness gain associated with the growth trajectory, in which a slowing of the trajectory would imply decreasing fitness gain for feeding longer at sea. Fish appear to delay maturity when the growth rate is consistently high throughout life, and mature early if growth rate starts to level off early (see e.g. Jonsson & Jonsson 1993; Hi & Steward 2002).

2.2.2 Within populations and the evolution of alternative reproductive phenotypes

Even within populations, Atlantic salmon show considerable variability in size and age at maturity, surpassing that of other salmonid fishes (Fleming 1998). The expression of this



Figure 2.2 Anadromous male in breeding condition. The jaws of the anadromous males such as this elongate more than 50% during maturation and grow long, recurved 'breeding' teeth. A large hook or 'kype' made of connective tissue forms at the anterior end of the lower jaw and fits into a hollow in the upper jaw when the mouth is closed. Anadromous males also develop an intense red mottling colouration that runs the length of their body. This secondary sexual character may be an important status signal during intrasexual contests and mate choice. Photo: Jörg Schneider.

variability differs between the sexes and reflects the differing forces of natural and sexual selection acting on them. Male salmon show a greater recognisable diversity of life-history tactics associated with reproduction than females and, as a result, the variability in body size within populations tends to be greater among mature males than females (Fleming 1998). This is partly a consequence of male fecundity being less constrained by body size than that of females, whose potential egg production closely tracks increases in body size (reviewed in Fleming 1996). It is also a consequence of males having alternative tactics available to them to gain access to fertilisation opportunities, including satellite and sneaking behaviours where large size may even hinder success. As a result, some male Atlantic salmon mature in fresh water as parr at less than a hundredth the weight of their anadromous male counterparts and rather than 'fight' for access to ovipositing females the mature parr attempt to 'sneak' fertilisations. Moreover, mature male parr will be more cryptic in appearance than anadromous males that exhibit elaborate secondary sexual characters for fighting and courtship (Fig. 2.2 and Fig. 2.3). The anadromous male's elongated and hooked lower jaw (known as a 'kype'), with its specialised breeding teeth, presents a formidable weapon, perhaps equivalent to horns, antlers or tusks, and his bright breeding colouration provides a gaudy display. While female Atlantic salmon rarely mature prior to seaward migration (Klemetsen *et al.* 2003), anywhere from 10% to nearly 100% of males in a population may do so during the freshwater parr stage of their life cycle (Bohlin *et al.* 1986; Myers *et al.* 1986; Baum *et al.* 2004; Heinimaa & Erkinaro 2004).



Figure 2.3 Two mature male parr lying within the nest excavated by the anadromous female (upper right). By contrast to anadromous males, mature male parr do not develop elaborate secondary sexual characters and appear to rely on crypsis for mating success. Photo: Anders Lamberg.

The evolution of such alternative reproductive phenotypes is believed to arise from intense breeding competition (Gross 1996; Shuster & Wade 2003), which occurs within salmonid breeding systems due in large part to the strongly male-biased operational sex ratios. While the individual fertilisation success of parr may frequently be more than an order of magnitude less than that of anadromous males (reviewed in Jordan *et al.* 2007), early maturation does involve increased survival to maturation. Moreover, it may afford greater opportunity to breed again in subsequent years either as a parr or as an anadromous male following migration to sea (i.e. maturing early does not preclude subsequent anadromy).

The coexistence of the two male phenotypes in Atlantic salmon is likely to represent alternative tactics within a single conditional strategy (Bohlin *et al.* 1990; Hutchings & Myers 1994), the equilibrium of which is determined by the combined effects of frequency- and condition-dependent selection (Gross 1996). It is likely to be negatively frequency-dependent in that each of the tactics, fighting and sneaking, is most successful when rare. As a result, neither tactic in itself is evolutionarily stable, but rather it is a mixture of the two that is stable. The equilibrium is also likely to be condition-dependent in that the success an individual gains using a tactic depends on its competitive ability or 'state' relative to others in the population. Thus, while the tactics may have unequal average fitnesses, the switch-point between them (i.e. their frequencies) will be evolutionarily stable even when the status cue (e.g. body size, lipid reserves, growth rate) influencing the switching 'decision' shows some heritability (Hazel *et al.* 1990; Hutchings & Myers 1994; Gross & Repka 1998; Tompkins & Hazel 2007). There is evidence both for a heritable basis to early maturity (Glebe & Saunders 1986; Garant *et al.* 2003a; Duston *et al.* 2005) and an environmental component (Myers *et al.* 1986; Bohlin *et al.* 1990; Metcalfe 1998; Aubin-Horth *et al.* 2005a) to the determination of early maturity. Recently, Piché *et al.* (2008) showed that thresholds for the alternative reproductive tactics differ genetically among populations, indicative of

the existence of discontinuous reaction norms (Box 2.2) for age and size at maturity (see also Aubin-Horth & Dodson 2004; Aubin-Horth *et al.* 2006). The propensity for early maturation among populations is thus likely to be sensitive to environmental conditions that affect the costs and benefits, such as growth opportunities, mortality rates, migration costs and habitat structure.

In populations where only a proportion of the males mature early as parr, it has often been presumed in the past that salmon adopting the sneaker tactic have lower average fitness than those that fight. However, recent evidence suggests that the opposite may be true, with faster-growing/larger and thus probably higher-status juveniles adopting the sneaker life-history tactic (e.g. Thorpe 1986; Gross 1996; Garant *et al.* 2002; Aubin-Horth & Dodson 2004). In such populations, only the largest or most dominant males may be able to effectively adopt the early maturation tactic, while other males are better off delaying maturity. Recent evidence of Aubin-Horth *et al.* (2005b) that brain gene expression profiles of sneaker males were more similar to those of immature females than immature males indicates that early maturation as a sneaker may, in fact, be the default developmental pathway. The males that fail to reach the threshold size or condition to develop into sneakers are those that appear to adopt the *alternative* tactic of actively repressing maturation.

2.2.3 Anadromous and resident phenotypes

Atlantic salmon also exhibited fully resident populations that never migrate to sea, many of which are landlocked by impassable barriers and mature at considerably smaller sizes than anadromous salmon despite similar ages at maturity (reviewed in Klemetsen *et al.* 2003). In some populations, however, both resident and anadromous Atlantic salmon exist sympatrically (e.g. Leggett & Power 1969; Hutchings 1986; Verspoor & Cole 1989; this is the predominant situation for river systems with lakes in Newfoundland [Adams 2007]), raising intriguing questions about how they arose and how coexistence persists. Two main hypotheses may be proposed: (1) they are genetically distinct, reproductively isolated populations that have arisen either sympatrically or allopatrically, and have since come into contact; or (2) they are alternative ecological life-history phenotypes within a single population. Distinct genetic differences between the anadromous and resident forms of Atlantic salmon have been demonstrated supporting the former hypothesis (e.g. Birt *et al.*, 1986, 1991; Verspoor & Cole 1989; Tessier & Bernatchez, 1999, 2000). This pattern of life-history polymorphism involving genetically distinct, reproductively isolated populations appears to not to be uncommon within salmonids and other fishes (reviewed in Schluter & McPhail 1993). The above studies of Atlantic salmon, however, have tended to sample parapatric populations (i.e. reproducing in adjacent but distinct habitat that may act as a barrier to gene flow) or the two life-history forms from distinct habitats within a watershed (Adams 2007). Recent work by Adams (2007), sampling truly sympatric populations, however, provides compelling evidence that the expression of the two different life-history forms of Atlantic salmon can evolve as alternative tactics within a single reproductive strategy. The expression of the alternative tactics, like that of early maturity in male parr, varies with environmental conditions such as aquatic productivity and density-dependent effects on growth and survival (Hutchings 1986; Adams 2007). Thus, it appears that the coexistence of anadromous and non-anadromous forms of Atlantic salmon may arise through both mechanisms depending on circumstances.

2.3 Reproductive investment

Together with age and size at maturity, reproductive investment sets the stage for the breeding system and the patterns expressed reflect the different ways in which males and females achieve success. In Atlantic salmon, reproductive investment extends beyond the simple production of gametes to include time and energetic expenditures on breeding migrations, secondary sexual traits, competition for nesting resources and mates, courtship and mate choice. These investments to maximise the numbers of offspring parented are likely to be traded off against costs to survival and future breeding attempts (*sensu* Williams 1966).

Atlantic salmon are typified by high investment in each reproductive bout, as well as differences between the sexes in the allocation of the investment. In anadromous populations, both males and females expend, on average, 59% of their total energy reserves to breed, with larger individuals expending more than smaller individuals (Jonsson *et al.* 1991b, 1997). The amount expended, however, scales more steeply with increasing body size for females, so that large females expend significantly more than similarly sized males (Jonsson & Jonsson 2003). Not surprisingly, energetic expenditures differ among salmon populations, with those having longer migrations and lengths of freshwater residence expending more energy during reproduction (e.g. River Drammen [primarily multi-sea-winter fish] 60–70% versus River Imsa [primarily one-sea-winter fish] 40–50%; Jonsson *et al.* 1991b, 1997). Among the salmonid fishes, this high level of reproductive investment appears to be surpassed only by that of the semelparous Pacific salmon (Fleming & Reynolds 2004). Non-anadromous forms of Atlantic salmon, however, are likely to expend somewhat less energy during reproduction, with their reproductive expenditure probably comparable to that of other non-anadromous salmonids (*c.* 47–52%; reviewed in Fleming 1998). Similarly, mature male parr appear to expend less energy during reproduction than their anadromous counterparts (Jonsson & Jonsson 2003, 2005; Fleming *unpublished data*).

2.3.1 Differences between the sexes

Much of the female investment in reproduction is in the form of eggs, with 30–31% of their total energy devoted to them (17–21% of total body weight; Jonsson & Jonsson 2003). They represent more than 60% of the female energetic investment during reproduction (Jonsson & Jonsson 2003) and therefore shape female reproductive behaviour. The numbers of eggs (fecundity) an anadromous female produces from this energetic investment may range from 1700 to over 10000 depending on her body size (reviewed in Fleming 1996). Fecundity, however, increases with body size at a diminishing rate, such that larger females produce fewer eggs per unit body size than small females, a pattern common to salmonid fishes (Fleming 1996). This pattern reflects an increase in egg size with female size, with larger females forgoing more eggs (i.e. having fewer eggs per unit body size) to have larger eggs than smaller females. The eggs of salmonids are among the largest in the fish world (Einum & Fleming 2002), with those of Atlantic salmon averaging 105 mg (range 94–127 mg) for anadromous populations and 87 mg (range 72–116 mg) for resident populations (Fleming 1998). Much of the other reproductive costs of females appear to come in the form of behaviour directed towards offspring survival, particularly nest digging (Økland *et al.*

2000). Overall, the level of investment in egg production is similar to that of other anadromous salmonids, but greater than that of non-anadromous forms (Fleming 1998). The reduced probability of repeat breeding associated with anadromy (see Section 2.3.3 below) theoretically favours an increase in present versus future reproduction.

By contrast, investment in gonads by anadromous males is less than a seventh that of females, with 3–4% of a male's total energy devoted to testes (excluding production costs; Jonsson & Jonsson 2003) or 2–6% of their total body weight (Fleming 1998). The difference between the sexes is due both to a greater allocation of mass to gametes by females and a higher energy density of eggs (due to lipids) than testes (Jonsson & Jonsson 2003). Thus, gonads represent less than 10% of the energetic expenditure by anadromous males during reproduction. This implies that much of their energy loss occurs due to behavioural activity (e.g. mate competition), development of secondary sexual traits and maintenance. Breeding-related activities, such as chasing, aggressive display and quivering (a form of courting) can carry significant energetic costs (Økland *et al.* 2000; Hendry & Beall 2004), similar to that observed in Pacific salmon (Healey *et al.* 2003; McVeigh *et al.* 2007).

2.3.2 Differences between reproductive phenotypes

Gonadal investment by males will be shaped by sperm competition, which ensues when the ejaculates of two or more males compete to fertilise a female's ova (Stockley *et al.* 1997). Sperm competition is a common phenomenon in Atlantic salmon, where fertilisation is external and sneaking is a successful tactic, particularly for mature male parr. Within species, such sneaker phenotypes that face a high risk of sperm competition often have relatively larger testes and milt volume for their size than fighter phenotypes that face a lower risk (Taborsky 1998). This pattern holds for Atlantic salmon, with mature parr investing relatively more in gonads than anadromous males, both in terms of their body mass (5–10% versus 2–6%, Fleming 1998) and their body energy (*c.* 10% versus 3–4%). Gonadal differences between anadromous and parr males also extend to sperm characteristics. Mature male parr may have greater spermatozoa concentrations and motility, as well as longer spermatozoa lifespan than anadromous males (Daye & Glebe 1984; Gage *et al.* 1995; Vladić & Järvi 2001). Thus mature parr are apparently investing relatively more in both gamete production and gamete quality for sperm competition than are anadromous males.

2.3.3 Survival costs

The high reproductive investment by anadromous Atlantic salmon also carries a steep cost in terms of the probability of surviving to breed another year, which typically averages less than 10% (Fleming & Reynolds 2004). This level of repeat breeding is amongst the lowest for iteroparous salmonids (Fleming & Reynolds 2004), though it has been recorded to reach as high as 43% in some populations from the Bay of Fundy, Canada (Ducharme 1969). Interestingly, these populations have experienced dramatic declines in repeat breeding during the past two decades associated with declines in overall marine survival. This is likely to have contributed to the recent collapse of these populations, which are now considered in danger of extinction and are being conserved largely by a living gene bank (O'Reilly & Doyle 2007).

The probability of repeat breeding decreases with increasing fish size, reflecting a general increase in energy expended during reproduction (Jonsson *et al.* 1997). In addition, males are less likely to survive the breeding season than are females (Baglinière *et al.* 1990, 1991; Jonsson *et al.* 1990; Fleming *et al.* 1997), which may explain why they are less likely to breed again (Shearer 1992). This occurs despite similar energy expenditures by the sexes during reproduction, suggesting that costs, other than energy, of the intense male–male competition for mating opportunities (e.g. wounding and risk of predation; Jonsson *et al.* 1990; Fleming *et al.* 1997) are partly responsible. The greater propensity for repeat breeding by females than males is a pattern common to other iteroparous Salmoninae (Fleming 1998).

Mature male parr are not immune to the survival cost of breeding, much of which is imposed upon them by anadromous spawners. Both anadromous males and females attack parr in the vicinity of active nesting sites. Experiments in semi-natural settings indicate that 15–51% of mature male parr may incur wounds from such attacks over the course of a spawning season and 10–15% of them may die (Hutchings & Myers 1987; Garant *et al.* 2003b; Weir *et al.* 2005). Some male parr may even be ingested by anadromous fish (Weir *et al.* 2005) or entombed during female nest covering (Sægrov & Urdal 1993). While there are no measures of wounding rates incurred by mature male parr in nature for Atlantic salmon, evidence for brown trout (*Salmo trutta*) indicates rates of at least 28–37% (Bohlin 1975; Broberg *et al.* 2000). The likelihood of breeding again, however, appears to vary among Atlantic salmon populations, reflecting the harshness of the freshwater environment, particularly during winter when energy reserves may be critical to parr survival. In some populations with high rates of precocious maturation (*c.* 80% of males) and inhabiting harsh winter environments, survivorship of mature male parr is low (e.g. Codroy River, Newfoundland, Canada; Myers 1984; see also Berglund *et al.* 1992) and reflected in a strongly female-biased sex ratio among the anadromous spawners (i.e. few previously mature male parr survive to smolt and return as large spawners; Fleming 1998). By contrast, other populations showing similarly high rates of precocious maturation (e.g. River Imsa, southern Norway, *c.* 70–80% of males; Bohlin *et al.* 1986), but inhabiting less harsh environments, may experience relatively high survivorship (Jonsson *et al.* 1998) and show male-biased sex ratios among anadromous spawners (Fleming 1998). Surviving parr may either smolt or remature as parr in subsequent years; however, the factors that influence this decision remain unknown.

2.4 Breeding behaviour and success

Like other aspects of the reproductive ecology of Atlantic salmon, breeding behaviour is shaped by the different means by which the sexes achieve reproductive success. Females direct much of their behaviour towards activities that ensure oviposition success and offspring survival, and males towards activities that ensure mating success. This has implications for reproductive investment and the probability of breeding again, and influences the patterns of breeding success (i.e. number of embryos produced).

2.4.1 Females

Females largely dictate when and where eggs will be deposited, and thus the conditions under which the embryos will incubate and the environment into which the juveniles will

enter upon emergence. Breeding time correlates with water temperature during incubation, and is likely to ensure emergence and initial feeding at an optimal time (Heggberget 1988; see also Brannon 1987). While incubation rates can differ by a few days among populations (Berg & Moen 1999), there is much greater scope for evolution in emergence time by adjustments in breeding time, which can vary up to four months among populations (Fleming 1996). Within populations, there is likely an evolutionary game, with early breeding affording females access to high-quality nest sites and the likelihood of their offspring emerging to establish territories and begin feeding and growing before those of later breeding females. This is, however, not without costs in the form of increased susceptibility to nest destruction by the digging activity of later-breeding females (e.g. Taggart *et al.* 2001) and the probability of unfavourable environmental conditions during emergence early in the season. The dynamics of this trade-off are not fully understood, but are likely to be affected by female phenotype (e.g. size, energy stores, physical condition) through effects on nest depth (Crisp & Carling 1989; Fleming *et al.* 1996, 1997) and thus susceptibility to nest destruction, as well as through egg size and thus offspring size at emergence and survival (see Section 2.6).

The choice of nesting location by the female is an active process, at least at the scale of river reaches, in which she may dig at several different locations (test digging) before selecting a site for excavation. As with breeding time, this choice appears to be in response to factors likely to improve reproductive success, such as habitat conditions. Female Atlantic salmon show a preference for nesting on the upstream side of riffles or gravel bars, where water depth is decreasing, and current is accelerating and upwelling through the gravel (e.g. Beland *et al.* 1982; Crisp & Carling 1989; Moir *et al.* 1998, 2004, 2006). These areas are often characterised by low concentration of fine sediments and high permeabilities (Peterson 1978; Crisp & Carling 1989; Moir *et al.* 1998), and thus high intragravel dissolved oxygen and low sediment compaction, which are important for embryo survival and successful fry emergence (reviewed in Sear & DeVries 2008). Although nesting sites may appear non-limiting within rivers, females often clump nests in particular areas (Heggberget *et al.* 1988; Moir *et al.* 1998), which may reflect continuous rather than discrete (threshold) preference criteria. This may explain why nest superimposition occurs even at low population densities (Fleming 1996; Taggart *et al.* 2001). Female phenotype may also affect the choice of nesting location, with larger females tending to spawn in coarser substrates, and deeper and faster flowing waters (Crisp & Carling 1989; Moir *et al.* 1998) and competition forcing other females (smaller or later arriving individuals) to occupy less-preferred sites, as evidenced in other salmonids (e.g. Blanchfield & Ridgway 1997; Hendry *et al.* 2001a). At larger spatial scales, the choice of breeding location may be in response to local homing to a specific tributary or location within a river where the fish had reared as a juvenile. This may lead to population substructuring within rivers (e.g. Garant *et al.* 2000; Primmer *et al.* 2006; Vähä *et al.* 2008), and be an adaptation to match genotypes with environments and/or a form of traditionality that evolves when complete resource assessment is costly and previous experience (e.g. as a juvenile) provides insight into current resource quality.

To excavate the nest, females use a tail-beating motion where they turn to one side and undertake a series of rapid beating sequences with their caudal fin (2–21 tail beats at a frequency of 4.0–4.3 beats s⁻¹; Johnstone *et al.* 1992). In the process of vigorously pressing her caudal fin against the gravel and then rapidly lifting it to generate suction, the female displaces gravel and creates a depression in the stream bed for the nest (described in detail

in Jones 1959). Initially, such digging is weak and less directed (i.e. exploratory) and then progressively becomes more vigorous and concentrated as the nest develops. As the nest nears completion, digging becomes interspersed with periods of probing, where the female crouches down into the nest with her anal fin erect, thus pressing it into the gravel. It is believed that this behaviour is important in assessing nest readiness. Once satisfied with conditions (nest, mate, etc.), she deposits her eggs amongst the large stones remaining in the nest pit; the finer gravels having been removed during digging. The number of eggs deposited varies directly with female size and tends to decrease from a female's first to last nest (Fleming 1996; Fleming *et al.* 1997; de Gaudemar *et al.* 2000a). Immediately after egg deposition and fertilisation, the female begins to rapidly cover her eggs to protect them from predators and disturbance. Here, digging occurs around the upstream edges of the nest, thereby lifting gravel back into the nest and covering the eggs. As the female fills the nest pit, a new nest emerges upstream of the previous one and digging slowly switches from covering to excavation. It usually takes from 4 to 24 hours to complete the construction of a single nest, but may take up to several days (for detailed descriptions see Jones 1959; Fleming 1996; de Gaudemar & Beall 1999; Esteve 2005). The total number of nests a female constructs for her eggs increases with her size, reflecting her fecundity, and usually varies between 4 and 9, but may range up to 14 (Fleming 1996; de Gaudemar *et al.* 2000a). These nests need not be concentrated in a single area or 'redd', but may be distributed among two or more redds (Baglinière *et al.* 1990; Barlaup *et al.* 1994; Taggart *et al.* 2001). The whole nesting process is usually completed within three to six days (Fleming 1996; de Gaudemar *et al.* 2000a).

Female breeding success is a function of fecundity, nesting success and fertilisation. Because female fecundity increases rapidly with body size, body size is commonly the most important determinant of female breeding success. Retention of unspawned eggs at the end of the breeding season is rare among wild fish, seldom exceeding 1% of total fecundity (Baglinière *et al.* 1990; Jonsson *et al.* 1990; Fleming *et al.* 1996, 1997). Fertilisation rates are typically high, often exceeding 95% (Jones 1959; de Gaudemar *et al.* 2000a). Here, behavioural sequence chaining between the sexes can be important in ensuring fertilisation (de Gaudemar & Beall 1999), with poor timing between the sexes reducing fertilisation, as is often observed in farmed salmon (Fleming *et al.* 1996; Weir *et al.* 2004). Survival of the fertilised eggs through to fry emergence from the nest will be a function of nest quality and nest survival (see Section 2.5). Overall, breeding success of females (i.e. number of embryos surviving to the eyed stage) has been found to relate positively to body size ($r^2 = 0.72$; Fleming 1998).

Beyond successful breeding, a female's reproductive success will be affected by her maternal influences on her offspring (see Section 2.6) and, potentially, paternal influences through her choice of mating partner(s). The latter may influence offspring success through the effects of genetic quality and/or genetic compatibility (Neff & Pitcher 2005). Female mate choice may be expressed through aggression toward males (Fleming *et al.* 1997), delays in breeding (de Gaudemar *et al.* 2000b), incitation of male-male competition (*sensu* Cox & Le Bouef 1977) and/or adjustments in the number of eggs deposited at oviposition (*sensu* Côté & Hunte 1989). The latter two behaviours, while possible, have not been documented in salmonid fishes. The ability for female Atlantic salmon to express choice, however, is likely to be constrained or circumvented by male-male competition because of the ability of dominant males to limit access to females (Fleming & Reynolds 2004; see also Garner 2009). The

only evidence for choice based on genetic criteria in Atlantic salmon is somewhat indirect and comes from non-random increases in heterozygosity at the major histocompatibility complex (MHC) (Landry *et al.* 2001) or in MHC dissimilarity between parents and offspring (Consuegra & Garcia de Leaniz 2008). The latter was shown to increase parasite resistance in the offspring. Contrary to these findings, Yeates *et al.* (2009) found that Atlantic salmon eggs favour, rather than disfavour, sperm in competition that have similar MHC alleles. Overall, genetic evidence suggests that female reproductive success increases with body size (Taggart *et al.* 2001; Garant *et al.* 2001, 2003a), though the relation is not as tight as for breeding success. This is not surprising given the additional factors that come into play to affect offspring success, including environmental variability.

2.4.2 Anadromous males

The arrival time of males relative to females on the breeding grounds for Atlantic salmon is poorly understood. If it is like that of other salmonid fishes, protandry predominates, in that males arrive 1–5 days, on average, before females (Morbey 2000). It is hypothesised that this allows males to maximise their opportunities to mate with females. Male Atlantic salmon do not participate in either nest acquisition or construction, but rather search and compete for access to breeding females. Such competition is intense, particularly because the operational sex ratio will often be male-biased (see Section 2.1, above). As a result, anadromous males invest heavily in behavioural activity and are considerably more aggressive than females (Fleming *et al.* 1997). This aggression is characterised by both combat (fighting) and display, and is used predominately to intimidate male rivals during mate acquisition and guarding (described in Jones 1959; Fleming 1996).

Anadromous males will often form local dominance hierarchies around nesting females, with the largest males frequently being dominant (Järvi 1990; Fleming *et al.* 1997). There may also be two or more males occupying secondary or ‘satellite’ positions downstream of the female and dominant male (Belding 1934; Jones 1959; Webb & Hawkins 1989; Järvi 1990; Fleming *et al.* 1997). The dominant male performs most of the courting behaviour towards the female, which may include quivering (vibrating his body next to the female’s), nudging (prodding the female about her mid-body) and crossing over (crossing from one side to the other over the female’s tail) (detailed in Jones 1959; de Gaudemar & Beall 1999; de Gaudemar *et al.* 2000b). During this time, there is good reason to believe that males may express mate choice for females that are nearing oviposition, as has been observed in Pacific salmon (Schroder 1981; Hamon *et al.* 1999). They may also be choosy about female size and nesting stage, both of which affect the number of eggs she is likely to deposit at a spawning. The ability to express and the form of male mate choice, however, are likely to be constrained by interactions with other males (e.g. dominance).

As spawning approaches, the frequency of male courting intensifies (de Gaudemar & Beall 1999). Males may follow the female into her nest when she crouches to probe, particularly if she gapes during probing. This can lead to a false spawning, where the males ejaculate because they appear to perceive that the female is about to spawn, but in the end does not expel eggs (Jones 1959; De Gaudemar & Beall 1999). Such false spawnings may be more frequent in spawning hierarchies, where males more distant from the female have difficulty interpreting her behaviour (Fleming 1996). Petersson & Järvi (2001) suggested that it may

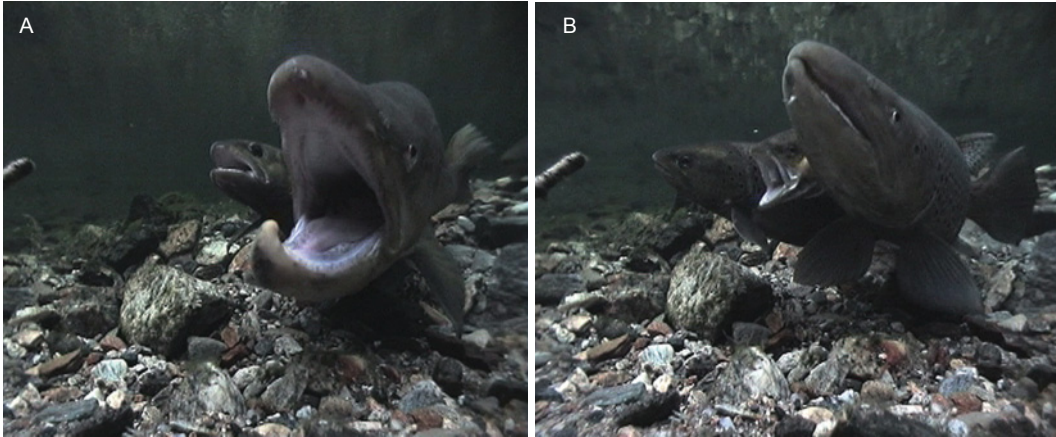


Figure 2.4 A female (left) and a single, dominant anadromous male (right) initiate spawning (A). Both gape as they release gametes into the nest. Seconds later they are joined by a subordinate (satellite) male, who enters between the couple, gapes and releases sperm (B). At this time, both the female and dominant male have just completed gamete deposition (i.e. have ceased to gape). Photos: Anders Lamberg.

also be a means for females to apply some control over matings by increasing the number and/or quality of mates. Males are likely to risk false spawnings because sperm competition can be intense, and both proximity and precedence are key to fertilisation success (Mjølenrød *et al.* 1998; Yeates *et al.* 2007). True spawning usually lasts for 5–10 seconds (Belding 1934; Jones & King 1949), after which the males may depart in search of other breeding opportunities.

Male breeding success (i.e. the number of embryos fathered) over the course of the breeding season will be a function of the number of matings achieved, and the number of eggs deposited and fertilisation success at each mating event. Most spawnings involve a single anadromous male, though multiple anadromous male spawning is not uncommon (Fig. 2.4; Fleming *et al.* 1997; Jones & Hutchings 2002; see also Martinez *et al.* 2000; Taggart *et al.* 2001). Despite a preponderance of spawnings involving single anadromous males, polygamy appears to be the norm, with males and females mating with different partners across breeding events (Fleming *et al.* in prep.; see also Garant *et al.* 2001; Taggart *et al.* 2001). Among anadromous males, access to breeding events and the ability to monopolise them are facilitated by male body size (Fleming *et al.* 1996, 1997). Body size, however, has been found to explain less than 20% of the variation in the number of spawnings that males participated in and in the number of embryos they fathered (Fleming 1998). This is similar to genetic studies quantifying reproductive success through to the parr life stage (Garant *et al.* 2001, 2003). The low explanatory power of body size is indicative of different means by which males can establish dominance and different tactics by which they may gain access to spawning events (e.g. sneaking, female mimicry).

2.4.3 Mature male parr

Mature male parr use an alternative mating tactic of sneaking to gain access to spawning females. They attempt to do so by being cryptic, either lying deep within the nest as oviposi-

tion approaches (Fig. 2.3) or darting into the nest from surrounding cover at oviposition (Jones 1959; Armstrong *et al.* 2001). This behaviour allows the male parr to position themselves below the female during oviposition and thus be closer to the female's vent as the eggs are released than the anadromous male(s). Male parr will compete for such access and proximity (Jones & King 1952; Myers & Hutchings 1987), and parr–parr aggression may be common (>1 aggressive act per 5 min; Fleming *et al.*, in prep.). This aggression, however, carries the risk of drawing the attention of and inciting an attack by the anadromous spawners, which can be fatal. Traits that appear to favour access and precedence to ovipositing females during parr–parr competition include parr body size, dominance and prior residence in the vicinity of the nest site (Fleming *et al.*, in prep.). This is not dissimilar from traits that favour mating access for anadromous males.

Despite risks of injury and death, spawning participation by mature male parr is common. Moreover, their fertilisation success in comparison to that of anadromous males is often greater than might be expected on the basis of relative body masses (reviewed in Jordan *et al.* 2007). This is likely to be due to their ability to sneak proximity to the female vent at egg release and their relatively large investment in gametes (see Section 2.3). Even so, the paternity of individual male parr at a spawning event is only about a tenth that of anadromous males (reviewed in Fleming & Reynolds 2004). However, as a group, the genetic contribution of parr during a breeding season can be considerable (11–65%; reviewed in Fleming & Reynolds 2004). For example, in a three-year study on the Girnock Burn, Scotland, mature male parr contributed genetically to at least 91% of redds, with average yearly contributions of 40–50% per redd (Taggart *et al.* 2001). There is evidence that reproductive success is density-dependent, with the group contribution of parr increasing with the number of parr present at the spawning and the mean contribution of each male declining (Hutchings & Myers 1988; Thomaz *et al.* 1997; Garant *et al.* 2003b). The latter effect may result largely from increased sperm competition. Among parr, body size appears to increase the chance of achieving fertilisations and the number of nests to which a parr contributes (Jones & Hutchings, 2001, 2002; Garant *et al.* 2002). By contrast, the degree to which parr body size promotes fertilisation is somewhat equivocal, with some studies reporting an effect (Thomaz *et al.* 1997) and others not (Jones & Hutchings 2001, 2002; Garant *et al.* 2003b).

2.5 Reproductive success through effects on the next generation

2.5.1 Egg and larvae development

Following the dramatic events during reproduction, life calms down in salmon rivers. The spent salmon are either dead, have left for the sea, or are awaiting spring conditions suitable for outmigration. With water temperatures following spawning commonly being below 5 °C, egg development within the gravel is slow. For example, at an average incubation temperature of 2.5 °C, hatching will not occur until more than 4.5 months after fertilisation (Crisp 1988). The embryo within the egg has then developed into a larva which is attached to a large, nutritious yolk-sac. In general, survival rates during this period are in most situations high. However, during the egg stage, oxygen required for metabolism may become limiting. This may be due either to insufficient flow of water through the nests (e.g. due to siltation, Soulsby *et al.* 2001), or exposure to hypoxic groundwater (Malcolm *et al.* 2005). Following hatching, the yolk-sac larvae may evade such conditions. Throughout the whole period

mortality may occur due to mechanical disturbance of nests (i.e. hydrological scour) during flood events (DeVries 1997). In the spring, a few weeks following hatching, the larva has absorbed most of its yolk-sac and transformed it into body tissue, and the fully developed juvenile salmon emerges from the gravel.

2.6 Maternal influences on offspring

The story of Atlantic salmon reproduction may be considered to be completed by the time the juveniles emerge from their nests. However, the trail of events culminating in spawning can influence the lives of offspring even after emergence (Fig. 2.5). In particular, there can be tight, direct links between maternal traits and offspring success. Usually, these links are described as maternal effects (Box 2.3). For Atlantic salmon, egg size, spawning time and spawning location represent three of many maternal traits that can produce such effects. Considerable empirical progress has been made in understanding the importance of these three traits during the last decade, and we will therefore focus on them below.

2.6.1 Egg size

Egg size is probably the trait with the longest history of scientific interest with regard to maternal effects. The Norwegian fish biologist Knut Dahl devoted a whole chapter on this topic in his book *Ørret og ørretvann* ('Trout and trout lakes') (Dahl 1943), concluding that



Figure 2.5 Maternal effects represent an important route through which juvenile Atlantic salmon are influenced by events occurring prior to and during their parents' spawning. Egg size, spawning time and spawning location determine their initial size, timing and location of emergence. This, in turn, influences their success in terms of growth rates and probabilities for survival, and hence represents a crucial component of their ecology. Photo: Sigurd Einum.

Box 2.3 Maternal effects

Traditionally, organisms have been thought to vary phenotypically (i.e. the way they look and perform) for two reasons: genetic and environmental variation. The genotype each individual receives from their ancestors influences their development from fertilised egg to adulthood. Additional variance stems from the external environment experienced by the individuals themselves during development. These two 'traditional' causes of phenotypic variation do not, however, include the important aspects of variation caused by maternal effects. Definitions of maternal effects are abundant and diverse, often reflecting the biological sub-discipline practised by the user (discussed in Rossiter 1996). One rather comprehensive definition states that maternal effects 'represent developmental influences extended across life cycle stages in which genetic or environmental differences in the maternal generation are expressed as phenotypic differences in the offspring' (Mousseau & Dingle 1991). Maternal effects are commonly stronger than paternal effects, basically because the mother usually provides the offspring with most of the initial energy, mitochondrial DNA and cytoplasmic factors (e.g. hormones and mRNA), and determines where, when and how the offspring are born/dispersed. In general, maternal traits seem to have pervasive effects on fitness of the offspring, and may thus be important for population dynamics.

brown trout that originated from large eggs outgrew those from small ones. A number of subsequent studies using more refined methods and controlled experimental conditions have showed juveniles originating from larger eggs to be larger and having improved competitive abilities, increased resistance to starvation, reduced risk of predation and increased survival and growth rates (e.g. Hutchings 1991; Kristjánsson & Vøllestad 1996; Einum & Fleming 1999; Heath *et al.* 1999; Einum & Fleming 2000a).

Given this positive correlation between egg size and offspring fitness, why do females not produce eggs that are as large as physically possible? The answer to this question must take into account a trade-off between the number of eggs a female can produce and the amount of resources invested in each of them. Maternal fitness increases both with egg number and egg size. Yet, due to a limited amount of resources available for gonad production, one of these traits cannot be increased without decreasing the other. Thus, the size of eggs imposes a constraint on fecundity, resulting in negative phenotypic and genetic correlations between these traits in many organisms, including salmon (Gall & Neira 2004). The optimal solution to the trade-off is therefore to produce some intermediate egg size which maximises maternal fitness, with the exact value depending on the shape of the curve describing the relationship between egg size and offspring fitness (Smith & Fretwell 1974).

Although decades have passed since the model predicting the optimal egg size was proposed by Smith and Fretwell, it has rarely been tested in the wild. One exception is provided by an experimental study of Atlantic salmon (Einum & Fleming 2000a). Egg size was manipulated by rearing parents to adulthood in captivity, a procedure that can result in some females producing more variable egg sizes than in the wild (Einum & Fleming 2004). Juveniles originating from different egg sizes were allowed to develop in artificial nests, and emerging juveniles were group marked before being released in a natural stream. Recaptures of resulting juveniles revealed strong directional selection towards larger egg size, both with respect to offspring and maternal fitness. Furthermore, significant stabilising selection for maternal fitness was found. This means that females producing too small or too large eggs would have reduced fitness. The relation between egg size and estimated survival was best described by an asymptotic regression in accordance with the Smith-Fretwell model (Fig.

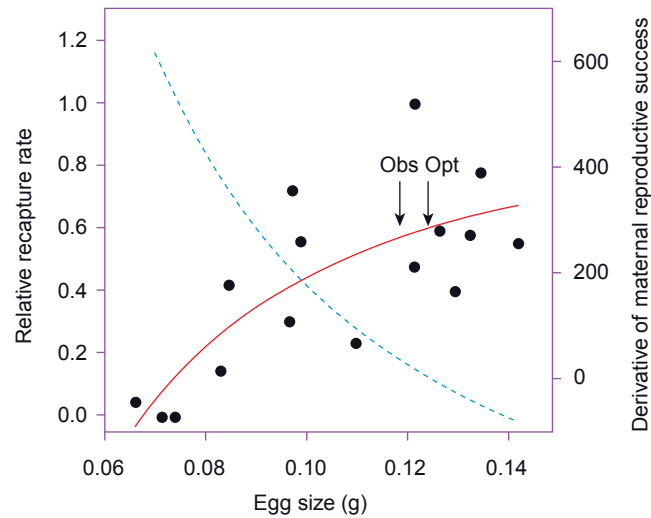


Figure 2.6 Relationship between egg size and relative recapture rate of juvenile Atlantic salmon one month after emergence from nests. The asymptotic function (solid line) relating offspring recapture rate to egg size (m) is of the form $f(m) = 1 - (m_{min}/m)a$, where m_{min} is the minimum viable egg size and a is a constant. The dashed line gives the derivative of the function relating maternal reproductive success to egg size. The derivative equals zero for the egg size that maximises maternal reproductive success (Opt). Observed mean (Obs) egg size of the native population is given. From Einum & Fleming 2000a.

2.6). Finally, the optimal egg size estimated from these data fitted well with the mean egg size observed in the native population. This indicates that egg size in Atlantic salmon has evolved primarily as a response to selection on maternal fitness via effects on offspring fitness. The close fit between predictions and observations demonstrates that the Smith-Fretwell model represents an important contribution towards understanding how mothers solve the trade-off between the number of eggs and their size.

Atlantic salmon egg sizes vary across different levels; within females (i.e. within clutch), among females within populations, and among populations. Variation within females is generally low in wild reared fish, constituting less than 3% of the overall variation (Einum & Fleming 2004). Among females within populations, egg size is positively correlated with female body size (Fleming 1996). It is not clear why this is so. According to the Smith-Fretwell model females within a given population, experiencing a common environment, should produce eggs of a single optimal size. Thus, one potential explanation could be that female body size influences offspring environment during incubation or early juvenile stages (e.g. due to effects of female size on abiotic habitats experienced by offspring, or effects of fecundity, and hence female body size, on intra-clutch competition), and that they therefore have different optima (e.g. Parker & Begon 1986; Hendry *et al.* 2001b). This idea has received some empirical support from a comparative study. Across fish species, those where mothers have a higher potential for influencing offspring environment also have a higher among-female within-population variation in egg size (Einum & Fleming 2002).

Some of the variation in egg size among salmon females within populations can also be related to their juvenile growth rate. Females that experience higher juvenile growth produce smaller eggs relative to their body size when maturing (Jonsson *et al.* 1996). This may rep-

resent adaptive phenotypic plasticity, whereby offspring from females having grown fast in their juvenile stage are more likely to experience advantageous environmental conditions themselves, which in turn will cause a decrease in the optimal egg size (Hutchings 1991; Einum & Fleming 1999). Given the plasticity in Atlantic salmon egg size, variation among populations will to a large degree be determined by differences in body size and potentially also juvenile growth rates. Yet, estimated heritabilities for salmonid egg size (Gall & Huang 1988) suggest a significant scope for evolutionary responses to diverging selection. Thus, although it is not known to what extent the observed variation in egg size among wild Atlantic salmon populations (Aulstad & Gjerdem 1973) is genetically based, the conditions required for genetic divergence and local adaptation appear to be present in this trait, as for many others (Garcia de Leaniz *et al.* 2007).

2.6.2 Spawning time

One of the important decisions that a mature female salmon has to make is when to spawn during a given season. Spawning early may increase the risk of having the nests excavated by later spawning individuals (van den Berghe & Gross 1989; McPhee & Quinn 1998). In addition, early spawning causes early emergence of offspring from nests, and if emergence coincides with unsuitable environmental conditions such as spring floods this is expected to have negative effects on survival rates (e.g. Jensen & Johnsen 1999). Early emergers, being few in number, may also get the undivided attention of predators in the environment (Brännäs 1995). There are therefore many potential disadvantages of emerging early. Emerging late, however, may also have negative consequences. Late emergence may negatively influence performance when in competition with earlier emergers, who will have accrued a size advantage. Moreover, in territorial species such as the Atlantic salmon, early emergence can afford a prior residence advantage (Chandler & Bjornn 1988; Cutts *et al.* 1999). Thus, timing of spawning may strongly influence offspring growth and survival through effects during the post-emergence period. Strong evidence for this has been obtained in a field experiment where timing of fertilisation was artificially delayed and the survival of the resulting groups of juvenile Atlantic salmon was compared to that of eggs fertilised at a normal time, showing strong directional selection against late emergence (Einum & Fleming 2000b). A similar field experiment comparing the survival of juveniles from three different stocking periods, and where stocking of the early group was significantly advanced compared to the normal situation, suggested stabilising selection on timing of emergence, with highest survival being observed for the middle group (Letcher *et al.* 2004). Thus, for a given population there is likely to be an optimal timing of emergence that female spawning time should evolve to match. Differences in temperature regimes and other environmental characteristics across the range of distribution of Atlantic salmon suggest that there is a potential for differences in this optimal timing of spawning among populations. This, combined with this trait's heritability (Su *et al.* 1999), predicts local adaptations in spawning time. For chinook salmon, introduced populations originating from a common origin have been shown to diverge in this trait over short evolutionary time (Quinn *et al.* 2000). Local adaptations would explain the strong negative correlation observed between latitude and spawning date among populations of Atlantic salmon (Fleming 1996), and also potentially differences among upper and lower reaches within larger rivers where environmental conditions differ (Webb & McLay 1996).

2.6.3 Spawning location and consequences for population productivity

If streams extend over a sufficiently large spatial scale, an individual emerging at a particular location is unlikely to have access to all other locations, or to interact to an equal extent with all other individuals within the population. Thus, an individual emerging from a nest in an area with many other such nests is likely to experience stronger competition than if it emerged in an area with no other nests. From a population productivity perspective, an important question is to what extent does the dispersion of eggs (nests) within a stream affect offspring distribution and, hence, the intensity of competition due to local density dependence? Salmonid fishes are among those organisms that are best suited for conducting controlled experiments to study such processes. One reason for this is that it is easy to produce fertilised eggs that can be planted out in different spatial configurations, and to map the distribution of the resulting juveniles. Furthermore, this can be done in habitats that are known to be suitable for the species, but where it is absent due to migration barriers. Using such an approach it has been shown that the spatial distribution of juvenile densities can be shaped by egg distributions over a surprisingly small spatial scale compared to the large scale of typical salmon rivers (Einum *et al.* 2008a; Fig. 2.7). Furthermore, the physical habitat requirements for salmon spawning (Finstad *et al.* 2011 [Chapter 3]) often result in patchy spatial distributions of nests (Geist & Dauble 1998; Moir *et al.* 2004; Isaak & Thurow 2006) that would be expected to produce spatial variation in juvenile densities. Finally, Foldvik *et al.* (2010) found relatively strong links between the spatial distribution of nests and that of the resulting juveniles in natural populations of brown trout and Atlantic salmon. This link was apparent despite a relatively homogenous spatial distribution of spawning activity compared to what is probably the norm for most salmon rivers. Thus, there seems to be a large potential for spawning distributions to influence the spatial distribution of offspring.

Recent results have also demonstrated how interactions that negatively affect fitness-related traits among emerging juvenile Atlantic salmon occur over a very limited spatial scale. In the study by Einum *et al.* (2008a), variation in juvenile density among recapture sections, caused by the spatial distribution of spawning, resulted in a corresponding variation in growth rates. In a different study, the number of eggs in nests being located 150 m apart was strongly and positively correlated with the resulting mortality rates among the juveniles (Einum & Nislow 2011 [Chapter 11]). Given the effects of the spatial distribution of spawning on the distribution of juveniles, and the corresponding effects on their performance, how does this translate into production of smolts and adults? Empirical data shedding light on this question are lacking. Yet, for management of Atlantic salmon populations this is a very relevant question in many situations. Degradation of spawning habitat due to anthropogenic disturbance is well documented in salmonids (Opperman *et al.* 2005), and a number of river restoration projects aim to improve the abundance of suitable spawning habitat (Bash & Ryan 2002; Barlaup *et al.* 2008). Furthermore, one might wonder whether exploitation of salmon populations in rivers influences their spatial distribution during spawning, and if so what consequences this can have for production. Population modelling suggests that effects of spawning distributions on subsequent adult returns and maximum sustainable yields will depend strongly on the amount of habitat available for different juvenile life stages (Einum *et al.* 2008b). This relates to how habitat availability influences the potential for density-dependence. The effect of having a well dispersed

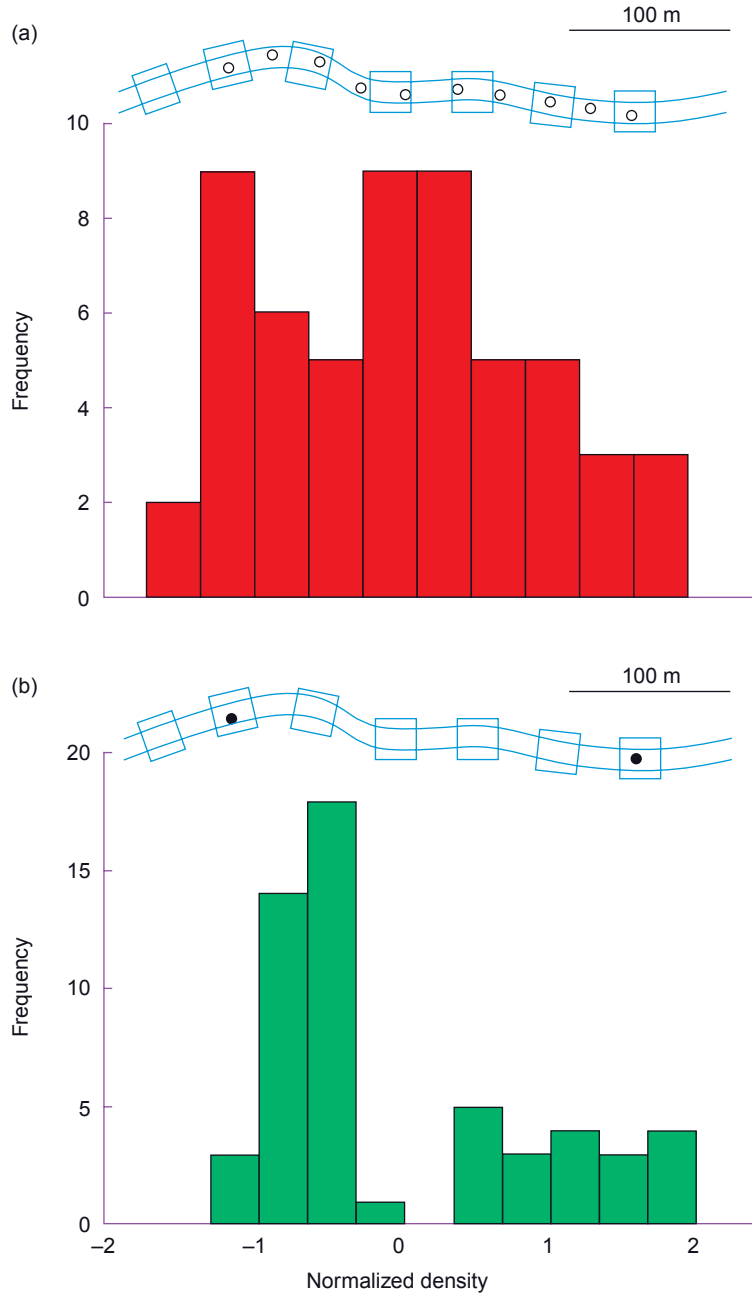


Figure 2.7 In a study of effects of the spatial distribution of Atlantic salmon eggs within streams, eggs were planted out in either (a) ten nests (open circles) distributed uniformly along streams or (b) in two nests (closed circles) located 250 metres apart. Two months after emergence from nests, juvenile densities were quantified in sampling stations (square boxes). The ten-nest treatment resulted in a frequency distribution of densities that closely approximated normality. This was caused by a gradual increase in density when going downstream, suggesting that juveniles originating from an increasing number of nests were present. In contrast, the two-nest treatment had a pronounced tail towards high densities, as sample sections adjacent to nest sites had relatively high densities, and as a result differed significantly from a normal distribution. (Figure reproduced from Einum *et al.* 2008a, with permission of Blackwell Publishing Ltd.)

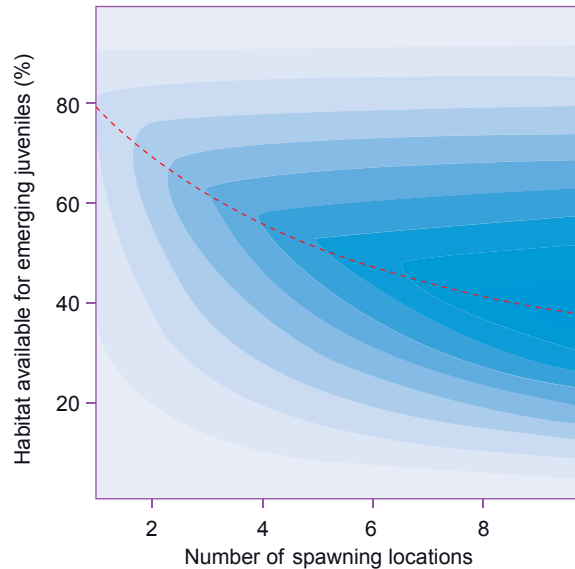


Figure 2.8 Predicted adult Atlantic salmon abundance based on a spatially explicit population model, which quantified effects of number of spawning locations and habitat abundance for fry (juveniles <1g). In the model, spawning locations were uniformly distributed along the length of a 50 km-long stream, and total stream area was divided into habitat suitable either for fry or larger juveniles. Darker shading indicates higher adult abundance, and the dotted line indicates the fry habitat value maximising adult abundance for different numbers of spawning locations. (Figure reproduced from Einum *et al.* 2008b, with permission of Blackwell Publishing Ltd.)

spawning distribution is predicted to be strongest under intermediate levels of habitat availability for the smallest juvenile stage (Fig. 2.8). If the stream habitat is predominantly suitable for emerging juveniles and little habitat is available for older stages, then the population is most likely to be regulated during these older stages, and increasing survival for the emerging juveniles will have little or no effect on the production of smolts and adults (Einum *et al.* 2008b). Thus, restoration of spawning habitats may be an efficient measure to conserve threatened populations and increase yield in exploited salmonid populations, but uncritical efforts in the absence of juvenile habitat considerations may in some cases be inefficient.

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3 Freshwater Habitat Requirements of Atlantic Salmon

Anders G. Finstad, John D. Armstrong & Keith H. Nislow

Abstract

Atlantic salmon deposit their eggs in fresh water. Some individuals, predominantly male fish, may then complete their life cycle in fresh water but most individuals migrate to sea before returning to rivers to spawn. This text considers a number of aspects of the freshwater requirements of Atlantic salmon and focuses in particular on the problem of defining and managing the quality of abiotic habitat. This issue is of particular importance for river managers seeking to conserve fish stocks and influence fisheries. A process-based approach is adopted to explore how habitat affects potential for growth via the energy budget. Consideration is then given to integration of mortality risks to define consequences of habitat structure for fitness of individual fish. The scope for using available descriptive information on habitat use by salmon to define a meaningful niche – defined as a fitness function – is discussed and the links between large- and local-scale processes are described. The text then moves on to discuss general principles of management of salmon habitat through application of existing model frameworks, development of optimum habitat-production landscapes and definition of reference conditions. We conclude by identifying key areas of information deficiency as priorities for research management focus.

Key words

Habitat management, enhancement, carrying capacity, bioenergetics *Salmon salar*

3.1 Introduction

There are few species for which the habitat use has been so extensively described as the Atlantic salmon in its freshwater phase; numerous scientific publications have addressed this issue (see reviews by Gibson 1993; Heggenes *et al.* 1999; Bardonnnet & Baglinière 2000; Armstrong *et al.* 2003). This volume of effort reflects the longstanding interest in salmon as a subject for commercial and recreational fisheries, as well as the use of this species as a model organism for examining fundamental relationships between animals and their physical and biological environment.



Figure 3.1 Stretch of the River Nausta, western Norway, showing a typical rearing area for juvenile salmon consisting of riffle sections with boulder and cobble substrate providing shelter opportunities for the fish. Photo: Anders G. Finstad.

It is well established that habitat used by juvenile salmon is diverse and variable on both temporal and spatial scales (Fig. 3.1). This is partly due to changes in the requirements of the fish as they grow (Armstrong & Nislow 2006) and across seasons and throughout the day, but it also reflects the complexity and variation in the biological systems with which they interact (Armstrong *et al.* 2003). Understanding variation in habitat use is important for devising appropriate strategies for managing salmon habitat. Habitat constitutes the resource that determines the fates of individuals, and therefore ultimately the spawning stock and numbers of salmon returning to fisheries. Any changes in habitat, through collateral disturbance by man, positive management intervention and other natural processes, may affect the nature of the fish, the populations and the fisheries. In this brief overview, we proceed from consideration of the functional theoretical framework that encompasses the mechanisms at the local level that influence each individual fish, through to population consequences and scope for management intervention. This approach is underpinned by the contention that a mechanistic understanding of underlying processes, particularly when projected spatially and temporally, provides a robust structure upon which ultimately to develop predictive models of the responses of populations to changes in habitat.

The focus of this chapter is on abiotic habitat factors. Interactions between Atlantic salmon and other biological parts of the habitat are more thoroughly covered in the following chapters on freshwater feeding, competition and predation (Johansen *et al.* 2011 [Chapter 4], Nislow *et al.* 2011 [Chapter 7] and Ward & Hvidsten 2011 [Chapter 8]). However, since the main effects of abiotic habitat factors are often mediated through biotic components of the ecosystem, a discussion of habitat requirements would be inadequate without some reference to such connections. The important point here is that the habitat requirements of juvenile salmon throughout the freshwater phase are governed by a range of factors woven together in a net of interdependence (Armstrong *et al.* 2003; Fig. 3.2) and acting across a range of spatial scales (Armstrong *et al.* 1997).

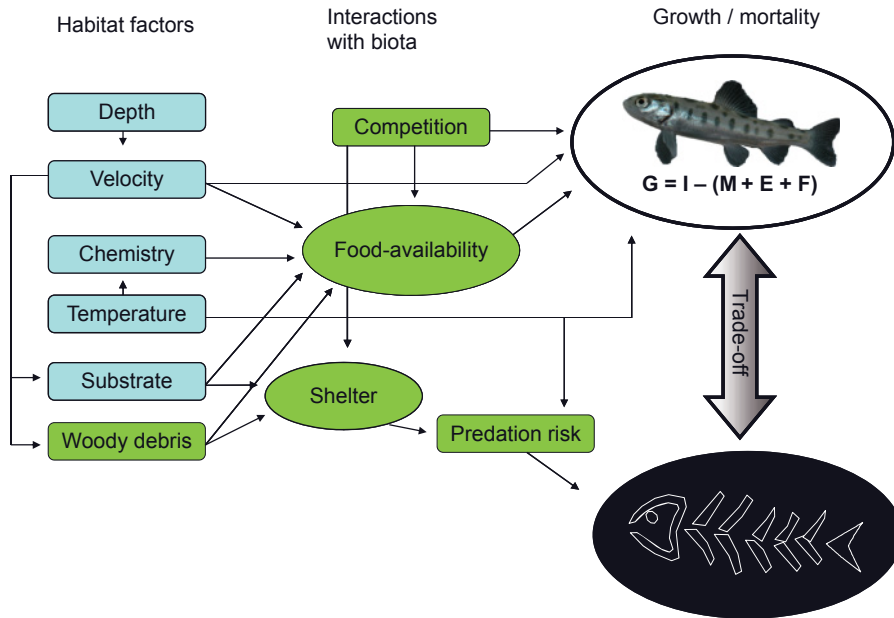


Figure 3.2 Flow diagram illustrating how different abiotic (blue boxes) and biotic (green boxes) habitat factors interact to shape the growth and mortality risk in juvenile Atlantic salmon.

3.2 The fundamental niche and freshwater habitat requirements

3.2.1 Scope for growth

To contribute directly to the future gene pool, a fish needs to survive and to grow to a size at which it can complete its life cycle and generate sufficient successful progeny. Fast growth may increase fitness through production of more and/or larger eggs and/or through reduced generation time. Growth in the currency of energy gain, g , is determined by the balanced energy budget:

$$g = I - (M_s + M_a + M_{sda} + F + E), \quad (1)$$

where I is energy intake (as food), M_s is resting metabolic rate of a starved, inactive fish with no oxygen debt due to anaerobic activity, M_a is the metabolic cost of activity, M_{sda} is the metabolic cost incurred during handling, digestion and assimilation of food and $F + E$ represent energy of ingested food that is lost faecal and ureic waste. Habitat affects growth by influencing parameters in the energy budget; it tends to be beneficial if it increases food intake (I) and reduces other parameters on the right-hand side of the energy budget.

Resting metabolic rate (M_s) includes the basal energetic costs of physiological maintenance together with an additional excitation metabolism from stress that is ill-defined but can be associated with assumed predation risk. This psychological factor is commonly reduced in species of shoaling fish when they aggregate and thereby shelter among one another (Parker

1973). In Atlantic salmon, M_s was reduced by about 30% when fish were provided with a shelter (Millidine *et al.* 2006). This reduction seemed to be associated with fish having knowledge of the presence of a nearby shelter rather than use of it *per se*. This finding implies that habitat such as large stones or boulders that generate shelter possibilities, and perhaps riffled water surface and overhead cover, may reduce energy costs and hence increase growth rate. Direct observations of salmon in near-natural habitats are consistent with this prediction (Finstad *et al.* 2007). M_s also varies with local social environment, being elevated in subordinate salmon in the presence of dominants and reduced in dominant fish living in association with conspecifics of similar age (Millidine *et al.* 2009a). Hence, the way that physical habitat influences social structure may be important in determining M_s . The fish also have a large scope of moderating growth rate (g) by varying food intake (I) through behavioural means to balance energy drains (e.g. Orpwood *et al.* 2005). Further work is required to determine how energy budgets are matched to local habitat characteristics and respond to changes in the environment.

The metabolic cost of activity (M_a) may also be influenced by habitat in a number of ways. Fish are active to feed, to move among habitat patches, to escape predators and in competition with conspecifics and other animals. Any components of the habitat that increase the presence of predators and competitors can be expected to tend to increase M_a or, alternatively, induce compensatory changes in space use that may have other costs such as reduced food intake (Metcalf *et al.* 1987). Increased water discharge may cause a reduction in the amount of space used and activity of salmon parr, presumably because of an increase in the associated metabolic costs of swimming (Kemp *et al.* 2006). The presence of boulders can increase activity through time spent in the water column (Kemp *et al.* 2005). Hence, boulders may reduce M_s by providing shelter, but at the same time increase M_a . We are aware of no evidence for effects of habitat on (M_{sda}), or energy lost in faeces or urea (F or E). However, the costs associated with M_{sda} are strongly influenced by standard metabolic rate (M_s) (Millidine *et al.* 2009b), but probably more associated with basal metabolic components rather than stress levels associated with habitat type.

Food consumption (I) is strongly influenced by habitat. The general trophic state of the river catchment coupled with local physical habitat structure and vegetation affects background levels of invertebrate production (see Ugedal & Finstad 2011 [Chapter 13]) and hence food availability. For fish feeding on invertebrate drift, I is also determined by local water velocity, which is a function of discharge, gradient and local topography. An increase in velocity results in an increase in food abundance but a decrease in capture efficiency. The net result is a parabolic relationship between I and velocity, with an optimum value at intermediate levels (Nislow *et al.* 1999). The optimum velocity for growth increases with overall food richness of the environment due to energy costs of swimming (Armstrong 2009). This shift will be more pronounced in habitat where salmon spend a relatively high proportion of their time in the water column, such as may be associated with abundant boulders.

Temperature affects many components of the energy budget (Elliott 1976). At superabundance of food, growth can occur across the range 0–25 °C (Jonsson *et al.* 2001; Finstad *et al.* 2004) and is optimal at 16 °C (Elliott and Hurley 1997; Forseth *et al.* 2001; Jonsson *et al.* 2001). Poor water chemical quality may have direct effects on metabolism and reduce growth rates through increased metabolic costs (Coghlan & Ringler 2005; Hosfeld *et al.* 2008).

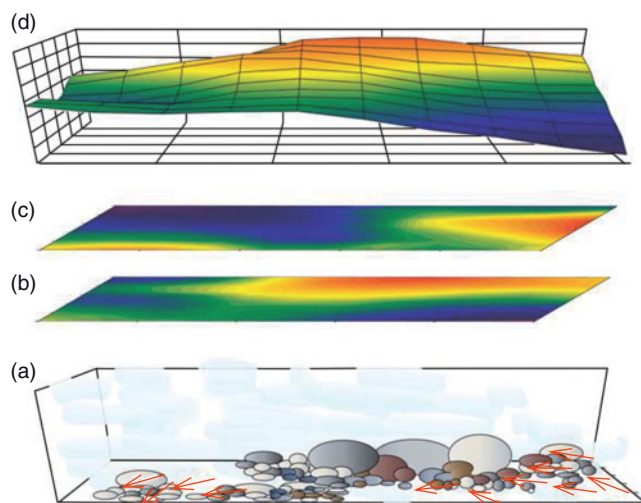
3.2.2 Trading off growth and survival

When salmon parr are not feeding, they tend, where possible, to minimise risk by occupying secure shelters, usually in the form of crevices among boulders or other large substratum particles (Fraser *et al.* 1993; Valdimarsson & Metcalfe 1998). Shelter occupation is density-dependent among wild salmon (Armstrong & Griffiths 2001). Therefore, both habitat structure and population size determine overall availability of shelter (Box 3.1).

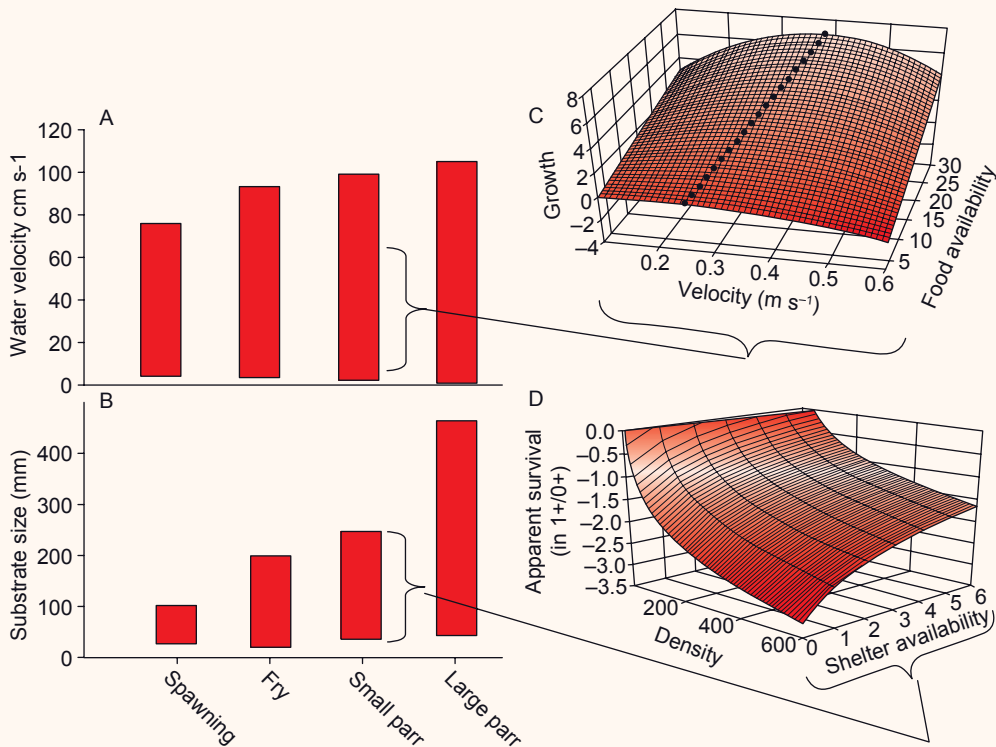
Shelter for feeding fish may also include proximity to bolt holes in coarse substratum, a broken water surface that visually obscures them from surface predators and water depth that provides cover and distance from the surface. Shelter is also available in the form of ambient light, which at low levels may prevent the fish being seen. Secure shelters that also provide feeding opportunities are highly selected (Valdimarsson & Metcalfe 1998). However, feeding usually involves temporary departure from secure shelter and exposes salmon to risk of predation and attack from competitors for foraging patches.

Although most information pertains to habitat use by salmon during daylight hours, they appear to be preferentially nocturnal in both summer (Orpwood *et al.* 2005) and winter (Valdimarsson & Metcalfe 1999), at least as overyearlings. Feeding efficiency is low at night (Fraser & Metcalfe 1997). However, abundance of drifting invertebrates is high at night (Brittain & Eikeland 1988) and it is therefore not clear whether or not in wild settings low nocturnal foraging efficiency results in a reduced rate of food intake compared to that of the day. Decrease in food availability caused salmon parr to extend foraging further into daylight hours to maintain a fixed growth rate rather than reducing growth to balance any increased predation risk associated with daytime foraging (Orpwood *et al.* 2005). However, such a balance between mortality risk, μ , and growth has been inferred from switches in the behaviour of salmon parr during winter (Metcalfe *et al.* 1987). This balance is termed the 'minimise μ/g rule', where g is the current growth rate (Gilliam & Fraser 1987; Werner & Hall 1988). The minimise μ/g concept is illustrated in Fig. 3.3, showing how different sections of a river may have either good shelter opportunities due to coarse substratum (high

Figure 3.3 A schematic diagram of a river stretch providing juvenile salmon habitat (a), with red arrows indicating areas with higher velocity. Patches with coarser substrate give higher survival probability by providing abundant shelters among interstitial spaces, illustrated by survival probability surface (b) where increasingly warmer colours illustrate higher survival. Scope for growth varies throughout the river area due to local variations in water velocity as illustrated by growth surface (c) – see text for further details. The combination of local growth opportunity and mortality risk generates a fitness surface (d).



Box 3.1 Observed habitat, preferred habitat and habitat limitation



Observations of habitat used by salmon in the wild vary greatly among studies (Figs. A and B above) (Armstrong *et al.* 2003). Such data provide information on overall niche breadth but may be inadequate to determine which particular habitat characteristics are optimum and preferred. There are two distinct factors that may confound simple interpretation of such data. First, the optimum value of a habitat parameter may vary among locations. This effect is illustrated in Figure C above in which the optimum local water flow (shown by the dotted line), in terms of growth of salmon that it supports, varies depending on the overall food richness of the environment (see Armstrong 2009). Secondly, many fish may occupy suboptimal locations because of competitive exclusion from preferred sites and may even exist, for a time, in habitats that cannot support long-term growth and survival (Box 3.2).

The importance of particular habitat parameters as limiting factors can depend on the nature of the population of fish occupying the stream. Substrate size (Fig. B) is recognised as a potentially important habitat factor, being a proxy for sheltering opportunities in interstitial spaces between rocks (Valdimarsson & Metcalfe 1998; Finstad *et al.* 2007). However, competition for shelters among wild Atlantic salmon (Armstrong & Griffiths 2001) results in juveniles seldom sharing shelters (Milner *et al.* 1993, Harwood *et al.* 2002). The effect of substrate size (as a proxy for shelter capacity of the streambed) is thus dependent on interspecific competitive interactions and population density (Finstad *et al.* 2009). Figure D illustrates how apparent survival (including both migrations and mortality) from 0+ fry to one-year-old juveniles the subsequent year may depend on the combination of shelter availability and density. At low densities, apparent survival was high and shelters were available in excess. However, as density increased, so the relative number of available shelters decreased and the shelter capacity of the substrate became increasingly important. It follows that the effect of shelter capacity on apparent survival varies with density from almost no relationship at low, to an asymptotic function at high values of density.

survival) or high potential for growth due to water velocities giving rise to abundant availability of drifting invertebrates. The optimal areas are not necessarily those that provide either the highest survival probability or highest scope for growth, but more likely to be those that reflect the μ/g balance.

Salmon parr may reduce their feeding efficiency by seeking relatively safe habitats in the presence of high mortality risk (Metcalf *et al.* 1987). However, it is not clear that this short-term behaviour ultimately results in reduced growth; it may be that foraging bouts are extended to compensate to some extent for reduced rate of food intake.

A problem with the 'minimise μ/g rule' approach applied to stream fishes is that it does not consider habitats providing negative energy intake, which in time also will result in mortality, depending on the time until the fish moves (e.g. emigrating as a smolt) or the local habitat improves. One way around this issue is to treat survival over a future time horizon as a common 'currency' for food intake and mortality where the current energy state and energy intake of the fish is used to predict the risk of future starvation (Railsback & Harvey 2002). This currency is state-dependent, allowing individuals with different energy reserves to follow different decision trajectories.

However, to provide realistic predictions, habitat selection rules should also include density- and frequency-dependent components of fitness. The fish may not only respond to resource availability but also the demand on that resource (Tyler & Gilliam 1995). These principles have been incorporated in habitat selection theory from the early formulations of the Ideal Free and Ideal Despotism distributions (Fretwell & Lucas 1970; Fretwell 1972) (Box 3.2).

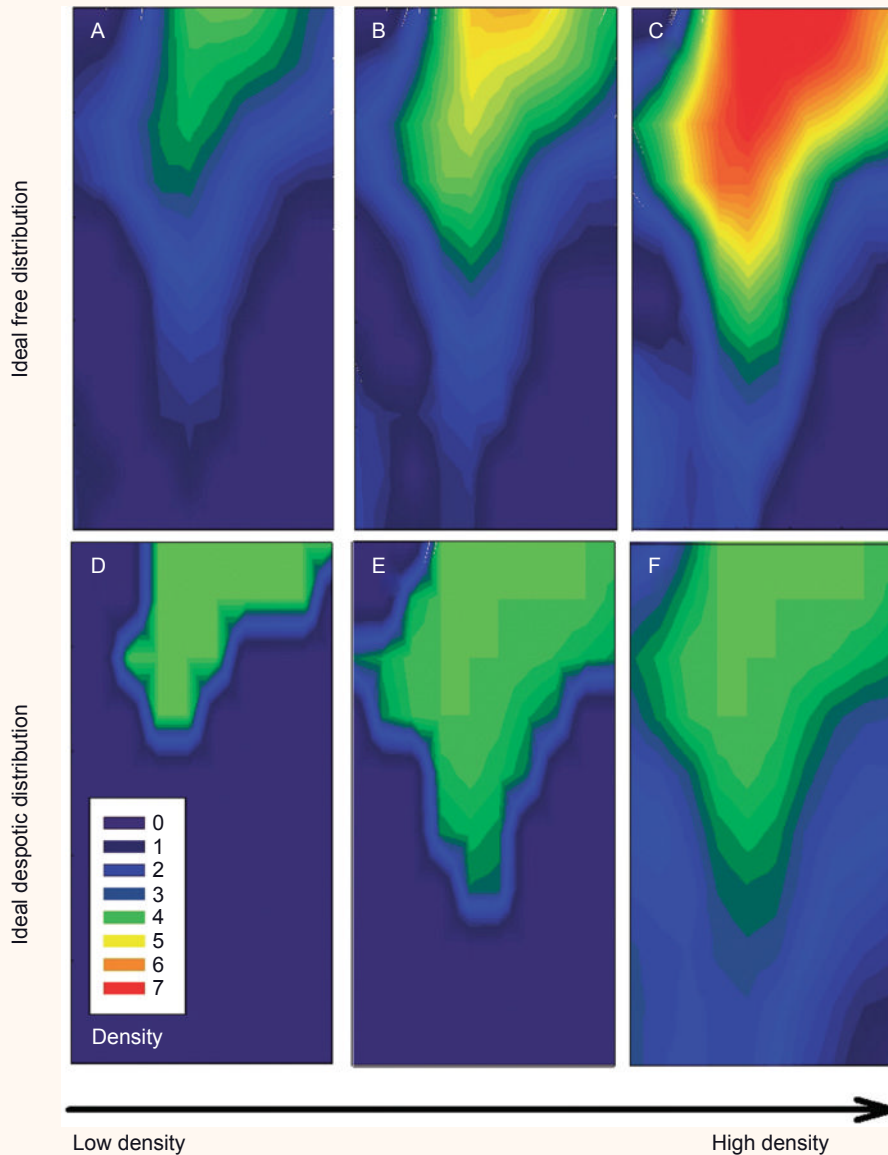
3.3 Realised niche and observed habitat use

There is extensive variation in the range of habitats used by Atlantic salmon both within and among populations. A detailed review focusing on streams is provided in Armstrong *et al.* (2003) and a summary of characteristics of habitats used is listed in Table 3.1. Juvenile salmon are also found in lakes, estuaries and river reaches from small headwater tributaries to deep pools in main stems (Fig. 3.4). It is evident that the physical requirements for fulfilling the fundamental freshwater niche might be met by a large proportion of northern fresh waters. However, salmon are frequently absent from sites that have suitable physical and chemical conditions. This is probably due to migration barriers, interspecific interactions such as predation or competition, or distance from habitat that is needed by earlier life stages.

Habitat requirements of adult salmon in the pre-spawning phase are not extensively described. However, they probably rely on pools as holding stations on their upriver migration. Specific characteristics of such habitat have not been correlated with survival but are likely to include depth, together with instream shelter, such as boulder density, and near-stream shelters such as overhanging banks (Bardonnnet & Baglinière 2000). These fish also require habitat that allows free access upstream at the times when they want to move. Obstructions such as dams and weirs obviously may interfere with such movements.

The range of habitat characteristics for spawning and early rearing are rather narrow compared with the other life stages (Armstrong *et al.* 2003). Salmon often bury their eggs so that they incubate below gravel, secure, to an extent, from desiccation, predation,

Box 3.2 Density-dependent habitat selection



Habitat use by the population is likely to be affected by competition for limited resources (Chapter 7). The response of habitat use to changes in density is commonly described by two conceptual distribution models. Firstly, the 'Ideal Free Distribution' (IFD), where the spatial frequency distribution of individuals among habitat types remains constant (Fretwell & Lucas 1970) assuming limited but non-defended resources that are increasingly depleted at higher densities. Figures A to C show density-dependent habitat selection for the river stretch from Fig. 2 viewed from above under simplified assumptions of the IFD. With increasing density, the fish spread out so that realised density at each habitat patch is equivalent to the level of limiting resources at that patch.

At high densities (C), all patches giving positive survival rates are filled up and the distribution of local densities of individuals mimics the fitness surface curve of river stretch.

In contrast, the 'Ideal Despotic Distribution' (IDD), assumes that dominant individuals are able to monopolise highly profitable resources or habitat patches (Fretwell 1972). Increase in abundance will then lead to increased utilisation of suboptimal habitat by the subdominant individuals not able to compete for the best habitat patches (Fig. D to F). At high densities, subdominant fishes may be forced in to marginal habitats, where there is low growth or energy loss and/or high mortality risk. Observing fish at specific sites does not guarantee observation of good or even a viable combination of habitat characteristics. In this case, observations of habitat use give no information on preference or quality.

Although the IDD has been recognised as appropriate for describing habitat utilisation by juvenile Atlantic salmon in experimental settings (Bult *et al.* 1999), studies from wild populations provide contrasting indications as to whether the IDD or IFD applies (Rodríguez 1995; Hedger *et al.* 2005; Gibson *et al.* 2008). There are several reasons why empirical studies from wild populations may provide divergent results. Variation in density may not be large enough to cause patterns expected under the IDD or the simple fixed territoriality in juvenile salmon may not always apply (Hedger *et al.* 2005). Atlantic salmon parr may form hierarchies within overlapping territories and relative qualities of patches may vary across time and space (Martin-Smith & Armstrong 2002; Økland *et al.* 2004). Under such conditions salmon parr do not necessarily conform to basic predictions of the IDD (Macleay *et al.* 2005).

physical disruption, freezing and washout. Spawning tends to occur where substrate is of a size that can be excavated by the female, where flow allows sufficient oxygenation of the eggs and where fine material does not impede such flow (Table 3.1). Suitable areas are often located at the tails of pools.

Emergent fry tend to use areas of relatively slow flow, probably due to constraints in their abilities to capture prey (Nislow *et al.* 1999). The ranges of flows and depths that are used tend to increase with size of parr, possibly reflecting reduction in constraints from inter-year class competition and increased capacity for occupying high energy flows (Box 3.1, Table 3.1). Substrate size used by parr tends to increase with their size (Box 3.1), probably reflecting the availability of shelters of suitable size (Finstad *et al.* 2007; Finstad *et al.* 2009). During winter, parr are closely associated with shelters among substrate (Roussel *et al.* 2004; Scruton *et al.* 2005; Stickler *et al.* 2008) or may use deep pools (Bremset 2000) or cover from surface ice (Linnansaari *et al.* 2008).

Where predation and competition are low (O'Connell & Ash 1989, 1993), salmon parr can also prosper in lakes (Dempson *et al.* 1996; Halvorsen & Jørgensen 1996; Klemetsen *et al.* 2003), mainly using rocky substrates and macrophytes in the littoral zone (Halvorsen & Jørgensen 1996). Similarly, they can occur in pools in main rivers (Bremset & Berg 1997, 1999) if predation risk is sufficiently low (Robertson *et al.* 2003). Juvenile salmon may also utilise estuarine environments before smolting (Power & Shoener 1966; Cunjak *et al.* 1989, Pinder *et al.* 2007).

Although this information on habitats used by salmon is valuable, there is seldom any indication of how well individual fish prosper in the locations where they are recorded. Such information is needed to determine the values of habitats to the population. A further complication is that fish are likely to use a variety of habitats within their home range at different times and for different activities (e.g. feeding and sheltering). Hence, although the contours illustrated in Fig. 3.3 provide an instantaneous value for fitness, the relationship between

Table 3.1. Literature values for Atlantic salmon habitat use during spawning¹, fry stage² and the parr stage³. Habitat variables considered are water velocity (either snout velocity⁴ or mean column velocity⁵), water depth and substrate sizes. For spawning salmon, the percentage of fine material (particles <1 mm) and depth of egg deposition in the gravel is given. Measures are given either as range, minimum and maximum observed values across studies, as range of mean values across studies or as observed preferences. Values are taken from Tables 1 to 3 in Armstrong *et al.* (2003), and references to individual studies can be found therein.

Life stage	Habitat variable	Measures	Values
Spawning	Velocity	Means	35–80 cm s ⁻¹
		Minimum	>15–20 cm s ⁻¹
	Water depth	Mean	25–50 cm
		Range	17–76 cm
	Substrate size	Median	5.4–78 mm
		Mean	20.7–100 mm
Fry	Deposition depth	Mean	15–25 cm
		Range	2.3–8.0%
	Percentage fines	Range	5–30 cm s ⁻¹
		Range	20–40 cm s ⁻¹
	Snout velocity	Minimum	>5–15 cm s ⁻¹
		Maximum	<100 cm s ⁻¹
	Column velocity	Range	10–30 cm s ⁻¹
		Minimum	<10 cm
	Water depth	Range	20–40 cm
		Preference	<25 cm
	Substrate size	Range	5–65 cm
		Maximum	<100 cm
Parr	Substrate size	Range	16–256 mm
		Range	5–50 cm
	Snout velocity	Maximum	>60 cm
		Maximum	<120 cm
	Column velocity	Minimum	<20 cm
		Preference	10–65 cm
	Depth	Range	20–70 cm
		Range	64–512+ mm

¹ Site of egg deposition;

² life stage from swim-up and throughout the first summer;

³ juveniles from after the fry stage and until smoltification;

⁴ water velocity measured at the position of the fish;

⁵ water velocity measured throughout the water column.

overall habitat occupied by a parr and its fitness value requires integration of multiple patches across a complex time axis incorporating seasonal and diel variations. Furthermore, individual fish may choose different strategies in terms of prioritising growth and survival dependent on, for example, life-history characteristics or inherent differences in metabolic rate (Finstad *et al.* 2007). Such factors may result in different fish using the same habitat patch in different ways; for example, adopting different feeding strategies (Armstrong *et al.* 1999).

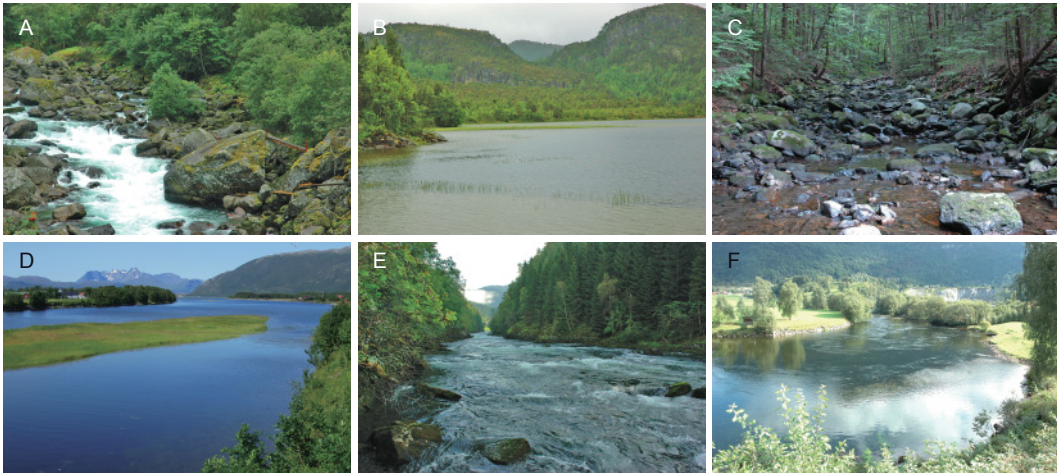


Figure 3.4 Juvenile Atlantic salmon utilise a wide range of habitats including steep rapids (A), vegetated and stony littoral areas of lakes (B), headwaters and small streams (C), estuaries (Photo: Eva Thorstad) (D), shallow, fast-flowing riffles (E) and deep, slow flowing pools in larger rivers (F). Photos except (D): Anders G. Finstad.

3.4 Large-scale determinants of Atlantic salmon habitat

Thus far, we have considered juvenile salmon habitat in terms of the physical conditions experienced largely within an individual's territory or home range. However, rivers and streams are, like other ecosystems, governed by a spatially nested set of controlling environmental factors. There are a number of important reasons for considering the larger-scale determinants of physical habitat for juvenile Atlantic salmon.

First, over the course of their juvenile life-history, individuals may make extensive migrations through sections of rivers, including movements between lake and river habitats. In part, these movements are the consequence of ontogenetic changes in habitat requirements. The initial density and distribution of each cohort are determined by the mothers' choices of spawning locations, which are commonly unevenly distributed. For example, in some rivers, spawning occurs in large, gravel-bedded mainstem sections, which provide appropriate spawning habitats and easy access for spawning adults; however, the juveniles subsequently move to smaller tributaries that provide suitable overwintering habitat and prey resources (Erkinaro & Niemela 1995). In many systems, juveniles also make downstream movements in autumn prior to outmigration as smolts in the spring (McCormick *et al.* 1998). The use of natural geochemical tracers in otoliths has shown that individual salmon parr varied considerably in their movement and large-scale space use strategies (Kennedy *et al.* 2000).

The spatial scale of a typical salmon river (Ugedal & Finstad 2011 [Chapter 13]) makes it likely that ideal free distributions of fish may be hampered both by dispersal limitations and dispersal costs. Given these patterns, Kocik and Ferreri (1998) suggested that not just the overall amount of suitable habitats for different ontogenetic stages, but their spatial arrangement within river systems, need to be considered with respect to estimates of smolt production.

Second, processes that operate at large spatial and temporal scales may set the ultimate limits on juvenile production. Folt *et al.* (1998) reviewed the characteristic scales of important determinants of Atlantic salmon habitat, concluding that many of the important limiting factors on salmon production operate at scales larger than the river reach. Changes in physical habitat structure may have little influence on juvenile production, for example, in rivers that are subject to chronic or episodic acidification due to the interaction between atmospheric pollution and poorly buffered soils and bedrock (Clair & Hindar 2005), processes which operate at the watershed and ecoregional scale. Many of these large-scale influences are discussed by Ugedal and Finstad (2011 [Chapter 13]). The interaction between climate, geology and land cover, as modified by human action, provides the ultimate geographic template for juvenile Atlantic salmon habitat (Elliott *et al.* 1998) and can ‘trickle down’ to influence habitat at micro- and meso-scales. For example the availability of shelters, a key determinant of juvenile rearing habitat quality, is a joint function of substrate size, spatial arrangement and permeability, which are determined by flow and sediment regimes at the watershed scale or larger. Similarly, many other habitat-forming processes are the results of legacy effects with long time scales. The legacy of Pleistocene glaciation, which covered essentially the entire range of wild Atlantic salmon, remains a primary influence on drainage patterns, channel form and sediment supply. More recently, extensive land use conversion throughout most of northwestern Europe and northeastern North America greatly changed the structure and function of riparian forests along salmon rivers. One probable effect has been a marked reduction in the supply rate and size distribution of large woody debris (LWD) in Atlantic salmon-rearing streams (Magilligan *et al.* 2008; Nislow 2009). LWD in streams provides shelter and increases habitat heterogeneity, and has been associated with increased habitat quality for juvenile salmon (Nislow 2009). Finally, management efforts designed to protect salmon habitat (such as land use restrictions and pollution controls) are frequently implemented at large spatial scales. Understanding the ultimate effects of these efforts at the level of habitats used by individual fish requires monitoring plans that account for the way in which these efforts are manifest at local scales.

3.5 Managing Atlantic salmon freshwater habitats

3.5.1 General principles

Managing Atlantic salmon freshwater habitat may seek to achieve one or more of a variety of goals ranging from biological conservation to increasing social or economic value of stocks. This may involve maintaining a status quo (conservation) or changing to a new state that is more beneficial to salmon than the existing conditions (enhancement). In some cases, enhancement may restore habitat to a previous state (restoration). Conservation requires a defensive strategy of monitoring habitat condition (physical, chemical and biological variables) and responding to changes when these parameters exceed or fall below some threshold level. Restoration requires knowledge of the historic habitat condition and identification and remediation of the factors that have subsequently changed. Enhancement implies an understanding and active manipulation of habitat features in any given situation to reach a specified goal; for example increasing numbers of returning salmon of certain biological characteristics.

The potential to change habitat for the better requires an understanding of how the production potential, in terms of numbers and size of salmon smolts generated, is influenced by habitat factors. Habitat requirements change with fish size. The combination of habitat availability and size-specific requirements will determine the life-stages at which habitat limits abundance (Armstrong 2005). Identifying life stages under density-dependent regulation is thus crucial to determine the focus of management efforts. Finally, to determine the value of habitat change in terms of adult fish, stage-specific models need to be incorporated into full-life cycle population dynamics models (Einum 2011 [Chapter 11]).

The maximum number and size of any of the life stages supported in a specific habitat determines its carrying capacity. Of the three main forms of modelling available (Box 3.3),

Box 3.3 Habitat modelling concepts

(i) Empirical correlation models

In this case, population parameters (e.g. density, biomass) are related via a multiple regression approach to a range of habitat parameters, e.g. HABSCORE (Milner *et al.* 1993).

Key strengths: This is a simple, direct approach.

Key weaknesses: It is difficult to relate local measures to a true carrying capacity unless populations are stocked to saturation. Correlation among habitat variables complicates the model structure. It is also difficult to ensure standardisation of habitat descriptions, which is a requirement when merging data from several studies into a common model.

(ii) Application of preference curves with habitat surveys

In this case, local density of fish or frequency of occupation (preference) in each type of habitat is used to weight habitat types in terms of quality to generate a preference curve. Frequency of occurrence of each habitat type is assessed at one discharge and predicted at others. Preference and relative availability of habitat types are combined to give a weighted useable area (WUA) at each discharge, e.g. PHabSim (Bovee 1986; Heggenes *et al.* 1999; Bardonnet & Baglinière 2000; Armstrong *et al.* 2003).

Key strengths: the method is relatively easily applied. Potentially the approach can include the fish's perception of mortality risk.

Key weaknesses: Preference curves often do not indicate preference or performance in a habitat type but rather usage (see Boxes 3.1 and 3.2). The fitness potential of habitats cannot be assumed to match habitat usage (Railsback *et al.* 2003). Furthermore, preference curves can vary with discharge (Holm *et al.* 2001) and therefore have poor predictive value. WUA is seldom related to fish population parameters such as population density, size or time of sampling. Also, pure stochastic variation, often ignored when presenting preference curves, can yield considerable uncertainties in predictions (Williams 1996).

(iii) Bioenergetic modelling

Habitat patches are assessed in terms of the energy balance they would afford occupying fish and summed to give an overall quality for a defined area.

Key strengths: The method directly estimates energy flow through fish, and hence growth potential, and may therefore be readily linked to population level parameters. It provides mechanistic, and therefore potentially system-independent, understanding of habitat requirements and usage.

Key weaknesses: Conceptually the approach can be extended to include mortality risk and hence fitness attributes afforded by habitat patches to fish (Armstrong 2009). However, making this extension is not a trivial matter. Parameterisation of bioenergetic models and measurement of local habitat characteristics may be very costly in terms of resources.

carrying capacities might in principle be estimated from correlation approaches. However, this may be the case only if the relationship between local fish densities and habitat variables is derived when recruitment is not limiting. Alternatively, time series may be used to estimate local stock recruitment functions and hence habitat-specific carrying capacity (Finstad *et al.* 2009). However, there appears to be no example in which these methods have been applied to rivers known to be at saturation level with fish. Furthermore, correlative methods are notoriously noisy and only a modest proportion of the variation in densities of salmon is typically explained (Milner *et al.* 1993). A bioenergetics approach does not suffer from this problem and can be applied without the need for sampling of fish and manipulation of populations to achieve saturated levels for calibration. However, the bioenergetics method does not incorporate the mortality risk, although such data in theory may be derived using habitat preference data (Armstrong *et al.* 2003). Full bioenergetics models also require substantial information across the community to accommodate variations in prey species with habitat types.

3.5.2 Optimum habitat-production landscapes

With knowledge of carrying capacities across a range of habitats it is possible to envisage assessment of costs (in terms of resource input) and benefits (in terms of enhanced production of fish) of changing from one state to another. The notion of an optimum habitat is useful in providing a potential maximum target and also because it is important to know in which direction it lies from any current state. Defining optimum habitat for a given size of fish is not a simple matter for several reasons, including complexity in the response of fish populations to habitat variables and interactions among those variables. In some cases there is an optimum intermediate parameter value with respect to any specific variable. For example, if food is not limiting then salmon growth peaks at temperatures of about 16°C (Elliott & Hurley 1997; Jonsson *et al.* 2001) and ceases at low and high levels within the seasonal range. Similarly, salmon biomass production may be enhanced through moderate shading of an open tree canopy but seriously impeded as cover increases further (O'Grady 1995). In contrast to such near dome-shaped or parabolic relationships, the response to some other variables, such as food supply, may follow an increase to an asymptote at a saturating level.

The response of fish to any one habitat variable may depend on the levels of other variables. The relevance of this interaction concept to management is illustrated in general terms in Fig. 3.5 in which two habitat parameters, a and b , exhibit interacting parabolic effects on salmon biomass across a habitat-production landscape. When a is at level 1, a moderate increase in b will result in an increase in salmon biomass. However, the same change in b from the same starting value would be detrimental when parameter a is at level 2. Evidently, a fundamental starting requirement in managing a stream is to establish its position on the multi-parameter habitat-production landscape, at least to the degree that it is possible to predict whether changes in any specific habitat variable will have positive or negative consequences for the salmon population. Fig. 3.5 considers only two interacting variables; a realistic model would include multiple habitat parameters that are not readily illustrated in only three dimensions. Such complex interactions among variables can be appreciated by reference to the aforementioned examples, since increase in tree canopy cover may increase allochthonous food, decrease autochthonous production through reduction of light, and

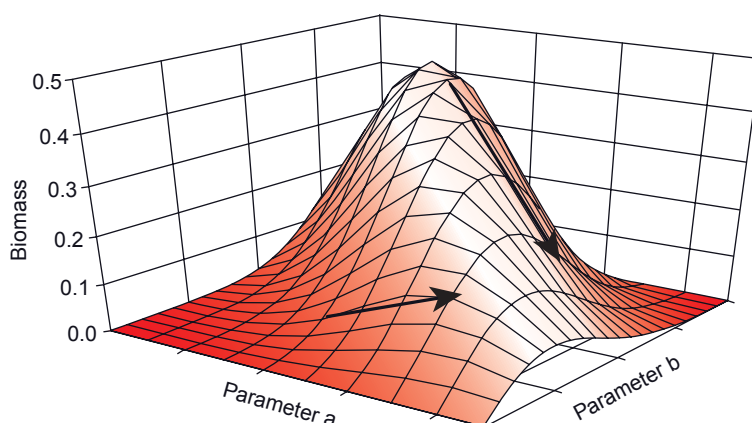


Figure 3.5 Habitat-production landscape illustrating the interdependent effects of two hypothetical habitat parameters, *a* and *b* on maximum biomass of juvenile Atlantic salmon. The arrows show how the same change in parameter *a* can have a positive or negative effect on biomass depending on the value of parameter *b*. An example of such interactions is between local water velocity and general trophic state of the habitat (illustrated in Box 3.1).

reduce temperature. The net result on biomass of salmon can be expected to depend very much on starting levels of temperature and food availability.

3.5.3 Management strategies

Ideally, models would be available to define optima and forms of response curves of population parameters (e.g. density and biomass) for levels of a broad range of habitat variables and across a number of salmon populations that may show specific local adaptations. If this was the case, then it would be possible to make measurements of habitat at a given site and derive the limiting factors and the degree of change in populations achievable for various levels of intervention. Such data are available for some populations and habitat variables. For example, precise optima have been derived for local flow velocities for drift-feeding salmon fry (Nislow *et al.* 1999; Armstrong 2009) and for growth in relation to temperature (Elliott & Hurley 1997; Jonsson *et al.* 2001). For other habitat parameters, general ranges of suitable levels are available (Armstrong *et al.* 2003); these define niche breadth but optimal values and response curves are not made clear from empirical studies (Box 3.1). Thus management decisions must be based on a fuzzy understanding in which it may be clearly evident when certain habitat factors are limiting (e.g. an absence of large substrate particles to provide in-stream cover), but an optimal level is often unknown. When this situation is confounded further by potential for complex interactions (Fig. 3.2), it is evident that managers of salmon habitats face a considerable challenge.

Faced with such uncertainty and a need for pragmatic action, an important approach is adaptive management (Naiman & Latterell 2005), whereby efforts are made to monitor the effectiveness of actions and to modify subsequent actions accordingly. Even if the statistical power of individual monitoring exercises is low, meta-analyses, in which results of multiple studies are combined, can add additional value. Many habitat management initiatives have failed to produce positive results and reporting of such efforts, as well as significant findings,

provides important information for improving our ability to predict correctly in the future (Roni *et al.* 2008).

3.5.4 Reference conditions and habitat management

Uncertainties in the associations between management actions and habitat conditions, and in the mechanistic relationships between habitat features and individual salmon performance, have led some to consider alternative, and in some cases complementary, approaches to habitat management. One approach is to view the habitat conditions present in relatively undisturbed systems as a reference point, and design management actions to conserve or restore these conditions in other systems. In particular, the restoration of natural flow regimes has become an important goal in river conservation and restoration. The expectation is that restoring this key process will result in across-the-board improvements in habitat conditions for a wide range of riverine and riparian species (Poff *et al.* 1997), and may capture critical aspects of physical habitat that have been overlooked by more focused studies. Recently, a natural flow regime-based approach was used by Enders *et al.* (2009) to define flow requirements for specific salmon life-history stages in a maritime Canadian river influenced by flow alteration.

In spite of some advantages, this approach poses significant challenges, particularly in the context of Atlantic salmon management. For Pacific salmonids, large tracts of wilderness in the northwestern US and Canada and eastern Siberia provide useful reference conditions for natural regimes (Naiman *et al.* 2002). In contrast, much of the current and historic distributions of wild Atlantic salmon lie within intensively developed landscapes (Parrish *et al.* 1998). In some cases, anthropogenic landscape change has been so long-term and pervasive that it has essentially become established as a reference condition. For example, although the UK was a largely forested landscape in prehistoric times (Angelstam 1996), a long history of intensive land use has resulted in moorland landscapes being considered as a characteristic reference condition, with forests, particularly managed plantation forests, considered to be a disturbance, and essentially no intact native forests to serve as adequate references. This long history of disturbance is not an insurmountable barrier. For example, in the absence of adequate reference systems, Nislow (2010) used simulation modelling of forest dynamics to provide targets for LWD restoration in New England salmon restoration streams. Further, without a strong basis for habitat-performance relationships, it is difficult to determine which aspects of natural regimes to restore or conserve. Perhaps the best approach is to try and combine both natural regime and species-requirements viewpoints, looking for opportunities that can benefit from both approaches (Nislow 2010).

3.5.5 The future

There is a large body of information describing habitats used by Atlantic salmon in natural streams, which is valuable to an extent. However, there is now an urgent requirement for studies to make a more quantitative effort to derive habitat optima that will greatly enhance the abilities of managers to make sound decisions in *focusing* resources on habitat management. For example, there are no clear guidelines for optimum levels of nutrients, canopy cover, large woody debris and boulder densities, even though these are all known to be important habitat features. A combination of controlled field experiments (e.g. Williams

et al. 2009) and detailed studies of mechanisms in tightly controlled laboratory streams of appropriate dimension (Flodmark *et al.* 2006; Kemp *et al.* 2006; Finstad *et al.* 2009) appears to be a powerful approach in this regard.

Another important area is the development and application of new technologies, particularly remote sensing of in-stream and riparian conditions to expand the scale of habitat assessment efforts. This approach is especially valuable in the context of major restoration efforts, for example in assessing potential habitat gain from removal of barriers to the upstream migration of adult salmon.

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4

The When, What and Where of Freshwater Feeding

Morten Johansen, Jaakko Erkinaro & Per-Arne Amundsen

Abstract

This review summarises the current state of knowledge on salmon freshwater feeding, emphasising the issues of what to eat, and when and where feeding activity occurs. It also provides a brief introduction to optimal foraging theory and drift-feeding models. We focus primarily on juvenile salmon freshwater feeding, as the adult salmon feed very little while in fresh water. The juveniles actively select prey items both in terms of prey types and sizes, with large-sized prey types usually being preferred. The diet composition, both in terms of taxa and average prey size, changes with fish size. Most of the diet consists of invertebrates, but there are also some records of juvenile salmon eating fish. In running water, the salmon can feed from invertebrates drifting either on the water surface or in the water column, or from benthic invertebrates on the streambed surface. In temperate areas, juveniles are predominantly daytime drift-feeders, whereas they spend more time feeding on the benthos at night in northern areas. The relative extent of benthic feeding also increases with decreasing light and temperature through the season. The highest feeding rates are observed during spring and early summer. However, although feeding rates decrease with falling water temperatures in the autumn, juveniles also feed during the winter. Thus, juvenile salmon are versatile fish, being able to feed successfully in different habitats ranging from small streams to large lakes and under different conditions (e.g. changing light levels and seasons).

Key words

Competition, diet overlap, functional response, juvenile fish, ontogenetic variation, optimal foraging, *Salmo salar*, spatial patterns, temporal patterns

4.1 Introduction

In the natural world of fishes the struggle for existence is in large measure the technique of eating and not being eaten. – P.A. Larkin

The resident freshwater phase of juvenile Atlantic salmon represents a growth stage where fish prepare for smoltification (Klemetsen *et al.* 2003). There are a multitude of factors, both biotic and abiotic, that influence the growth rate of individuals (Forseth *et al.* 2011 [Chapter 6]), but ultimately growth is limited by the quantity of food that is consumed (Higgins & Talbot 1985). Despite this, surprisingly few studies of Atlantic salmon directly link or incorporate food availability and feeding behaviour into models of growth, habitat and survival, and most freshwater feeding studies are, thus, empirical. This review aims to summarise the current state of knowledge on salmon freshwater feeding, emphasising the issues of what to eat, and when and where feeding activity occurs. In the final section, we also point to some key aspects deserving further attention.

4.2 Diet selectivity

Many fish species are generalist feeders with a broad diet at the population level, even if individuals may specialise through experience and learning on a single or a few prey categories (see references in Dill 1983). Optimal foraging theory (Schoener 1971) provides a useful framework for explaining the mechanisms that cause individuals to select a restricted diet from a range of possible food items (see Box 4.1). In terms of diet selectivity, optimal foraging theory predicts that fish should maximise net energy gain by choosing optimal prey type and size. In this sense, prey selection is important for enhancing the feeding efficiency of fish.

Juvenile salmon are often described as opportunistic feeders (Egglishaw 1967; Thonney & Gibson 1989) with a diet reflecting food availability (e.g. Lillehammer 1973a; Erkinaro & Erkinaro 1998). Yet, they can learn to focus on common prey items (Box 4.2), and demonstrate quickly rising consumption rates of novel prey as experience is gained (Reiriz *et al.* 1998), showing a functional response similar to Type 3 in Box 4.1.

Box 4.1 Foraging theory

Theoretical approximations of what foraging animals *are* doing arrived with the work of Holling (1959a) detailing the functional response of a predator, while theoretical framework on what foraging animals *should* do came in the 1960s with the seminal works of MacArthur & Pianka (1966) and Emlen (1966). The current status of foraging theory is reviewed in Stephens *et al.* (2007).

The relation between prey density and average number of prey consumed by each predator in an area can be described by functional responses. For all predators, two constraints are present: searching time (the time spent by the predator in finding the prey; decreasing with increasing prey density) and handling time (the time the predator spends handling the prey; depends on characteristics of both the predator and prey species). There are three generalised response types (Fig. B4.1.1). The type 1 response describes a predator whose feeding rate increases linearly with prey density, meaning that the predator eats the prey in direct proportion to the prey

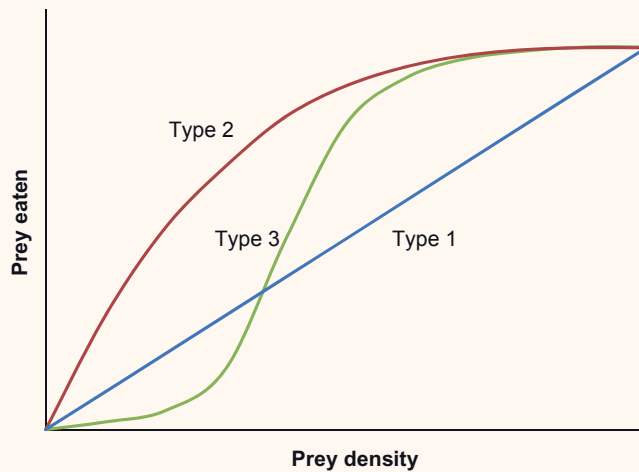


Figure B4.1.1 Functional response curves of Type 1 (passive predators), Type 2 (limited handling time) and Type 3 (learned responses).

abundance. With the type 2 response, feeding rate increases rapidly with prey density but gradually levels off as the relative time spent handling the prey increases. In a type 3 response, the predator mostly ignores a prey species at low densities, but with increasing prey densities the predator makes a dietary switch and rapidly increases its predation rate of this specific prey. The feeding rate eventually levels off as the relative time spent handling increases.

The response curves can be generalised into a simple equation:

$$\text{net rate of energy intake} = \frac{\text{energy gain}}{(\text{handling time} + \text{searching time})}$$

It is evident from this equation that each prey has both a cost (the time and energy spent handling and searching) and a benefit (the prey energy content). The relative value of each determines the prey profitability. In other words:

$$\text{profit} = \frac{\text{prey energy content}}{\text{time}}$$

The above thinking can be developed into the general equation known as Holling's Disk Equation (Holling 1959b):

$$R = \frac{\lambda \cdot e - s}{1 + \lambda \cdot h}$$

where R is the net rate of energy intake, λ is the prey encounter rate, e is the average energy gain per prey item, s is the cost of searching per unit time and h is the average prey handling time. The handling time includes capturing, killing, eating and digesting the prey. This approach forms the basis for optimal foraging models.

Optimality models provide a formalisation of how animals are expected to behave (i.e. maximising fitness or some trait correlated with fitness) and, thus, a framework for describing and testing traditional problems

like attack or exploitation models (the former are also known as prey, optimal diet or contingency models and the latter as patch departure or marginal value models). The former models deal with questions of *what* to eat, i.e. whether a predator should accept a prey item or continue searching, while the latter models deal with questions related to *when* and *where* to eat.

A simple optimal diet model provides a useful example of how optimal foraging theory can be applied. The profitability of an encountered prey item i is given by e_i/h_i . Assume two available food types with the profitability of food item 1 given by $p_1 = e_1/h_1$ and prey item 2 by $p_2 = e_2/h_2$. Further assume that item 1 is more profitable than item 2 ($e_1/h_1 > e_2/h_2$). Which of the two food items should the predator eat? According to optimal foraging theory, the predator should eat the food item if, while handling and eating the item, the predator cannot find a better food item. So, when encountering a prey of type 2, the predator should eat it if $e_2/h_2 \geq e_1/(h_1 + s_1)$ and ignore it if $e_2/h_2 < e_1/(h_1 + s_1)$. In other words, the predator should eat prey 2 if this is more profitable than ignoring it, and keep on searching for prey 1 (or *vice versa* ignore it). This enables us to predict when the predator should specialise (i.e., include only the most profitable prey types) or generalise (i.e., include lower ranked prey types as well). The most profitable prey should never be ignored, but less profitable prey should be ignored depending on the search time for the most profitable item 1. If it takes longer to handle item 2 than it takes to search and find item 1, so that $e_2/h_2 < e_1/(h_1 + s_1)$, then the predator should always ignore items of type 2 regardless of their abundance.

As an example, the above reasoning can be directly applied to prey size. On the benefit side, increased prey size usually means increased energy content of the prey. On the cost side, handling time is short for small prey but increases rapidly over a critical prey size depending upon the mouth size of the predator. These estimates of costs and benefits can be used to predict the optimal size composition of the diet (Fig. B4.1.2).

Optimal foraging can also be used to make predictions about how animals should exploit resources distributed in different patches. An example of this is the marginal value theorem (Charnov 1976), which describes when an animal should leave a patch to search for the next patch (Fig. B4.1.3). The theorem predicts, for instance, that individual animals should stay longer in a patch as the distance between patches increases (Fig. B4.1.3a) and stay longer in a high productivity than a low productivity patch (assuming the same distance between patches, Fig. B4.1.3b).

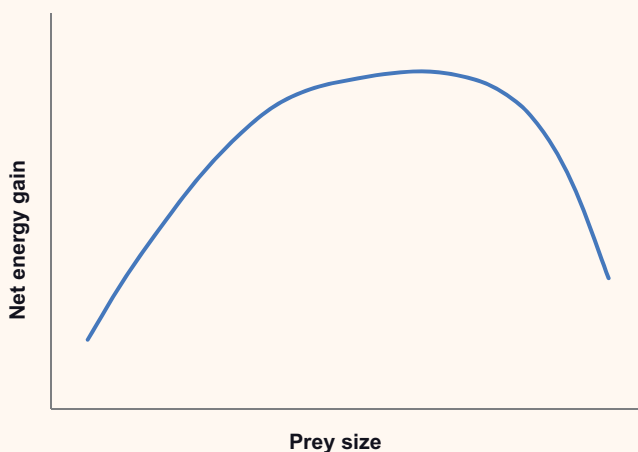


Figure B4.1.2 An example of the relationship between net energy gain and prey size. Net energy gain initially increases rapidly with increasing prey size, before levelling off due to increasing penalties associated with handling time. With increasing handling time, the net gain eventually starts to drop.

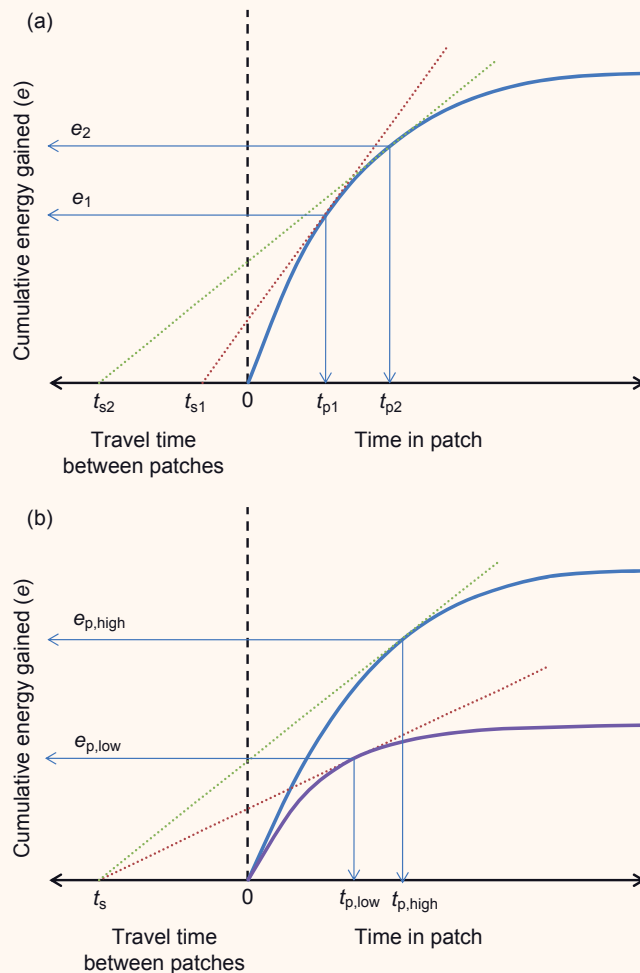


Figure B4.1.3 Marginal value theorem. When a predator enters a patch, the rate of energy gain is initially high and then declines with time as the patch becomes depleted. Cumulative energy gained from a patch is shown with curves in the figure. The optimum stay time within a patch is given by a line tangential to the curve. (a) An example of how different search times (short search time t_{s1} vs. long search time t_{s2}) results in different optimal feeding time within a patch (t_{p1} and t_{p2}). (b) Given the same search time between patches (t_s), a predator should stay shorter in a low productivity ($t_{p,low}$) than a high productivity patch ($t_{p,high}$).

Comparing salmon stomach contents with drift and benthic samples often demonstrates a feeding preference for some taxa. For example, Trichoptera larvae dominate the autumn diet of both fry and parr in the large River Tana, although the larvae are found only in very low numbers in drift and benthic samples (Amundsen *et al.* 2001). Given a choice of three different prey in a laboratory study, juveniles most frequently selected a mayfly (*Ecdyonurus*) instead of a caddis (*Hydropsyche*) or *Gammarus* (Reiriz *et al.* 1998). Conversely, *Gammarus* were most often rejected. The prey selection by the fish became more pronounced as the fish got closer to satiation. Such changes in selectivity are expected from optimal foraging theory,

which predicts that fish should reduce their selectivity (and hence have a broader diet) in a situation with high energy requirements or low food availability.

Juvenile salmon also select with respect to prey size, with larger fish eating larger prey (Keeley & Grant 2001). Newly emerged fry feed on prey smaller than the average available in the drift, while parr feed on larger prey than average (Keeley & Grant 1997). This is confirmed in an experimental setup, where fish took the larger prey when presented with a choice (Reiriz *et al.* 1998). Selection for large prey, e.g. large Plecoptera nymphs and Trichoptera larvae, is most pronounced in large parr (Stradmeyer & Thorpe 1987; Thonney & Gibson 1989; Erkinaro & Erkinaro 1998; Dineen *et al.* 2007). In contrast, small chironomids and nymphs of the mayfly genus *Baetis* often dominate the diet of fry and small parr (Bergersen 1989; Erkinaro & Erkinaro 1998) but decrease in importance as the parr grow larger (Keeley & Grant 1997).

Box 4.2 Common freshwater prey items

Mayflies (Ephemeroptera)

Mayflies (Fig. B4.2.1) are common in both lentic and lotic water bodies. Most species have a one-year life cycle, and their larvae (nymphs) feed on periphyton and fine-particled organic matter, actively searching for food and frequently being exposed to predation. Most species hatch on the water surface, with the nymph actively swimming from the bottom to the surface. There, the adult emerges directly from the nymph (i.e. there is no pupae stage) onto the surface, where it waits for a few moments before it is dry and able to fly away. Mayflies are the only insects with two adult stages (subimago and imago). The female imago returns to the water surface to lay eggs, again exposing them to fish predation.



Figure B4.2.1 Adult subimago mayfly (Ephemeroptera). Mayflies, both nymphs and adults, are important prey items for juvenile salmon. Photo: Morten Johansen.

Stoneflies (Plecoptera)

Stoneflies (Fig. B4.2.2) are mostly associated with lotic waters. Generation length varies with most species having a one-year life cycle, while some larger species have a two-year life cycle (or even more in northern areas). Stonefly nymphs are shredders of large organic particles or predators. The nymphs are exposed to predation both on the substrate surface and while drifting. Stoneflies hatch by crawling up on the shore, where the adult emerges directly from the nymph (i.e. no pupae stage). The adults crawl back into the water to lay eggs.



Figure B4.2.2 Adult stoneflies (Plecoptera), both long- and short-winged individuals. Stoneflies are an important prey item, especially during the winter, and are taken mostly as nymphs. Photo: Morten Johansen.

Caddisflies (Trichoptera)

Caddisflies (Fig. B4.2.3) are a diverse family common to all water bodies. They have a complete metamorphosis (i.e. larvae, pupae and adult stages). Generation length varies, depending on species and latitude, with most smaller species having a one-year life cycle whereas some larger species have a two-year life cycle (or even several years in northern areas). Caddis larvae show a remarkable diversity in feeding ecology, from free-living ranging predators via net-spinning filter feeders to leaf shredders and algal grazers. The larvae of many species carry with them a protective case made by spinning silk and attaching gravel, sand or debris particles. The pupal stage is spent hidden in a house fastened to the bottom. When fully developed, the pupa swims to the surface and emerge as an adult (in some species, the pupa swims on the surface to the shore, where the adult emerges).

Chironomids (Chironomidae)

Chironomids (or non-biting midges) are small insects with complete metamorphosis which belong to the family Chironomidae (order Diptera) and are common to all water bodies, usually in high densities and with many species. The majority of species have a one-year life cycle (but there also many examples of species with several



Figure B4.2.3 Reversing the roles, case-building caddis (Trichoptera) larvae of the family Limnephilidae feeding on a dead anadromous Arctic charr (*Salvelinus alpinus* L.). Caddisflies are frequently positively selected by the juveniles, with a higher occurrence in stomachs than in drift and benthic samples. Photo: Morten Johansen.

generations per year). Most species are detritivores, but there are also some algae grazers and predators. Chironomids are available to fish predation in all life cycle stages, and can be taken from the bottom surface, in the water column or on the water surface.

Blackflies (Simuliidae)

Blackflies belong to the family Simuliidae (order Diptera) and are common in running water, particularly below lake outlets where they can occur in huge densities. They have a complete metamorphosis, and the majority of the species have a one-year life cycle (but there are many species with several generations per year). Blackfly larvae are filter feeders, staying on top of stones where they use foldable fans to catch passing particles (small organic particles, algae and even bacteria). This exposes them to fish predation during the larval stage.

Terrestrial invertebrates

Terrestrial invertebrates accidentally falling into freshwater systems can be an important food source for juvenile salmon. Most common are adult terrestrial insects, but spiders, ants, slugs, snails and earthworms can also form considerable inputs.

4.3 Drift vs. benthic feeding

The food of freshwater fish can be taken from one of three feeding habitats: bottom (benthos), water column or water surface. The benthos encompasses invertebrates appearing

either on the substratum surface or in the hyporheos (interstitial spaces between or under stones and gravel). Organisms in the water column and on the water surface together constitute invertebrate drift, which has four sources: 1) benthic organisms dislodged from the substratum and transported downstream, 2) emerging aquatic insects actively moving from the bottom to the water surface, 3) adult aquatic insects returning to the river to oviposit, and 4) terrestrial invertebrates that have accidentally fallen into the river (Brittain & Eikeland 1988). Within this context, freshwater fish can be described as either benthic or drift-feeders (Allen 1969). Benthic feeders take prey almost exclusively from the benthos, while drift-feeders flexibly take prey at the surface, in the water column and on the bottom.

Atlantic salmon are commonly described as visual drift-feeders, relying on eyesight to detect and intercept drifting prey (Keenleyside 1962). This drift feeding mode has received considerable theoretical modelling attention (summarised in Box 4.3). Drift-feeders may change feeding mode both diurnally and seasonally depending on relative prey availability, light level and water temperature. It was initially claimed that salmon feed mainly on drifting invertebrates (Kalleberg 1958; Keenleyside 1962; Wankowski 1981), but there have also been many reports of benthic feeding (Keenleyside & Yamamoto 1962; Sosiak *et al.* 1979; Vignes 1999; Amundsen *et al.* 2001), especially at night (Amundsen *et al.* 2000), during the first feeding of the fry after emerging from the gravel (Williams 1981) and during periods of low drift availability (Nislow *et al.* 1998). Juveniles staying in large rivers where drift rates and benthic densities are low also feed frequently from benthic invertebrates (Amundsen *et al.* 2001). The relative contribution of drift-feeding both in streams and larger rivers seems to decrease with decreasing water temperature (Erkinaro & Erkinaro 1998), possibly an effect of increasing relative costs connected to feeding forays and prey interception in the water column as temperature gets lower. Salmon feed more frequently from the benthos than other salmonids such as brown trout (Thomas 1962) and brook trout (Thonney & Gibson 1989).

Box 4.3 Drift-feeding models

Drift-feeding is an important feeding strategy for juvenile salmon. In this feeding mode, the fish attain a sit-and-wait state, selecting energetically profitable holding positions of relatively low water velocity from which they can make short movements into adjacent faster water to capture prey (Chapman & Bjornn 1969). This feeding situation is well suited for energy intake models based on a cost–benefit framework similar to optimal foraging theory. Foraging against a current has metabolic costs that should be balanced against the benefit of higher prey encounter rates in faster water (Fausch 1984). The fish gross energy intake rate (GEI), estimated as total prey energy per time unit, can be calculated from the number of captured prey, while the net energy intake rate (NEI) is determined by subtracting the energy costs (EC) of prey capture from GEI (Hughes & Dill 1990). Energy costs include basal metabolism while maintaining holding position in the current and prey capture costs. NEI then becomes:

$$\text{NEI} = \frac{\text{NET ENERGY GAINED}}{\text{TOTAL TIME}} = \frac{e}{h + s}$$

where e is the prey energy content, h is the handling time and s the search time.

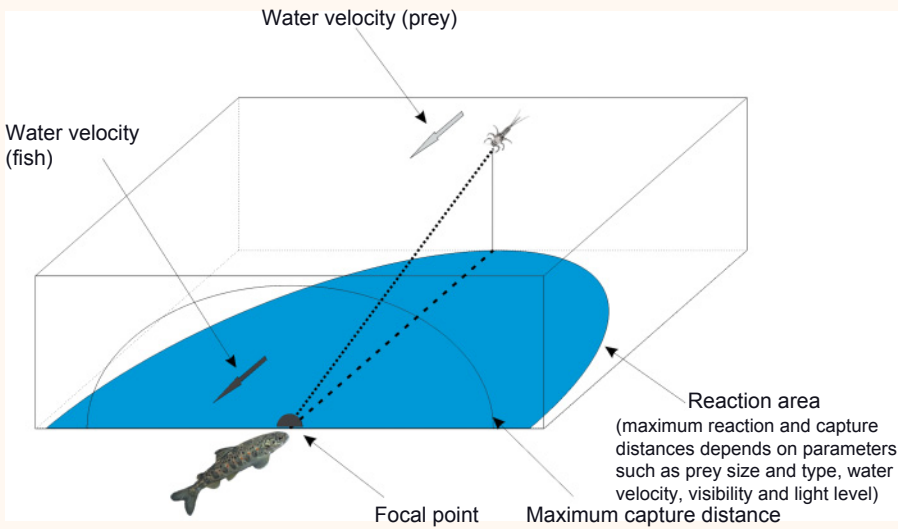


Figure B4.3.1 A summarised diagram of variables used in a drift-feeding model.

The spatial geometry involved in the prey capture for a drift feeding fish is summarised in Fig. B4.3.1. Following the derivation in Guensch *et al.* (2001), the following equation for NEI can be obtained for a drift-feeding fish:

$$NEI = \frac{\sum_{i=1}^n (DD_i MCA_i v_i PC_i (e_i - CC_i)) - SC}{1 + \sum_{i=1}^n DD_i MCA_i v_i h_i}$$

where DD_i is the drift density of prey i , MCA_i prey capture area at a location (given depth and water velocity), v_i mean water velocity, PC_i probability of successful capture, e_i energy content of prey i , CC_i prey capture costs, SC swimming costs and h_i handling time. This is essentially a formulation of Holling's Disk Equation, extended to account for multiple prey types and swimming costs.

Models like this can be used to simulate feeding using parameters related to the fish (size, swimming speed and reaction distance), water (velocity, depth, temperature and turbidity) and food (drift density and prey size composition), and then allow for predicting the growth rate of drift-feeding fish.

4.4 Ontogenetic changes in diet

Different age groups of juvenile salmon might find themselves competing directly with each other for food. The salmon diet is size restricted with a maximum, minimum and optimum prey size defined by the gap width of the fish (Wankowski & Thorpe 1979b), and this may influence the prey choice of different salmon age groups. Larger body size corresponds with increasing prey size (Keeley & Grant 1997; Vignes 1998). Direct observations show that older parr use surface drift-feeding more frequently than younger parr (Keenleyside 1962; Peterson & Martin-Robichaud 1986; Stradmeyer & Thorpe 1987), indicating size-related differences in feeding habitat and behaviour. Considerable diet overlaps between different

age groups have been found on both sides of the Atlantic (e.g. Amundsen *et al.* 2001; Grader & Letcher 2006).

4.4.1 Fry

Early-season food and habitat availability are considered key factors for fry survival (Einum & Nislow 2005). When the newly emerged fry start dispersing from the nest, they enter a critical period of the life cycle. The yolk from the egg is exhausted, so the fry need to find suitable habitat quickly to start feeding. During the first few weeks after the onset of independent feeding, over 50% of all individual fry had consumption rates that were insufficient to meet metabolic demands (Kennedy *et al.* 2008). Further, variation in consumption among sites was correlated with growth and survival, giving clear evidence for foraging habitat limitations for fry. Later in the summer, consumption rates of fry increased greatly and were frequently close to predicted maximum consumption (Kennedy *et al.* 2008).

Fry feed most frequently on relatively small invertebrates, and the most numerous food items in the diet are usually chironomid larvae and small nymphs of Plecoptera and Ephemeroptera (Lillehammer 1973a; Bergersen 1989; Keeley & Grant 1997). When comparing habitat food availability and fry stomach contents, it appears that all the common food items also are numerous in the environment and the fry stomach contents therefore resemble the composition of the bottom fauna (Allen 1941; Lillehammer 1973a; Bergersen 1989). Most of the feeding forays are directed towards drift, especially early and late in the summer (Nislow *et al.* 1998), while surface feeding is rare.

4.4.2 Parr

The diet composition of parr follows the seasonal food availability, but to a lesser degree than that of fry (Bergersen 1989). Stoneflies (Plecoptera) provide an example of such seasonality (see Box 4.2). Many stoneflies have a winter life cycle, they hatch from their eggs in late summer/early autumn and grow through the winter with high drift and benthic densities in the autumn, winter and spring (Lillehammer 1988). During this period, Plecoptera nymphs are frequently eaten by parr, but less so in the summer months (e.g. Amundsen *et al.* 2001). Surface food items (both terrestrial and adult aquatic insects) are available, and correspondingly mostly eaten, during the summer months (June–August; e.g. Amundsen *et al.* 2001; Dineen *et al.* 2007). Older parr feed more frequently from the surface than younger parr (Keenleyside 1962; Peterson & Martin-Robichaud 1986; Stradmeyer & Thorpe 1987), indicating size-related differences in feeding habitat and behaviour.

There are observations of piscivory among parr, including a couple of notes of cannibalism (Mills 1964; Henderson & Letcher 2003), and some reports of salmon parr eating sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*) in northern Scandinavian lakes (Erkinaro *et al.* 1995; Halvorsen 1996; Erkinaro *et al.* 1998).

4.4.3 Smolt

Few studies exist of the food of salmon smolt during their downstream smolt migration. Smolts feed during the migration, mainly on the same type of prey as large parr (Mills 1964; Södergren & Österdahl 1965; Mitans 1970; Garnås & Hvidsten 1985). However, the

observed passive displacement of smolts (Thorpe & Morgan 1978; Tytler *et al.* 1978; Hansen & Jonsson 1985; but see Davidsen *et al.* 2005) might reduce effective feeding (Garnås & Hvidsten 1985), and most feeding probably takes place during resting stops in pools near the bottom (Mitans 1970; Garnås & Hvidsten 1985). This has been suggested to cause the large benthic component observed in the diet of smolts, in contrast to the more drift-orientated feeding of salmon parr (Wankowski & Thorpe 1979a; Stradmeyer & Thorpe 1987). Smolt are, however, also clearly capable of drift-feeding, demonstrated through the occurrence of surface prey in the diet. Heinimaa & Erkinaro (1999) showed that feeding activity and the amount of surface prey in stomachs were inversely correlated with proportion of high water velocity habitats in different parts of the large Tana River system (northern Norway and Finland). Surface prey constituted 11–88% of the smolt diet in Tana, while the proportion has typically been 15% or less in other northern salmon rivers, e.g. the Salatsa in Latvia (Mitans 1970), the Rickleån in northern Sweden (Södergren & Österdahl 1965) and the Orkla, central Norway (Garnås & Hvidsten 1985). The Tana figures resembled those of the River Bush, Northern Ireland (Kennedy *et al.* 1984) and the Merrimack River, USA (Johnson *et al.* 1996), where the proportion of surface prey varied within the range of 10–21% and 47–86%, respectively.

4.4.4 Adults

It is commonly stated in the literature that the adults do not feed during their upstream spawning migration (Mills 1989; Bardonnnet & Baglinière 2000), although there is some evidence of adult stomachs containing food items of both terrestrial and freshwater origin (Johansen 2001). Very little is known about winter feeding of kelts after spawning and premature late autumn migrants, but results from River Alta (northern Norway) indicate no feeding (A. Rikardsen & E. Halttunen, unpublished data). Large adult landlocked salmon are often piscivorous (e.g. Hyvärinen *et al.* 2000), while parr and adults of a Norwegian lacustrine dwarf population predominantly feed on zooplankton (Barlaup *et al.* 2005).

4.5 Temporal feeding patterns

The juveniles do not spend all their time feeding; rather they seem to feed efficiently for short periods and then retreat to more sheltered locations (Gries & Juanes 1998). The salmon are, thus, balancing their time budget between energy gain and costs (Forseth *et al.* 2011 [Chapter 6]). The balancing of this time budget depends on a multitude of interconnected environmental factors such as water temperature, current velocity, streambed composition, food availability and predation risk. The profitability of a feeding site may vary with time of day due to variations in light level as feeding is most efficient during daylight and declines with lowered light levels (Fraser & Metcalfe 1997). In contrast to this, however, drift availability is usually higher at dim to no light (Brittain & Eikeland 1988), and day-active salmon are more exposed to predation risk from visually hunting predators. From day to day and season to season, the juveniles must balance their behaviour between actively feeding and seeking refuge. This trade-off is reflected in the observation that juveniles become nocturnal at low temperatures and more day-active as temperature and energy needs increase (Fraser *et al.* 1993).

4.5.1 Day vs. night

Early literature on salmon feeding states that juveniles feed mostly during the day and relatively little at night during spring, summer and autumn (e.g. Hoar 1942; Ali 1964; Wankowski & Thorpe 1979a; Wankowski 1981; Higgins & Talbot 1985; Browman & Marcotte 1986; Thorpe *et al.* 1988). The salmon eyesight is adapted for daylight feeding (Ali 1961), and at lower light levels drift-feeding efficiency becomes greatly reduced. At a light level of 1 lx, less than 50% of juveniles were able to obtain drifting food items, and below 0.01 lx only minimal drift feeding rates were observed (Fraser & Metcalfe 1997). Prey detection distances decrease with decreasing light levels, and this gives the juveniles less time to react and capture drifting prey (see Box 4.3). The most intensive drift foraging is thought to take place around dusk and dawn, which are periods with sufficient light levels and high drift food availability due to high drift rates (Brittain & Eikeland 1988).

At night, juveniles likely feed predominantly from the benthos. Juvenile salmon changed feeding behaviour from drift to benthic feeding when moved from light to darkness in a lab experiment (Jørgensen & Jobling 1992), and night-time stomach samples from subarctic areas indicate predominantly night-time benthic feeding (Bergersen 1989; Gabler & Amundsen 1999; Amundsen *et al.* 2000). Subarctic areas have continuous daylight from May to early August, so feeding efficiency is not constrained by low light levels at night. There is no day–night difference in food availability, as seen in the lack of a diel drift periodicity (Müller 1973; Johansen *et al.* 2000), and salmon, accordingly, have high feeding rates both during day and night. Later, as the season change from summer to autumn, nights get darker and invertebrates become more night-active. Juveniles respond to this change in food availability by becoming more nocturnal (Amundsen *et al.* 1999, 2000).

The day–night pattern in feeding activity varies with water temperature. Juvenile salmon become increasingly nocturnal in experimental studies at water temperatures below 13 °C (Fraser *et al.* 1993, 1995), a finding that agrees with some field observations (Amundsen *et al.* 1999, 2000). There are, however, also examples of nocturnal feeding in temperate areas at higher water temperatures (13–23 °C, Gries *et al.* 1997), demonstrating that the relationship is not as clear in the field as experimental setups indicate. Breau *et al.* (2007) found 1+ parr to be mostly night-active, while fry were almost exclusively day-active. Another study (Imre & Boisclair 2004) found the same nocturnal activity for parr (1+ and older), while fry were equally active at day and night. This demonstrates that summer feeding behaviour is more complex than a simple story of day or night feeding. Breau *et al.* (2007) revealed great individual variability among the studied juveniles, both in pattern and in how each fish responded to changes in environmental variables. This individual variability and how it relates to feeding clearly deserves further study.

At very low water temperatures, during winter, the day–night activity pattern changes with the presence or absence of ice. Juveniles are nocturnal in temperate areas without ice (Fraser *et al.* 1993), while there are only small differences between day and night (Stickler *et al.* 2007) or even a tendency towards diurnal activity (Erkinaro *et al.*, unpublished data) in more northern areas with ice.

4.5.2 Season

A temperature-based food consumption model predicts increasing food consumption with increasing temperature, up to a maximum consumption at temperatures of 19.5–19.8 °C

(Forseth *et al.* 2001). The highest food consumption is, thus, expected in late spring, summer and early autumn, which is indeed often observed (Kennedy *et al.* 2004; Mookerji *et al.* 2004; Amundsen & Gabler 2008). There are, however, also observations of lower gut fullness during the summer despite high food availability (e.g. Grader & Letcher 2006), which might be caused by the water temperature becoming suboptimally high.

While water temperatures fall during the autumn, juvenile salmon activity levels decrease and the juveniles switch their positions towards hiding in overwintering refugia between stones in the river bed (e.g. Heggenes & Saltveit 1990; Valdimarsson & Metcalfe 1998). The limited food intake of juveniles during the winter can be characterised as a state of overwintering anorexia (Metcalfe & Thorpe 1992). This state of anorexia is upheld even in the presence of excess food (Higgins & Talbot 1985). Salmon do feed in the winter (Cunjak 1988; Thonney & Gibson 1989; Grader & Letcher 2006), but the high number of empty stomachs and the overall dominance of highly digested prey remains observed in stomachs that contain food indicate low overall feeding levels (Cunjak 1988; Finstad *et al.* 2004). The winter feeding patterns depend on life-history, as the fish that will smoltify the following spring maintain relatively high activity (Metcalfe *et al.* 1988; Morgan *et al.* 2000), while the fish that will remain in fresh water for at least another year show lower activity levels (Valdimarsson & Metcalfe 1998). The former group had significantly higher food consumption rates than the latter at the start of the winter, while rates became equal in mid-winter and the latter group exceeded the former in early spring (Morgan *et al.* 2000).

There are notable differences in prey composition between seasons. Dominant orders in the overall diet are Diptera, Ephemeroptera and Trichoptera (Box 4.2; Thomas 1962; Thonney & Gibson 1989; Cunjak 1992; Gabler & Amundsen 1999; Amundsen *et al.* 2001; Grader & Letcher 2006). In general, the seasonal transition in diet moves from Ephemeroptera, Diptera and Plecoptera in spring, to Ephemeroptera, Diptera and terrestrial insects in summer. By autumn, Trichoptera larvae become dominant, while in winter the diet shifts to a combination of Plecoptera, Ephemeroptera and Trichoptera.

4.6 Spatial feeding patterns

River systems are inherently variable on several spatial scales, as detailed in the patch dynamics concept (Townsend 1989). This concept emphasises differences in life cycles and colonisation abilities of aquatic organisms within the ever-shifting spatial and temporal mosaic of patches and habitats within a river. Juveniles live in an environment of contrasting feeding possibilities on different scales, from microhabitat feeding station decisions via mesohabitat movements between riffles and pools to large-scale migrations between major habitats (for instance nursery streams or lakes).

The relative food availability among patches in running water can change over a very short time-scale (Martin-Smith & Armstrong 2002). This variability creates a need to track the relative quality of adjacent habitat patches, and individual juvenile salmon respond by becoming mobile with extensively overlapping home ranges, in contrast to the sharply defined single local territories found in the more predictable environment of the laboratory (Armstrong *et al.* 1999). Little is known about the extent to which juveniles are able to track the relative food availability of patches. There are indications that the juveniles are able to track quality on the habitat scale (Nislow *et al.* 1998), but this tracking seems more



Figure 4.1 Juvenile salmon in holding position close to the streambed. The water current carries drifting prey items past the juvenile, while holding station against the current and darting out into the current to catch prey items both require energy expenditure. The juvenile salmon use their large pectoral fins as hydrofoils to hold position on the streambed with minimal energy use. Photo: Panu Orell.

limited within local microhabitats where small-scale changes occur quickly and frequently (Macleán *et al.* 2005).

4.6.1 Microhabitat scale

Juvenile salmon occur in a wide range of conditions, and these local conditions govern the microhabitat characteristics of the juveniles' feeding behaviour. In slow-flowing or still water, e.g. in lakes, the juveniles move actively around searching for food items (Gibson 1978; Erkinaro *et al.* 1998), while in running water the juveniles behave more like a 'sit-and-wait' predator, at least while drift-feeding. When drift-feeding, juveniles select focal points (holding positions on or just above the river bed; Figs. 4.1, B4.3.1), from which they forage by darting out to intercept food items that are carried past in the current (Keenleyside 1962; Stradmeyer & Thorpe 1987). Preferred feeding points are near areas where the highest drift rates occur, patches in the river that provide a good balance between energy gained through feeding and energy expended for metabolism and growth (Fausch 1984). Water velocity is a key factor here as it determines the prey encounter rate, the prey capture probability and the energetic costs incurred by the fish while feeding (see Box 4.3 for more details).

4.6.2 Mesohabitat scale

Most studies of juvenile salmon have been conducted at the mesohabitat level of riffles and runs. Deep slow-flowing areas have received comparably little interest, despite documented

extensive usage of pools (Saunders & Gee 1964). The larger size-at-age of parr in pools (Bremset & Berg 1997) can either be explained through the movement of large, dominant parr into pools, or by favourable conditions in the pools that give pool-dwelling fish a higher net energy gain than their riffle-living conspecifics. We have, unfortunately, little knowledge about feeding within deeper slow-flowing areas and how this relates to the possible advantageous conditions within pools.

4.6.3 Habitat scale

Fish undertake movements over larger scales to obtain better food resources and growth possibilities (Northcote 1978). Salmon movements into habitats such as lakes, small streams and estuaries have been widely documented, and for all three migratory alternatives it is found that growth, body composition and energy status of the juveniles undertaking the migration differ from those left behind in the original habitat (e.g. Cunjak 1992; Erkinaro & Niemelä 1995; Dempson *et al.* 2004), reflecting habitat changes that provide the juveniles with better feeding possibilities.

Within a lake, the fish can feed on benthic invertebrates from the lake bottom, zooplankton from the water column and insects from the water surface. In Newfoundland lakes, dipteran larvae, pupae and adults were the most important prey items (Pepper *et al.* 1985). Reports on the diet of stocked salmon from lakes in the United Kingdom revealed a diet consisting of benthic invertebrates, plankton and surface insects (Morrison 1983). In a north Norwegian lake, juvenile salmon fed primarily from the water column and lake surface during the summer, and not so much directly from the benthos (Jørgensen *et al.* 2000). In the Tana River system in Finland, stomach fullness was found to be higher for juveniles within the lake compared with fluvial counterparts, and also higher in sandy, vegetated areas of the lake compared with stony, unvegetated areas (Erkinaro *et al.* 1998). In addition, there was a tendency towards more individually specialised prey use among lacustrine parr than in fluvial parr, e.g. for zooplankton and fish prey.

Parr use of river estuaries has been documented from North America (Power & Shooner 1966; Cunjak *et al.* 1989; Cunjak 1992). During spring, riverine parr had higher average stomach fullness (61%) than estuarine parr (50%), while in summer and autumn, estuarine parr had the highest stomach fullness (76%); markedly higher than the average (40%) observed in the river (Cunjak 1992).

Parr migration into nursery streams (defined here as small tributary streams without spawning activity based on lack of salmon fry, spawning redds and spawners) are found on both sides of the Atlantic (Erkinaro 1995; Erkinaro & Gibson 1997). Growth rates in nursery streams are higher than growth rates in the main natal river despite lower water temperatures in the nursery streams (Erkinaro & Niemelä 1995). This indicates higher feeding rates within the nursery streams, and when comparing benthos and drift densities between the main river and tributaries (Figs. 4.2 and 4.3), it is clear that food availability (especially drift of terrestrial invertebrates) is highest in the small nursery streams (Erkinaro & Erkinaro 1998; Johansen *et al.* 2005). The diet composition also differed between the main river sections and nursery streams, with large Plecoptera and Trichoptera being dominant in the stomachs of stream fish and smaller Simuliidae and *Baetis* (Ephemeroptera) in the main river.

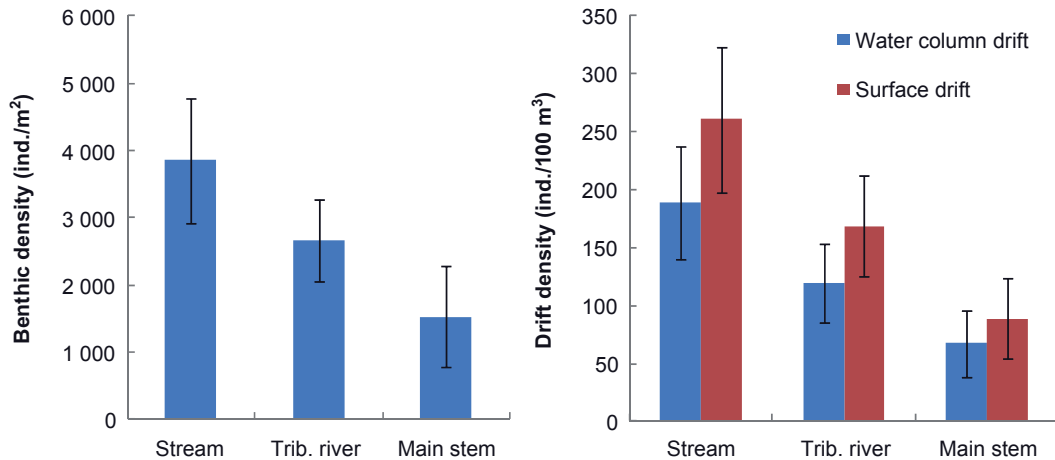


Figure 4.2 Food availability comparison between a highly productive small tributary stream (see Fig. 4.3a), a larger tributary river, and the large Tana River main stem (see Fig. 4.3b) on the border between Norway and Finland (data from August 2002, recalculated after Johansen *et al.* 2005 and Johansen, unpublished data).

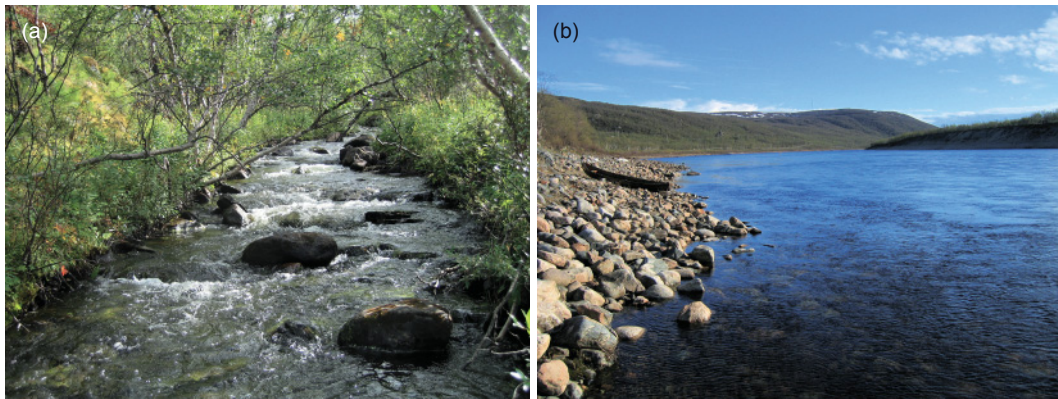


Figure 4.3 An example of (a) a small tributary stream with dense riparian vegetation and abundant supply of both benthic and drifting food items, and (b) a large river habitat for juvenile salmon with relatively low abundance of both benthic and drifting food items. Photos: Jaakko Erkinaro.

4.7 Interspecific food resource partitioning

Limited resources create the possibility for resource competition (Schoener 1986). Competitive interactions for food are, however, difficult to study as it is hard to document food limitation under natural conditions (Werner 1986; Schoener 1989). For this reason, food competition involving salmon has only rarely been addressed and results from the available studies are more suggestive than conclusive and also mixed (see Poff & Huryn 1998). Empirical evidence for food limitation has been found in two northern rivers (Amundsen & Gabler 2008), with interspecific food competition in one of the populations and intraspecific food competition in another.

What, then, are the salmon's expected responses to food competition? Niche theory states that, if food is limiting, the competing species should narrow their niches and become specialised (i.e. feed selectively on certain prey) when sympatric, and feeding should become more generalised when allopatric (Schoener 1989). Optimal foraging theory, on the other hand, suggests that individuals should specialise on optimal prey when prey are abundant and include suboptimal prey in their diet when prey are scarce. The abundant prey situation corresponds to few competitors (low density in allopatry), while the scarce prey situation corresponds to the presence of competitors (sympatry or high population density in allopatry). Initially, these predictions may sound contradictory. However, optimal foraging deals with individuals, whereas niche theory deals with species (or populations) that differ in their competitive ability for different resources. The presence of a competing species will increase the costs in terms of search time for some prey types (i.e. those that the competing species are good at catching). The alternative prey (those that the competitor is not good at catching) would then be the most profitable, and both optimal foraging theory and niche theory would predict a switch to alternative prey.

The habitat use of sympatric brown trout (*Salmo trutta*) and salmon overlap considerably. Both species have a fundamental microhabitat preference for low snout water velocity (Heggenes & Saltveit 1990), which suggests the potential for interference, feeding overlap and resource competition. Brown trout have the same preference for daylight feeding during the summer that is reported for salmon, and both species have the same ability to find food items at night as well (Hoar 1942). Salmon in sympatry with brown trout exhibit more daytime feeding activity than allopatric salmon (Harwood *et al.* 2001). The diet overlap between brown trout and salmon is considerable both in running water (Frost 1950; Thomas 1962; Maitland 1965; Egglisshaw 1970; Lillehammer 1973b) and standing water (Jørgensen *et al.* 2000), but the salmon diet has lower prey species diversity than trout (Dineen *et al.* 2007). Terrestrial invertebrates are more important for trout than for salmon (Jørgensen *et al.* 2000; Dineen *et al.* 2007), indicating a higher use of surface drift. The relatively high incidence of surface drift-feeding among brown trout compared to salmon can be important in facilitating salmon feeding on aquatic invertebrates, and has interesting consequences for the management of river systems with both species. Terrestrial invertebrates form a significant part of the surface drift, and landscape changes that negatively affect the production of terrestrial invertebrates can consequently affect the dynamics between brown trout and salmon (Dineen *et al.* 2007).

Salmon and brook trout (*Salvelinus fontinalis*) often co-exist as juveniles (Fausch 1998). In sympatry, the two species have been found to partition the available food by utilising different food items (Mookerji *et al.* 2004). Brook trout were generalist feeders with a wide diet breadth (wider in sympatry than allopatry). Surface drifting adult insects were the most important prey item. Salmon had a narrower diet breadth and were more specialised on Ephemeroptera nymphs.

Sympatric salmon and rainbow trout (*Oncorhynchus mykiss*) have a high diet overlap (Coghlan *et al.* 2007). In allopatry, salmon had a wider diet breadth than rainbow trout, with comparatively little overlap. This overlap increased in sympatry, with the diet composition of rainbow trout changing most. A semi-natural experiment demonstrated no effect of rainbow trout on salmon feeding success, only an increase in daytime activity (Blanchet *et al.* 2008). Coho salmon (*O. tshawytscha*) had no effect on the foraging success of Atlantic salmon (Scott *et al.* 2005).

In the River Reisa (northern Norway), sympatric Arctic bullhead (*Cottus poecilopus* Heckel) and salmon have a high diet overlap (Gabler & Amundsen 1999). This is an empirical example of food limitation affecting salmon, as salmon parr have low food consumption rates compared to other river systems in the region (Amundsen & Gabler 2008). Bullhead (*Cottus gobio*) were accidentally introduced to the River Utsjoki (a tributary of the large River Tana) in the 1970s (Pihlaja *et al.* 1998). Bullheads and salmon show a consistent segregation in food niches, with the bullhead feeding mainly on interstitial prey while salmon feed mainly on substrate surface and drifting prey (Gabler *et al.* 2001).

4.8 Concluding remarks and future perspectives

Salmon freshwater feeding has received a lot of attention over the years, and perhaps one of the central tenets that can be derived is that juveniles are inherently flexible with a wide range of responses to environmental conditions. Although a great deal of attention has been given to the field of salmon freshwater feeding, we still have unresolved issues that deserve additional study. In particular, there is a lack of rigidly designed field studies that can test the combined interactive effects of the feeding behavioural mechanisms found in the large body of laboratory studies. The role of food availability in the habitat selection of juveniles, and the interaction between food and habitat in determining the distribution of juveniles on different scales, are relatively little studied. Also, feeding is seemingly well studied at the population level, but much less so on the individual level. This is illustrated by a general focus in the literature on the average diet, while variability on different scales (both for individuals and populations) has received comparatively little focus.

The modelling approaches, e.g. through drift-feeding models that combine foraging theory, energetics and behaviour, are promising. However, most models still focus only on salmon as a drift-feeding fish on the mesohabitat scale of a riffle. The juvenile salmon are remarkably flexible and opportunistic, being able to inhabit and feed in a large range of differing habitats, ranging from small nursery streams to large rivers, and in water velocity from still-standing lakes to fast-flowing riffles. The salmon juveniles are able to choose from different habitats and different feeding modes (e.g. taking food items that are on the substratum surface, drifting in the water column, and drifting on the water surface), and these choices will affect their growth patterns and eventually their life-histories. To incorporate this flexibility will be a major challenge for future population models.

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5

Dietary Life-Support: The Food and Feeding of Atlantic Salmon at Sea

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Abstract

Atlantic salmon, *Salmo salar*, are opportunistic feeders, utilising a wide variety of available prey throughout all life stages while feeding at sea. It is during this time that they build up the bulk of their final body size with many fish increasing in weight 1000-fold or more. Their main prey are different species of fish and fish larvae and planktonic crustaceans, and successful marine feeding is a key factor for enhancing the survival and production of salmon at sea. However, any changes in the marine environment on both spatial and temporal scales may affect the availability of prey and hence impact the subsequent survival and abundance of salmon. In particular, the first few months at sea are often regarded as an important feeding period in order for young salmon to rapidly enhance their growth and reduce their risk of predation. Drawing on past as well as recent studies, we review current knowledge related to similarities and differences associated with spatial and temporal aspects of Atlantic salmon feeding during various stages of their marine migration from nearshore coastal waters and out into the open sea. As salmon are likely affected by ecosystem structure rather than directly influence it, we note that future studies should focus on direct linkages between prey abundance and the prey that salmon consume, along with how these associations affect survival and productivity of stocks in the context of a changing climate.

Key words

Life-history, *Salmo salar*, anadromy, marine migration, North Atlantic Ocean, growth, top-down, bottom-up, climate change

5.1 Introduction

At sea, Atlantic salmon (*Salmo salar*) are usually pelagic feeders that often forage close to the surface, covering large areas of the North Atlantic (Hansen *et al.* 2003; Rikardsen *et al.* 2004). Most spend from 1 to 4+ years at sea and during this period they accomplish the bulk of their lifetime growth, increasing in weight from about 15–50 g to 1–25 kg or even

Box 5.1 Why migrate to sea? – ‘The food availability hypothesis’

An anadromous life-history is most common at higher latitudes (McDowall, 1987), and Northcote (1978) proposed that this latitudinal trend in anadromy could be a result of oceanic waters being less productive in the tropics than in temperate or polar areas. Expanding on this hypothesis, Gross (1987) and Gross *et al.* (1988) postulated that anadromy evolved as a response to the relative differences in the productivity of the marine and freshwater environments. Thus, by migrating from fresh water to the sea, the fish in northern latitudes could increase the possibility of growth, resulting in higher fitness¹ and the evolution of anadromy.

Although this food-availability hypothesis is still under discussion (e.g. McDowall 1988, 1992, 1993, 1997, 2008; Northcote 1992; Stearley 1992; McLennan 1994; Dodson 1997), it is agreed that the migration model of Gross seems to be valid: anadromy will be an evolutionary stable life-history strategy as long as the growth and survivorship advantages at sea, minus the cost of moving between habitats, exceed the advantage of staying only in fresh water for the same period (Gross 1987).

¹ In this context defined as the lifetime product of reproductive success x survivorship

more. In temperate and Arctic latitudes, the marine production of potential prey for Atlantic salmon, and other anadromous fishes, is usually much higher than the corresponding freshwater production at similar latitudes (Gross *et al.* 1988). Therefore, the availability and quality of food at sea are key elements that provide the dietary life-support required to enhance growth and survival of salmon in the ocean environment (Box 5.1).

In recent decades, marine survival and growth of various salmon populations have declined in both the northeast and northwest Atlantic even though many marine fisheries for salmon have been reduced or closed (Parrish *et al.* 1998; Friedland *et al.* 2003a; Dempson *et al.* 2004; Jonsson & Jonsson 2004a; ICES 2008a). The reduction in growth and survival affects the subsequent abundance of salmon that return to spawn in fresh water and has been associated with changes in the marine climate, especially sea surface water temperature (SST) along with other larger-scale climate indices such as the North Atlantic Oscillation (NAO) and Atlantic Multi-decadal Oscillation (AMO), with evidence building for both European (e.g. Friedland *et al.*, 1998, 2000, 2009; Dickson & Turrell 2000; Jonsson & Jonsson 2004b; Boylan & Adams 2006) and North American (e.g. Friedland & Reddin 2000; Friedland *et al.* 2003a, 2003b, 2005) populations. We acknowledge, however, that the NAO does not always correlate with size or abundance in all areas (e.g. Niemelä *et al.* 2004; Todd *et al.* 2008; Friedland *et al.* 2009). Water temperature and other abiotic environmental factors may mainly act indirectly, so that changes in the production and availability of suitable food items may more likely be the primary cause affecting salmon as well as other species (e.g. Brander 2007; Friedland *et al.* 2003b, 2009).

Except for Friedland *et al.* (2009), few studies have tried to address the linkages between abiotic marine environmental factors, the different trophic levels of the marine food web, and the subsequent effects on Atlantic salmon as a top predator. Many of the earlier investigations provided descriptive details on the marine feeding of Atlantic salmon during different periods of their ocean migration and usually with emphasis on a specific life-history stage (e.g. Lear 1972, 1980; Hislop & Shelton 1993; Jacobsen & Hansen 2000, 2001; Sturlaugsson 2000). With the advent of more efficient surface trawls, more extensive sampling of small and young first-time migrating salmon, both within fjords in coastal areas and in the open ocean, has been carried out in recent years to examine spatial and temporal variation in early salmon feeding during their first months at sea (Holst & McDonald 2000; Holm *et al.* 2003). In particular, these months are regarded as a key feeding period for the

young salmon in order to grow out of the ‘risk size window’ of being eaten by larger predators, as well as ensuring a healthy body condition important for subsequent survival, migration and growth opportunity during their whole sea residency (Levings 1994; Salminen *et al.* 2001; Hvidsten *et al.* 2009).

Accordingly, this chapter focuses on the present knowledge of feeding of Atlantic salmon at sea. Here, we follow terminology used in earlier feeding analyses where the salmon are termed post-smolt during their first months following sea entry, usually May–October (Jacobsen & Hansen 2000). Pre-adult and adult salmon are defined as non-maturing and maturing fish, respectively, feeding in the open offshore region or while on their homeward migration in coastal areas with sizes generally greater than 30 cm in fork length. Much of the information presented is based on more recent studies carried out in the northeast Atlantic, owing to the general dearth of comparable up-to-date investigations in the northwest Atlantic. Thus, drawing on past as well as current studies we begin with a review of the feeding of post-smolts in nearshore coastal waters (e.g. fjords) and then summarise dietary information as post-smolts move out into the open ocean and later during the pre-adult and adult feeding stages. Similarities and differences in feeding on both spatial and temporal scales are noted to the extent possible for the various life-history groups. This is followed by a synthesis of how salmon may be affected by ecosystem processes in the North Atlantic and then concludes with suggestions for further research.

5.2 Post-smolt nearshore feeding

The period of sea entrance and the first few months of marine life have been considered as the time at which most marine mortality in Atlantic salmon occurs (Hansen & Quinn 1998; Anon. 1999; Jacobsen & Hansen 2000; MacLean *et al.* 2000; Potter & Crozier 2000; Sturlaugsson 2000). During this time post-smolts begin feeding extensively on marine fish larvae, particularly sand eels (*Ammodytes* spp.), herring (*Clupea harengus*), gadoids and crustacean prey (Rikardsen *et al.* 2004) and often experience a rapid increase in growth (Dutil & Coutu 1988). Thus it is important that post-smolts quickly obtain sufficient food to enhance growth, improve migration success and avoid predators. While several papers have addressed the relationships between open ocean sea water temperatures and salmon abundance (see references in Section 5.1), Hvidsten *et al.* (2009) also found a positive relationship between the local sea temperature at post-smolt sea entry and the abundance of returning adults of the same smolt year, as well as evidence for higher returning rates of post-smolt year classes that fed extensively on marine fish larvae. They hypothesised that the correlation between returning rate and sea temperatures at smolt sea entry was related to a combination of higher prey abundances at higher coastal sea temperatures (Vikebo *et al.* 2005) and better growth opportunities at sea temperatures $>8^{\circ}\text{C}$ (Hvidsten *et al.* 1998; Hadeland *et al.* 2008), thus supporting the importance of the early post-smolt phase. Indeed, as growth cannot be compromised, successful early marine feeding is a key factor for the survival of young salmon at sea (Levings 1994; Levings *et al.* 1994; Salminen *et al.* 2001; Hvidsten *et al.* 2009).

A high growth rate of larger fish is usually associated with piscivory (fish eating) behaviour, or by selecting abundant high-energy crustaceans (Elliott & Hurley 2000; Rikardsen *et al.* 2000; Salminen *et al.* 2001; Jensen *et al.* 2008). In fresh water, salmonids must often attain a size of 15–25 cm or more in order to start feeding on fish, but this varies by species



Figure 5.1 A fish-eating post-smolt (15 cm L_T) captured shortly after its sea entry to the Alta Fjord, northern Norway. The post-smolt had eaten sand eel and herring larva (prey:predator relationship = 27%) and also some pelagic amphipods (*Themisto* spp.) and one krill (Euphausiacea) Photo: Stig Sandring

(e.g. East & Magnan 1991; L'Abée-Lund *et al.* 1992; Mittelbach & Persson 1998; Jonsson *et al.* 1999). In contrast, Atlantic salmon smolts, even at sizes less than 15 cm, immediately after entering the sea may feed extensively on fish larvae (Rikardsen *et al.* 2004; Fig. 5.1); a prey that they never have encountered or eaten before while in fresh water. In a river, the small juvenile fish (fry) usually hide within the substrate, making them inaccessible as a prey for salmon pre-smolts. While in the sea, however, marine fish larvae may occur in large densities in estuaries, fjords and open oceans, making them potentially more easily accessible due to their large size compared with other and smaller prey items in this habitat (e.g. insects and planktonic crustaceans). From an energetic perspective, feeding on marine crustaceans or fish larvae instead of insects will be highly beneficial due to their larger size and a lipid content of >50% (of dry mass), which is two to seven times greater than the lipid content of most invertebrate prey in fresh water (Falk-Petersen *et al.* 1990; Rikardsen *et al.* 2000).

Studies of other anadromous salmonids in fjords in the North Atlantic have also shown a strong reliance on herring larvae. For example, both sea trout (*Salmo trutta*) and anadromous Arctic charr (*Salvelinus alpinus*) feed extensively on herring larvae when available, and have a high diet overlap with each other and with Atlantic salmon post-smolts within the same fjord systems in years when herring abundance is high, but a low overlap in years when herring are less prevalent (Grønvik & Klemetsen 1987; Rikardsen & Amundsen 2005; Rikardsen *et al.* 2004, 2006, 2007).

5.2.1 Geographical and annual differences

There are large geographical differences in the type and amount of prey eaten by post-smolts after entering salt water (Fig. 5.2). However, one apparent aspect is that there is a general tendency for certain pelagic fish species' larvae to be eaten, if present. For example, in west Scotland, sand eels were the principal component in the diet of post-smolts (16.7–20.2 cm

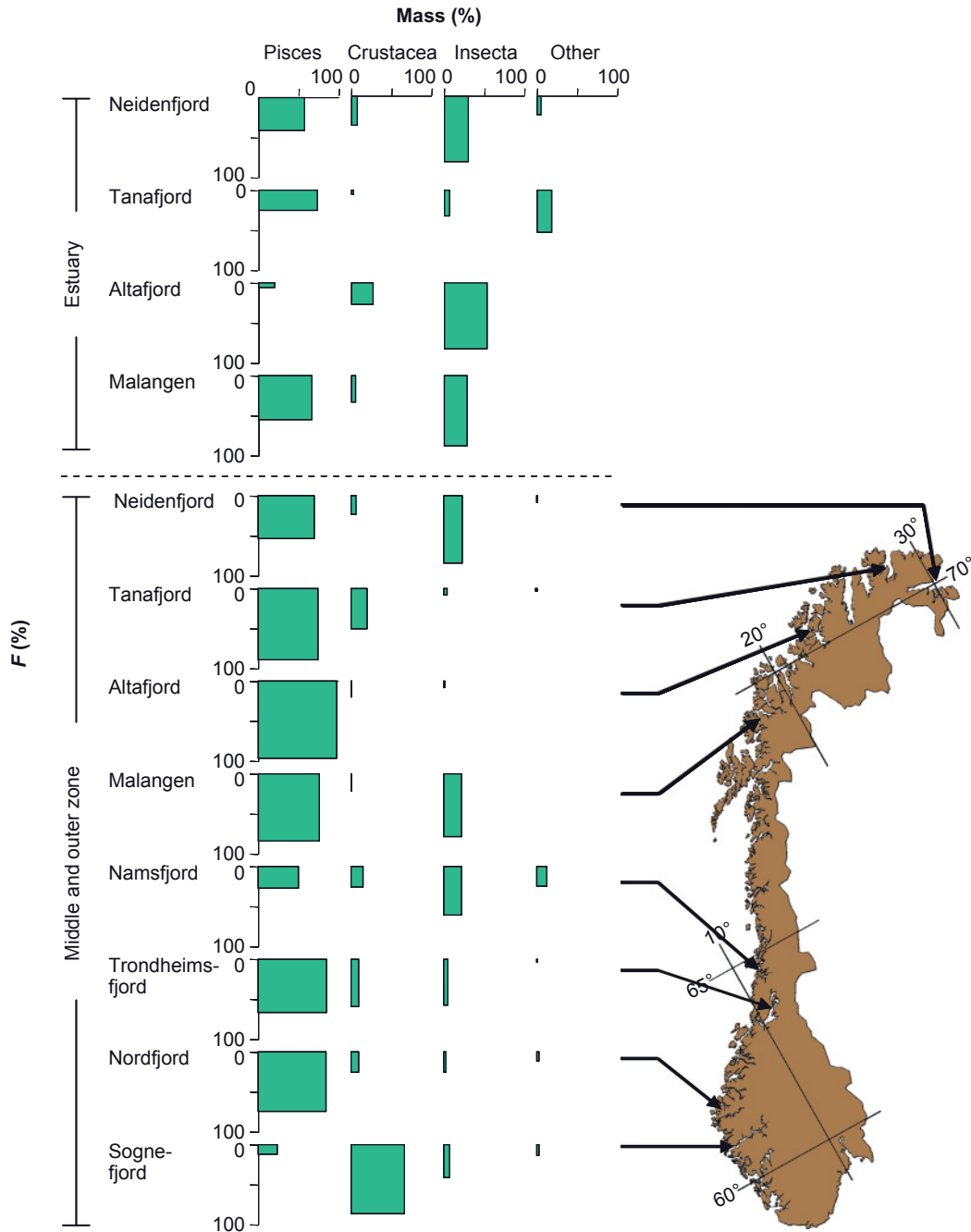


Figure 5.2 The relative importance of main prey groups for post-smolts in different Norwegian fjords expressed as combinations of frequency of occurrence (F%), i.e. the percentage of fish in which a particular prey occurred of the total number of fish with food in their stomach) and stomach fullness (mass%), i.e. the percentage mass of a prey taxon of the total mass of the stomach content in all predators) for post-smolts divided by the estuary zone and a combination of the middle and outer zone. Within each zone, the fjords are arranged from the most northeasterly one (top) to the most southeasterly one (bottom). Redrawn from Rikardsen *et al.* (2004).

in fork length, L_F) shortly after their migration out of a river (Morgan *et al.* 1986). This corresponds with Rikardsen *et al.* (2004) who found that herring and sand eel larvae were the dominant prey in a study of eight Norwegian fjords (Fig. 5.2). In contrast, other studies in Norway, Iceland, Canada and the Baltic show that insects and different crustaceans often make up the largest contribution to the diet of post-smolts (~10 to 34 cm) shortly after entering the ocean (Levings *et al.* 1994; Sturlaugsson 1994; 2000; Andreassen *et al.* 2001; Lacroix & Knox 2005). This could be a situation where fish larvae either are not present or accessible to the post-smolts, or where more energetically profitable crustacean prey occurs in high densities.

Salminen *et al.* (1994, 2001) examined the shift in diet of Baltic salmon to piscivory after fish had attained a critical size of about 24 cm (L_F) and the subsequent impact on growth rate. They suggested that the lack of piscivory of smaller post-smolts may be due to the fact that the available fish (herring) were too large to be eaten by most post-smolts in the Bothnian Sea. Their observed average prey-length:predator-length relationship was 21% (11–36%), and was similar to that reported by Rikardsen *et al.* (2004) in Norwegian fjords. In the latter case the smallest Atlantic salmon (*c.* 10 cm L_F) were feeding on fish larvae in the estuarine zone (see Fig. 5.1). As the abundance and size range of available fish larvae may vary considerably within and between seasons (Fiksen & Slotte 2002; Vikebo *et al.* 2005; Toresen & Østvedt 2008), the timing of the smolt runs will thus be important for maximising immediate growth efficiency, and may give rise to a match-mismatch situation among years and within seasons (Box 5.2).

Box 5.2 The importance of timing the sea entry: the ‘match-mismatch scenario’

The onset of the salmon smolt migration is triggered by several environmental factors (see Chapter 1.2) and is assumed to be adjusted to advantageous conditions at sea (Hvidsten *et al.* 2009). However, the type, size and abundances of prey items they encounter while entering the sea for the first time may vary greatly within seasons, as well as among seasons and at different locations and latitudes. This means that if smolt enter the sea too early or too late in the spring or early summer, they might miss the abundance maximum of suitable prey or the prey may be too big or too small for consumption. Consequently, post-smolts may suffer from reduced growth and survival. On the contrary, if they enter the sea at a time when the suitable prey availability is most abundant, they may be rewarded with a higher immediate growth rate and a corresponding potential for higher overall survival. Thus, the timing of the smolt migration in relation to the size range and abundance of suitable prey (especially fish larvae) in the fjords may therefore be important for maximising immediate growth efficiency, and may give rise to a *match-mismatch situation* (Cushing 1975, 1990) within seasons and between years.

The availability of fish larvae at smolt sea entry is, however, dependent on the availability of suitable zooplankton prey (Maravelias 1999; Beaugrand and Reid 2003). For simplicity, we have used the North Atlantic copepod *Calanus finmarchicus* as an example here, although other copepods or crustaceans can also be important (Friedland *et al.* 2009). *C. finmarchicus* is regarded as a key species in the marine production and an important prey for marine fish larvae (Tande 1991, 1992; Peyronnet *et al.* 2008). However, the abundance of *C. finmarchicus* may vary by a factor of 100 among years, seasons and localities (Tande and Slagstad 1992), often representing >90% of the total zooplankton biomass in northern and Arctic seas and fjords (Tande, 1992; Falkenhaug *et al.*, 1997). This variation is dependent on environmental and oceanographic conditions (in particular temperature), internal production within the area, predation and the extent of horizontal movement (advection) of zooplankton from coastal and oceanic waters (Aksnes *et al.* 1989; Mann and Lazier 1991; Unstad and Tande 1991; Tande 1991, 1992). However, *C. finmarchicus* usually has its highest biomass in the upper water column in spring, and when they reach the copepodide stage V they migrate to deeper water to spawn and overwinter and are then unavailable for pelagic marine fish larvae like herring and sand eel. Thus, for fish

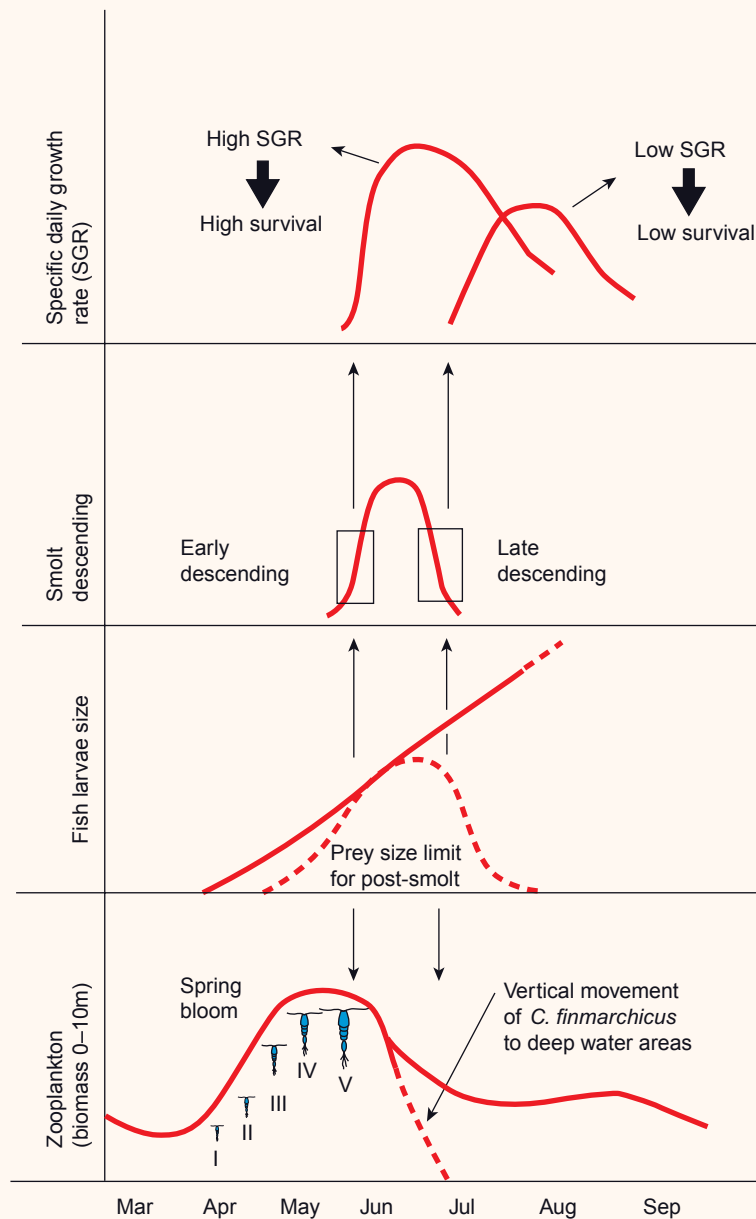


Figure B5.2.1 The spring maximum of e.g. *Calanus* spp. may give rise to a high production of fish larvae of a size available for post-smolts within a restricted time window, which in turn can result in a high immediate specific growth rate (SGR) and subsequently a high survival rate if the smolt migration is timed correctly.

larvae it is important that they hatch at a time when the abundance of suitable prey is profitable. As marine fish larvae generally make a large contribution to the post-smolt diet, *C. finmarchicus* or other abundant crustaceans may therefore potentially have a considerable indirect impact on post-smolts and may contribute to match-mismatch scenarios (Fig. B5.2.1).

In the absence of studies that consider both geographical area and time, it can be difficult to determine whether observed differences in feeding are due to spatial rather than temporal variation. However, Rikardsen *et al.* (2004) studied eight fjords along the southwestern to northeastern coast of Norway during 1998–2001. Post-smolts from southern Norway generally showed low feeding intensity within fjords where they often consumed insects and crustaceans (Fig. 5.2). In contrast, post-smolt fed more extensively in fjords in the central part of Norway, and particularly in the northernmost region where they fed more extensively on fish larvae (mostly sand eels and herring). They concluded that extensive feeding immediately after sea entrance may be more common for post-smolts in the northern and central parts of Norway, than in the southern fjords, possibly as a result of spatial and temporal differences in prey availability within and between the different types of fjord systems. Spatial variation may be explained in terms of fjord dynamics where the shorter and more open northern fjords are usually more influenced by a high advection from the Norwegian coastal current (Aksnes *et al.* 1989; Tande 1991; Box 5.2) and are generally regarded to be more productive than the longer, narrower and often more closed southern sill fjords (Reigstad 2000).

Spatial differences in feeding also occur within fjords. Much of this insight was obtained from detailed investigations carried out within Norwegian fjords (e.g. Rikardsen *et al.* 2004), while comparatively little information is available from the northwest Atlantic. The Norwegian studies show a general tendency for post-smolts to increase their feeding intensity when migrating from the estuary and throughout the fjord before entering the open ocean (Levings *et al.* 1994; Andreassen *et al.* 2001; Stefansson *et al.* 2003; Rikardsen *et al.* 2004; Knudsen *et al.* 2005). Insects and intertidal crustacean prey (especially gammarid amphipods) were frequently taken in the estuary, although fish larvae can also make a large contribution in terms of the overall mass of stomach contents (Levings *et al.* 1994; Hvidsten *et al.* 1995; Andreassen *et al.* 2001; Rikardsen *et al.* 2004; Fig. 5.2). In contrast, fish larvae, and to some extent various crustaceans (particularly Hyperiidæ, Gammaridæ, Euphausiacea and Copepoda) often dominated the diet in the middle and outer parts of the fjords, where post-smolts usually feed more extensively than in the inner part. This may be due to growing familiarity with the marine physical environment and the prey organisms encountered and possibly the increasing availability of various marine prey species further out in the fjord. Many of the insects found in post-smolt stomachs in the estuary may be a relict of the diet consumed while fish were still in the river, or from insects drifting down into the estuary (Cunjak 1992; Granås & Hvidsten 1995; Rikardsen *et al.* 2002).

Limited feeding studies of a few post-smolt from the northwest Atlantic (the Bay of Fundy and Gulf of Maine) similarly illustrate differences in feeding among locations (Lacroix & Knox 2005). Here, more fish, particularly larval *Ammodytes*, were found when surveys were conducted within the Bay of Fundy, but more crustacean species, particularly amphipods and euphausiids, were recorded when surveys extended farther out into the Gulf of Maine.

Besides spatial differences, feeding intensity and prey species consumed also vary annually when examined at different latitudes (Levings *et al.* 1994; Hvidsten *et al.* 1995; 2009; Andreassen *et al.* 2001; Rikardsen *et al.* 2004). In general, fish were the dominant prey in most Norwegian fjords. In years with high feeding intensity, fish larvae usually made a larger contribution to the diet than in years with a lower feeding intensity where various crustaceans and sometimes insects made important contributions to the diet.

In summary, there are substantive geographical and annual differences in the quality and quantity of early marine feeding of post-smolts due to both abiotic and biotic factors affecting the availability of suitable prey. This variability is likely to contribute to spatial and temporal differences in early growth and survival of salmon post-smolts, suggesting that populations may also respond differently to environmental changes affecting the early post-smolt phase of salmon (Hvidsten *et al.* 2009).

5.3 Open ocean feeding of post-smolts

Most Atlantic salmon populations eventually feed in the open North Atlantic, where the bulk of their lifetime growth takes place during their 1–4+ year migration (Klemetsen *et al.* 2003). After leaving the estuaries and coastal areas, many use only a few days to move into the open ocean (Thorstad *et al.* 2007; Davidsen *et al.* 2009), some European populations following the North Atlantic Current (NAC) with minimum migration rates of 6–26 km day⁻¹ (Shelton *et al.* 1997; Holm *et al.* 2003), while in the northwest Atlantic salmon are often concentrated in the Labrador Sea gyre (Reddin & Shearer 1987). Hence, knowledge pertaining to their marine distribution and feeding areas at sea is important in understanding how the oceanic environment influences feeding and production of different salmon stocks. While this topic is partly covered in another chapter in this volume (Thorstad *et al.* 2011 [Chapter 1]), a brief summary follows because it is key to understanding the marine feeding ecology.

Figure 5.3 provides a generalised overview of the presumed distribution of Atlantic salmon in the North Atlantic based on our current understanding of salmon at sea (Hansen &



Figure 5.3 Assumed ocean feeding areas for Atlantic salmon based on available literature, with names given for the main ocean areas discussed in the text. Figure by Frøydis Strand and Audun H. Rikardsen.

Jacobsen 2000; ICES 2008b; Rikardsen *et al.* 2008), along with the names of the main feeding areas noted throughout this text. While the distributional limit of salmon is not necessarily known at any particular time, it is likely that it changes with regard to biological and environmental factors both in time and space.

Existing information indicates that salmon from North America can be found, and are likely to feed, in the western North Atlantic including the Labrador Sea and areas on and east of the Grand Bank of Newfoundland (Reddin 1985; Reddin & Shearer 1987; Ritter 1989; Reddin & Friedland 1993; ICES 2008b). Salmon from southern and central parts of Europe are believed to feed mostly in the northeast Atlantic, particularly in the North and Norwegian seas (Holm *et al.* 2000, 2003; Holst *et al.* 1993, 2000). European salmon, particularly those from southern Europe, the United Kingdom and Ireland, are also abundant off West Greenland along with potential multi-sea-winter (MSW) salmon of North American origin (Swain 1980; Reddin & Friedland 1999). There is also evidence of intercontinental migrations of salmon occurring between North America and Europe (Reddin & Friedland 1999; Hansen & Jacobsen 2003; Spares *et al.* 2007).

While much information on a number of North American and European salmon populations has been compiled over the years, there is still relatively little data identifying feeding areas of the Atlantic salmon stocks from northern Norway and Russia (Jensen *et al.* 1999; Rikardsen *et al.* 2008). A few tagged pre-adult and adult fish of Russian origin have been captured north of the Faroe Islands (Hansen & Jacobsen 2000; Holm *et al.* 2003) and salmon from the White Sea basin may utilise different feeding areas from those populations that migrate directly into the Barents Sea (Jensen *et al.* 1999). Atlantic salmon post-smolts have been caught in surface trawls at 70–75°N in the Norwegian and Barents Sea in July (Holm *et al.* 2003), but their origin is not known. Rikardsen *et al.* (2008) recovered a salmon tag from the stomach of a Greenland halibut (*Reinhardtius hippoglossoides*) captured southwest of Bear Island (72.5°N) at >600m depth in the Barents Sea, a tag that was applied to a smolt released in the River Alta, northern Norway (70°N) one month earlier. In addition, two tagged sub-adults originating from the same Alta Fjord region and one from the Drammen River (southeastern Norway) were captured between 70.5° and 78°N in the western Barents Sea. This new information suggests that northern stocks may utilise different feeding areas than southern European, southern Norwegian and North American stocks, during most or part of their life cycle, and may also partly explain why the productivity of salmon originating from these areas may cycle differently from those at more southern areas (Anon. 1999; Jensen *et al.* 2002; ICES 2008a).

5.3.1 Post-smolt diet in the open ocean

Most of the information on the feeding characteristics of salmon migrating away from nearshore coastal areas has been obtained by studies conducted in the northeast Atlantic region. Observations to date show that upon reaching the open ocean, post-smolts continue feeding on many of the same prey groups they utilised during their initial migration in nearshore areas. Focusing on the area west of the British Isles and the Norwegian Sea, Haugland *et al.* (2006) found large variations in post-smolt diet among areas and years (Fig. 5.4). As the occurrence of post-smolts was closely associated with the North Atlantic Current, their diet was characterised by the potential prey species carried along by this current system. For example, in the Southwestern Area, blue whiting (*Micromesistius pou-*

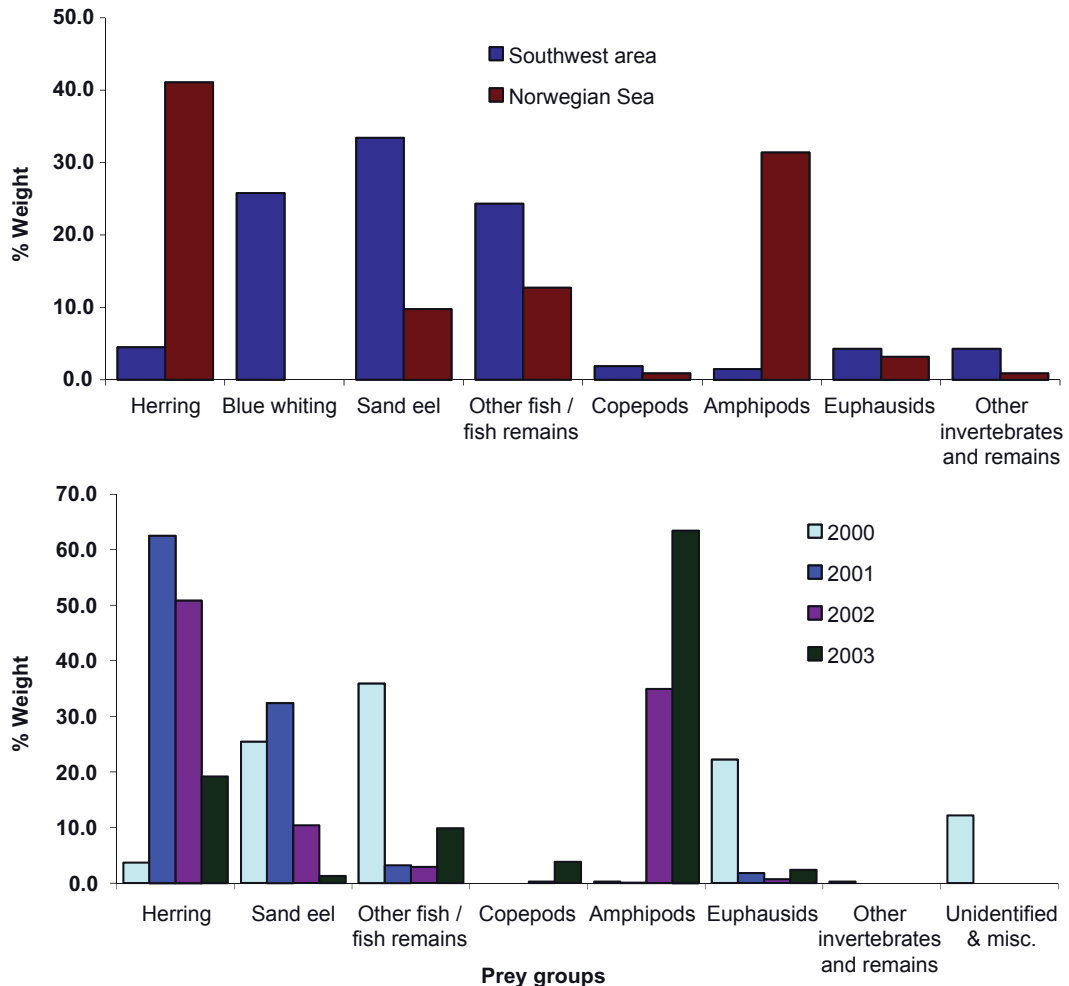


Figure 5.4 Relative importance (% by weight) of different prey items in the diet of post-smolt Atlantic salmon from the southwest and Norwegian Sea areas of the northeast Atlantic (upper chart), with annual differences in prey species consumed from the Norwegian Sea highlighted in the lower chart. Data were obtained from Haugland *et al.* (2006) where the mean length of sampled post-smolts ranged from 16.5 cm to 25.7 cm with specimens captured from June to August.

tassou) and sand eels were important prey in that section of the North Atlantic Current that runs along the continental slope transporting larvae from the spawning areas west of the United Kingdom into the North and Norwegian seas. In the North Sea, 0+ sand eel were also a key prey item; a species that traditionally has been very abundant in this area (see references in Haugland *et al.* 2006) although the number of post-smolt specimens obtained from this area was rather limited. In contrast, 0+ herring were the most important fish prey within the Norwegian Sea, followed distantly by sand eels, while amphipods, particularly *Themisto abyssorum*, dominated the invertebrate species consumed (Fig. 5.4). The importance of 0+ herring in the Norwegian Sea is further illustrated by a positive relationship

between forage ratio and the amount of herring found in post-smolt stomachs and an increased condition factor of post-smolts in years with a high forage ratio of herring (Haugland *et al.* 2006).

From limited investigations in the northwest Atlantic, Dutil & Coutu (1988), found that there was a transition in the diet of post-smolts in the northern Gulf of St Lawrence from mainly insects and gammarids in mid- to late July to largely preying on sand eel and somewhat on capelin (*Mallotus villosus*) from August to October. Earlier we noted that post-smolts sampled in the Gulf of Maine tended to feed more on amphipods and euphausiids by comparison with those feeding on sand eels that were captured within the Bay of Fundy itself (Lacroix & Knox 2005). Thus, regardless of whether investigations are carried out in coastal areas of the northwest or northeast Atlantic, sand eels are frequently one of the most common prey items utilised in both regions whereas – similar to the situation in fjords – herring are typically more common in the northeast Atlantic. Collectively, these investigations again illustrate that the prey species utilised can vary among areas as well as annually within the same location.

In some areas, seasons or years in the northeast Atlantic with less fish larvae apparently available, the Atlantic salmon post-smolts feed proportionally more on different crustacean zooplankton, and in particular on large planktonic amphipods (Hyperiididae, *Themisto* spp.), but also occasionally on krill (Euphasiacea), copepods (e.g. *Calanus finmarchicus*) and a few other groups (Isopoda, Decapoda and Caligoida) (Haugland *et al.* 2006). The copepod *C. finmarchicus* or other abundant copepods species may, however, play a key role as a bottom-up driven key species for both Atlantic salmon and other pelagic fish species in the North Atlantic, in particular as a main prey for marine fish larvae (Peyronnet *et al.* 2008; Friedland *et al.* 2009; Box 5.2). Thus, as seen in their early nearshore post-smolt stage in the open ocean, fish larvae are utilised when present, whereas in years with less piscivorous prey available, crustacean zooplankton, particularly amphipods, become more important.

High abundances of herring or other zooplankton-feeding pelagic fishes may, however, also have a potential negative effect on post-smolt feeding as hypothesised by Haugland *et al.* (2006). For example, high abundances of 1+ or older herring may result in less availability of zooplankton for the young salmon, as well as for their fish-larvae prey. Herring, then, may also act as a competitor and a potential negative factor to salmon growth and survival, rather than as a preferred food resource as with 0+ herring larvae. Thus, high abundances of different year-classes of herring within the feeding areas of post-smolts might act as a ‘double-edged sword’, being both a preferable and important prey as juveniles and a competitor for food (particularly crustaceans) for post-smolts as adults (Fig. 5.5).

5.4 Open ocean feeding of pre-adults and adult pre-spawning salmon

Following their first summer and autumn as post-smolts at sea, Atlantic salmon maintain their opportunistic feeding by availing themselves of a wide variety of both fish and invertebrate prey. Current information suggests differences in feeding patterns between salmon of European and North American origin. Here we summarise dietary information for pre-adult and adult Atlantic salmon captured in the northwest and northeast Atlantic Ocean.



Figure 5.5 Looking for the ‘needle in the haystack’ (post-smolts among herring). One-year-old (1+) herring may potentially compete with post-smolts for food, either indirectly or directly, and often occur in high densities in the same habitat as post-smolts both in fjords and the open ocean. However, in fjords this may also lead to less predation pressure for post-smolts, as the predators have a very abundant alternative prey to feed on. Photo: Audun H. Rikardsen.

5.4.1 Northwest Atlantic Ocean

Pre-adult and adult salmon in the northwest Atlantic Ocean feed mostly on different species of fish, with capelin, sand eels, herring, lantern fishes (*Myctophidae*) and barracudinas (*Paralepididae*) being the most common prey consumed (Fig. 5.6). Knowledge of pre-adult and adult salmon diet exist from several main areas in this region: the coast of West Greenland, Labrador Sea and Davis Strait (offshore areas), and coastal areas of Atlantic Canada (Fig. 5.3).

In a review of marine feeding information of more than 2000 pre-adult and adult salmon in the Northwest Atlantic during 1969–1971, Lear (1972, 1980) found that capelin and sand eels often dominated (>65% by weight) their diet along the coast of West Greenland up to ~64°N during autumn (August to November) (Fig. 5.6). However, in the southwestern part of Greenland, amphipods and euphausiids (krill) made up a greater portion of the diet (>25% by weight) than at ~64°N. Amphipods were also the most common prey by weight in salmon caught off the tip of northern Labrador (Port Burwell, ~60°N), with sand eels being the most important of the fish species eaten (Neilson & Gillis 1979). In contrast, the autumn (September–October) diet of pre-adult and adult salmon specimens obtained from sampling offshore in the Davis Strait and Labrador sea areas (see map, Fig. 5.3) were dominated by barracudinas (*Paralepis coregonoides borealis*) and some lantern fish (Fig. 5.6). These results were somewhat similar to those reported for the Labrador Sea by Templeman (1967) from samples collected in late summer (July and August). Similar to the coast of West Greenland at ~64°N, capelin and sand eels contributed over 80% of the diet by weight in salmon captured during May 1979–80 in coastal areas outside the northeastern tip of Newfoundland (Grand Bank). However, salmon captured in the more oceanic waters east of this area fed more on barracudina and deep sea smelt (family Bathylagidae) along with

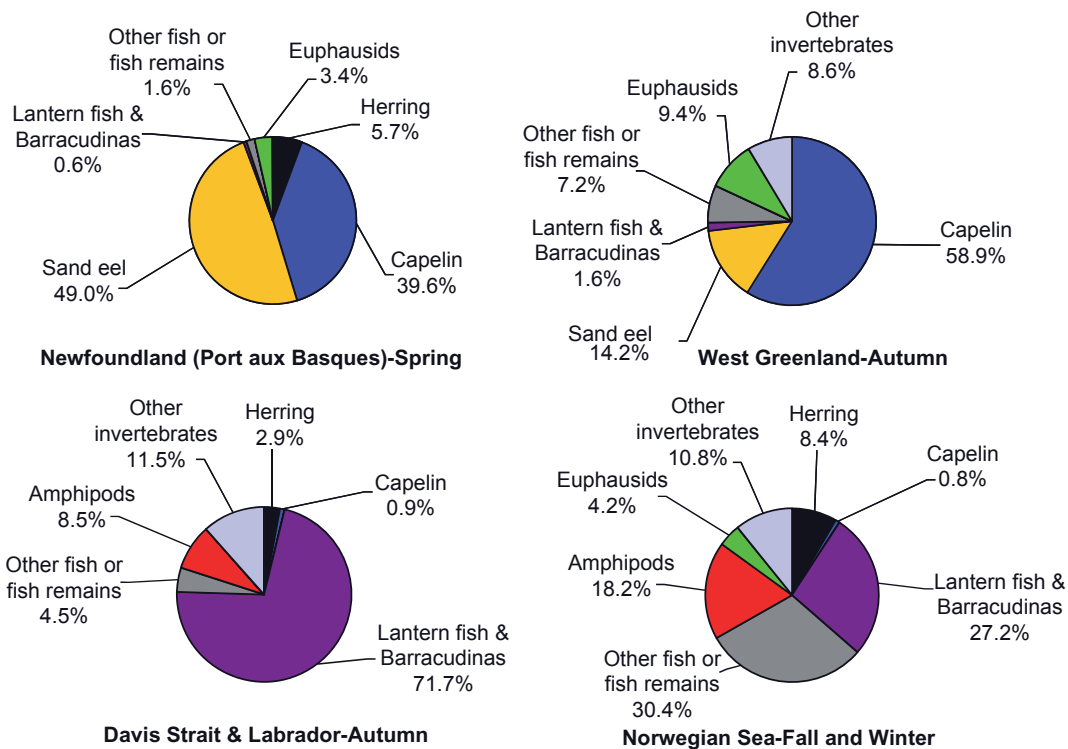


Figure 5.6 Relative importance (% by weight) of prey items in the diet of pre-adult and adult Atlantic salmon from various areas of the North Atlantic. Newfoundland, West Greenland and Davis Strait – Labrador Sea data were from Lear (1972, 1980) while Norwegian Sea feeding data were obtained from Jacobsen and Hansen (2001).

amphipods (Reddin 1985). Templeman (1968) also found a predominance of barracudina (*P. coregonoides*) and lantern fish (*Notoscopelus* sp.) in salmon stomachs from sampling during the spring (March–April) in oceanic areas of the northwest Atlantic.

Along coastal areas of Atlantic Canada, the diet of adult salmon approaching home waters was often dominated by one or two species, typically with capelin and sand eel, or capelin and herring, while amphipods and euphausiids generally made up less than 5% of the mass of stomach contents in these nearshore areas (Lear 1972). Approaching home waters, many salmon had empty stomachs, a finding also reported by Blair (1965) for salmon in the Bay of Islands area of Newfoundland and by Power (1969) for salmon returning to Ungava Bay rivers.

In total, all these investigations indicate that barracudinas and lantern fish were important prey for pre-adult and adult salmon in offshore areas in the northwest Atlantic from spring to late autumn in the 1960s and 1970s, while in the more coastal areas their diet usually consisted of capelin, sand eels, herring and crustaceans (Fig. 5.6). Collectively over all areas, seasons and years, the contribution of different prey organisms also seemed to vary by size of salmon in the same period (Fig. 5.7). Capelin was by far the most consistent item in the diet of salmon across the smallest (44–59 cm) to largest (90–99 cm) length intervals. Sand eels were also present in all size groups but their importance decreased as the size of salmon increased, while the contribution of herring in the diet increased along with the size of the salmon (Fig. 5.7). Amphipods and euphausiids represented less than 2% of the mass of all stomach items in salmon >70 cm in length. With the closure of directed commercial fisheries for Atlantic salmon in Canadian waters, coupled with limited catches of salmon during marine research surveys, diet information for salmon in recent decades has been largely non-existent from this area.

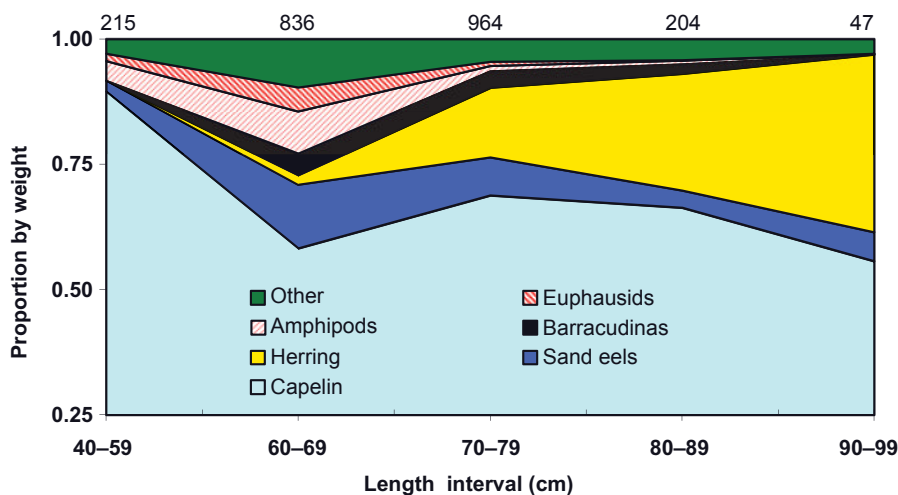


Figure 5.7 Relative importance (proportion by weight) of various prey items in the diet of pre-adult and adult salmon captured in the northwest Atlantic, stratified by length intervals. Data obtained from Lear (1972). Sample sizes for each length interval are given across the top.

5.4.2 Northeast Atlantic Ocean

Detailed investigations and reviews of diet information in the northeast Atlantic have been compiled by various researchers (e.g. Hansen & Pethon 1985; Jacobsen & Hansen 2000; Sturlaugsson 2000; Jacobsen & Hansen 2001) where pre-adult and adult salmon were found to feed proportionally more on pelagic crustaceans by comparison with the salmon in the northwest Atlantic (Fig. 5.6), although the latter studies were carried out several decades earlier and thus may not accurately reflect current feeding patterns. Northeastern studies have generally included salmon caught in three main areas: coastal Norway, the Norwegian Sea north of the Faroe Islands and along coastal western Iceland, but some information is also available on the Baltic Sea and coastal waters of the British Isles.

Along the middle and northern part of the Norwegian coast, various species of fish including myctophids, herring and capelin were reported during the May to June period in 1969–72 (Hansen & Pethon 1985). Crustaceans, particularly euphausiids and amphipods, were also common and in general were more prevalent than squid (e.g. *Gonatus fabricii*) during the same period. Differences in feeding were also found depending upon whether salmon were caught over a shelf area or from oceanic waters proximate to the coast. By comparison with investigations from the coastal northwest Atlantic Ocean, fish species such as capelin and sand eel seem to be of lesser importance in the coastal northeast Atlantic Ocean, with the exception of a few limited studies of salmon feeding in Scottish coastal waters where returning salmon fed mostly on sand eels and some on herring (Fraser 1987; Hislop and Shelton 1993). Recent analyses of stable isotope signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ also provide additional support for differences in feeding between some salmon populations in the northeast versus the northwest Atlantic (Dempson *et al.* 2010).

The diet of almost 3000 wild pre-adult and adult salmon caught during 1992–95 in the open ocean of the Norwegian Sea, north of the Faroes, was examined in detail by Jacobsen and Hansen (2000, 2001). In this area, crustaceans (mainly amphipods, *Themisto* spp.) contributed more than 50% of the mass of stomach content material in fish sampled during the autumn (November–December), while in winter (February–March) the amount of crustaceans was reduced by half (~25%). The contribution of fish was quite low during the autumn (<20%), but increased in the winter months (~50%). However, mainly blue whiting (*Micromesistius poutassou*) and mackerel (*Scomber scombrus*) were commonly taken during the autumn (~25% by weight) and these were virtually absent from the diet from samples obtained in the winter period when particularly pearlides (*Maurolicus muelleri*), barracudinas, lantern fishes and herring dominated among fish preys. This shows that the ocean diet of salmon may vary extensively by season within the same area, probably due to seasonal changes in availability of prey.

Jacobsen & Hansen (2001) also examined prey availability relative to diet and concluded that Atlantic salmon utilised fish over crustaceans and that pelagic amphipods were fed upon to a greater extent than euphausiids. Also, one-sea-winter (1SW) and two-sea-winter (2SW) salmon had similar feeding patterns, but there were substantial differences between 1SW and three-sea-winter (3SW) salmon as well as low diet overlap index (Horn 1966). This was due to the greater contribution of larger fish species in the diet of 3SW salmon compared with the much smaller 1SW fish that tended to feed more on amphipods and lantern fishes. Thus, larger salmon seem to prefer larger prey. Different size groups of salmon may therefore respond unequally if they feed in an area where prey type and size may vary in space and time.

Feeding studies of adult salmon in Icelandic coastal waters during summer (June and July) similarly showed a high utilisation of fish prey, particularly sand eels and herring (>60% by weight), with more diverse feeding apparent in only one location (Jokulfjords) where half of the diet included amphipods, euphausiids, and decapods (megalopa larvae) (Sturlaugsson 2000). There was a general tendency for salmon to feed largely on a few species in nearshore coastal waters in most of the Icelandic areas sampled. This was similar to findings in other areas during the same summer period, including the nearshore Senja in northern Norway (predominately herring and sand eels) (Grønvik & Klemetsen 1987), the northern Baltic Sea where herring were the most common species (>90% occurrence) (Salminen *et al.* 2001), and in coastal Irish waters where sprat (*Sprattus sprattus*) was the dominant species observed in salmon stomachs (Twomey & Molloy 1974).

In summary, pre-adult and adult salmon in the open ocean of the northeast Atlantic feed more extensively on crustaceans (especially pelagic amphipods) than salmon in the northwest Atlantic, although fish (e.g. lantern fish, barracudinas and herring) were important prey in this area as well during certain times of the year. Overall, the wide variety of invertebrates and particularly fish species found in the stomachs in all areas of the North Atlantic underline their opportunistic feeding behaviour. Differences were apparent by location, whether between offshore versus nearshore or in terms of large-scale differences between northwest and northeast Atlantic studies (Fig. 5.6), and by season.

5.5 Summary and conclusions

Atlantic salmon are opportunistic feeders, utilising a wide variety of available prey throughout all life stages while feeding at sea. Their main prey are different species of fish and fish larvae, and planktonic crustaceans, consistent with other anadromous salmonids in the Northern Hemisphere, including various species of Pacific salmon, Arctic charr and sea trout (e.g. Dempson *et al.* 2002; Kaeriyama *et al.* 2004; Rikardsen *et al.* 2002, 2007; Quinn 2005). Post-smolts, pre-adult and adult Atlantic salmon have been reported to feed on more than 40 different fish species or species groups from at least 19 families, and consume invertebrates from more than 10 major taxonomic groups. The relative importance of each salmon prey group observed during their different life-stages at sea is summarised in Table 5.1 and illustrates that the variety of prey taken and their respective size range increases from the estuary, throughout the fjords, along the coast and into the open ocean. What is quite apparent is that independent of life-stage at sea, habitats, geographical areas, year or season, fish such as sand eels, herring, capelin and cod (Gadidae), and planktonic amphipods, are frequently the most important components of their diet and hence commonly provide the dietary life-support needed by salmon to survive. However, although Atlantic salmon feed on a wide variety of prey, it is common to find only 1 to 3 marine prey species in their stomach at the same time (Hansen & Pethon 1985; Jacobsen & Hansen 2000; Rikardsen *et al.* 2004). This suggests that not only does the available prey vary considerably depending on the area in question, time of day and season, but also that individual salmon may specialise somewhat in their consumption of a certain prey organism (Andreassen *et al.* 2001; Jacobsen & Hansen 2001).

To some extent it is understandable why salmon frequently utilise, and perhaps even select certain forage species such as capelin, herring and lantern fishes (myctopids). These prey, as

Table 5.1 The relative importance of different prey groups for post-smolts in estuary and fjord/coast and for post-smolts and pre-adults/adults in oceanic waters in the Northern Atlantic

Prey organism	Post-smolts Estuaries	Post-smolts Fjord and coast	Post-smolt Oceanic	Pre-adults / adults Oceanic
Pisces				
Ammodytidae (Sand eels) (3<)	•••	••••	••••	••••
Clupeoids (4)				
Herring (<i>Clupea harengus</i>)	•••	••••	••••	••••
Other Clupeoids	—	—	—	••
Capelin (<i>Mallotus villosus</i>)	—	•••	•••	••••
Gadidae (Cod fishes) (9)	•••	•••	•••	•••
Atlantic cod (<i>Gadus morhua</i>)	••	•••	••	••
Saithe (<i>Pollachius virens</i>)	••	•••	••	•
Blue whiting (<i>Micromesistius poutassou</i>)	—	—	•••	••
Other Gadidae	—	—	••	••
Myctophidae (Lantern fishes) (8)	—	—	••	••••
Paralepididae/ Barracudinas (2)	—	—	—	•••
Perlside (1<)	—	—	•	•••
Scorpaenidae (Red-fish)	—	—	•	•
Gasterosteidae (Stickleback)	•*	—	—	•
Scombridae (Mackerel, <i>Scomber scomber</i>)	—	—	—	•
Anarhichadidae (Wolf-fish fry) (2<)	—	—	—	•
Belonidae (Garpike)	—	—	—	•
Pleuronectidae (Flatfish) (1<)	—	—	—	•
Osmeridae (2)	—	—	—	•
Cyclopteridae (Lumpfish) (1)	—	—	—	•
Stichaeidae (1)	—	—	—	•
Cottidae (Sculpins, fry) (1<)	—	—	—	•
Cottunculidae (1)	—	—	—	•
Agonidae (1)	—	—	—	•

Table 5.1 Cont'd

Prey organism	Post-smolts Estuaries	Post-smolts Fjord and coast	Post-smolt Oceanic	Pre-adults / adults Oceanic
Crustacea				
Copepoda (4<)	••	••	••	•
Amphipoda				
Planktonic	••	•••	•••	••••
(Hyperiididae) (5<)				
Benthic (Gammaridae)	•••	••	—	—
Isopoda	•	•	•	•
Mysidacea (Mysids)	—	•		
Euphausiacea	•	••	••	•••
(Euphausiids)				
Decapoda				
Planctonic larvae	•	•	•	•
Shrimps (2<)	—	—	•	•••
Other crustacean	—	•	•	•
Mollusca				
Cephalopoda	—	—	•	••
(Squids) (2<)				
Gastropods (sea slugs)(2<)	—	•	•	•
Bivalvia (pelagic)	—	—	—	•
Insecta (30<<)	••••	•••	•	•
Polychaeta	•	•	•	•
Chaetognatha (Arrow worm)	—	•	—	•
References:	Rikardsen <i>et al.</i> 2004 Levings <i>et al.</i> 1994 Andreassen <i>et al.</i> 2001 Dutil & Coutu 1988 Morgan <i>et al.</i> 1986 Cunjak 1992*	Rikardsen <i>et al.</i> 2004 Jacobsen & Hansen 2000 Levings <i>et al.</i> 1994 Andreassen <i>et al.</i> 2001 Dutil & Coutu 1988 Hvidsten <i>et al.</i> 2009 Lacroix & Knox 2005 Sturlaugsson 2000	Haugland <i>et al.</i> 2006 Jacobsen & Hansen 2000 Shelton <i>et al.</i> 1997 Dutil & Coutu 1988**	Jacobsen & Hansen 2000 Jacobsen & Hansen 2001 Hansen & Pethon 1985*** Hislop & Shelton 1993 Reddin 1985 Lear 1972; 1980
	*Estuarine feeding of parr		**Most of these fish were caught close to the coast	***Some fish were caught not too far from the coast

•••• = very important prey (>50%W if taken), ••• = prey often found in stomachs and important if less profitable prey is assumed not available, •• = occasionally found, but in low abundance, • = rare (<1%W) and — = not reported. Number given in parenthesis behind the prey family name represents number of individual species within this family found in salmon stomachs.

well as zooplankton species such as *Calanus finmarchicus*, often have much higher lipid contents and energy densities (e.g. Falk-Petersen *et al.* 1990; Van Pelt *et al.* 1997; Lawson *et al.* 1998) than many other potential prey organisms and thus are more qualitatively beneficial to the fish. However, since the energy density of some of these species can change throughout the year and between areas (see Mårtensson *et al.* 1996; Lawson *et al.* 1998; Michaud & Taggart 2007; Trudel 2009), salmon must still be able to switch and utilise a wide array of prey items at different times. In fact, a recent study of Pacific salmon shows that high survival and growth of these is often closely correlated to times when lipid-rich northern copepods dominate the zooplankton community (Trudel 2009). As for Atlantic salmon (Box 5.2), copepods generally constitute a small fraction of their diet in the open ocean. Therefore, these results may simply reflect profound changes that occur at the base of the food chain with respect to lipid dynamics and quality, rather than a direct effect of copepods on salmon growth.

The production of prey at sea is highly dependent on climatic and oceanographic factors that can influence the entire ecosystem. Hence, differences in productivity among areas, seasons and years, may contribute to some of the variability observed in salmon abundances on spatial and temporal scales. It has been suggested that growth of salmon at sea is controlled by bottom-up processes where production is dependent on the larvae production, which in turn is dependent on zooplankton production, and where zooplankton is dependent on primary productivity (Peyronnet *et al.* 2008; Todd *et al.* 2008; Trudel 2009; Box 5.2). An example of bottom-up control was noted earlier in regard to the match/mismatch timing of successful smolt migrations into nearshore areas (Box 5.2). However, top-down control may also be occurring in some areas. High predation from seabirds (Montevecchi *et al.* 2002), marine mammals (Middlemas *et al.* 2003), and various species of fish (Hvidsten *et al.* 1987, 1988; Hislop & Shelton 1993) can affect salmon smolts by top-down predation pressure. In addition, salmon may also be influenced by the interplay between bottom-up and top-down processes as has been noted in other marine ecosystems (e.g. Hunt & McKinnell 2006).

Perhaps of greater importance is the recent documentation of large-scale trophic cascades in various parts of the North Atlantic (Frank *et al.* 2005, 2007; Bundy *et al.* 2009). Selective removal of top fish predators as a result of high rates of fishing have been noted for a number of areas in both the northwest and northeast Atlantic Ocean that has resulted in changes in the composition of top predator species and subsequently affected the productivity at lower trophic levels. Recent investigations of various North Atlantic ecosystems have suggested that colder, northern, often species-poor areas are likely influenced more by top-down control whereas warmer, southern areas are more probably structured by bottom-up processes (Frank *et al.* 2006, 2007). Salmon are not abundant in the Northern Atlantic by comparison with other top-predator fishes, nor are they static and they hunt widely throughout the North Atlantic. As a result they could potentially be influenced by a variety of processes at different times in different areas. Thus, we believe that Atlantic salmon are affected by ecosystem structure rather than directly influence it. However, unlike most marine fish species, a great advantage in studying Atlantic salmon is that many of the life-history parameters (e.g. survival, growth, age, sex ratio and maturation) of almost the entire population can be recorded during at least two different life-history stages (smolts and adults) by trapping or other enumerating methods when the fish are migrating between fresh

and salt water (e.g. Hvidsten *et al.* 2009). Therefore, by understanding how the life-history of salmon is affected by the marine ecosystem structure including information related to the availability of potential prey items, future studies of Atlantic salmon could provide valuable information associated with large scale environmental changes in marine ecosystems as a whole.

Friedland *et al.* (2009) have recently shown that salmon survival can be linked with changes in potential planktonic food resources in the northeast Atlantic, but they also noted that the changes in trophic structure that appear to impact salmon still need to be fully resolved. Future coordinated studies with multidisciplinary approaches that incorporate both biological and physical environmental factors over large spatial and temporal scales would be important to understand how changes in the ocean environment and ecosystem affect salmon abundance and other marine species over time, as well as indirect techniques that can utilise both new and historical long-term data. For example, efforts to better understand changes in feeding ecology are now being explored by way of stable isotope analyses (e.g. Dempson *et al.* 2010) including those that make use of archived collections of salmon scales (e.g. Trueman & Moore 2007; Sinnatamby *et al.* 2008, 2009). Analyses such as these may help understand spatial and temporal variability in the feeding ecology of salmon coincident with biological and environmental changes in different areas in the North Atlantic. This is particularly relevant given the dearth of recent long-term information on food and feeding of Atlantic salmon from the northwest Atlantic, particularly at the pre-adult and adult life-history stages, by comparison with information available from the northeast Atlantic.

With the general pattern of decline in many North Atlantic stocks of salmon, their recovery may depend, in part, on at least one factor that is probably common to the successful recovery of any fish species, and that is the availability of ample food resources (Dolgov 2009). Accordingly, future studies should focus on direct linkages between prey abundance and the prey salmon consume, along with how these associations affect survival and productivity of stocks in the context of a changing climate.

Additional knowledge is also needed in order to better map the different feeding areas for salmon of different sizes (1SW *vs.* MSW), from different geographical areas, and how this is related to changes in the marine environment. Recent developments in genetic identification and electronic tracking (Thorstad *et al.* 2011 [Chapter 1], Box 1.4) will become especially important in this regard. Investigations such as those discussed above will ultimately build on current attempts (e.g. Friedland *et al.* 2009; Hvidsten *et al.* 2009; Trudel 2009; Todd *et al.* 2011 [Chapter 16]) to understand better the functional relationships of salmon and the biological and physical environment in which they live.

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6 The Behavioural Flexibility of Salmon Growth

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Abstract

Atlantic salmon exhibit massive variation in growth, and here we review the patterns and allometric, genotypic, maternal and environmental sources of the variation. However, growth is also behaviourally flexible and influenced by behavioural trade-offs with survival-related traits. We suggest a conceptual framework that addresses growth variation throughout the salmon life cycle based on such behavioural trade-offs. Under this framework both seasonal freshwater growth variation and the large difference in growth between fresh water and sea water are related to the trade-off between feeding to maximise growth and sheltering to avoid predation under different seasonal conditions and habitat characteristics. A link has recently been established between female spawning behaviour and variation in offspring growth (through local density regulation of growth), further emphasising the importance of behavioural traits for growth variation. Finally, growth is also state-dependent, with growth being accelerated or depressed according to physiological or life-history states. No model has so far been developed that accounts for the complex interactions of abiotic factors, biotic interactions, physiological and life-history states and the behavioural flexibility of growth. However, even the simple temperature-driven growth models have proven their value as baselines for Atlantic salmon performance. Currently, field-based models are being developed that incorporate more sources of growth variation, and if extended into generic models they should become valuable tools in many aspects of the science and management of Atlantic salmon.

Key words

Compensatory growth, growth constraints, interspecific competition, marine growth, thermal adaptation

6.1 Introduction

Atlantic salmon exhibit massive variation in growth in both freshwater and marine environments. While the mean size at migration to sea (smolt size) in Atlantic salmon does not vary



Figure 6.1 Both are sea-run mature salmon males – the upper is a 17 kg fish caught in the River Alta in northern Norway (note the size of the adipose fin!) and the lower is less than 1 kg sampled in a small river in central Norway. The size difference is due to differences in growth rates and life-history. Photos: Anders G. Finstad.

that much (typically between 12 and 16 cm), the mean age at migration varies between one and five years among populations, and within populations the smolt run may consist of three age-classes or more. Similarly, sea-run adult size varies from less than 1 kg to more than 20 kg (Fig. 6.1), and even within a sea age group (e.g. one-sea-winter) adult weight may vary fourfold. Population or individual differences in growth rates are the major sources of variation in size at age, and knowledge about this is vital for our understanding of the population dynamics, life-history, evolution and ecology of Atlantic salmon. Here we review the patterns, mechanisms and sources of growth variation in Atlantic salmon with the focus on recent advances. Our overarching goal is to outline a mechanistic understanding of growth rate variation necessary for modelling of salmon growth. While doing so, we focus on the influence of behavioural trade-offs on the regulation and variation in growth. In the

final sections we give examples of recent models and their application in the science and management of Atlantic salmon.

6.2 Patterns of Atlantic salmon growth

A fundamental pattern of growth in fishes is the allometric scaling of growth rates, causing mass specific growth rates (G_m , the change in mass over time relative to the size of the fish; Box 6.1) to decline with increasing body mass. The allometric mass exponent has been estimated at 0.31 for Atlantic salmon (Elliott & Hurley 1997). Allometric growth in fishes has been related to allometric growth of gill surface area (Pauly 1981), or surface area of the digestive system (Wootton 1998), relative to body mass of the fish. By using a proper metrics for growth (Box 6.1), the allometric pattern of growth can easily be accounted for and the ecological and life history patterns of Atlantic salmon growth can be explored.

The most striking pattern of Atlantic salmon growth is the difference between growth in fresh water and at sea. While naturally recruited juveniles in fresh water may increase in mass by a factor of two to 20 annually, salmon may increase their mass 50 times or more during their first year at sea. Does this imply that the physiological potential for growth in the marine environment is much higher than in fresh water? Due to the obvious difficulties

Box 6.1 Measurements of growth

Early studies of fish growth focused on estimating parameters at the population level using models such as the von Bertalanffy (1938) growth equation, parameterised by data on average fish size (usually length, but sometimes mass) at age throughout life. While such size-at-age models are useful for comparing growth in many fish populations they are less useful for species like Atlantic salmon with substantial habitat shifts (anadromy) and strong habitat-dependent growth (much faster marine growth compared with freshwater growth). Thus, salmon researchers typically estimate growth independently for each age class. When individual tagging is possible, individual-based growth rates can provide improved growth rate estimates at the population level because processes that are potentially size-dependent (e.g. mortality or emigration/immigration) cannot bias estimates by removing or adding fish. The simplest characterisation of body growth (G) based on repeated observations of tagged individuals is the change in length (L) over time (t); $G_L = (L_2 - L_1)/t$. Because growth in length is generally linear (Ostrovsky 1995) and metabolic rates scale linearly with length (Sigourney *et al.* 2008), G_L is not biased by initial size. However, different energy allocation strategies over ontogeny may to varying degrees decouple growth in length from growth in mass (Sigourney *et al.* 2008), and growth in mass (G_m) is often necessary to properly describe growth patterns. While the most commonly used growth metric for mass (m), instantaneous growth $G_m = (\log(m_2) - \log(m_1))/t$, appears to be size-independent, it is indeed biased low for larger fish because proportional gains in mass necessary for similar instantaneous growth rates of small and large fish require that larger fish grow an unrealistically high proportion of initial mass. Because G_m scales allometrically with initial size ($G_m = a \cdot mb$), comparison of G_m for groups of fish with different initial sizes can be misleading and we strongly caution against the use of G_m unless initial sizes of fish for comparison are similar.

Two alternatives exist for estimating growth in mass that are independent of initial size. Ostrovsky (1995) provides a metric, Ω , which includes an estimate of b (0.31 for Atlantic salmon; Elliott & Hurley 1997), the slope of the relationship between $\ln G$ and $\ln m_1$; $\Omega = (m_2^b - m_1^b)/(bt)$. Ω , often termed the mass standardised growth rate, is independent of m_1 (Ostrovsky 1995; Sigourney *et al.* 2008). A second alternative involves examining relationships between m_2 and m_1 , either as a regression with m_1 as a covariate and m_2 as dependent variable, or as an analysis of residuals from the regression of m_2 and m_1 (Carlson *et al.* 2007). Both regression approaches effectively eliminate the allometry, but because time is not included, they are limited to comparisons over similar time intervals.

of representative sampling of Atlantic salmon at sea, there is little information on their growth rates during this life stage. Annual growth or monthly relative growth (Peyronnet *et al.* 2007; McCarthy *et al.* 2008), can be estimated by analyses of scales from returning adults or in smolt tagging programmes. However, since such data cannot be used to estimate growth rates over finite time intervals with continuous growth (e.g. months), there are no direct comparisons available of growth rates in fresh water and at sea. Some simple calculations can, however, provide some insights. Assuming that a 1.5 kg returning one-sea-winter salmon has grown for six months at sea, its average mass standardised growth rate (Ω ; Box 6.1) would be in the order of four times higher than the growth rate of a typical juvenile salmon during its first summer (three months). However, there are indications that salmon can grow at lower temperatures at sea than in fresh water (Handeland *et al.* 2003) and the fish may thus grow during winter. Under the assumption of positive growth during the whole sea journey (e.g. 14 months), mass standardised growth rate at sea for a one-sea-winter salmon will be in the same order as the early juvenile growth.

Handeland *et al.* (2003) provide some rare data on monthly post-smolt growth rates (G_m) of wild Atlantic salmon under controlled tank environment in sea water. From their average initial mass and growth rates, standardised growth (Ω) can be approximated for three temperatures and compared to model predictions for maximum growth in fresh water (five Norwegian populations; Jonsson *et al.* 2001). Both experiments were performed using commercial dry food (but differing in particle size) and similar day lengths. At the highest temperature (14.3°C), predicted growth in fresh water was similar or even higher (one population) than growth in sea water (Fig. 6.2). At 9.4°C no predicted freshwater growth rates could match growth in sea water (approximately 30% lower for fish from the fastest-growing freshwater population), and whereas positive growth was obtained at 4.3°C in sea water, the lower temperatures for growth of summer acclimatised salmon in fresh water range from 5–6°C. While this may indicate adaptive differences in thermal growth performance in fresh water and sea water, a simpler explanation may apply. It has been shown that the lower temperature for freshwater growth decreases with increasing energy intake (Jonsson *et al.* 2001). If this pattern is general for Atlantic salmon, higher consumption of larger (Wankowski & Thorpe 1979; Keeley & Grant 2001) and more energy-efficient food items (such as fish in the wild and larger food pellets in the experiments), causing higher energy intake, may explain positive growth at low temperatures in the marine environment.

It can be hypothesised from these simple calculations and comparisons that the tremendous growth at sea compared to freshwater growth is not due to generally higher growth potential at sea, but due to higher growth at low temperatures and thus that growth may occur during the whole sea journey (Box 6.2). Obviously, prey availability and prey size (Keeley & Grant 2001) is essential for maintaining such high growth at sea and these effects will be discussed below (see also Rikardsen & Dempson 2011 [Chapter 5]).

Another distinct pattern of Atlantic salmon growth is the seasonal pattern. Across latitudes, freshwater growth is ultimately limited by cold, dark winters with longer periods of zero growth in the north compared to the south (Jensen *et al.* 2000). In northernmost populations (70°N), conditions are suitable for growth during only three months of the year (Jensen 2003), while positive growth is possible year-round, although very slow in winter, in southern populations (Letcher & Gries 2003). However, beyond this temperature-driven seasonal pattern of no or negative growth during winter, a distinct pattern has repeatedly been shown for freshwater growth of Atlantic salmon and other salmonids, in which large

percentages of annual growth occur during a short spring or early summer period (Mortensen 1985; Jensen 1990, 2003; Jones *et al.* 2002; Letcher & Gries 2003; Bacon *et al.* 2005). Field studies with relatively short sampling intervals and individually tagged fish have estimated that approximately 75% of the yearly growth in juvenile salmon occurs during a couple of months in spring (Letcher & Gries 2003; Bacon *et al.* 2005). Indeed, growth rates during this period have been shown (Jensen 2003; Bacon *et al.* 2005) to exceed estimated maximum growth for Atlantic salmon predicted from laboratory-based models (Elliott & Hurley 1997; Forseth *et al.* 2001). While it has been suggested that the relatively high prey availability in the spring may explain this rapid growth (Vøllestad *et al.* 2002; Bacon *et al.* 2005), it is likely to be insufficient for explaining growth rates that exceed maximum growth in tank environments. One additional mechanism (see below) may be compensatory growth after winter starvation. Interestingly, growth rates in the autumn are much lower than expected despite adequate food availability (Vøllestad *et al.* 2002 [for *Salmo trutta*]; Jensen 2003), suggesting strong behavioural regulation of growth rate in the autumn. The extensive studies exploring the behavioural trade-offs between feeding and sheltering (or activity levels) in salmonids (Heggenes *et al.* 1993; Valdimarsson & Metcalfe 1998; Metcalfe *et al.* 1998, 1999; Imre & Boisclair 2004; Johnston *et al.* 2004; Orpwood *et al.* 2006; Finstad *et al.* 2007) may provide a suitable framework for understanding this seasonal pattern. As prey availability, growth potential and energetic status of the fish changes with progression of the season, the behavioural trade-off between feeding and sheltering changes towards increasing the priority of sheltering and survival (Box 6.2).

Box 6.2 A conceptual framework for behaviourally driven differences in freshwater and marine growth

The massive increase in growth from the freshwater to the marine habitat may be due to physiological shifts during smoltification, influencing traits such as maximum growth capacity, feeding efficiency and thermal optimum. While the possibility of adaptive shifts is intriguing, there is currently no documentation for such shifts. Here we suggest an alternative conceptual framework based on behavioural changes. In fresh water food availability is strongly seasonal, prey items are generally small (also relative to body size) and many of the predators (at least birds and mammals) are not gape-limited. During spring, food is abundant, prey items are relatively large due to the general phenological pattern of aquatic insects (Poff & Huryn 1998) and the energetic state of overwintering salmon is poor (Gardiner & Geddes 1980; Finstad *et al.* 2004b). Both feeding conditions (Orpwood *et al.* 2006) and energetic state (Metcalf *et al.* 1998) cause the fish to prioritise feeding over sheltering and they obtain high growth. As the summer progresses food availability decreases (Poff & Huryn 1998), the potential for fast growth is reduced, the energetic state is substantially improved, and the fish make different trade-offs and prioritise survival by increasing time in shelter (or reducing activity levels; Martin-Smith & Armstrong 2002) over feeding and high growth. There is now ample evidence that shelter availability and sheltering is important for juvenile salmon (e.g. Valdimarsson & Metcalfe 1998; Finstad *et al.* 2007; Finstad *et al.* 2009). In the marine environment, prey availability is less seasonal, prey items are larger (the prey to fish size ratio typically doubles or more from invertebrate to fish prey; Keeley & Grant 2001) and many of the potential predators (fish and birds) are likely to be gape-limited. Moreover, there are no sheltering structures available in the open ocean. Fast growth is thus vital to reduce predation risk. The combination of large food items (Wankowski & Thorpe 1979), allowing high food consumption, and the lack of behavioural trade-offs makes growth possible at low temperatures (see main text) and less seasonally restricted. Support for such a behaviourally driven scenario is provided from the very similar growth acceleration of piscivorous salmonids (L'Abée-Lund *et al.* 1992; Jonsson *et al.* 1999) that occurs without any salinity changes and physiological smoltification.

Seasonal growth rate variation in the sea appears much less pronounced than seasonal growth variation in fresh water. While direct comparison is difficult due to lack of representative samples from the marine system, the seasonal pattern at sea can be explored by analyses of otoliths and scales (Wells *et al.* 2003) of fish captured at sea or as they return to rivers (Friedland *et al.* 1993). In an Irish population (Peyronnet *et al.* 2007) scale circuli spacing distances were largest during the 'first summer maximum' and smallest during the 'first winter minimum'. Circuli spacing also varied between seasons in a Canadian population (Hubley *et al.* 2008). In both cases, growth at sea was estimated to be fastest in the summer and slowest in the winter, but the seasonal difference in growth was much smaller in the sea compared to the seasonal difference in fresh water. This may also be related to differences in behavioural trade-offs in fresh water and at sea (Box 6.2).

Predictions from temperature- or seasonal-driven models may also fail to represent growth trajectories accurately when growth depends on current state. One example is life-history-dependent growth (see below). Another is growth compensation, which is enhanced growth compensating for mass or energy losses after periods of slow growth due to food deprivation or cold temperatures, documented for Atlantic salmon and several other fish species (e.g. Wilson & Osburn 1960; Weatherley & Gill 1981; Nicieza & Brana 1993; Boersma & Wit 1997; Nicieza & Metcalfe 1997; Ali *et al.* 2003). The rapid growth that allows growth compensation generally seems to be triggered (but see Nicieza & Metcalfe 1997) by reduced lipid reserves. Fish respond to low lipid reserves by increasing feeding rates if sufficient food is available, which, over the short term at least, replenishes lipid reserves and often allows fish to catch up in size to fish that did not experience food deprivation. The existence of a phenomenon such as compensatory growth raises several questions related to trade-offs between growth and other fitness-related traits that will be discussed later. However, there are costs of growth compensation *per se* that are observed long after the period of accelerated growth. Morgan & Metcalfe (2001) found reduced performance (slower growth, lower lipid reserves) of fish that had undergone growth compensation compared to controls, months after the period of low growth rates. The lower lipid reserves of the growth compensation fish even resulted in altered life-history expression a year later; fewer males matured as parr in the growth compensation group. Although fish may appear to have regained a similar body size following growth compensation, delayed costs of growth compensation can cause the fish to underperform compared to fish that did not need to catch up in size (Morgan & Metcalfe 2001). While most studies of growth compensation have been conducted in the laboratory, some studies have also shown growth, condition and energetic compensation in the field (Carlson *et al.* 2004; Alvarez & Nicieza 2005; Johnsson & Bohlin 2006), and Johnsson & Bohlin (2006) demonstrated mortality costs of compensation. Whether growth compensation is an important process for wild Atlantic salmon remains an open question, but as mentioned above, it may be involved in the spring growth burst.

A final striking feature of Atlantic salmon growth variation is the strong size and growth bimodality between early and late smolts (Thorpe *et al.* 1982). Fish that will smolt in a particular spring are substantially larger than fish that delay smolting for one or more years. This size bimodality is set up as early as age 0+ in rivers with relatively fast growth (Letcher & Gries 2003) and may be related to metabolic rate and intrinsic competitive ability of fry (Metcalfe *et al.* 1989; Metcalfe 1991). A less obvious, but still important component of size variation is the complex interaction between smolt age and male parr maturation. Male parr

can mature in autumn before emigration, but they are less likely to smolt the following spring compared to males that did not mature (Whalen *et al.* 2000). While early smolts are generally larger than late smolts, only the fastest-growing, largest fish combine parr maturation and early smolting (Letcher & Gries 2003). Because there is a growth cost to parr maturation, however, these fish do not end up as the largest smolts. Previously mature early smolts are about one-half of a standard deviation unit smaller than previously immature early smolts (mostly females, Letcher & Gries 2003).

6.3 Environmental sources of growth variation

6.3.1 Abiotic factors

Among the abiotic environmental factors, temperature is by far the most important source of growth variation (Fig. 6.2). Under laboratory conditions and fed *ad libitum*, summer acclimatised Atlantic salmon generally (across seven populations) show positive growth from 5–7 to 24–26 °C and grow fastest at 16–20 °C (Elliott & Hurley 1997; Jonsson *et al.* 2001). The thermal range declines with reduced food consumption, whereas the temperature for maximum growth appears not to change (Jonsson *et al.* 2001). Winter acclimatised salmon (short day lengths and low temperatures) under similar conditions can, however, obtain positive growth at temperatures at least as low as 1 °C, indicating some kind of adaptation to seasonal thermal regime (Finstad *et al.* 2004b).

The effects of temperature on growth of wild salmon in sea water are poorly described. Handeland *et al.* (2003) established a regression model that indicates a thermal growth range from close to 0 to 19.5 °C and maximum growth at 13 °C. The model is, however, based

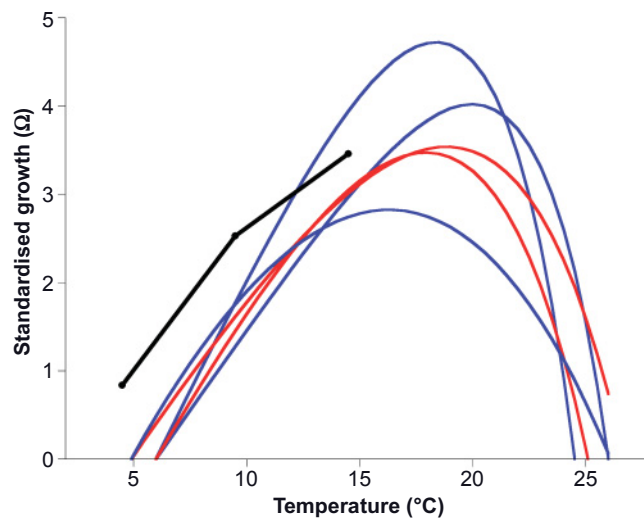


Figure 6.2 Predicted (from Jonsson *et al.* 2001) maximum standardised growth rates (%/day) for freshwater reared juvenile Atlantic salmon from three Norwegian rivers with low summer temperatures (blue lines) and two warmer rivers (red lines), and growth rates at three temperatures for post-smolts in sea water (black line and circles, estimated from Handeland *et al.* 2003).

on only three growth observations (see Fig. 6.2) of wild salmon (from central Norway) that were combined with data from two farmed strains. The model is also based on data from relatively few temperatures, rendering particularly large uncertainty for optimum temperature for growth, and should thus be used with caution in studies of wild salmon growth at sea. The lack of a proper model for Atlantic salmon marine growth hampers interpretation of correlative studies on relationships between temperature, growth and survival at sea. Friedland *et al.* (2005) found, respectively, positive and negative correlations between post-smolt growth and temperature in the migration corridors of Scottish and Canadian populations, despite relatively small temperature differences. Because the thermal growth relationship is not properly described, the effects of growth below and above the thermal optima could not readily be separated from other ecosystem effects on growth.

The significant contribution of sea surface temperatures to salmon population dynamics was outlined as early as the 1980s (Reddin & Shearer 1987), and since then the importance of sea temperature has been clearly established (Friedland *et al.* 1993; Friedland 1998; Friedland *et al.* 1998; Jonsson & Jonsson 2004a; Jonsson & Jonsson 2004b; Todd *et al.* 2011 [Chapter 16]). The mechanisms of the relationships, however, remain poorly understood. Most authors point to some kind of temperature-growth-survival causality (Friedland *et al.* 2000; Friedland *et al.* 2005; Peyronnet *et al.* 2007; Todd *et al.* 2008; but see Crozier & Kennedy 1999), but cascading ecological effects influencing food availability (Beaugrand & Reid 2003) may also be important (Rikardsen & Dempson 2011 [Chapter 5]).

Another important abiotic factor in fresh water is river discharge. Field studies in Norway (Arnekleiv *et al.* 2006) and Canada (Arndt *et al.* 2002) have shown that large proportions of the among-year variation in growth could be explained by differences in water discharge. The negative impact on growth was related to episodes of high discharge. During high flow conditions, salmon parr become less active, use a smaller area for feeding and use more energy at their holding positions compared with lower flow conditions (Kemp *et al.* 2006). High flow incidents also reduce food availability as invertebrates are washed out or experience increased mortality (Hildrew & Giller 1994). All these effects are further amplified in situations with rapid variations in flow, as can be seen in regulated rivers (Lauters *et al.* 1996; Arnekleiv *et al.* 2006). Besides these effects of extreme events, the relation between discharge and salmon growth remain poorly described (Armstrong *et al.* 2003), although progress is currently being made (Armstrong 2005; Kemp *et al.* 2006; see also Finstad *et al.* 2011 [Chapter 3]).

Chemical composition of the water may also influence salmon growth. The level of dissolved oxygen and carbon dioxide in water may have severe impacts. A medium-level increase in carbon dioxide has been shown to significantly reduced parr growth, and at high levels mortality increased greatly (Fivelstad *et al.* 2003). Conversely, increased oxygen levels increased parr growth (Hosfeld *et al.* 2008). Acidification of rivers has been a major cause of salmon decline on both sides of the Atlantic (e.g. Lacroix 1989; Hesthagen & Hansen 1991). Interestingly, the lowered production from the acidic rivers is due to increased mortality of eggs, fry and parr at lower pH levels, while growth rates of parr are not negatively impacted (Lacroix 1989; Hesthagen & Hansen 1991). Indeed, in some cases higher growth has been found at low pH, probably due to reduced fish densities (Lacroix 1989).

The smoltification process includes the development of high salinity tolerance, enabling the smolt to migrate out of the river with only minor disruptions to the osmotic balance and no negative growth effects. In contrast, parr are not similarly adapted, and transfer of

parr to sea water results in high mortality and stunted growth (Duston 1994). However, parr use of estuaries in water with salinity ranging from 1–24 ppt has been documented, with growth rates comparable to (and even higher than) parr of the same age living entirely in fresh water (Cunjak 1992).

Finally, levels and patterns of light may influence salmon growth. Photoperiod manipulations in aquaculture research have demonstrated seasonal variations in growth that are strongly influenced by photoperiod changes, with exposure to additional daylight enhancing growth for parr (Berrill *et al.* 2003), smolt (Handeland *et al.* 2003) and adults (Oppedal *et al.* 2003; Guerrero-Tortolero & Bromage 2008). Reductions of day lengths also enhanced growth at low temperatures in offspring of wild salmon (Finstad *et al.* 2004a). Recently, changes in light conditions due to reduced winter ice cover (Magnuson *et al.* 2000) have been shown to potentially influence growth and energy cost of salmon parr (Finstad *et al.* 2004c), and northern populations appear more sensitive to ice cover removal than southern ones (Finstad & Forseth 2006).

6.3.2 Biotic factors

Within the limitations of the physical factors, biotic factors have strong effects on the growth of Atlantic salmon. Among these, the availability of prey is obviously of prime importance for the growth of fish. Interestingly though, a direct study of the effects of food availability on growth rates revealed that, within the range studied, food availability did not impact parr growth rates (Orpwood *et al.* 2006). Rather, the parr responded to lowered food availability by changing behaviour and increasing activity. This study is particularly interesting as it highlights the behavioural influence on the growth of salmon parr (see also Box 6.2). Parr may compensate for reduced food availability by increasing the time spent foraging, but at the cost of higher predation exposure and lower probability of survival (Martin-Smith & Armstrong 2002). Prey availability varies through both space and time (Johansen *et al.* 2011 [Chapter 4]), but it is not yet known to what extent it can represent a limiting factor for salmon population dynamics in fresh water (see Nislow *et al.* 2011 [Chapter 7] and Einum & Nislow 2011 [Chapter 11]). Similarly, the high marine production of suitable prey items forms the foundation for the large size increments of salmon at sea. However, since salmon at sea are generalists and opportunistic feeders (Rikardsen & Dempson 2011 [Chapter 5]), the relative importance of food availability and other environmental and biotic factors for growth and survival at sea remains unresolved (Jacobsen & Hansen 2000).

In most freshwater systems, the available habitats of salmon are shared with one or several other fish species, providing opportunity for competitive interactions with potential consequences for juvenile salmon growth rates. The competition can be exploitative, with the fish competing for invertebrate prey, or interference, with the fish competing for space. Unravelling the mechanisms causing observed patterns is, however, notoriously difficult (Fausch 1998; Ward *et al.* 2007). Most evidence for interspecific competition is interpreted as interference competition (Fausch 1998), and effects on salmon growth and behaviour have been seen from a wide range of species such as brown trout (*Salmo trutta*, Kennedy & Strange 1986), brook trout (*Salvelinus fontinalis*, Gibson & Dickson 1984) and rainbow trout (*Oncorhynchus mykiss*, Blanchet *et al.* 2007). In comparison, evidence for exploitative competition is scarce, probably because it is difficult to prove that the fish really is experiencing limited food resources. A candidate example comes from the River Reisa, northern Norway, where

salmon and Arctic bullhead (*Cottus poecilopus*) live in sympatry with high habitat and diet overlap (Amundsen & Gabler 2008). Salmon food consumption and growth rates were low in this river compared to nearby rivers without Arctic bullhead, which at least indicates that food limitations are involved in the competition.

There is now ample evidence for density regulation of freshwater growth in juvenile Atlantic salmon (e.g. Nislow *et al.* 2004; review in Grant & Imre 2005; Imre *et al.* 2005; Juttila *et al.* 2006; Einum *et al.* 2006; Gibson *et al.* 2008), showing that variation in conspecific densities is a major source of growth variation. The relationship between growth and density for Atlantic salmon can, in parallel to other fish species (Jenkins *et al.* 1999), be described by a negative power relationship showing particularly strong effects as densities change from low to medium levels (Grant & Imre 2005). The mechanisms (competition by interference or exploitation) are still debated (Imre *et al.* 2005; Ward *et al.* 2007; Nislow *et al.* 2011 [Chapter 7]). However, the lack of knowledge on the relative importance of intra- and intercohort competition is more critical, particular for modelling exercises. In contrast, there is no evidence of density-dependent intraspecific effects on growth in the sea (Hansen & Quinn 1998; Jonsson *et al.* 1998). There are, however, some observations that might be tracked back to results from density effects in fresh water. Comparisons of smolt size and post-smolt growth have demonstrated both positive (Lundqvist *et al.* 1994; Salminen 1997) and negative correlations (Skilbrei 1990; Nicieza & Braña 1993). Moreover, positive correlations have been found between smolt size and post-smolt survival (e.g. Jonsson & Jonsson 2004a; Kallio-Nyberg *et al.* 2004), and a negative relationship between annual mean smolt size and the densities they have experienced in the stream (Juttila *et al.* 2006) may therefore serve as an example of a density-dependent relationship that has consequences for the marine phase of the salmon life cycle.

6.4 Maternal sources of growth variation

Behavioural, physiological and life-history traits of the Atlantic salmon female may influence the growth of her offspring. Such maternal effects on growth are likely to be more important than previously recognised (Einum & Fleming 1999). The most obvious maternal source of growth variation in Atlantic salmon is egg size. Einum (2003) showed that large eggs produced large body mass at yolk absorption and that juveniles from large eggs outgrew siblings from smaller eggs. By using siblings, and manipulating egg size by rearing the females to maturity in a hatchery environment, genotypic sources of growth variation were excluded. While this study, to our knowledge, is the only study on the relationship between egg size and juvenile growth in Atlantic salmon that controlled for genotypic differences, there is sufficient evidence from related species (Einum & Fleming 1999, 2000; Einum *et al.* 2004) to conclude that variation in egg size is an importance source of growth variation in juvenile Atlantic salmon.

A female's influence on offspring growth, however, exceeds her allocation of energy to individual eggs. Timing of spawning determines the time of hatching, emergence from the gravel and first feeding (Heggberget 1988; Fleming 1996; Webb & McLay 1996). It has been shown in stream channel and field experiments that late-emerging juveniles were smaller than early-emerging siblings (Einum & Fleming 2000). Surprisingly, growth rates (controlled for temperature differences and allometry) were higher in the late than early

emerging juveniles in the stream channel experiments. Thus, prior residency (e.g. Harwood *et al.* 2003), which should favour early-emerging juveniles, appeared not to be a major factor influencing growth rates. However, the size advantage of the early-emerging individuals remained for the duration of the experiments (26 days). In the field experiment growth rates were similar and the established size differences persisted for the whole period (120 days). Such size variation due to variation in time of spawning may amplify over time and influence life-history patterns and decisions (e.g. Jonsson & Jonsson 1993; Letcher *et al.* 2004).

Finally, the female choice of spawning location may strongly influence offspring growth due to local density effects (see Einum & Nislow 2011 [Chapter 11]). A female may deposit different numbers of eggs in each redd and she may visit more than one of the often patchily distributed spawning grounds within a river (see Fleming & Einum 2011 [Chapter 2]). This behaviour produces large local variation in fry densities (siblings and other conspecifics). It has now been convincingly shown that the resulting density regulation operates at small spatial scales due to limited early juvenile mobility (Einum & Nislow 2005; Einum *et al.* 2006; Einum *et al.* 2008). While the density regulation among emerging fry appears to be expressed mainly as differences in local survival without effects on growth, by the end of the first summer spatial variation in body size is established (Einum *et al.* 2006). Dispersal ability increases through ontogeny, but may not be sufficient to produce ideal free distributions even for older juveniles (Einum *et al.* 2008). More research is needed on ontogenetic changes in dispersal and maintenance of patchy juvenile distributions, but available studies clearly show that female choice of spawning location has the potential to produce growth variation during the first summer and possibly beyond.

6.5 Genetic sources of growth variation

Somatic growth is closely linked to fitness in fishes (e.g. Roff 1992) through its effect on mortality risk (e.g. size-dependent predation) and reproduction (e.g. size-dependent fecundity, age at maturation). The native distribution of Atlantic salmon spans broad environmental gradients from, for example, the temperate climate regions of northwestern Spain and Connecticut (US) to sub-Arctic areas in northern Norway and Russia, and biotic gradients from simple few-species communities to multiple-species communities with as many as 20 fish species or more. Thus growth rates are expected to be under strong selection during adaptation to local conditions (e.g. thermal regime, competition, predation pressure). Moreover, estimates of heritability of growth rates (Gunnnes & Gjedrem 1978; Gjerde *et al.* 1994; Garant *et al.* 2003), body size (Garcia de Leaniz *et al.* 2007) and strong responses to selection for enhanced growth in the salmon aquaculture industry (e.g. Gjedrem *et al.* 1991; Gjedrem 2000), indicate extensive genetic variation in growth potential in Atlantic salmon. Despite this obvious potential for local adaptation of growth or related traits, the evidence for such adaptation in Atlantic salmon is rather weak (Garcia de Leaniz *et al.* 2007).

Because temperature has pervasive effects on growth and varies greatly among salmon rivers, thermal adaptations are particularly likely. There are two contrasting hypotheses for thermal adaptation in ectotherms (Box 6.3); adaptation to local optima (Levinton 1983) and the countergradient variation hypothesis (Levins, 1969). Thermal growth performance curves (Fig. 6.2) have been established based on laboratory data on juvenile fish from a total of seven populations of Atlantic salmon from Norway (Jonsson *et al.* 2001) and Britain

Box 6.3 Hypotheses of thermal adaptation

There are two contrasting hypotheses for thermal growth adaptation in ectotherms: adaptation to local optima (Levinton 1983) and the countergradient variation hypotheses (defined by Levins 1969; reviewed by Conover & Scultz 1995) that differ in their assumptions on trade-offs. The first hypothesis implies that natural selection can shift the optimal temperature for growth to match the prevailing temperature in a new or changed thermal niche (Fig. B6.3.1), and assumes that growth at one temperature is traded off against growth at another. Such trade-offs are often referred to as specialist-generalist trade-offs (Angilletta *et al.* 2003). The alternative countergradient variation hypothesis suggests that populations from hostile environments (low temperature, short season for growth, strong competition) grow faster than conspecifics from benign environments at all temperatures, without any obvious specialist-generalist trade-off. However, there may be other trade-offs such as poorer swimming performance influencing survival (Lankford *et al.* 2001) or behavioural trade-offs (Biro *et al.* 2006).

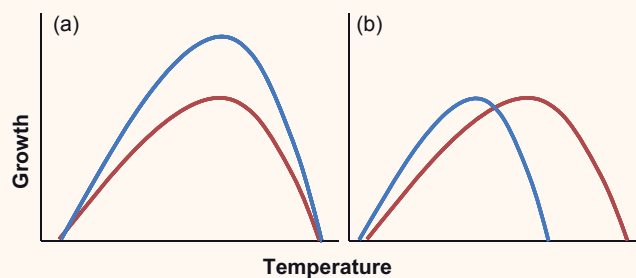


Figure B6.3.1 Theoretical thermal growth curves in populations experiencing low (blue lines) and high temperatures (red lines) during the growth season according to the countergradient (a) and local optima (b) hypotheses for thermal adaptation.

(Elliott & Hurley 1997), allowing evaluation of thermal adaptation hypotheses for Atlantic salmon (see also growth modelling below). Jonsson *et al.* (2001) concluded that the common environment experiments and modelling provided no support for either of the thermal adaptation hypotheses. They found small and insignificant (after accounting for modelling uncertainty) differences in thermal growth optima and thermal range for growth among five populations ranging largely in thermal conditions in their natal streams. However, significant differences (in the order of 60%) were found among populations in maximum growth at the optimum temperature (i.e. the height of the performance curves), but no correlation was found between maximum growth and thermal conditions such as mean temperature or length of growth season in natal rivers. The growth curves of Norwegian and British salmon were also very similar (Forseth *et al.* 2001). In apparent contrast to these studies, Nicieza *et al.* (1994a) found support for countergradient variation in growth in common environment experiments on juvenile Atlantic salmon from Spain and Scotland. Fish from the northern population grew faster than southern fish in a common environment, and food passage time and digestion rates were higher in northern than southern fish across three temperatures (Nicieza *et al.* 1994b). However, only two populations were compared and other selection agents than thermal regime may be responsible for the difference.

Why do Atlantic salmon populations appear to lack growth adaptation to local thermal conditions? Jonsson *et al.* (2001) suggest that Atlantic salmon growth at sea in a common

thermal environment in the North Atlantic (Friedland *et al.* 2000) is more important than fresh water growth in divergent thermal conditions. They also discussed different trade-offs between growth and other fitness-related traits that may prevent adaptation to local thermal conditions (see below).

Jonsson *et al.* (2001) did, however, find rather large genetically based differences in growth potential among Norwegian populations. Similarly, Obedzinski & Letcher (2004) found significant differences in alevin and early parr growth in common environment experiments using five New England populations from a more restricted geographical and climatic gradient. Moreover, there is some evidence for genotypic variation in marine growth. In common marine net-pen experiments Sheehan *et al.* (2005) found significant differences in lengths between two of three North American populations over a 25-month period, and the genotype effect accounted for 2.8% of the total variation (variation among sites dominated). Jonsson & Jonsson (2007) found consistent differences in adult size related to life-history pattern among eight Norwegian populations. The fish were reared under similar conditions in the same hatchery and released in the River Imsa, southwestern Norway, over a 21-year period. Returning adults from populations dominated by one-sea-winter salmon were on average smaller both after one and two years at sea than fish from multi-sea-winter populations.

Overall, genotypic variation in growth is likely to be a significant source of growth variation among Atlantic salmon populations, although there are surprisingly few studies that provide solid evidence and estimates of its relative importance. The adaptive patterns, and the underlying selection pressures, remain largely unexplored. While there is no solid evidence for thermal adaptation, there is a suite of other abiotic and biotic factors that may select for certain body sizes or growth rates. Finstad & Forseth (2006) found an adaptive latitudinal gradient in growth response to artificial ice cover, and for other salmonids there are indications that genetic population differences in growth rates are related to life-history characteristics or diet (*Salvelinus alpinus*; Larsson *et al.* 2005, *Salmo trutta*; Forseth *et al.* 2009) rather than thermal conditions.

Obviously, there is also genotypic variation in growth among individuals within Atlantic salmon populations. One important pattern is related to the alternative reproductive tactics. It has been shown that offspring fathered by mature male parr have higher early juvenile growth than those fathered by anadromous males, indicating an inherited fitness advantage in favour of mature male parr (Garant *et al.* 2002). Moreover, Garant *et al.* (2003) found that offspring fathered by one-sea-winter fish grew larger than those fathered by multi-sea-winter fish, and that heritability of juvenile growth was significant and varied according to both habitat quality and male reproductive tactics.

6.6 Constraints to growth

Growth rates are constrained, from both an evolutionary and ecological point of view, by costs of growth or trade-offs. As shown above, fish can on one hand accelerate growth beyond their normal maximum in response to periods of starvation and on the other hand growth rates are frequently far below species maximum even when food is abundant. It is now well established that maximum growth, or indeed growth above the normal maximum, cannot be maintained over longer periods due to physiological and ecological costs of fast

growth or trade-offs between growth and other fitness-related traits. Physiological costs of rapid growth in fishes include reduced swimming performance (Billerbeck *et al.* 2001; Munch & Conover 2003), reduced developmental stability (Arendt 1997; Arendt *et al.* 2001) and lower investment in tissue maintenance (Morgan *et al.* 2000), reduced immune capacity (Arendt 1997; Jhingan *et al.* 2003), and reduced starvation tolerance (Cook *et al.* 2000) and egg tolerance to hypoxia (Sundt-Hansen *et al.* 2007), which is likely to be due to elevated metabolic rates. Ecological costs are behaviourally mediated and increased susceptibility to predators due to increased activity and risk taking is particularly well documented (Johnsson *et al.* 1999; Munch & Conover 2003). These costs or trade-offs imply that growth is optimised rather than maximised (Arendt 1997; Metcalfe & Monaghan 2001). The behavioural trade-off between active feeding and predator avoidance is well described for juvenile Atlantic salmon, and as outlined above, is likely to be a major factor explaining patterns of salmon growth. Less is known about the physiological cost of rapid growth in Atlantic salmon. Reduced starvation tolerance due to elevated metabolic rates has been documented (Cook *et al.* 2000) and there are indications that fish from populations with fast marine growth are more susceptible to salmon lice infections (Glover *et al.* 2004).

6.7 Growth modelling

Growth models are valuable tools in almost any aspect of the science and management of Atlantic salmon. From simple temperature-driven laboratory models, salmon scientists are now expanding into more complex field-based explanatory and predictive models.

6.7.1 Laboratory models

Based on the pioneer work of Brett (1971) and Elliott (1975), laboratory-based thermal growth models have been established for at least 28 populations of salmonid fishes (e.g. Nicieza *et al.* 1994a; Elliott & Hurley 1997; Jonsson *et al.* 2001; Larsson *et al.* 2005; Forseth *et al.* 2009), including seven populations of Atlantic salmon. These models predict maximum growth from initial body size and ambient temperature (Box 6.4), and are powerful methodological tools in ecological and evolutionary studies. First and foremost they are baseline models with which fish performance in nature or experiments can be compared. The developed models can be used to control for differences in body size and temperature, and therefore facilitate direct comparisons of growth performance among individuals or groups of fish. By expressing growth as ratios between observed and maximum growth (relative growth), new insights have been gained on topics ranging from maternal effects on growth (Einum & Fleming 1999, 2000), density dependence and interspecific competition (Vøllestad *et al.* 2002), growth effects of fluctuating water level and temperature (Flodmark *et al.* 2004) and hydrological regime (Nislow *et al.* 2004), and seasonal patterns of growth (Craig 1982; Mortensen *et al.* 1988; Vøllestad *et al.* 2002; Bacon *et al.* 2005). The models can also be used to compare performance of different species enabling competitive effects (reduced growth of the inferior competitor) to be separated from evolutionary (phylogenetic) differences in growth potential between the species (Persson *et al.* 2000; Forseth *et al.* 2003).

Evolutionary studies are a second major field of application for laboratory-based growth models. Given sufficient genetic representation of the populations, the established growth

Box 6.4 Laboratory-based growth models

There are two types of models used in modelling of laboratory data on growth of Atlantic salmon, the Elliott *et al.* (1995) model (Elliott model) and the re-parameterised version of the Ratkowsky *et al.* (1983) model. The first describes a sharply peaked thermal response, whereas the latter performs better for flatter thermal responses around the optimal temperature (Elliott & Hurley 2003; Forseth *et al.* 2009). Both models can be parameterised by using individual standardised mass-specific growth rates (Ω , Box 6.1) as the dependent variable. The Elliott generic model for fish growth consists of five biologically meaningful parameters: the lower (T_L), optimal (T_M) and upper (T_U) critical temperatures for growth, the height of the growth curve (c , the growth rate of a 1 g fish at the optimal temperature) and the mass scaling constant b . When using mass standardised growth (Ω), and thus account for allometric variation, the Elliott growth model is given as:

$$\Omega = \frac{c(T - T_{LIM})}{(T_M - T_{LIM})}$$

where T (°C) is the experimental temperature, T_{LIM} substitutes for the lower critical temperature for growth (T_L) for temperatures below, and the upper critical temperature (T_U) for temperatures above, the optimal temperature (T_M), and c as defined above. Since T_{LIM} is a parameter that takes different values (T_L or T_U) depending on another estimated parameter (T_M), it must be replaced with a Boolean expression: $T_{LIM} = (T \leq T_M)T_L + (T > T_M)T_U$, to fit the model by non-linear least squares regression.

The re-parameterised version of the Ratkowsky *et al.* (1983) model (Forseth *et al.* 2001) describes the relationship between standardised mass-specific growth rates (Ω) and temperature (T) as:

$$\Omega = d(T - T_L)\{1 - e^{g(T - T_U)}\}$$

This model consists of two of the same biologically meaningful parameters as the Elliott model, the lower (T_L) and upper (T_U) critical temperatures for growth, and two shape parameters d and g , that can be used to estimate the two final parameters of the Elliott model (T_M and c). The optimal temperature for growth (T_M) is estimated by solving:

$$\ln(1 + g(T_M - T_L)) = -g(T_M - T_U)$$

Finally, the height of the growth curve (c) is estimated by calculating the equation for $T = T_M$.

models are continuous norms of reactions describing relationships between genotypic (population) growth and temperature (Huey & Kingsolver 1989; Kingsolver *et al.* 2004). Establishment of inter-population variation in such curves allows tests of thermal adaptation hypotheses (Angilletta *et al.* 2003; Kingsolver & Gomulkiewicz 2003), and evaluation of the potential trade-offs of performance (Angilletta *et al.* 2003). Such tests, based on comparing performance curves or performance at selected parts of the thermal range, have been used to explore thermal adaptation in salmonids (e.g. Nicieza *et al.* 1994a, b; Jonsson *et al.* 2001; Larsson *et al.* 2005; Forseth *et al.* 2009). Along the same lines are studies that explore geographical variation in performance, and the potential for local adaptations, by studying residual growth variation after accounting for differences in body size and temperature across local (Allen 1985; Mortensen *et al.* 1988; Vøllestad *et al.* 2002; Nicola & Almodovar 2004), regional (Edwards *et al.* 1979; Jensen 1990) or continental climate gradients (Jensen *et al.* 2000). Understanding the ability of populations to respond to changes in thermal conditions by evolutionary changes in thermal performance is vital for predicting long-term effects of climate change.

Finally, laboratory-based growth models can also be used to simulate growth in nature (Bacon *et al.* 2005) for use in population models and in other predictive or exploratory biological models (e.g. Ugedal *et al.* 1997) and to predict growth after anthropogenic changes in thermal conditions (Jensen 2003). However, models for salmonid growth using temperature and body size alone, cannot accurately predict the range of growth experienced by wild fish at different seasons and in different physiological or life-history stages (Bacon *et al.* 2005). Field-based models represent promising alternatives.

6.7.2 Field-based models

Individual tagging programmes in small streams have provided data for more complex models that seek to explain sources of variation in individual growth rates. Recapture rates of tagged individuals in fresh water may be relatively high in such systems (0.5–0.8; Letcher & Horton 2008), allowing parameter fitting of complex models based on field data (Juanes *et al.* 2000). Jones *et al.* (2002) fitted data on individual captures to a dynamic energy budget model that explicitly modelled changes in body length and mass. After adding an individual-specific food assimilation coefficient, their model accounted for about 90% of the variation in both length and mass. Working with data from the same system, Bacon *et al.* (2005) developed an empirical multiple regression model aimed at explaining the strong seasonal growth dynamics observed in fresh water. The model captured the key seasonal patterns of very rapid growth in the spring with a small growth spurt in the fall. The model was also used to examine growth variation between life histories, demonstrating faster growth, especially in length, for mature male parr in the early part of the year.

One difficulty with empirical growth models is the accounting for the repeated observations of individuals. Davidson *et al.* (2009) used mixed general linear models to evaluate the effects of environmental variables (stream flow and temperature) on growth of individually tagged salmon. In the mixed models, year, cohort and individual were treated as random effects. Treating individual as a random effect effectively accounts for the variation in growth introduced by repeated observation of specific individuals. In the model, the variance effect size for year was an order of magnitude greater than variance effect sizes for either cohort or individual. Overall, the model accounted for about 95% of the variation in growth rates, with yearly variation in stream discharge accounting for about 30% and temperature accounting for about 15% of the growth rate variation. As more and more data are collected on individual fish in more systems, it will be critical to develop modelling strategies that can accommodate the extremely complex dynamics that control growth rates in the field. Hierarchical Bayesian models (e.g. Gelman *et al.* 2004; He *et al.* 2008) offer a promising platform for the development and parameter estimation of complex models based on field data.

The main challenge for models developed from tagging programmes in specific systems is transferability. While models developed in one system may accurately describe growth variation and predict effects of environmental or population changes in that system, it may fail in another system. Indeed, model performance may be poor even for new cohorts within the same system. To overcome this limitation, factors explaining growth variability should be tested across different systems or explored in laboratory studies. To obtain generic models, applicable for management challenges, we advocate gradual expansion from simple temperature-driven growth models to more complex models by the inclusion of functional

model descriptions of the most important sources of growth variation. While simple models with relatively few parameters may not mimic natural growth accurately, the relative effects of different changes (natural or anthropogenic) may be adequately described.

6.8 Perspectives for management

The growth of Atlantic salmon is environmentally sensitive and closely linked to fitness. In view of this, monitoring of changes and modelling of growth may serve as early warnings of, or predictions for, negative population changes. However, for interpretation we need to consider the complex relationships between growth, fish density, predation risk and behaviour. The most obvious application of growth models is in predictive models for effects of climate change. While the knowledge is available for successful modelling of the freshwater phase, much work is needed before the marine phase can be satisfactory modelled. Meanwhile, we also advocate continuous efforts towards development and application of freshwater models to address a suite of management challenges (e.g. river regulation, pollution, stocking strategies, habitat change and fragmentation and restoration), and sampling programmes that can account for the variation in growth at appropriate spatial and temporal scales.

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7

The Role of Competition in the Ecology of Juvenile Atlantic Salmon

Keith H. Nislow, John D. Armstrong & James W.A. Grant

Abstract

Juvenile Atlantic salmon compete amongst themselves and with other species for critical resources such as food and space. Competition between juvenile salmon of the same age-class is a well-established mechanism underlying population dynamics and population regulation. Competition between territorial individuals, which awards favourable territories to the winners on the basis of size, prior residence and energetic status, appears to be a primary way in which juvenile abundance is adjusted to ‘fit’ the carrying capacity of local environments. Recent studies have refined our understanding of these dynamics and explored their consequences for management and conservation, including interactions between wild and farmed salmon. In contrast to the large literature dealing with intraspecific competition, there have been relatively few studies examining competition between juvenile Atlantic salmon and other species. Those studies that have been conducted suggest that some of the important mechanisms underlying intraspecific interactions (size and prior residence) may also influence competition among co-occurring salmonid species. It also appears that the ‘residence’ advantage may provide a general rule for interactions between migratory Atlantic salmon and resident salmonids. However, researchers have yet to take full advantage of the challenges and opportunities provided by the accidental and planned manipulations of species assemblages that have affected Atlantic salmon rivers worldwide. Further, we have yet to fully understand how these interactions depend on changes in resource availability and environmental conditions such as streamflow and temperature. The overall challenge for the next generation of research may be to better integrate the role of competition in the context of ecosystem change.

Key words

Competition, density-dependent dynamics, interspecific competition, intraspecific competition, *Salmo salar*

7.1 Introduction

Stream-dwelling salmonids, including Atlantic salmon in their juvenile phase, show some of the clearest and best-studied examples of density-dependent population dynamics in the



Figure 7.1 Juvenile Atlantic salmon (*Salmo salar*) and signal crayfish (*Pacifasticus leniusculus*) competing for shelters in a laboratory stream.

natural world Einum & Nislow 2011 [Chapter 11]. Competition is one of the three classic mechanisms, along with predation Ward & Hvidsten 2011 [Chapter 8] and parasitism Harris *et al.* (2011) [Chapter 9]; Finstad *et al.* (2011) [Chapter 10] underlying density-dependent dynamics. The way in which individual Atlantic salmon compete with members of their own species (intraspecific competition) and with co-occurring species (interspecific competition) has been the subject of considerable interest and research. Further, widespread changes in the structure of freshwater species assemblages make understanding interspecific interactions all the more critical. These efforts have been aided by the relative tractability of manipulative experiments using salmon in both laboratory and field settings in ways that are difficult or impossible in other species, yielding information that has contributed to our general knowledge of the causes and consequences of competition in the natural world. In this review, we consider the mechanisms and consequences of intra- and interspecific competitive interactions in Atlantic salmon, highlight recent findings in this area, identify critical data gaps, and point out directions for future research. We deal exclusively with competition for resources (food, habitat, etc.); reproductive competition is covered separately in Chapter 2.

Competition for resources is most likely to occur amongst individuals with similar requirements and ecological niches. We therefore begin the chapter by considering intraspecific competition within cohorts, then move on to consider intercohort and interspecific interactions. Our goal is to address the way that an understanding of competitive interactions in Atlantic salmon can aid in conservation and management, and might also serve as an important model for competition that may be widely applicable across species and systems.

7.2 Intraspecific competition

A number of attributes of salmon natural history contribute to the idea that competitive interactions underlie density-dependent dynamics. Perhaps the most obvious is the strong territoriality exhibited by juvenile salmonids where space-holding individuals actively exclude other fish (sometimes including fish of other species) from their foraging areas. In contrast, there is little evidence for competitive interactions or density-dependent population regulation in the adult stage (Box 7.1.).

Box 7.1 Resource competition in the Atlantic salmon adult stage

The role of resource competition in the ecology of adult Atlantic salmon in marine and freshwater environments is poorly understood. Manipulation experiments are generally not possible, and studies are therefore limited to correlative and 'natural' experiments. The lack of evidence for density-dependent survival or growth of Atlantic salmon in the marine environment (Jonsson *et al.* 1998) suggests no strong role for intraspecific competition at sea in Atlantic salmon. Intra- and interspecific competition for prey resources, as inferred by negative correlations between abundance and growth rates of co-occurring species in the ocean, may occur among Pacific salmon species (Martinson *et al.* 2008). This has been most strongly suggested by negative effects of large-scale stocking of pink salmon (*Onchorhynchus gorbuscha*) on native species in the northern Pacific (Ruggerone *et al.* 2003). As yet, there has been no evidence for similar effects on Atlantic salmon. However, given that pink salmon have now become established in Atlantic salmon rivers in northern Norway (Berg 1977), along with general concerns about the ecosystem-level effects of overfishing in the north Atlantic (Lotzke & Milewski 2004), negative effects of interspecific competition in the marine realm remain a possibility.

Although adult Atlantic salmon returning from sea do not require prey resources during their river residence, they may compete for suitable habitat. Strong competition for suitable spawning gravels has been observed in mass-spawning Pacific salmonids such as sockeye (*Onchorhynchus nerka*), resulting in strong density-dependent recruitment due to overcutting and exposing previously constructed nests (Fukushima *et al.* 1998). While some studies have suggested that suitable spawning habitat may be strongly limited in some Atlantic salmon rivers (Armstrong *et al.* 2003), smaller run sizes may be the reason why redd overcutting and competition for spawning sites have received relatively little attention in this species. Adult Atlantic salmon, particularly individuals that return to rivers in the spring and spend several months before spawning, require suitable holding habitats, generally large deep pools. These habitats may be in short supply in some situations, particularly in small rivers and streams that have been canalised, and adults may compete for the best sites, but there is essentially no quantitative information on such potential interactions.

The complex life-history and annual breeding schedules of Atlantic salmon result in the formation of discrete cohorts (year-classes) which overlap in time and space and potentially compete. It is therefore useful to distinguish within the broader category of intraspecific competition among members of the same cohort (intracohort) and competition among members of different cohorts (intercohort). In addition, the tremendous expansion of Atlantic salmon farming and ranching (Gross 1998) has resulted in the potential for competitive interactions between wild and farmed salmon, which may pose a considerable threat to wild populations. In this section we review the mechanisms underlying intraspecific competition in Atlantic salmon and explore some implications for management and conservation.

7.2.1 Intracohort interactions

Juvenile Atlantic salmon emerge from nests in the stream bottom (referred to as redds) in the spring to encounter a high-density world in the vicinity of the nest. They then begin feeding, some near the redd, whereas others disperse, primarily downstream, to find suitable habitat with fewer competitors. They also establish a territory (Kalleberg 1958; Gustafson-Greenwood & Moring 1990; Keeley & Grant 1995): a more or less exclusive area maintained by active defence (Wilson 1975). Intrinsic dominance and prior-residence advantage (the importance of being there first) are both important for acquiring and holding a territory at this early stage (Harwood *et al.* 2003). Thereafter, territories are a special case of site-limited dominance, where individuals are dominant to conspecifics within their territory and subordinate to others outside these boundaries.

Territorial mosaics occur when a habitat is subdivided into a number of contiguous territories (Keenleyside 1979). This social system is often observed in the first summer of life when high densities of salmon of similar size occupy sections of stream. Territorial mosaics are an uneasy blend of aggressive territoriality amongst competitors and cooperation amongst neighbours – a society of ‘dear enemies’ (*sensu* Wilson 1975), which focus attacks on intruders rather than each other. As salmon grow larger, territorial mosaics tend to break down. This change may result from an increase in size variation within a cohort, such that dominant individuals extend their influence into the space used by others. In addition, juvenile salmon increasingly interact with older cohorts and other species, which may have priority of access to the space. The antithesis of a territorial mosaic of ‘equals’ is the size-structured dominance hierarchy that is often observed in non-migratory, stream salmonid populations (Bachman 1984; Nakano 1995).

Because some individuals of virtually all stream salmonid populations defend feeding territories, salmonid biologists tend to overlook the rarity of this social system. Most fish species engage in territorial behaviour during reproduction (Grant 1997), whereas few freshwater fish species other than salmonids defend territories exclusively for feeding (Barlow 1993). Hence, there must be something peculiar about the foraging niche of juvenile salmon in streams that makes territories economically defensible (see Box 7.2).

Juvenile salmon feed extensively on drifting aquatic invertebrates (hereafter ‘drift’) (Keeley & Grant 1995), although they can switch to feeding directly from the benthos when necessary (Nislow *et al.* 1998). Because drift is a mobile and constantly renewing resource, a sit-and-wait tactic is optimal for drift-feeders. The abundance of drift flowing through a cross-sectional area of stream (i.e. drift rate, *sensu* Elliott 1970) increases with current velocity, so that the average abundance of food differs markedly among sites, and is highly predictable in space. These characteristics make territories economically defensible (Box 7.2) for juvenile salmonids and for other drift-feeders including aquatic insects such as blackfly larvae (Diptera: Simuliidae) and net-spinning caddisflies (Trichoptera: Hydropsychidae), and as well as birds such as pied wagtails (*Motacilla alba*) (Davies & Houston 1981; Hart 1987).

Juvenile salmon are classic central-place foragers that encounter their food at a distance (Schoener 1971). At high population densities, they typically rest on or near the substrate at a single central place, face into the current, defend a two-dimensional territory around the central place, and intercept drift as it flows over the territory (Keeley & Grant 1995). The radius of the defended area corresponds closely to the maximum distance at which a salmon can see the largest prey in the drift (Dunbrack & Dill 1983; Keeley & Grant 1995). Because of the directional nature of the flow, salmon defend further upstream than downstream, as if protecting access to their drift resource.

The size of a territory within a mosaic likely represents the smallest area in which an individual can obtain enough food to grow and also have access to shelter from predators and adverse environmental conditions. Territory size increases with body size as the visual acuity, prey size and metabolic requirements of the salmon increase. Juvenile salmon also shift to deeper, faster habitats as they grow (Keeley & Grant 1995), presumably to increase their encounter rate with food (Hughes & Dill 1990).

Box 7.2 Economics of territoriality

Cost/benefit analyses of territoriality typically address two fundamental questions: (1) do individuals defend territories? and (2) what is the optimal territory size?

Jerram Brown (1964) provided the conceptual breakthrough to answer question 1: individuals should defend territories only when the benefits exceed the costs of defence. As the idea of alternative strategies emerged from the literature on evolutionary game theory (e.g. Maynard Smith 1982), Brown's concept was refined to suggest that territoriality will be the best strategy when the net benefits of defence exceed the net benefits of alternative strategies, such as being non-territorial or floating (e.g. Puckett & Dill 1985). Whether or not territories are economically defensible depends crucially on how resources are distributed in space and renew in time. A synthesis of predictions from models and experimental data suggests that resources are defensible when they are predictable in space and time, clumped in space, dispersed in time, found at intermediate densities, and are contended for by an intermediate number of competitors (for a review, see Grant 1993, 1997).

Optimal territory size models address the question of how large a territory to defend. Territory size is predicted to decrease with an increase in both the benefits: typically food abundance, and costs: typically intruder pressure (see Figure B7.6.1). These predictions assume that territories are not contiguous, so that individuals are free to expand and contract their territory when needed. The general support for these two predictions (Adams 2001), even in species with contiguous territories, suggests that optimal territory size models are broadly applicable for many territorial species and situations. Important exceptions occur when contiguous territories are forced well below their non-contiguous optimum by the pressure of intruders and neighbours (Adams 2001), as in some coral reef fishes (Norman & Jones 1984; Tricas 1989), and salmonid fishes at high density (e.g. Imre *et al.* 2004).

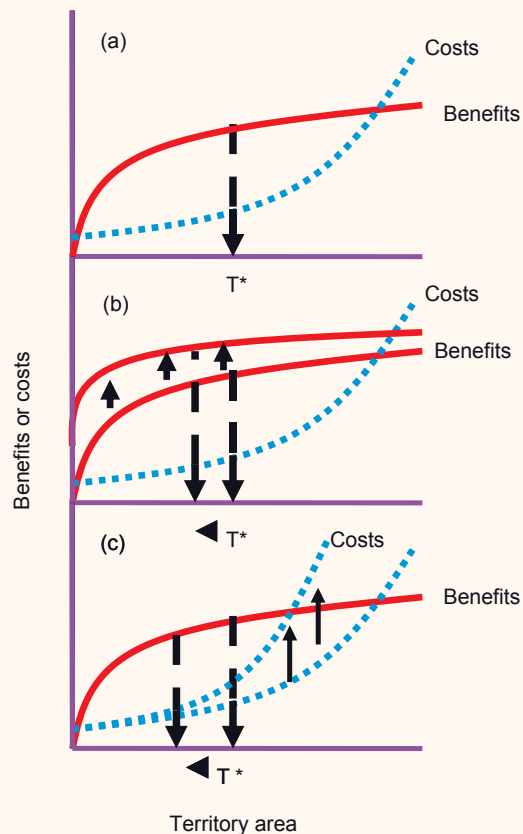


Figure B7.2.1 The benefits and costs of defence increase with increasing territory size, leading to (a) an optimal territory size (T^*). This optimal size decreases as (b) the benefits of defence increase, or (c) as the costs of defence increase.

As predicted by optimality models (Box 7.3), the territories of juvenile salmon typically decrease with increasing food abundance, population density, or a combination of both factors (Slaney & Northcote 1974; Keeley 2000). While there has been less experimental

Box 7.3 Exploitation vs. interference competition

The distinction between exploitation and interference is based on how individuals interact when competing for a limiting resource. Exploitation occurs when individuals interact indirectly, solely through the reduction of the available supply of the resource, whereas interference involves direct interactions via threat, aggression or territoriality (Keddy 1989). Both mechanisms are likely to operate in stream salmonid populations.

Imagine two individual salmon at a low population density settling at the most favourable foraging site within each of two adjacent riffles, separated by one pool (Fig. B7.7.1). These sedentary fish are unaware of each other, but the upstream fish has first access to rare and rich drifting prey, which originate upstream. Such an example of shadow competition (*sensu* Elliott 2002), when the individual closer to the source has first access to the resource, is a case of exploitation competition. As the population density increases, however, territoriality limits the number of settlers in each riffle – a classic example of interference competition (Figure b). Within each riffle, some territories will be closer to rich sources of drift than others. Because aggressive interactions determine the position of territories in relation to the food sources, shadow competition within habitats is also a clear case of interference. At the larger spatial scale, however, shadow competition between the salmon in the two riffles still appears to be a case of exploitation competition, unless aggressive interactions play an important role in how the adjacent riffles are settled. While determining the actual mechanisms of competition that are operating in the wild will not necessarily be easy (e.g. Imre *et al.* 2005; Ward *et al.* 2007), the outcome may have important implications for population regulation and management decisions (Chapter 11).

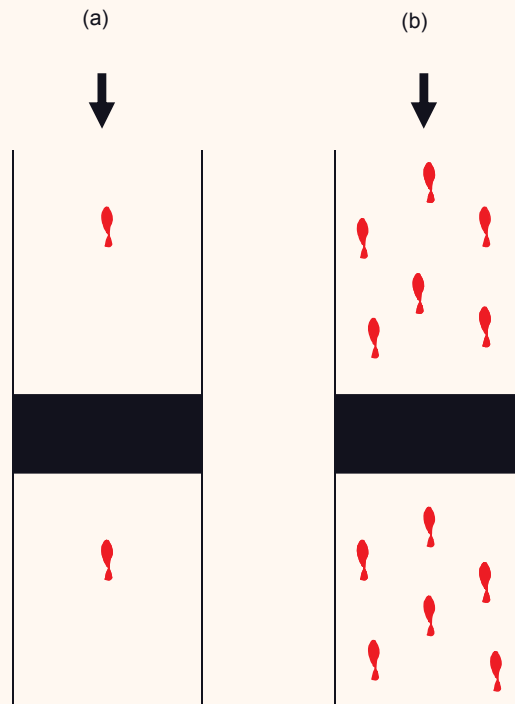


Figure B7.3.1 Schematic diagram depicting the spatial arrangement of juvenile salmon experiencing both interference competition (within a section) and exploitation competition (from upstream sections). Arrows give the direction of flow.

work with Atlantic salmon, observational studies suggest that territory size is inversely related to food abundance (Keeley & Grant 1995) and a combination of current velocity and population density (Kalleberg 1958). The costs of territoriality can also be increased by decreasing the visibility within the environment, which impairs the ability of defenders to detect and eject intruders (Eason & Stamps 1992), or by increasing the risk of predation.

Physical structure of the habitat may influence local densities and growth rates of salmon (Kalleberg 1958) through a combination of mechanisms that impinge on the intensity of intraspecific competition. The presence of physical shelter reduces the resting metabolic rate of salmon parr, presumably by lowering their perceived risk from predators and competitors (Millidine *et al.* 2006), and may also reduce metabolic costs of aggression among conspecifics. Visual isolation from larger conspecifics lowers resting metabolism of relatively small salmon; conversely, larger salmon seem to acquire a metabolic benefit from association with smaller conspecifics (Millidine *et al.* 2009). The net result of these and potentially other effects of large substratum on food supply can be a decrease in mean territory size of age-0 fish and increase in their density with no effect on body size (Imre *et al.* 2002; Venter *et al.* 2008). However, in some situations, larger substratum may force salmon to spend more time in the water column, with potential increase in energy expenditure and risk of predation (Kemp *et al.* 2005).

The territorial behaviour and space use of juvenile salmon suggest a simple model for juvenile competition regulating population and production dynamics. Fish whose territorial requirements for space exceed its availability experience one or more of higher mortality, reduced growth and increased propensity to emigrate (Elliott 1993; Grant *et al.* 1998; Nislow *et al.* 2004) and the population is thereby regulated (Einum & Nislow 2011 [Chapter 11]). Population regulation is sometimes accomplished during a critical period early in life or via self-thinning throughout juvenile ontogeny (Nislow *et al.* 2004; Kennedy *et al.* 2008; Armstrong & Nislow 2006). Further, the effects of intracohort competition appear to be manifest largely via mortality in the early fry stage (in the first several weeks after emergence) and more via reduced growth and increased propensity to emigrate later in juvenile life-history (Einum *et al.* 2006). This general model is consistent with a growing body of literature relating variation in the availability of suitable territories to variation in juvenile survival (Nislow *et al.* 2000; Letcher *et al.* 2004; Einum & Nislow 2005; Einum *et al.* 2006) at the scale of local interactions between territorial individuals.

As in any simple model, a number of inadequacies have been pointed out in recent studies. Perhaps most important are results which indicate that negative effects on growth and survival are observed at densities well below saturation/space-based carrying capacity (Grant *et al.* 1998; Nislow *et al.* 1999; Einum & Nislow 2005; Einum *et al.* 2006). Simply stated, if territory size is well predicted by body size, we would expect the abundance of juvenile salmon to be directly proportional to the number of territories that would 'fit' into a given area. Density-dependent effects would only be manifest when habitats were close to saturation. However, Grant *et al.* (1998) found that habitat saturation tended to be quite low (<25% total stream area). Further, analyses of long-term data for Catamaran Brook, eastern Canada, and a meta-analysis including data for a number of different salmonid species (Imre *et al.* 2005; Grant & Imre 2005) found that the strongest effects of density on growth occurred at low densities, with the strength of the relationship declining at the highest densities. This appears to be in direct conflict with the general model, which would predict

density-dependent effects to increase slowly at low densities, then grow stronger as densities increased. What is the explanation for these apparent discrepancies?

Studies conducted in the last decade suggest some answers. It appears likely that the spatial requirements of juvenile salmon are more complex than those predicted by previous body size/territory size relationships. Due to strong habitat limitation and high mortality in the few weeks following emergence (Nislow *et al.* 2004; Kennedy *et al.* 2008), only a small percentage of total stream area may be suitable for foraging. Competition may therefore be particularly severe in the few weeks following emergence and the onset of independent feeding (Nislow *et al.* 1999; Nislow *et al.* 2000). During this period the majority of fry at high densities may fail to find suitable territories and subsequently die of starvation (Kennedy *et al.* 2008). As a result, density-dependent population regulation will have occurred while habitat for older juveniles remains unsaturated. Steingrímsson & Grant (2008) also found that individual salmon fry at low densities display multiple central place foraging and use much larger stream areas than found previously for single-place foragers in tightly packed groups, which would increase spatial requirements and habitat saturation. Such fish essentially appear to adopt a similar patch sampling strategy to that exhibited by dominant older parr (Martin-Smith & Armstrong 2002; Maclean *et al.* 2005). In addition, the availability of shelters appears to be an important limiting resource for juvenile salmon, which may spend the majority of their time sheltering (Finstad *et al.* 2007, Breau *et al.* 2007a.). There is some evidence that juvenile salmon compete for shelters (Armstrong & Griffiths 2001) with potential density-dependent consequences. Finally, Imre *et al.* (2005) suggested that the common pattern of density-dependent growth in age-0 salmon (strong effects at low densities, weaker effects at higher densities) is more consistent with exploitation competition for prey (see Box 7.3) than interference competition for space. Taken together, these results underscore the need to incorporate multiple environmental axes (including prey and shelter abundance) in combination with a detailed understanding of stage-specific population dynamics to further our understanding of the population consequences of intracohort competition in juvenile Atlantic salmon.

7.2.2 Intercohort competition

Although generation time and cohort structure are highly variable across the range of wild Atlantic salmon populations, in the large majority of rearing environments, at least two and frequently more age-classes co-occur (Hutchings & Jones 1998) (Fig. 7.2). In order to fully address intraspecific competition, we must consider the potential interactions between age-classes. These issues are not simply of academic interest. From a population dynamics perspective, the strength and direction of competitive interactions between juvenile age-classes can have a major influence on stock-recruitment curves. Specifically, in both empirical and mechanistic models (Einum *et al.* 2008; Einum & Nislow 2011 [Chapter 11]), when strong younger age-classes have negative effects on older age-classes, overcompensation (Ricker-type) responses are predicted. In such cases, increases in early recruitment, for example by increasing habitat availability for young juveniles or stocking above carrying capacity, can cause a decrease in overall population size, population growth rate, and sustainable yield. In contrast, if younger cohorts fail to influence the growth and survival of older cohorts (for example, if larger, older individuals are competitively dominant) asymptotic (Beverton-Holt) dynamics are expected, with no overcompensation (Fig. 7.3).



Figure 7.2 Three age-classes of juvenile Atlantic salmon co-existing in a small rearing stream in central Massachusetts, northeastern USA. Photo: Benjamin H. Letcher.

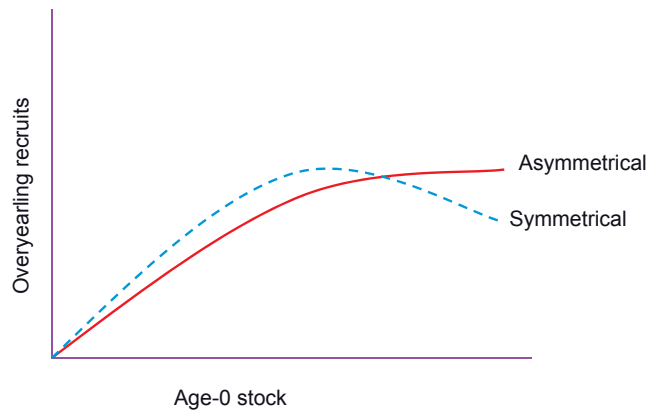


Figure 7.3 Graphical depiction of different stock recruitment curves resulting from model scenarios with symmetrical competition (juveniles of different cohorts competitive equivalents) compared to asymmetrical competition (older cohorts dominant over younger cohorts (modified from Eium *et al.* 2008).

So, an important question is ‘Are individuals from different cohorts competitive equivalents?’ A number of factors will influence the answer. Size and experience will generally favour older, larger individuals in pairwise contests (Metcalf 1998) (Box 7.4), which will in most cases favour individuals from older over younger cohorts. However, there are several factors that may complicate this simple size- and experience-based advantage of older fish. Juveniles at different points in their life-history may have substantially different habitat and resource-use strategies, and correspondingly different perspectives on the costs and benefits of competitive interactions. For example, age-0 fish tolerate warmer water temperatures better than older parr (Breaux *et al.* 2007a, b), which may give them a competitive advantage during the low-flow periods of summer. An important conceptual framework here is the ‘asset protection principle’ (Clarke 1994) which states that individual behaviour should become more risk-averse as the reproductive value of that individual increases over ontogeny. Several general observations of behavioural changes are consistent with increased risk aversion of older Atlantic salmon juveniles, with important implications for intercohort

Box 7.4 Dominance interactions in salmonids: causes and consequences

The earliest observers of juvenile salmonids were struck by the strong dominance interactions exhibited by captive juvenile salmon. In aquaria containing several fish, generally one individual would completely dominate the entire space, with all the other fish cowering in a corner. The ability to quickly assess the dominance status of individuals with these competition 'assays' has allowed researchers to map out dominance relationships among many individual fish and to examine the determinants of dominance at a level of detail and with sample sizes that would not be possible with most other species. Figure B7.8.1 shows a conceptual diagram of the causes and consequences of dominance of dominance status for juvenile Atlantic salmon.

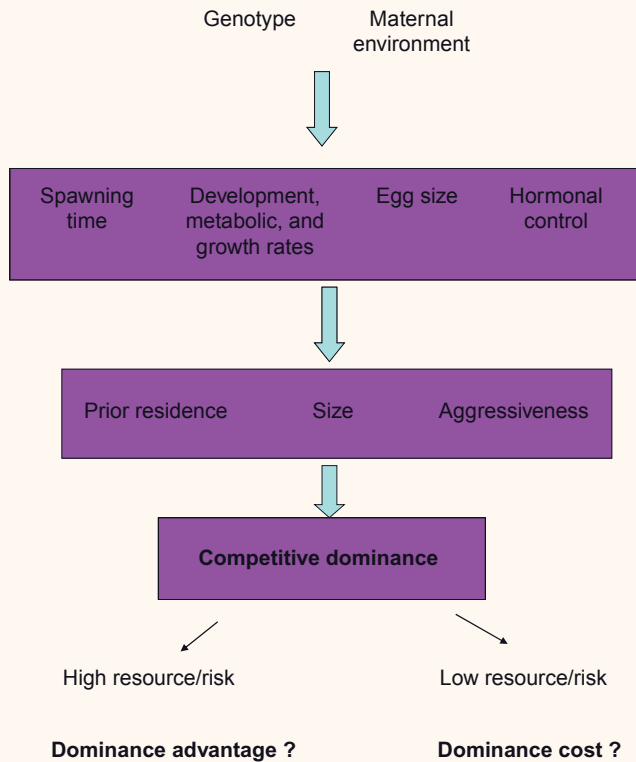


Figure B7.4.1 Causes and consequences of dominance status for juvenile Atlantic salmon.

As in many other species of fish, size and prior residence appear to be important determinants of competitive dominance (Cutts *et al.* 1999). In some cases, however, it appears that standard metabolic rate may be the strongest factor (Metcalf 1998). Size may therefore be more of a consequence than a cause of dominance, as dominant individuals monopolise resources and grow faster, achieving larger body sizes (Metcalf 1998).

Dominance status may have major consequences for growth, survival, and life-history expression. As reviewed in Metcalf (1998), in laboratory studies, dominant individuals are more likely to grow faster, smolt earlier, and (for males) mature as parr than are subordinates. However, these advantages are likely to incur measurable costs, so that the ultimate consequences for individual performance and population dynamics are likely to be highly context-dependent. For example, energy costs of the high standard metabolic rates and increased aggressiveness of farmed juveniles may be part of the reason why they fail to outperform wild juveniles in low-food, high predation risk environments (Metcalf *et al.* 2003). As another example, while prior residence associated with early emergence may result in competitive advantage (Einum & Fleming 2000; Einum & Nislow 2005)

harsh environmental conditions can select against early emergers (Letcher *et al.* 2004; Armstrong & Nislow 2006). Figure B7.8.2 shows in graphic form the costs and benefits of different emergence times in Atlantic salmon.

Salmon may also be impeded from expressing dominance behaviour if they run the risk of exposing themselves to attack from predators or competitors (Höjesjö *et al.* 2009). These complicating factors, as well as challenges for dominant fish in tracking variations in local quality of the habitat (Maclean *et al.* 2005), may be a reason why dominance interactions determined in the laboratory may not always predict individual performance in the field (Martin-Smith & Armstrong 2002; Harwood *et al.* 2003).

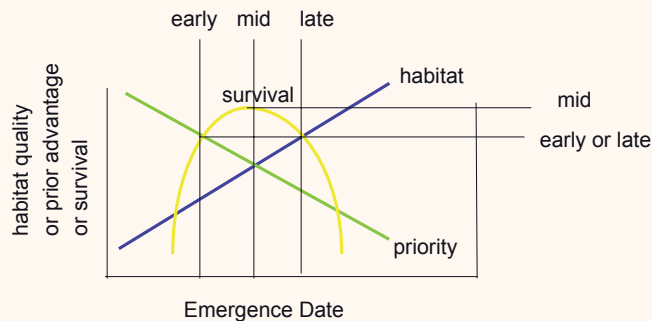


Figure B7.4.2 Graphical model depicting the cost and benefits of emergence time for juvenile Atlantic salmon. Modified from Armstrong & Nislow (2006).

interactions. Assuming that diurnal foraging behaviour is ‘risky’ relative to sheltering or nocturnal feeding (Orpwood *et al.* 2006), it has been observed that overyearlings:

- are more likely than age-0 fish to be night-active
- in some rivers, achieve their growth over a short time period (spring) then feed primarily for maintenance, mainly at night (Letcher & Gries 2003) whereas age-0 fish continue to grow through the summer and feed extensively during daylight hours (Imre *et al.* 2005)
- take longer to emerge from hiding after exposure to alarm cues from predators than do age-0 fish (Kim *et al.* 2009).

Taken as a whole, these differences between age-classes may reduce overlap in resource and habitat demands between cohorts, and potentially reduce the strength of intercohort competitive interactions. At the same time, differences in behaviour and resource use may reflect to some extent the outcome of intercohort competition.

Given these considerations, what is known about intercohort competition in juvenile Atlantic salmon? There have been few published studies looking directly at pairwise interactions between individuals of different cohorts, either in the lab or in the field. There is some evidence that overyearlings are dominant over underyearlings in some situations (Kennedy & Strange 1986a), but little evidence of negative effects of overyearling presence or abundance on age-0 fish. In fact, Adams *et al.* (2000) in a laboratory study found that the presence of overyearlings, by reducing aggression levels among age-0 fish, actually increased age-0 growth, in spite of the fact that they directed some aggressive attacks towards, and were dominant over, the age-0 fish. Although this is an interesting finding, its application to wild fish is uncertain (Sloman & Armstrong 2005). With respect to population level

consequences, intercohort effects appear to be substantially smaller than those from intracohort competition. For example, while Imre *et al.* (2005) found that overyearling density had a significant negative effect on age-0 growth, it explained a very small percentage of the variation; substantially less than that due to age-0 density. Overall, compared to our knowledge of intracohort interactions, intercohort competition is quite poorly understood. In essence, the appropriate experiments or the appropriate analyses of long-term datasets have not been attempted. This is particularly evident in the lack of studies looking explicitly at effects of age-0 fish on older juveniles.

7.2.3 Competition among wild and farmed Atlantic salmon

As the numbers and production of farmed Atlantic salmon now vastly outnumber those of wild fish (Gross 1998; Parrish *et al.* 1998), interactions between wild and farmed salmon have been the subject of an increasing body of research (reviewed in Jonsson 1997). A number of studies have highlighted the differences between farmed and wild adult reproductive behaviour and competition (Fleming *et al.* 1996; Einum & Fleming 1997; this topic is also reviewed by Fleming & Einum (2011) [Chapter 2]).

Hatchery and farmed juveniles are behaviourally distinct from wild salmon (Jonsson 1997). In general, farmed and hatchery fish appear to be substantially more aggressive (Holm & Ferno 1986; Einum & Fleming 1997) and less risk averse (Einum and Fleming 1997). They also appear to have higher intrinsic growth rates, which can lead to larger size-at-age (Einum & Fleming 1997). These differences have been observed across a number of salmonid species (Jonsson 1997), suggesting common effects of domestication on behavioural traits that influence competition. Further, these differences appear to be highly heritable and consistent with the vastly different selective environments experienced by wild and hatchery fish (Gross 1998; Ruzzante 1994; Einum & Fleming 1997).

These differences between farmed and wild juveniles may strongly affect competitive interactions. Increased aggressiveness can favour farmed juveniles in pairwise dominance interactions with wild fish. Metcalfe *et al.* (2003) found that hatchery-origin juveniles were dominant over wild-origin juveniles when both groups were raised in common laboratory conditions. However, this advantage disappeared when the fish were tested under conditions more representative of the field. In fact, in terms of the consequences of competition for survival and growth under natural or semi-natural condition, most evidence suggests a substantial advantage of wild fish over farmed fish (Fleming & Einum 1997; McGinnity *et al.* 2003). However, in some cases this advantage, due in part to large numbers of sea-ranched or aquaculture escapees, does not prevent the presence of hatchery-derived fish from lowering the fitness and reducing population growth rates of wild fish, either from introgression of maladapted genes into wild populations, or from competition for space or other resources (McGinnity *et al.* 2003).

7.3 Interspecific competition

7.3.1. Species assemblages in Atlantic salmon rivers

Salmon exist within complex communities of plants and animals, some of which are potential competitors for space and resources. Interspecific competition includes a broad range of

interactions that affect the local habitat of salmon. At a local scale, direct interference competition from fish and other animals within the stream may reduce space and food available. However, exploitative competition may also occur at much larger scales; for example, by invasive species that substantially alter aquatic food webs. Here we focus on interactions between juvenile Atlantic salmon and species that co-occur in rearing streams. Based on similarity of habitat and/or resource requirements, we emphasise fishes, but also consider certain macroinvertebrates and other aquatic vertebrates.

In global comparative terms, the fish assemblages of coastal North Atlantic river systems are species-poor. A number of factors contribute to this lack of diversity. Decreasing vertebrate diversity with increasing latitude is a general biogeographical rule (Hillebrand 2004). In addition, in freshwater habitats, coastal drainage basins in the northern latitudes were unconnected to glacial refugia and have correspondingly lower diversity than large continental basins such as the Mississippi and St Lawrence basins in North America.

Although general species diversity is low, assemblages of co-occurring species exhibit substantial natural variation in space and time across the range occupied by salmon. For example, in some wild salmon rivers of the northern UK and Scandinavia, brown trout *Salmo trutta* (either resident or anadromous) are the only other species commonly co-occurring with salmon in juvenile rearing streams. In contrast, in other river systems, juvenile salmon commonly co-occur with at least five (Ward *et al.* 2008) and as many as 13 other species (Mitchell & Cunjak 2007). Species assemblages have changed over time, and will continue to change substantially in the future. In their initial radiation and diversification at the end of the Pleistocene, anadromous salmonids were likely to have been some of the pioneer colonists as rivers and streams opened up after glacial retreat, and were subsequently joined by later colonists (Milner *et al.* 2008). More recently, faunal change has been more closely associated with anthropogenic causes. These include both extirpations and/or major reductions in abundance, particularly of anadromous species (Saunders *et al.* 2006), as well as widespread introductions of freshwater fish (Rahel 2000), which have influenced the large majority of rivers and streams worldwide. For example, cyprinids such as the European minnow (*Phoxinus phoxinus*), are now widespread through rivers in northern Scotland and Norway (Hesthagen & Sandlund 2004). In the future, global climate change may have a major influence on fish assemblages, as warm- and cool-water species expand into formerly coldwater habitats.

Not just the overall diversity, but the general characteristics of salmon streams are important in setting the context for interspecific competition. Species that co-occur with juvenile salmon comprise a limited taxonomic range, these being most frequently both resident and anadromous forms of other salmonids, as well as cyprinids (frequently demersal species), cottids (bullheads), anguillids (eels) and lampreys. For the most part, species in these low-diversity streams and rivers tend to be very widely distributed, and to be habitat and trophic generalists. For example, these systems generally lack specialised piscivores and herbivores, with most species being highly dependent on aquatic invertebrates as prey. From the perspective of classical ecological theory, the presence of co-occurring generalists with wide fundamental niches sets up the possibility of strong interspecific interactions (Fausch 1998).

Although general patterns of diversity and assemblage structure are useful in setting the context of potential interactions, these patterns are of limited utility. For example, a high degree of niche overlap may be consistent either with a high potential for competition, or evidence that competition is not a significant factor structuring communities. This uncer-

Box 7.5 Additive vs. substitutive designs in the study of competition

Two types of experimental designs may be used to test for competition between species (or age-classes). In experiments using additive designs, the density of one species is manipulated while the other is held constant, resulting in differences in total fish density among treatments as well as the relative density of each species. In experiments using substitutive designs (also known as replacement series), only the relative densities of each species vary across treatments, with total fish density remaining constant.

Both designs have their advantages and disadvantages. In the strictest sense, additive designs cannot directly measure the strength of interspecific competition, or estimate the relative strength of inter- vs. intraspecific competition. This is because it is impossible to distinguish interspecific effects from the influence of changes in total fish density. However, this design effectively represents situations involving species introductions or removals, which are of paramount interest for management and conservation. In contrast, substitutive designs maintain total densities constant across treatments, manipulating only the relative densities of the two competitors. Substitutive designs can provide unbiased estimates of the strength of interspecific competition, but may not effectively represent natural situations. Further, it is often unclear whether to control for total numerical density (number of individuals per unit area) or some other parameter, such as total metabolic demand (based on biomass). Additionally, if interaction strength actually depends on total density, then estimates derived from a single, often arbitrarily assigned total density may not be particularly relevant. Perhaps the most thorough way to assess interspecific competition is by careful consideration of the results of both approaches.

tainty underscores the need for experimental approaches (including natural and unplanned perturbations in some cases).

Fausch (1998) reviewed the state of the science regarding the role of interspecific competition between juvenile Atlantic salmon ecology and co-occurring fish species, focusing on experimental studies where densities of either salmon or potential competitors were directly manipulated. He found that compared to the number of studies on other aspects of juvenile salmon ecology (e.g. intraspecific competition, habitat selection), relatively few studies addressed interspecific competition. Further, all but one of these involved salmonids, and only a small percentage had been replicated and/or conducted at relevant spatial and temporal scales. The studies also tended to use additive rather than substitutive designs (see Box 7.5), limiting their ability to distinguish the strength of intra- vs. interspecific competition. These limitations strongly constrained the ability to support any general conclusions about the nature or significance of interspecific competition for juvenile Atlantic salmon. For example, in models of competing species, the relative strength of intra- compared to interspecific competition is one of the most important determinants of coexistence (Connell 1983). Lack of good estimates therefore strongly constrains our ability to predict when and where species are likely to coexist with juvenile Atlantic salmon. There was some indication that species which were dominant in pairwise tests tended to have either a size advantage or a prior residence advantage, suggesting similar mechanisms of competition for space as observed in intraspecific interactions. This was particularly evident in the interactions between age-0 fish where, under natural emergence regimes, species which emerged earlier and were therefore larger were dominant, but this advantage disappeared when fry were matched for size and age (Fausch 1998).

What have we learned in the last approximately ten years since Fausch's review? In the rest of the chapter we will review more recent studies on interspecific interactions, with particular attention to general patterns and findings.

7.3.2 Competitors other than fish

Aside from fishes, juvenile salmon co-occur with aquatic invertebrates and vertebrates that may compete for some aspects of habitat and prey resources; interactions that were not covered by Fausch (1998). There are essentially no studies on interactions between salmon and large predatory aquatic insects, or between salmon and aquatic salamanders, which are common inhabitants of North American streams and rivers. An exception is the American signal crayfish (*Pacifastacus leniusculus*), which is an invasive species of crustacean invertebrate native to the Pacific Northwestern region of the United States. It has been introduced and is spreading rapidly through river systems in the UK and Scandinavia (Crawford *et al.* 2006). Signal crayfish are potential competitors of juvenile salmon. Their presence may reduce the abundance of invertebrate prey used by juvenile salmon (Crawford *et al.* 2006). Perhaps more importantly, they may compete for refuges within the river substratum that are also the favoured habitat for salmon (Fig. 7.1). The potential competition between the species for such habitat was tested using both substitutive and additive designs (Griffiths *et al.* 2004). Crayfish dominated shelters over salmon in both treatments. Salmon had no effect on shelter use by crayfish. The relevance of these laboratory studies to the situation in the wild can be expected to depend on the local abundance of shelters relative to population densities of salmon and crayfish and has yet to be thoroughly evaluated.

7.3.3 Non-salmonid fishes as competitors

Quantitative studies on the effects of non-salmonid fishes on juvenile Atlantic salmon are rare. Ward *et al.* (2008) examined whether salmon re-introduced into tributaries of the Connecticut (USA) might be influenced by competition from the native fish fauna with which they previously had evolved. They found no evidence of competition, but rather a positive relationship between abundance of non-salmonids, overall ecological productivity and salmon growth. From comparisons among populations inhabiting a small number of streams, it has been suggested that demersal fishes in the family Cottidae (known commonly as sculpins in North America and bullheads in Europe) have a potentially negative influence on populations of salmon (Amundsen & Gabler 2008), although diet studies suggest little competition for food (Gabler *et al.* 2001). It is evident, however, that cottids may be vigorous predators of salmon at early life stages with substantial consequences for population processes (Ward *et al.* 2008; Ward & Hvidsten 2011 [Chapter 8]), making it difficult to attribute negative effects to competitive interactions.

In addition to being affected by non-salmonids, juvenile Atlantic salmon may in turn influence non-salmonid presence and abundance. This may be particularly important in situations where Atlantic salmon are farmed outside their native range and escapees have entered river systems (Volpe *et al.* 2001), or in systems where wild salmon have been eliminated from parts of their historic range and then re-introduced (Gephard & McMenemy 2004). In the only controlled laboratory-based study reviewed by Fausch (1998), Symons (1976) found that juvenile salmon were competitively dominant over four sympatric North American species in habitats that the salmon strongly preferred (open stream, boulder substrate), easily displacing them from these habitats, which were occupied by the non-salmonids when salmon were absent. More recently, in a field survey in Catamaran Brook, eastern Canada, Mitchell & Cunjak (2007) found that sections where salmon were absent due to semiper-

meable obstructions (beaver dams) were more likely to contain non-salmonid species (primarily slimy sculpin), suggesting an influence of salmon on species diversity.

7.3.4 Competition with other salmonid species

The large majority of studies on interspecific competition in Atlantic salmon ecology involve salmonid species. Juvenile salmon co-occur with three salmonid species across their native range: brook charr (*Salvelinus fontinalis*) in North America, brown trout in Europe, and occasionally with Arctic charr (*Salvelinus alpinus*) in the northern part of their distribution on both continents (Klemetsen *et al.* 2003). Brown trout is originally a European species, but has been widely introduced to many parts of the world (Elliott 1994), and become well established in the wild in many Atlantic salmon streams in North America. Rainbow trout (*Onchorhynchus mykiss*), a Pacific-drainage species, has been established in a number of wild anadromous Atlantic salmon rivers in both North America and Europe (Fausch 1998). Native populations of landlocked Atlantic salmon in Lake Ontario (within the Great Lakes region of the USA) have experienced the introduction of three species of Pacific salmonids (Fausch 1998). Pink salmon (*O. gorbuscha*) have been introduced to Russian rivers with native Atlantic salmon in the Kola Peninsula and are now also present in northern Norway (Berg 1977).

There is evidence that brown trout tend to be more aggressive than, and socially dominant to, salmon of similar size (Kalleberg 1958; Harwood *et al.* 2002; Bremset & Heggenes 2001; Heggenes *et al.* 1995; Höjesjö *et al.* 2005). However, in competition for shelter during winter, dominance depended solely on the size and not the species (Orpwood *et al.* 2003). Both intrinsic dominance (which often relates directly to relative size) and prior residence in a patch of streambed are important factors in establishing outcomes of competition between pairs of fish (Harwood *et al.* 2002a, 2003). Furthermore, among other salmonids, early experience of success or failure in competition influences the future dominance status of individuals (Rhodes & Quinn 1998).

Although these behavioural mechanisms may be important features of inter-specific competition between salmon and trout during the establishment of territories by emerging fish in natural systems, direct information in this regard is scarce. Eggs and emergent fry of trout are typically much smaller than those of Atlantic salmon (Fleming 1998) but both brook charr (Fausch 1998) and brown trout hatch earlier in the spring (Jensen & Johnsen 1999). Early hatching is likely to expose trout to a particularly unpredictable and hostile environment early in the year (Armstrong & Nislow 2006). However, it may also permit the early establishment of territory and hence prior residence advantage required to compete effectively against salmon in the early life stages, as well as an early size advantage due to a longer period for growth following emergence. There is evidence that olfactory cues from the presence of brown trout may induce earlier emergence of salmon (Jones *et al.* 2003), tending to support the prediction that early acquisition of territory confers an advantage. In his review, Fausch (1998) found that in a number of studies of pairwise interspecific interactions, size advantage and prior-residence advantage appear to be associated with success. For example, with respect to interactions with Pacific salmonids, the earlier emergence and resultant size advantage allowed coho salmon (*O. kisutch*) to outcompete Atlantic salmon, which was not the case when individuals were size-matched. In contrast, Atlantic salmon generally emerge earlier than steelhead (or resident rainbow trout). As potentially invasive Atlantic salmon escapees from fish farms may enter wild steelhead rivers in northwestern North America

(Volpe *et al.* 2001), and wild Atlantic salmon are currently being reintroduced where valuable introduced steelhead and rainbow trout fisheries have been well established in eastern North America, this issue has attracted some attention. However, given that anadromous Atlantic salmon have never been successfully established outside their native range, and the re-introduction of extirpated populations has had limited success, negative effects of juvenile Atlantic salmon may not be a major concern (Waknitz *et al.* 2003).

Patterns of habitat use with and without co-occurring species may also shed light on the nature and consequences of inter-specific competitive interactions. Atlantic salmon are often strongly associated with riffle habitats in the wild, whereas brown trout, arctic charr and brook charr tend to use slower-flowing areas more extensively (e.g. Heggenes *et al.* 1999; Heggenes & Dokk 2001; Heggenes & Saltveit 2007). Salmon are particularly well adapted to fast-flowing water due to their large pectoral fins, which may be used as hydrofoils to hold station with low expenditure of energy (Arnold *et al.* 1991). However, salmon appear to prefer pool habitat both as fry (Blanchet *et al.* 2006; Holm *et al.* 2001) and parr (Höjesjö *et al.* 2009). Therefore, their extensive use of riffles might be seen as character displacement due to competition with trout ('the ghost of competition past' (Connell 1980)). In contrast, Rodriguez (1995), based on changes in habitat use as a function of population density, suggested that juvenile Atlantic salmon were competitively dominant over brook charr, displacing them from riffles (the preferred habitat for both species based on preferential occupancy) into pool habitat.

Even in situations where the strength and direction of pairwise interactions can be tested, the consequences of these interactions for habitat use and population dynamics can be complex. Höjesjö *et al.* (2009) found that the presence of trout facilitated increased pool use among overyearling salmon even though the dominant trout tended to use the pools themselves. This facilitatory effect was apparently mediated through a reduction in intraspecific competition due to inhibition of dominance behaviour among salmon. Other studies have observed a similar inhibition of dominance among salmon during summer due to brown trout (Harwood *et al.* 2002a) and rainbow trout (Blanchet *et al.* 2006). However, the presence of brown trout in winter forced salmon into shallower habitat (Harwood *et al.* 2002b). Salmon can feed in the presence of trout by switching to a 'sneaky feeding' strategy of cryptic coloration and short localised bursts (Harwood *et al.* 2002b; Höjesjö *et al.* 2005). It remains to be determined whether a behavioural facilitation of pool habitat due to the presence of brown trout translates to growth and survival benefits to Atlantic salmon at a population level, since they experienced additional aggression from trout (Höjesjö *et al.* 2009). Similarly, the potential negative effects of exotic brown trout and chinook salmon (*O. tshawytscha*) on Atlantic salmon due to an increase in agonistic interactions has been highlighted (Scott *et al.* 2005). As well as affecting the type of habitat that is used, competition can affect the times of day that it is used. Atlantic salmon appear to be preferentially nocturnal feeders in summer and winter, but extend activity into the day to maintain growth rate (Orpwood *et al.* 2006; Metcalfe *et al.* 1998). Presence of non-native rainbow trout (*Onchorhynchus mykiss*) (Blanchet *et al.* 2006) and sympatric resident brown trout (Harwood *et al.* 2002b) can cause salmon to increase daytime activity, which can maintain growth rate in the presence of the competitor but would be likely to increase mortality risk in natural conditions. In addition, the presence of non-native trout substantially disrupted dominance hierarchies and behavioural strategies of juvenile Atlantic salmon in laboratory and natural settings, resulting in reduced individual growth of salmon (Blanchet *et al.* 2007).

Dominance by sympatric resident brown trout and associated salmon habitat shifts in laboratory studies suggest asymmetrical effects of changes in trout and salmon abundance at larger scales. Kennedy and Strange (1986a, b), using field enclosures, found that the presence of brown trout overyearlings decreased survival and caused habitat shifts in juvenile salmon, while the presence of salmon had minimal effects on trout. These studies, along with earlier correlative observations (Egglishaw & Shackley 1980) supported the view that re-establishing salmon (via stocking or by making previously blocked habitats accessible to spawners) would have minimal impact on resident trout populations. However, these studies had some major limitations. The field experiments were unreplicated, were unable to follow individual growth responses, and did not allow for a response via changes in emigration rates. To date, adequately replicated field experiments examining competition between resident trout and juvenile Atlantic salmon have not been conducted.

Due to the general reliance of stream salmonids on aquatic invertebrates, there is opportunity for prey resource competition between co-occurring species. Atlantic salmon largely feed opportunistically on drifting invertebrates. Larger fish eat larger prey, and there can be selectivity for smaller than the average size available in small salmon and larger than average items in salmon larger than 4.6 cm (Keeley & Grant, 1997). The prey species richness and diversity of prey consumed increases with fish size (Dineen *et al.* 2007). Co-occurring brown trout tend to feed more on surface drift of terrestrial origin than do salmon (e.g. Dineen *et al.* 2007). However, there is extensive overlap in diets between these two species. Interestingly, diets of rainbow trout and Atlantic salmon overlap little in allopatry but extensively in sympatry (Coghlan *et al.* 2007). This study emphasises the need for carefully controlled studies to tease apart competitive effects on diet overlap among other salmonid species pairs. The facilitatory effect on habitat use – generating increased sharing of pools among salmon and brown trout (Höjesjö *et al.* 2009) – would be a mechanism that could increase dietary overlap but this change *per se* would not necessarily have negative effects on biomass of salmon. Competitors might also cause a switch to benthic feeding in salmon if they reduce the density of drifting invertebrates (Nislow *et al.* 1998) by shadow competition (Elliott 2002).

Context-dependent interactions

An increasing emphasis in community ecology is the extent to which species interactions are context-dependent (Ricklefs 2008). For example, competitive dominance may depend on temperature regime, as in a laboratory study by Reeves *et al.* (1987), where juvenile coho salmon which were dominant over redbreasted shiner at cold temperatures, were subordinate at warmer temperatures. Similarly, steelhead were only negatively affected by co-occurring pikeminnow (*Ptychocheilus grandis*) at higher temperatures (Reese & Harvey 2002). For Atlantic salmon, temperature was found to mediate competition between rainbow trout and salmon (Coghlan & Ringler 2005). In this case competitive effects were intense at 15 °C and absent at 25 °C, presumably due to differences between the species in thermal optima and energy budgets. Given that the Atlantic salmon thermal optimum is the highest of any salmonid yet tested (Elliott & Hurley 2003), it is likely that they will compete well with other salmonids at high temperatures with implications for the community response to climate change.

Variation in hydrologic regime provides another important context for interspecific interactions. For example, low flows and associated low rates of drifting invertebrates may

influence competition for prey resources. In northern temperate systems, low summer flows appear to result in an energetic crunch time for drift-feeding salmonids (Nislow *et al.* 2004; Sotiropoulos *et al.* 2006). For Atlantic salmon, competition between trout and salmon might be expected to be most intense when local population densities are elevated during periods of low water. However, brown trout did not exclude salmon from pools under such conditions in the short term (Stradmeyer *et al.* 2008). Pools were dominated by a single despotic individual, which was always a trout when salmon and trout coexisted. For subordinate fish, it made little difference whether the despot was a trout or salmon and hence the effect of interspecific competition was predominantly on the dominant salmon of the group.

Low flows may also create an ecological crunch for prey resources and exacerbate the potential for interspecific competition for prey. In the many northern temperate systems, low flows in the summer create low flux rates of drifting invertebrate prey, particularly in comparison to the spring period. As a consequence, both overyearling salmon and trout have very low growth rates in summer compared to spring. In looking at seasonal changes in diet and stomach fullness, Ojala (2007) found that all three co-occurring salmonids in a small stream in central Massachusetts, northeastern USA, fed largely on aquatic-derived invertebrates that were common in the drift, and that most individuals had full stomachs. In contrast, during the low-flow summer, stomach fullness in all species was low, and species appeared to pursue different feeding strategies. The two resident salmonids switched to terrestrial-derived invertebrates, while salmon diets contained a large proportion of aquatic invertebrates that did not occur in drift samples, suggesting a possible switch to epibenthic feeding in response to low availability of drift, as found by Nislow *et al.* (1998) in response to an experimental reduction of drift, and providing an example of context-dependent character displacement.

7.4 Conclusions

In the ten years since Grant *et al.* (1998) and Fausch (1998) reviewed important aspects of intra- and interspecific competition, respectively, our understanding of the causes and consequences of competition for Atlantic salmon have been addressed by new research.

For intraspecific competition, particularly with respect to intracohort interactions, the idea that competition for food and space among age-0 fish is an important mechanism underlying population dynamics and population regulation has received support from the results of a number of studies combining experimental manipulations, new analytical techniques, and simulation models. These efforts have continued to establish juvenile Atlantic salmon as a model species to study the economics of territoriality and central-place foraging, the causes and consequences of dominance interactions, and the application of self-thinning concepts to mobile animals. At the same time, an understanding of competitive interactions has helped to guide management strategies. Considerably less progress has been made with respect to intercohort interactions, in spite of several studies indicating that their direction and magnitude may have important implications for population dynamics and management. Finally, competition between wild and cultured Atlantic salmon juveniles has been recognised as a major threat to wild populations. Studies of competitive interactions between wild and cultured fish have helped us to understand the basic nature of juvenile competition. These studies have underscored the importance of growth, size and aggression in determining

pairwise contests. At the same time, they have revealed that the consequences of these interactions are highly context-dependent. Traits that confer competitive advantage may increase survival and fitness when food is highly available and predation risk is low, but decrease fitness when conditions are harsh and risky.

In strong contrast, while conservation and management concerns have identified the need to understand interspecific interactions better, there is still a relative lack of studies addressing this issue. At this point, it is still unclear whether the species assemblages of salmon rivers are best thought of as a community of strong interactors, or as a collection of species responding independently to their environment. Those studies that have been conducted suggest that some of the important mechanisms underlying intraspecific interactions (size and prior residence) may also influence competition among co-occurring salmonid species. It also appears that the 'residence' advantage may provide a general rule for interactions between migratory Atlantic salmon and resident salmonids, which appear to outcompete juvenile salmon for habitat and dominate pairwise interactions. However, researchers have yet to take full advantage of the challenges and opportunities provided by the accidental and planned manipulations of species assemblages that have affected a large proportion of Atlantic salmon rivers worldwide. Further, we have yet to understand fully how these interactions depend on changes in overall resource availability and environmental conditions such as streamflow and temperature. The overall challenge for research may be to develop a better integration of the role of competition in the context of ecosystem change. Finally, given the cost and resources involved in studies performed at appropriate spatial and temporal scales, better integration amongst disparate investigations is an increasing priority.

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8

Predation: Compensation and Context Dependence

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Abstract

Atlantic salmon are vulnerable to predators at every stage of their incredible life cycle. To some extent, selective pressure by predators is likely to have played a role in the very development of the salmon life-history. So, is predation currently a strong driver of Atlantic salmon population dynamics? If so, which predators are important and when are they important? We take up these questions here, reviewing the major predators of Atlantic salmon from freshwater rearing streams to the open ocean. Salmon populations display important compensatory mechanisms that can ameliorate impacts of some predators. Further, predator impact on salmon populations varies depending on the habitat and community context of the interaction. However, we identify two general situations when predation is especially likely to suppress salmon recruitment and population growth: (1) predation on older life stages and (2) predation on populations that are already suppressed by other factors. Finally, we identify areas for future research, including the effects of anthropogenic habitat changes on salmon vulnerability to predators and the demographic consequences of predator avoidance behaviour, which will further clarify the impacts of predators on Atlantic salmon populations.

Key words

Predation mortality, predator control, predator swamping, trait-mediated predation risk

8.1 Introduction

From small fish gulping fry in freshwater streams, to birds snatching parr from above and seals waiting in estuaries and the open ocean, Atlantic salmon run a lifelong gauntlet of predation risk. Predators are probably among the key factors driving the evolution of the diverse Atlantic salmon life-histories and behaviours we know today (Box 8.1). But are predators currently an important driver of Atlantic salmon population dynamics? And how important are predation losses for salmon conservation and management? These are

Box 8.1 Predation and evolution

Predators clearly exert strong natural selection on salmon populations. Most clearly for current populations, downstream-migrating salmon smolts face a suite of predators that exert size-biased mortality, preferentially taking small individuals (Rosseland 1978; Dieperink *et al.* 2002). As individual growth rate and body size at migration of salmon are heritable (Garcia de Leaniz *et al.* 2007), such size-biased predation represents potentially strong directional selection for faster growth and larger size. However, evolution of increased growth rates may itself be constrained by predation because fast-growing individuals likely show increased movement and foraging activity (Sundt-Hansen *et al.* 2009) that increase their vulnerability to predators. The complex suite of salmon behavioural responses to predation risk, balancing the current risk of predation with the future survival and fecundity benefits of growth, attests to a long history of predator-driven evolution (Metcalf *et al.* 1987).

But, in a broader sense, was the evolution of the anadromous life-history itself driven by predators? Life-history theory suggests that, for species such as salmon where reproduction is related to body size, the optimal pre-reproductive life-history minimises the ratio of mortality rate to individual growth rate (Werner & Gilliam 1984). For small juvenile salmon that are very vulnerable to predators, this ratio may be minimised in freshwater rearing streams where both predation risk and growth potential are relatively low. However, as individuals grow and become less vulnerable to predators, the minimum ratio may shift to marine habitat with higher predation risk but much higher growth potential (reviewed in Willson 1997). This is a difficult hypothesis to test, but the relationship suggests that shifting predation regimes should alter the optimum size at migration – e.g. reducing predation risk at sea should lead to migration at a smaller size. Therefore, one potential approach to evaluating this hypothesis would be to compare reaction norms for individual size and growth rate at migration to sea across populations that face distinct predator regimes (Hutchings & Jones 1998), but this is a test that remains to be done.

questions with a contentious history in fisheries management, yet there is little data available to assess the impacts of most predators on salmon populations. In reviewing predation on Atlantic salmon we seek to identify the situations when predation is likely to be an important driver of Atlantic salmon population dynamics, and thus a concern for salmon conservation and management.

In the rest of this chapter, we describe the major predators of Atlantic salmon throughout their life cycle, then review basic conceptual models of the magnitude and variation in the effects of predators on prey populations and discuss the potential impacts of predators on salmon populations. We restrict discussion specifically to predators of salmon that immediately kill the individuals they consume and that can consume multiple individuals over a lifetime. Parasites are covered in Harris *et al.* (2011 [Chapter 9]) and Finstad *et al.* (2011 [Chapter 10]). The special case of predation on Atlantic salmon by human fisheries is covered by Hindar *et al.* 2011 [Chapter 12]. Much of the general conceptual framework of predation impacts that we describe can apply to all of these situations.

8.2 Major salmon predators

The life cycle of Atlantic salmon is complex and variable (see comprehensive overview in Thorstad *et al.* 2011 [Chapter 1]). Salmon lay eggs in freshwater streams in autumn, fry hatch over the winter, and then emerge from the spawning gravel in spring (individual mass <0.3 g). Salmon then reside in streams as parr until reaching sufficient size to migrate to sea as smolts (*c.* 10–80 g; usually 2–4 years in streams). Post-smolts migrate through estuaries to the open ocean, where they feed and grow to adult size (*c.* 2–20 kg; usually 1–3 years at sea) before returning to their natal freshwater streams to spawn the next generation. Given



Figure 8.1 Even small, generally innocuous fish like slimy sculpin *Cottus cognatus* are potentially important predators of vulnerable newly hatched Atlantic salmon fry. Photo: D.M. Ward.

their wide range in body size and habitat, Atlantic salmon face an incredible diversity of predators, ranging from <10g sculpin in freshwater streams (Fig. 8.1) to >100kg seals at sea. Here, we briefly review the major predators of Atlantic salmon throughout their life cycle in each of these habitats (Table 8.1).

8.2.1 Eggs

Most fish species in salmon streams (including older Atlantic salmon cohorts), along with predaceous insects, crayfish, and birds, undoubtedly consume Atlantic salmon eggs opportunistically. However, there is little quantitative information available about the magnitude and importance of predation on Atlantic salmon eggs. In considering predation on eggs of Pacific salmon, Moyle (1977) suggested that egg predators have little impact on populations as the eggs most readily available to predators are those that are not successfully buried in the substrate and these are unlikely to survive in any case. Furthermore, strong density-dependent survival of later juvenile stages (Jonsson *et al.* 1998) may compensate for predation losses of eggs, ameliorating impacts of egg predators on recruitment and population growth (see Section 8.3.1).

8.2.2 Fry

Salmon fry are particularly vulnerable to piscivorous fish upon emerging from gravel nests to seek a territory and begin feeding (Brännäs 1995; Table 8.1). While no studies have measured the demographic effects of predation on naturally emerging wild salmon fry, stocking experiments show that predatory fish can consume a substantial proportion of stocked salmon fry (Henderson & Letcher 2003; Ward *et al.* 2008a, b). However, these estimates of predation on stocked fry may overestimate the impacts of predators on wild salmon populations, as hatchery-reared fry are disproportionately vulnerable to predators

Table 8.1 Some of the major documented predators of Atlantic salmon, by habitat and predator type

Habitat/ Predator type	Predator species	Life stages eaten	References
Fresh water	Fish		
	Brook charr, <i>Salvelinus fontinalis</i>	Eggs, fry, parr	(Henderson & Letcher 2003)
	Brown trout, <i>Salmo trutta</i>	Eggs, fry, parr	(Mills 1964; Henderson & Letcher 2003)
	Burbot, <i>Lota lota</i>	Fry, parr, smolts	(Larsson & Larsson 1975; Jones <i>et al.</i> 2003)
	Pike, <i>Esox lucius</i>	Fry, parr, smolts	(Bakshanskiy 1976; Mann 1982; Kekalainen <i>et al.</i> 2008)
	Slimy sculpin, <i>Cottus cognatus</i>	Eggs, fry	(Ward <i>et al.</i> 2008a; Ward <i>et al.</i> 2008b)
	Striped bass, <i>Morone saxatilis</i>	Smolts	(Blackwell & Juanes 1998; Beland <i>et al.</i> 2001)
	Bird		
	Belted kingfisher, <i>Megaceryle alcyon</i>	Parr	(Elson 1962)
	Cormorant, <i>Phalacrocorax carbo</i> , <i>P. auritus</i>	Parr, smolts	(Kennedy & Greer 1988; Koed <i>et al.</i> 2006; Blackwell <i>et al.</i> 1997)
Mammal	Mergansers, <i>Mergus merganser</i> , <i>M. serrator</i>	Parr, smolts	(White 1939; Elson 1962)
	Mink, <i>Mustela vison</i>	Parr, smolts	(Heggenes & Borgstrøm 1988)
	Otter, <i>Lutra lutra</i>	Parr, smolts, adults	(Carss <i>et al.</i> 1990; Kruuk 1993)
Marine	Fish		
	Cod, <i>Gadus morhua</i>	Post-smolts	(Hvidsten & Møkkelgjerd 1987; Hvidsten & Lund 1988; Svenning <i>et al.</i> 2005a)
	Pollack, <i>Pollachius pollachius</i>	Post-smolts	(Thurow 1966)
	Saithe, <i>Pollachius virens</i>	Post-smolts	(Hvidsten & Møkkelgjerd 1987; Jepsen <i>et al.</i> 2006)
	Bird		
	Sea trout, <i>Salmo trutta</i>	Post-smolts	(Hvidsten & Møkkelgjerd 1987)
	Cormorant, <i>Phalacrocorax carbo</i> , <i>P. auritus</i>	Post-smolts	(Dieperink <i>et al.</i> 2002; Koed <i>et al.</i> 2006)
	Gannet, <i>Morus bassanus</i>	Post-smolts	(Montevecchi <i>et al.</i> 2002)
	Merganser, <i>Mergus merganser</i>	Post-smolts	(Kålås <i>et al.</i> 1993; Svenning <i>et al.</i> 2005b)
	Herring gull, <i>Larus argentatus</i>	Post-smolts	(Reitan 1988; Dieperink <i>et al.</i> 2002)
	Shag, <i>Phalacrocorax aristotelis</i>	Post-smolts	(Greenstreet <i>et al.</i> 1993)
	Mammal		
	Grey seal, <i>Halichoerus grypus</i>	Post-smolts, adults	(Jounela <i>et al.</i> 2006; Matejusova <i>et al.</i> 2008)
	Harbour seal, <i>Phoca vitulina</i>	Post-smolts, adults	(Greenstreet <i>et al.</i> 1993; Middlemas <i>et al.</i> 2006)

(Berejikian 1995; Hawkins *et al.* 2008). Numerous studies show that naturally emerging salmon fry alter their emergence time and behaviour in response to predator cues in order to minimise individual predation risk (Jones *et al.* 2003; Hawkins *et al.* 2004; Hawkins *et al.* 2007).

Interestingly, stream-resident trout (*Salmo trutta*) and charr (*Salvelinus fontinalis*) often prey heavily on stocked fry, consuming up to 60% of the population (Henderson & Letcher 2003), yet abundant trout generally do not suppress early survival of Atlantic salmon fry (Raffenberg & Parrish 2003; Ward *et al.* 2008a). In contrast, slimy sculpin (*Cottus cognatus*)

predation on stocked salmon fry can suppress salmon survival, even leading to complete recruitment failure in streams with abundant sculpin (Ward *et al.* 2008a, b). This contrast between the population-level effects of trout and sculpin predation may be driven by different predator feeding modes that generate individual variation in predation risk for salmon: drift-feeding trout may prey on drifting, moribund fry that failed to find a territory (Bujold *et al.* 2004), whereas benthic-feeding sculpin may consume territory-holding fry that otherwise had a higher probability of surviving (see Section 8.3.1).

8.2.3 Parr

Like fry, Atlantic salmon parr are vulnerable to numerous predatory fishes (Table 8.1). In addition, salmon parr are also targeted by terrestrial piscivores in many systems (Table 8.1). Abundant avian and mammalian predators can take a heavy toll on salmon parr recruitment (Elson 1962; Heggenes & Borgström 1988). Given these potential impacts, and the conspicuous nature of terrestrial predators, predator control efforts are sometimes implemented for fish-eating birds and mammals on salmon-rearing streams. Such predator control efforts have had some success (Elson 1962), but removing predators can also be counterproductive (see Section 8.3.6) and predator control efforts are generally very controversial.

Due to the increased size and speed of parr, and the rapid development of effective predator-avoidance behaviours (Metcalf *et al.* 1987), predation rates on salmon parr are likely to be lower than for newly emerged or newly stocked fry (Henderson & Letcher 2003). The primary predator-avoidance behaviour of parr is sheltering, or hiding in substrate crevices or other shelters. While sheltering effectively reduces predation risk, sheltering salmon do not feed. Thus, avoiding predation risk from both predatory fish (Metcalf *et al.* 1987; Vehanen 2003; Hawkins *et al.* 2004) and birds (Gotceitas & Godin 1991; Dionne & Dodson 2002; Blanchet *et al.* 2007) reduces foraging effort of juvenile salmon, with a potential long-term cost in terms of reduced individual growth. Salmon balance this trade-off between hiding and eating in response to other factors, including hunger level and social status (Gotceitas & Godin 1991; Vehanen 2003).

These adaptive behavioural responses of Atlantic salmon parr to increased predation risk may explain some puzzling aspects of parr behaviour. For example, in cold winter conditions salmon parr feed at night when low visibility limits their foraging efficiency (Fraser & Metcalf 1997). This nocturnal foraging may be a response to increased daytime predation risk by visual avian and mammalian predators, which unlike salmon maintain quick response times when winter temperature drops (Fraser *et al.* 1993). As mentioned above, these behavioural-trait responses to predation risk could indirectly affect salmon individual growth and hence life-history expression, but the demographic and population-level effects of these behavioural responses of salmon parr to predators are unknown.

8.2.4 Smolts

Migrating Atlantic salmon smolts face many of the same predators as parr (Table 8.1), but smolts may be more vulnerable to predation than parr. Increasingly mobile, smolts spend less time sheltering than parr and smolts may be more conspicuous to predators as social interaction and increased movement replace the sedentary, territorial behaviour of parr (Hvidsten *et al.* 1995). Furthermore, migrating smolts must pass through dangerous areas

Box 8.2 Context-dependent predation

Most of the salmon predators described in this chapter are native species that have long co-existed with Atlantic salmon populations. Yet, in some cases, there is concern that predation is driving local salmon populations towards extinction. Have the rules of the predator–prey interaction changed in favour of the predators in these situations? It does appear that humans have significantly altered some predator–prey interactions by changing the physical and biological habitat context of predation. In the simplest case, human-caused habitat change and harvest have reduced salmon abundance, which in itself makes salmon disproportionately vulnerable to the effects of some predators (see text; Ward *et al.* 2008b). Further, hatchery-reared salmon are clearly more vulnerable to predators than wild salmon, probably due to undeveloped predator-avoidance behaviours (Ruggles 1980; Hansen 1987; Berejikian 1995; Hawkins *et al.* 2008; Kekalainen *et al.* 2008). However, the effects of humans on interactions between salmon and their predators can be more subtle than a direct reduction in salmon abundance or stocking of vulnerable hatchery-produced fish.

There follow three brief examples of human-caused factors that could exacerbate the effect of predators on salmon populations: 1) One of the major human impacts on salmon habitat is dam construction. Dams directly suppress salmon reproduction by restricting access to upstream breeding habitat. However, dams also slow outmigration of smolts and concentrate salmon at flow-ways and reservoirs (Blackwell *et al.* 1998), increasing feeding opportunities for piscivorous fish and birds (Blackwell *et al.* 1997; Blackwell & Juanes 1998; Koed *et al.* 2006), and potentially exacerbating predator impacts. 2) The impact of predation on salmon during short-term periods of vulnerability, such as smolt migration, may be reduced by the availability of abundant alternative prey (Svenning *et al.* 2005a, b), termed prey buffers. Anadromous river herring, whose spring migration coincides with the smolt run, were once very abundant in some salmon rivers – potentially providing an effective prey buffer. However, habitat change and harvest have caused many herring stocks to decline precipitously (Gephard & McMenemy 2004), leaving fewer alternatives for predators. 3) Even human activities remote from salmon streams may alter the interaction between salmon and predators. For example, when pH drops to even weakly acidic levels, salmon parr fail to respond to the chemical alarm cues produced when conspecifics are attacked by predators (Leduc *et al.* 2004; Olivier *et al.* 2006), potentially increasing predation losses. Furthermore, smolts reared in acidic environments suffer gill damage that increases osmotic stress and potentially interferes with predator avoidance behaviour upon transition to salt water (Rosseland & Kroglund 2011 [Chapter 15]). These examples suggest that, in some cases where predators are the direct source of increased mortality, human-caused habitat change may be at the root of the problem.

that sedentary parr are able to avoid, such as reservoirs or lakes with little shelter and high predator abundance (Mann 1982; Blackwell & Juanes 1998; Koed *et al.* 2006).

Estimates of predator-caused mortality during the smolt run vary widely, but range up to 60% in streams with abundant avian predators (Kennedy & Greer 1988). As with fry, predation rates on hatchery-reared smolts are higher than for wild individuals, potentially explaining their much lower survival rates through migration (Ruggles 1980; Hansen 1987; Kekalainen *et al.* 2008). Further, predation on migrating smolts depends on large-scale habitat factors that determine migration speed and predator access. Whether natural (e.g. lakes, falls) or built (e.g. dams), obstructions that slow migration, concentrate smolts, and increase foraging opportunities for piscivorous birds, likely exacerbate predator impacts on migrating smolts (Box 8.2; Blackwell *et al.* 1998; Koed *et al.* 2006).

8.2.5 Post-smolts in estuaries

Upon entering estuaries, post-smolts face a new suite of marine predators (Table 8.1). Many predators, including cod (*Gadus morhua*) (Fig. 8.2), seabirds, and seals (*Phoca vitulina*) congregate in estuaries with large smolt runs to feed on migrating salmon (Hvidsten &



Figure 8.2 During smolt predation studies, hundreds of predatory cod *Gadus morhua* were caught with lures, and afterwards some of them were hung up to dry. About 5000 specimens of cod were estimated to have been gathered in the estuary of the River Surna during the smolt migration (Hvidsten & Møkkelgjerd 1987). Photo: N.A. Hvidsten.

Møkkelgjerd 1987; Greenstreet *et al.* 1993) and the extent of this aggregative response partly determines predator impact (see Section 8.3.3). Predation on salmon post-smolts is especially intense where no other prey is available. Post-smolt mortality exceeds 20% in some estuaries where salmon are a primary prey (Hvidsten & Møkkelgjerd 1987; Hvidsten & Lund 1988), while Svenning *et al.* (2005a, b) report very little predation on salmon smolts in the Tana River estuary where abundant sandeel (*Ammodytes marinus*) provide an effective prey buffer (Box 8.2). Overall, estimates of predator-caused mortality of post-smolts in estuaries range from negligible (Hvidsten 2000; Nygård 2001; Johnsen 2008) to >40% (Dieperink *et al.* 2002).

Post-smolts are particularly vulnerable to predation during an initial period of acclimation to salt water (c. 48 hrs), when increased osmotic stress reduces predator avoidance behaviour (Järvi 1989; Handeland *et al.* 1996). Juvenile salmon reared in acidic environments suffer gill damage that increases this osmotic stress during the transition to sea water (Monette *et al.* 2008), potentially increasing predator-caused mortality (Box 8.2; Kroglund & Finstad 2003). As smolts progress through the estuary, predation may also be mediated by foraging conditions for the salmon. Numerous studies have linked variation in post-smolt recruitment to variation in sea temperature and other climatic conditions that affect prey availability and energetic costs of salmon (Friedland 1998; Friedland *et al.* 2003; Hvidsten *et al.* 2009). Predation may be an important proximate source of mortality driving these trends, as increased foraging effort by salmon under energetic stress may increase vulnerability to predators.

As in fresh water, hatchery-produced post-smolts are potentially more vulnerable to predators than wild fish (Larsson & Larsson 1975; Ruggles 1980; but see Hvidsten & Lund 1988; Thorstad *et al.* 2007). However, the larger size of hatchery-reared post-smolts may

counteract other characteristics that increase their vulnerability to predators. Stocking agencies can minimise the exposure of post-smolts to predators by stocking fish outside estuarine areas where predators concentrate or under turbid, high-flow conditions (Gunnerød *et al.* 1988; Hvidsten & Hansen 1988). Furthermore, stocking smolts at high density and into large shoals of wild fish can minimise predation risk by swamping estuarine predators (see Section 8.3.2).

8.2.6 Post-smolts at sea

Because predation on salmon in the open ocean is very difficult to detect, the extent of predation on post-smolts beyond estuaries is largely unknown. The few documented cases of predation on Atlantic salmon in the open ocean are from the chance discovery of salmon in the stomach contents of captured marine fish, including sharks (*Lamna cornubica* and *Somniosus microcephalus*), skate (*Raja batis*), cod, and halibut (*Hippoglossus vulgaris*) (Wheeler & Gardner 1974; Mills 1989). Although not explicitly linked to predators, recent studies that follow the fate of tagged salmon in near-coastal areas suggest that early marine mortality is very variable among stocks and potentially high, suggesting this may be an important determinant of low adult return rates (Thorstad *et al.* 2007, Lacroix 2008). Nonetheless, the overall predation rate and factors that drive predation risk in the open ocean remain a mystery.

8.2.7 Adults

Predation on adult Atlantic salmon returning to spawn is particularly conspicuous, as when seals (*Halichoerus grypus* and *Phoca vitulina*) congregate in estuaries when adult salmon return (Middlemas *et al.* 2006) or take salmon directly from fishing nets (Korsen 1983; Henriksen & Moen 1997; Jounela *et al.* 2006). This predation on returning adults generates considerable concern, as adult salmon eaten are direct losses from the river fishery and the spawning population. However, Butler *et al.* (2006) used a model to estimate seal predation impacts and suggested that, due to the functional and numerical responses of seals to salmon abundance (see sections below), seals actually have little effect on the total number of adult returns to the river, except in the smallest salmon populations.

8.3 Conceptual models of predation

The likely effect of predators on Atlantic salmon populations seems obvious: predators remove individuals from the population resulting in a decline in salmon abundance. However, crediting a predator with a given effect on prey recruitment or population growth rate simply based on the number of prey killed is often misleading. In many prey populations, including Atlantic salmon, strong compensating mechanisms can ameliorate the effects of losses to predation. Yet, the mere presence of predators can affect salmon traits or behaviour, potentially reducing survival and growth so that predators could suppress salmon populations without eating any salmon at all. Here, we briefly review simple conceptual models of compensatory mortality, the functional response of predation rate to variation in prey abundance, the response of predator abundance to variation in prey abundance, and the role of

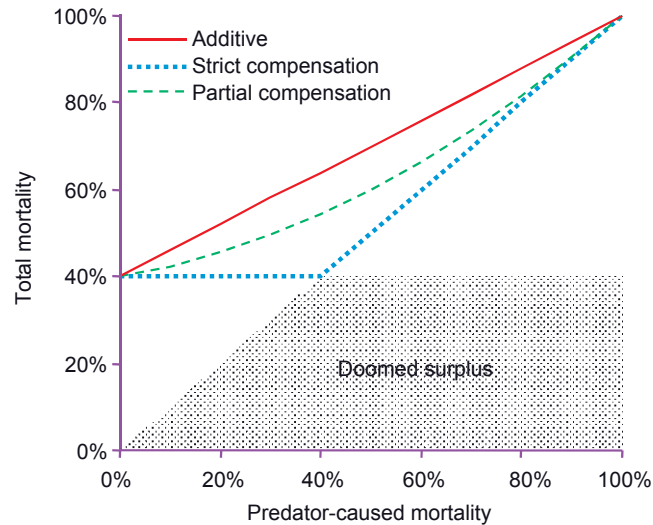


Figure 8.3 Conceptual model of compensatory mortality due to variation among individuals in predation risk, shown by the relationship between total mortality rate and the mortality rate cause by predators. In each case, there is background mortality rate of 40% without predators. Strict compensation occurs when predators only consume those individuals that would have died of other causes ('doomed surplus', indicated by the stippled area), up to the point where they consume all of the doomed individuals. Partial compensation occurs when predators preferentially consume individuals that would have died of other causes, but also take potential survivors.

trait-mediated effects of predators on prey. These are the general processes that determine the impact of predators on salmon recruitment and population dynamics.

8.3.1 Additive and compensatory mortality

Many predators kill salmon, but salmon also suffer some mortality in the absence of predators. The interaction of predation mortality with other sources of mortality is a key determinant of the impact of predators on salmon populations. Consider a cohort of juvenile salmon with two sources of mortality: predation and starvation. Would an increasing predation rate reduce the number of recruiting smolts or just reduce the number of individuals lost to starvation? In the first case, termed additive mortality, the two sources of mortality are independent. In the second case, termed compensatory mortality, increased predator mortality is compensated by reduced mortality from other sources. Thus, compensatory mortality moderates the impacts of predators on prey recruitment and population growth.

Individual variation in predation risk can generate strong compensatory mortality. Predation limited to individuals that are bound to die before recruiting (a 'doomed surplus') has no impact on total mortality rate (strict compensation, Fig. 8.3; Errington 1963). A clear example of this type of compensatory mortality is that noted above for predators of salmon eggs which primarily target unburied eggs that could not survive (Moyle 1977). Such compensation will operate to some extent even if predation is simply biased towards individuals that have a higher risk of mortality due to other causes (partial compensation, Fig. 8.3). For

example, many of the predators described above preferentially take smaller individual salmon (Rosseland 1978; Dieperink *et al.* 2002). This size-biased predation can lead to partial compensation if small individuals also have higher non-predator mortality risk – potentially due to lower energy reserves.

Density-dependent mortality of prey can generate compensatory mortality without individual variation in predation risk. For Atlantic salmon populations, density-dependent mortality is frequently observed and described in terms of curvilinear stock-recruitment relationships between life stages (see overview in Hindar *et al.* 2011 [Chapter 12]); as when the number of smolts recruited from a stream (R) is an asymptotic or dome-shaped function of the stock of eggs deposited (S): $R = f(S)$. If a predator consumes a constant proportion P of the salmon population, then additive predator mortality is modelled as $R = f(S) \cdot (1 - P)$ whereas compensatory mortality is modelled as $R = f(S \cdot (1 - P))$. Conceptually, if predators reduce the density of the prey prior to the action of density-dependent mortality, then mortality is compensatory.

If the stock-recruitment relationship is an asymptotic function, as often observed for juvenile salmon recruitment (Jonsson *et al.* 1998), then compensation by density-dependent mortality can dramatically reduce the predicted effect of predation on salmon recruitment compared to additive mortality (Fig. 8.4). This strong compensatory effect occurs even with identical parameters for the stock-recruitment relationships and the same proportion of the salmon population consumed by predators. Furthermore, although compensatory mortality ameliorates the impacts of predators on recruitment, the number of salmon consumed by predators is much larger when mortality is compensatory (Fig. 8.4). Clearly, then, the impact of predators on recruitment and population growth is not a simple function of the number of individuals consumed.

The strength and form of density-dependent mortality determines the degree of potential compensation for predatory losses. If density dependence is weak, yielding a stock-recruitment relationship close to linear, then compensation will not significantly reduce the effect of predators on recruitment (Fig. 8.5). Such weak density dependence is characteristic of older Atlantic salmon life stages, beyond the first year or two of life (Jonsson *et al.* 1998). If density dependence is very strong, yielding a hump-shaped stock-recruitment relationship, then compensation could actually yield a positive effect of predators on salmon recruitment. This occurs at high salmon population density when the stock density exceeds the level of peak recruitment (Fig. 8.5). However, the likelihood of such hump-shaped stock-recruitment curves for salmon populations remains a subject of some debate (Milner *et al.* 2003).

Compensatory mortality is not the only potential compensatory response of salmon populations to predation losses. For juvenile Atlantic salmon in freshwater rearing streams, individual growth increases due to relaxed intraspecific competition when predators reduce salmon population density (Imre *et al.* 2005; Ward *et al.* 2009). Further, due to size-biased predation towards smaller individuals (Rosseland 1978; Dieperink *et al.* 2002), the mean size of surviving salmon should be larger than average. Therefore, streams where predators reduce juvenile salmon population density should produce generally larger smolts (but see an alternative trait-mediated effect of predators on growth below). Size is a key determinant of salmon fitness, not least because larger smolts are less vulnerable to marine predators (Dieperink *et al.* 2002), so increased mean growth could be an important compensatory response of salmon populations to predation loss.

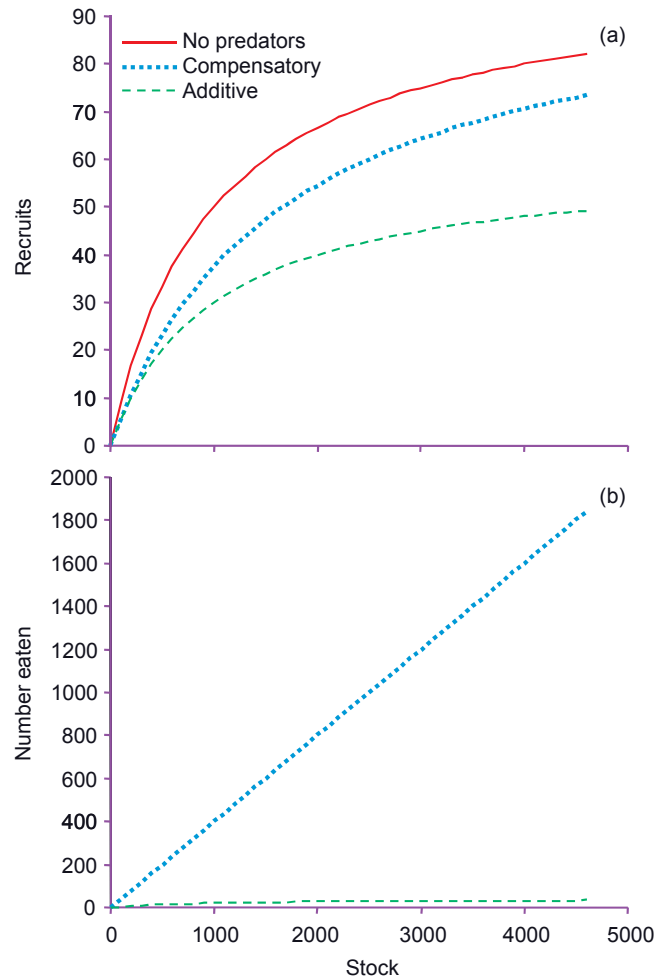


Figure 8.4 (a) Stock-recruitment relationships showing the relative effects of predators with additive and compensatory mortality. The stock-recruitment model is $R = \alpha S / [1 + (S/K)^\beta]$, where R is the number of recruits (e.g. smolts) S is the stock (e.g. egg input), K is threshold abundance (half saturation) and α and β are coefficients (Shepherd 1982). Parameters for the stock-recruitment functions here are $\alpha = 0.1$, $\beta = 1$, $K = 1000$ (from Jonsson *et al.* 1998). In both cases, a constant 40% predator-caused mortality rate was applied to the stock (compensatory mortality) or the recruits (additive mortality). (b) The number of prey consumed by predators in the additive or compensatory mortality models at different stock levels.

8.3.2 Functional response

Functional response relationships define the change in an individual predator's predation rate with increasing prey abundance. A key characteristic of realistic functional response relationships is an upper limit to individual predation rate, determined by the number of prey that a predator has the time and stomach capacity to capture and consume when prey abundance is unlimited (Holling 1959b). Given this upper limit, the proportion of the prey population consumed by a given number of predators declines with increasing prey

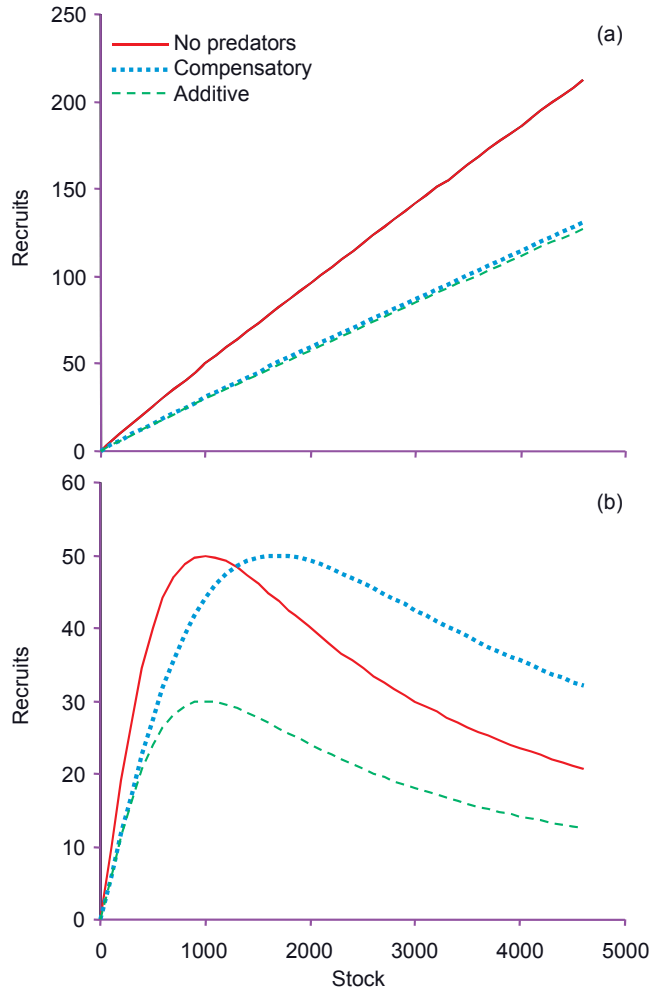


Figure 8.5 (a) Stock-recruitment relationships showing the relative effects of predators with additive and compensatory mortality for weak density dependence (model as for Figure 8.4, parameters are $\alpha = 0.1$, $\beta = 0.1$, $K = 1000$). (b) Relative effects of additive and compensatory mortality for strong density dependence with a dome-shaped stock-recruitment function (b, $\alpha = 0.1$, $\beta = 2$, $K = 1000$). In both cases, a constant 40% predator-caused mortality rate was applied to the stock (compensatory mortality) or the recruits (additive mortality).

abundance because the predators are consuming as many prey as they can (Holling 1959a), a phenomenon called predator swamping. Predator swamping means that, if predator numbers are relatively constant, predation will have little effect on recruitment of very abundant prey (Fig. 8.6).

At low prey density, the proportion of the prey population consumed by predators depends on predator behaviour. If predators are opportunistic and take a particular prey even when it is rare, termed a type II functional response (type I is a constant proportion consumed at all prey densities), then predators will have a disproportionate impact on rare prey populations (Fig. 8.6). If the predators tend to ignore rare prey so predation rate is an

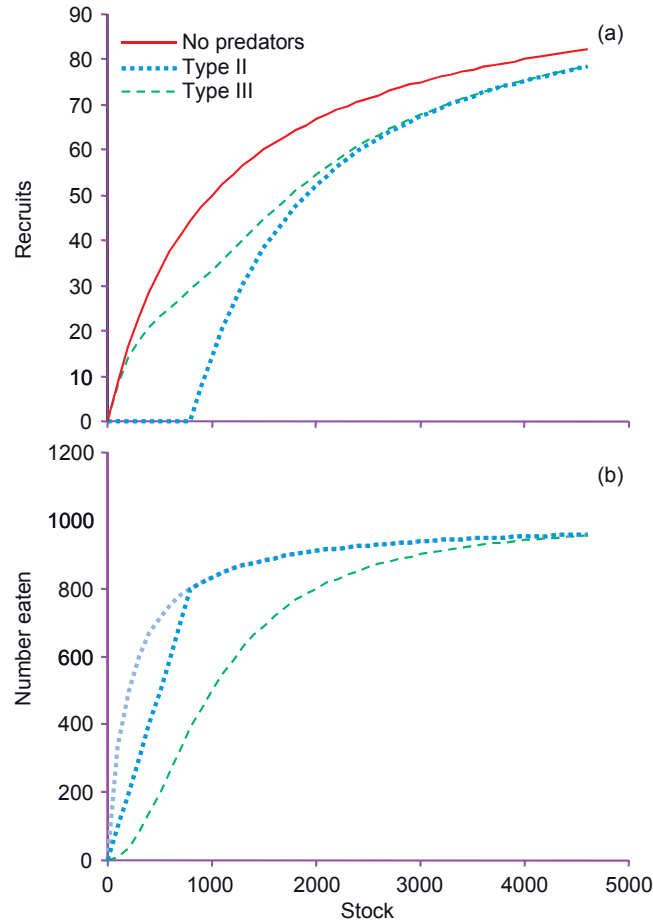


Figure 8.6 (a) Stock-recruitment relationships showing the relative effects of predators with type II or type III functional responses, modelled with compensatory mortality and 100 predators. Stock-recruitment model and parameters as in Fig. 8.4. The type II response model used to determine the number of prey consumed per predator (C), is $C = aS/(1 + aT_h S)$ where S is salmon stock size, a is a coefficient that describes predator efficiency, and T_h is the inverse of the maximum number of prey consumed per predator. The type III response model is $C = aS^2/(1 + aT_h S^2)$, with parameter definitions as for the type II. Parameters for the type II functional response here are $a = 0.05$, $T_h = 0.1$ (over the whole recruitment period); parameters for the type III functional response are $a = 0.01$, $T_h = 0.1$. (b) The total number of prey consumed by all 100 predators. The grey portion of the type II curve indicates where all available prey were consumed.

accelerating function of prey abundance when prey are rare, termed a type III functional response, then predators will have little impact on rare prey populations and a larger impact as population size increases – up to the point where predators are swamped (Fig. 8.6).

Characterising the predator functional response is essential for understanding the impact of predators on salmon population dynamics (Middlemas *et al.* 2006). The disproportionate effect of predators on small prey populations and negligible effect on large prey populations, characteristic of the type II functional response, is inversely density dependent and inherently destabilising (note extinction of small populations in Fig. 8.6). In this case, as

prey abundance declines, the proportion of prey consumed by predators increases, further decreasing prey abundance and driving the population towards extinction. In contrast, the accelerating predation rate of a type III functional response can generate stabilising density-dependent mortality (Murdoch & Oaten 1975; Hixon & Jones 2005). In general, type II functional responses are characteristic of opportunistic generalist predators that are relatively sedentary relative to prey. Type III functional responses are likely when predators specialise on abundant prey species and ignore rare species or when prey compete for limited space in a refuge from predators (Murdoch & Oaten 1975; Hixon & Jones 2005).

So, what are the functional responses of important salmon predators? Synchronous emergence of salmon fry and shoaling behaviour of migrating smolts reduce individual predation risk (Hvidsten & Johnsen 1993; Brännäs 1995), suggesting that high density does lead to predator swamping. This benefit of high population density is somewhat counterintuitive for juvenile salmon, as high population density clearly has a cost in terms of increased competition for resources for juvenile salmon in streams. Nonetheless, Ward *et al.* (2008b) show that increasing the abundance of stocked Atlantic salmon fry to swamp predators can increase the recruitment rate through the first summer, but only when predators are abundant and salmon population densities are very low.

While predator swamping is likely to offer salmon some protection in numbers when populations are large, the functional response of salmon predators at low prey density is more variable. Middlemas *et al.* (2006) show that seals in Scottish estuaries have a type III response to abundance of returning adult salmon, so rare populations may have a respite from predation. In contrast, sculpin in New England streams are likely to have a type II functional response, as they have disproportionately large effects on recruitment of fry mortality when salmon are at low density and can even cause complete recruitment failure (Ward *et al.* 2008b).

8.3.3 Predator abundance

While the functional response defines the predation rate of an individual predator, the total number of salmon consumed depends on the number of predators. Predator abundance can respond to changes in salmon abundance in two important ways: first, predators may respond through space to patches of high salmon abundance by aggregating (Middlemas *et al.* 2006); second, predator populations may respond to increased salmon abundance through time with an increase in predator population growth. Spatial aggregation behaviour of predators can mimic the effects of the predator functional response as described above (Folt & Schulze 1993). Spatially ubiquitous predators exert disproportionate destabilising effects on small populations, analogous to a type II functional response, while dispersed predators that fail to aggregate until salmon are abundant may exert stabilising density-dependent mortality. For example, the rivers Hals and Orkla in Norway produce ~1000 and ~300 000 smolts, respectively (Hvidsten *et al.* 2009); in the Hals estuary, the low-density smolt run encounters few predators, while in the Orkla estuary as many as 5000 cod assemble to feed on the migrating smolts (Hvidsten & Lund 1988).

Predator population responses through time, often called a numerical response, have an inherent lag time. The classic predator-prey population models predict cyclic dynamics: predator populations increase when prey are abundant, predators suppress prey abundance, then predator numbers crash due to lack of prey, prey recover, and the cycle starts over.

Yet, most predators of Atlantic salmon are generalists that consume many prey species, so they may not respond numerically to changes in Atlantic salmon abundance alone. We know little about the population-level numerical response of most predators to changes in Atlantic salmon population abundance. However, in the Connecticut River basin in New England, freshwater predators of juvenile Atlantic salmon remain abundant enough to suppress survival of reintroduced salmon even though salmon have been extinct in the basin for nearly 200 years (Ward *et al.* 2008a). Similarly, cormorant populations in Europe have increased sufficiently to spur predator control efforts to protect Atlantic salmon and other fish despite widespread declines in salmon abundance (Kinderman 2008). Such generalist predators that remain abundant and forage opportunistically on salmon are much more likely to cause extinction than predators that decline in abundance when salmon are rare (Sinclair *et al.* 1998).

8.3.4 Trait-mediated effects

The effects of predators on salmon populations are not limited only to direct mortality or even to the indirect effects of reduced intraspecific competition. Just the risk of predation can induce important changes in prey traits or behaviour (Relyea 2002; Werner & Gilliam 1984; Lima 1998). Juvenile Atlantic salmon have been something of a model system for studies of predator-induced changes in foraging behaviour. As described above for parr, individuals shelter more and forage less under risk of predation (see also Leduc *et al.* 2004; Olivier *et al.* 2006). Similar trade-offs play out during the emergence of newly hatched salmon fry from the gravel, when fry balance the risk of exposure to predators with the need to begin exogenous feeding and obtain a territory (Brännäs 1995; Jones *et al.* 2003), and potentially at other life-history transitions as well (e.g. smolt migration timing and size thresholds). Given strong predator-induced trait shifts, predators can suppress mean growth, survival, and fecundity of prey without actually consuming any prey at all (Werner & Peacor 2003). However, the long-term demographic effects of predator-induced changes in traits and behaviour for Atlantic salmon largely remain an open question.

8.3.5 Implications of predation for salmon populations

From the review above, we highlight two general situations where predators are likely to have strong, negative effects on salmon populations. First, predation on older parr, smolts, and marine life stages is a particular concern. Recruitment of juvenile salmon early in freshwater rearing is often strongly density dependent, whereas recruitment of older life stages and salmon at sea is often density independent (Jonsson *et al.* 1998; Milner *et al.* 2003). Thus, compensatory mortality is more likely for predation early in the juvenile stage, whereas predation mortality for older stages is likely to be more additive, directly reducing recruitment and population growth. This may be a particular problem where human impacts increase the vulnerability of older salmon to predators (Box 8.2).

Second, rare populations face a disproportionate risk of predator impacts. Many of the predators of Atlantic salmon described above are opportunistic generalists whose abundance is not strongly dependent on the salmon population (but see Middlemas *et al.* 2006). Such predators are particularly likely to decimate rare prey populations, greatly increasing extinction risk when population size declines due to other factors (Ward *et al.* 2008). Nonetheless,

while these general guidelines may indicate situations where salmon populations are at particular risk, we emphasise that the effects of predation are inherently context-dependent (Box 8.2; Mather *et al.* 1998) and efforts to conserve salmon populations by managing such predators face enormous challenges.

8.3.6 Predator control

Birds, seals, and other conspicuous predators described here are often the only visible source of natural mortality for salmon populations. Whenever salmon populations decline, which occurs with increasing regularity, there is often suspicion that these predators are eating the population, and fishery, into oblivion. Removing predators to reduce salmon predation losses is one potential technique for protecting these declining populations. A major point of this chapter is that the effects of predators are rarely this straightforward. Furthermore, there is the real possibility that the negative indirect effects of removing predators, mediated through changes in the rest of the food web, will outweigh any benefits of reduced predation on salmon (Yodzis 2001).

Wiese *et al.* (2008) provide a compelling example of the potential for unintended impacts of predator control. They modelled the efficacy of controlling piscivorous bird abundance to reduce predation losses and enhance recovery of endangered Pacific salmon (*Oncorhynchus* spp.) populations. Birds, conspicuously concentrated at dams, consume thousands of out-migrating salmon smolts annually in the Columbia River basin. However, estimates of bird predation losses were less than 1% of available salmon smolts. Furthermore, northern pikeminnow (*Ptychocheilus oregonensis*), a piscivorous fish and alternative prey species for the birds, were predicted to benefit dramatically from bird control. Pikeminnow are salmon predators themselves, and are also the subject of an ongoing predator control effort (in 2008 anglers on the Columbia River could collect a bounty of US\$4–8 for each pikeminnow killed; Pacific States Marine Fisheries Commission 2008). Wiese *et al.* (2008) predict that controlling seabirds would counter the efforts of the pikeminnow control programme and potentially increase overall predator losses for the salmon population. Such indirect interactions may be common in predator control efforts (Yodzis 2001; Harvey & Kareiva 2005; Lessard *et al.* 2005), suggesting that magnitude and even the direction of prey population responses to predator control efforts are very difficult to predict.

Nonetheless, there is at least one case of improved recruitment of Atlantic salmon with predator control. When Elson (1962, 1975) removed piscivorous birds from a 10-mile stretch of the Pollett River in New Brunswick for six years, the proportion of stocked Atlantic fry surviving to smolt age increased 2–4 fold relative to a pre-control year with similar salmon stocking density – suggesting that controlling predators can benefit some salmon populations. More recently, in December 2008, the European Parliament voted to support a pan-European Cormorant Management Plan to protect salmon and other fish stocks from cormorant predation (Kinderman 2008), but the success of this effort remains to be seen.

In practical terms, predator control efforts are often inordinately expensive and may fail to substantially reduce predation losses (Goodrich & Buskirk 1995). For example, Butler *et al.* (2006) show that removing seals from estuaries in Scotland Atlantic salmon would only substantially increase returns when salmon abundance was very low (see Jounela *et al.* 2006 for an alternative case of seal predation on salmon). Furthermore, predation is strongly

context-dependent (Box 8.2) so benefits of predator control are very difficult to predict. Finally, the ethical dilemma presented by killing predators to favour salmon frequently raises public controversy. Therefore, while predator control is potentially necessary to prevent extinction of some severely suppressed populations (Lessard *et al.* 2005), the decision to undertake predator control efforts requires case-specific justification and is as much a societal choice as a scientific one (Brennan & Rodwell 2008).

8.4 Conclusions

Predation plays an important role driving individual behaviour, recruitment and population growth of Atlantic salmon. The impacts of predation on salmon populations are likely to be particularly severe for predators of older life stages and for populations already suppressed by other factors. Yet, even in these cases, predation is one factor among many that can affect salmon populations, and interactions between predation and other factors can yield surprising outcomes. Here, we note cases where changes in the habitat and community context of predation and adaptive shifts in salmon individual traits and behaviour can mediate the effects of predation. These interactions suggest that we need to examine the effects of predators across a broader spatial and temporal scale to understand the role of predation. Across space, the same predator may decimate salmon populations in one context, but be relatively innocuous in another (e.g. Butler *et al.* 2006; Ward *et al.* 2008b). Through time, interactions that affect individual growth early in life may determine vulnerability to predators at later stages – not to mention the longer-term responses of predator and prey population size that we know very little about. Productive future research will integrate our growing knowledge of the extent of predation on Atlantic salmon for individual places and times across these scales to identify the interacting factors, beyond just direct predator-caused mortality, that determine predator impacts.

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9 The Parasites and Pathogens of the Atlantic Salmon: Lessons from *Gyrodactylus salaris*

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Abstract

This chapter reviews the parasite community of Atlantic salmon (Eastern Atlantic and Baltic races) in the various phases of their life cycle; as juvenile fish in fresh water, the maturational marine phase, and the return to fresh water to spawn. The compartmentalisation of the salmon life cycle means that these various phases of the life cycle are infected by entirely different sets of parasites; perhaps a strategy to minimise exposure of each life cycle stage to the pathogens of the previous stage. Although parasites may affect salmon at any stage of their life cycle, the most crucial phases are the early freshwater juveniles, and the subsequent migration to sea as smolts and post-smolts. We know almost nothing about the potential for disease in the latter stage, and research into the fate of parasitised smolts is urgently needed. Within the early freshwater phase, two pathogens are particularly significant. *G. salaris* has been causing epidemic disease in wild Norwegian salmon since the mid-1970s, while PKD, caused by the myxozoan *Tetracapsuloides bryosalmonae*, is an emerging pathogen in wild fish, linked to rising water temperatures brought about by climate change. The complexity of the *G. salaris* problem is discussed from the perspective of the ‘epidemiological triangle’, focusing on the interaction of host genome, parasite genome and environment. The role of the environment in modulating infectious disease interactions is particularly stressed, considering the role of environmental temperature, water chemistry and river substrate type as possible modifiers of the *G. salaris*–salmon interaction. Management of parasitic disease in wild salmon is briefly discussed, in particular the eradication strategy for *G. salaris* using rotenone. We recommend that the best hope for the sustainable management of widespread pathogenic disease in salmon populations is through the use of immunisation strategies and/or selective breeding for resistance.

Key words

Gyrodactylus salaris, PKD, *Tetracapsuloides*, epidemiology, aquatic wildlife disease

9.1 Introduction

Most species on Earth are parasites and almost all vertebrates are assailed throughout their lives by a range of pathogens attempting to obtain from them their energy for metabolism

and reproduction (Poulin 1997; Windsor 1998). Some may cause fatal diseases, whereas others exert only a slight but nevertheless deleterious energetic cost on the host. Parasites and pathogens may be drawn from a variety of taxa; some 200+ are known for wild Atlantic salmon, ranging from very poorly known bacteria and viruses, to some of the more spectacular marine crustaceans which have been known for centuries as markers of freshly sea-run fish.

The precise composition of pathogens and parasites able to infect Atlantic salmon varies depending on a range of environmental conditions, because in almost every case, transmission between fish depends on the parasite experiencing a phase free living in the external (macro-)environment. Not surprisingly, therefore, marine salmon experience a different parasite challenge to those in the freshwater phase, and alevins, fry, parr, precocious males and smolt experience a different subset of parasites to adult fish after their return to fresh water. Equally, the fish themselves represent a different (micro-)environment for parasites at the different stages of their lives. Salmon show considerable fidelity to their natal river, and the low migration between river systems may lead to specific genetically differentiated stocks (King *et al.* 2001; Verspoor *et al.* 2005). This may predispose this fish and its parasites for local adaptation, a term coined for the phenomenon whereby a local parasite strain becomes optimally adapted for the most frequently encountered local host genotype. Adult fish, after their return to fresh water, are relatively immuno-compromised (Slater & Schreck 1993; Maule *et al.* 1996), and this may allow a different set of freshwater pathogens to colonise them than would be the case for pre-smolt stages. Alevins in particular have an immature immune system, and must therefore experience a different set of parasitic challenges to parr in the same environment at the same time. Finally there are smolts, which experience massive changes to physiology and structure to prepare them for marine living. These certainly experience a very different challenge from parasitic organisms than do either parr or fully adapted marine salmon.

In this chapter we set out to describe the ecology of the parasite faunas of Atlantic salmon, both in the freshwater and marine phases. For the non-specialist, an account of the potential importance of pathogens and parasites for vertebrate hosts is presented in Box 9.1. We have reviewed this topic previously, and so this chapter does not intend to provide exhaustive species lists for salmon pathogens. The interested reader is referred to Bakke & Harris (1998) for this level of detail. Here instead we concentrate on the local adaptation of Atlantic salmon to their parasite faunas, and the extent to which freshwater salmon populations are

Box 9.1 The ecological role of parasites

What is the role of parasites and pathogens in the natural ecology of organisms such as the Atlantic salmon? The individual consequences of parasitism may be spectacular (as in the case of some fish lice, larger tapeworms, or 'red vent disease' due to *Anisakis*). The big question, however, is whether parasites can regulate or influence the population dynamics of their vertebrate hosts, and then whether they can have a selective role in the evolutionary trajectory of their hosts. The answer to both questions is a qualified 'yes', but evidence of selective or regulatory effects in specific cases is difficult to find. Theoretically all parasites can influence host population biology. The distinction (Anderson & May 1979) between microparasites (which reproduce *in situ* upon the host, have a short generation time and low individual biomass) and macroparasites (reproduction obligately linked to transmission, generation time long, often with complex life cycles, individual biomass rela-

tively large) is a useful one. Microparasites can destabilise host-parasite population dynamics, and often exert significant pathogenic effects (Anderson & May 1979). Macroparasites, on the other hand, theoretically have more stable population behaviour. However, work on parasites of terrestrial vertebrates suggests that macroparasites may also exert significant impacts upon their host populations. For example, Scott (1987) demonstrated that the nematode *Heligmosomoides bakeri* can influence the total size of free-ranging laboratory mouse populations, while a range of nematode macroparasites exert significant effects upon the fecundity or survival of their terrestrial vertebrate hosts (Tompkins & Begon 1999). Examples from aquatic vertebrates are much harder to find, because experimental interventions with a wild fish such as the Atlantic salmon are difficult to design. However, the inadvertent 'experiment' with salmon lice (Finstad *et al.* 2011 [Chapter 10]) is strongly suggestive of the role of macroparasites in limiting population size. The accidental introduction of *Gyrodactylus salaris*, in this case a microparasite (it gives birth to live young directly on the host), to Norway also clearly demonstrates the potential of parasites to limit salmon populations (Bakke *et al.* 2007). Atlantic salmon has an ecological strategy which seems selected to reduce the impact of infectious disease. Breeding in fresh water, but feeding largely in the sea, separates the vulnerable younger stages from adult fish which may act as a reservoir of infectious stages. In the case of both *G. salaris* and salmon lice, it is precisely these vulnerable stages, parr and sea-running smolts respectively, which are most susceptible to infection.

Both *G. salaris* and salmon lice have dramatic effects on host survival. What is less well explored, and may be an issue, is the role of disease in causing sub-lethal effects on fish biology. Disease ecology is tightly linked with host population biology, to the point where observed density-dependent effects may or may not be disease-mediated. For example, critical factors in the life-history of salmon, such as the age at smolting, have a density-dependent component with the need to achieve a critical body mass before smolting. Impacts of diseases which reduce host growth rates (e.g. *Gyrodactylus*; see Bakke *et al.* 2007) are not clear, but may be significant. Similarly, the effects of parasitism may synergise with, and exacerbate, dominance hierarchies during the parr stage, as fish which are genetically susceptible to particular pathogens may be unable to secure favourable feeding territories, and consequently their growth and survival may be impaired indirectly by parasite infection. Impacts such as this can perhaps lead to modified life history strategies as a result of selection at particular stages of the life cycle.

It is normally assumed that parasites evolve to reduced virulence, because by prolonging host survival they maximise their own reproductive output and transmission. In fact, this is not necessarily always true. Where transmission does not depend critically on the lifetime of the infectious host (as may be the case when parasites are highly mobile, or in the case of vector transmission), then there is little selective pressure for reduced virulence in the parasite. In a managed fishery such as that of Atlantic salmon, restocking must be approached with caution, because it may simply offer more naïve hosts to the pathogen responsible, rather than allowing an epidemic to run its course. This may lead to increased pathogenicity, because parasites then become adapted to an ecological regime in which naïve hosts are always available.

Vertebrates possess sophisticated immunological defence mechanisms with which to reduce or eliminate infections. For parasite communities the consequences of immunity are complex, and poorly understood. Most fish for example, develop immunity to gyrodactylid monogeneans. However, this immunity is not sterile, and immune individuals continue to support viable, reproducing populations of gyrodactylids. We know from terrestrial vertebrates that immunity to one parasite can impact upon other parasites, but the only detailed study for salmon (Kjøglum *et al.* 2008) failed to find correlations between resistance for three important microbial pathogens. Selection for resistance to particular pathogens in natural salmon populations does now appear to have been demonstrated (Dionne *et al.* 2009), albeit to an introduced pathogen. For a fish such as salmon, with natal fidelity, one might predict that individual stocks evolve immune responses optimal for the parasite fauna to which they are exposed, and that this would differ from river to river. Indeed, it is possible that parasites represent a major force in shaping local microevolution of salmon stocks.

susceptible to particular pathogens. We focus much more on the interaction between host genome, parasite genome and environment, which shapes any particular interaction. In particular we pay attention to the recent epidemic of the monogenean flatworm *Gyrodactylus salaris* in Norway that has received enormous public attention due to the economic and ecological implications for the countries involved (Bakke *et al.* 2007). Scientifically, *G. salaris* may offer insights into the processes of parasite speciation in real

time (Bakke *et al.* 2007; Hansen *et al.* 2007b), and from a parasitologist's perspective is equivalent in interest to, for example, the adaptation of the tephritid fly *Rhagoletis pomonella* to apple trees in the United States during the twentieth century.

9.2 The parasite community of Atlantic salmon

Atlantic salmon are exposed to a range of pathogens from the time of hatching until their death. However, the unique compartmentalisation of the salmon life cycle into freshwater, marine and then freshwater phases limits the range of pathogens which can afflict them (Table 9.1). This compartmentalisation has hampered our efforts to study the parasite fauna of Atlantic salmon; although the parasites of sea-run salmon have been known for centuries, and indeed have been regarded as markers of a 'fresh' newly returned adult, the pathogens of the initial freshwater phase are much less well known, and the diseases which particularly afflict smolts during smoltification and migration, and later, marine-phase salmon on their feeding grounds, are hardly explored (De Clers 1993). Much of our knowledge of infectious agents in marine salmon comes from studies of the pathogens of farmed salmon (Bakke & Harris 1998), and a few studies of wild salmon (e.g. Bristow & Berland 1991a, b; Bristow *et al.* 1996; Ieshko *et al.* 2008), and it is difficult to assess the significance of these infectious agents in natural populations of salmon (Bakke & Harris 1998). For example, the lethal viral infection Infectious Salmon Anaemia (ISA) is known primarily from farmed salmon (Raynard *et al.* 2001; Lyngstad *et al.* 2008). Is this because wild fish carrying this infection rapidly die and cannot be sampled, or is it because the disease is sufficiently virulent that transmission in the natural environment is very limited, and therefore the virus remains temporally or spatially rare? Although the epidemiology of salmon diseases has a history of over 100 years, in many ways it remains in its infancy, and we lack the basic data and tools necessary to begin to answer questions such as these (Bakke & Harris 1998).

A number of factors make the study of wild salmon parasite epidemiology difficult. In the first place, there has been a close intertwining of wild and managed salmon populations and farmed salmonids for over 100 years. Historically, an epidemic of furunculosis (caused by the bacterium *Aeromonas salmonicida*, first described in Europe by Emmerich & Weibel 1894) kick-started research into wild salmonid epidemiology in 1911, with the establishment of a Board of Investigation to investigate the outbreak of the disease (Masterman & Arkwright 1911). Quite surprisingly, roughly a century later we are still not clear about the causes of this epidemic, or the relationship between the epidemic in wild salmon and human-mediated movements of cultured salmonids, nor do we have a clear picture of the epidemiological relationships between wild and cultured salmonids. Escapes of cultured salmonids remain embarrassingly frequent, allowing intermingling (and interbreeding) of these fish and their pathogens with locally adapted wild stocks (Hansen & Bakke, 1989). Furthermore, in many river systems, smolts must migrate to sea past open sea-culture pens containing large numbers of salmon with their own parasite fauna (Bakke & Harris, 1998). The risks that such cultured fish pose to wild smolt at this critical stage in the salmon life cycle, apart from sea lice (Finstad *et al.* 2011, [Chapter 10]) remain entirely un-assessed.

The other factor making the study of wild salmon parasite epidemiology difficult has been the widespread extirpation of salmon stocks throughout the northeast Atlantic and Baltic

Table 9.1 Life histories of some representative salmon parasites in relation to the life cycle of the host

	Early freshwater stages (alevin, fry and parr)	Smolts running to sea	Marine feeding stages	Returning adults and kelts
Viruses			Infectious salmon anaemia an issue in farmed fish – a problem for wild as well?	
Bacteria	<i>Aeromonas</i> can infect early FW stages, impact unknown		<i>Aeromonas</i> of different strains? An issue for wild fish?	Epidemics of <i>Aeromonas</i> in adults – complex epidemiology, originating in fresh water?
Fungi	<i>Saprolegnia</i> infects weakened fish, especially in disease syndrome with <i>G. salaris</i>			<i>Saprolegnia</i> acquired on return to fresh water, infects weakened fish or wounds
Myxosporidia	<i>Tetracapsuloides bryosalmonae</i> accumulates but cannot develop further; pathology above 12 °C (Sterud <i>et al.</i> 2007)	→ May cause pathology in sea-running smolts, but unlikely to remain a threat in marine feeding stages	<i>Parvicapsula</i> in marine farms (Sterud <i>et al.</i> 2003) – an issue for wild fish?	→ ?
Monogenea	<i>Gyrodactylus salaris</i> infections acquired (Bakke <i>et al.</i> 2007)	→ Killed by exposure to sea water (Soleng & Bakke 1997)	<i>Gyrodactyloides bychowskyi</i> acquired in sea	→ Lost on return to fresh water
Cestoda	<i>Eubothrium crassum</i> freshwater race, mature in parr	→ Mature in smolts, release eggs in fw	→ Die in marine environment	
Nematoda			<i>Eubothrium crassum</i> marine race acquired in sea (Kennedy 1978) <i>Anisakis</i> larvae acquired during feeding at sea (Smith & Wootten 1978) continue to accumulate throughout feeding phase.	→ Persist in adults in freshwater, but eggs die → Accumulated <i>Anisakis</i> visible – ‘red vent disease’ (Beck <i>et al.</i> 2008)
Crustacea		<i>Lepeophthirius salmonis</i> , <i>Caligus elongatus</i> , begin to be accumulated on passage to open sea	→ Continue to be accumulated in open sea?	→ Eventually lost in fresh water

regions. Human activity, including the increase in aquaculture, dam and weir construction, and degradation of freshwater habitats, have all reduced and fragmented salmonid populations (Einum *et al.* 2008). Due to local extinctions following pollution and river improvement during the nineteenth and twentieth centuries, it is impossible to get a full picture of the natural parasite community affecting the Atlantic salmon in Europe. The fish was lost from many lowland river systems (e.g. those bordering the North Sea) in the nineteenth century, and the remaining salmon rivers tend to be in uplands, where parasitology is expected to be simplified (Wiśniewski 1958; Chubb 1964). Indeed, it is only through reintroduction schemes, as in the Elbe River in Germany and the Czech Republic, that we can gain an idea of the parasite fauna of salmon in more eutrophic habitats (Moravec 2003).

9.2.1 The parasite community of freshwater immature stages

Salmon show high fidelity to their natal stream, although this is not absolute. Furthermore, most of the marine pathogens with which adult fish are infected are unable to breed after the return of their hosts to fresh water. As a result, it is difficult for parasites to spread between river systems and parasite communities of juvenile salmon are highly spatially compartmentalised. Local selection of pathogens might be expected in these circumstances, with pathogens in particular watersheds being optimally selected for their sympatric host race. Human-mediated transfer of pathogens at this particular stage of the life cycle can have serious consequences, as demonstrated by the Norwegian *G. salaris* epidemic (Fig. 9.1).

Knowledge of the range of pathogens and parasites infecting juvenile (pre-smolt) salmon in fresh water is relatively restricted (Larsen & Lund 1997; Thoen *et al.* 1998), partly because there are so few studies based on lowland, eutrophic rivers. The study by Moravec (2003) is interesting in this regard, showing the colonisation of parr by parasites after reintroduction into the Elbe River system. Parr were soon infected with a range of ectoparasites, digenean metacercariae, and adult intestinal helminths, most shared with brown trout. Most interestingly, *Gyrodactylus truttae* was also found to have infected Atlantic salmon from brown trout (Moravec 2003). In upland rivers in Scandinavia, the sharing of parasites with brown trout has also been noted and *Gyrodactylus derjavini* (= *G. derjavinoides*; Malmberg *et al.* 2007), a trout parasite, can infect salmon at a relatively high prevalence in the River Sandvikselva (Mo 1997), which lacks the pathogenic *G. salaris*. This parasite also infects salmon at low intensities in several rivers where *G. salaris* is present, potentially muddling estimates of the abundance of the latter. Experimentally this parasite seems unable to persist on salmon (e.g. Bakke *et al.* 1999), and there is no reason to believe these infections in nature are anything other than transient. Zięta *et al.* (2008) similarly recorded many casual gyrodactylid infections of salmon, by species normally found infecting sticklebacks or minnows. In other fish, juvenile stages are infected by a community of ectoparasitic or ectocommensal protists including the peritrich ciliates *Trichodina* and *Apiosoma*, some of which may be epizootic; Khan (1991) for example recorded *Trichodina* in association with dying salmon kelts in Canada. These organisms might be more abundant and species-rich on parr in mesotrophic river systems, as, although some peritrichs are primarily fish pathogens (Huh *et al.* 2005), they also utilise waterborne bacteria as a food source. There is an important need for further studies of this ectoparasite community of salmon alevins, fry and parr.

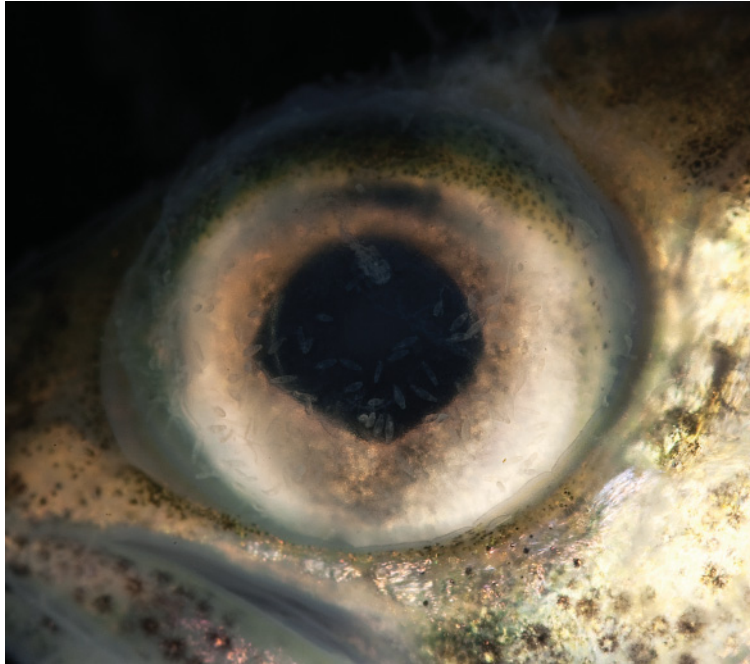


Figure 9.1 Flukes before the eyes. The head of salmon parr, heavily infected with *Gyrodactylus salaris*. Such a fish may sustain an infection of several hundred to thousands of these parasites, which will cover all the fins and much of the body surface, before dying. Photo: Karsten Sundt, Natural History Museum, Oslo.

There are other organisms recorded from aquaculture which might prove a problem in wild salmon populations but have not been found in them, probably because they have never been sought. Thus the flagellate *Spironucleus salmonicida* was described after it was found to cause losses in pen-reared salmon (Sterud *et al.* 1998; Jørgensen & Sterud 2006). The problem of the intertwining of the management of exploited salmon stocks, salmon farming, and the conservation of salmon as a species, is nicely illustrated by consideration of the intranuclear microsporidian parasite *Nucleospora salmonis*, described nearly 20 years ago by Chilmonczyk *et al.* (1991). Although it causes disease in fish farms, it is harder to say whether it is important in wild salmonid populations. El Alaoui *et al.* (2006) surveyed salmonids from the French Auvergne region, an area remote from intensive farming, where one might expect isolates of *Nucleospora* to represent forms naturally occurring in the salmonid population. Although the isolates were genetically distinct from those more commonly associated with farming, they were almost all collected from moribund fishes in hatcheries! Thus the identification of truly indigenous parasite strains, given the mixing of salmonids in cultivation, in management and in the wild, is likely to be very difficult in Europe.

An enigmatic group of pathogens which might be important in natural salmon populations, but about which little is known, are the myxozoans, plasmodial organisms infecting the internal organs of fish. The most important causes Proliferative Kidney Disease (PKD) in salmonids. When our previous review was published (Bakke & Harris 1998), the identity of the causative organism was unknown, and was referred to as 'PKX', thought to be close



Figure 9.2 *Plumatella fructicosa*, one of many freshwater bryozoans able to host the myxozoan *Tetracapsuloides bryosalmonae*, responsible for PKD in salmon. The round brown statoblasts visible within the colony are responsible for long-distance dispersal of the bryozoan (e.g. with waterfowl), and possibly also of *T. bryosalmonae* (Henderson & Okamura 2004). Photo: Karsten Sundt, Natural History Museum, Oslo.

to, but not identical with, a species of the genus *Sphaerospora* (Kent *et al.* 1998). Subsequently Canning *et al.* (2000) identified the PKX organism as a representative of a new group, the class Malacosporea, within the Myxozoa, naming it *Tetracapsuloides bryosalmonae* to reflect its two-host life cycle, alternating between salmonids and freshwater bryozoans (Fig. 9.2). The pathogen was subsequently found to be closely related to *Buddenbrockia plumatellae*, originally described in Europe in 1910, although *T. bryosalmonae* itself is thought to have originated in North America and subsequently colonised Europe, probably via natural means (Henderson & Okamura 2004). *T. bryosalmonae* has been held responsible for an epidemic of PKD in salmon parr in the River Åelva in central Norway (Sterud *et al.* 2007). The potential of this organism as an emerging pathogen of wild salmon is worrying, and is discussed in more detail in Section 9.3 below.

9.2.2 The parasite community of salmon in the sea

Salmon within the marine phase represent the least studied part of the life cycle from a parasitological perspective. A certain amount is known about large adult salmon, during their return migration, especially after they enter coastal waters and estuary mouths (Bristow & Berland 1991b; Bristow *et al.* 1996). However, virtually nothing is known about the parasitology of young salmon running to sea immediately after smoltification. Even for adult fish from the open sea, our knowledge of the parasite fauna is little more than species lists (see e.g. Bakke & Harris 1998). Most freshwater parasites which infect parr and survive smoltification are lost shortly after entry into the sea. For example, *Gyrodactylus salaris*

cannot survive the salinity of the open sea (Soleng & Bakke 1997; Soleng *et al.* 1998) although it may reproduce and transmit in estuaries up to 7.5‰ salinity. Instead marine phase salmon may be infected by the marine gyrodactylid, *Gyrodactyloides bychowskii*. Most of our knowledge of this parasite, originally described from wild fish (Albova 1948; Pålsson & Beverly Burton 1983), comes from net pen culture (Mo & Mackenzie 1991; Bruno *et al.* 2001). It is not clear how, or when, wild salmon first acquire this infection, as its presence infers close contact with other previously infected salmon (Bakke *et al.* 1992). The significance of other marine pathogens of salmon and other salmonids is well known; in particular the copepod sea lice *Lepeophtheirus salmonis* and *Caligus elongatus* are the subject of a separate chapter in this book (Finstad *et al.* 2011, [Chapter 10]). Again, the epidemiology of these organisms in relation to wild salmon in the open sea, in the absence of net pen culture is poorly understood. Before net pen culture began, both caligid and salmincolid copepods were well known (e.g. Kabata 1979), but they were not considered to have any specific pathological or epidemiological significance.

The smolt stage of Atlantic salmon is particularly poorly understood from a disease perspective, and yet this life cycle stage is peculiarly vulnerable to infectious diseases. In Norway, for example, post-smolts contain a range of internal parasites, some acquired from fresh water, such as *Crepidostomum* spp., and others which infect them during the marine phase (Knudsen *et al.* 2005). Presumably, the marine parasites eventually replace the freshwater forms entirely, but the impact of freshwater parasites such as *G. salaris* on the estuarine survival of smolts is unstudied. The question of smolts acquiring infections during their run through estuaries containing sea pen cultures has been highlighted previously (Bakke & Harris 1998), and remains an emotive issue (Butler & Watt 2003; Finstad *et al.* 2011 [Chapter 10]). In particular, the issue of smolts and post-smolts, possibly compromised by exposure to acid conditions or aluminum ions in freshwater (Kroglund & Finstad 2003; Kroglund *et al.* 2007), succumbing to sea lice during their migration into the sea has attracted considerable attention (Finstad *et al.* 2007). A particular concern has to be the potential of *Tetracapsuloides bryosalmonae* infections, acquired in fresh water, to trigger PKD when smolts reach the sea, a risk factor not yet recognised for Atlantic salmon, but identified in chinook salmon smolts in California (Foott *et al.* 2007). Other myxosporidians may be significant in the marine phase, as the genus *Parvicapsula* is associated with mortalities ranging from low-grade to significant in farmed Atlantic salmon (Sterud *et al.* 2003; Nylund *et al.* 2005), and may be epidemiologically relevant in other salmonids, such as *Ceratomyxa shasta*. In general, the impact of smolt infections on survival to maturity is a topic which would repay further investigation.

9.2.3 The parasite community in adult fish returning to fresh water

Adult salmon often bear characteristic ectoparasitic crustaceans: marine parasites which are unable to complete their life cycle in fresh water, and will usually die while the host is in the river system (Mo & Heuch 1998). The more specialised *Salmincola* species may also be present (see Kabata 1979 for a full description of these species), but these euryhaline forms are not killed by fresh water. The large tapeworm *Eubothrium crassum* is naturally acquired at sea (e.g. Kennedy 1978), and has been recorded as pathogenic in marine pen culture (Bristow & Berland 1991a). However, in larger wild fish this tapeworm is not known to have any significant impact on fish survival or health. Marine nematodes such as *Anisakis*

spp. may be present, and may indicate the feeding grounds of the adult salmon. *Anisakis* is contracted during the pelagic phase, and the longer the fish spends at sea, the greater are its burdens (Smith & Wootten 1978). The recent description of 'red vent disease', caused by *Anisakis simplex*, in adult salmon within coastal waters (Beck *et al.* 2008) may indicate an emerging problem with this nematode, possibly linked to increasing whale populations in the North Atlantic. *Anisakis* larvae are highly pathogenic to humans if uncooked or unfrozen salmon flesh containing larvae is eaten. Perhaps the biggest enigma concerning the epidemiology of wild adult salmon remains the UDN (Ulcerative Dermal Necrosis) epidemic of the 1960s. Despite many years' study, a single pathogen causing UDN could not be identified, and today it is regarded as a complex disease syndrome of adult salmon, which, weakened and perhaps immuno-suppressed during freshwater migration or spawning (Murphy 1981), became susceptible to a range of pathogens including the oomycete fungus *Saprolegnia parasitica*. This opportunistic fungus quickly kills infected fish (van West 2006), and is observed to be an important component of the disease syndrome with *G. salaris* (see below).

9.3 *G. salaris* and the epidemiological triangle

9.3.1 *G. salaris*: 'The Russian doll killer'

The most important pathogen of natural salmon parr populations in fresh water has turned out to be the monogenean flatworm *Gyrodactylus salaris* (Fig. 9.1). This species has largely rewritten paradigms of wild disease epidemiology, and therefore demands detailed coverage. The epidemic of *G. salaris* in Norway and along the Russian White Sea coast threatens the continued existence of the infected East Atlantic salmon stocks of *Salmo salar*. Not only does it have the potential to greatly reduce the number of salmon returning to existing rivers, with associated economic costs from loss of fishing and tourism revenues, it also threatens the reintroduction of salmon to parts of their range (such as the North Sea Basin and the rivers of Central Europe) from which they have been lost. Almost uniquely, it is a metazoan threat to the integrity of a wild vertebrate species, although it requires epidemiological expertise more appropriate to controlling bacteria and viruses. Finally, and most interestingly, *G. salaris* may turn out to be a newly emerged pathogen, resulting from a host shift of a strain of parasites from grayling (*Thymallus thymallus*) in the recent post-glacial past.

G. salaris was not a significant pathogen of wild fishes until the mid-1970s when severe gyrodactylosis was reported in Norway (Johnsen 1978; Johnsen *et al.* 1999). Since then, the parasite has been found in 46 wild Atlantic salmon and several Arctic charr (*Salvelinus alpinus*) populations in Norway, and it has been recorded additionally from 40 hatcheries and farms cultivating both rainbow trout (*Oncorhynchus mykiss*) and Atlantic salmon (Bakke *et al.* 2007). All previously infected hatcheries and farms in Norway were, at the time of writing (September 2009), parasite-free, as were 15 previously infected rivers, while a further 11 rivers are awaiting a decision on their parasite-free status and 20 rivers remain infected. The parasite was introduced (1992) into the River Keret in Russia, where it has also caused significant problems (Kuusela *et al.* 2009). Given this history of dissemination in Norway and Russia during the last 35 years, along with the dramatic economic and ecological consequences associated with it (Bakke *et al.* 2007), it is not surprising that *G.*

salaris has been a notifiable pathogen since 1983, and that it is of great concern within Europe. However, in most European states the primary host of *G. salaris* is rainbow trout, and human activities related to this farmed salmonid pose the greatest threat for further dissemination of *G. salaris*, as in the recent discovery of the parasite in Italy (Paladini *et al.* 2006).

It is noteworthy that, while *G. salaris* has also been found in 13 out of 23 salmon rivers on the west coast of Sweden, the picture of pathogenicity in these rivers is confusing. In some, such as the River Ätransälv, into which the parasite was almost certainly introduced, and was present from at least 1991, burdens of up to 1000 parasites per parr have been found (Alenäs *et al.* 1998). Overall, a decline in this river over the 10 years post-introduction of *G. salaris* resembles that seen in Norwegian rivers (Alenäs *et al.* 1998), although not as dramatic; however, this pattern has not been observed in every Swedish west coast river, and the pattern is complicated by other environmental factors (see Section 9.3.3 below); the epidemiology of *G. salaris* on the Swedish west coast would repay closer investigation. In general, the key question, why *G. salaris* has become a major killer of Atlantic salmon in Norway and White Sea Russia, but not in Baltic Sweden, Finland or Denmark, and more surprisingly, not throughout the Swedish west coast, comes down to the interplay between the agent (the *G. salaris* genotype), the host (the Atlantic salmon genotype) and the physico-chemical environment (the river conditions), an interplay which illustrates perfectly the concept of ‘The Epidemiological Triangle’ (see Box 9.2).

9.3.2 The agent: pathogenic or benign? Taxonomic issues surrounding *G. salaris*

Gyrodactylus salaris was originally collected from Atlantic salmon at the Hölle laboratory, close to the River Indalsälv, Sweden, in 1952 (Malmberg 1957). At this time there was no suggestion that this species would or could be a pathogen. Most *Gyrodactylus* species descriptions have been based on morphology, and when *G. salaris* was designated notifiable (1983), there was hardly any discussion concerning the species concept in *Gyrodactylus*, the extent to which morphology can indicate species boundaries, or the extent to which host identity is used as an implicit character in diagnosing infections (Harris *et al.* 2004). Nevertheless, these issues have turned out to be fundamental and limited awareness of their importance has definitely delayed recognition of the scale of the *G. salaris* problem.

Traditional (morphological) taxonomy of *G. salaris*

Identification of gyrodactylids using morphology is far from trivial and requires analysis of the structurally invariant opisthaptor hooks and bars. A comparison of the closely related *G. salaris* and *G. thymalli* from grayling (*Thymallus thymallus*) illustrates the difficulties of morphological approaches. Malmberg (1993) established a relationship between these species, based on a general resemblance of their marginal hooks, although the hooks of *G. thymalli* are somewhat larger than those of *G. salaris*. Shinn *et al.* (2004) examined the morphometry of two different populations of *G. salaris* (rivers Lierelva and Rauma, Norway) and two of *G. thymalli* (River Rena, Norway; River Test, UK). All except the Test population were maintained in the laboratory under identical environmental conditions. These were chosen because they had distinct mitochondrial haplotypes (see below). All specimens could be assigned to the correct species using a combination of eight morphometric variables, and only three specimens of *G. salaris* were wrongly assigned to the wrong population, but not

Box 9.2 The epidemiological triangle

A host population may live with or without a particular pathogen, and most pathogens have a particular spectrum of host species which they can exploit. Both host and parasite are also influenced by all aspects of their environment, such that the precise outcome of a particular infection, whether benign co-existence, pathogenic disease or extinction of host and/or parasite, is dependent upon the interaction of these three sets of factors (Fig. B9.2.1). This is referred to as 'the epidemiological triangle'. The outcome of the interaction may vary between epidemic (sudden onset of parasitic disease, death of a large proportion of the host population, often followed by disappearance of parasite) and endemic (stable cycling of parasite and host, no evident episodes of host mortality). The balance between these two extremes is determined by the basic reproductive rate, R_0 (the number of secondary infections generated from a primary infection) in relation to pathogenicity (the probability that the host will be killed by an infection), and the rate at which the host population increases. Both R_0 and the rate of increase of the host population are strongly influenced by external environment, hence the importance of this set of factors in the epidemiological triangle. A further complication is introduced by the existence of time lags within the system. Just as in predator–prey cycles, the time lags introduced by the parasite life cycle result in the parasite population tracking the host population imperfectly, which can either stabilise or destabilise the host–parasite interaction. Perhaps the greatest stability is introduced by the introduction of a second host into the interaction, often in a food chain, in which case the overall relationship can be described in terms of two epidemiological triangles, joined by a predator–prey interaction.

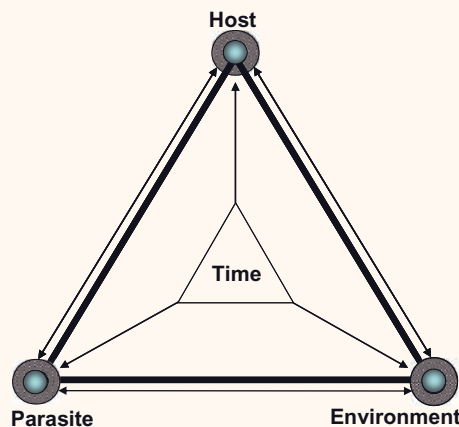


Figure B9.2.1 The epidemiological triangle, relating parasite genotype, host genotype and environmental factors.

to the wrong species. This implies that morphometrics targeting the subtle variation in the shape and size of the attachment hooks can discriminate between these sibling species.

Extending this, Olstad *et al.* (2007b) undertook a more detailed analysis using 27 measurements of the hooks and bars. Again they found that amongst 10 field collections, all could be assigned to the species as expected based on host identity. Only the grayling-infecting *G. thymalli* from the Norwegian River Trysilelva grouped with salmon-infecting *G. salaris* and was therefore misassigned. Although Olstad *et al.* (2007b) rightly caution that there is therefore no unambiguous morphological identification of the two species, on a positive note this morphometric study did discriminate *G. salaris* populations from Arctic charr and rainbow trout from each other and from *G. salaris sensu stricto*, and it did suc-

cessfully distinguish *G. thymalli* from Slovakia and from other Norwegian populations from classical *G. salaris*. A peculiarity of the results was the morphometric difference between classical *G. salaris* from salmon in the rivers Rauma and Skibotnelva, despite molecular evidence that these populations are closely related. Later, Olstad *et al.* (2009) used a geometric morphometric methodology to evaluate traditional morphological methods concluding that marginal hook shape represented the most important available taxonomic character, and that morphometric variation observed was fully in line with *a priori* species assignments based on host species among the analysed populations of *G. salaris* and *G. thymalli*. However, these studies show that the boundaries between *G. salaris* on salmon, rainbow trout and Arctic charr, and *G. thymalli* on grayling are not prominent, and only sophisticated morphological methodologies can distinguish them. These morphometric studies also highlight the need for more controlled analyses of the influence of environmental factors on gyrodactylid morphometrics. Phenotypic plasticity of the infective agent in interplay with the other two important epidemiological factors, host and environment, may compromise the morphological diagnostics of gyrodactylid infections (Olstad *et al.* 2009).

The specific affinities of *G. salaris* remained obscure until the advent of molecular markers for these parasites. A discussion of the problems in differentiating *G. salaris* and *G. thymalli* using both morphological and molecular markers is informative in illustrating the difficulties in diagnosing these parasites.

Molecular taxonomy of G. salaris

The first molecular markers for diagnosis of *G. salaris* became available during the mid-1990s (Cable *et al.* 1999; Cunningham 2002; Matejusová *et al.* 2001, Ziętara & Lumme 2002; Ziętara *et al.* 2002). The Internal transcribed spacer regions (ITS-1 and ITS-2) of the ribosomal DNA have since become markers of choice for molecular systematic studies, and Ziętara & Lumme (2003) went as far as to suggest that a sequence difference of *c.* 0.5% in the ITS loci can informally discriminate gyrodactylid species. It quickly became apparent (Cunningham 1997) that these ribosomal fragments were identical in *G. salaris* and *G. thymalli*, and only limited sequence variation has ever been detected between these taxa. The diagnostic value and ecological significance of this limited sequence variation at this locus is not understood, presenting a practical, diagnostic and conceptual problem for researchers; Based on Ziętara & Lumme's (2003) rule of thumb, these two forms should be considered identical, despite the clear biological and more subtle morphological differences between them.

Following the discovery of almost invariant ITS, the repetitive regions of the intergenic spacer (IGS) of the ribosomal gene cluster of *G. salaris* and *G. thymalli* were investigated for their diagnostic utility (Sterud *et al.* 2002; Cunningham *et al.* 2003; Hansen *et al.* 2006). Although this locus was considered taxonomically informative (Cunningham *et al.* 2003), this was challenged by Hansen *et al.* (2006), who concluded that the IGS region best supports the hypothesis that *G. salaris* and *G. thymalli* represent a single polytypic species. These taxa may represent nascent speciation with the sibling taxa either being semispecies (one or two polytypic species) or a superspecies (several sibling species using the nomenclature of Mallett, 2007), partly isolated by host preference.

Further resolution came from sequencing the mitochondrial cytochrome oxidase I (COI) gene of *G. salaris* and *G. thymalli* from a broad geographic range of populations (Hansen *et al.* 2003, 2006, 2007a, b; Meinilä *et al.* 2004). A total of 44 haplotypes, 12 from *G.*

salaris and 32 from *G. thymalli*, have been compiled (see Hansen *et al.* 2007b). These group into 12 well supported haplogroups (clades), most corresponding to both the specific ecology (host infected) and the geographical origin of the specimens (Hansen *et al.* 2007b and references therein), which came from a wide range of localities in Scandinavia, Central Europe and the United Kingdom. Each haplogroup (3 for *G. salaris*, 9 for *G. thymalli*) is thought to represent an independent evolutionary lineage. However, it is puzzling that these clades do not support monophyly of either *G. salaris* or *G. thymalli*. Instead, they are more in line either with a rapid spread and diversification of mitochondrial lineages after the Last Glacial Maximum (LGM) as a result of isolation and genetic drift (bottlenecking), or due to survival in numerous refugia close to the ice sheet (Harris 2008). Increased sampling, especially to the south and west of the range of grayling, is certain to discover further mitochondrial lineages. The grayling is itself highly structured genetically, because it survived in a variety of refugia during the LGM (Koskinen *et al.* 2000; Gum *et al.* 2005). *G. thymalli*, where it has been studied, is also highly structured, with haplotype groups associated with major drainage basins inhabited by the hosts (Bakke *et al.* 2007; Harris 2008). Several authors (especially Cunningham *et al.* 2003 and Meinilä *et al.* 2004) interpret the COI phylogeography as indicating that *G. salaris* is a salmon-infecting form derived from grayling-infecting *G. thymalli* via a host shift. As *G. salaris* was described before *G. thymalli*, this name has priority, and, if *G. salaris* and *G. thymalli* should be accepted as con-specific, we should refer to salmon-races and grayling-races or host ecotypes of *G. salaris*. However, the current molecular evidence is inconsistent and certainly does not provide the full story. Furthermore, it does not take into account morphological (McHugh *et al.* 2000; Shinn *et al.* 2004) and ecological and experimental host preference (Soleng & Bakke 2001; Bakke *et al.* 2002; Sterud *et al.* 2002) data. For example both *G. salaris* and *G. thymalli* occur sympatrically on their respective host species in the River Tornionjoki (Anttila *et al.* 2008). Reasoning based solely on molecular data may oversimplify the taxonomic and diagnostic problem, and must be considered preliminary until further sampling allows a more in-depth analysis.

There has been much confusion over the 'rainbow trout variant' of *G. salaris*, partly because this name has been used in two ways. Mo (1991) described a form collected from several rainbow trout farms in the River Drammen watershed in southeast Norway. The name subsequently became attached to *G. salaris* collected from rainbow trout farms in Scandinavia and elsewhere which have the mitochondrial haplotype F (e.g. Hansen *et al.* 2003; Meinilä *et al.* 2004; Zięta *et al.* 2006). In fact, the original 'rainbow trout variant' (Mo 1991) was never sampled for mitochondrial DNA, having been extirpated several years before mitochondrial haplotyping became common. However, it is assumed in the literature that this variant was identical to forms from rainbow trout elsewhere in Europe. *G. salaris* infecting salmon of the rivers Lærdalselva, Lierelva and Drammenselva in southeast Norway do share the same mitochondrial haplotype F as specimens from rainbow trout farms (Hansen *et al.* 2003), but nuclear IGS studies (Sterud *et al.* 2002; Cunningham *et al.* 2003; Hansen *et al.* 2006) make it unambiguously clear that these Norwegian parasites have distinct nuclear genomes. The origin of parasites on rainbow trout therefore remains speculative, but they are relatively variable, showing ITS polymorphisms and having variable host preference and pathogenicity; some are non-pathogenic to salmon (Lindenstrøm *et al.* 2003; Jørgensen *et al.* 2006, 2007; Rokicka *et al.* 2007). *Gyrodactylus bohemicus* (see Ergens 1992) may be an early report of one of these forms from farmed rainbow and brook trout.

Ziętara *et al.* (2006), using an uncharacterised nuclear marker, ADNAM-1 (Anonymous DNA Marker 1), suggested that the *G. salaris* clade from rainbow trout was triploid, as one allele was considered twice as bright on agarose gels as the other. This result has not been confirmed by cytogenetic methods.

Most remarkably, the presence of *G. salaris* on Arctic charr in several lakes in southeast Norway (Kravikfjorden, Norefjorden, Tunhovdfjorden, Pålbufjorden and Skurdalsfjorden), above the anadromous stretches of the Numedalslågen river system, has recently been confirmed (Robertsen *et al.* 2007, 2008). This parasite strain is also similar to rainbow trout-infecting forms of *G. salaris* (mitochondrial haplotype F) but is of only limited infectivity (and is non-pathogenic) to salmon (Olstad *et al.* 2007a). It may have originated following a host shift from rainbow trout probably imported from Denmark during the 1960s (Robertsen *et al.* 2008). This represents the first record of a viable *G. salaris* population infecting a wild salmonid host population in the absence of both salmon and rainbow trout.

Recently the whole mitochondrial genomes of selected strains of *G. salaris* and *G. thymalli* have been sequenced to find further suitable markers for addressing taxonomic and diagnostic questions (Huyse *et al.* 2007; Plaisance *et al.* 2007). These efforts have identified genes such as the Cytochrome Oxidase III and NADH dehydrogenase 4 genes, which are equally or slightly more variable than COI, but their use did not improve the resolution of the molecular phylogenies of these species.

Overall, many questions remain unanswered in this account of the origins of *G. salaris* as a pathogen of salmon. However, the potential of nuclear markers for interpreting the evolutionary history of gyrodactylids is clear, as is the importance of developing more of them.

The host: susceptible or resistant? The status of salmon stocks as hosts for G. salaris

Since research into the biology of *G. salaris* began, a great deal of work has focused on the susceptibility or not of different salmon stocks, and of different salmonids, to this parasite. Given the plurality of parasite strains, and the obvious complexity of the taxonomy of this apparently rapidly evolving parasite, there is a need for accurate definition of the strain used in host susceptibility studies. The vast majority of studies on the susceptibility of salmonids to *G. salaris* have utilised the parasite strain from the River Lierelva in southern Norway (Bakke 1991; Bakke *et al.* 1990, 1991a, b, 2002; Jansen & Bakke 1991, 1993a, b). Although not entirely typical of pathogenic strains in other Norwegian rivers (it has mitochondrial haplotype F), all results obtained with this strain are comparable, and allow a picture of its host range to be established. Limited data are also available for parasite strains from the River Batnfiordselva (Bakke *et al.* 2002), and from the River Figga in central Norway (Bakke and MacKenzie 1993; Bakke *et al.* 2004), both more typical of the Norwegian pathogenic strains.

Gyrodactylid monogeneans generally evoke a distinct host response which eventually limits the infection (Lester & Adams 1974; Scott 1985; Bakke *et al.* 2002; van Oosterhout *et al.* 2003; Buchmann & Uldal 1997). The first, most dramatic finding concerning the host spectrum of *G. salaris* (River Lierelva strain) was that this response was not evoked in infections of Norwegian Atlantic salmon stocks from the rivers Lone and Altaelva, although both populations and individually isolated fish of a Baltic stock from the Neva River (Russia) showed a 'normal' host response (Bakke *et al.* 1990). The results of these classic experiments were striking; on susceptible salmon the gyrodactylid populations increased without

check, while on the Baltic Neva strain, infections rarely increased above 100 parasites, and were either limited by a host response when they reached this level, or failed to grow in the first place. The primary reproductive rate R_0 of *G. salaris* (the number of secondary infections resulting from a primary infection) includes too many imponderables for calculation. However the best proxy measure of R_0 , the total reproductive output of an infection, can be estimated. Bakke *et al.* (2002) presented crude reproductive rates for *G. salaris* on a variety of salmon strains, and found almost a doubling in the exponential rate between the least susceptible strains and the most susceptible. There is considerable heterogeneity in the performance of *G. salaris* on individual fish, even when all of the fish tested are full sibs or come from relatively few parents. For this reason, Bakke *et al.* (2002, 2007) classified individual fish according to their response; on highly susceptible fish infections grow without check until the fish dies; innately resistant fish entirely fail to support population growth; while on moderately susceptible but responding fish the infection initially grows, but then is checked by the immune response. This last group is sometimes termed resistant; but such fishes can sustain breeding infections for short periods, and in the field may be important in sustaining infections even after developing an immune response. This classification allows further dissection of the response when breeding resistance into salmon stocks. Although salmon able to mount a response against *G. salaris* are rare, they do occur. They were observed experimentally in the Russian Neva stock (Bakke *et al.* 1990, 2002) but most significantly they were also observed within hatchery-reared salmon populations from several different Norwegian rivers (Bakke & MacKenzie 1993; Olstad *et al.* 2007a; Bakke *et al.* unpublished observations). At least some of this resistance is genetic, as shown by a mass selection experiment using River Drammenselva salmon (Salte *et al.* 2010). Families of known pedigree demonstrated both additive genetic variation and significant heritability in resistance to *G. salaris*, suggesting that this is under polygenic control and giving hope for the use of selective breeding to develop resistant salmon. In more complex experiments, Bakke *et al.* (1999) investigated the susceptibility of Norwegian salmon (River Alta stock), brown trout (Fossbekk stock) and hybrids between the two from the same parental generation to both *G. salaris* and *G. derjavini* (= *G. derjavinoides*). The hybrids were produced using salmon as both sires and dams. All hybrids could be infected to some extent by parasites of both species, but susceptibility followed more closely that of the maternal parent. The outcome of these hybridisation experiments is fascinating not only because it shows the complex, multigenic nature of resistance / susceptibility to gyrodactylids, but also because natural salmon / trout hybrids have become abundant in Norwegian river systems where *G. salaris* has reduced salmon numbers significantly. The epidemiological consequences of such hybrids in sustaining and disseminating the parasite remain to be investigated.

The immune response to gyrodactylid monogeneans is not fully understood and has been studied most thoroughly in non-salmonids such as the *G. turnbulli*-guppy system (e.g. Scott 1985; Scott & Anderson 1984; van Oosterhout *et al.* 2003), which are more tractable to analysis. Firstly, the response is heritable, and resistant and responding hosts can be selected. Secondly, it is induced. Initially the gyrodactylid population grows without check, but then a response is initiated and the gyrodactylid population begins to decline. This occurs a characteristic period after infection, and is not dependent on the size of the gyrodactylid population (Bakke *et al.* 2002). Thirdly, the response shows elements of memory, as secondary infections are limited at a smaller size than primary infections (Scott & Robinson 1984). Cross-resistance to species of *Gyrodactylus* not involved in the primary infection also occurs

(Richards & Chubb 1996). Finally, the response is dependent on an intact immune system, as X-irradiation of goldfish increases susceptibility to gyrodactylids (Schechmeister *et al.* 1962), and immunosuppression greatly increases the susceptibility of salmonids to *G. salaris* (Harris *et al.* 2000). Buchmann (1997) and Lindenstrøm and Buchmann (1998) showed similar increases in susceptibility of rainbow trout to gyrodactylids following administration of testosterone and dexamethasone, respectively. This chapter does not speculate on the mechanism of immunity, or on how immunosuppression acts to allow gyrodactylid infections; the reader is referred to Bakke *et al.* (2007) for a more detailed account. What is interesting in the current context are the epidemiological consequences of the interactions between the environment and the salmonid immune system. Stressors such as environmental degradation, starvation or crowding, may all reduce the ability of fish to deal with gyrodactylid infections. Environmental stressors might be an issue today in, for example, infections of resistant hybrid fishes, which may carry higher burdens of *G. salaris* because of stress than would otherwise have been the case (Harris *et al.* 2000). Environmental stressors might also be important following rotenone treatment, when *G. salaris* on salmonids such as Arctic charr might survive because their hosts are stressed and unable to eliminate them. Finally, there is an argument that *G. salaris* kills salmon through the stress response. The parasite is itself a stressor, large populations immunosuppressing the salmon to the point where they succumb either to the gyrodactylid infection, or to a secondary infection such as *Saprolegnia*. Reduction of environmental stress could in some cases reduce the risk of lethal outbreaks of *G. salaris* in a river, by increasing herd immunity overall to the parasite.

9.3.3 The physicochemical environment: The role of environment in shaping infection outcomes

As an obligate freshwater ectoparasite *G. salaris* is constrained both by the biotic environment of the living fish epidermis, and by the non-living physicochemical conditions of the aquatic environment. Biotic conditions may differ individually but are well defined structurally, physiologically and biochemically. In contrast, the aquatic environment which the parasites inhabit is highly diverse and is dynamic in both time and space. Many environmental variables are probably important in determining the outcome of gyrodactylid infections (see Box 9.2). We focus on three: water temperature, the chemical characteristics of the water body, and the substrate quality of the river. Temperature is the most important environmental variable influencing poikilothermic gyrodactylids and their hosts. A great deal of experimental work links *G. salaris* directly to water chemistry, but the importance of natural water chemistry in the field has never been considered. Finally, substrate quality has never been considered important for gyrodactylid infections previously, but we choose to review this in light of substrate choice by salmon parr.

Water temperature

Salmon and *G. salaris* are both critically influenced by water temperature. For gyrodactylids, the reproductive rate as observed experimentally doubles with a 5 °C increase in temperature (Jansen & Bakke 1991). Lifespan, however, declines with increasing temperature, from an average of more than 33 days at 2.6 °C down to less than 5 days at 19 °C (Jansen & Bakke 1991). At medium temperatures individual parasites may give birth up to four times, but at the extremes of temperature only two daughters may be born, at low temperature because

embryo development is so extended; at high temperature because adult survival is so reduced (Jansen & Bakke 1991). Although embryo development becomes prolonged at low temperature, *G. salaris* populations can survive throughout the winter at ambient temperatures as low as 0°C (Jansen & Bakke 1993a, b; Mo 1992; Appleby & Mo 1997). The survival of detached *G. salaris* is also temperature-dependent, and at low temperatures parasites can survive away from the host for many times longer than at high temperature (Olstad *et al.* 2006). This could be interpreted as an important survival mechanism during winter, when individuals may potentially survive for weeks off the host and still be able to re-infect salmon (Soleng *et al.* 1999a; Olstad *et al.* 2006). At high temperature, other gyrodactylid species are limited by a host response, but although it has not been specifically tested, it is assumed that salmon at high temperature remain entirely susceptible to *G. salaris*. Nevertheless, Jansen & Bakke (1993a) noted a decline in infections of *G. salaris* on wild salmon in the River Lierelva before the summer peak temperature, and it may generally be the case that these fish may respond more efficiently to infection at temperatures encountered during the hottest part of the summer. In southern Norway, the peak reproductive output of this parasite, and greatest host mortality, therefore comes during the spring and autumn, as temperatures rise and fall through their intermediate range, between 5 and 15°C (Jansen & Bakke 1993b).

Theoretical studies predict that gyrodactylids have unstable population dynamics, requiring the regular availability of naïve hosts if they are to persist. This has been experimentally confirmed in closed aquarium systems (Scott & Anderson 1984; Bakke *et al.* 1991b) when the parasite shows oscillatory population dynamics with cycles of host susceptibility and refractoriness. The amplitude of oscillations depends on features such as the rate of parasite reproduction, and the rate at which hosts become immune, or conversely lose their immunity. At high temperatures, the obvious instability of gyrodactylid population dynamics is such that the parasite frequently goes extinct, unless a very high replacement rate of naïve hosts is maintained. These complex, emergent aspects of parasite population growth make the interaction with environmental temperature complex, and seasonal cycles represent one of the strongest sources of information on the influence of external variation in natural populations. However, the seasonality of *G. salaris* population dynamics in relation to host ecology has been relatively little explored. To date, seasonality of *G. salaris* has been studied in only six rivers in Norway (Johnsen & Jensen 1988; Johnsen & Jensen 1992, 1997; Jansen & Bakke 1993a, b; Mo 1992; Appleby & Mo 1997; Johnsen *et al.* 2004; Knudsen *et al.* 2004, 2007; Winger *et al.* 2008). The yearly surveillance and control programmes of the Norwegian Veterinary Institute seek only to identify the spread of *G. salaris* to new localities, and do not take place unless eradication of the parasite or other circumstances justify surveillance. In other parts of its total range, only two studies have reported on the seasonality of *G. salaris*; one within the presumed original range draining to the Baltic Sea (the River Tornionjoki between Sweden and Finland; Anttila *et al.* 2008), and the other considering an introduced population in the River Keret in Russia (Ieshko *et al.* 2008). Of other *Gyrodactylus* species infecting wild salmonids in Fennoscandia only *G. derjavini* (= *G. derjavinoidea*) in the River Sandvikselva, Norway, has been subject to a closer study on its seasonality (Mo 1997). Nevertheless, these studies do indicate some general trends in the seasonal population dynamics of *G. salaris* (Bakke *et al.* 2007). There is a prominent spring increase in parasite abundance concurrent with rising water temperature and the emergence of fry from the spawning redds. The abundance of the parasite is either bimodal with peaks

in late summer and autumn, or there is a single peak in late summer or autumn depending partly on the age of the salmon pre-smolts and the seasonal temperature regime. The population then declines to a low level throughout winter and early spring. Highly infected adult salmon sometimes survive late into the winter and may represent a reservoir of infection for parr (Soleng *et al.* 1998).

There are of course interactions between host biology and environment which complicate this analysis of the impact of temperature on the *G. salaris*–salmon interaction. Perhaps the most important is the global effect of climate on salmon life-histories. In the south of the European range, Atlantic salmon parr may remain in the river for only a single year before smoltification and migration to sea. In the north of Norway and Russia this phase might be prolonged for five years. The impact of this effect of temperature on the host fish is profound. *G. salaris* would be extremely unlikely to persist without an alternative host species in rivers where parr smoltify and migrate to sea before the annual production of alevins has emerged from the gravel and become available for infection. In northern rivers multiple parr generations provide a reservoir for infection even if mortality within a single age cohort is severe. All available evidence suggests that in rivers containing multiple parr generations, the infestations are larger on 1+ fish, but then, where parr survive to a second year (2+ year class) in the river, they then may carry fewer parasites. In the best study of this type (Johnsen & Jensen 1992), on a single census occasion in October 1989 in the River Lakselva, 0+ (young of the year) parr carried a mean *G. salaris* burden of 356 parasites, while 1+ and 2+ fish carried mean burdens of 2537 and 955, respectively. Appleby & Mo (1997) similarly recorded this phenomenon in female parr in the River Batnfjordselva, although in their case, the situation amongst male parr was complicated by the onset of precocious maturity. Precocious males carried significantly more parasites in both age classes than their sexually immature counterparts, presumably due to hormonally induced immunosuppression. The same trend, of highest infection in 1+ or 2+ fish, and reduced infestation of older parr, is also evident in the data of Johnsen & Jensen (1997) from the River Lærdalselva; from 11 samples collected along the river in October 1996, in general 2+ and older fishes carried substantially lower burdens than did 1+ fish. Johnsen & Jensen (1992) appear to interpret this drop in infection level between year classes in the same cohort of fishes as due to parasite-induced mortality. This is likely, but it is also possible that a degree of genetic resistance or induced immunity also prevents burdens increasing further on these particular survivors.

A great deal remains to be investigated concerning the impact of water temperature on the gyrodactylid–host interaction. The rivers of the Norwegian epidemic area have relatively low temperatures throughout the year, because they receive their water flow from alpine areas, sometimes from glaciers, and rarely attain 20 °C, although the three most southerly infected rivers, the rivers Sandeelva, Drammenselva and Lierelva, do exceptionally attain these temperatures. Rivers draining to the Baltic, within the endemic zone, tend to be generally warmer in summer as they experience a more continental climate. What then of the Swedish west coast rivers harbouring the East Atlantic salmon? The parasite was introduced into these rivers and potentially should cause epidemic problems. However, these rivers also attain relatively high summer temperatures, and it is tempting to think that this might also lead to a higher level of resistance amongst the resident salmon. These differences in temperature and seasonality within the range of *G. salaris* need to be analysed more closely for a better understanding of the parasite epidemiology.

Water chemistry

Water chemistry may also influence the abundance and distribution of gyrodactylids in fresh water. The clearest indication of this was the discovery that a combination of acidified water and aqueous aluminium ions (Al^{3+}) eliminated *G. salaris* (after 4 days at $202\text{ }\mu\text{g Al/l}$), without killing the salmon (Soleng *et al.* 1999b). This effect was relatively independent of pH, except at the lowest pH when the effect of Al was enhanced. Acidified water also impaired parasite survival in the absence of metal ions, and at pH 5.0, *G. salaris* was eliminated from salmon within 9 days (Soleng *et al.* 1999b). Later, Soleng *et al.* (2005) demonstrated that the toxic effect of aluminum on *G. salaris* survival and reproduction is reversible, and that, if *G. salaris* is not killed by exposure to Al^{3+} ions, it will resume reproduction. Another study by Poléo *et al.* (2004) confirmed these observations of Al^{3+} as a parasiticide and also demonstrated that zinc (Zn^{2+}) ions increased parasite mortality at concentrations which do not kill the host. No measurable effect was observed with iron (Fe), copper (Cu) and manganese (Mn) ions except Cu at the highest concentrations tested. The mechanism behind this effect of metal ions on *G. salaris* is unknown.

The role of metal ions on gyrodactylid infections in natural water bodies is entirely unknown. Aluminum is now being used as an alternative to rotenone to treat *G. salaris* infections in Norway (see Bakke *et al.* 2007 and Section 9.4 below) with some limited success, raising the question as to whether natural levels of metal ions in groundwater could ever limit *G. salaris* distribution. Salmon rivers today tend to be in upland regions, and much of the existing range of salmon extends over hard granitic and basaltic rocks, where the river water can contain high concentrations of aluminum ions at low pH, and in areas of acid soils rainfall can enrich aluminum ions temporarily in river water (Neal *et al.* 2004). This can be seasonally constrained into an acid pulse as snow melt feeds spring flood waters (Buffam *et al.* 2008). The impact of such a rise in aluminum ions in rivers on gyrodactylids is not clear, but anecdotally we have noted that gyrodactylids can be very rare in British river systems such as the Tweed or the Spey which drain areas of basaltic rock. The levels attained during such pulses are comparable to the highest used by Soleng *et al.* (1999b) in their experiments; thus Buffam *et al.* (2008) record Al^{tot} concentrations in headwaters of the Krycklan catchment (Sweden) of between 135 and $175\text{ }\mu\text{g l}^{-1}$, sufficient to eliminate *G. salaris* within 4–10 days according to Soleng *et al.* (1999b), while in the outlet, aluminum concentration spiked to almost $200\text{ }\mu\text{g l}^{-1}$. Particularly in southwestern England and northern France (Brittany), many rivers drain metalliferous serpentine rocks, containing a range of metal ions extending far beyond aluminum; the impact of these watersheds on gyrodactylids is entirely unknown. Acidification due to acid rain in the 1970s resulted in the extinction of salmon in several rivers in southern Norway (Mills 1989), although the decline in air pollution in recent years, with remedial liming, has resulted in their return. An interesting observation in this respect has been the correlation between rising water pH due to liming and the increasing importance of *G. salaris* in the River Ätran on the Swedish west coast (Alenäs *et al.* 1998).

Substrate type

An aspect of the gyrodactylid–host interaction which has not been considered before is the substrate type that the fish inhabit, and the influence this may have on parasite transmission. Lacking a specialised transmission stage (Bakke *et al.* 2007; Boeger *et al.* 2005), *G. salaris* can transmit to a new host only by direct transfer during host–host contact, by contact with

detached parasites attached to the substrate or in the drift, or by transmission from dead infected fishes (Bakke *et al.* 1992; Soleng *et al.* 1999a; Olstad *et al.* 2006). An important aspect of *G. salaris* transmission may be its survival for extended periods (up to 6 days at 12°C) on dead salmon (Olstad *et al.* 2006), an unusual characteristic for a gyrodactylid. Little is known of the relative importance of these routes, apart from that overall, transmission is highly efficient; the prevalence of *G. salaris* on previously uninfected marked salmon introduced into an infected river reached 44.4% after only one day (Soleng *et al.* (1999a)! Soleng *et al.* (1999a) also showed that transmission via host–host contact was positively correlated with temperature (between 1.2 and 12.2°C) and that drifting *G. salaris* could infect up to 6.4% of test fishes in one day. Transmission behaviour of gyrodactylids is crucially dependent on factors related to both host biology and to the environmental conditions. Host–host contact is highly efficient for transmission, but as parr are territorial the main opportunity for contact comes during agonistic interactions between them. If, for example, *G. salaris* impairs the ability of infected fishes to gain and hold territories, do these fish then become dispersive, spreading infections to new areas of the river bed? Dead fish usually attract the attention of living con-specifics which investigate and perhaps feed from the body. In a flowing river, dead bodies tend to be washed downstream, potentially providing important foci of infection for populations of salmon parr occupying different riffle stretches. However, they can also lodge amongst stones and become inaccessible to investigating con-specifics. Similar considerations apply for the attachment and transfer of dislodged parasites to bottom-dwelling salmon parr. Transmission of *G. salaris*, and hence the epidemiology of the infection as a whole, may therefore depend on the substrate structure of any particular river. In particular, an extensive three-dimensional substrate, giving fish shelter from current and predators within the matrix, may give gyrodactylids much greater access to resting fish. Considerations such as these, with catchment-level water chemistry (Buffam *et al.* 2008) may be important in interpreting contradictory data on the distribution of *G. salaris* within individual river systems (e.g. Johnsen & Jensen 1997; Anttila *et al.* 2008).

9.4 Managing disease in wild salmonid populations

Disease is natural in wild vertebrate populations. On the other hand, however, in the case of Atlantic salmon we are dealing with a species which is relatively rare, of high conservation and economic value, and in which pathogen-mediated disease exacerbated during the management of the stock, in the broadest sense, is an established fact. In almost every river with a salmon run in northwestern Europe, intervention is practised for stock management, often to maintain a healthy returning stock for angling. All management practices carry some element of risk. *Aeromonas*, *G. salaris* and the myxozoan identified by Dionne *et al.* (2009) were all originally translocated beyond their natural range as a direct result of farming or stock management. Salmonid farming can also establish foci for infection with parasites, which can spill over and infect natural salmonid populations. Sea lice (Finstad *et al.* 2011 [Chapter 10]) provide perhaps the clearest and most controversial example of this. A more subtle version of this problem, however, is the stocking of river systems with salmon parr; undoubtedly, this practice assisted the early spread of *G. salaris* within Norway (Bakke *et al.* 2007), and it has the important disadvantage that it slows the evolution of resistance through natural selection in the fish population. Dionne *et al.* (2009) have

demonstrated that MHC alleles for increased susceptibility quickly become replaced by more resistant alleles within salmon populations exposed to infectious agents; restocking of rivers with naïve parr may delay this. Secondly, restocking with parr may modify parr densities within the river system, tipping the parasite's R_0 from the point at which endemic coexistence is possible into the range where epidemic disease becomes more likely.

So how then should disease in wild salmon populations be managed? In Norway the approach to *G. salaris* has been to eradicate the parasite, and in Europe in general to prevent its further translocation. Eradication is achieved by excluding returning reproducing salmon and then either through treatment with the biocide rotenone, or more recently, by the use of toxic aluminum sulphate (Soleng *et al.* 1999b; Poløe *et al.* 2004). Rotenone can in some ways be seen as the ideal biocide. It kills all aquatic vertebrates within the treated river very quickly (within a matter of hours) and then breaks down, leaving no residual toxicity. Once all salmon and their parasites have been killed, the river is either restocked with parr of the same genetic stock from gene banks or fish are allowed to recolonise the river from the sea. The difficulty with this strategy is ensuring the complete coverage of the river system at the appropriate concentration of rotenone needed to achieve eradication. Because of these problems, nine rivers have become reinfected, some several times, after treatment, and a further 10 must wait five years before they are declared parasite-free. Aluminum is being considered for wider use because rotenone is being phased out as a legal biocide within the European Union, and although the Norwegian government had a special exemption to continue use until 2010, there are concerns over the future supply of the poison. At present, no other alternatives to these methods of eradication have advanced beyond the experimental stage.

The problem with disease management, as opposed to eradication, is that, as in the UK foot and mouth disease epidemic of 2001, it offers at best a non-sterile solution. Acceptance of the fact that *G. salaris* will continue to infect Norwegian rivers would place significant long-term constraints on the future development of the Norwegian wild salmon industry, and have wide-ranging economic impacts across a large part of northwestern Europe. However, such a non-sterile solution may be inevitable, given the complexity of some larger river systems and the discovery of apparently non-pathogenic *G. salaris* populations on charr in southern Norway (Olstad *et al.* 2007a; Robertsen *et al.* 2007, 2008; Section 9.3.2 above). In fact, it is clearly possible for wild salmonid populations to co-exist with *G. salaris* within parts of the range of the parasite, suggesting that pathogenicity may, as suggested above (Section 9.3.3), be limited by environmental factors. More research, for example into the distribution of pH, Al^{tot} and temperature conditions lethal to *G. salaris* in natural water bodies across Scandinavia, and the ways in which these parameters may change following global warming, may allow us to achieve a more balanced perspective of the likely future trajectory of the *G. salaris* epidemic.

On the other hand, the focus of attention on eradication of *G. salaris* in Norway, and on exclusion elsewhere in Europe, has diverted attention away from the question of overall disease management in wild populations of Atlantic salmon. For example, the emerging problem of *Tetracapsuloides bryosalmonae* may represent a potentially huge risk to wild salmon stocks, and attempts at salmonid restoration in European waterways. While we do not go so far as Tops *et al.* (2006), who speculate that the spread of *T. bryosalmonae*, coupled with global warming, could lead to a terminal decline in European salmonids, we nevertheless do consider that this organism presents as great a threat to the Atlantic salmon in the early decades of the twenty-first century as *G. salaris* did in the latter part of the

twentieth century. The particular problem is that *T. bryosalmonae* has a catholic range of bryozoan hosts in which it can replicate, which can be found in rivers throughout much of the range of salmon. Bryozoans have highly resistant dispersal stages, within which the parasite is thought to survive (Henderson & Okamura 2004), and so their spread in response to increasing global temperature is assured. Finally, the clinical disease in salmonids manifests itself at temperatures in excess of 12 °C. Thus upland populations of salmon currently escape the disease syndrome because their rivers stay below this temperature even in mid-summer. Water abstraction and management can lead to water temperatures exceeding 12 °C more regularly (Sterud *et al.* 2007), especially as global warming becomes more significant. Even now, this pathogen may present a significant problem in restoring salmon to lowland river systems. Control of *T. bryosalmonae* by eradication or by restriction on stock movements is not an option.

Two long-term approaches suggest themselves for controlling pathogens of wild salmon which otherwise pose an intractable problem of epidemic disease; one is based on selective breeding, the other on immune enhancement. Both approaches might work for *G. salaris*, but only selective breeding would seem feasible for *T. bryosalmonae*. Attempts to enhance immunity to *G. salaris* have never been tried, partly because such an approach would be non-sterile, and therefore compromise the potential ‘*G. salaris* free’ status of Norwegian rivers, and partly because of the paradigm that *G. salaris* does not induce any immune response in Norwegian salmon strains. In fact, this is not true. As discussed above, several field and laboratory studies (Jansen and Bakke 1993b; Bakke and MacKenzie 1993; Bakke *et al.* 2002, 2004; Olstad *et al.* 2007; Salte *et al.* 2010) have demonstrated that some Norwegian Atlantic salmon, from several stocks, develop some immunity, or are resistant, to the parasite. A number of possibilities for enhancing herd immunity in the salmon population then arise, given that restocking rivers with parr is a routine management tool. The first possible approach is that salmon parr be released sufficiently late in the year that they acquire a small *G. salaris* population which they carry through the winter before the water begins to warm in the following spring. It might then be hoped that these fish would smoltify and escape the parasite by migration to the sea before parasite pathogenicity becomes an issue in the spring. The second possible approach is to expose parr before release to *G. salaris* at a high temperature (15 °C), above the optimum for the parasite. At higher temperatures, parasite fecundity and population growth rate are compromised (Jansen & Bakke 1991), potentially reducing their pathogenicity. At the same time, at the higher temperature, the immune response of the fish is more efficient, and we would envisage that a short pulse infection at high temperature might induce sufficient immunity to protect the fish when they are subsequently released into the wild. Herd immunity, the protection of a few un-immunised wild fish by the presence of a majority of immunised restocked individuals, might then be expected to control the infection within tolerable limits. Solutions based on immunity in the case of *T. bryosalmonae* are currently impossible, because the PKD syndrome is itself a manifestation of an inappropriate immune response (Chilmonczyk *et al.* 2002).

The second long-term approach is the breeding of genetic resistance into the specific salmon populations under threat. This is feasible today; the heritability of resistance to *G. salaris* has been clearly demonstrated (Bakke & MacKenzie 1993; Bakke *et al.* 1998, 2002, 2004; Olstad *et al.* 2007a), breeding experiments have given promising results (Salte *et al.* 2010), and resistant natural hybrids (Johnsen *et al.* 2004) confirm earlier laboratory experiments (Bakke *et al.* 1998). Several methods of breeding resistance into salmon are possible,

potentially countering the arguments against the release of genetically modified (albeit by traditional methods) organisms into the wild. For example, surviving wild salmon parr at the point of smoltification may be removed from rivers, their level of infection assessed, and the least infected reared to maturity for use in a selective breeding programme. Each river system has its own genetically unique stock of Atlantic salmon, resulting from the bottlenecks and drift caused by the return of only a small number of breeding adults (Mills 1989). Conservation of this diversity remains the first priority of the North Atlantic Salmon Conservation Organisation (NASCO) and therefore of Norwegian conservation bodies, and artificial selection for resistance has been ruled out. However, for complex river systems (e.g. the Drammenselva, Lierelva and Drammensfjord system), which cannot be treated chemically, there is little alternative to artificial selection. Within Drammenselva, artificial mass selection for resistance to *G. salaris* has been in progress for several years (Salte *et al.* 2010). The arguments in favour of selective breeding are even more persuasive in the case of *T. bryosalmonae* in wild salmonids, as this pathogen is widely distributed in Europe and North America, and it is difficult to see how any other control strategy could be feasible.

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10 The Effect of Sea Lice on Atlantic Salmon and other Salmonid Species

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Abstract

Sea lice were historically observed in rather low numbers on wild salmonids, with few adverse effects on the host being reported. Since the late 1980s, however, there have been several reports of sea lice epizootics on salmonids in Norway, Scotland, Ireland, and more recently Canada. Infested post-smolts and adult fish often have been reported to be in poor physical condition, with some showing severely damaged caudal and dorsal fins and skin lesions. It has been suggested that the apparently increased infestation rate of sea lice on salmonids is correlated with the presence of salmon farms. This has been the focus of a long and controversial debate. Management improvements on fish farms have therefore aimed specifically at enhancing husbandry of cultured fish by reducing their infestations of sea lice. This approach has been taken with the additional objective of reducing their potential impact on wild salmonids. Here we give an overview of the differing experiences and responses of national bodies and the farming industry to the environmental challenges presented by sea lice in Norway, Canada, Ireland and Scotland. Whilst the emphasis is on the effect of sea lice on Atlantic salmon performance, some additional information on sea lice impacts on sea trout, Arctic charr and Pacific salmon is included.

Key words

Aquaculture, *Caligus*, disease, *Lepeophtheirus*, life cycle, *Oncorhynchus*, prevalence, parasite abundance, parasite intensity, populations, *Salmo salar*

10.1 Introduction

Wild Atlantic salmon (*Salmo salar*) are parasitised by two species of caligid copepod sea lice (*Lepeophtheirus salmonis* [Fig. 10.1] and *Caligus elongatus*, Kabata 1979, 1984). Historically, sea lice have been observed in rather low numbers on wild salmonids, and few adverse effects on the host have been reported. Since the late 1980s, however, there have



Figure 10.1 Adult salmon lice on a wild, two-sea winter Atlantic salmon (6 kg). Mature females often prefer this area around the anal fin. Salmon lice can cause severe skin lesions in these areas also on adult salmon. Photo: Christopher D. Todd.

been several reports of sea lice epizootics on salmonids in Norway, Scotland, and Ireland, and in more recent years also in Canada (Heuch *et al.* 2005; Revie *et al.* 2009). Infested post-smolts and adult fish often have been reported to be in poor physical condition with some showing severely damaged caudal and dorsal fins and skin lesions. It has been suggested that the apparent increased infestation rate of sea lice on salmonids is correlated with the presence of salmon farms. This has been the focus of a long and controversial debate for some years but management improvements on fish farms have aimed specifically at enhancing husbandry of cultured fish to reduce their infestations of sea lice. This approach also has the additional objective of reducing their potential impact on wild salmonids.

Here the main focus is on the salmon lice (*L. salmonis*), which almost exclusively parasitises salmonids (Kabata 1979, 1984) throughout the North Atlantic. It is also recorded from the North Pacific, where it parasitises all species of Pacific salmon (*Oncorhynchus* spp.). Whilst the emphasis is on the effect of salmon lice on Atlantic salmon performance, valuable additional information on sea lice impacts on sea trout (*Salmo trutta* L.), Arctic charr (*Salvelinus alpinus* L.) and also Pacific salmon (*Oncorhynchus* spp.) is included. Our objective is to give an overview of the sea lice story from Norway, Canada, Ireland and Scotland, and the different experiences and responses of national management bodies and the farming industry to the environmental challenges presented by sea lice.

10.1.1 Sea lice biology

The salmon lice is considered to be restricted to the Northern Hemisphere, and to have a circumpolar distribution (Kabata 1979). Adults are light to dark brown in colour, and the sexes are easily distinguished by body size (females ~11 mm when gravid, males ~6 mm, Schram 1993). The life cycle of the salmon lice (Fig. 10.2) comprises five phases and 10

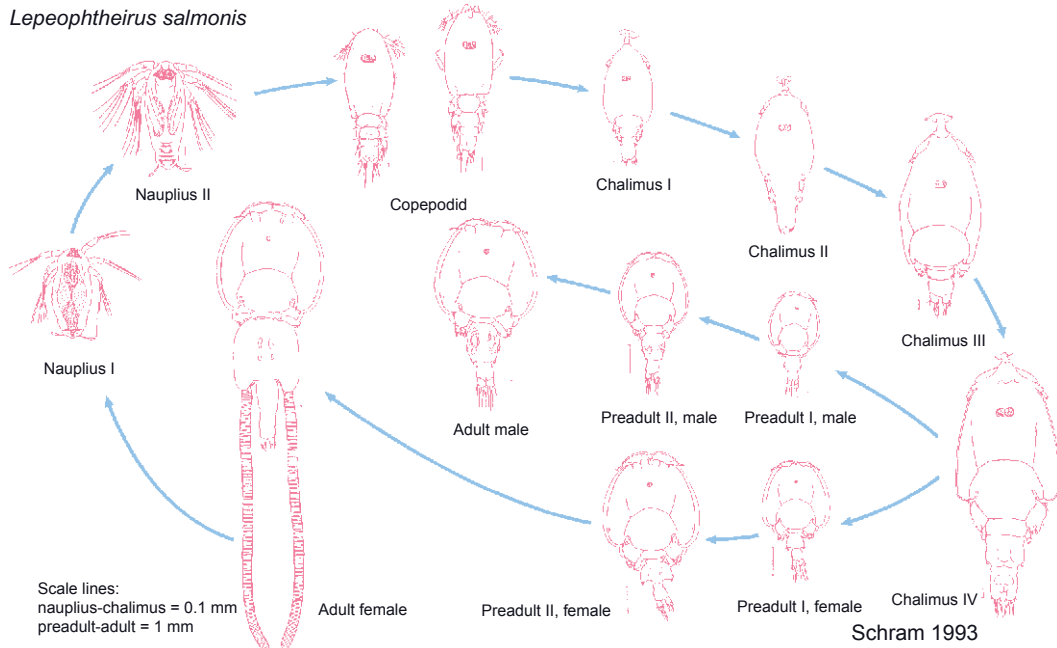


Figure 10.2 The moult stages and life cycle of salmon lice *Lepeophtheirus salmonis*. The gravid female extrudes a pair of eggstrings containing the developing embryos and these are retained to the hatching stage (nauplius I). After two planktonic larval moults host infestation occurs at the final, free-swimming, copepodid stage and the subsequent four chalimus stages all are attached to the host fish by a thread. The pre-adult and final adult stages all are mobile over the host fish. No further moults occur after the adult status is attained (after Schram 1993). Reproduced with permission of the author.

stages; two planktonic nauplius stages, one infective copepodid stage (all non-feeding), four attached chalimus stages, two mobile pre-adult stages, and one adult stage (Johnson & Albright 1991; Schram 1993; Pike & Wadsworth 1999). Sea lice are poorly adapted to hyposaline conditions <20 psu (Bricknell *et al.* 2006) and are shed after a few days when the host fish re-enters fresh water (McLean *et al.* 1990; Finstad *et al.* 1995).

Adult male salmon lice are generally found on the anterior dorsal area of the host, while females prefer the ventral post-anal area (Todd *et al.* 2000). Location on the host is, however, modified by a number of factors (intraspecific competition, host size, lice developmental stage), and unmated adult females often are found in the dorsal anterior region when pairing with adult males (Jaworski & Holm 1992; Pike & Wadsworth 1999). Reproduction in salmon lice is complex. The smaller males develop at a faster rate than females, such that adult males co-occur with pre-adult II females of the same age. Copulatory pair-forming occurs between an adult male and a newly moulted, virgin, adult female or, if not available, a pre-adult II female (Hull *et al.* 1998; Ritchie *et al.* 1996; Pike & Wadsworth 1999). Once a suitable female is found, the male clasps the female's genital segment and applies two external spermatophores on the female's ventral surface (see Pike & Wadsworth 1999 for details). After mating, the long-lived female salmon lice often move to post-anal areas of the host and may extrude up to 11 pairs of sacs with fertilised eggs (Ritchie 1993; Pike & Wadsworth 1999) over a period of months. Early reports indicated *L. salmonis* to

be monogamous and that the attached spermatophores effectively sealed the female's genital openings. DNA paternity analyses have, however, shown promiscuous mating and multiple paternity in at least a proportion of adult females infesting both wild and farmed Atlantic salmon (Todd *et al.* 2005). Because each egg sac may contain 100–1000 eggs (see Pike & Wadsworth 1999 and Nordhagen *et al.* 2000 for details), a large number of offspring may be produced over the female's lifespan and this has implications for the infestation dynamics within farms and between farmed and wild host fish.

Upon hatching, the nauplius I larva is released to the water column. Nauplius I and II are non-feeding, and depend on internal stored reserves for nutrients. The mean duration of the nauplius I is 52.0, 30.5 and 9.2 h at 5, 10 and 15 °C, respectively (Johnson & Albright 1991). The duration of the nauplius II is 170.3, 56.9 and 36.6 h at 5, 10 and 15 °C, respectively (Johnson & Albright 1991), before attaining the moult to the infestation stage, the copepodid.

The copepodid is positively phototactic, and remains non-feeding but is a much more active swimmer than the nauplius. The copepodid has a finite time to locate and infest a host and behavioural positioning of the copepodid at an appropriate depth in the water column probably maximises its likelihood of encountering a salmonid host (Genna *et al.* 2005). Because wild salmonids at sea are surface-orientated (Thorstad *et al.* 2007; Davidsen *et al.* 2008; Plantalech Manel-la *et al.* 2009), copepodids position themselves in the upper water layers (Hevrøy *et al.* 2003). They seem also to perform vertical movements and concentrate at pycnoclines >20 psu and in turbulent water where wild salmonids often migrate and feed (Heuch 1995; Heuch *et al.* 1995). The entire planktonic phase of these three louse stages may last up to 1 month at Norwegian spring temperatures (Heuch *et al.* 2005). This means that in areas with strong currents, for example along open coastlines, the free-swimming and infestation stages are capable of drifting tens to hundreds of kilometres and can be widely dispersed from their point source host fish. The successful copepodid then settles on a passing salmonid, probably through larval swimming responses to the low-frequency pressure waves created by a swimming fish (Genna *et al.* 2005), and initially connects to the host by the prehensile antennae and the maxillipeds (Pike & Wadsworth 1999; Boxaspen 2006). The preferred locations on the host, both for the copepodid and the later chalimus stages, are the fins but chalimi can be found all over the body at high infestation intensities (Jaworski & Holm 1992; Finstad *et al.* 1994; Bjørn & Finstad 1998).

Immediately following infection the copepodid moults into the first of four sessile chalimus stages. The chalimus now is able to feed on the host mucus, skin and body fluids, but remains constrained and attached by the chitinous frontal filament. Feeding-induced skin damage caused by the chalimus stages is therefore restricted, although extensive pathology has been observed at high infestation intensities, especially on the dorsal fin (Bjørn *et al.* 2001; Gargan *et al.* 2003). After the fourth and last chalimus stage the filament is lost and the sea lice moults progressively through two mobile pre-adult stages (I and II, Fig. 10.3), and finally to the adult stage. The time span of the life cycle is strongly temperature-dependent, with a generation time at 10 °C of ~40 d for males and 52 d for females (Johnson & Albright 1991).

10.1.2 General effects of sea lice on fish physiology

The effects of salmon lice on host physiology of Atlantic salmon, sea trout, Arctic charr and Pacific salmon are now well understood (e.g. Grimnes & Jakobsen 1996; Grimnes *et al.*



Figure 10.3 Hatchery-reared Atlantic salmon post-smolt with pre-adult salmon lice. More than 50 lice are dispersed all over the body surface of the fish and feed on the host mucus, skin and body fluids. Infestation intensities at this level will severely impact fish physiology through feeding-induced skin damages and stress. Photo: Bengt Finstad.

1996; Bjørn & Finstad 1997, 1998; Nolan *et al.* 1999; Finstad *et al.* 2000; Bjørn *et al.* 2001; Wagner *et al.* 2004, 2008; Wells *et al.* 2006; Jones *et al.* 2006, 2008; Finstad *et al.* 2007). Major primary, secondary and tertiary physiological effects (Wendelaar Bonga 1997; Iwama *et al.* 2006) – including elevated plasma cortisol (Bjørn & Finstad 1997; Finstad *et al.* 2000) and glucose (Wells *et al.* 2006), reduced osmoregulatory ability (Grimnes & Jakobsen 1996; Bjørn & Finstad 1997; Nolan *et al.* 1999; Finstad *et al.* 2007) and reduced non-specific immunity in the host – occur when the lice develop from the sessile chalimus 4 stage to the mobile first pre-adult stage. Sublethal tertiary effects, such as reduced growth, reduced reproduction, reduced swimming performance and impaired immune defence have also been reported (Bjørn & Finstad 1997; Nolan *et al.* 1999, 2000; Finstad *et al.* 2000; Bjørn *et al.* 2001; Wagner *et al.* 2003, 2004, Tveiten *et al.* in press).

Burdens of >30 chalimus larvae can kill a 40 g Atlantic salmon smolt, once the larvae have developed to the mobile pre-adult stages. This relative intensity of ~ 0.75 lice g⁻¹ body weight suggests that as few as 11 chalimus larvae may have a detrimental effect on 15 g wild salmon smolts (Finstad *et al.* 2000). The consequences for salmon smolts also have been shown by Holst *et al.* (2003) who examined >3000 wild fish taken in the Norwegian Sea for lice, but found none carrying >10 adult lice, further suggesting a lethal dose around this level.

Bjørn & Finstad (1997) showed that infection intensities of >90 salmon lice copepodids, or 50 pre-adult or adult lice, may result in mortality of sea trout post-smolts (60 g). In subsequent studies, Wells *et al.* (2006) concluded that 13 mobile lice fish⁻¹ was the critical abundance which elicited sublethal stress responses in post-smolt sea trout (weight range 19–70 g). Fewer studies have been performed on Arctic charr, but in early laboratory

experiments (Grimnes *et al.* 1996) this species also was found to suffer from stress and mechanical skin damage which resulted in severe osmoregulatory consequences. Reduced growth, increased mortality and reduced total fecundity of Arctic charr have also been recorded among adult spawners (Tveiten *et al.* in press).

Studies on Pacific salmon have shown that the patterns of infestation on these species differ from that observed on the genus *Salmo* (Fast *et al.* 2002). This might indicate that Pacific salmon possess elevated resistance to salmon lice and innate resistance apparently varies among *Oncorhynchus* spp. (Fast *et al.* 2002; Jones *et al.* 2006, 2008), and probably also in response to different parasite species. The mechanisms by which some juvenile *Oncorhynchus* spp. to a certain extent avoid the consequences of sea lice infestations are not well understood, but appear to be associated with inflammation at the site of attachment and the local and systemic elaboration of protein inflammatory cytokines (Johnson & Albright 1992; Jones *et al.* 2006, 2008).

Based on the foregoing, perhaps a conservative and precautionary management approach would be for wild fishery managers to adopt a critical level of <10 mobile lice fish⁻¹ as a conservation target for juvenile Atlantic salmon post-smolt and post-smolt sea trout and Arctic charr in their first year at sea.

10.1.3 General effects of sea lice on fish populations

When the net harm that a parasite causes to the host is severe, parasitic diseases can be major contributors to host mortality rates (e.g. Threlfall 1968; Johnsen & Jensen 1992; Bjørn *et al.* 2001; Krkošek *et al.* 2007a), and even act to regulate host population size (e.g. Anderson & May 1978, 1979, 1981; Tompkins & Begon 1999; Krkošek *et al.* 2007a). However, detecting the effects of parasitism in wild fish populations is inherently difficult (e.g. Anderson & Gordon 1982; Lester 1984). For salmon lice, the registration and quantification of effects in wild salmonids have been hampered by difficulties in capturing infested fish (Holst & McDonald 2000; Bjørn *et al.* 2001), as well as a lack of detailed knowledge of salmonid post-smolt marine ecology (Moore *et al.* 2000) and salmon lice epidemiology both in intensively farmed and unfarmed fjords (Heuch *et al.* 2005). Atlantic salmon post-smolts may be infested initially by salmon lice during their short transit period through fjords and outer coastal areas (Finstad *et al.* 2000; Hvidsten *et al.* 2007). In Norway, sea trout essentially remain within the inner fjord systems throughout their marine residence (e.g. Jonsson 1985; Knutsen *et al.* 2001; Finstad *et al.* 2005; Thorstad *et al.* 2007) and may be susceptible to repeated re-infestation with salmon lice. Pacific *Oncorhynchus* spp. display rather different migratory strategies (Groot & Margolis 1998). Pink and chum salmon tend to reside in coastal waters for longer than the three other Pacific species and may therefore be especially vulnerable to nearshore sources of infestation. None the less, just as for wild Atlantic salmon, all these Pacific species might be subject to salmon lice infestation in their earliest marine phase.

In the pre-farming situation, or in areas without fish farms, salmon lice epidemics in wild salmonids have seldom been reported (White 1940; Johnson *et al.* 1996). Salmon lice have typically been found at rather high prevalence but low intensity, probably also in a quite regulated and stable host-parasite system; few adverse effects on the host population have been observed (Boxshall 1974; Pemberton 1976; Tingley *et al.* 1997; Bjørn *et al.* 2001; Krkošek *et al.* 2005, 2006a, b). Under such stable host-parasite situations, if host

population densities decline either because of parasite epidemics or for other unrelated reasons, this will reduce the parasite success. This feedback mechanism prevents negative effects of the parasite in weak host populations. However, salmon farming has fundamentally changed the number of salmon lice hosts and also the epidemiology of the host–parasite system (Heuch & Mo 2001; Heuch *et al.* 2005). Even if wild salmon populations decline in abundance, the remaining individuals can be exposed to large numbers of lice being produced in farms. This external input of lice may therefore produce negative population growth rates in the salmon even for very small population sizes, when one would normally expect positive population growth that prevents extinctions (Hindar *et al.* 2011 [Chapter 12]). In Norway, salmon lice hosts are now up to 400 times more abundant than they were before fish farming (Heuch *et al.* 2005; Anon 2009), permitting continuous production of the infestation stages into the surrounding waters (Costello *et al.* 1993; Costello 2009a). As plankton, the lice larvae will drift and be dispersed over potentially long distances and aggregate in various fjords and nearshore coastal areas. These locations are exploited by feeding and migrating post-smolts. Increased encounter rates between the parasite and host are therefore highly facilitated compared to the pre-farming situation, and severely increased infestation intensities have been observed in intensively farmed areas (Bjørn *et al.* 2001, 2007; Krkošek *et al.* 2005, 2006a, b). In combination with the relatively high salmon lice pathology (see Section 10.1.2), high levels of direct parasite-induced mortality can be expected. In Norway, direct parasite-induced mortality in Atlantic salmon post-smolts has been predicted to vary between 0 and 95% among years and fjords of the intensively farmed area of western Norway (Holst *et al.* 2003; Bjørn *et al.* 2009). Similar mortality estimates have been predicted for sea trout in intensively farmed areas in northern Norway (Bjørn *et al.* 2001), as well as for pink salmon in areas of western Canada (Krkošek *et al.* 2007a, b). Salmon lice epidemics may, therefore, if not controlled, be capable of decimating host populations in intensively used fish farming areas.

10.2 The sea lice story from Norway

10.2.1 Historical data

Soon after salmon farming was established in Norway in the 1970s, both salmon lice and *Caligus* sp. emerged as a problem (Heuch *et al.* 2003, 2005, Fig. 10.4). In 1990, sea trout in salmon farming areas along the coasts of Norway were observed returning to rivers and estuaries shortly after they had descended to sea. These ‘prematurely returning’ sea trout were heavily infested with salmon lice, and the infestation was associated with significant host skin pathology and observations of badly emaciated individuals (Jakobsen *et al.* 1992; Finstad *et al.* 1992; Finstad 1993; Finstad *et al.* 1994; Birkeland 1996; Birkeland & Jakobsen 1997). Norwegian investigations in the early 1990s indicated that infestation of sea lice larvae also occurred on fjord-migrating Atlantic salmon post-smolts descending the long and intensively farmed fjords of western and central Norway (Finstad *et al.* 1994, 2000; Holst *et al.* 2003), and also that Arctic charr of northern Norway probably were subject to heavy infestations in areas with salmon farms (Finstad 1993; Bjørn *et al.* 2001). It therefore seems likely that salmon lice epidemics may be partly responsible for the decline of certain populations of wild anadromous salmonids along the Norwegian coast.



Figure 10.4 A large fish farm in Norway, which often contains approximately 1 million fish, or 5000 tonnes. Farms are usually located in fjords or sheltered coastal areas and fish are constrained in open net-pens, clustered individually, or like in this picture, inside a larger steel frame. Photo: John B. Pedersen, reproduced with permission of Egil Lund.

10.2.2 Infestation levels of Atlantic salmon post-smolts

In Norwegian waters, reliable monitoring of sea lice infestation levels on wild Atlantic salmon post-smolts has been undertaken by means of a specially designed trawl, the Ocean Fish Lift (Holst & McDonald 2000). The results have shown large variations in salmon louse prevalence and mean intensity among years and fjords.

The farmed Sognefjord of western Norway was trawled annually between 1998 and 2004, and mean infestation intensities have varied from 1 to 104 lice fish⁻¹. Based on a conservative mortality threshold at 15 lice fish⁻¹, parasite-induced mortality has been predicted to vary between 0 and 95% (Holst *et al.* 2003, 2005). In the later years (2002 to 2004), the situation improved (<2.3 lice fish⁻¹), presumably because of improved husbandry measures on farms during winter and spring (Holst *et al.* 2005). In another intensively farmed fjord of western Norway (Hardangerfjord), results from 2004 to 2006 indicated only low infestation levels (0.6 to 1.9 lice fish⁻¹). During these years synchronised delousing of fish farms in the fjord system took place. No significant differences were recorded before (2004) and after (2005 and 2006) delousing. However, in 2007 and especially 2008, prevalence (90%) and intensity (33) had increased, indicating that the measures taken had not been sufficient (Bjørn *et al.* 2008, 2009).

In the unfarmed Trondheimsfjord (central Norway), sea lice burdens on post-smolt Atlantic salmon have been monitored since 1992 (Finstad *et al.* 1994, 2000; Hvidsten *et al.* 2007). The results from this long-term study show that in some years (1992, 1998 and 2003) there was a moderate infestation pressure (e.g. in 1998, 11% had >10 lice) (Finstad *et al.* 2000; Hvidsten *et al.* 2007). For most of the other years infestations were low, and no

negative effects on smolts were assumed (Hvidsten *et al.* 2007; Bjørn *et al.* 2007, 2008, 2009).

In northern Norway, the intensively farmed Altafjord was trawled annually between 2000 and 2004, and the unfarmed Malangen in 2000 to 2002 (Rikardsen *et al.* 2004; Holst *et al.* 2005; Bjørn *et al.* 2007). These results showed almost no salmon lice on migrating Atlantic salmon post-smolts in either fjord (Holst *et al.* 2005; Bjørn *et al.* 2007). Sea trout and Arctic charr were, however, moderately infested later in the summer in both fjord systems. This indicates that a ‘mismatch’ exists between the time of migration of wild Atlantic post-smolts and the seasonal rise in infestation pressure in northern fjords, despite intense farming activity (Bjørn *et al.* 2007).

10.2.3 Sea lice effects on Atlantic salmon – adult returns

Individually tagged salmon and sea trout smolts have been experimentally protected against lice by an in-feed medication (Slice® – emamectin benzoate), or bath treatment (Substance EX, Pharmaq; this protects fish for several weeks through the prevention of synthesis of chitin by sea lice). Both protected and unprotected smolts were released in the vicinity of their native river to investigate the effects of salmon lice on populations of Atlantic salmon. Results from Agdenes (central Norway, Hvidsten *et al.* 2007) and Daleelva (southwest Norway, Finstad & Jonsson 2001) for Atlantic salmon show that in years with high salmon lice infestation pressure, the returns of protected fish have been higher than returns of unprotected control groups. These studies are supported by Skilbrei & Vennevik (2006), who also showed highest recapture rates in the treated groups, and Hazon *et al.* (2006), who showed enhanced marine growth in protected compared to unprotected fish.

10.3 The sea lice story from Canada

10.3.1 Historical data

The Atlantic salmon farming industry developed in very different circumstances on the east and west coasts of Canada (Anderson 2007). On the east coast, farming began in the early 1980s, and there is an intense concentration of the industry principally in an area around the border between Maine (USA) and New Brunswick, with limited development in other Canadian Atlantic Provinces. This had major implications for the transmission of pathogens. The sea lice epidemic did not erupt until after 1992, and infestations spread rapidly among farm sites because of the concentrated nature of the industry (MacKinnon 1993). By 1994, sea lice were costing the industry ~20% of the yearly market value of the fish, with *L. salmonis* being the principal cause of damage (MacKinnon 1997).

The larger west coast (Pacific) industry is, with the exception of a small US site in Washington State, located entirely in the Canadian Province of British Columbia (Anderson 2007). The British Columbia coast has favourable conditions for salmon farming over much larger areas than does the Canadian east coast and farms commonly are separated by tens of kilometres. The west coast industry dates back to the late 1960s (USA) and early 1970s (Canada) with the culturing of native Pacific salmonids. The Canadian west coast switch to principally Atlantic salmon production was for technical and market reasons and

began in the mid-1980s. There have been no reports from the west coast salmon farming industry of a catastrophic, industry-wide sea lice infestation similar to that on the east coast, and this may be due to the greater separation among salmon farms on the west coast. However, sea lice do parasitise both wild and farmed salmon in this region, and the industry is required by the British Columbia government to monitor farm fish for lice burdens, and to treat their fish when pre-set thresholds are reached.

10.3.2 Effects of sea lice on Atlantic salmon – east coast

Limited work has been done in this region to examine the impacts of lice from farm sites upon wild Atlantic salmon populations. Salmon farming has been suggested to be a possible contributor to observed recent declines in the area's wild salmon populations (Cairns 2001). The two studies that have examined the issue have failed to document a link between sea lice from farms and the present low numbers of wild Atlantic salmon. Carr & Whoriskey (2004) assessed sea lice burdens on wild fish returning to a river in the centre of the east coast farming industry, and found the majority of returning adults in all years monitored since 1992 generally had low lice burdens, even in the years when the industry was suffering a lice epidemic. However, that study did not address lice infestations that could have impacted the smaller and more susceptible smolts as they emigrated to sea. Lacroix & Knox (2005) captured wild, hatchery origin, and escaped farmed post-smolts over a three-year period (2001–2003) in proximity to the salmon farming industry, soon after those post-smolts had entered the ocean. No *L. salmonis* were found on any of the 398 post-smolts examined, and prevalences of *C. elongatus* ranged from only 2.4 to 4.4%, with a maximum infection intensity of 1 parasite fish⁻¹.

Presently, in the east coast salmon farming region, local wild Atlantic salmon populations are close to biological extinction. Despite this, *L. salmonis* continues to be an annual problem for the region's salmon farming industry. This suggests that, at least in the Canadian east coast region, ongoing *L. salmonis* infestations in the salmon farming industry originate from sea lice occurring on farmed fish, rather than resulting from an annual infestation from wild fish. This has important implications for the development of lice resistance to prophylactic treatments.

10.3.3 Effects of sea lice on salmonids – west coast

The issue of the impacts of farm-origin sea lice upon wild Pacific salmon on the Canadian west coast remains highly controversial. Precipitous declines in returns of wild pink and chum salmon to the Broughton Archipelago region of British Columbia were linked by a series of studies to the presence of lice from salmon farms in this region (Morton *et al.* 2004; Morton & Routledge 2005; Krkošek *et al.* 2005, 2006a, 2007a, b; Orr 2007). However, many of these links were correlative, or the data sets used were incomplete, and this has led some investigators to question the extent of the declines of Pacific salmon abundance in the Broughton Archipelago and the role played by sea lice (Beamish *et al.* 2005, 2006; Brooks 2005; Jones *et al.* 2006; Brooks & Jones 2008). Rebuttals have been provided for these critiques (Krkošek *et al.* 2006b, 2008), and new research suggests that elevated levels of sea lice (*L. salmonis* and/or *C. clemensi*) are occurring in pink, chum and sockeye salmon, and on Pacific herring (*Clupea pallasii*; the louse species on Pacific herring was *C. clemensi*) in

other west coast salmon farming areas outside of the immediate Broughton Archipelago region (Morton *et al.* 2008). The controversy has stimulated a burst of new sea lice research especially in the Broughton area, but this effort may fail to provide the definitive evidence that some are seeking (Ackerman 2008; Harvey 2008). However, a mounting weight of scientific evidence points to farm-origin lice having impacts on the wild salmon populations in the region.

10.4 The sea lice story from Ireland

10.4.1 Effects of sea lice on Atlantic salmon

Little information has been available on the impact of sea lice from marine salmon farms on wild Atlantic salmon stocks in Irish waters. Salmon rod catch data for a number of mid-western rivers have shown large reductions in catches of one-sea-winter adults (grilse) in years following high sea lice levels on marine salmon farms, anecdotally suggesting a link between salmon smolt migration success and an impact from sea lice infestation on marine survival. Preliminary data supporting this possibility became available when survey netting in an aquaculture bay in the west (Killary harbour) recorded salmon smolts with low numbers of juvenile sea lice (Anon. 2004). This was the first record of sea lice on salmon smolts in Ireland. Furthermore, a significantly higher adult return rate of experimentally Slice[®]-treated salmon smolts has been observed in areas impacted by salmon farms (Hazon *et al.* 2006). These data suggest that protection from sea lice infestation, and hence reduced early marine mortality, was beneficial to smolts in the treated groups.

10.4.2 Effects of sea lice on sea trout

In contrast to the limited information on effects of sea lice on Atlantic salmon, there has been a large body of research in Ireland targeted at quantifying the impact of sea lice from salmon aquaculture on wild sea trout stocks. The best documented sea trout angling fisheries are located in the mid-western area including the Connemara District. Salmon aquaculture began to develop in bays in mid-western Ireland in the early 1980s, and by the end of that decade ~7000 tonnes of farmed salmon was produced. Concurrent with the development of salmon farming in western bays, heavy sea lice infestations were observed on sea trout returning to rivers. In late May 1989, sea trout were first observed in the lower pools of the Delphi fishery with heavy sea louse infestations (Anon. 1992). Sampling of rivers began in 1990 to determine if this phenomenon was widespread, and prematurely returning sea trout post-smolts and some sea trout kelts were recorded with infestations of predominantly juvenile sea lice in all rivers sampled (Anon. 1992), indicating recent transmission (Tully *et al.* 1993a, b). This has been linked with the development of marine salmon farming in the mid-west zone at that time (Gargan *et al.* 2003).

The occurrence in the late 1980s of heavy sea lice infestations on sea trout in mid-western rivers entering aquaculture bays also coincided with stock collapses. Annual sea trout rod catches for the period 1985–2003 for 22 mid-western fisheries displayed an overall trend for the period of decreasing catches until 1988, followed by a stock collapse in 1989/90 (Gargan *et al.* 2007). The Connemara District rod catch, which comprises a large proportion

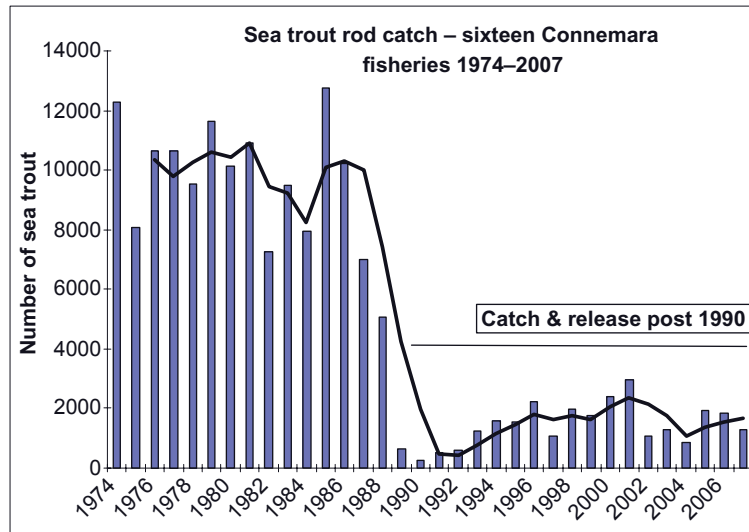


Figure 10.5 Sea trout rod catch, sixteen Connemara fisheries, 1974–2007. Data from Western Regional Fisheries Board, Weir Lodge, Earls Island, Galway, Ireland. Reproduced with permission from P. Gargan.

of the mid-western data (Fig. 10.5), fell from an average of 9,570 sea trout over the period 1974–88 to 646 in 1989 and only 240 in 1990.

The ‘sea trout problem’ observed in fisheries in the mid-western region can thus be summarised as follows: premature return to fresh water of sea trout post-smolts with heavy sea lice infestation, infestations predominantly of juvenile sea lice, a collapse in sea trout rod catches, and a change in sea trout population age structure (Anon. 1994a, b). The history of the mid-western sea trout stock collapse and subsequent events has been well documented (Poole *et al.* 1996; Whelan 1993; Gargan 2000).

Salmon aquaculture also developed to the north in Donegal (Ballyshannon & Letterkenny Districts) and to the south in the Kerry District by the late 1980s. In the early 1990s premature returning lice-infested sea trout also were recorded in rivers entering salmon aquaculture bays in Donegal and south Kerry (Tully *et al.* 1999).

10.5 The sea lice story from Scotland

10.5.1 Historical data

Salmon farming in Scotland was developed initially during the 1960s by Unilever at a site near Lochailort. The first commercial smolts were put to sea in 1972, and as early as in 1976 it became apparent that *L. salmonis* was problematic to the industry (Rae 2002). In Scotland the greater public concern and focus of research has been on the impacts of sea lice (especially *L. salmonis*) on wild sea trout rather than on wild Atlantic salmon. To a large extent this is a reflection of the considerable difficulty of capturing wild salmon smolts once they have emigrated from their home river estuary, and the rapidity with which they

leave coastal waters for the open ocean (see Section 10.2.2). Thus, due to methodological limitations, sea lice impact studies of Atlantic salmon in Scottish waters have relied on monitoring of infestation levels of returning adults.

10.5.2 Effects of sea lice on Atlantic salmon

Wild salmonids around the British Isles maintain a population of sea lice throughout the year (Tingley *et al.* 1997; Todd *et al.* 2000; Copley *et al.* 2005) and all life stages of *L. salmonis* occur on wild salmon on their oceanic feeding grounds. In the Norwegian Sea, north of the Faroes, Jacobsen & Gaard (1997) reported *L. salmonis* prevalence on wild salmon at >99%. Similarly, Todd *et al.* (2006) recorded 100% prevalence of wild one-sea-winter (1SW) salmon returning to Scotland, and Todd *et al.* (2000) showed that returning two-sea-winter (2SW) adults bear heavier average infestations than do 1SW fish. Cross-infection in the open ocean is therefore a persistent process throughout the marine migrations of wild salmon. The abundance of *L. salmonis* on wild 1SW salmon returning to Scotland typically is high and the annual geometric mean varies between 17 and 31 mobile *L. salmonis* fish⁻¹ (Todd *et al.* 2006); individuals have been recorded with total sea lice burdens (*L. salmonis* plus *Caligus elongatus*) as high as 150, and yet appear to be in good physiological condition.

As far as can be judged, the natural salmonid host–sea lice association is stable but it has to be reiterated that, by definition, monitoring time series of returning adult wild salmon, such as those reported by Todd *et al.* (2006), are confined to surviving fish. No inferences can be drawn on the causes of mortality of post-smolts in the absence of information on the newly migrating smolt stage.

Time series monitoring of sea lice infestations of adult wild salmon in Scotland has been best achieved by collaboration with commercial salmon netsmen who operate in fixed locations and fish gear in a consistent manner, year on year. But their fishing season is strictly regulated, and legally (as well as voluntarily) excludes the autumn, winter and early spring months. An additional problem for scientific monitoring is that most commercial netting of wild salmon in Scotland now is focused on estuarine (or ‘in river’) locations, and the use of seine nets. With seine nets the fish are abraded against the net meshes and thrash in the shallow water as the net is retrieved. Counts of even the sessile chalimus stages, let alone the mobile stages, of caligids are therefore very prone to error for seine-netted fish. But equally important is the influence of brackish water on sea lice: sea lice counts from hyposaline locations (be they shorelines of semi-enclosed sea lochs, river outfalls, or areas adjacent to the estuarine reaches of rivers (MacKenzie *et al.* 1998; Marshall 2003; Urquhart *et al.* 2008)) are liable to be severe underestimates of true abundances of *L. salmonis* and especially *C. elongatus* which perhaps has the greater propensity to detach from the host fish in response to reduced salinity (Todd *et al.* 2006).

10.6 Management

The global economic costs of sea lice to the salmonid farming industry are estimated to be ~€305 million (Costello 2009b) and are a considerable challenge for the farming industry. In addition, sea lice have a significant influence on wild fish globally (Revie *et al.* 2009) and

appropriate treatment regimes in fish farms are needed to reduce the impact of sea lice on wild fish populations. Here we summarise the differing management structures for sea lice treatment by the aquaculture industries in Norway, Canada, Ireland and Scotland.

10.6.1 Sea lice management in Norway

The routine monitoring of sea lice on Norwegian fish farms in recent years has entailed counts of parasites at water temperatures $>4^{\circ}\text{C}$ and the results are reported to the Norwegian Food Safety Authority (NFSA). A new 2009 regulation requires that the average numbers of lice on each salmon in a net pen shall not exceed either 0.5 females (with or without eggstrings) or >3 mobile stages (all mobile stages, excluding females) during the period 1 January–31 August and shall not exceed 1 female or >5 mobile stages during the period 1 September–31 December. In addition, mandatory and synchronised delousing during late autumn and early spring at very low lice levels (>0.3 or 0.1 female lice) are planned along most of the Norwegian coastline to reduce infestation pressure during the spring run of wild salmonids (Stian Johnsen, Norwegian Food Safety Authority, pers. comm.). Several chemicals, including Slice® (Emamectin benzoate), are licensed and routinely used for lice treatment in farms (Heuch *et al.* 2003; Revie *et al.* 2009). However, increasing observations of treatment failure of the most used medicines in Norway are of considerable concern (Nilsen *et al.* 2008).

The establishment of Norwegian National Salmon Fjords (NNSF), which are protected fjord areas in which salmon farming is prohibited, was a further management effort to protect wild salmonids from sea lice impacts (Anon 2006). Some NNSFs, especially the larger systems, appear to have been effective at protecting local wild salmonid populations, but a longer time-series of data is needed before firm conclusions can be drawn. Furthermore, irrespective of the designation of NNSFs, migrating salmonids do commonly encounter a relatively high infection pressure from sea lice once they have migrated to the outer fjords and coastal areas.

10.6.2 Sea lice management in Canada

On the Canadian east coast, a monitoring system has been developed for farms whereby sea lice counts are conducted in December and May and cages having >5 pre-adult lice fish^{-1} , or >0.25 gravid female lice fish^{-1} are required to be treated (National Working Group on Integrated Management of Sea Lice 2003). Slice® is presently the only effective treatment agent available for sea lice. The industry has implemented a coordinated Bay Area Management Strategy, in which all farms within a given region (1) culture fish of the same age, (2) coordinate their fish health treatments, and, perhaps most importantly, (3) synchronously fallow for a full year all sites in the region at the end of a two-year grow-out, in order to break parasite and pathogen life cycles (Chang *et al.* 2007). These measures seem to have been beneficial (e.g., Westcott *et al.* 2008) because there have been no reports of industry-wide sea lice outbreaks since implementation.

For the Canadian west coast, monthly counts of sea lice are required at all farms. Since 2005, the aquaculture industry in British Columbia has had a year-round lice trigger level of 3 mobile lice fish^{-1} . During the period of out-migration of wild salmon smolts, any farm that reaches the trigger level must take action, either through treatment (Slice®) or harvest

of its fish. At other times of year the first response to the trigger level can be to increase the frequency of lice counts to bi-weekly intervals. If lice levels continue to increase, treatment or harvest will be required.

10.6.3 Sea lice management in Ireland

Each year-class of salmon on each farm is monitored for sea lice 14 times a year, twice a month during March, April and May and monthly for the remainder of the year. The critical period for wild salmonid (Atlantic salmon and sea trout) smolt migration to sea is considered to be from March to May. The sea lice monitoring and control strategy sets out lice treatment trigger levels for salmon farms. Treatment triggers in spring were set at 0.3–0.5 ovigerous female lice fish⁻¹. Outside the critical spring period, a level of 2 ovigerous females acts as a trigger for treatment. If monitoring indicates that these trigger levels have been exceeded, fish farmers are instructed to treat for salmon lice. One of the purposes of monitoring is to provide management information, at the earliest opportunity, to drive implementation of the control and management of sea lice. The sea lice monitoring and control strategy has five principal components: (1) separation of generations, (2) annual fallowing of sites, (3) early harvest of two-sea-winter fish, (4) targeted treatment regimes, including synchronous treatments, and (5) agreed husbandry practices.

In response to severe sea lice infestations on salmon farms in 2007, a new strategy (Anon. 2008) is being implemented as the mechanism to achieve effective sea lice control on salmon farms in a ‘real time’ management regime. The new strategy sets out a number of initiatives which need to be addressed to ensure effective sea lice management on Irish salmon farms. Among these strategies are single-generation sites, ‘all-in all-out’ bay-by-bay production and a new approach to the use of licensed sites.

10.6.4 Sea lice management in Scotland

A 10-year retrospective (Lees *et al.* 2008a) has recently summarised the overall levels and patterns of sea lice infestation on Scottish farmed salmon. In general, the levels of sea lice (predominantly *L. salmonis*, but to a lesser extent also *C. elongatus*) on farms have dropped and become more effectively controlled (Revie *et al.* 2002a, b). This is due partly to industry access to more efficacious in-feed chemical treatments (e.g. Slice®), but also to the establishment of Area Management Agreements (AMAs) involving both the industry and local wild fishery interests (Revie *et al.* 2003; McKenzie *et al.* 2004). These studies have taken place despite the fact that there is no statutory requirement to publish farm sea lice data in any public forum. The Scottish model, based on the creations of AMAs (see also below), thus provides an interesting alternative approach to the statutory counting and reporting that happens in, for example, Ireland (Revie *et al.* 2005a; 2007).

The range of sea lice management strategies in Scotland, and the diversity of chemotherapeutic treatments applied over the years, has resulted in an overall decrease in sea lice infestation problems on farms over the past decade, but there is some evidence of changing efficacy of the currently most widely used medicine, Slice® (Lees *et al.* 2008b, c). Between 2002 and 2006, there was evidence of decreasing efficacy for the 0 to 83 day period following treatment. Further analysis and modelling of the efficacy of available medicines and how they are used in the field is required to determine if observed patterns are consistent with

resistance developing and what impacts this might have on best practice (Revie *et al.* 2005b; Robbins *et al.* 2010). Biological lice treatment by use of cleaner fish (wrasses of the family Labridae; Treasurer 1994, 2002; Costello 1993, 2006) has been successfully applied over many years (Revie *et al.* 2009), with the goldsinny wrasse (*Ctenolabrus rupestris*) the most widely used in Ireland, Scotland and Norway.

10.7 Concluding remarks

Sea lice have historically been observed in low numbers on wild salmonids, and few adverse effects on the host have been reported. However, since the late 1980s, in parallel with the expansion of fish farming, there have been several reports of marked sea lice outbreaks on salmonids in Norway, Canada, Ireland and Scotland. Infested post-smolts and adult fish have often been reported to be in poor physical condition, with some having severely damaged caudal and dorsal fins and skin lesions.

The risks and consequences of lice infestation vary according to the species of parasite and host fish. Amongst other factors, these will depend both on the encounter rate between the host and the infective parasite stage as well as the host's susceptibility to infestation, and specific differences in host life-history and migratory behaviour. The latter may have especially important implications on the risks of individual host fish to salmon lice infestation. The smolt migrations of Atlantic salmon, sea trout and Arctic charr usually extend over a 3- to 7-week period between April and July. The timing varies among species and populations and is especially influenced by latitude. The final 'decision' for a smolt to migrate to sea is determined by environmental factors including water temperature, light levels, photoperiod and water discharge during springtime, resulting in annual and regional variation in the peak of the migration for each species. The risks of sea lice infestation are similarly likely to vary geographically and amongst host species.

Given the frequently high numbers of gravid *L. salmonis* carried by the large numbers of cultured fish throughout the year, it is likely that the development of the salmon aquaculture industry has led to changes in the natural host-parasite relationship, and made possible the production of large numbers of the infective dispersal lice stages over and above the natural production of lice by wild salmonids. As planktonic organisms, these larvae drift and disperse over large distances. The density of infective salmon lice stages is, therefore, likely to be greatest in nearshore coastal areas and enclosed fjords that are subject to constrained tidal flushing. These locations, which are ideal for the location of farm net pens, also are exploited by feeding and migrating post-smolts and this inevitably may lead to increased potential encounter rates between the parasite and the host.

Management measures to reduce farmed to wild infestation pressure have been a priority of the aquaculture industry in the various Northern Hemisphere countries. Somewhat different delousing strategies have been developed and include the use both of chemicals and biological treatments. These are variously underpinned by governmental regulations with respect to 'legal' lice levels (treatment triggers) on fish in cages, site fallowing, separation of culture generations, the introduction of synchronised delousing, and single bay/area management. Yet, in areas subject to intensive salmon aquaculture, the total biomass of farmed salmon in a given region may be so high that even ensuring very low levels of sea lice on each farmed fish may not be sufficient to reduce the overall infestation pressure on wild fish

to a sustainable level. Further research into basic lice biology, epidemiology, vaccine development, new chemicals and biological treatment methods, as well as more optimal use of existing treatments, modelling of 'safe farming sites' and development of 'farm production-infestation risk' carrying capacity models, are urgently needed to reduce infestation pressure to a sustainable level. If not, a reduced production of farmed salmonids or a change to closed containment farms in the most affected areas may be necessary.

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11

Variation in Population Size through Time and Space: Theory and Recent Empirical Advances from Atlantic Salmon

Sigurd Einum & Keith H. Nislow

Abstract

A major challenge for ecologists is to understand the underlying mechanisms and processes that shape population size variability. Here we review the basic theoretical and empirical components of our understanding of such variability for Atlantic salmon, including population dynamics models and empirical documentation of juvenile density dependence. We then highlight three major issues that we feel deserve particular emphasis. First, there is a need to distinguish between environmental factors that act directly on population growth rates *vs.* those that act on the habitat's carrying capacity. Both these possibilities appear plausible for a range of environmental factors, and both can produce fluctuation in population size over time, but they are undistinguishable *a priori*. We illustrate this using water discharge data combined with a habitat model as an example. Second, we need to understand how the intensity of juvenile competition, and hence the timing of density dependence, changes throughout juvenile life. At present, evidence appears mostly to be consistent with an early phase (first summer) of density-dependent mortality followed by density-independent losses until smoltification, but the generality based on the few existing studies remains uncertain. Finally, we need to acknowledge the potential for spatial density heterogeneity within populations, particularly during early juvenile stages, to determine levels of density-dependent mortality. Incorporating the current knowledge regarding these three issues and obtaining further empirical data will yield a more comprehensive understanding of Atlantic salmon population dynamics in general, and provide a framework within which management of specific populations can be developed.

Key words

Brown trout, environmental stochasticity, ideal free distribution, logistic growth, niche shift, ontogenetic, population regulation, *Salmo salar*, *Salmo trutta*, self-thinning

11.1 Introduction

Why does salmon population size vary among rivers? And what causes populations to vary in size among years? What happens to the salmon population if we alter particular

characteristics of the physical habitat (Fig. 11.1)? What can be done to increase the natural production of salmon in a given river?

These are all questions that are commonly encountered among salmon scientists, managers and anglers. Unfortunately, clear answers are much less common. Admittedly, this is true for most organisms. However, there exists a solid theoretical framework for addressing such questions, which lies within the realm of population dynamics (Box 11.1). Our understanding of the important processes determining the production of salmon in rivers has increased

Box 11.1 Definitions

Carrying capacity (K): The maximum population size a given environment can accommodate.

Density compensation: A decrease in population growth rate with increasing density.

Density dependence: A feedback mechanism whereby demographic rates (births, deaths) depends on density.

Density depensation: A decrease in population growth rate with decreasing density.

Environmental stochasticity: variation in demographic rates (births, deaths, migration) in response to factors external to the population.

Maximum population growth rate (r): a theoretical quantity describing population growth rate under given environmental conditions (i.e. mean environmental conditions of habitat inhabited by a given population) in the absence of density effects.

Ontogeny: The development of an individual organism from embryo to adult.

Population dynamics: The study of short- and long-term changes in numbers of individuals within populations.

Population growth rate: The change in population size over time.

Population regulation: The prevention of unbounded deviation in population size from equilibrium or a trend.

Self-thinning: a continuously working density-dependent mortality that causes a decrease in population abundance as its per capita resource requirements (food or space) increase with increasing body size.



Figure 11.1 Juvenile Atlantic salmon emerge from nests containing hundreds of eggs, thus creating localised patches of high density. This causes intense competition and high mortality rates during the first few weeks of their lives. However, whether measures implemented to change the mortality rate during this period influence smolt production depends on the nature of density dependence throughout the juvenile stage. This exemplifies how development of a successful management strategy depends on detailed knowledge of population dynamics. Photo: S. Einum.

considerably through time, and perhaps particularly over the last decade. Thus, the lack of reliable answers to the types of questions posed above may primarily be due to missing site-specific empirical data rather than a failure to understand the important general mechanisms. Yet, there is great promise in having a strong theoretical framework, because it enables us to ask relevant questions and collect relevant data.

The core of this theoretical framework is the concept of density dependence (Box 11.2). For a population experiencing density dependence, a high density of individuals causes demographic rates such as fecundity or survival to decrease. Conversely, a low density causes these rates to increase. ‘Low’ and ‘high’ here refer to the density compared to the carrying capacity (Box 11.1) of the specific population. Thus, if we are able to understand and quantify how the carrying capacity varies among rivers and within rivers over time (including effects of changes in the environment), and how environmental conditions disturb populations, we should be heading in the right direction towards answering questions such as those posed at the beginning of this chapter.

11.2 Temporal variation in Atlantic salmon abundance

As for any organism, populations of Atlantic salmon vary in size over time. A major challenge for ecologists has been to understand the processes that shape such variability. Year-to-year variation in environmental conditions is likely to be causing variation in survival rates both in fresh water and at sea (for review of Atlantic salmon survival rates see Hutchings & Jones 1998). Thus, populations may fluctuate to different degrees due to differences in the magnitude of environmental variation. However, do different populations also differ in their sensitivity to such variation? In a comparative study of salmonids, Einum *et al.* (2003) found significant among-species variation in temporal variation of adult counts (Fig. 11.2). Atlantic, chinook (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*)

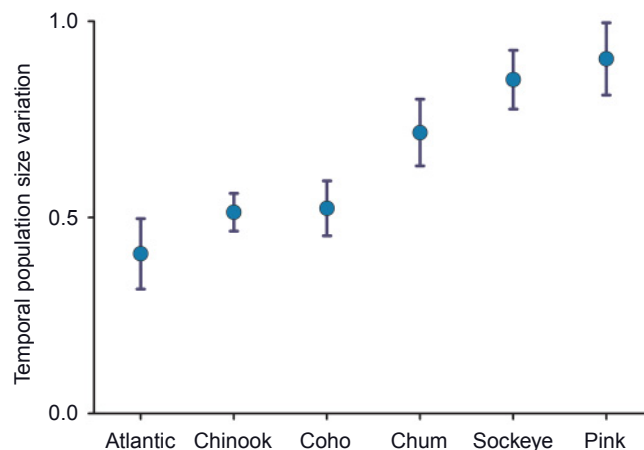


Figure 11.2 Temporal (among-year) population size variation (mean \pm SE) in Atlantic salmon and five Pacific salmon species after adjustment for mean population sizes, numbers of years sampled, and long-term linear trends. In addition to the differences among species shown here, larger populations were less variable when comparing within species. From Einum *et al.* 2003.

were less variable than sockeye (*O. nerka*) and pink salmon (*O. gorbuscha*), with chum salmon (*O. keta*) being intermediate.

Although causal explanations for such differences among species are hard to test due to the pronounced differences in life-histories and habitat use, it was speculated that the timing of migration to the marine environment may contribute to these observed patterns. Whereas Atlantic, coho and components of chinook salmon populations typically spend substantial amounts of time (months to years) growing in rivers or estuaries prior to their migration to sea, pink and chum salmon migrate to sea shortly after they emerge from their gravel nests. Thus, due to their small size at migration, pink and chum salmon may be more susceptible to temporal variation in the marine environment of coastal areas (e.g. temperature, prey abundance, predation) than are the larger juveniles of Atlantic, coho or chinook salmon. Circumstantial support for this hypothesis comes from release experiments of Atlantic salmon smolts, where annual variability in survival decreased with increasing smolt size (Salminen *et al.* 1995). At first glance, sockeye salmon do not appear to fit this pattern because they migrate to sea at a large size. However, shortly after emergence they undertake a migration from their natal river to a lake, and may thus experience an associated temporal variability in survival, although somewhat diminished relative to that experienced by pink and chum salmon migrating to sea. Moreover, the mean variability in the sockeye salmon was highly influenced by one of the few sockeye populations that shows strong cyclic fluctuations, the reasons for which remain unclear (see Myers *et al.* 1998).

Given the observed temporal variation in Atlantic salmon population sizes, is it conceivable that changes in population size from one year to the next are independent of population density? Or are patterns of temporal population fluctuations consistent with the idea that Atlantic salmon populations are regulated by density dependence? Rather than answering this question in the traditional way (we return to this later), we would like to illustrate here what would happen to populations in the absence of such regulation. To do this we use the observed distributions of variation in annual population growth, assume that such variation is random (i.e. the change in size from one year to the next is independent of population size), and simulate the fate of extant populations (Fig. 11.3). When doing this for the ten North American populations analysed by Einum *et al.* (2003), we see that for five of these the simulated trajectories go rapidly to extinction (Fig. 11.3). This happens despite the fact that all arithmetic mean growth rates used in the simulations were equal to or larger than 1. The remaining five populations increase in size beyond what can be reasonably expected to occur in reality. Clearly, our proposed population model that assumed random variation in growth rates did not perform well. Based on the observed fluctuations in population size we would not predict long-term stability of salmon populations in the absence of internal regulation. Thus, in addition to external disturbances that causes population growth rates to vary among years, there must be a tendency for population growth rates to become large at small population sizes, and vice versa.

11.2.1 Density dependence vs. density independence

Causes for temporal and spatial variation in population abundance are commonly divided into two categories: density-dependent and density-independent processes. In the most common form of density dependence, population growth rates will decrease with increasing population density. These *compensatory* mechanisms exert a strong regulatory effect on

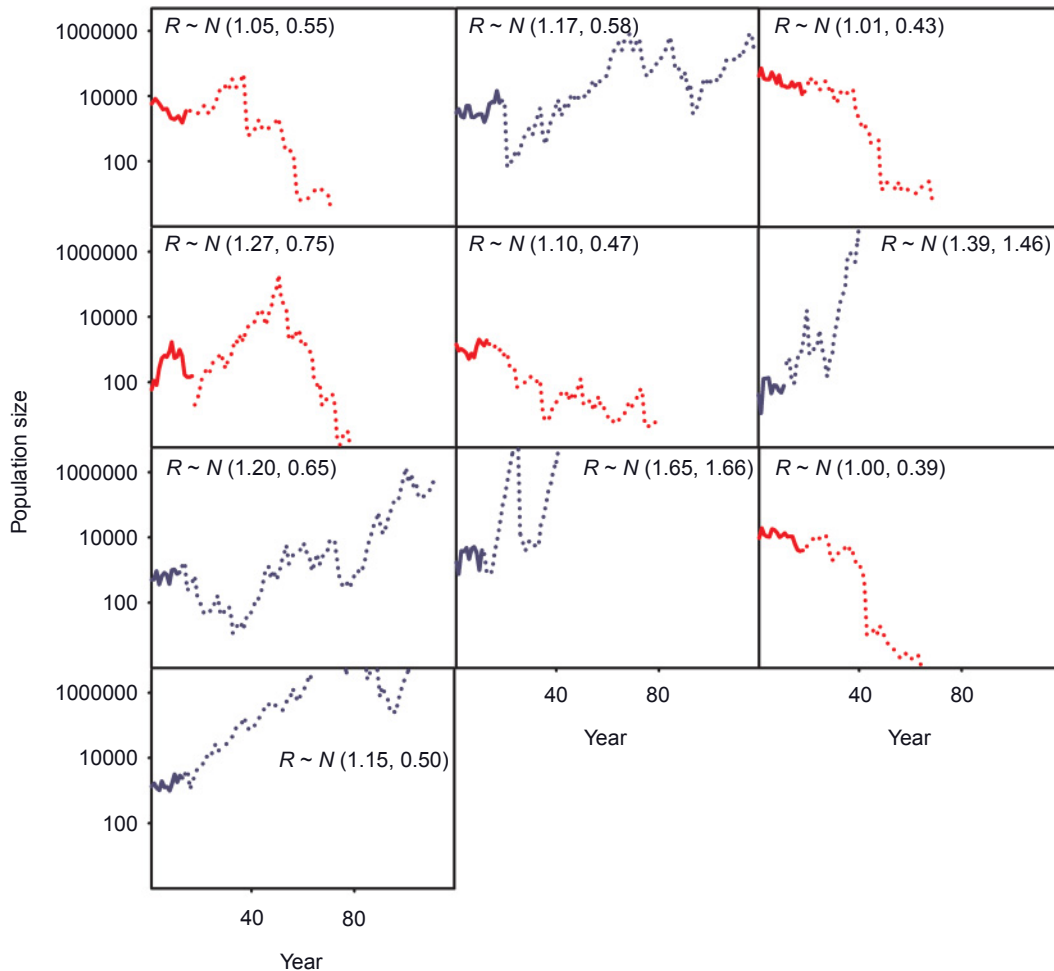


Figure 11.3 Observed variation in population size (solid lines) and simulated population trajectories (dotted lines) of ten Atlantic salmon populations when assuming no internal regulation (i.e. no density dependence). A single random time series of annual growth rates ($R = N_{t+1}/N_t$, normally distributed based on mean and SD of observed data from given population, constrained to be >0) was used to produce each trajectory. In the absence of density dependence, populations are predicted to either increase to unrealistic large sizes (blue lines) or to go extinct (red lines). This suggests that density dependence is responsible for the relative long-term stability of Atlantic salmon populations. Data from O'Connell *et al.* 1996; O'Neil *et al.* 1997; Burgeois *et al.* 1998; Dempson *et al.* 1998 a, b; Chaput & Prevost (1999); Ransom Myers' stock-recruitment database <http://www.mscs.dal.ca/~myers/welcome.html>.

populations (i.e. prevention of unbounded fluctuations and extinctions) (Murdoch 1994), and form the basis of sustainable exploitation (Hindar *et al.* 2011 [Chapter 12]). It is possible, however, for some processes to cause inverse density dependence, where population growth rates decline as densities decrease. These *depensatory* mechanisms, also known as Allee effects (review by Liermann & Hilborn 2001), are strongly destabilising, and can lead to rapid extinction of small populations. While some depensatory mechanisms have been suggested to be relevant to anadromous salmonids (Chen *et al.* 2002; Barrowman *et al.*

2003), there has been little evidence for their importance for Atlantic salmon populations, and the focus of this chapter will be on compensatory density dependence.

In contrast to density-dependent processes, factors external to the organism (i.e. environmental factors) may influence population growth rates directly through density-independent processes (Box 11.2). In the marine environment, large-scale climate oscillations, particularly the North Atlantic Oscillation (NAO), appear to have a strong, but density-independent, influence on stock size (Todd *et al.* 2011 [Chapter 16]). In fresh water, catastrophic disturbance events such as floods (Jensen & Johnsen 1999) may also have strong density-independent effects on population size via direct mortality. Although the division between density-dependent and density-independent processes may in some cases be convenient, the two processes are not necessarily easily distinguishable. For example, if survival during flooding depends on the availability of shelters from high current speeds and mobile substrate, and the number of shelters available for the population is fixed, a larger proportion will survive when pre-flood density is low than when it is high. Thus, environmental factors may cause temporal (year-to-year) variation in the carrying capacity, and the presence of density dependence causes the population size to track these variations (Box 11.2). Clearly, in this case, the process that causes populations to fluctuate in response to the environment can no longer be thought of as being density independent.

This may appear to be a rather academic discussion. It is not! As will be seen later, our ability to predict the effects of environmental disturbance depends crucially on our understanding of the mechanism. Furthermore, in conservation biology, density dependence is often ignored because threatened populations are believed to be too small to be constrained by density dependence (e.g. Doak *et al.* 1994; Kareiva *et al.* 2000). This is unfortunate, because the low density may be a result of a new, reduced carrying capacity (e.g. due to habitat degradation). If so, the population may still experience density-dependent mortality, as indicated in threatened populations of chinook salmon that have population sizes far below historical levels (Achord *et al.* 2003). Thus, density-dependent processes are probably relevant to most organisms and under most circumstances. Understanding how they work and interact with environmental fluctuations is crucial for predicting natural variation in abundance among and within populations. Furthermore, knowledge of how populations are

Box 11.2 What is density dependence?

Density dependence is the internal feedback mechanism that prevents unbounded population growth and extinction. Theoretically, it is perfectly possible that a population can exist without such regulation. However, in most circumstances this appears unlikely. We will not go into details regarding the semantics surrounding the debate of regulation (see Berryman 2004 and White 2004 for a recent exchange of views), but will mention some consequences a lack of regulation would have. For the population to persist, the average mortality and reproductive rates for the whole population must be those that give a long-term average net reproductive rate of exactly one. In the absence of regulation, this value would be *exactly* one *just by chance*, and a slight long-term environmental change would cause the population to increase without bound or to go extinct. Furthermore, introducing exploitation in such a system would lead to a steady decline in population size and eventually extinction. This happens because no compensation for the decreased adult density will occur; non-harvested females still produce only one successfully reproducing female offspring. Such a lack of resistance and resilience to disturbance seems unlikely for most extant populations.

We can therefore safely assume that most extant closed populations (i.e. not dependent on immigration) persist due to internal regulating forces. The size of such populations can be modelled according to the discrete version of the logistic model:

$$N_{t+1} = N_t + N_t \cdot r \cdot \left(1 - \frac{N_t}{K}\right) \quad (11.1)$$

(Maynard Smith 1968), where N_t and N_{t+1} are the population sizes at years t and $t + 1$, respectively, and r is the annual per capita growth rate of the population in the absence of density effects. K is the carrying capacity of the population, and can be thought of as the maximum equilibrium population size, being limited by resources.

By dividing 11.1 by N_t on both sides you will see that population growth decreases linearly with increasing density. This also means that for $N_t > K$, N_{t+1} will become smaller than if $N_t = K$, such that a plot between N_t and N_{t+1} gives a dome-shaped curve. This may be realistic for some organisms, for example when large numbers of individuals decrease the quality of the environment through resource depletion, and as a result all individuals get a decreased survival probability. However, problems for this model arise if $N_t \gg K$, which may cause N_{t+1} to become negative. This is clearly biologically infeasible. An alternative expression for logistic growth that avoids this problem is given by:

$$N_{t+1} = N_t e^{r \left(1 - \frac{N_t}{K}\right)} \quad (11.2)$$

This model is structurally similar to the Ricker stock-recruitment model commonly applied in management of fish stocks (Hindar *et al.* 2011 [Chapter 12]). Alternative models for organisms with different competitive mechanisms (e.g. territorial) also exist in which N_{t+1} goes toward an asymptotic value with increasing N_t (e.g. the Beverton-Holt model, Hindar *et al.* 2011 [Chapter 12]). A common feature for all these models is that in their basic formulations the environment is assumed to be stable over time, and as soon as the population reaches its carrying capacity it remains there indefinitely (Fig. B11.2.1a). This is clearly not realistic for natural populations, as there is no scope for environmental stochasticity to influence population size. For simplicity we use model 11.1 and modify it into:

$$N_{t+1} = N_t + N_t \cdot r \cdot \left(1 - \frac{N_t}{K}\right) - N_t \cdot m_t \quad (11.3)$$

where m_t represents density-independent changes in population growth caused by stochasticity in an environmental variable E_t (Fig. B11.2.1b).

Model 11.3 is equivalent to some models that deal with fishing mortality, but obviously applies equally well to other density-independent sources of mortality. This type of effects of environmental stochasticity is sometimes referred to as vertical perturbation effect, because it is independent of population size (Royama 1992,

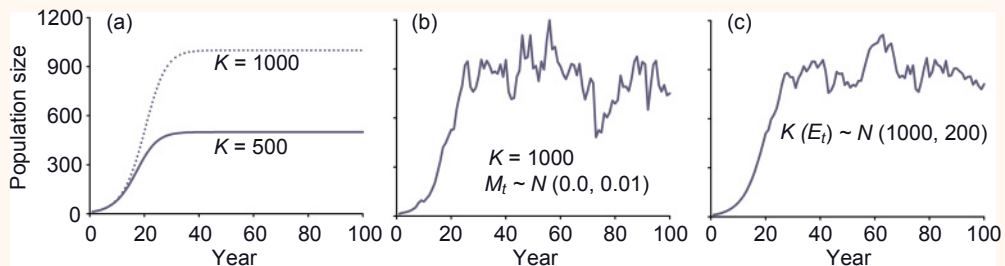


Figure B11.2.1. Population growth according to (a) 11.1, (b) 11.3 and (c) 11.4.

p. 35). Thus, a given magnitude of environmental disturbance always produces a proportional change in population growth.

Effects of environmental stochasticity may also manifest themselves in a fundamentally different way. For example, consider a situation where environmental stochasticity influences the amount of food available for a population, and where individuals compete for and deplete the food resource. In years of low population density, environmental stochasticity may have little effect on population growth, as there will always be sufficient food resources. However, this will not be the case in high-density years. Such effects of environmental stochasticity can be modelled by letting the carrying capacity be a function of the environmental factor E :

$$N_{t+1} = N_t + N_t \cdot r \cdot \left(1 - \frac{N_t}{K(E_t)} \right) \quad (11.4)$$

Here, the amount of the limiting resources for a population varies randomly among years, and due to density-dependent processes, the population size tracks this temporal stochasticity (Fig. B11.2.1c).

The most important lesson to be learnt from these simple models and figures is that variation in abundance among and within (over time) populations may be caused by environmental stochasticity influencing population growth rate (11.3), the carrying capacity (11.4), or both. Variation in density over time *may* be a consequence of direct density-independent effects of environmental stochasticity on population growth rates, but cannot be assumed to be so *a priori*. For more detailed discussions on these topics see Royama (1992).

regulated naturally is necessary to predict how they will respond to various conservation and management strategies.

11.2.2 Empirical evidence for density dependence in Atlantic salmon

The long-term study of anadromous brown trout (*Salmo trutta*) in Black Brows Beck, England, provides detailed evidence for salmonid density dependence (reviewed in Elliott 1994). Although a different species, anadromous brown trout share many common biological characteristics with Atlantic salmon, having to some extent similar breeding biology and juvenile behavioural patterns. By making detailed observations of a small stretch of the stream over decades, Elliott's work has provided a textbook example of how density dependence during early juvenile stages can regulate populations of stream-living salmonids (Elliott 1984, 1985). For that population, density dependent losses from the population (mortality and dispersal) occurring over a 'critical period' of 1–2 months following juvenile emergence from nests were shown to be followed by density-independent losses from the population for the remaining period of freshwater residence (Elliott 1989).

Although studies that parallel Elliott's in extent and detail are generally lacking, many examples of density-dependent losses during early juvenile stages exist also for Atlantic salmon (e.g. Gee *et al.* 1978; Egglisshaw & Shackley 1980; Gardiner & Shackley 1991; Crozier & Kennedy 1995; Dumas & Prouzet 2003; Einum & Nislow 2005; Einum *et al.* 2006). In one of the few well-controlled whole-population studies conducted to date, Jonsson *et al.* (1998) counted the number of females entering the River Imsa on the south-west coast of Norway as well as the number of outmigrating smolt over a period of 20 years. By plotting the number of smolt produced for each cohort against the number of eggs that the same cohort originated from, they were able to estimate the shape of the stock-

recruitment curve for this system (see Fig. 12.5 in Hindar *et al.* 2011 [Chapter 12]). From this it is clear that there is a maximum limit to how many smolts can be produced from this system, and that the mortality rate from the egg to smolt stage increases with increasing egg deposition according to density dependence. During the sea stage, no such processes were detected, and a simple linear model with constant mortality rates described the relationship between number of outmigrating smolts and the resulting number of adult returns.

Density dependence such as that observed by Jonsson *et al.* (1998) may come about through a direct density response in survival rate, whereby sources of mortality such as starvation and predation become more important with increasing density for a given cohort. Alternatively (or in addition), such density dependence may be an indirect effect of density-dependent body growth rates. The growth rate of salmon can be of importance because key life-history events (e.g. parr maturation, smolting) are strongly size dependent. For a given annual survival rate, an increased smolt age due to a reduced growth rate causes more individuals to die before smoltification. Furthermore, if different age-classes compete for the same resources (i.e. intercohort competition), the presence of additional age-classes due to density-dependent growth and delayed smoltification may reduce survival rates. In a recent analyses of time series data from the Girnock Burn in Scotland the relative importance of direct density-dependent survival and changes in smolt age were assessed. In this system there has been a marked decrease in spawner abundance over the last four decades, but this has not led to large responses in smolt production. Over the same period there has also been a decreasing trend in the smolt age. Yet, this change in smolt age does not appear to be responsible for the resistance towards decreasing spawner abundance. Rather, an increase in survival rates from spawning to young-of-the-year juveniles appears to be responsible for the population regulation in this system (Gurney *et al.* 2008).

A second interesting point that can be made about density-dependent growth is that it may represent an important link between processes occurring in fresh water and at sea. Smolt from cohorts having experienced high density may be smaller when entering the sea (e.g. Chadwick 1987, Jutila *et al.* 2006), and this may translate into reduced sea survival (Kallio-Nyberg *et al.* 2007, Salminen *et al.* 1995). However, compared to the well documented influence of density-dependent mortality on population dynamics of Atlantic salmon, the potential effect of changes in smolt size has received much less attention both from a theoretical and empirical point of view.

Although data sets allowing analyses of the population dynamics of whole populations of Atlantic salmon remain rare, Milner *et al.* (2003, p. 115) in their review conclude that 'The evidence for density-dependent regulation of abundance in the salmonid life cycle is overwhelming ...'. Thus, based on both *a priori* arguments, a wide range of experimental data, and the observed dynamics of natural population, it appears that density-dependent regulation of Atlantic salmon populations is indisputable. This gives a starting point in understanding variation in population size among populations. There is an upper limit to the number of smolts produced, and this limit is set by the amount of limiting resources available. The type of resource that is limiting may vary among systems, and density-independent mortality acting directly on growth rates may take the production below this limit (see Section 11.4). Identifying the role of environmental factors in resource limitation and density-independent influences on population growth rate is therefore crucial in our understanding of salmon productivity.

11.3 Environmental influences on population dynamics

Any features of the environment that can influence immigration/emigration, births or survival will also influence population dynamics. Thus, an almost indefinite range of factors can be of potential importance. Some of these factors are obvious (e.g. interspecific interactions such as competition, predation and parasitism, physical habitat, climate, water chemistry, food availability) and are covered in other chapters of this book. Here we will focus on how one of these, water discharge, influences survival rates as an example.

High water discharge has been shown to negatively influence survival rates of Atlantic salmon during early juvenile stages (Jensen & Johnsen 1999). This can occur through two processes: by influencing mortality directly in a proportional way, or by reducing the carrying capacity and influencing mortality through density-dependent processes. Both mechanisms appear plausible. Direct mortality may occur through mechanical damage from mobile substrates, or due to random downstream displacement of individuals with the eventual fate being predation by drift-feeding organisms (e.g. larger salmonids or other piscivorous fish) or being flushed all the way to the sea. In contrast, density-dependent processes may occur if water discharge influences the carrying capacity of the river. These alternatives give qualitative differences in mortality patterns over time (Box 11.3). In the first of these scenarios, the negative effect of the environmental disturbance will continue even at very low population sizes. In the second scenario an increase in mortality rates due to environmental disturbance is seen only when population size is close to carrying capacity. Thus, this example illustrates the difficulty that we mentioned above (Box 11.2) which arises when trying to distinguish *a priori* whether a given environmental factor has a density-dependent or density-independent effect.

For many applied issues the distinction between density-dependent and density-independent effects of a given environmental factor is particularly relevant. For example, if survival rates for Atlantic salmon at sea continue to decrease (Todd *et al.* 2011 [Chapter 16]) juvenile population sizes may be less likely to approach the carrying capacity. Measures to increase smolt production will then most likely be successful if targeting environmental factors that act directly on mortality rates rather than those that influence the carrying capacity. However, it should be mentioned here that for Atlantic salmon, environmental factors influencing the carrying capacity during the first post-emergent stage are likely to be important even under low adult population density due to their aggregated distribution of eggs (Fleming & Einum 2011 [Chapter 2]) and the local spatial scale over which density-dependence operates during this period of their lives (see Section 11.5). Thus, barring self-thinning (see Section 11.4), increasing the carrying capacity during this stage may therefore be likely to increase smolt production under most situations, independent of overall population density.

There are strong reasons to believe that water discharge can influence carrying capacities. At the coarsest level, low water discharge (as in a drought) decreases the total habitat area available to a stream fish population, and to the extent that resources scale with space, the carrying capacity will be reduced (Fig. 11.4). However, total stream area may not adequately describe the amount of food, space and shelter available to juvenile salmonids, and water discharge may therefore have a more complex relationship with carrying capacity. For example, bioenergetic modelling suggests that early juvenile stages have a very narrow window of water currents in which they are able to feed successfully (Nislow *et al.* 2000; Kennedy *et al.* 2008). Too slow currents provide insufficient amounts of food drifting

Box 11.3 Interactions between environment and population density

Knowing whether environmental factors have a direct effect on population growth rates or work through influencing carrying capacities is of outmost importance when predicting effects on population size. To illustrate this, consider a situation where a given cohort of a salmon population experiences unfavourable events such as high (or low) flows that increase mortality rates. To predict the change in cohort strength over time, its size on day $t + 1$ is formulated as a function of the population size on the previous day t and the per capita daily mortality rate d :

$$N_{t+1} = N_t - dN_t \quad (11.5)$$

A model for the mortality rate to depend on the environmental disturbance E and population size can be given as:

$$d = g(E) + \alpha \left(\frac{N_t}{K - h(E)} \right)^\delta \quad (11.6)$$

where $g(E)$ is the direct effect of environmental disturbance on mortality, and $h(E)$ determines how the environmental disturbance influence carrying capacity. α and δ are parameters that determine the strength and shape of density-dependent mortality, respectively.

Using this model we can choose to let the effect of population density be independent of the environmental disturbance by setting $g(E) \neq 0$ and $h(E) = 0$. Alternatively, if $g(E) = 0$ and $h(E) > 0$, the effect of the environmental disturbance will be influenced by population size. These two alternatives give qualitative differences in mortality patterns over time (Fig. B11.3.1).

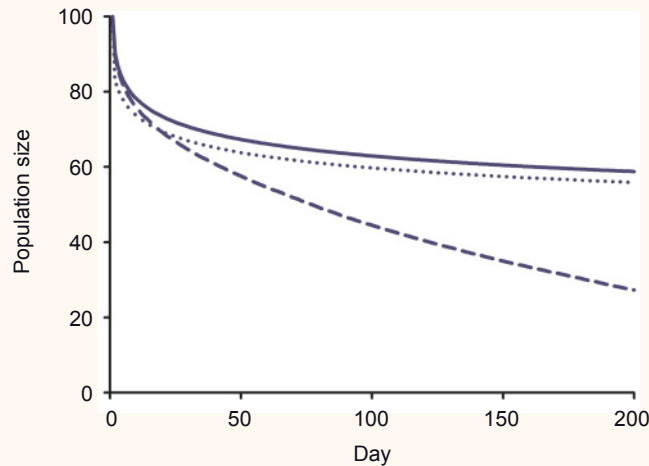


Figure B11.3.1. Changes in population size over time according to (11.6) when environmental disturbance is absent (solid line, $E = 0$), environmental disturbance is present and acts on the carrying capacity (dotted line, $h(E) = 10E$, $E \sim \text{Logn}(0.5, 0.05)$), and when environmental disturbance is present and acts directly on mortality rates (dashed line, $g(E) = 0.01E$, $E \sim \text{Logn}(0.5, 0.05)$). Parameter values used: $K = 100$, $\alpha = 0.1$, $\delta = 10$.

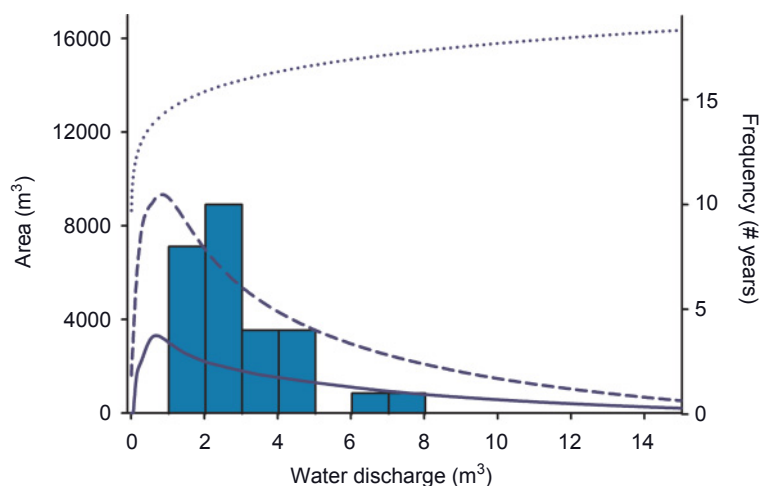


Figure 11.4 Discharge-area relationships of River Imsa, Norway. Models are based on measurements of water depth, stream width and substrate diameter taken at different discharges in combination with the equation describing how water width (W) changes with discharge (Leopold & Maddock 1953) and a statistical description of velocity distributions (Lamouroux *et al.* 1995). Whereas total wetted area increases monotonically with discharge (dotted line), the area where drift-feeding is possible for emerging juvenile Atlantic salmon (dashed line) and the area where currents enable feeding rates within 10% of predicted maximum (solid line) decrease over the observed range of mean discharge during the main period of emergence (1–14 May) in the period 1978–2005 (bars indicating frequency of observations). Thus, if the carrying capacity is linked to either of these latter two areas, years with high discharge are predicted to cause reduced survival, and particularly so during years of large numbers of emerging juveniles. The effect of water discharge will then be density-dependent.

through their territories, whereas too rapid currents prevent successful capture of such drifting items.

Among-year differences in water discharge in a given stream reach will therefore change the proportion of potential territories capable of providing adequate consumption rates, and therefore the carrying capacity of the stream during the emergence period (Fig. 11.4). This model suggests that effects of discharge will be modulated by density, and hence that they are density dependent. However, as of yet, such interactions between initial density and discharge on survival rates remain to be shown in empirical studies of Atlantic salmon.

11.4 Density dependence throughout the juvenile stage

An additional temporal axis of population dynamics concerns changes in the carrying capacity relative to developmental changes over the ontogeny of the organism. So far we have only considered the Atlantic salmon life cycle to be divided into two stages: one freshwater and one marine. However, Atlantic salmon, like many other organisms, have complex life cycles in which more or less distinct morphological, physiological and behavioural changes occur throughout ontogeny (Thorstad *et al.* 2011 [Chapter 1], Finstad *et al.* 2011 [Chapter 3], Johansen *et al.* 2011 [Chapter 4], Forseth *et al.* 2011 [Chapter 6]). As a result of this, the salmon change their resource requirements as they grow. One obvious change is the

increased resource requirements with body size. However, there may also well be qualitative changes in resource requirements. Such changes are commonly referred to as ontogenetic niche shifts, and represent the change in habitat use and/or diet that is associated with an increase in age. Ontogenetic niche shifts are of particular importance for organisms where body size changes considerably with age, and where body size to a large degree influences resource use and predation risk (Werner & Gilliam 1984; Miller *et al.* 1988). Salmon juveniles are definitely among such organisms, ranging in body mass by two orders of magnitude, and having associated changes in habitat (Finstad *et al.* 2011 [Chapter 3]) and diet (Johansen *et al.* 2011 [Chapter 4]). These niche shifts have one very important implication; because individuals at different ontogenetic stages depend on different types and amounts of resources, the carrying capacity for a population is also likely to change throughout ontogeny. Rather than thinking of the carrying capacity as a single value that exists for each population, it may be useful to consider different carrying capacities for different size- or age-classes.

This brings us to the concept of self-thinning. Originally developed for plants, self-thinning is the process that causes a decrease in population abundance as its per capita resource requirements increase with increasing body size. This can also be thought to apply for Atlantic salmon. As the juveniles grow, their territory size and food requirements increase (Nislow *et al.* 2011 [Chapter 7]). Hence, for a given cohort, the larger they become, the fewer the numbers that can be supported by a given area of stream. If no other process than intraspecific competition causes mortality, and the initial density is sufficiently high, this is very likely to be the mechanism that causes the carrying capacity to decrease with increasing body size. In the absence of self-thinning (or other forms of density-dependent population losses occurring at older juvenile stages), populations will be regulated at earlier juvenile stages. Salmon experience massive mortality rates, sometimes referred to as 'bottlenecks', during the first few weeks following emergence from nests (Einum & Fleming 2000a, b; Nislow *et al.* 2004). If these are sufficiently large, and if resource availability for older juveniles is sufficiently high, self-thinning becomes less likely. Graphically, the issue is whether early mortality is sufficient to keep the population below a predicted thinning line, taking into account density-independent mortality (Armstrong & Nislow 2006).

At present, there is a lack of empirical data to evaluate the importance and frequency of self-thinning among salmon populations. In fact, and perhaps surprisingly, this is true for salmonids in general. Studies examining this issue are for a large part limited to observational studies that ask whether the observed patterns of decreases in numbers with age/size are consistent with space or food limitation. One rather rough way to study this has been to estimate an overall density and mean body size of all age-classes present either on the same location in different years (e.g. Bohlin *et al.* 1994) or at different locations in the same year (e.g. Dunham & Vinyard 1997). However, this approach has the obvious limitation that any relation between density and body size may to a large degree be driven by variation in age structure. For example, years or sites with high recruitment (i.e. high density of under-yearlings) will have a high overall density (because under-yearlings can be very numerous) and also a low mean body size.

The alternative approach to study self-thinning, which is to follow changes in densities and sizes of individual cohorts through time, is less biased. Using this, Steingrimssohn & Grant (1999) found thinning lines that had slopes consistent with space limitation in Atlantic salmon. However, that study only observed changes occurring throughout the first three months following emergence from nests, and is therefore consistent with the early density

dependence observed in other studies, but says little about the potential for density dependence at older ages. Following 23 cohorts of brown trout from emergence to smoltification, Elliott (1993) found a perfect fit between predictions based on food limitation and observed self-thinning lines. Yet, these results were from the same population where he had previously demonstrated a lack of density dependence following the critical period (Elliott 1989), and re-analyses suggested that the perfect fit was more likely coincidental (Armstrong 1997). Rincón & Lobón-Cerviá (2002) followed 10–11 cohorts of brown trout at four sites within the same stream and found a relatively flat relation between body size and density after the critical period up until a body size of *c.* 15 cm. In fact, slopes were significantly different from 0 for only four of the 42 cohorts for this size range, suggesting extremely low mortality rates and/or significant immigration to the four sampled sites (which were relatively small; mean of *c.* 230 m²). If ignoring the possibility for immigration, this suggests no self-thinning for the size range that is relevant for Atlantic salmon (i.e. salmon smoltify before reaching 15 cm in most populations). For older fish the slopes became steeper (see also Lobón-Cerviá & Mortensen 2006; Lobón-Cerviá 2008), which may suggest increased competition for more limited resources as fish become larger (e.g. deeper pools). However, movement of older fish out of sites that are sampled to areas with more suitable (i.e. deeper) habitat rather than mortality may also explain such patterns. Since the issue of self-thinning is an empirical one with particular relevance for management one would usually be interested in the situation on a whole-population level, and not on site-specific patterns. Finally, increased mortality associated with maturation may cause steeper slopes for larger fish.

Apart from methodological challenges with empirical studies of self-thinning, we also know that predictions in terms of thinning line slopes from space or food limitations assume that the amount of resources available for the population is constant throughout ontogeny. The considerations of ontogenetic niche shifts discussed above suggest that this is unlikely to be true. Thus, we do not even appear to have a clear prediction about the slope of thinning lines against which to compare observations. Fish die for a wide range of reasons even in the absence of competition, so describing decreases in density with increasing size becomes trivial unless one has a robust theoretical prediction against which to compare observations. Evaluation of patterns (thinning lines) is therefore unlikely to provide much information about underlying processes (density dependence). However, comparisons of age-specific mortality rates among populations and links between these and age-specific habitat availabilities may provide some information on the likelihood for density dependence to occur at different ages in different types of environments.

The lack of knowledge about density-dependent mortality at different ages in Atlantic salmon populations is a major hindrance for efficient management. For example, consider a situation where a physical disturbance causes increased mortality during one of the earliest juvenile stages. Should measures to improve this situation be given a high priority relative to measures targeting older stages? If we know that this particular population experiences strong self-thinning, the answer is probably no (Fig. 11.5). Without knowledge about the relative importance of self-thinning *vs.* early bottlenecks, such a question is extremely difficult to address. One approach is to use modelling in combination with experiments to provide management ‘rules of thumb’ for prioritising improvements in carrying capacity. For example, both graphical (Armstrong & Nislow 2006) and mechanistic (Einum *et al.* 2008) modelling approaches have indicated that at early fry survival levels of <20%, populations are likely to remain below carrying capacity for older juveniles over a wide range of

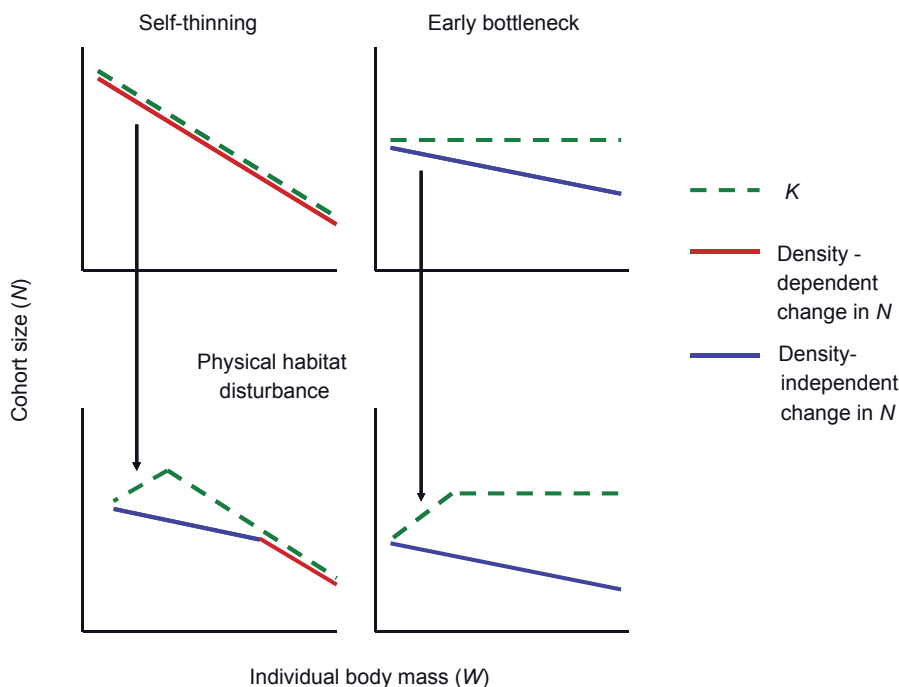


Figure 11.5 Illustration of how the effect of a physical disturbance during the first juvenile stage depends on the ontogenetic nature of density dependence. Under self-thinning, reduced survival at the earliest juvenile stage is compensated for and may have little influence on smolt production. In contrast, if regulation occurs only through an early bottleneck, subsequent changes in N over ontology will be determined by density-independent processes. Thus, no compensation for increased early mortality will occur, and a reduced smolt production will be expected. Adapted from Armstrong & Nislow 2006.

older juvenile habitat availabilities. By referencing this threshold, and obtaining appropriate survival estimates, managers can prioritise habitat improvements designed to increase either fry or parr survival.

11.5 Spatial aspects of density dependence

So far we have ignored spatial aspects in our discussion on Atlantic salmon density dependence. However, because spatial locations within and among juvenile rearing sites differ in their carrying capacities, and there are constraints on the ability of individuals to assess, find and occupy the most favourable sites, density-dependent dynamics may be strongly influenced by the spatial variation in both habitats and juvenile distributions. If individuals distribute themselves through space according to what is known as the Ideal Free Distribution, fitness variation due to spatial location is minimised. This, of course, does not mean that densities (or production of smolt) will be equal among locations, so from a management perspective some areas of a stream will still be more valuable than others. Yet, ignoring the spatial dimensions when considering various aspects of population dynamics may then be

a good approximation to reality (Box 11.4). For Atlantic salmon this is, however, unlikely to be true. Females require particular habitats for creating nests, and deposit large numbers of eggs in patches (Fleming and Einum 2011 [Chapter 2]). The survival rates of the resulting juveniles during the first period following emergence from these nests has been shown to be locally density-dependent (Fig. 11.6), whereas dispersal rates are only weakly related to nest size (Einum & Nislow 2005). Furthermore, maternal choices with regard to spawning locations have the potential to produce spatial variation in density and growth rate of resulting juveniles over small spatial scales, and may even influence population abundance (Fleming

Box 11.4 Ideal free distribution

If all individuals within a population are free to move without cost across the whole spatial extent of the habitat and have perfect knowledge about variation in habitat qualities they are predicted to distribute themselves over space in a way that minimises variation in fitness. A distribution in which all individuals obtain equal fitness is called the Ideal Free Distribution (IFD). Deviations from such distributions will have consequences for population dynamics (Fig. B11.4.1). Recent research on Atlantic salmon demonstrates how deviations from such distributions can be expected among juveniles, particularly during early stages, due to patchy distribution of eggs and limited juvenile mobility.

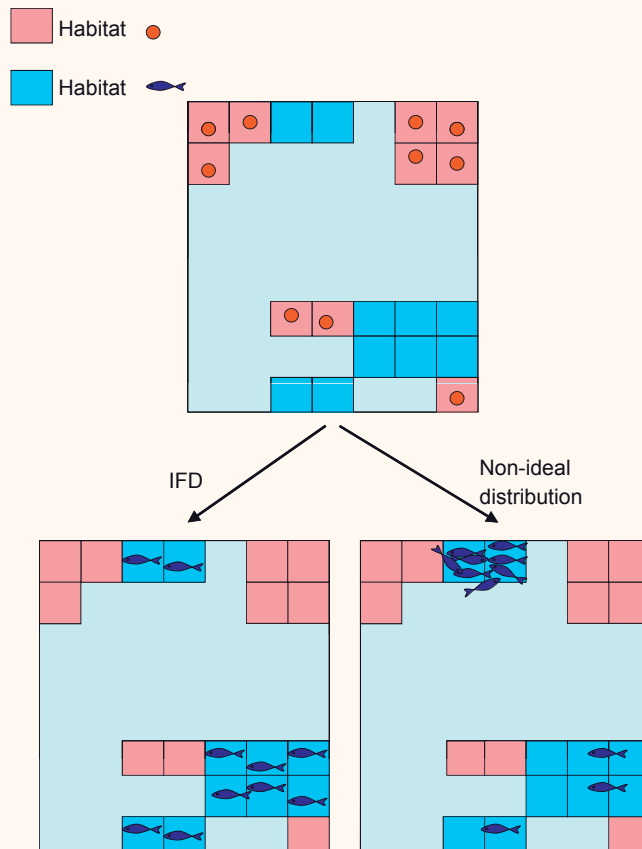


Figure B11.4.1.

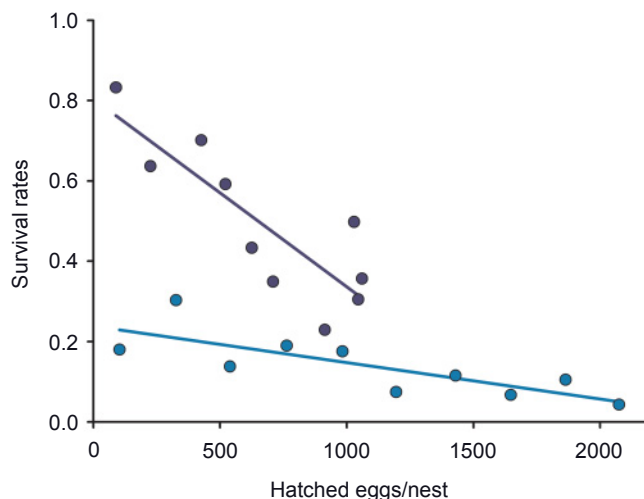


Figure 11.6 Effect of nest size (eggs per nest) on survival rates of resulting juveniles during the first 1–2 months following emergence in two years (dark blue: 2002, light blue: 2003). Eggs were outplanted in artificial nests located 150 m from one another along the River Bjørnbettelva, central Norway, and otolith marks applied prior to outplanting enabled identification of juveniles at recapture. Such local density dependence suggests an important role for spatial structure of populations to influence their dynamics. From Einum & Nislow 2005.

and Einum 2011 [Chapter 2]). Thus, including effects of spatial structure gives a much more comprehensive understanding of Atlantic salmon population dynamics (Fig. 11.7).

As juveniles grow, their ability to move over larger distances is likely to increase. Consistent with this expectation, whereas dispersal rates of emerging juveniles were only weakly related to nest size (Einum & Nislow 2005), Einum *et al.* (2006) found dispersal of juveniles being outplanted 2–3 months after onset of feeding to be strongly density dependent. Thus, it appears that the ability to reduce spatial patchiness in density and approach a more ideal distribution should increase with increasing body size.

Ontogenetic changes in mobility and degree of deviation from ideal distributions has implications for how density dependence acts throughout the juvenile stage. Density dependence on the population level is a result of the influence of effective density, which can be thought of as the density that each individual experiences at a given time (e.g. number of encounters with other individuals per time interval; Lloyd 1967; Folt & Schulze 1993). This measure of density will be more closely related to the level of interactions among individuals than the more conventional density measure expressed as total number of individuals divided by total area, and will therefore to a greater extent represent the potential for density dependence. In addition to effects of total age-class abundance, individual territory size and area of suitable habitat, age-class patchiness will influence effective density (Nislow *et al.* 2004). Everything else being equal, two age-classes differing in the degree of patchiness will also differ in their effective density. Thus, the increased mobility of older age-classes should act to reduce levels of competition, and should therefore be taken into account when considering the potential for early bottlenecks *vs.* self-thinning in salmon populations.

The extent to which populations exhibit spatial structure may also significantly influence temporal variation and population regulation. Metapopulation theory predicts that the flow

of individuals between subpopulations with different population vital rates increases population stability (Hanski 1998). There is some evidence that these considerations may apply to juvenile Atlantic salmon. In the study by Einum *et al.* (2003), in addition to differences among species (see temporal variation section) temporal variation *within* species decreased with increasing population size. Yet, the measures of variability used should be independent of population size (McArdle *et al.* 1990). A number of potential explanations were proposed to explain this pattern, but perhaps the most likely one is that large populations usually have a more complex spatial structure than small populations, consisting of sub-units that do not fluctuate in perfect synchrony. Thus, such spatial structuring may act as a stabilising



Figure 11.7 Experimental field studies of Atlantic salmon population dynamics commonly depend on controlled outplanting of eggs in artificial nests (A–C), or releases of hatchery reared juveniles (D–E). The spatial distribution, survival rates and growth of resulting fish are assessed through recaptures after a certain period (F–H). Usually, this requires identification of recaptures to a particular release group (e.g. initial local density) by means of external marks (e.g. visible elastomer implants, D), otolith marks (the six thickest lines towards the centre of the otolith) that can be applied during the egg stage (I) or genetic parentage analyses. Photos: S. Einum.

force if the relative success of different segments of a population varies from year to year. In other words, the effect of exogenous forces on the total population is averaged out across years (Kindvall 1996; for a salmon model see Kocik & Ferreri 1998). This indicates a potential role for spatial structure in shaping the stability of salmon populations. Studies of spatiotemporal autocorrelations, yielding information on how synchrony in population fluctuations depends on distance within stream systems, would shed light on the potential for such a mechanism to cause larger populations to be more stable.

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12 Stock, Recruitment and Exploitation

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Abstract

Management of Atlantic salmon populations has for decades been carried out in the near absence of quantitative information, except in a few cases. Since the 1960s an increasing number of rivers have been monitored for the number of upmigrating spawners and outmigrating smolts. We are now in the position to capitalise on the quantitative information accumulated by this monitoring. This chapter describes methods for modelling relationships between spawning stock and recruitment in the subsequent generation, and how to extract information on conservation limits and spawning targets from the models. We review spatial and temporal variation in stock-recruitment relationships, assess uncertainties in deriving spawning targets from data-rich populations, and review suggestions for transferring spawning targets from data-rich to data-poor populations. Even for well studied rivers, the uncertainties in setting spawning targets are pronounced. This is a challenge for management as there is usually limited opportunity to obtain precise information on pre-fishery abundance, and limited understanding of variation in exploitation rates. We describe how fishing for Atlantic salmon has moved from fresh water into sea water and back into fresh water through history, and show how fishing can have evolutionary and ecological consequences for harvested populations. We end by discussing some of the management implications of the current knowledge on stock-recruitment relationships and exploitation. The overriding challenge is to apply the increasing knowledge to securing viable populations of Atlantic salmon in an era of declining population sizes.

Key words

Spawning population, juvenile density, wetted area, catch statistics, fisheries management, applied population dynamics, conservation limit, density dependence

12.1 Introduction

Active management of Atlantic salmon populations is necessary for several reasons. First, Atlantic salmon has considerable commercial value as wild, hatchery-produced and farmed

populations. Second, salmon populations occupy broad geographical areas in fresh water and in the ocean, crossing several national borders during their migrations. Third, the abundance and distribution of wild salmon have declined strongly during the past 30 years and are probably at all-time lows. Fourth, salmon populations are naturally regulated, suggesting that there is some threshold density of spawners above which more spawners do not increase recruitment but may instead be fished on without compromising the population's productivity or viability. This, however, demands proper knowledge about stock-recruitment relationships, and also careful management of the fisheries in the open ocean, along the coasts and in fresh water. Whereas Chapter 11 (Einum & Nislow 2011) dealt with the underlying mechanisms of population regulation, this chapter deals with applied aspects of the population dynamics. Although the focus is on Atlantic salmon, we also use information from other (salmonid) fishes when necessary.

The Atlantic salmon has been exploited throughout its history of co-existence with humans. Forty thousand year old bone remains of salmon in Spanish caves and 6000- to 10000-year-old paintings and carvings of Atlantic salmon on rock in Scandinavia suggest that humans and salmon colonised northern environments together. Early legislation has commandments that limited the exploitation of salmon during its migrations; for example, the Norwegian Gulating Law states that the salmon should have free passage to the uppermost part of the river, if the salmon decided to migrate there ('Ganga skal Gudsgåva til fjells som til fjæra, um ganga ho vil' ['Running to mountains and shore God's gift should do, if running she wants']; from Gulatingsloven, c. 1200 AD).

The Atlantic salmon is exploited for food and recreation, both of which have strong economic implications. This generates conflicts between commercial and recreational fishing interests, and also between nations that share the same salmon resources. The high economical value of salmon also invites over-exploitation, which has been a problem for many salmon populations and may also be so in the future.

Major changes have taken place in the application of population dynamics theory to Atlantic salmon since Derek Mills's 1989 textbook on Atlantic salmon ecology. The first is a change in primary management objectives, from one of targeting (maximum sustainable) yield of salmon, to one of targeting conservation of the populations. The second is a change in the fisheries for salmon, from a majority of the fish being caught at sea to a majority of the fish being caught in fresh water. The third is an increase in the number of Atlantic salmon populations for which long-term data exist on stock and recruitment. This development is summarised by Prévost & Chaput (2001) and Crozier *et al.* (2003) and has been accompanied by a more elaborate use of models to describe stock-recruitment relationships in fishes in general, including the compilation of a database on stock-recruitment data from more than 600 fish populations by the late Ransom Myers (http://ram.biology.dal.ca/~myers/about_site.html). Also, achievements have been made on how information extracted from stock-recruitment data can be used to identify biological reference points for the population. The most important change since Mills's 1989 textbook, however, has been that the abundance of wild salmon is declining, despite strong reductions in fishing mortality and an increased understanding of the population dynamics of Atlantic salmon and of the factors threatening wild populations.

In this chapter, we review the status of Atlantic salmon worldwide and the knowledge about population sizes, recruitment and exploitation of Atlantic salmon. We describe methods for modelling stock-recruitment relationships from temporal data, and how to

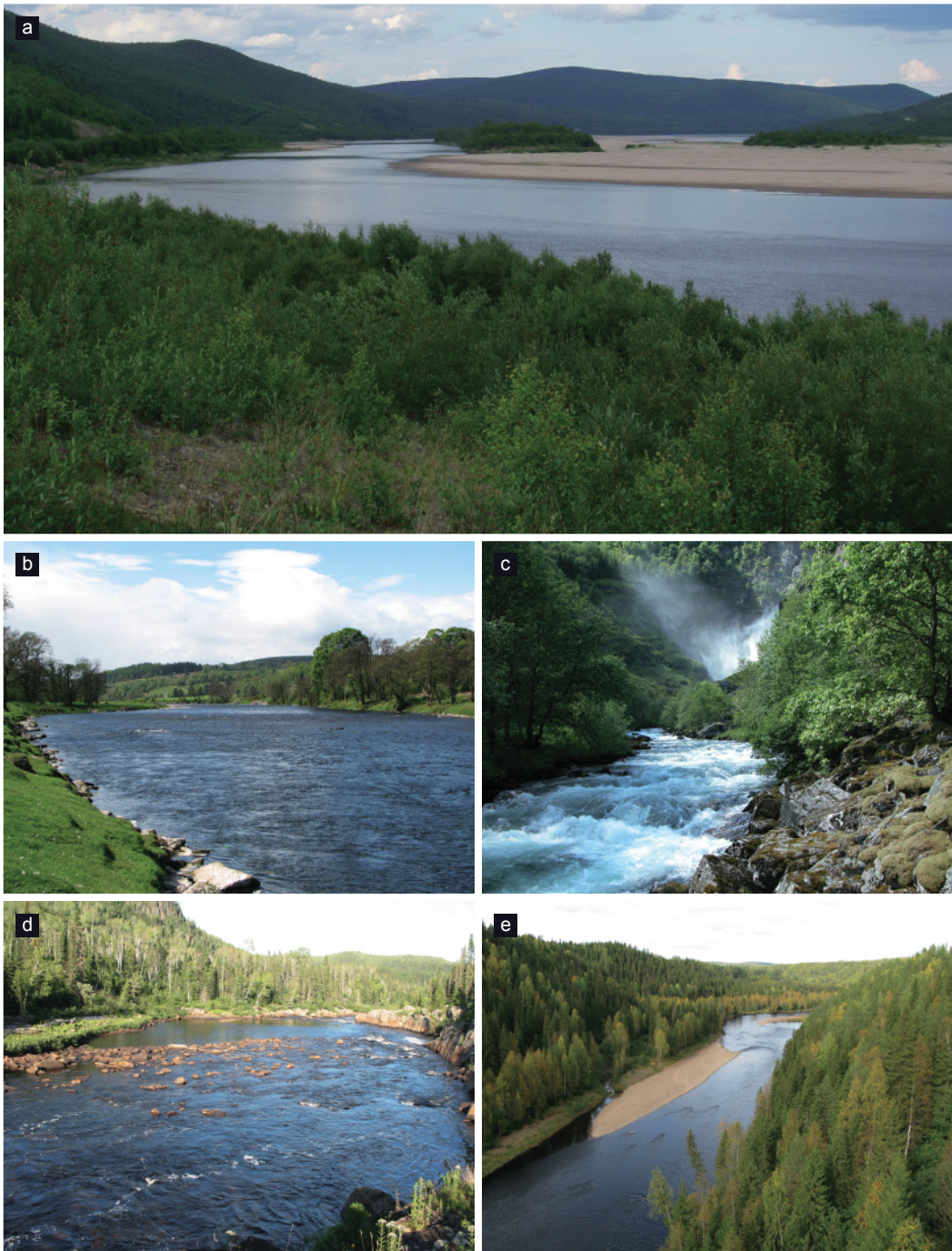


Figure 12.1 Environmental variation among rivers holding Atlantic salmon represents a challenge when attempting to transfer spawning targets. (a) River Tana/Teno (Norway/Finland, photo: Eva B. Thorstad), (b) R. Spey (Scotland, photo: Odd Terje Sandlund), (c) R. Nærøydalselva (Norway, photo: Leif Magnus Sættem), (d) R. Sainte-Marguerite (Canada, photo: David Paez), (e) R. Öreälven (Sweden, photo: Eva B. Thorstad).

Box 12.1 Concepts and definitions (from Crozier et al. 2003 and references therein)

Biological reference points (BRP): A calculable quantity that describes a population's state and which is estimated from the life-history characteristics of the population.

Conservation limit (CL): Demarcation of undesirable stock levels; the ultimate objective when managing stocks is to ensure that there is a high probability that the undesirable levels are avoided.

Management target, or spawning target: A desirable (spawning) stock level, which may be used as an aiming (or reference) point to achieve management objectives. The spawning target is typically higher than the conservation limit (in number of spawners or egg density) as it incorporates some measure of uncertainty, taking natural variability and measurement error into account.

Maximum sustainable yield (MSY): The largest average annual catch that may be taken from a stock continuously without affecting the catch in future years.

Replacement line: Represents the number of recruits needed to replace the corresponding spawning stock in the absence of fishing. When assuming no density-dependent mortality from the recruit stage to spawner, the replacement line is a straight line with slope determined by post-recruit survival and growth (Hayes et al. 1996).

extract information on biological reference points (Box 12.1), such as conservation limits and spawning targets, from the models. We review suggestions for transferring these reference points from populations with established stock-recruitment relationships to populations for which little information exists. This is a major challenge, considering the wide variety of salmon habitat and life-histories throughout the species range (Fig. 12.1). We review the history, methods and intensity of fishing for Atlantic salmon, and describe how fishing can have ecological and evolutionary consequences on harvested populations. Finally, we discuss some of the management implications of our findings, particularly as they relate to securing viable populations of salmon in an era of declining population sizes.

12.2 State of Atlantic salmon populations

Atlantic salmon is a genetically structured species, with a number of genetically distinct populations spawning in different watercourses and/or in different locations within the same watercourse (Verspoor *et al.* 2007). The exact number of Atlantic salmon populations worldwide is not known, and may well never be known, as the delineation between them is not absolute, except between landlocked populations. Whereas the river may in most cases be viewed as a surrogate for a single population, genetic and demographic data are often suggestive of two other possibilities. The first is that several neighbouring rivers may comprise a single (meta-)population. The second is that several (sub-)populations may exist within a single river.

One example of a putative meta-population is that of salmon inhabiting the River Lærdalselva and neighbouring rivers in western Norway. Counts of spawners in the River Lærdalselva (Sættem 1995) and in six smaller neighbouring rivers (Sættem 1995) suggest that while the Lærdalselva had >500 anadromous spawners (1985–94), the others had between 10 and 60 spawners each. Even a small level of straying from the River Lærdalselva to neighbouring rivers is therefore likely to comprise a significant proportion of the spawners in the other rivers (Hindar *et al.* 2004). At the same time, even high straying rates from the

small populations will only make up a small proportion of spawners in the Lærdalselva. This system of one big and several small populations may therefore better be treated as a meta-population. The same may hold true for areas where a number of small populations is located within a limited geographical area, or in environmentally very similar locations. Such an example may be that of some Canadian rivers associated with the inner Bay of Fundy (Fraser *et al.* 2007).

On the other hand, genetic evidence suggests that several genetically distinct populations can exist within the same river system (Verspoor *et al.* 2007); for example, among tributaries within rivers, and also among geographically separated spawning and rearing areas of the main river, such as in the River Tana/Teno in northern Norway and Finland (Ståhl & Hindar 1988; Vähä *et al.* 2007).

Comparisons across several large river systems suggest that the within-river genetic structure of Atlantic salmon is variable, from well differentiated to undifferentiated (Dionne *et al.* 2009). Ideally, this genetic structure should be known before assessing stock and recruitment relationships for Atlantic salmon populations. Catch statistics and other numerical information about Atlantic salmon populations are usually scaled to the level of rivers. For this chapter, we therefore use a pragmatic view adopted from Simon & Larkin (1972) that a population is a group of organisms that share habitat and gene pool, and is sufficiently different from other such groups to be treated as a self-reproducing system that can be managed.

The current status of Atlantic salmon worldwide has been assessed by WWF (2001), which collated information on 2600 rivers from national representatives in all of the countries holding self-reproducing populations of wild salmon. Of these, information was considered sufficient for a rough classification of status in 2005 rivers, which can be summarised as country-by-country averages (Fig. 12.2). Atlantic salmon populations are considered ‘extinct’ from 309 rivers (15%) worldwide and from the following countries: Germany, Switzerland, Netherlands, Belgium, Czech Republic and Slovakia. They are considered ‘endangered’ in Estonia, Portugal, Poland and the United States. At the other end of the scale, Atlantic salmon populations are considered ‘healthy’ in 867 rivers (43%), most of which are located in Iceland, Scotland, Norway and Ireland (WWF 2001). We note, however, that although the WWF classifications may have some utility, they can provide misleading information on status at smaller scales. For example, the classification identifies most (excluding ‘unknown’) Canadian populations of Atlantic salmon as being endangered, when only those at the southern extreme of the species’ Canadian range can be defensibly classified as such (COSEWIC 2006). Few, if any, populations in Newfoundland, for example, are at heightened risk of extinction.

12.2.1 Migratory populations

The population sizes of Atlantic salmon are commonly much lower than those of several species of Pacific salmon, which may have (river) population sizes in the order of hundred thousands to millions (Quinn 2005). Direct counts of the number of spawners in Atlantic salmon populations exist for only a few rivers. In others, the number of spawners can be estimated from catch statistics, freshwater exploitation rates, and mark-recapture studies. The catch statistics from 361 Norwegian rivers suggests that the most common classes of catch per river are 10–100 and 100–500 salmon (Fig. 12.3), the average being 330 (standard

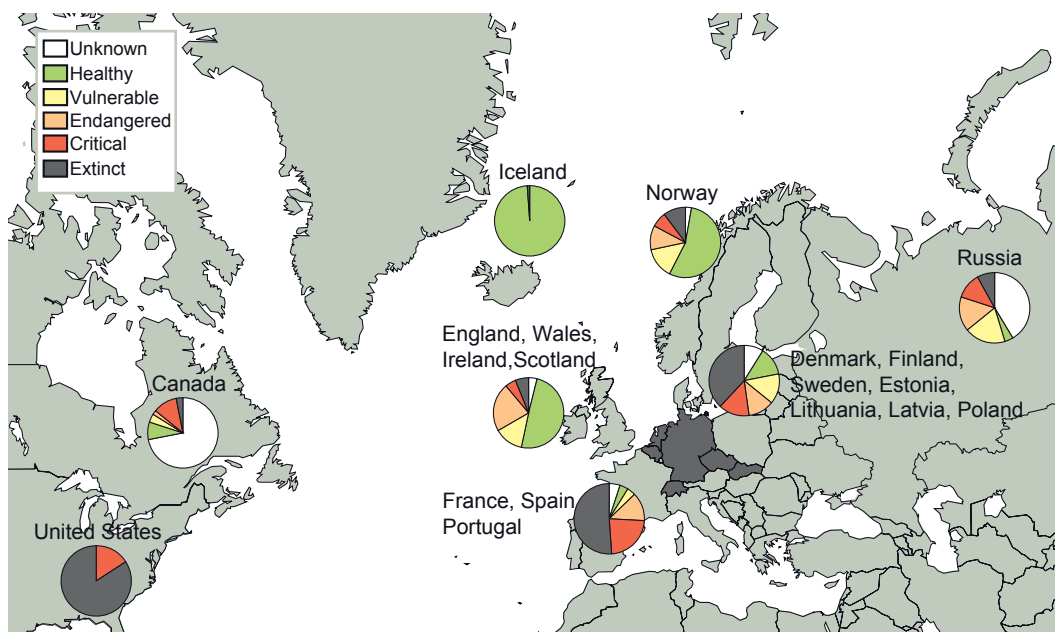


Figure 12.2 Status of Atlantic salmon populations based on WWF (2001) classification of 2005 rivers as Healthy (green), Vulnerable (yellow), Endangered (orange), Critical (red), Extinct (black), or Unknown (white). Updates for Norway from www.dirnat.no. In countries coloured black (Germany, Switzerland, the Netherlands, Belgium, the Czech Republic and Slovakia) all salmon populations have gone extinct.

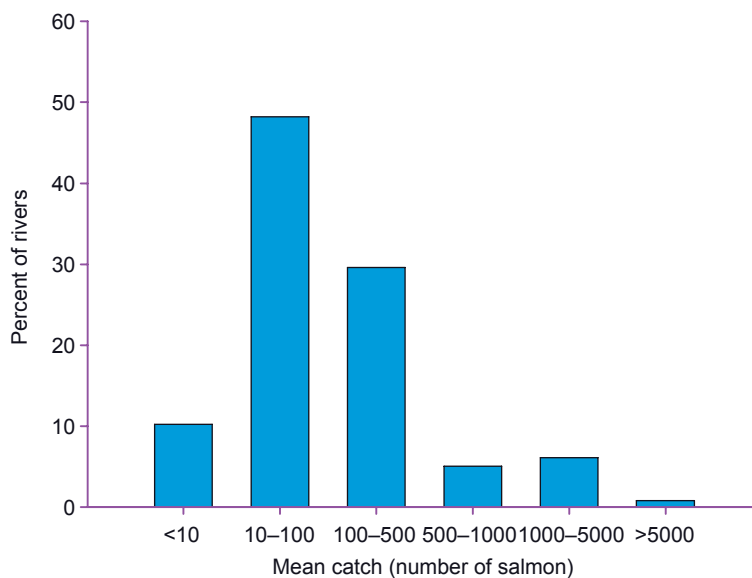


Figure 12.3 Frequency distribution of mean catches (number of salmon) in the period 1979–2006 for 361 Norwegian rivers. Only rivers reporting their catches in at least 10 years in the period are included.

deviation = 1143) and median being 71. If the catch rate is 50% (see Section 12.5), then the figure gives a rough impression of the distribution of spawning population sizes that could go into stock-recruitment (SR) considerations for a large number of populations. If the catch rate is 33%, the size ranges for each class in the figure should be doubled.

Long-term downward trends in the catches of Atlantic salmon since the 1960s and 1970s suggest that salmon populations are at all-time lows (Hindar *et al.* 2007a). These negative trends have initiated international reports to protect wild Atlantic salmon (NASCO 1998) as well as government reports in Norway (NOU 1999) and the USA (Fay *et al.* 2006), among other countries. Even longer time series suggest large-scale temporal and regional variation in the catches of Atlantic salmon, as suggested by Vøllestad *et al.* (2009) based on long-term data series on river catches in Scotland and Norway.

Catches may, however, give a biased picture of stock sizes. Therefore, international efforts have been put into estimating total stock size by ‘working backwards’ from the catches, building up the number of salmon based on assumptions of exploitation rates, extent of unreported catches and natural mortality in the period from when the catches took place until the date that the stock size is estimated for. The basic structure of this procedure is given in Potter *et al.* (2004) and Chaput *et al.* (2005) for estimating the so-called pre-fishery abundance (PFA), which is the estimated number of Atlantic salmon alive on 1 January in the northeast Atlantic Ocean and on 1 August in the northwest Atlantic Ocean.

Current estimates by ICES (2009) suggest that PFA of Atlantic salmon in the North Atlantic Ocean decreased from 6.5 million to 3.5 million between the 1980s and 2008 (Fig. 12.4). This is also suggested by a dramatic decrease in the catches of Atlantic salmon during the same period. Estimates of pre-fishery abundance (PFA) from the 1970s suggest that the number of salmon have been even higher than in the 1980s (Potter *et al.* 2004). Better catch statistics, and an increasing proportion of farm escapes in the catches during this period (Hansen *et al.* 1999), mask a possibly stronger negative trend of wild fish in some areas.

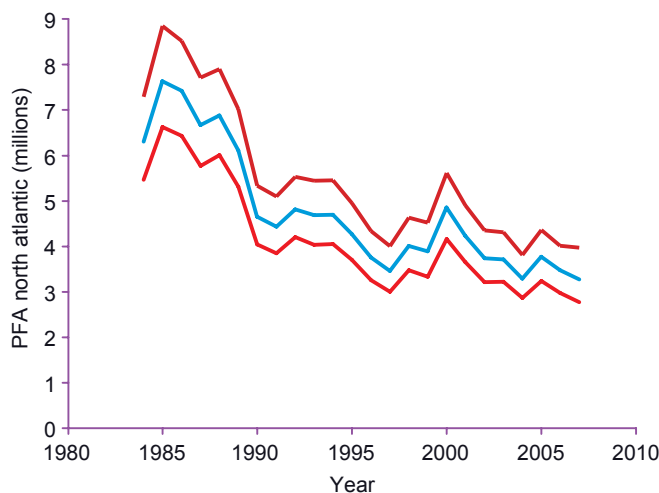


Figure 12.4 Estimated pre-fishery abundance (PFA) of Atlantic salmon in the North Atlantic in the period 1984–2007 (blue line). Red lines encompass 95% of the simulations. Data collated from ICES (2009).

12.2.2 Non-migratory populations

Some populations of Atlantic salmon lead their entire life in fresh water (Berg 1985). Although rare in Europe, non-migratory populations of Atlantic salmon are not uncommon in North America. Various terms 'ouananiche' or 'landlocked salmon', these populations inhabit waters that may or may not have barriers to migration to and from the sea. In Maine (where they are called 'lake' or Sebago salmon; Warner & Havey 1961) and Quebec (Chambers 1896; Riley *et al.* 1989), the populations are truly landlocked, preventing genetic or ecological interactions with anadromous populations. However, throughout Newfoundland, where non-migratory salmon are most abundant, ouananiche frequently co-exist with anadromous populations. Not only does this co-existence raise interesting questions concerning the evolutionary stability of both life-history forms (Hutchings 1986, 2002), but it also has consequences for the establishment of reference points for stock assessment. Since the early 1990s, the conservation targets used in Newfoundland have distinguished riverine habitat from lacustrine waters (O'Connell & Dempson 1995).

12.3 Stock and recruitment in Atlantic salmon populations

Stock-recruitment relationships are much less developed for Atlantic salmon populations than for Pacific salmon (Prévost & Chaput 2001). There are relatively few long-term data sets for Atlantic salmon populations, and most of them are from small rivers or tributaries to larger rivers. On the other hand, several of these data sets are from controlled locations where both the number of spawners and the number of recruits are counted with high precision over several cohorts.

For single-spawning, or semelparous, species Hilborn & Walters (1992) suggested that stock (S) and recruitment (R) be expressed in the same units because this allows for the estimation of management-related parameters such as maximum sustainable yield (MSY), spawning target, and exploitation rate at MSY (Box 12.1 and Box 12.2). Whereas semelparity holds true for most species of Pacific salmon, it is at best an approximation for Atlantic salmon. Atlantic salmon populations having largely multi-sea-winter females can be treated as effectively semelparous because repeat spawners are rare and do not comprise a significant part of the spawning population (Jonsson *et al.* 1991). Alternatively, populations having females maturing sexually as one-sea-winter salmon may have much higher proportions of repeat spawners that constitute a significant part of the spawning population (especially when quantified on a weight or fecundity basis). Therefore, adult-to-adult relationships do not necessarily reflect the most important biological processes that govern stock-recruitment relationships in Atlantic salmon. Unlike some Pacific salmon populations (Quinn 2005), important density-dependent regulation of Atlantic salmon populations takes place early in life (Einum & Nislow 2005; Einum & Nislow 2011 [Chapter 11]) whereas density-independent processes seem to prevail in the ocean (Jonsson *et al.* 1998). Thus, although we favour SR relationships based on adult-(or egg)-to-smolt relationships, we also present adult-to-adult relationships in this chapter.

Box 12.2 Stock and recruitment: concepts, models and biological reference points

The concept

The relationship between the size of the spawning population, or stock, and the number of recruits in a fish population is commonly described by a stock-recruitment (SR) model. SR-models include both density-independent survival and a possible density-dependent survival between two consecutive life stages of the population, or over the whole life cycle from adult to adult. Different types of data can be used as input for establishing stock-recruitment relationships, depending both on the data available and the part of the salmon's life cycle that is to be modelled. In rivers having counts of ascending adults, size and sex distributions from catch records, and counts of outmigrating smolts, the stock can be given as the number of adults of both sexes, as the number or biomass of females or – by fecundity-weight relationships – as the number of eggs. The recruitment can be given as the number of outmigrating smolts or the number of returning adults one generation later. Age determination from scale samples ensures that the recruits are allocated to the correct cohort. If the river (wetted) area available to the salmon is known, densities can be estimated and used instead.

Most salmon populations cannot be counted directly, so the stock-recruitment relationship must be established from other types of data. For the stock, we usually rely on catch statistics and estimates of catch rates to give the estimated number of spawners. This approach is especially sensitive to the catch rate estimate, since small errors in this can have large effects on the spawning stock estimate. Older catch statistics may also be somewhat biased (ICES 2009).

For the recruitment, the available information on juveniles (underyearlings, parr or pre-smolt) is usually obtained from electrofishing performed at some stations along the river. The estimated overall juvenile density is then calculated as the average over all stations. When there is information on meso-habitat categories (Caron *et al.* 1999) for the river, the densities from different habitats can be weighted according to their relative proportions. The smolt production can also be estimated by mark-recapture approaches. Finally, if the full life cycle is studied, the recruitment represented by the returning adults can be estimated from catch records and age determination either by individual scale samples or by river-specific smolt- and sea-age distributions.

Models

Establishing river-specific SR-models is a prerequisite for the use of spawning targets in fish population management. Although SR-relationships have been well documented for salmonids in general (e.g. Ricker 1954; Elliott 1994), comparatively few exist for European Atlantic salmon populations.

Here, egg density [egg m⁻²] will primarily be used as the stock unit, making it easier to compare rivers with different body size distributions, and allowing one to depict survival from eggs to recruits. The recruitment will be given as density of fish that survive to a given age or life-history stage (e.g. parr or smolt). Although the SR-observations are usually assumed to be independent, they can be auto-correlated because of shared environmental conditions and/or intercohort competition. The SR data should always be checked for temporal changes, or trends, in recruit survival rates due to environmental factors, since such changes almost always lead to changes in SR parameters at the same time (Walters & Korman 2001). If such changes are found, the time series should be split into sub-series with relatively constant river and marine conditions.

SR-models all conform to the general structure $R = aSf(S)$ (Elliott 2001), where R is the recruitment, S the stock, the parameter a the density-independent contribution to fish mortality and the function $f(S)$ the density-dependent regulation of the population. The SR-models therefore differ only by the assumed shape of the density regulating function. Some common SR-models (Elliott 1994) are as follows:

- Ricker (1954): $R = aSe^{-bS}$, giving a dome-shaped curve.
- Beverton-Holt (1957): $R = aS / (1 + bS)$, giving an asymptotic curve.
- Cushing (1971): $R = aS^{1-\beta}$, giving an infinitely increasing curve.
- Shepherd (1982): $R = aS / (1 + (bS)^\beta)$ where
 - $\beta > 1$ gives a Ricker-shaped curve,
 - $\beta = 1$ gives the Beverton-Holt model, and
 - $\beta < 1$ gives a Cushing-shaped curve.

The Shepherd model will be preferred in our applications because it does not require that the form of the curve is defined *a priori*, but rather estimated from the data. Caution must be exercised when interpreting these *SR*-models since there are often few, if any, observations in some parts of the range of possible *S*-values, typically either at the very low or very high stock densities. At these extremes, there will probably be factors affecting survival additional to those captured by the modelled *SR* relationship, such that extrapolations beyond the observed range may be very misleading. Fig. B12.2.1a presents a Shepherd *SR*-model with replacement line (Box 12.1). Maximum sustainable yield (*MSY*) is obtained for the stock density that maximises the difference between the *SR*-model and the replacement line. The replacement point is the intersect of an *SR*-curve and the replacement line, and represents the approximate equilibrium for an unexploited population.

Another interesting *SR*-model is the so-called Hockey-Stick model (Barrowman & Myers 2000). Barrowman and Myers were concerned by the unrealistically high survival rates often estimated for low stock densities by the existing *SR*-models, and suggested a simple, piece-wise linear model with initial density-independent mortality for low *S*-values. Above a threshold, we assume that all territories are occupied, or that the habitat is exhausted, and that density-dependent mortality will prevent any further increase in recruitment. We thereby end up with a hockey-stick shaped curve describing the *SR*-relationship. For computational convenience, we will here apply the generalised and smoothed version of the model, the so-called Logistic Hockey Stick model (Barrowman *et al.* 2000; Diserud *et al.* in prep.).

For some of the data sets, we fit both the Shepherd and the Logistic Hockey-Stick (LHS) models in order to compare the two, both with regard to their fit and the spawning targets they produce. A proper model validation is always required, both visually and by a cross-validation approach, especially given that some results can depend heavily on starting values chosen for the fitting algorithm. An r^2 -value (explained variance) close to zero may indicate that the population has had egg densities above the density regulation threshold during the entire study period such that any variation in egg density will not be reflected in the recruitment. The variation in recruitment will then be caused by other factors, e.g. a fluctuating environment or sampling randomness.

Spawning targets

NASCO has defined the conservation limit in Atlantic salmon fisheries management as the spawning stock level below which recruitment starts to decline significantly (NASCO 1998, and Box 12.1). The Precautionary Approach then dictates that the populations should be maintained above the conservation limit by use of a management, or spawning, target. The spawning target can be defined as the spawning stock level that ensures population viability. It may comprise the conservation limit with an added safety margin.

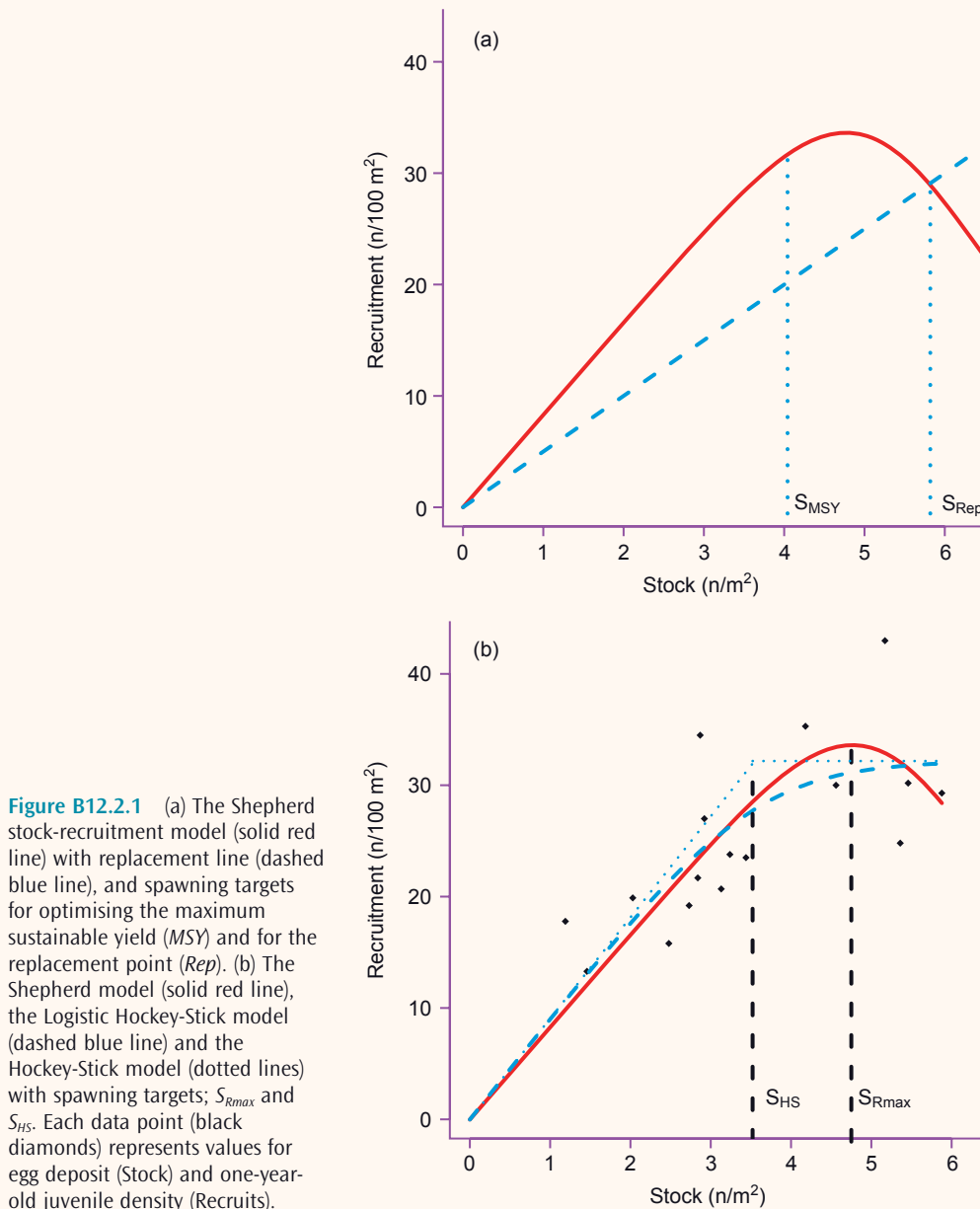
Spawning targets can be estimated for each river that has time series observations of the stock and the recruitment. A thorough review of both parametric and non-parametric spawning stock reference levels can be found in Potter (2001); we will present only the essentials here. The different spawning targets are adapted in part to the type of information available, but also to the different management criteria that can be applied. Some targets focus on the lower, critical limit of spawners needed for population viability, some identify the stock required for obtaining the maximum sustainable yield, while others may target the number of spawners needed to reach maximum recruitment.

Some common parametric spawning targets are presented in Fig. B12.2.1. The stock density giving maximum sustainable yield S_{MSY} and the replacement point S_{Rep} will necessarily depend on the *SR*-model used; in Fig. B12.2.1a we have illustrated this with a Shepherd model. The spawning target S_{Rmax} marks the top point of the dome-shaped Shepherd curve (Fig. B12.2.1b), i.e. the stock density that gives the maximum recruitment. For some rivers we have little or no information on maximum recruitment because all observed stock densities are below this reference point. The target S_{HS} estimates the threshold between density-independent mortality for low stock values and the asymptote where density-dependent mortality will prevent further increase in recruitment. Hayes *et al.* (1996) discuss in more detail the basic features of *SR*-curves and the information that can be obtained from them.

Modifications of these spawning targets have also been suggested, particularly as percentages of the more conservative targets. The proposed percentage has then been chosen according to the risk for stock depletion that managers are willing to accept. For dome-shaped *SR*-curves with adequate observations at low stock size, Mace (1994) suggested the use of 50 % of S_{Rmax} as a conservation limit, but added that they 'should be treated as absolute thresholds in the sense that the probability of crossing them should be vanishingly small'. Another approach might be to examine the gradient of the *SR*-model, and set the target where the increase in recruit-

ment falls below some predefined threshold. The problem with these two latter approaches is in deciding upon the 'biologically appropriate' percentage or gradient.

The observed SR relationship will necessarily be affected by both observation and process (unexplained biological) errors. When these nuisance parameters are ignored, assessments of uncertainty in the SR models are usually far too optimistic (Walters & Korman 2001). In order to calculate the safety margin of the conservation limit, required by the Precautionary Approach, these error parameters need to be quantified. The uncertainty of the models is usually best illustrated by the confidence limits of the SR relationship, thereby also giving the confidence interval for the spawning target. Spawning target uncertainties are discussed in more detail in the main text.



12.3.1 Spatial variation in stock and recruitment relationships

The first SR relationships for Atlantic salmon populations were established by Elson (1957, 1975). Combining information about parr and smolt density after planting underyearlings in tributaries to the Miramichi River, and by letting salmon spawn above a counting fence in the Pollett tributary to the Petitcodiac River, New Brunswick, Canada, he suggested that 2.4 eggs m^{-2} was sufficient to achieve a target number of outmigrating smolts (Elson 1957). The first report was based on only three cohorts of spawners and smolts, whereas a larger data set was based on spawning for the years 1953 to 1960 (Elson 1975). For this latter data set, Elson (1975) found little evidence of population regulation between the egg and underyearling stage, but near-significant evidence for regulation between the underyearling and smolt stage. He suggested that the population seemed to reach a plateau of 3–5 smolts 100 m^{-2} at an egg deposition of 2.4 eggs m^{-2} , but acknowledged that a particularly good year suggested a higher optimal egg density, as indicated in Fig. 12.5a. Re-analysis of

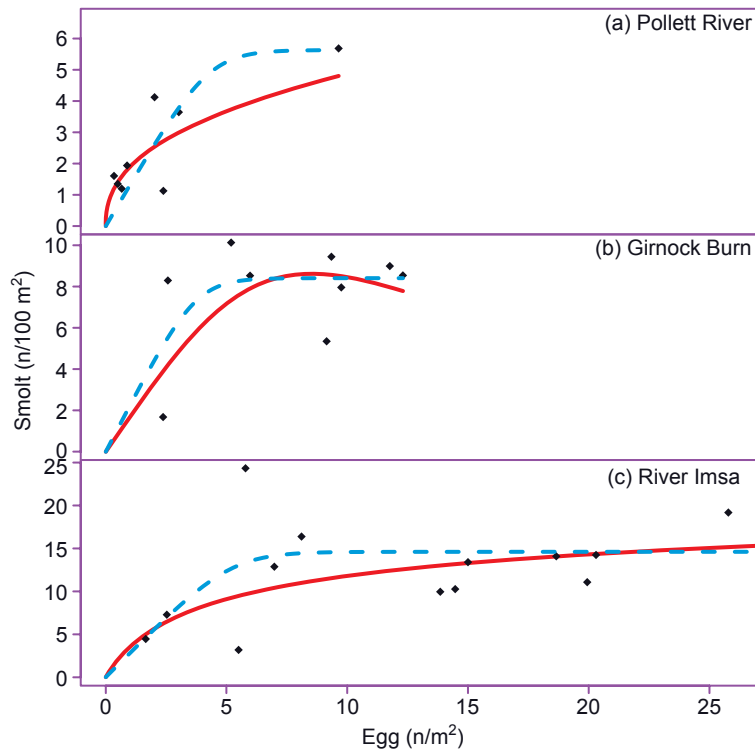


Figure 12.5 Shepherd (solid red line) and Logistic Hockey-Stick (dashed blue line) stock-recruitment models for one North American and two European rivers where stock was given by density of eggs (hatch year) and recruits were given as the density of smolts. Note that the scale of the y-axes (smolts 100 m^{-2}) varies. (a) Pollett River, tributary of the Petitcodiac system, New Brunswick, Canada (from Elson 1957; 1975). (b) Girnock Burn, tributary to River Dee, Scotland (from Buck & Hay 1984). (c) River Imsa, Norway (from Jonsson *et al.* 1998). Two years had stock densities above 60 eggs m^{-2} following releases of first-generation hatchery-produced smolts of R. Imsa origin. We have truncated this curve at 25 eggs m^{-2} to prevent the SR-curves for the Pollett River and Girnock Burn becoming too compressed.

Elson's data suggests that the *SR* relationship he fitted by eye results in an underestimate of the optimal number of eggs (*S*) resulting from *SR* modelling, as noted previously by Potter (2001).

Elson described his means of estimating optimal egg densities as the *ecological approach* (Elson 1975), as it was based on ecological aspects of the river life of Atlantic salmon. In contrast, he referred to Ricker's (1954, 1958) analyses of stock and recruitment of Pacific salmon as the *statistical approach*, being based on statistical analyses of the interrelationships of adult fish between parental and filial generations. In the 1980s and 1990s, several *SR* relationships were published based on full count data. We have shown two of them in Fig. 12.5b and 12.5c; one from the Girnock Burn tributary to the River Dee, Scotland (Buck & Hay 1984), and the other from the small River Imsa, Norway (Jonsson *et al.* 1998). These rivers differ from the Pollett both in the number of smolts produced per area, and in the egg densities sufficient to reach these levels of smolt production.

Stock-recruitment relationships of 15 rivers from Europe were analysed by Crozier *et al.* (2003) and Prévost *et al.* (2003) based on monitoring data from 1985 onwards. Analyses of stock (spawners) and recruits (pre-fishery abundance), using a Ricker model, suggested a wide range of S_{MSY} values (i.e. stock size that results in the highest maximum sustainable yield), from approximately 1 egg m^{-2} (rivers Nivelle, France, Mourne, N. Ireland, and Vesturdalsá, Iceland) to 10 egg m^{-2} or more (rivers North Esk, Scotland, Lærdalselva, Norway, and Ellidaár, Iceland) (Fig. 12.6).

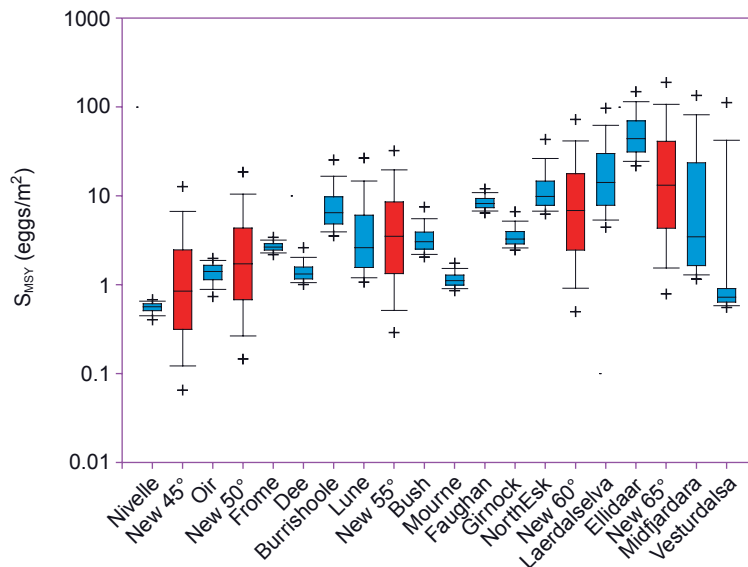


Figure 12.6 Box plots of the posterior distributions of S_{MSY} for the index rivers (blue) and any new river (red) without *SR* data located at latitude 45°, 50°, 55°, 60° and 65° North (from Crozier *et al.* 2003, with permission; Prévost *et al.* 2003), expressed in eggs m^{-2} of riverine wetted area accessible to salmon. Each box plot displays on a log scale the 10, 25, 50, 75, 90 percentiles and all values outside the 10 to 90 percentiles interval. Rivers are ordered according to latitude from south (River Nivelle, France, at 43° N) to north (River Vesturdalsá, Iceland, at 65° 30' N).

12.3.2 Temporal variation in SR relationships

Whereas few observations make estimation of relationships between stock and recruitment uncertain from statistical considerations, a high number of SR observations, spanning several decades in time, are unlikely to produce a SR relationship that is stable over time (Walters & Korman 2001). Changes in oceanographic conditions affecting growth and survival rates (Friedland *et al.* 2000), and human-caused changes in stock composition¹ and/or freshwater habitat, are among the factors that are likely to influence stock-recruitment relationships over time.

Temporal heterogeneity, so-called ‘non-stationarity’, of SR relationships was addressed for six European rivers by Crozier *et al.* (2003). Splitting these SR data series into an early time period (before the mid-1980s) and a late time period (after the mid-1980s), an analysis using the Ricker model suggested that both (1) the slope at the origin and (2) the maximum recruitment per m² accessible to salmon declined from the early to the later time period. A detailed analysis on one of these rivers, the Burrishoole in Ireland, suggested multiple causes of the temporal trends in recruitment (McGinnity *et al.* 2009).

A time series of recruitment from the River Lærdalselva, western Norway (Fig. 12.7), illustrates how the recruitment observations may show non-stationary characteristics. The river went through a watercourse regulation in 1974/75 and a second regulation in 1988/89, both affecting the spawning success and the juvenile survival rate. From 1961 (year of hatching) until the first regulation in 1974 the pre-fishery abundance (PFA) fluctuates around a recruitment of 63 eggs m⁻² (obtained for $S_{Rmax} = 9.3 \text{ eggs m}^{-2}$; Diserud *et al.*, in preparation). For the second period between 1975 and 1988 we see a steady decline in recruitment that violates the stationarity assumption required for an SR-model, i.e. that the average SR relationship is constant over time and that environmental conditions randomly affect survival, independent of stock size or time (Hilborn & Waters 1992).

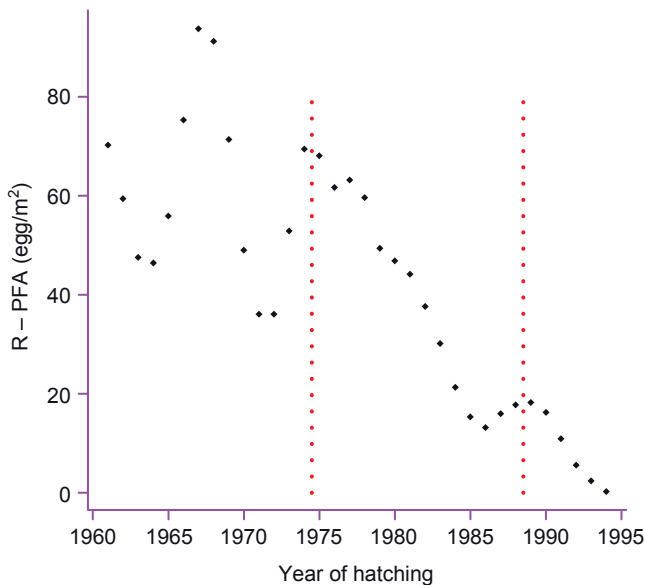


Figure 12.7 Non-stationarity in the salmon recruitment time series from the River Lærdalselva, western Norway, for the years of hatching 1961–1994 (from Diserud *et al.*, in prep.). The recruitment is estimated as the number of eggs at pre-fishery abundance; i.e. the estimated egg number of females upon entering the coastal fisheries. Watercourse regulation took place in the river in 1974/75 and 1988/89 (dotted vertical lines); *Gyrodactylus salaris* was discovered in 1996.

¹Of particular concern is evidence that stocking and ranching, as well as escaped farmed salmon, depress recruitment of the redipient wild populations (Verspoor *et al.* 2007; McGinnity *et al.* 2009; Vøllestad *et al.* 2009).

12.4 Spawning targets: from single populations to nation-wide levels

Stock and recruitment relationships can be used to establish biological reference points, such as spawning targets, for the population in question (Box 12.2). Whereas this task may be challenging in itself, a much greater challenge is to transfer this type of information to the vast majority of rivers where such information is non-existent.

12.4.1 Methodology – transfer from data-rich to data-poor rivers

The simplest means of transferring estimates of spawning targets (number of spawners or egg deposition) from data-rich to data-poor rivers is to assume that different rivers have the same area-specific egg density requirements (Prévost *et al.* 2001). Differences between rivers in spawning targets thereby reflect differences in wetted area accessible to salmon. If spawning targets are to be expressed as number of female spawners, egg density must be translated into number of female spawners by egg-weight relationships (Klemetsen *et al.* 2003) and average weight of females. This method has been used to provide spawning targets for a large number of Atlantic salmon populations in Canada (Elson 1957; Chadwick 1985), as outlined in more detail below.

This simple method is attractive for several reasons, as wetted area can be estimated with reasonably high precision by GIS methods from digital maps (Erikstad *et al.* 1999) that easily lend themselves to large-scale analysis. Another approach is to quantify the area of limiting habitat within rivers, based on the assumption that habitat requirements of juvenile salmon lead to some habitat types being limiting for smolt production (Prévost *et al.* 2001). This method is biologically attractive but requires a more detailed knowledge about each river. Recent analyses suggest that not only areas of preferred habitat are important for determining juvenile production indices, but also their distribution relative to spawning sites (Einum & Nislow 2005; Finstad *et al.* 2009).

In an analysis of several European salmon rivers, Crozier *et al.* (2003) and Prévost *et al.* (2003) assumed that geographical position (latitude) represented one easily available type of data that could be used to transfer information from data-rich to data-poor rivers. Latitude is also biologically relevant as it may be associated with smolt age and production of juveniles in salmon populations (Metcalf & Thorpe 1990) and possibly with marine survival rates. In a hierarchical Bayesian analysis of SR relationships from egg (spawners)-to-egg (pre-fishery abundance), Prévost *et al.* (2003) found that spawning targets in 13 European rivers between 43 and 64°N increased linearly with latitude (Prévost *et al.* 2003). The slope of this linear increase was lower when including two Icelandic rivers at 65° 30' N (Crozier *et al.* 2003), which had a much lower spawning target than predicted by latitude (see Fig. 12.6). One reason which led Prévost *et al.* (2003) to exclude these populations was that the populations in these rivers do not use the same oceanic feeding ground as many other European populations.

Characteristics of the population have also been used to put different rivers into different classes of spawning targets. Symons (1979) argued that smolt age was associated with a population's carrying capacity, which could be estimated from survival rates from eggs to smolt, growth rates to smolt stage, and space requirements of juvenile salmon. As rivers having comparatively young smolts seemed to have much higher smolt carrying capacity

than rivers having older smolts, Symons (1979) argued that the former rivers required a higher egg deposition to meet the potential smolt production.

12.4.2 Spawning targets for North America

The application of biological reference points to Atlantic salmon populations in Canada is one that reflects remarkably little change over the past half-century. The spawning escape-ments required to meet the conservation target of a particular population have been, and still are (for the most part), based on the number of eggs per unit area of fluvial rearing habitat (or lacustrine rearing habitat in Newfoundland) estimated to maximise the number of smolts produced by each population (i.e. 2.4 eggs m⁻² of fluvial rearing habitat as estimated by Elson [see Section 12.3.1]; Potter 2001; Chaput 2006). In the early 1990s, in acknowledgement of the importance of lakes and ponds to the production of salmon in Newfoundland, spawning requirements for several Newfoundland rivers were defined based on the additional requirement of either 1.05 or 3.68 eggs m⁻² of lacustrine habitat (CAFSAC 1991; O'Connell & Dempson 1995), depending on latitude.

The conservation egg requirement of 2.4 eggs m⁻² of fluvial rearing habitat has been transported to all Canadian Atlantic salmon rivers, despite the high probability that smolt production varies considerably throughout the species' Canadian range. By applying a general smolt production model to a sample of 10 rivers for which egg deposition and smolt abundance estimates were available, Chaput *et al.* (1998) estimated that the 2.4-egg target was likely to be more than twice that required to maximise yield, i.e., S_{MSY} . Although they suggested that a target of 90% of maximum smolt production would represent an appropriate risk-averse management strategy, the 2.4-egg conservation requirement is still applied. To date, conservation egg requirements have been defined for 55 rivers and all Salmon Fishing Areas in Newfoundland, and for more than 150 rivers in the Canadian Maritime provinces of Nova Scotia, New Brunswick and Prince Edward Island.

In the late 1990s, Quebec changed its conservation requirements for 110 rivers from one based on the aforementioned 2.4 eggs m⁻² target to one defined by Caron *et al.*'s (1999) analysis of egg-to-egg stock-recruitment data for six rivers: Matane, Cascapédia, Saint-Jean, York, Dartmouth, and la rivière de la Trinité. Fitting a Ricker model to the available data, Caron *et al.* (1999) estimated S_{MSY} for each stock and found a good fit between these optima (based on yield) and a metric of productivity for each river, as defined by their Units of Production (UPs). The number of UPs in a given river is a function of the physical characteristics of the rivers (e.g. width, flow regime, substrate morphology) per m² of usable fluvial habitat, expectations of parr growth rate (based on the number of days that the air temperature exceeds 5.6 °C), and relative juvenile densities. The Bayesian approach adopted by Caron *et al.* (1999) allowed them to construct a frequency distribution of probable values of S_{MSY} . They selected the 75th percentile of this distribution of S_{MSY} as their reference level, which resulted in a conservation egg requirement of 1.67 eggs UP⁻¹. This conservation target has since been applied to all 110 salmon rivers in Quebec (Chaput 2006).

Recent attempts have been made to establish targets for the salmon rivers in Labrador, which are thought to be less productive than those further south, leading to the high probability that S_{MSY} may be lower for Labrador rivers than elsewhere in North America. Given the absence of an adequate time series of stock-recruitment data for a single Labrador river, Reddin *et al.* (2006) adopted three approaches (which variously included fishery-generated

SR data and smolt production estimates from Sand Hill River) to estimate conservation egg requirements. Until recruitment data associated with high escapements have been obtained, they recommended that the standard of 2.4 eggs m^{-2} used elsewhere in Canada be applied as a management target, but that 1.9 eggs m^{-2} be adopted as a conservation limit, i.e., a threshold level below which the population should not be permitted to fall. Reddin *et al.* (2006) also recommended that the value of 1.05 eggs m^{-2} of lacustrine habitat be maintained for Labrador rivers.

In the USA, spawning targets have been established based on the 2.4 eggs m^{-2} reference level from Canada and historical observations on the populations in New England rivers (Baum 1995). Given local stock characteristics and the areas of juvenile salmon habitat currently accessible to spawners, Baum (1995) estimated that a minimum number of 29 200 2-sea-winter female salmon was required for New England rivers. Adult returns to these rivers have, however, not exceeded 18% of this level at any time during the past 25 years (Potter 2001).

The need for population-specific data for establishing reference points was underscored by Gibson (2006) who posed three questions of fundamental importance:

- 1) At what age is density dependence most evident in fresh water?
- 2) Is overcompensation characteristic of Atlantic salmon populations?
- 3) Can the strength of density dependence be quantified from stock-recruit data?

Using juvenile density data for nine rivers in New Brunswick and Nova Scotia, and smolt-to-adult return-rate data for 15 rivers located throughout eastern Canada, Gibson (2006) fit three spawner-recruit models: Beverton-Holt, Ricker, and a one-parameter density-independent model. To the three questions he initially posed, Gibson (2006) proffered the following answers. Firstly, the timing of population regulation varies among populations and appears most frequently between ages 0 and 1 yr. Interestingly, density-dependent effects appear to be manifested rapidly, in single age-classes in some populations, but to extend over multiple age-classes in others (see also discussion on self-thinning in Einum & Nislow 2011 [Chapter 11]). Secondly, none of the data were consistent with the hypothesis that over-compensation is a general feature of the population dynamics of Canadian Atlantic salmon populations; the Beverton-Holt model consistently provided statistically better fits to the data than did the Ricker model. Thirdly, the degree to which density dependence could be detected by the available data was, in general, surprisingly weak. Of considerable interest was Gibson's (2006) finding, estimated in two ways, that the carrying capacity for age-1 parr differs by a factor of 16 among populations.

The practice of establishing invariant conservation egg targets across broad spatial scales in Canada and the USA is recognised as being potentially fraught with difficulties. On the one hand, there will be a tendency to set risk-averse targets. Although the 2.4 eggs m^{-2} target was not initially based on a need to err on the side of caution, it has since been recognised as such (Chaput *et al.* 1998; Potter 2001). From a catch perspective, unduly cautious targets will result in foregone angling opportunities under some circumstances. If population-specific stock-recruitment data were routinely available, reference points could, in theory, be established on a river-by-river basis, ideally resulting in an optimisation of yield. Nonetheless, given the depleted status of many fisheries worldwide (Hutchings 2000; Worm *et al.* 2006), a condition generated in large part by a lack of appropriate reference points,

the initially fortuitous and currently intentional caution exercised by Atlantic salmon managers in Canada and the USA is laudable.

12.4.3 Spawning targets for Europe

The first European-wide attempt to establish biological reference points for Atlantic salmon populations was provided by the EU project SALMODEL (Crozier *et al.* 2003), which led to several papers with relevance to setting spawning targets. Methods developed by that project were used to estimate spawning targets for 70 rivers in England and Wales (Prévost *et al.* 2003), based on the latitudinal cline in European rivers which included three data-rich rivers from England and Wales (the Frome, Welsh Dee and Lune). The median optimal egg density with respect to yield (i.e. S_{MSY}) in these rivers was approximately 4.4 eggs m^{-2} , with the 10th and 90th percentiles of the estimate located at 2.4 and 8.0 eggs m^{-2} , respectively, reflecting the relatively wide confidence intervals for data-poor rivers.

A similar analysis of salmon populations in Ireland (Ó Maoiléidigh *et al.* 2004) suggested a median optimal egg deposition of approximately 4.3 eggs m^{-2} wetted area, with the 10th and 90th percentiles of the estimate located at 2.9 and 7.4 eggs m^{-2} , respectively. This estimate was somewhat lower than another one based on a 'pseudo stock-recruitment' model for which the eggs deposited were back-calculated from estimates of pre-fishery abundance of 1SW salmon (Ó Maoiléidigh *et al.* 2004). The estimate derived for Ireland by using this method was 7 eggs m^{-2} .

In their European analysis, Prévost *et al.* (2003) noted significant variation among rivers within a narrow latitudinal range, and considerable within-river uncertainty in some rivers (the River Lærdalselva at 61°N , the only Norwegian river in the analysis, being one of them). For Norwegian high-latitude rivers, then, the predicted optimal stock size for a data-poor river at 60°N or 65°N is to a large extent determined by observations from an Icelandic river (River Ellidaár) at 64°N (Prévost *et al.* 2003). The uncertainty associated with this prediction, as well as the observation that other northern (Icelandic) rivers may have very low egg deposition rates (Crozier *et al.* 2003), suggests that alternative strategies must be employed to specify spawning targets for Norwegian rivers.

Based on analyses of stock-recruitment relationships in nine rivers having optimal egg densities with respect to recruitment (and not yield) ranging from approximately 1 egg m^{-2} to more than 6 eggs m^{-2} , Hindar *et al.* (2007b) suggested that spawning targets for salmon populations in Norway could be grouped into four categories of egg densities: 1, 2, 4 and 6 eggs m^{-2} wetted area. Assessment of productivity (category of egg density) was for most rivers based on catch statistics converted to catch per area, smolt age distribution and other available knowledge about each river. From the spawning target (expressed as eggs m^{-2}), the number of eggs necessary to seed the whole river was estimated, and the number of females needed to meet that number was calculated from catch statistics (giving female weights) and an egg-weight relationship of $1450 \text{ eggs kg}^{-1}$, which seems to be representative for a large number of Norwegian rivers.

The spawning targets for most of the 80 watercourses treated by Hindar *et al.* (2007b) lie between 2 and 4 eggs m^{-2} . In the River Tana (Teno in Finnish), one of the largest salmon-producing rivers worldwide, the total spawning target was estimated at approximately 100 million eggs, equivalent to a female spawning biomass at $55\,000 \text{ kg}$ per year. Considering that this river holds several genetically distinct populations (Vähä *et al.* 2007; 2008), local

spawning targets were suggested for major tributaries and the main river. When this information was held against local catch statistics in the Tana/Teno, it became clear that the upper reaches are most likely far from reaching the local spawning target (Anon. 2009).

In rivers with small wetted areas and big fish, a small number of females (in some cases fewer than 20) may be sufficient to meet the spawning target. In such rivers, factors other than *SR*-relationships may be used to set the conservation limit, given that smaller numbers of spawners are increasingly vulnerable to genetic drift and demographic and environmental stochasticity (*cf.* Lande 1993).

12.4.4 Spawning target uncertainties

The observed *SR*-relationship, described by model type and parameters, is characterised by uncertainty due to both process error, i.e. stochastic environmental variability, and observation error. Further, for most rivers we have limited temporal information, so that only a small subsample of possible stock levels is available. Finally, *SR*-models describe just a small part of the complete population dynamical model for Atlantic salmon; a complete model should include a stochastic environmental term and stochastic age-structured survival rates (Lande *et al.* 2003).

To illustrate the effect stochasticity in reproduction may have on the spawning targets, we have included a stochastic term in the Shepherd *SR*-model $R = \frac{aS}{(1 + be^{BS})} e^{\varepsilon}$, where ε is a normally distributed variable with expectation 0 and variance σ_{ε}^2 (Diserud *et al.*, in prep.). This approach is in accordance with Walters and Korman (2001), which assumes that both process and measurement errors are, empirically justified, log-normally distributed. Following Walter and Korman's (2001) definition, ε may represent both unmodelled sources of natural variation in R and errors in measurement of R . A log-normally distributed recruitment is also expected under the Central Limit Theorem if a combination of normally distributed random factors affects multiplicatively the instantaneous mortality rate from egg to recruitment (Quinn & Deriso 1999; Salmon Technical Team 2005). Hence, the variance σ_{ε}^2 can be estimated from the residuals and subsequently used in the simulation of new *SR*-data sets. For each observed S -value we simulate a new R -value by drawing from a lognormal distribution with expectation obtained from the original *SR*-model and variance σ_{ε}^2 . This simulation procedure is repeated 1000 times so that we can obtain uncertainty estimates for model parameters and spawning targets. Fig. 12.8 shows 10 of the *SR*-models fitted to simulated data sets (red dotted lines) while the blue solid line is the original model. Note how the right tail of the curve 'flaps' depending on whether the highest simulated S -value have a high or low recruitment, illustrating the lack of robustness of the Shepherd model in the right part of the interval. This also illustrates the problem of choosing the 'right' *SR*-model (Ricker; Beverton-Holt; Cushing), since we can recognise all three types of curves fitted to data simulated from a 'true' Shepherd-model. Nevertheless, the estimated spawning target from the Shepherd model (S_{Rmax}) is rather robust and rarely gives estimates far below the original value.

Fig. 12.9 presents the distribution for the spawning target S_{Rmax} , estimated from each of the simulated data sets. For simulated data sets where the fitted *SR*-curve is infinitely increasing, or reaching the asymptote at higher stock values than observed, we have used the maximum stock level (5.9 eggs m^{-2}) as a minimum value for the spawning target. This will

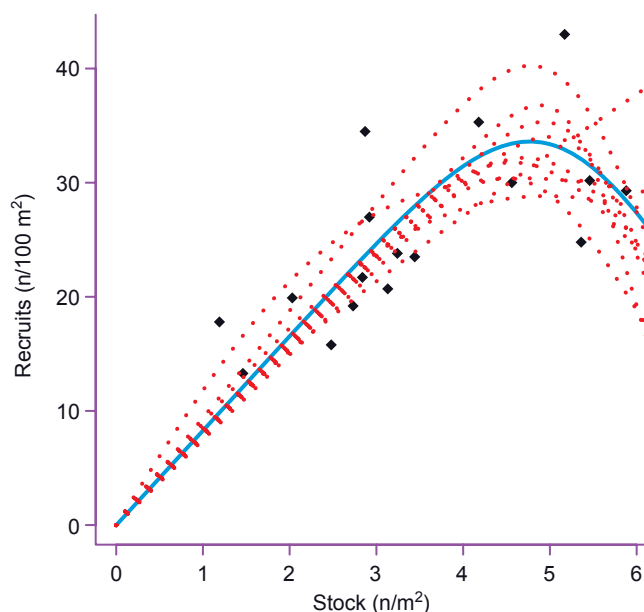


Figure 12.8 The stochastic variance in reproduction σ_ε^2 can be estimated from the residuals between the Shepherd model (black line) and the SR-data (black diamonds). The dotted red lines illustrate SR-curves fitted to 10 simulated data sets where the recruitment is obtained from a lognormal distribution with the prediction from the original model as expectation and variance σ_ε^2 .

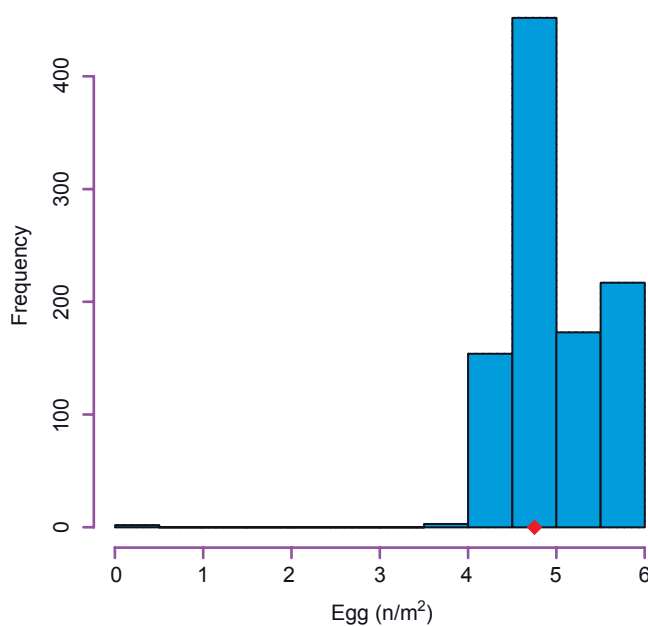


Figure 12.9 The frequency distribution for the spawning targets S_{Rmax} estimated from each of the 1000 simulated SR data sets. The red diamond at the base of the bars indicates the spawning target (4.8 eggs m⁻²) estimated from the original data set.

give a right truncated distribution for S_{Rmax} (Fig. 12.9), but is done in order to avoid excessive extrapolation. One simulation gives, by chance, a spawning target close to zero, due to large, positive residuals (higher recruitment than predicted by the model) for the lower S -values and negative residuals for the higher S -values. When the SR -model is then fitted to this simulated data set, we get a linear, slightly negative, relationship between S and R . If very favourable environmental conditions were experienced during the years with the lower stock densities, and random environmental fluctuations led to very bad survival during the years with the highest spawning stocks, this unlikely situation could occur. Besides this single extreme simulation, S_{Rmax} is relatively robust, with the lower 95% confidence interval limit at 4.2 eggs m^{-2} . The upper confidence limit is not calculated due to the right truncation of the distribution.

From similar simulations for the other spawning targets, Hindar *et al.* (2007b) found that S_{Rmax} from the Shepherd SR -model was the most robust spawning stock reference point, and appropriate for use as spawning target.

12.5 Exploitation

Fishing for Atlantic salmon has changed considerably over time, both with respect to fishing methods (Fig. 12.10), locations, effort and exploitation rates. The following historical review focuses on data from Norway, with additional information from other areas.

12.5.1 History of exploitation

In historical time, Atlantic salmon was traditionally exploited in the rivers or in the sea close to rivers. Rock carvings suggest that salmon played an important role for people in Scandinavia in the stone age. However, studies of bone remains suggest that salmon may have contributed less to the diet of people in northern Scotland from 3500 BC to AD 1500 than other fishes such as species from the cod family (Barrett *et al.* 1999).

Exploitation of salmon was probably moderate and the fish were mainly exploited in the rivers from deglaciation 10 000 years ago until approximately 1800 when effective gear for capture of salmon in the sea was developed. The fishing in the rivers was mainly a subsistence fishery, using different nets, traps, hooks and gaffs (Shearer 1992; NOU 1999). However, some trade with dried and salted salmon has also been documented (NOU 1999).

By the 1800s river owners could secure better income by letting their fisheries to anglers (Shearer 1992; NOU 1999). Angling has since remained the main fishing method in the rivers, and today traditional traps and netting methods are only used in a limited number of rivers (Numedalslågen, Tana and Neiden in Norway, and by indigenous fishermen in North America (NOU 1999)). Initially, angling was mainly an upper-class sport, but gradually a larger number of people took part in the activity (Aas 2001). Today, angling has moved from 'fishing for food' towards 'fishing for fun' and catch and release angling has increased in most countries (ICES 2009).

In the mid-1800s, gear was developed that enabled salmon to be caught effectively on their migration along the coast (Shearer 1992; NOU 1999), and this led to an increase in exploitation. In Norway, the number of bag-nets increased up until the early 1900s, but has decreased since 1960 (NOU 1999, Fig. 12.11). In the 1960s and 1970s, the use of bend-nets



Figure 12.10 Fishing for Atlantic salmon with rod and line (upper) and with bend-nets (below). Photos: Dag H. Karlsen and Roar A. Lund.

(Fig. 12.10) increased along the Norwegian coast, and during the same period a drift net fishery developed close to the Norwegian coast (Fig. 12.11). This fishery has been closed since 1989 and the number of bag-nets and bend-nets has also decreased. Furthermore, the time period during the season in which fishing for salmon is allowed using these gears has been reduced. Salmon have also been harvested by long-line fisheries in the Norwegian Sea and close to the Faroes, and by a net fishery off the coast of West Greenland. Towards the end of the 1970s, the high seas fishery in the northern Norwegian Sea was banned, and fishing was limited to the Faroes Economic Exclusion Zone (Hansen & Jacobsen 2000) and Greenland. In the 1990s, only a limited fishery took place at the Faroes, and since 2000 there have been no salmon catches at the Faroes (ICES 2009). The effort in the sea fishery

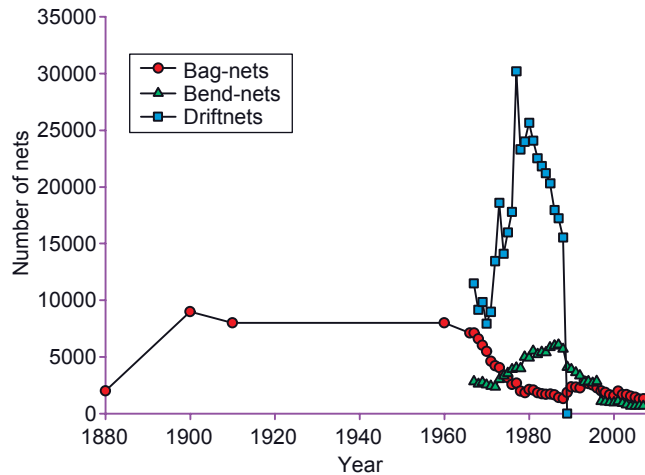


Figure 12.11 Approximate number of nets used in the Norwegian salmon fishery in the sea in the period 1880 to 2007. The numbers in the period 1880 to 1966 are approximate figures based on the information from NOU (1999). Figures from 1966 to 2007 are data from the Directorate for Nature Management in Norway. In addition to the methods presented here a limited number of lift-nets (<60) were in use in the period 1880 to 1992.

of Norwegian Atlantic salmon is therefore currently much lower than it has been during the last 130 years, and the fishery is once again mostly undertaken in or close to the rivers.

In short, the salmon has been exploited in, or close to, its home rivers for most of the period during which humans have exploited salmon. Only in a relatively short period (in evolutionary time) has a mixed-stock fishery dominated the catches. The mixed-stock fishery was most intense from approximately 1960 to 1990. Since 1990, there has been a shift towards a greater proportion of the catches being taken in or close to the rivers.

12.5.2 Exploitation rates

Exploitation in the marine fisheries varies among populations and among stock components (Potter & Dunkley 1993). In general, multi-sea-winter salmon were more heavily exploited than one-sea-winter salmon in the distant water fisheries (Potter & Dunkley 1993). Tag recoveries suggest that the Faroes fishery may have taken on average 25% (range 3–50%) of multi-sea-winter salmon from southern Norwegian populations in the 1980s (Potter & Dunkley 1993). Furthermore, before the closure of the Norwegian drift net fisheries, 80–95% of returning multi-sea-winter salmon from the River Imsa in southern Norway were taken in the home-water fisheries, leaving a low proportion returning to the river (Potter & Dunkley 1993). After the closure of the drift-net fishery, the home-water exploitation rate for multi-sea-winter salmon from Imsa was reduced to approximately 45% (Hansen *et al.* 2008).

Exploitation rates in UK rivers have been estimated to vary between 5 and 35% in different studies (summarised by Thorley *et al.* 2007; Hindar *et al.* 2007a), and vary among different stock components with early running fish experiencing the highest exploitation rates (Thorley *et al.* 2007). For Norwegian rivers, higher rod exploitation rates have been

estimated for small salmon (mean of approximately 50%) than for medium sized (mean of approximately 40%) and large salmon (mean of approximately 30%) (Anon. 2009). However, there was large variation among different studies (Anon. 2009). In the Icelandic River Hvítá, a rod exploitation rate of between 39 and 52% is suggested (Einarsson & Gudbergsson 2003). In the River Lune in northwest England, the rod exploitation rate was estimated at approximately 26% in the years 1989 to 1998, but the rate fell to approximately 14% in the period 2000–2004 as a result of introduction of a bag limit of four fish per angler per season (Aprahamian *et al.* 2006). The exploitation rates reported from Norwegian rivers (Anon. 2009) have generally been higher than those reported from UK rivers and more in line with the rates reported from Iceland and Spain (Hindar *et al.* 2007a).

In their stock and recruitment analysis referred to above, Prévost *et al.* (2003) estimated the exploitation rate at MSY for some data-rich European rivers. Northern populations seemed to be able to withstand higher exploitation rates than southern populations, with most rivers from the River Dee (Scotland) and northwards sustaining exploitation rates at 50% or higher, with the highest rates (70–80%) being sustained by populations in Northern Ireland (rivers Bush, Mourne and Faughan). These exploitation rates refer to exploitation from pre-fishery abundance, i.e. in coastal areas and rivers combined, whereas the exploitation rate summarised in Anon. (2009) refers to exploitation in rivers only.

12.5.3 Composition of catches

The sea fisheries have been a size-selective fishery (Reddin 1986; Strand & Heggberget 1996; Jensen *et al.* 1999). For example, the drift-net fishery along the Norwegian coast mainly targeted large grilse and small multi-sea-winter salmon (Jensen *et al.* 1999). After the drift-net fishery in Norway was banned in 1989, the proportion of large grilse increased in nearby Norwegian and Russian rivers (Jensen *et al.* 1999).

In some areas, such as Scotland and Canada, concern has been expressed that large fish, or multi-sea-winter (MSW) salmon, appear to be the stock component showing the most rapid decline (Youngson *et al.* 2002; Chaput *et al.* 2005). Even longer time series suggest that large-scale temporal variation exists in the stock composition of Atlantic salmon (e.g. Summers 1995) for reasons that remain obscure. Also, regional variation exists in the relationship among 1SW and MSW salmon, and recent trends in Norway and Russia suggest that 1SW salmon are declining more rapidly than MSW salmon in the northeastern Atlantic (ICES 2009).

12.6 Evolutionary and ecological effects of fishing

Fishing has the potential to generate significant phenotypic and genotypic changes to exploited populations, in addition to affecting the ecological interactions that exist between harvested populations and their competitors, predators, and/or prey. Traits in Atlantic salmon thought to have been influenced by fishing include age and size at maturity, growth rate, body size, run timing, and incidence of anadromy.

Notwithstanding the considerable difficulties associated with establishing a firm causal relationship between fishing and genetic change (Kuparinen & Merilä 2007; Hutchings & Fraser 2008), there is good reason to believe that some of the life-history changes associated

with fishing can be attributed to harvest-induced selection. Although many contemporary studies of fisheries-induced evolution have focused primarily on marine fishes (Jørgensen *et al.* 2007; Kuparinen & Merilä 2007; Hutchings & Fraser 2008), some of the earliest work was undertaken on salmonid fish. Handford *et al.* (1977), studying a Canadian population of lake whitefish (*Coregonus clupeaformis*), ascribed reductions in body size and individual growth rate to fisheries-induced selection against large, fast-growing individuals. Long-term declines in size at maturity among sockeye (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) were attributed by Ricker (1981) to genetic responses to exploitation. Haugen (2000) and Haugen & Vøllestad (2000) have made a convincing case for angling-induced evolutionary shifts in life-histories of grayling (*Thymallus thymallus*) in central Norway.

In Atlantic salmon, potential examples of fisheries-induced evolution have been limited to long-term shifts in size at maturity and the timing of the seasonal return of adults from the sea to fresh water (Hindar *et al.* 2007a). Bielak & Power (1986), for example, attributed century-long declines in mean weight-at-age for two-sea-winter and previously spawned Atlantic salmon angled from Quebec's Godbout River as genetic responses to increased fishing mortality, although they did not examine potential environmental correlates of these changes. Concomitant with 30- to 70-year declines in average mass, Quinn *et al.* (2006) documented temporal shifts in the run timing of Atlantic salmon in three Irish rivers (Blackwater, Owenduff, Newport), which they postulate may be attributable to fishing-induced selection against specific temporal components of the run (see also Consuegra *et al.* (2005) for Iberian salmon populations, and Gee & Milner (1980) for River Wye, Wales). Shifts in the run timing of sockeye salmon in the Bristol Bay area of Alaska have also been attributed to temporally differential, fishing-induced selection pressures (Quinn *et al.* 2007). It has also been hypothesised that increased mortality during the adult stage, attributable to the direct or indirect effects of commercial or recreational fishing, might select against seaward migration by male salmonids (Myers *et al.* 1986). Under these circumstances, fishing might effect genetic shifts in threshold reaction norms, resulting in increases in the frequency of the mature male parr reproductive strategy within affected populations (Piché *et al.* 2008; Thériault *et al.* 2008).

Irrespective of whether changes to life-history traits are genetic or phenotypic in origin (the latter being attributable to phenotypic plasticity or changes in density), they will almost certainly have negative consequences for population growth rate, thus affecting sustainable rates of exploitation and probability of recovery following depletion. If one assumes that trait distributions in the absence of fishing are optimal, such that individual fitness has been, on average, maximised for the natural environments in which the populations evolved (Fraser *et al.* (2008) provide one such example for Atlantic salmon), then changes to these traits will almost certainly decrease average fitness and, thus, population growth rate and/or carrying capacity. If the changes are genetically based, as might be anticipated under fisheries-induced selection, they are unlikely to be readily reversible (Stokes & Law 2000; Law 2007; Hutchings & Fraser 2008).

12.7 Management implications

Stock and recruitment analyses of Atlantic salmon have come a long way since Mills's 1989 salmon ecology book. By the end of the 1980s, stock-recruitment relationships were largely

based on Elson's (1957, 1975) analyses of a handful of populations from Canada and Ireland. New trapping facilities on several rivers increased the number of monitored populations during the 1970s and 1980s, and stock-recruitment relationships were developed for salmon populations in several North American and European rivers. Now these analyses have been applied to setting both population-specific and nation-wide spawning targets. In Ireland, stock and recruitment analyses also regulate the total allowable catch, firstly by region (Ó Maoiléidigh *et al.* 2004) and from 2005 onwards, by individual rivers (Anon. 2008). The total allowable catch per river is based on a risk analysis (by simulations) of the probability of the spawning stocks exceeding the conservation limit given different catches under the assumption that the stocks' size are as in the latest years. The total allowable catch is given as the catch that gives a 75% probability of the spawning stocks exceeding the conservation limit (Anon. 2008). If the 75% probability is not reached given any catch, the catch advice is either only open for a catch-and-release fishery or no catch. In rivers with no catch options the spawning stocks must be monitored by other means than by examining catch statistics, for example redd counts, counters of upstream migrating adults, survey draft netting or electrofishing of juveniles (Anon. 2008).

Management goals have changed dramatically since Mills's 1989 book, from one based on yield to one based on population viability and conservation. Accompanying this change is incorporation of a precautionary approach to salmon management (NASCO 1998; Crozier *et al.* 2003). This includes taking uncertainty into account when estimating pre-fishery abundance and the size and characteristics of spawning populations, and also when regulating fisheries that target several (often unknown) populations in so-called mixed fisheries.

Major oceanic fisheries have been closed or strongly regulated, such as the fisheries around the Faroes and off West Greenland, and the drift-net fishery on the Norwegian coast. International organisations have been key players in this change, in particular the North Atlantic Salmon Conservation Organisation (NASCO), which suggests fishery regulations based on scientific advice from the International Council for the Exploration of the Sea (ICES). In 2008, approximately 61% of North American catches, and approximately 67% of northeast Atlantic catches, took place in rivers (ICES 2009).

A central question for management is to what degree run size and thereby total allowable catch, can be based on information about stock-recruitment relationships and the strength of current cohorts. Can foresight (in-season) management be practised, or can it only be executed in hindsight (using the last few seasons)?

The survival at sea is highly variable (Friedland *et al.* 2000), so even in the case where one has complete knowledge about the number of smolts leaving a river, predicting the number of one-sea-winter salmon returning the following year is difficult. Survival appears to be positively correlated between different sea-age-classes from the same smolt cohort (Friedland *et al.* 2000), thus one may be able to predict the number of two-sea-winter salmon from the number of one-sea-winter salmon (grilse) returning the previous year. In rivers where multi-sea-winter salmon constitute a large proportion of the population, it may be possible to predict the number of two-sea-winter and three-sea-winter salmon returning the following years from the number of grilse returning the same smolt cohort. This opens up the possibility of giving crude predictions about the expected salmon return. Comparing this predicted return to the spawning target for the river thus shows if there is expected to be a harvestable surplus that could be used for setting size-class-specific quotas in the rivers. This may open the possibility to perform foresight management. If most of the fisheries on one

stock is performed close to or in the rivers, assessing the size of the population will be easier than it was in the past when harvest was taking place over a larger area. It may thus be possible to explore the relations between the number of returning salmon at different sea-ages from the same smolt cohorts for an increasing number of rivers in the future, thus improving the ability to give catch advice based on predictions.

However, for the majority of rivers one probably still has to base management advice on hindsight management (for example, Norwegian management authorities are basing management on fulfilment of the spawning target in the previous four years). This is not a bad strategy since in most rivers one smolt cohort consists of several river ages, and applying strong regulations to rivers that have not fulfilled the spawning targets in the most recent years may still ensure that the smolt production in the rivers is not substantially lowered in the long run. The strategy can probably be improved by looking at fulfilment of spawning targets per generation of the different populations, rather than for a fixed number of years. The future management of salmon is most likely going to be a combination of the various approaches.

Angler behaviour has contributed to the conservation focus by an increased practice of releasing rod-caught fish back into the river (catch-and-release). In the 2008 angling season, 86% of the rod catch of salmon in Russia was released back into the river, and other major salmon-producing areas like Canada and Scotland reported that around 60% of rod catches were released (ICES 2009). In Norway, catch-and-release has not been encouraged by management authorities except in a few rivers, but an increasing number of anglers are voluntarily releasing the salmon they catch.

Does the future of Atlantic salmon depend on the behaviour of anglers? For some populations, the complete abandonment of fishing must be accepted, given sufficient data to support a complete closure. A more challenging task will be to counteract size-selective fishing behaviour in the remaining river fisheries. If most of the fishing is carried out in such a way that specific size groups or fish with a specific life-history are being released and others are killed, rod-and-line fishing might be a stronger size-selective force than it historically has been. Still in its infancy, quota-based angling and catch-and-release fishing is not unproblematic, and its regulation for the long-term viability of the spawning population is a timely management measure that needs to be developed and investigated further.

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13

Landscape and Land Use Effects on Atlantic Salmon

Ola Ugedal & Anders G. Finstad

Abstract

Atlantic salmon spawn in more than 2000 river systems along both sides of the North Atlantic Ocean. A river's capacity for producing juvenile salmon is to a large degree dependent on the total amount of suitable freshwater habitat available for rearing, which varies extensively among rivers. This chapter focuses on how landscape and its anthropogenic land use modification contributes to the among-river variation in salmon production. We outline how landscape factors operate at widely varying spatial scales which are hierarchically nested within each other. Due to this hierarchy of river functioning, large-scale factors often override factors controlling salmon production at smaller scales. Human impacts and land use have influenced the historical and current status of Atlantic salmon productivity from the global to the catchment and local reach scales. Understanding how factors at different scales influence salmon productivity is thus obviously important in salmon habitat conservation and restoration. In light of this we discuss relevant spatial scales for assessment of anthropogenic land use impacts on salmon freshwater habitat and for carrying out habitat restoration strategies.

Key words

Riparian vegetation, sedimentary processes, forest clearance, forestry, fine sediments, Atlantic salmon

13.1 Introduction

There are more than 2000 Atlantic salmon rivers in the world (NASCO, North Atlantic Salmon Conservation Organisation, see www.nasco.in), distributed over large geographical areas along both sides of the North Atlantic Ocean. Consequently, river systems harbouring Atlantic salmon come in a variety of sizes and shapes that ultimately set the limits for the size of the salmon populations. For example, the River Tana (catchment area 16 386 km²), a border river between Norway and Finland, currently harbours one of the world's largest

stocks of Atlantic salmon. With more than 20 tributaries and approximately 1100 km of river accessible to salmon, the number of salmon ascending the river system peaks at more than 100 000 fish (Niemelä *et al.* 2004). In contrast, small rivers may drain catchments of less than 50 km², with annual runs at less than 100 adult salmon.

In general, the size of a salmon population is related to the total amount of suitable habitat available. The crudest measure of habitat availability is the total wetted area of the river system that can be used by salmon. There is a positive correlation between salmon catch (a proxy for freshwater productivity) and the amount of freshwater habitat available both in Canadian and Norwegian rivers (Chadwick 1985; Hindar *et al.* 2007). However, the variation in salmon catch per wetted area is rather large, suggesting that differences in system productivity and local habitat conditions are also important for salmon production. Estimates of smolt production confirm this variation among salmon populations (Chaput *et al.* 1998). In Norwegian rivers estimated smolt densities vary from less than 3 to more than 15 smolts per 100 m² of wetted area (Berg 1977; Jonsson *et al.* 1998).

The sources of variation in productivity among salmon rivers are a central issue in Atlantic salmon conservation and management. Population targets for management of salmon populations are commonly based on biological reference points (e.g. how many eggs need to be spawned to ensure full recruitment to the next cohort) derived from stock-recruitment relationships (www.nasco.int; Einum & Nislow 2011 [Chapter 11]). Biological reference points will vary from population to population, in large part due to variation in stream habitat features resulting from variation in large-scale landscape factors. One central challenge is therefore the transfer of reference points established for populations with high quality biological data to data poor systems. At present, transfers are typically based on comparative judgements of river productivity by using metrics such as densities of juvenile fish, runs of adult fish and/or habitat quality (Prévost & Chaput 2001). Establishing reference conditions, as well as understanding how anthropogenic land use or instream habitat modifications drive populations away from these conditions, are important topics in salmon habitat conservation and restoration that require knowledge about the interdependence of large-scale factors contributing to between-river variations in production.

In this chapter we address how landscape and land use may affect salmon production. We first outline how large-scale environmental factors in river ecosystems influence environmental factors at smaller spatial scales, highlighting the need for understanding the spatial nesting of environmental factors. Thereafter we review land use factors influencing the present-day status of Atlantic salmon productivity from the global to the catchment and local scales.

13.2 The multiple spatial scales of freshwater productivity

13.2.1 Global and regional scales

Rivers and streams, like other ecosystems, are under the influence of environmental factors that operate at widely varying spatial scales, and accordingly become hierarchically nested within each other (Fig. 13.1). Climate, geology and topography set the stage for environmental factors that shape and structure habitat factors at the local scale. Global atmospheric circulation patterns are determinants of local climatic factors, and

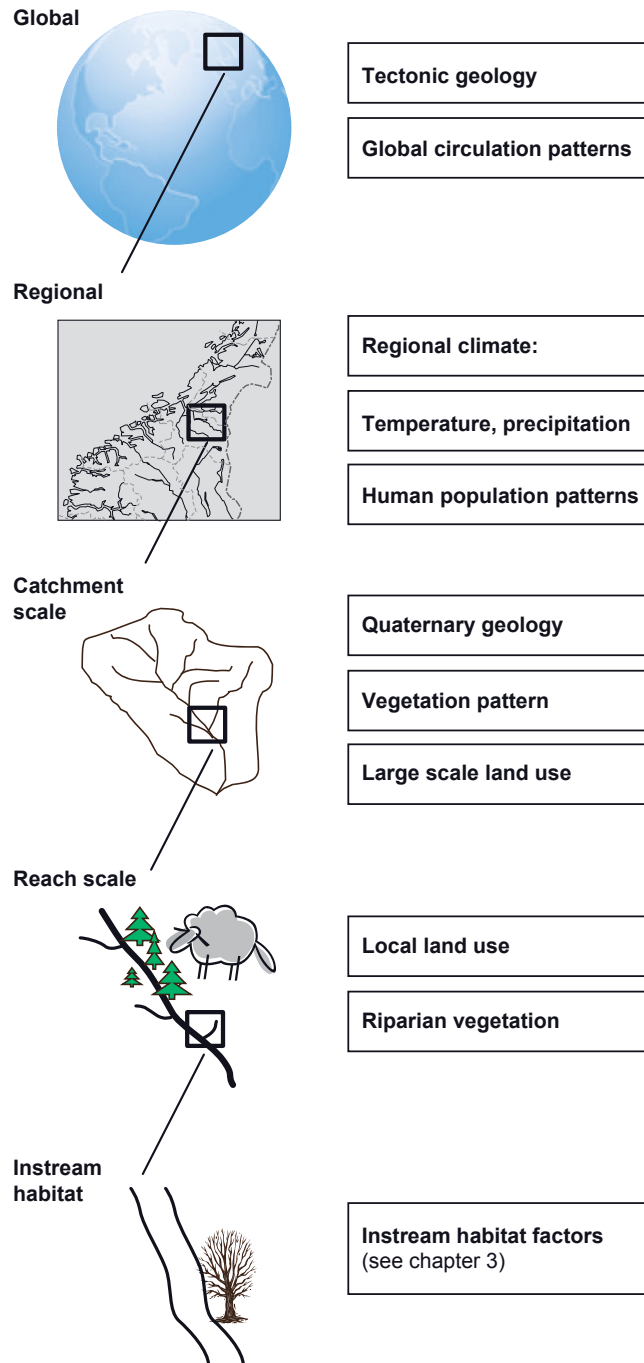


Figure 13.1 Hierarchical nesting of habitat factors influencing Atlantic salmon production. For practical purposes we divide the spatial scale over which habitat factors operate into five groups, reaching from global to instream habitat. Superimposed on spatially distributed factors are historical patterns. The composition of the biotic part of the ecosystem is governed by large-scale biogeographical processes shaped by geological and glacial history. Moreover, land use is dependent on the history of the human population density, which is also likely cross-correlated with historical potential for agriculture determined by abiotic parameters at various spatial scales.

the influence of these can be traced down to single Atlantic salmon populations. For example, does the North Atlantic Oscillation Index (NAOI) correlate with Atlantic salmon population parameters both in fresh and sea water (e.g. Jonsson & Jonsson 2004; Jonsson *et al.* 2005).

Elliott *et al.* (1998) divided the global distribution range of Atlantic salmon into five major regions based on geology, flow regime and climate, coupled with geographic position (Fig. 13.2). This regionalising of the distribution range of Atlantic salmon illustrates the interdependence of regional factors, where climate, geology and potential for agriculture interact to create large-scale differences in human population and anthropogenic impacts (Fig. 13.2).

The North American distribution range is divided into two major regions: I) New England and Nova Scotia region and II) the Northern Canadian shield (Elliott *et al.* 1998). Region I is characterised by mild to hot summers, with cool to cold winters with little ice cover and a geology characterised by glacial deposits overlying bedrock. Most likely as a result of favourable agricultural conditions, human population densities are high and urbanisation, agriculture and forestry have led to extensive landscape modifications (Nislow 2005). Region II, consisting of central-eastern Canada and northwards is characterised by granite bedrock overlaid by thin soils with a relatively flat topography. Summer climate is typically mild to cool with cold winters resulting in extensive periods of ice cover. Human impacts through land use are variable, with forestry being the most pronounced (Elliott *et al.* 1998).

The Atlantic Islands of Greenland and Iceland make up region III, where only Iceland holds numerous Atlantic salmon populations (Elliott *et al.* 1998). The geology of Iceland is heavily influenced by volcanic activity and the climate is typical Atlantic with mild and humid summers and moderately cold winters. The European distribution range is further divided into IV) Scandinavia and Russia, and V) Western Europe. Region IV is further divided into two distinct areas where Denmark and southern Sweden consist primarily of glacial moraine deposits and the rest of the region primarily of Archaean crystalline rocks (e.g. granites). The northern areas are characterised by heavy glacial scouring leading to steep topographic gradients and thin soil layers. Climate varies considerably from temperate with moderately hot summers and mild winters in the south to Arctic in the north. As a result of geological and glacial history and climate, human population densities are higher in the southern parts, leading to extensive landscape modifications through agriculture and urbanisation. Region V, Western Europe, is geologically diverse but characterised by high human population densities and more than a millennium-long history of land use (agriculture, forestry, industrialisation and urbanisation). Although the relative flat topography of Western Europe leads to rivers with long natural stretches accessible to anadromous fish, dam building and channel modifications in combination with pollution and eutrophication have considerably reduced the areas accessible to Atlantic salmon (*cf.* Lassalle *et al.* 2009).

13.2.2 Catchment and reach scales

The regional geology, in combination with the surface geomorphologic features resulting from the last ice age, determines the size and characteristics of catchments areas. Together with local precipitation patterns this determines the size and structure of river networks. For example, the river length (estimated along the main stem) accessed by anadromous Atlantic salmon in Norway range from about 1 km to 288 km with a median at 11.5 km

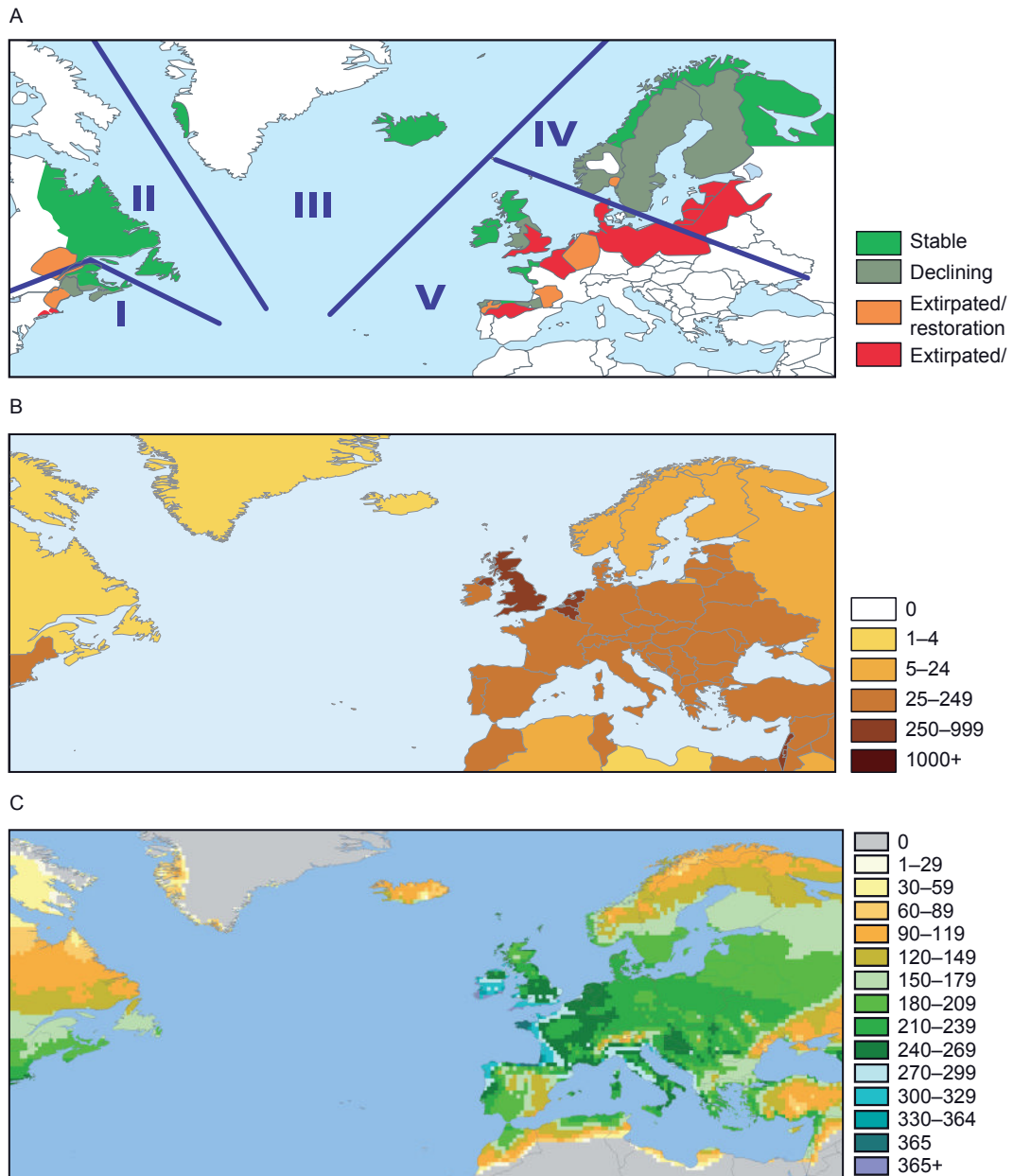


Figure 13.2 Climatic regions, illustrated as length of plant-growing season (lower panel), human population density (mid panel), and broad-scale population status of anadromous Atlantic salmon (upper panel) within the global distribution range of Atlantic salmon. A division of Atlantic salmon rivers into five major regions (I–V) based on geology, flow regime, climate and geographic position (Elliott *et al.* 1998) is also shown on the upper panel. Population status is based on Parrish *et al.* (1998) and represents a broad regional picture rather than giving an accurate picture of the status in individual rivers. Population status is classified based on numbers of adults returning to rivers as extirpated (no returns for at least 10 years), extirpated with restoration (no returns for many years followed by the initiation of a restoration programme), declining (long-term decline in numbers) and stable (no consistent decline).

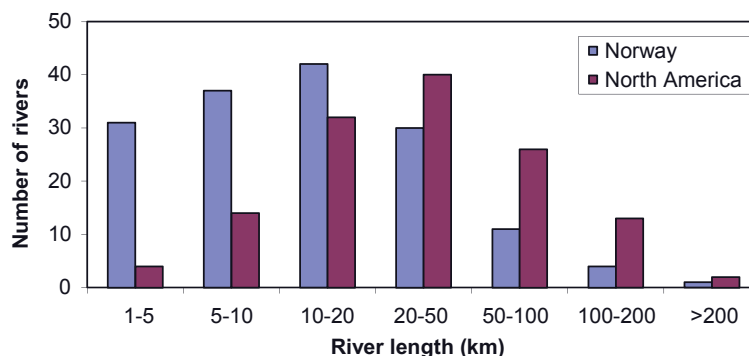


Figure 13.3 River length (in km along the main stem) accessed by Atlantic salmon in rivers from Norway and North America (mainly Canada). The figure is based on compilation of data from 165 Norwegian rivers (L'Abée-Lund *et al.* 2004) and 131 rivers from North America (Schaffer & Elson 1975).

(L'Abée-Lund *et al.* 2004). In contrast, data from 131 North American rivers (mainly from Canada) shows that the river length accessed by anadromous Atlantic salmon range from about 1 km to 343 km, with a median river length at 32.2 km (Schaffer & Elson 1975; Fig. 13.3). The difference probably reflects major differences in landscape topography.

River systems may range from low-gradient streams interspersed with lakes, ponds and wetlands, to high-gradient mountain streams dominated by cascades and waterfalls. Both the number of different habitat classes as well as their spatial distribution throughout the river system is likely to be of great importance for Atlantic salmon production (Kocik & Ferreri 1998; Finstad *et al.* 2009). The bedrock geology regulates the types and quantities of nutrients naturally available for dissolution and also affects the thermal regime. For example, watersheds consisting of carbonate bedrock or deep glacial deposits typically have higher concentrations of dissolved ions and less variable thermal and hydrologic regimes, providing the potential for higher total salmon production than streams draining other bedrock types (Krueger & Waters 1983). Vegetation characteristics of the catchment area also influence the nutrient load and runoff pattern. Open landscapes retain nutrients less effectively than forested landscapes, so that forest clearance results in increased runoff of nutrients from the cleared areas (Chamberlain *et al.* 1991). Invertebrate production transforms the stream's primary production and inputs of detritus and leaf litter from the surrounding land to a form available for Atlantic salmon (*cf.* Poff & Huryn 1998). In addition, terrestrial invertebrates from vegetation along the river (riparian vegetation) may constitute an important prey resource for stream fishes, at least in smaller streams and rivers (Nakano & Murakami 2001; Baxter *et al.* 2005; Saunders & Fausch 2007). This prey subsidy of terrestrial invertebrates can provide up to half the annual energy budget for drift-feeding fishes such as salmonids. Streams and their adjacent riparian zones are closely linked by reciprocal flows of invertebrate prey influencing food webs in both ecosystems (review in Baxter *et al.* 2005). All in all, watershed geology, vegetation cover, land use and land use history all interact to affect secondary and primary production in streams (Fig. 13.1).

Geological history, erosion and mass transport in the catchment will, together with hydrological conditions, affect the instream sedimentary processes that ultimately determine the size composition of the riverbed substrate, which in turn shapes the physical habitat available for the salmon. Riverbed substrate also influences the composition and production of

stream invertebrates (Rice *et al.* 2001). The size composition of substrate particles is governed by the interplay between deposition and mobilisation of different-sized sediment particles (i.e. source-sink dynamics). Connecting streams, local geomorphologic conditions and topographic formations will result in river stretches alternating between parts where substrate particles will either tend to be carried away with the current or deposited on the riverbed, creating a series of sedimentary links (Rice & Church 1998). This process is very closely dependent on the catchment scale geology, and sediment transport into the river networks may be highly associated with the glacial-era-valley organisation (Davey & Lapointe 2007).

Sedimentary processes ultimately determine the number and dispersion of suitable spawning grounds for salmon (Coulombe-Pontbriand & Lapointe 2004a; Davey & Lapointe 2007). Also, the distribution of favourable habitats for older juveniles in terms of shelter availability will be highly affected (Coulombe-Pontbriand & Lapointe 2004b). Both the spatial distribution and number of different substrate types therefore have a potentially large impact on the carrying capacity and population dynamics of the salmon stock (Einum & Nislow 2011 [Chapter 11]; Finstad *et al.* 2011 [Chapter 3]; Fleming & Einum 2011 [Chapter 2]). However, the interconnectedness of habitats suitable for various life stages is likely to be dependent not only on the spatial structure of the river, but also on the scale at which population dynamic processes operate (Isaak *et al.* 2007; Letcher *et al.* 2007). There is a profound lack of information on the spatial scaling of population regulation in Atlantic salmon, except for the very early life stages (Einum & Nislow 2011 [Chapter 11]; Fleming & Einum 2011 [Chapter 2]).

A stream reach can be defined as a length of stream channel that incorporates several local habitats (Poff & Huryn 1998). Typically a reach incorporates several pool/riffle sequences and may consist of one or more source-sink stretches in sedimentary processes (Davey & Lapointe 2007). Channel morphology and riparian vegetation interact to shape the distribution and quality of local habitats within reaches (Gregory *et al.* 1991). Riparian vegetation is more important for stream energy budgets in smaller streams (Vannote *et al.* 1980). Primary and secondary production at the reach scale is therefore determined both by stream width and the deposition of terrestrial litter and insects into the stream (Vannote *et al.* 1980; Baxter *et al.* 2005). At the reach scale, local land use patterns such as grazing of farm animals may have a strong impact on the riparian vegetation, reducing input of both allochthonous material and terrestrial invertebrates (Saunders & Fausch 2007). Removal of riparian vegetation may also increase streambed erosion and the inputs of fine sediments that may strongly influence invertebrate production and habitat conditions for salmonids (Larsen *et al.* 2009). However, at the same time, grazing from livestock could provide increased nutrient input, increasing instream production.

13.3 Land use and Atlantic salmon

Due to the hierarchical functioning of river ecosystems, large-scale factors can override factors controlling salmon production at smaller scales (Folt *et al.* 1998; Poff & Huryn 1998). Water chemistry, water temperature and sediment supply, important determinants of stream productivity, are largely controlled by catchment-scale processes. Changes in these factors can strongly influence the habitat complexity and stream productivity over large parts of a river. For example, excessive inputs of fine sediment due to land use in headwater

parts of a stream will be transported downstream and negatively affect habitat conditions and productivity in downstream reaches. The use of riparian buffer zones to reduce sediment inputs (see Broadmeadow & Nisbet 2004) will thus have minor effects on the local habitat conditions in these reaches, because sediment load is determined by the inputs from the headwater parts of the stream. It is therefore essential to understand the hierarchical functioning of river ecosystems for assessing land use effects on Atlantic salmon populations.

13.3.1 Global trends

Numbers of wild anadromous Atlantic salmon have declined throughout their native range. At the end of the twentieth century Parrish *et al.* (1998) addressed the question ‘why aren’t there more Atlantic salmon?’ They reviewed available information on the status of wild anadromous salmon based on numbers of adults returning to rivers to obtain patterns of salmon status across broad geographical areas (Fig. 13.2). In most catchments in the southern part of the salmon range, both in Europe and North America, salmon populations have experienced extirpation or great declines. These areas also have the highest human population densities within the salmon distribution range (Fig. 13.2). A recent study of the current distribution of European diadromous fishes, including Atlantic salmon, in relation to anthropogenic pressures supports the negative effects of increased density of human populations (Lassalle *et al.* 2009). Analysis of Atlantic salmon population status in Norwegian and Scottish rivers (Vøllestad *et al.* 2009) confirms the trend, with healthy populations in the rural north and declining populations in the more populated south.

Historically, there is also a connection between growth in the human population in an area and reduction and subsequent loss of salmon populations along river systems. For example, industrial and urban development during the industrial revolution in the nineteenth and twentieth centuries caused the extinction of Atlantic salmon from many rivers in England, Wales and Scotland (Netboy 1968; Doughty & Gardiner 2003; Mawle & Milner 2003). During this period certain areas became increasingly industrialised and the human population moved in large numbers to towns and cities, usually situated close to rivers. The loss of salmon populations was gradual and the last salmon in the River Thames, one of the first major rivers to lose its stock in Britain, was recorded in 1833. By 1900 salmon was extirpated in many rivers in Scotland, and the decline of salmon populations in the British Isles continued long into the twentieth century. Many of the historical declines and extirpations of Atlantic salmon can be more or less directly attributed to human activities in the catchment or within the river, such as construction of mainstem dams without fish passage (MacCrimmon & Gots 1979), severe pollution associated with industry, sewage and agriculture (Netboy 1968; Doughty & Gardiner 2003; Mawle & Milner 2003), and in a few cases total dewatering of streams (Parrish *et al.* 1998). However, industrial emissions often far from the point of deposition have also affected salmon populations negatively. In southern Norway, Atlantic salmon became virtually extinct in at least 25 rivers due to acid rain deposition (Hesthagen & Hansen 1991), and salmon rivers have also been negatively affected by acidification in other parts of the world.

Today, populations are recovering in parts of the salmon distributional range. During the mid-twentieth century stronger legal measures to control and reduce pollution from industry and sewage systems were implemented in England, Wales and Scotland (Doughty & Gardiner 2003; Mawle & Milner 2003). Large investments have been made in the effective treatment

of effluents, and heavy polluting industries are in decline. Recently, water quality in many rivers in Norway has improved due to reductions in the emissions of sulphur combined with extensive liming of rivers and their watersheds (Skjelkvåle *et al.* 2003, Rosseland & Kroglund 2011 [Chapter 15]). Following the progressive improvements in water quality combined with extensive restocking programmes in some cases, salmon have now recolonised many of their ancestral rivers both in Britain and in Norway (Mawle & Milner 2003; Hesthagen & Larsen 2003).

In many cases it is possible to identify single factors that have been responsible for extirpations of Atlantic salmon. The causes of observed declines of Atlantic salmon at the global scale are not always as obvious and a mix of interdependent factors is probably involved (Parrish *et al.* 1998). In addition to environmental factors directly reducing freshwater productivity of salmon, changes in marine survival rates of salmon may also have contributed to the declining trends in certain regions (Dempson *et al.* 2004).

13.3.2 Catchment effects

Atlantic salmon is managed at the population level, which in practical management terms is usually equivalent to management at a river system scale. Assessment of processes affecting Atlantic salmon production at the catchment scale (Fig. 13.4) is therefore important for habitat management considerations (Roni *et al.* 2008). Few if any studies have explicitly addressed the question of how land use affects the productivity of Atlantic salmon at the

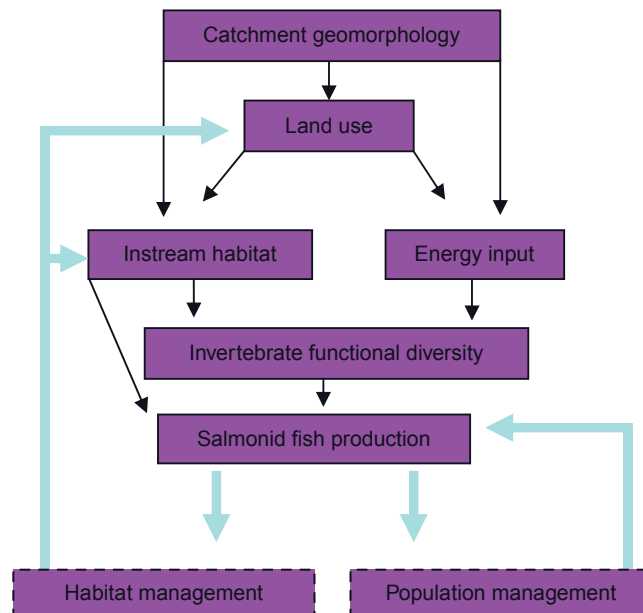


Figure 13.4 Flow diagram illustrating how catchment geomorphology, as well as anthropogenic land use, directly affects the physical stream habitat and the energy input to the system that influences salmonid fish production. Density-dependent population processes related to both the number and distribution of physical characteristics of the habitat as well as population and habitat management will ultimately determine the actual production of Atlantic salmon.

population level, but negative effects of different land use practices on Atlantic salmon productivity at a reach and local habitat scale have been demonstrated (e.g. Gilvear *et al.* 2002; Hendry *et al.* 2003; Deschênes *et al.* 2007). In other cases, negative effects can be predicted because of known effects on other species of salmonids and knowledge about the mechanisms at work. The total effect of changes in land use on a salmon population can, however, be hard to quantify from knowledge about local effects because of the problems of scaling up local habitat/reach-scale population effects to the entire river system.

At the catchment scale, land use affects both biotic and abiotic factors (Fig. 13.4). Large-scale catchment geomorphologies, as well as land use, determine both the physical stream habitat as well as energy input to the system. These factors will directly govern the functional diversity of invertebrates, and the effect of land use is also likely to interact with geomorphologic features of the river itself.

Forest clearance and forestry have been widespread throughout Western Europe and Eastern North America, to the extent that few Atlantic salmon rivers drain catchments with intact natural or late-successional forests (Elliott *et al.* 1998). Forest clearance is historically often carried out because of agriculture or urbanisation and may occur over large spatial scales, sometimes covering entire catchment areas. Stream fish populations are affected by the modification of key environmental features at multiple spatial and temporal scales (Chamberlain *et al.* 1991; Nislow 2005). One immediate effect of forest clearance is changes in hydrology (higher peak flows and lower base flow) due to a decreased water buffering capacity in the catchment. Changes in nutrients and chemistry (increased nutrients and acidity) and input of fine sediment (increasing due to soil disturbance from clearing) also follows. Moreover, removal of riparian canopy will increase light intensity, which affects the heat balance such that stream temperatures increases in summer and decreases in winter (Caissie 2006). Eventually, geomorphologic features in the riverbed may also change because of altered flow and sediment load patterns (Chamberlain *et al.* 1991). Forest clearing may also decrease the loading of large wood to streams. Large woody debris in streams increases habitat heterogeneity, and has been associated with increased habitat quality for juvenile salmon (Nislow 2005). In addition to these physicochemical changes associated with conversion of forested landscapes, the energy input to the stream ecosystem will be affected by the changes of vegetation in the catchment and particularly the changes occurring in the riparian zone (Broadmeadow & Nisbet 2004; Baxter *et al.* 2005).

In many cases it is obvious that conversion of forested land to open landscapes, such as agricultural land, have changed the stream physical habitat in such a way that fish production is reduced (Gilvear *et al.* 2002). Habitat deterioration is often associated with geomorphologic adjustments to streams, such as channel widening and loss of pools, due to changes in sediment input and hydrology (Gilvear *et al.* 2002). Many productive Atlantic salmon rivers, however, run through extensively cultivated and open landscapes (Elliott *et al.* 1998), showing that high fish production may be upheld in catchments that are largely deforested. The link between fish production and forest cover is complex. Nislow (2005) discusses how changes in forest cover may influence stream fish habitat and salmonid production in upland coldwater streams, as can be found in New England and in the British Isles (Fig. 13.5). He suggests that old-growth forest and open landscapes may be two alternative peaks for fish production in such streams, whereas young early-mid successional forests may be a potential production trough. Young-mature forests are highly effective filters for light, nutrients and sediments, such that levels of nutrients, light and temperature in streams may be driven



Figure 13.5 Upland coldwater streams in (A) extensively cultivated and open landscapes in Scotland and (B) densely forested areas in New England. Photos: Rasmus Kaspersson & Anders G. Finstad.

below what is optimal for fish production. For formerly forested landscapes, re-establishment of forest cover may be a restoration target, but due to the complex nature of fish–forest interactions it may be difficult to predict what effects such restoration measures will have on fish production (Nislow 2005). Moreover, the effects of forest cover certainly differ between regions due to differences in geology, topography, climate and fish species.

Forestry, harvesting of timber, will usually not result in a permanent clearance and environmental effects thus operate over shorter time scales and on smaller spatial scales. Invertebrate and fish production in upland streams may be nutrient and light limited (see Nislow 2005), such that increased runoff of nutrients and reduced shading may be beneficial

in the short run. Removal of the canopy due to forestry can therefore give increased production of invertebrates in small headwater streams, which may give increased density and biomass of salmonid fish (Nislow & Lowe 2006). However, several studies shows that forestry may influence salmonid fish populations negatively, and that one of the main environmental disturbances is erosion of fine sediments due to clearing of land and building of roads in connection with the harvest of timber (Waters 1995). Knowledge of how forestry affects Atlantic salmon is scarce, as most studies of forestry effects on salmon populations have focused on Pacific salmonids from forests of the western United States and Canada (Waters 1995). However, Deschênes *et al.* (2007) reported that the number of reaches where Atlantic salmon was present (incidence) and juvenile salmon density was negatively affected by forestry practices in the Cascapedia River basin, Canada.

Increased inputs of fine sediments to rivers as a result of human activity are a major cause of reduced instream habitat quality. The effects of excessive inputs of fine sediments on fish populations have received much attention in North America, and quantitatively, fine sediment has been labelled the most important pollutant in US streams and rivers (Waters 1995). Inorganic fine sediments: clay, silt and sand (particles <2 mm), are naturally present to some extent in all streams. In gravel-bed rivers, the storage of fine sediments is normally transient, as sediments enter and leave river channels naturally, being transported downstream to lowland reaches or the sea by gravel mobilising flows. Water abstraction from catchments or reduction of high flows due to hydropower developments (storage of water for power production) can seriously reduce gravel mobilisation flows and thereby reduce the self-cleaning capacity of the river (*cf.* Poff *et al.* 1997). Also, human activities such as agriculture, forestry and road building in connection with the development of urban and rural residential areas has led to the input of excessive fine sediments into rivers, which has greatly increased the accumulation of fine sediment in rivers throughout the world (Waters 1995; Opperman *et al.* 2005). Pulse inputs of fine sediments may eventually be cleaned from river reaches (Macdonald *et al.* 2003). However, redistribution and transport of deposited sediments to reaches further downstream may continue for many years, and the effects of input of fine sediments due to for example logging may be detected for decades after the actual disturbance (e.g. Swank *et al.* 2001). Such effects of historical land use were termed the 'ghost of the land use past' by Harding *et al.* (1998).

Deposition of fine sediments in spawning gravels can detrimentally affect salmonid spawning success (Chapman 1988). Moreover, inputs of excessive fine sediments affects juvenile fish habitat by filling up interstitial spaces that fish use for sheltering (Suttle *et al.* 2004). Fine sediments also influence fish indirectly by affecting the invertebrate fauna. Species of benthic invertebrates that are important as prey for juvenile salmonids, such as species of Ephemeroptera, Plecoptera and Trichoptera decline in density, whereas burrowing organisms such as Chironomidae and Oligochaeta increase (Waters 1995; Suttle *et al.* 2004; Larsen *et al.* 2009). Such changes in prey composition together with deteriorating habitat conditions negatively affect growth and survival of juvenile salmonids (Suttle *et al.* 2004; Bolliet *et al.* 2005).

Water quality problems arising from land use include pollution from point and diffuse sources. In urban environments, levels of different chemical pollutants such as heavy metals, excess nutrients, pesticides, and toxic organic compounds are typically elevated in rivers due to industrial and sewage effluents, and runoff from roads, yards and other sources (Paul & Meyer 2001; Rosseland & Kroglund 2011 [Chapter 15]). Poor water quality can have a

marked effect on salmonid stocks, but the impact can vary greatly in terms of scale and longevity. Agriculture typically increases nutrients in rivers due to both point sources and diffuse inputs (Fig. 13.6). Most rivers with Atlantic salmon are oligotrophic (Elliott *et al.* 1998), and moderate nutrient increases can have a positive effect on salmon productivity (e.g. Bergheim & Hesthagen 1990). On the other hand, excessive enrichment with nutrients causes eutrophication problems (e.g. reduced oxygen levels and habitat deteriorating) which may reduce fish production (Hendry *et al.* 2003).

The principal activities by which flow regimes in rivers are modified by human activities include changes in land use such as different agricultural and forestry practices within a catchment, water abstraction and transfers between catchments, impoundment and flow regulation, and hydropower generation (Hendry *et al.* 2003). Flow can be reduced or increased, or the seasonal pattern of flow fluctuations can be modified. The largest changes in flow regime and hydrological factors are connected to different types of hydropower installations (e.g. Johnsen *et al.* 2011 [Chapter 14]). Extensive construction of dams by humans has greatly dampened the seasonal and interannual stream flow variability of rivers (Poff *et al.* 2007), thereby altering the natural dynamics of ecologically important flows (i.e. gravel mobilisation flows, Poff *et al.* 1997).

13.4 Concluding remarks

Although large-scale global patterns show correlations between anthropogenic impacts and the status of Atlantic salmon stocks, we do not know to what extent changes in land use are responsible for or contribute to the continuous decline of populations in several areas.



Figure 13.6 The effect of anthropogenic land use on the freshwater production of Atlantic salmon is not clear, but is likely to depend both on local climate and geology. For example, many salmon rivers in northern systems run through highly cultivated landscapes but still hold thriving populations. Photo: Eva Thorstad.

Moreover, for rivers in regions where Atlantic salmon populations appear to be stable at present, we do not know if and eventually how much the freshwater productivity has been shifted away from its original levels. Given that several land use practices have been proven to generally negatively affect salmonid productivity, there are reasons to believe that some populations in this part of the Atlantic salmon distributional range may suffer reductions. At the same time, positive effects may also be expected in some oligotrophic river systems due to moderate nutrient enrichments.

NASCO has adopted and applies a precautionary approach to the conservation, management and exploitation of Atlantic salmon in order to protect the resource and preserve the environments in which it lives (www.nasco.int). One of the guiding principles of the precautionary approach is that priority must be given to conserving the productive capacity of the salmon resource. This implies that the remaining salmon habitats should be protected and that as much as possible of lost and degraded habitats should be restored. However, the spatial hierarchical structuring of environmental factors determining Atlantic salmon production means that choice of the appropriate management scales is crucial in this respect. Habitat restoration strategies will have to be planned and carried out based on the assessment of processes affecting Atlantic salmon production on the catchment scale (*cf.* Beechie *et al.* 2008; Roni *et al.* 2008). In order to provide cost-effective conservation and restoration measurements, future research focus should therefore be on understanding the appropriate spatial scale of such measures in order to maximising the likelihood of habitat quality improvement.

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14

Hydropower Development – Ecological Effects

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Abstract

Hydropower development has taken place in salmon rivers in different countries since the 1880s, and peaked during the 1950s and 1960s. In some countries there have been serious negative effects for Atlantic salmon populations, but in others the effects have been negligible. The negative effects on single populations vary greatly, ranging from complete extinction to small negative effects; there have even been a few cases where populations have actually benefited from the regulation. One major concern is that large dams may impair the upstream migration of Atlantic salmon and also affect the downstream migration of smolts and kelts through hydropower turbines and reservoirs. River regulations often change the hydrological scheme in rivers, thus affecting water discharge, water temperature and water quality, all of which are parameters that may affect the survival of salmon both directly and indirectly.

Traditional mitigatory measures in regulated rivers are fish stocking, weirs, fish ladders, downstream fish-passage facilities, and different kinds of habitat adjustments.

Minimum water flow has been one of the oldest mitigatory actions, and there is documentation of a positive correlation between winter discharge and the survival of juvenile salmon in winter. An improved understanding for a broader use of water for environmental purposes has in some cases resulted in new manoeuvring rules for power plants that should improve the environment for the salmon population.

It is imperative for future research to identify the bottlenecks that may cause high mortality, and a major task for the future management will be to maintain river-specific populations at levels that ensure natural reproduction and recruitment.

Key words

Hydropower development, river regulation, Atlantic salmon

14.1 Introduction

Hydropower produces one-sixth (16%) of the world's power (<http://www.hydropower.org>). The principle behind the concept of hydropower ultimately is the conversion of the potential energy of water into electrical energy. This conversion can be achieved through impoundment, diversion or pumped storage (http://www1.eere.energy.gov/windandhydro/hydro_plant_types.html). An impoundment facility, typically a large hydropower system, uses a dam to store river water in a reservoir. The water may be released either to meet changing electricity needs or to maintain a constant reservoir level. A diversion facility, sometimes called run-of-river, channels a portion of a river through a canal or penstock. Because this type of hydropower utilises the natural flow of the water, dams or impoundment are not necessary in many cases. A pumped storage facility stores energy, when demand for energy is low, by pumping water from a lower reservoir to an upper reservoir. During periods of high electrical demand, the water is released back to the lower reservoir in order to generate electricity.

Different types of hydropower facilities, depending on the landscape and the amount of water, have been developed in Atlantic salmon rivers throughout the world (Box 14.1). This development has resulted in serious negative effects for Atlantic salmon populations in some countries while the effects have been negligible in other countries. During the period of hydropower development, research in regulated rivers has produced a large bank of knowledge both on effects from different types of hydropower development and on mitigatory measures.

The main goal of this chapter is to present the key elements of this knowledge in order to contribute to a basis both for future research and future management in regulated rivers.

Box 14.1 The history of hydropower development and Atlantic salmon

Different types of hydropower facilities, depending on the landscape and the amount and distribution of water, have been developed in Atlantic salmon rivers. This development has resulted in serious negative effects for Atlantic salmon populations in some countries and rivers, while the effects have been negligible in other countries and/or rivers. As a backdrop, we present briefly the history of hydropower development in countries where the effects on Atlantic salmon have been substantial.

Norway

The first hydropower station in Europe was built in Norway in 1882 and this event initiated a period of construction of hydropower development for local use. Between 1945 and 1961, more than 200 new power stations were built (Hveding 1992). The period from 1961 to 1980 witnessed the completion of many large hydropower projects. Storage is the most common type of hydropower development in Norway. The impacts of this kind of hydropower development are very complex and depend on the running of power stations, the release strategy of water from reservoirs and the water quality in the different parts of the watercourse.

In Norway there are 452 rivers which have or have had a self-reproducing population of Atlantic salmon. In 84 (19%) of these rivers, hydropower development is a significant factor influencing the status of the salmon stock (Hansen *et al.* 2008). Among the 45 Norwegian salmon populations that have been lost, 19 (42%) were lost owing to hydropower development (Hansen *et al.* 2008).

According to Hansen *et al.* (2008) the most common negative effects of hydropower development are the permanent or partial drying of the riverbed, frequent changes in water flow leading to the stranding of fish

and smolt mortality due to downstream migration through turbines. Hydropower development has reduced the production of Atlantic salmon smolts in Norwegian rivers by 10–20%. In some rivers the salmon population has been exterminated while in others there are rough estimates of the increase in the annual smolt production following the hydropower development, mainly due to increased water discharge during winter (Hvidsten *et al.* 2004).

Sweden

The first hydropower-generating stations appeared in the 1880s and currently only two large salmon rivers remain unregulated. The total length of the regulated reaches is about 670 km. Regulation has often resulted in a complete loss of local populations (Svensson 2000). Regulated Swedish rivers typically consist of one or a few major storage reservoirs in the mountains, followed by a series of river impoundments in the downstream direction. The major regulated rivers are generally fully harnessed between the uppermost dam and the sea, and thus look like ladders when seen in profile (Svensson 2000). The river impoundments often store water for peaking power generation and water level fluctuates throughout the day and week. The river channel, between the dam and the power station outlet into the next dam below, acts only as a spillway. Sometimes, they have a certain minimum flow and are used for fish passage. This is mainly the case in northern Sweden, while the hydroelectric power stations in southern Sweden are comparatively small and are mainly of the run-of-river type.

Dams prevent upstream migration to spawning areas and smolt face problems during downstream migration owing to turbines and the altered fish populations in the reservoirs. Owing to the river impoundments, lotic species like Atlantic salmon are replaced (Henricson & Müller 1979). Base-flow measures to keep up natural populations of anadromous species were only consequentially used where spawning grounds were still available downstream from the lowermost dam (Svensson 2000).

Finland

The construction of hydropower in Finland started by the turn of the twentieth century and the main increase of capacity took place in the 1950s and 1960s when the share of hydropower of the country's electricity generation was 90% at its highest. Hydroelectric dams preventing spawning migration change the rivers below the dams and destroy the spawning and nursery areas above the dam. The demand for hydroelectric power has caused an almost total destruction of the migratory fish stocks in Finnish rivers discharging into the Baltic Sea. Only two rivers still support salmon runs (Ikonen 1984).

Denmark

Atlantic salmon occurred historically in nine Danish rivers. Today, however, natural salmon populations remain in only three river systems. The major cause of extinction of salmon in Danish rivers has been watercourse obstruction. The withdrawal of river water to supply about 450 trout farms has obstructed not only the upstream migration of adults, but also the downstream migration of smolt of salmon and trout. The wild salmon population in the most important salmon river, Gudenå, was entirely destroyed in the 1930s following the construction of a hydropower dam in 1920 (WWF 2001). A debate over the demolition of this dam has been going on for the last two decades.

Iceland

In Iceland, 88 rivers and river systems hold Atlantic salmon (Isaksson & Gudbergsson 2009), of which 62 are major salmon rivers (Isaksson 2002). Salmon mostly inhabit clear-water rivers or clear-water tributaries to glacial rivers. Most salmon rivers in Iceland have been spared hydroelectric development because rivers that have been or are being developed are large glacial rivers of limited value to salmon (Scarnecchia 1989).

Russia

Some Atlantic salmon rivers in the regions of Karelia and Murmansk have been affected by dams. Large dams constructed between 1934 and 1966 have prevented upstream migration in some of the more productive rivers and have reduced the potential salmon-production area (Johnsen *et al.* 1999; Karpinen *et al.* 2002). In one fish pass alone 3000 to 6000 salmon ascended annually in recent years (Tretyak *et al.* 1997; Jensen *et al.* 1999).

Great Britain

Great Britain has relatively little hydropower (only about 2% of the total electricity consumption) (Johnson 1988). The first hydroelectric power scheme was developed in Scotland in 1896, but the important period for hydropower construction occurred from 1948 to 1965. Today, there are over 80 hydropower stations in the Scottish Highlands and Islands (Fig. B14.1.1). All of the major rivers are regulated by dams or are influenced by upstream impounding reservoirs. Dams prevent upstream migration and increase the mortality on descending smolt. Below dams, generous compensation and freshets flow on many rivers have been generally beneficial for stocks (Johnson 1988). In 1965 the completion of Llyn Celyn reservoir in the River Dee caused the loss of 6 km of salmon spawning grounds by flooding and preventing adult migrants from reaching a further 10 km upstream (Brooker 1981).



Figure B14.1.1 The 15 m-high dam in Pitlochry on the Tummel River, a tributary to the Tay, Scotland. The dam was established in 1951. A fish ladder provides migration opportunities to the left of the dam seen from downstream. Photo: Eric Verspoor.

Ireland

There are 148 salmon rivers in Ireland and four major catchments are currently being used for hydroelectric power (Mathers *et al.* 2002). Hydropower development has resulted in a decline in salmon populations (Twomey 1991; O'Farrell *et al.* 1996; ESB 1998). However, on the productive Liffey, significant numbers of salmon passing the dam at Leixlip indicate that the fish lock and spillway gates are working satisfactorily for upstream migration (O'Farrell *et al.* 1996). Also, a reasonable number of smolt are passing the Kaplan turbines alive during downstream migration. The dam construction may thus have been less harmful here than in the other hydroelectric catchments (Mathers *et al.* 2002).

France

Hydropower has been used for electricity production in France since the end of the nineteenth century. The most active construction period was after the Second World War. Hydropower produces 15% of the total electricity production of EDF (Electricité de France). The presence of barriers is the main cause of the major decline in stocks of migratory salmon, together with overfishing (Couderc 1978; Decamps 1984; Gayou & Roguet 1996). One of the long-term consequences of hydropower on fish populations appears to be the progressive replacement of Salmonidae by Cyprinidae. Also in France, dam removals to restore and enhance anadromous fish populations, including salmon, have recently been implemented for instance, on the Allier River (http://www.rivernet.org/general/dams/decommissioning_fr_poutes/poutes_f.htm).

Spain

The first hydroelectric power plants in Spain were constructed at the end of the nineteenth century. In 1901, 40% of the electric power plants were hydroelectric and the energy is used most extensively for absorbing the peaks of energy demands. Most rivers are regulated and only a few important rivers are preserved (García de Jalón 1987). The building of large dams has blocked the Atlantic salmon run and has led to the decrease or the extinction of salmon populations (Brufao 2008). In the past decade, around 50 dams have been dismantled, mainly on northern rivers, to eliminate the risk of floods and to protect salmon stocks (Brufao 2008).

USA

The United States is the second-largest producer of hydropower in the world. The greatest rate of increase was from the late 1950s to the late 1970s (US Army Corps of Engineers 1996). Atlantic salmon have been lost in the southern part of the former distribution range, and are currently found only as an endangered population in Maine (US Fish and Wildlife Service 2000). Salmon populations were already extinct in the nineteenth century in many rivers and river barriers were one of the main reasons for the extinction of 42 river populations.

In eight river systems, the salmon are still considered wild (i.e. genetically corresponding to historic populations). In the other rivers, stocking of hatchery fish has maintained salmon populations at critically low levels (<http://www.asf.ca/docs/uploads/rivers/newengland.html>).

Although fish-passage facilities can alleviate difficulties that adults encounter in upstream migration, the effects of dams on the downstream migration of smolt have been recognised only recently and they are more difficult to reverse. By creating pools reservoirs behind them, dam change habitats by eliminating flowing water and riffles. Gravel and sediment that were formerly carried down the river and that provided spawning and rearing habitat are now stopped by dams. As a result, habitats below dams are also less suitable for spawning and juvenile rearing. Restorative and rehabilitative efforts, in the form of stocking and fish-passage constructions, are underway (Kocik & Sheehan 2006).

The Edwards Dam in the Kennebec River was dismantled between July and October 1999. The newly undammed stretch rebounded rapidly. Anadromous fish have begun returning (Meadows 2006) to a river that was historically renowned for its magnificent runs of salmon, sturgeon and other anadromous fish prior to the dam construction in 1837. Plans to remove more dams are currently being discussed in the USA.

Canada

Canada is the world's biggest producer of hydropower and hydropower represents nearly 62% of the country's total electricity production (Anon. 2008b). As in other countries, the first small plants were established in the 1880s.

Historically, Atlantic salmon appeared in Canada from Ontario eastward. In all, 875 rivers had healthy populations of wild salmon. Currently the number of Atlantic salmon rivers is down to 747 with reduced population size in most cases (<http://www.asf.ca/docs/uploads/rivers/introduction.html>). Watt (1989) has concluded that since 1870 there has been a net loss of 16%, of which 7% was due to impoundments, water diversion and obstruction.

The Atlantic salmon rivers in Canada are divided in 28 Atlantic salmon conservation units (DFO 2007) and hydroelectric and water-storage dams are considered a threat in most of the conservation units (Anon. 2008).

The Exploits River, on the island of Newfoundland, which has two large hydroelectric facilities, sustains one of the largest runs of wild adult Atlantic salmon in North America. This feature has been developed through a major enhancement programme and the construction of fish-passage facilities at major natural and man-made barriers in the watershed (Burgeois *et al.* 1994; Scruton *et al.* 2007).

Hydroelectric dams in Canada cause delays in upriver migration as fish are attracted to high-water velocities and discharge, both of which are hydrologic conditions associated with hydroelectric plant tail-races (Bernatchez & Dodson 1987; Scruton *et al.* 2007). The loss of smolt during downstream migration represents a population reduction in a life stage that does not allow for normal biological compensatory mechanisms to mitigate the potential population loss. Mortality at the smolt stage adversely affects adult recruitment and hence the potential yield from the stock originating from spawning and rearing areas above a hydroelectric development (Ruggles 1993; Scruton *et al.* 2003).

14.2 Changes in physical, chemical, hydrological and biological factors in rivers and fjord systems as a consequence of hydropower development

14.2.1 River systems

Physical and chemical factors

Studies have demonstrated that river regulations impose primary changes on flow and sediment transfer, the principal factors governing the alluvial channel regime (Church 1995). Gurnell *et al.* (1994) have identified spatial and temporal trends in the planform of the River Dee on the Welsh–English border over a 115-year period and Gurnell (1997) has found that there was a temporal trend of decreasing channel width during the study period and especially since the mid-1960s, the period of strongest flow regulation.

Another example of this finding is observed with the River Fortun, western Norway, which was regulated for hydropower in 1963. The hydropower scheme has resulted in a large reduction of the frequency of large magnitude flooding events. Repeated measures of 47 cross-profiles in 1973, 1989 and 1995 along a 1600 m-long reach showed a reduction in channel size and capacity since 1973. The upper part of the reach was subject to the greatest amount of aggradation, with the riverbed being raised up to 1.5 m while the lower part had degraded with lateral erosion cutting banks back by up to 30 m. Overbank flow occurred at lower discharges subsequent to, rather than prior to, regulation (Fergus 1997).

One study reveals the occurrence of primary changes on flow and sediment transfer in the regulated River Tummel, Scotland. Banks with inter-layered cohesive and non-cohesive sediments had undergone most erosion, while those consisting entirely of non-cohesive gravels also had quite high rates of erosion. In contrast, the erosion of banks of cohesive, laminated silts was generally very low. Of the total length of banks that were protected by rip-rap or were bedrock controlled, less than 1% suffered any erosion (Winterbottom & Gilvear 2000).

In the North Tyne river (Northumberland, UK), diurnal-stage fluctuations of 0–6 m took place during periods of peak hydropower flows. The main morphological adjustments were the degradation of riffle spawning grounds, the development of fine sediment berms along channel margins, the aggradation of pools, the vegetation of former gravel shoals and the growth of tributary confluence bars. Higher percentages of fines within spawning gravels,

the coarsening of surface gravels and the development of a stable, strong bed fabric, characterised the sedimentological adjustments (Sear 1995).

In regulated rivers, several factors can either improve or reduce the water quality for wild salmon (see Rosseland & Kroglund 2011 [Chapter 15]).

Supersaturation has been a serious problem in the USA. In Norway dead fish have also been found in the proximity of a few hydroelectric plants (Pettersen & Mellquist 1984).

Hydrological factors

With respect to hydropower development in rivers, the term ‘hydrology’ commonly denotes parameters such as water discharge, water velocity, water temperature and ice conditions.

Water discharge

A common effect of hydropower development is a reduction of large floods in rivers. For example, in the River Hallingdalselva the largest flood after hydropower development was about $300\text{ m}^3\text{ s}^{-1}$ lower than the largest flood before hydropower development (Tvede 1993).

Another possible effect of hydropower regulation is the increase of fluctuations in water discharge. For instance, Norway passed a new energy law in 1990 that permitted competition in the production and trade of electric energy (Thue 2006). This legislation has led to both more hydro-peaking at several Norwegian power stations and large variations in the water discharge within short periods of time. Such flow patterns may cause great variations in the water level, the water quality and the water temperature which in turn may have negative impacts on invertebrates and fish.

Water velocity

Further, changes in water discharge lead to changes in water velocity. In the River Suldalslågen at the outlet of the lake Suldalsvatn, for example, the average velocity has decreased from 0.8 m s^{-1} before hydropower development to 0.4 m s^{-1} during winter after the development and it has decreased from 1.6 m s^{-1} to 1.2 m s^{-1} during the spring flood (Kanavin 1971; Tvede 1993).

In winter, when a river is partly or totally covered with ice, the relation between water flow and velocity is more complex, especially where there are large accumulations of bottom ice on the riverbed. In such situations the water current will be concentrated in the parts of the riverbed with no bottom ice and the velocity of the water may be very high. If such a current is turned towards a riverbank with erosive material, considerable erosion can take place on both the riverbank and the river bottom even at moderate water flows (Tvede 1993).

Water temperature

The largest temperature changes in Norwegian rivers are connected to outlet water from power stations with an intake at great depth in high mountain reservoirs. The water temperature in rivers below such power stations is $1\text{--}5^\circ\text{C}$ lower in midsummer and $0.5\text{--}2^\circ\text{C}$ higher during winter (e.g. rivers Aurlandselva, Lærdalselva, Veflefjordselva, Surna, Orkla, Stjørdalselva).

There has, however, been an increase in the portion of ground water in many rivers with reduced water flow due to hydropower development. The summer temperatures in many rivers with considerably reduced water flow have dropped while the winter temperatures have risen. Increased ground water also increases the risk of CO₂ supersaturation, which can reduce the pH and mobilise Al and other metals (Norton & Henriksen 1983; Rosseland & Hindar 1991). The levels of CO₂ can reach to >12–15 mg CO₂/L, which is suboptimal to salmonides (Stefansson *et al.* 2007a, b).

Hydro-peaking power plants may have a great impact on the water temperature in the river downstream from the outlet. For example, when the Grana power plant in the River Orkla was running with frequent starts and stops in July, August and September, the water temperature in the river downstream from the Grana power plant varied up to 6 °C from one day to another (Tvede 2006).

Ice conditions

A pronounced increased ground water flow will lead to rivers that are either without ice cover or are partly covered with ice. In other rivers, a reduced water flow may lead to a faster formation of ice cover because of the faster cooling of the water. In rivers with increased water flow during winter, the ice cover will usually be more unstable; otherwise there will be no ice at all where the speed of the water is fast, or the winter climate is mild, or both. The water from reservoirs running through power plants may also play an important part in such cases.

At water currents with a speed of more than 0.6 ms⁻¹, ice cover will hardly occur (Flatjord 1963). In such cases ice crystals floating free in the water (frazil) will often be the result, an indication that the water has a temperature some hundredths of a degree below the freezing point. This kind of ice may attach to rocks or installations at the river bottom. In this way ice-dams may result, which in turn may lead to floods. Such ice problems are found in many regulated rivers in Norway. In most of these cases the solution has been to build run-of-river power plants on the reaches that had formations of bottom ice or by running the power plants in such a way that ice cover can materialise before the water flow is increased. In several regulated rivers, the water flow is manipulated in order to achieve desired ice conditions. The new manoeuvring rules for the power plant on the River Alta aim to attain hydrological conditions that will improve the environment for the salmon population. During the winter the power plant uses water from the upper intake in the reservoir, a practice that results in a lower water temperature than earlier manoeuvring rules and thus improves the conditions for ice formation in the Sautso region of the river (http://nve.no/modules/module_109/publisher_view_product.asp?identityID=23739).

Biological factors

Hydropower development can have substantial effects on macroinvertebrates, which represent several functions in the food web and are the most important food organisms for salmonids in running water. Water discharge, velocity, water temperature, water chemistry, bottom substrate and attached algae and mosses are all important factors that affect the quantity and composition of invertebrate benthos and the drift in running waters (Hynes 1970; Brittain & Eikeland 1988; Allan 1995).

There is evidence of short-term eutrophic effects. In the River Alta in northern Norway, for example, there was a eutrophic effect downstream the dam in the ice-free river section

after regulation. However, this effect decreased 6–17 years after the impoundment, and the reduction primarily concerned Chironomidae larvae (Koksvik & Reinertsen 2008).

Lakes and reservoirs may produce considerable amounts of zooplankton and microcrustaceans that are available as food for drift-feeding salmonids living downstream (Ward 1975; Lillehammer & Saltveit 1979; Petts 1984; Weisberg & Burton 1993). One study on the River Stjørdalselva, Norway, has calculated that as many as 1 170 000 000 individual microcrustaceans drifted past a given point per 24 hours (Arnekleiv *et al.* 2007). In lakes where the outlet is dammed the consequence for salmonids is negative due to reduced drift.

Water discharge

Typical effects of river regulation on macroinvertebrates include a decline in species diversity, increases or decreases in abundance, alteration in community composition and changes in trophic guilds (Armitage 1984; Cushman 1985; Ward & Stanford 1987; Brittain & Saltveit 1989). Flow and velocity are here key factors that determine substrate composition and interstitial spaces, distribution of attached algae and mosses and the amount of detritus that is the available food for the bottom fauna. A more constant seasonal flow will favour more stable substrate conditions and will often result in increasing amounts of attached algae and mosses. Some invertebrate species are favoured by moss and a more stable substrate and may increase in abundance, while others prefer substrate without vegetation (Bremnes & Saltveit 1992, 1997; Arnekleiv & Kjærstad 2003).

Certain studies have concluded that hydro-peaking adversely affects benthic communities by reducing biomass, diversity and taxa richness in the variable zone (Cushman 1985; Casado *et al.* 1989; Shaver *et al.* 1997; Céréghino *et al.* 2002; Clarke *et al.* 2008). The variable zone is the shoreline area that is repeatedly dewatered and inundated because of short-term fluctuations in flow. For example, daily hydro-peaking in the River Nidelva, Norway, resulted in the dewatering of the shoreline, but not the entire river transect owing to a minimum water discharge. In hydro-peaking periods, the density of macroinvertebrates in the variable zone was only 10% of that in the permanently wetted zone. There was a significant negative correlation between the number of dewatering episodes and the benthic densities in the variable zone. After a month of daily hydro-peaking, there were only tiny fauna, consisting mostly of chironomids and oligochaetes left in the variable zone. Recolonisation, probably from the permanently wetted area, took place in winter and spring with more stable high flow, but the diversity and density in benthos in the variable zone did not approach that of the permanently wetted area (Arnekleiv *et al.* 1994; Harby *et al.* 2004).

There are several cases of the adverse effects of hydro-peaking on benthic communities. In a river in Idaho (USA), the benthic community below a dam was severely altered and simplified, with high abundance of a few species but low overall diversity. The majority of the benthos was chironomids, which are known to be tolerant of rapid changes in discharge (Munn & Brusven 1991). Helešic *et al.* (1998) have sampled the Dyje River in the Czech Republic above and below a reservoir and dam with hydropower peaking. They found the highest number of invertebrate taxa (157) above the reservoir, and the lowest number of taxa below the dam (136), followed by an increase in taxa at a site 33 km downstream the dam (149 taxa). Céréghino *et al.* (2002) have also found that peaking affected the longitudinal zonation of several species, and they observed the low abundance of several taxa, below the impoundments.

Flow fluctuations also induce drift, and may result in stranding of invertebrates. Drift densities are reported to increase both with increased water flow (Perry & Perry 1986) and following flow reduction (Corrarino & Brusven 1983). Céréghino & Lavandier (1998) have found that Plecoptera and Ephemeroptera responded to peak-flow releases with catastrophic drift. The amplitude of disturbance (peaking) is probably important for determining drift rate and the impact on benthic density (Céréghino *et al.* 2004).

Water temperature

The release of cool water can have drastic effects on benthic communities. For instance, in the lowermost 20 km of the River Surna, northwestern Norway, where a hypolimnic release of cool water from a mountain reservoir takes place during summer, the benthic densities immediately below the power station were dramatically reduced. Even though the benthic densities increased downstream from the power station, they never exceeded the densities above (Saltveit *et al.* 1994).

14.2.2 Fjord systems

The water masses in the Norwegian fjords are more stratified than the coastal ocean water beyond the fjord and the transport of the fresh water from rivers is in a 1–10 m-deep brackish water-surface layer. The transport in the brackish layer is perhaps five times larger than the supplied fresh water due to the mixing with the fjord water. The salinity and extension of the brackish layer varies both between regions and throughout the year (Tollan 1984).

Fresh waters contain colloids and particulate matter, like humics, which will have bound metals, especially aluminium. As fresh water meets salt water and the salinity increases above 1–3‰, aluminium bound to humics and colloids will be released as low molecular weight forms. Because they are highly reactive to fish gills, as in freshwater ‘mixing zones’, they can impose mortality on fish (see Rosseland & Kroglund 2011 [Chapter 15]).

Most hydropower plants in Norway have large reservoirs, and the natural freshwater regime may, at least locally, be greatly changed (Pytte Asvall 1984). A well known hydrological consequence from hydropower development in Norwegian watercourses is the transfer of surplus water from the summer period to the winter period (Tvede 1993). There are also several examples of regulations that transfer freshwater discharge from one fjord to another. This practice will to some extent affect biological processes in fjords and coastal waters and may even alter the recruitment to fish stocks (Skreslet 1984).

The winter values of salinity decrease owing to increased freshwater discharge (Kaartvedt 1984). This condition leads to an increase of ice. On the other hand, a well defined brackish water layer will trap the energy from the wind and thus increase the wind driven flow as well as the level of mixing above the pycnocline, possibly reducing the local ice production (Svendsen & Thompson, 1978). Nevertheless, in some fjords there are mitigatory measures like air-bubbling systems (Rana and Holand fjords) or submerged outlet tunnels from power stations (Aurland and Luster fjords) in order to prevent the increase in ice cover.

The precipitation and runoff along the Norwegian coast have increased naturally in recent years as a consequence of a climatic change. This development also includes an increased presence of TOC in the water, possibly due to changes in precipitation quality (less acidic rain) (Monteith *et al.* 2007). Thus, a change in freshwater runoff is occurring as a result of river regulation, while there is also a natural change. These simultaneous processes make it difficult to distinguish between the effects of the different processes.

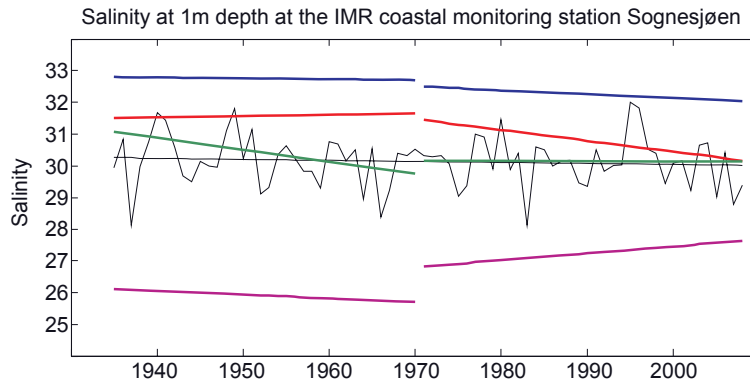


Figure 14.1 Yearly mean salinity at the Sognesjøen IMR coastal monitoring station in the outer part of the Sognefjorden. The coloured lines represent magnitude and trends for the quartiles of the year: January–March = blue, April–June = red, July–September = magenta, October–December = green.

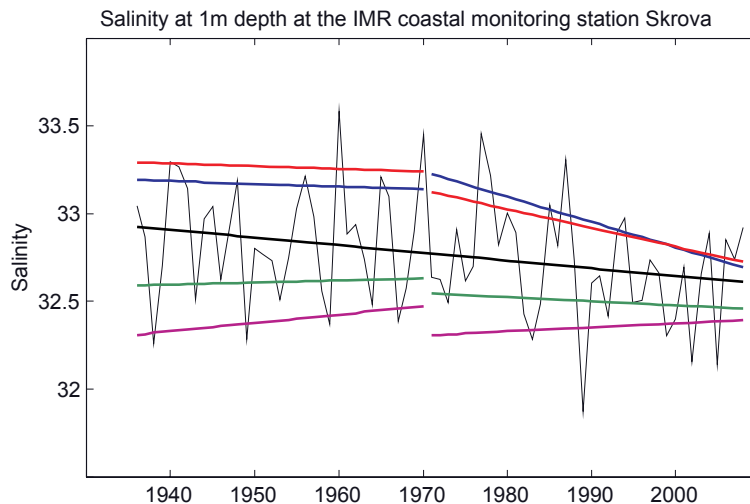


Figure 14.2 Yearly mean salinity at the Skrova IMR coastal monitoring station in the outer part of the Vestfjorden. The coloured lines represent magnitude and trends for the quartiles of the year: January–March = blue, April–June = red, July–September = magenta, October–December = green.

The long-time series from the outer parts of fjords are part of the coastal monitoring stations operated by the Institute of Marine Research (<http://atlas.nodc.no/stasjoner/>). Observations of both the Sognesjøen station in the outer part of the Sognefjorden on the western coast of Norway and the Skrova station (in the Vestfjorden inside the Lofoten archipelago in the northern part of Norway) reveal a noteworthy effect. We should expect the overall salinity trend at the surface to decrease owing to the general increase of precipitation and runoff. The yearly mean salinity values at 1 m depth also demonstrate this effect, although the values are rather weak at Sognesjøen (Figs. 14.1 and 14.2). The magnitudes and trends since 1970 for the quartiles of the year show that the largest decrease of salinity occurs in the winter and spring. However, we also find an increase of salinity in the third quartile (the magenta line in Figs. 14.1 and 14.2). This effect can be the result of river regulation that transfers fresh water release from the warm season to the cold season.

14.3 Changes in survival, growth, migration and production of salmon in rivers and fjords

Hydropower development may affect different life stages of Atlantic salmon with respect to survival, growth, migration and production. The effects on Atlantic salmon populations may be negative or even devastating, but there are also examples of hydropower developments that have had positive effects on salmon populations.

14.3.1 Rivers

Survival

The degradation and destruction of valuable spawning and rearing habitats due to anthropogenic changes (e.g. hydropower, flow modification and channelisation) is known to have dramatic impacts on fish populations (Enders *et al.* 2007). Increased siltation after spawning may result in reduced egg survival owing to oxygen depletion (Chapman 1988) or to the clogging of the gravel pores which leaves the fry unable to emerge from the gravel (Witzel & MacCrimmon 1980). Egg mortality can also result from the stranding of redds caused by low-water discharge during winter (Fig. 14.3). A high-water discharge during the spawning season relative to the following winter, is likely to increase the probability of stranding (Barlaup *et al.* 1994).

In temperate and sub-arctic regions, the energy intake of freshwater fishes is low during winter and several studies regard the depletion of energy as a major cause of mortality, including for the Atlantic salmon (Gardiner & Geddes 1980; Post & Evans 1989; Miranda & Hubbard 1994; Finstad *et al.* 2004b). For instance, in the regulated River Alta (Norway, 70°N), the winter is six to seven months long and the fish must feed to survive (Forseth *et al.* 2000). If the energy intake is too low, the salmon parr might die owing to energy deficits or predation caused by increased exposure. In 1992, five years after the opening of the power plant, the parr density in 7km of the river near the power plant was reduced to approximately 20% of the pre-regulation level (Ugedal *et al.* 2008). The regulation of the river caused both an increase in water temperature during the winter (mean increase 0.5°C) and a loss of ice cover (Næsje *et al.* 2005). Recognising the changed environmental conditions, some researchers have suggested energy-dependent winter mortality as one of the main



Figure 14.3 A spawning area at high water discharge (left picture) during the spawning time in late autumn and the same spawning area (picture to the right), stranded, during low discharge the following spring. Stranding of the redds caused 100% egg mortality. Photo: LFI-Unifob v/Bjørn T. Barlaup.

reasons for the reduction in parr densities. One mark-recapture experiment confirmed the reduced survival rates in the ice-free areas (Næsje *et al.* 2005). Juvenile salmon which were held in semi-natural channels without cover had a considerably higher energy loss (20%) than fish under simulated ice cover (Finstad *et al.* 2004a, 2005). Field data from the River Alta confirmed these results as the number for stomach fullness was lower and the number of empty stomachs higher in the area with reduced ice cover compared to ice-covered areas (Næsje *et al.* 2005).

Although floods may have positive effects on the juvenile-fish habitat, high floods, or peaking floods, may have harmful effects on newly emerged fry of salmonids. Downstream displacement of salmonid fry due to flow increase, from $12\text{--}15\text{ m}^3\text{ s}^{-1}$ to $>100\text{ m}^3\text{ s}^{-1}$, was documented in River Suldalslågen, Norway (Saltveit *et al.* 1995). Fry displaced downstream were lost from the population and the total loss was estimated to be between 75 000 and 100 000 Atlantic salmon fry, representing 5.6–11.1% of first-year mortality. Other investigations have also documented high mortalities of newly hatched fry due to high flows which influence the year-class strength of the juvenile salmon population (Jensen & Johnsen 1999; Cattaneo *et al.* 2003).

There is body of research on the causes underlying the stranding of fish. Field experiments have shown that sudden reductions in the river flow may cause high mortality of juvenile salmonids as a result of stranding. One study has found higher incidences of fish stranding during winter conditions, probably due to lower fish activity during the cold season (Saltveit *et al.* 2001). Another study showed that Atlantic salmon had larger home ranges and were more mobile during summer than winter and there was only anecdotal evidence of stranding in the summer (Scruton *et al.* 2005). In comparison with the summer, fish in winter remained relatively sedentary, a behaviour which may increase the likelihood of stranding. When the flow was reduced on average $0.23\text{--}0.31\text{ cm/min}$, there was a reduction in stranding. Cold water combined with coarse substrate, low gradient and high water velocity, led to the highest incidences of stranding. Yet, stranding is not necessarily tantamount to mortality; fish have been found to survive for several hours in the substrate after dewatering.

The restriction of movement of Atlantic salmon parr appears to be detrimental. Berland *et al.* (2004) have found that free-ranging Atlantic salmon parr moved considerable distances regardless of discharge. Yet, rapid reductions in water flow caused increased mortality in large parr in shallow habitats if their movements were restricted. However, rapid fluctuations did not appear to influence movements or to cause stranding by free-ranging Atlantic salmon parr.

In rivers with poor water quality in parts of their catchment area, hydropower development may affect the survival of salmon indirectly. One result of reducing the amount from the reservoirs is that water of poor quality from the tributaries or catchments might dominate or be mixed into the base flow water and create toxic mixing zones, thereby imposing toxic water on the Atlantic salmon population (see Chapter 15.3). In the regulated River Suldalslågen (Norway), tributaries of marginal water quality for salmon dominated the water quality in the main river during certain periods (Blakar & Haaland 2000; Kroglund *et al.* 1998a). Research has also documented that these conditions created massive fish mortality in the River Nidelva (Norway) in the late 1970s (Muniz *et al.* 1979). In the regulated River Vosso, tributaries draining the regulated lower catchment area had water qualities which today are known to be extremely critical to migrating salmon smolt. Such waters might have contributed to a large degree to the extensive reduction in the salmon population

in the river (Kroglund *et al.* 1993, 1998b). Also, the regulated River Otra (Norway) has downstream instances of low pH owing to water from acidified tributaries (Kroglund *et al.* 2008). In the regulated River Oga (Norway), a power station using waters from a catchment characterised with low pH and very high Al concentrations started running as Atlantic salmon spawners entered the river. These conditions led to massive fish mortality on the downstream river stretch (Skogheim *et al.* 1984).

Growth

There is evidence that hydropower development affects the growth of Atlantic salmon. In the River Surna (Norway), reduced growth below the power station of both Atlantic salmon and brown trout compared with fish in the upper section of the river, is due to the presence of cold water during the summer as a result of a hypolimnetic release in a mountain reservoir (Saltveit 1990). The slower growth below the power station causes both Atlantic salmon and anadromous brown trout to smoltify one year later compared with fish in the upper section of the river.

After the regulation of the River Alta (Norway) the effects on water temperature were a decrease of 1–2 °C during June, July and the first half of August, an increase up to 3 °C during late summer and a small increase during winter (Jensen 2003). Following the hydropower development, the growth rates of juvenile Atlantic salmon decreased during early summer, but increased correspondingly later in the season. There was close agreement between these growth changes and the altered annual regime of river temperature. Overall, only minor changes in annual growth rates have been observed after the hydropower development (Jensen 2003).

In contrast, one study has documented better growth in all parts of the River Stjørdalselva after regulation (1994–2000) compared to before regulation (1990–1993). The differences were greatest in the upper part of the river (Arnekleiv *et al.* 2002). This study found that the observed variation in growth rates between the years was explained by a variation in mean daily water discharge and spring temperature and has suggested that growth rates of juvenile salmon are governed by biotic and abiotic factors connected to water-flow regime and spatial variation in food availability (Arnekleiv *et al.* 2006).

Migration

Downstream migration of smolt and kelts

The effect of downstream migration of smolts and kelts through hydropower turbines is of great concern. Smolt mortality due to turbine passages has been reported to vary from 7 to 80% (Coutant & Whitney 2000; Skåre *et al.* 2006). Various circumstances can increase the mortality when fish pass the turbines. Fish may be killed in the water intake, in the turbines or in the outflow runway from the turbines (Montén 1985; Jepsen *et al.* 1998; Coutant & Whitney 2000). Generally, the presence of Kaplan turbines, fish passing the turbines at high-water discharge in the power plant, power stations with a low waterfall and a short outflow tunnel all led to the best rates of survival (Montén 1985). High mortality, however, is expected for kelts that move into the turbines.

There are also indications of increased mortality for smolts passing power-station through turbines (Montén 1985). One study has estimated a turbine mortality of 73% for smolts released into the intake at a power station in the River Orkla (Hvidsten & Johnsen 1997). The inlet to the hydropower station was designed to prevent smolt from entering the tur-

bines. This measure seems to function well in periods of high river flow. However, during periods of low flow there should be no diversion of water for hydropower generation, but if necessary, the diversion should probably not exceed more than 20% of the river flow (Hvidsten & Johnsen 1997).

Water discharge during smolt migration seems to be critical for the survival of hatchery-reared smolts and high water discharge at release can improve survival, possibly because of the reduction of mortality due to predation just after release. Conversely, it is probable that reduced water flow during smolt migration in regulated rivers may lead to reduced rates of survival. One study of the rivers Surna and Gaula appears to support these observations (Hvidsten & Hansen 1988).

Upstream migrating adult salmon

Large dams may impair the upstream migration of Atlantic salmon and thereby seriously affect the salmon population. In several cases salmon have become extinct above large dams. In France, the Atlantic salmon was eliminated from the Garonne and Dordogne Basin in the mid-nineteenth century by dam construction and probably by overfishing (Gayou & Roguet 1996). The River Kemijoki, in northern Finland, was one of the best salmon rivers in Europe until 1949, when the dam and the hydropower plant were completed close to the river mouth (Laine *et al.* 1998).

Angling catches of Atlantic salmon in the River Bidasoa, a river in the Basque Country of northern Spain and southern France that runs largely from south to north, decreased greatly during the twentieth century, leading to a risk of extinction during the last decades of the century (Alvarez *et al.* 1995). There was a noticeable reduction in the available spawning areas in the basin mainly because of the reduction of the water flow and the interposition of several dams.

A run-of-river type of regulation may affect salmon migration because the fish are attracted to the water flow from the power plant rather than to the reduced water flow in the river.

The discharge from the turbines in the regulated River Umeälven in northern Sweden, for example, attracted the salmon away from the bypass route while the increased spill in the bypass channel attracted salmon to the bypass (Lundquist *et al.* 2008). In the regulated River Nidelva, southern Norway, salmon migrated quickly from the site of release in the lower part of the river up to the tunnel outlet of the Rygene power station, but they were delayed at the outlet (Thorstad *et al.* 2003). The salmon stayed in the outlet area for 0–71 days (median = 20), and mainly took a position inside the dark power station tunnel. According to Scruton *et al.* (2007) conventional and electromyogram (EMG) radio telemetry studies have documented the occurrence of tail-race attraction and residency, and the associated energy cost, for migratory wild Atlantic at a power plant on the Exploits River (Canada). Turbine discharge was the primary factor contributing to ‘false attraction’.

The introduction of dams does not, however, always lead to detrimental effects on upstream migration. In a glacial river system in Iceland, a dam in the upper areas has led to a positive change in salmon abundance (Isaksson & Gudbergsson 2009). These stocks were small and the change in the flow pattern through water regulation and lower turbidity has both improved the conditions for upstream migration and significantly increased the salmon catch and fry production in the mid-section of that system (Isaksson & Gudbergsson 2009).

Production

The effects of hydropower development in salmon rivers may differ depending on how much effort is put into sustaining the Atlantic salmon population. The hydropower development in the Norwegian River Alta (70°N) is an example of positive changes in Atlantic salmon production following changed hydropower discharge regimes. The River Alta was, and still is, one of the best rivers for recreational salmon fishing in Norway, but for a period the production of salmon in the upper parts, near the outlet of the power plant, fell drastically (Ugedal *et al.* 2008). The river was regulated for hydropower in 1987, and the power plant is situated at the top of the salmon-producing stretch. The decline in salmon production and parr densities appeared to have begun during the main construction period of the dam, tunnels and power plant. The biological data indicate that the building process had a negative effect on the salmon population (Ugedal *et al.* 2008). During the first years of production, accidental or unforeseen close-downs of the turbines caused sudden drops in the water discharge with 10 to 80 cm reductions in the water level in the upper part of the river (Forseth *et al.* 1996). Using simulation models, Forseth *et al.* (1996) concluded that stranding mortality was partly responsible for the decline in the juvenile production in the early 1990s. Both the installation of a diversion valve ($33\text{ m}^3\text{ s}^{-1}$) in the power plant and improved operative routines since 1994 have minimised the problem of sudden drops in the water discharge (Brodtkorb 2002). In order both to reduce water temperature and to improve the ice conditions, the water-intake regimes in the power plant have been changed since 2002. With the aim of increasing the ice-cover, there was a reduction of the temperature reservoir in the hydropower dam during the autumn by means of a bottom intake to the power plant. During winter, an upper intake was in operation until the depletion of the dam and then the intake had to be switched to the bottom of the dam. The new water regime has reduced the water temperature during the winter from 0.5 to 0.2°C, and has improved the ice formation and juvenile survival (Næsje *et al.* 2005). In addition, increased and stable winter discharge has had a positive effect on juvenile survival (Ugedal *et al.* 2005). The average winter discharge increased from $14\text{ m}^3\text{ s}^{-1}$ before the regulation (1972–1986) to $29\text{ m}^3\text{ s}^{-1}$ after (1988–2003). Before the regulation, the lowest weekly winter minimum was $5.5\text{ m}^3\text{ s}^{-1}$; after regulation, the minimum winter discharge has been higher and seldom much below $20\text{ m}^3\text{ s}^{-1}$. The increased winter survival of juveniles at higher and stable discharges may be due to both an increased wetted area and improved habitat conditions (Cunjak *et al.* 1998). The production of smolt in the upper part has fallen to approximately 50% of pre-regulation level owing to increased juvenile mortality caused by the hydropower development. The development has, however, most likely caused an increase in juvenile production in the middle part, thus compensating for the reduced production in the upper part. The overall production of Atlantic salmon in the River Alta 20 years after hydropower development is as good as it was before the regulation (Næsje *et al.* 2005; Ugedal *et al.* 2008).

One study has hypothesised that high minimum discharge during winter increases the winter survival of parr (Hvidsten & Ugedal 1991). Moreover, because major changes in abiotic conditions relate to stabilised discharges, an increase in production area may increase smolt production. This study examined the River Orkla (Norway) where the water discharge has always exceeded $10\text{ m}^3\text{ s}^{-1}$ since its regulation for hydropower production in 1983. The high minimum discharge during winter has led both to improved rates of survival of parr and to increased smolt production (Hvidsten & Ugedal 1991).

Other researchers have found, moreover, that in the lower part of the River Stjørdalselva (Norway) and in the unregulated Forra tributary, juvenile salmon densities ($\geq 1+$) increased

significantly during the period 1991–2006, while the densities were unchanged or lower in the upper part of the river (Arnekleiv *et al.* 2007). However, there was no significant difference in the smolt production estimate for the whole river throughout the investigation period.

Hydro-peaking

Rapid reductions in flow have either a direct mortality effect on fish owing to stranding (Hunter 1992) or an indirect effect owing to desiccation or drift of the benthos (Cushman 1985; Lauters *et al.* 1996; Céréghino & Lavandier 1998). Hydro-peaking by changing the velocity of the current may also reduce the quality of fish habitat and alter fish-community structures (Valentin *et al.* 1994; 1996), but it does not seem to affect fish stress levels when peaking is done frequently in rivers with high minimum flow (Flodmark *et al.* 2002). In the River Stjørdalselva, energy resources of juveniles below a hydroelectric power plant differed from those at a reference station (Berg *et al.* 2006). Especially during the summer, the young of the year had 31% lower total energy content at the hydropower station than those at the reference station. The period of energy losses corresponded with a period of great variation in water flow owing to hydro-peaking operations in the power plant. One study found that sudden and strong reductions have affected Atlantic salmon populations in several Norwegian rivers (Saltveit *et al.* 2001). The lower densities of juvenile Atlantic salmon in the rivers Suldalslågen, Surna and Alta below dams or power stations are presumably a consequence of sudden reductions in flow.

Variable and rapidly changing discharge regimes can have negative effects. One study has suggested that this is the case in the regulated Afon Clywedog in the upper Severn catchment (Wales), where the juvenile recruitment of both Atlantic salmon and brown trout have declined steadily following the increased utilisation of the impoundment for regulation (Cowx & Gould 1989). On the other hand spawning success and juvenile survival of salmonids in the River Vyrnwy (Wales) has been relatively stable and Cowx & Gould (1989) have suggested that the flow regime in this river has been less destructive.

14.3.2 Fjord systems

Regulation from hydroelectric power production may have consequences for the ecology of the fjord systems (Kaartvedt 1984). The available quantitative information is sparse, especially for factors that influence Atlantic salmon, except on the creation of the ‘estuarine mixing zones’ (see Chapter 15.3). The task of discriminating between the changes in the environment from river regulations and changes from natural variability and other causes is difficult due to the large natural variability of the fjord dynamics.

Our knowledge of the effect of brackish water in fjords during the winter is quite restricted. In particular, a larger brackish water layer during the winter prevents vertical exchange in the water column. The supply of nutrients will thus drop and lead to a reduction in the primary production. The consequences of this effect throughout the food web are unknown.

Furthermore the reduced salinity of the fjord water masses also affects the light conditions, making the waters darker (Aksnes *et al.* 2009). This darkening affects a range of biota, from primary producers to visual predators. In recent years there has been increased precipitation and runoff along the Norwegian coast and the fjord and coastal waters have thus naturally become fresher (and darker). It is possible that freshwater hydropower regulation transfers fresh water from the spring and summer to the winter, thus making the winter water even

darker and the spring and summer water even lighter. This change again might affect salmon migration because the smolt on its way out of the fjord may be more susceptible to predation. No quantitative information on this possible effect exists, however.

The presence of a well defined brackish water layer in the fjords is also important for survival. Salmon lice pose a grave threat to the smolt (the presence of 10 salmon lice or more is assumed to be lethal for the smolt). A well defined brackish water layer in the fjords protects migrating salmon smolt from salmon lice (Heuch *et al.* 2005). Consequently, a reduction of the brackish layer due to hydropower development during smolt migration can lead to higher mortality of the salmon stock. In addition a well defined brackish layer might also act as a navigational aid for the salmon on their way in and out of the fjords. A reduced brackish layer might then negatively affect both the protection and migration of the salmon inside the fjords.

One study suggests the attraction of salmon to freshwater releases in fjords is minimal (Thorstad *et al.* 2003). The migration of Atlantic salmon returning to the River Suldalslaagen, Norway, was studied in relation to the redirection of freshwater flow through a power station which has an outlet situated in the Hylsfjord, a fjord adjacent to the river mouth. The researchers tagged 72 salmon with acoustic transmitters and released them in the outer part of the fjord system. The salmon were automatically recorded as they entered the Hylsfjord and the river. The release of water from the power station did not attract the salmon to a large extent during their return migration. Neither the proportions of salmon entering the river nor the time from release to entering the river differed among salmon tagged in the different periods. The recording of the salmon in the Hylsfjord took place both when the power station was running and when it was closed. There were no differences in the number of times, the number of days or hours recorded in the Hylsfjord among salmon tagged in the three periods. The only significant difference found between the periods was the duration of stays in the inner part of the Hylsfjord. This finding may indicate a slight attraction to the freshwater release, but the difference seems small (1.8 *vs.* 0.7 h) compared with the time the fish stayed in the fjord system before entering the river (16–85 days) (Thorstad *et al.* 2003).

There are other studies, however, that indicate the diversion of salmon to outlets from power plants is significant (Johnsen *et al.* 2005). The mouth of the River Daleelva in Høyanger (Norway) is situated close to a power plant that has its outlet directly into the fjord. Normally the water discharge from the power plant is significantly higher than the discharge from the river. The water from the power plant attracts Atlantic salmon and this effect leads to a yearly catch of about 100 specimens in the tail-water below the power plant. This number represents approximately 45% of the average yearly catch of Atlantic salmon in the River Daleelva. In 2004 the power plant was closed owing to maintenance work and that year's catch of salmon was the highest ever recorded (Johnsen *et al.* 2005).

14.4 Measures to compensate for negative effects of hydropower development

There are different mitigatory measures to compensate for the negative effects of hydropower development. The measures are divided into two main categories: the use of biological and physical measures and the use of water reserved for environmental purposes.

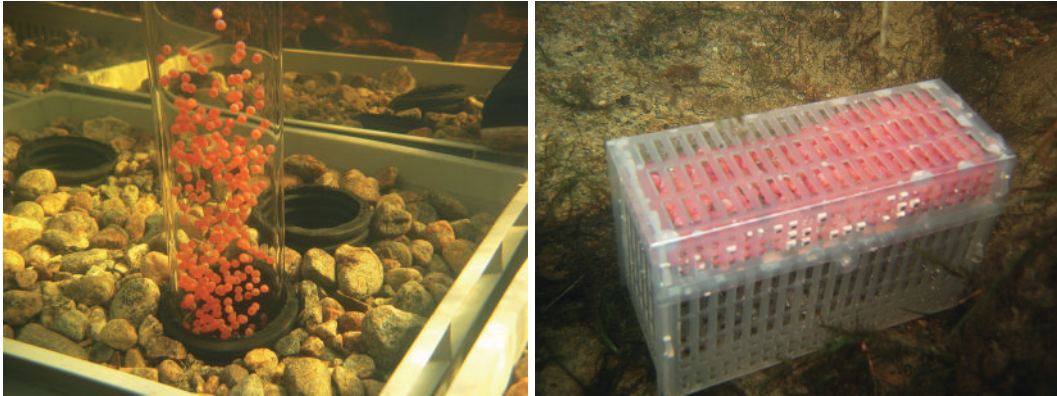


Figure 14.4 Planting of eggs by 1) use of a box filled with gravel and planting of eggs through a plastic cylinder (left picture), and by 2) use of a Vibert-box ready to be buried in the gravel. Photo: LFI-Unifob v/Tore Wiers.

14.4.1 Use of biological and physical measures

Some of the most important measures for compensating for possible negative effects in regulated rivers are fish stocking, weirs, fish ladders, downstream fish-passage facilities and different kinds of habitat adjustments.

Fish stocking

The stocking of fish has a long tradition in Europe, probably dating back to the Roman period (Welcomme 1998) and is a widely used strategy to mitigate negative environmental impacts on recruitment or to increase fish production and yield. While smolts are most commonly used as stocking material in for example Sweden and Finland (Ackefors *et al.* 1991), most of the fish stocked in Norwegian river systems are fry and fingerlings (Fjellheim & Johnsen 2001). In latter years the planting of eyed eggs has become a commonly used method in large-scale restoration projects in Norway (Moen *et al.* 2007; Barlaup *et al.* 2008; Hesthagen 2008).

Several studies on a variety of planting techniques and salmonid species have reported successful egg planting (Barlaup & Moen 2001). The techniques generally used are eggs incubated in boxes (e.g. Whitlock 1978) that are buried in the riverbed or eggs placed freely into a gravel structure which to some degree imitates a natural redd (Fig. 14.4.).

Stocking fry or parr is necessary and effective only when natural reproduction is negatively affected (Saltveit 1998, 2006) or the stocking takes place in an area upstream the natural run of salmon (Fjellheim & Johnsen 2001). In the regulated River Suldalslågen, Norway, less than 0.005% of the number stocked as one-summer-old hatchery-reared fish was recaptured as adults in the river. Their annual contribution to angling catches, varied from 7 to 334 kg, or less than 15% of the total number caught. The lack of positive response to stocking was possibly due to younger smolt, smaller size, later migration of hatchery smolts and poorly developed seawater tolerance of hatchery smolts (Saltveit 2006).

Another example of fish stocking in Norway took place in the River Drammenselva in an area where there was no natural run of salmon (Hansen 1991). The estimated return to the

river was 320 salmon, which was 2.3% of the number of one-summer-old hatchery-reared fish released. Based on the marine exploitation rate of the stock, the estimation of the total production of adult fish in this experiment was estimated to be 914 fish (6.5% of the number released) weighing about 6300 kg. This equals a production of 0.45 kg per 0+ released.

The Atlantic salmon was eliminated from the Garonne and Dordogne Basin in France in the mid-twentieth century by dam construction and probably overfishing (Gayou & Roguet 1996). The stocking programme that was initiated there developed from a stocking of less than 100 000 fed fry of foreign origin in the first years, to a stocking of 500 000 fish from French Loire-Allier and Adour wild stocks and the new-built Dordogne stock, ten years later. According to Gayou & Roguet (1996), the return rates range from 0.04 to 0.42% and the recapture of micro-tagged fish shows that Garonne and Dordogne fish derived from 2SW Adour and Connon stocks are subject to distant fisheries at the Faroes and by coastal gill-nets in western Ireland.

If we assume that an excess of spawners are used as parental fish, the stocking of smolt can be effective because stocked smolt immediately leave the river and therefore produced beyond the natural carrying capacity of the river (Russell 1994; McGinnity *et al.* 2004). But in Norway, survival rates of hatchery-reared smolts are low; approximately half those of wild smolts. The reduced survival rate may be due to a lack of adaptation to natural conditions as well as poor handling, transporting and releasing procedures (Finstad & Jonsson 2001).

In general, a perusal of the reviews on fish stocking points to the conclusion that the effects vary greatly depending on the species, population and environmental conditions (Einum & Fleming 2001).

Weirs

Weirs are generally divided into two groups, those made to compensate for loss of biotopes and those made to prevent erosion and mass transport. The latter can again be divided into two groups; basin weirs and current weirs. The latter type, also called the 'Syvde' weir, is also common in natural salmon rivers because it creates a fishing pool below the weir outlet.

In Norway there are more than 1000 weirs. Their main purpose has been to create a suitable habitat for fish and to maintain a certain water level in the river for aesthetic reasons (L'Abée-Lund & Brittain 1997).

Basin weirs present certain problems to Atlantic salmon. To compensate for loss of habitat, basin weirs are common constructions in rivers with strongly reduced flow. In general, the effects are positive compared to a river nearly without water. Basin weirs, however, often drastically reduce the water current and this affects the habitat conditions and therefore the relationship between different fish species. In this way Atlantic salmon are vulnerable because they have strong and defined preferences for different physical habitat parameters such as current, substrate and depth (Heggenes & Saltveit 1990; Heggenes *et al.* 1999) and this vulnerability indirectly affects stock size and reproduction. The current and the flow are probably the most important factors for Atlantic salmon habitat selection (Karlström 1977; Heggenes & Saltveit 1990), and basin weirs greatly affect these two factors. Weirs may also prevent the upstream migration of Atlantic salmon (Thorstad *et al.* 2006).

Fish ladders

A fish ladder is an artificial bypass that enables fish to ascend a regulation dam or a natural hindrance for upstream migration. Its main purpose is to increase the spawning and nursery area for salmon. A variety of fish-passage facilities has been developed to encourage or enable passage beyond such obstacles (Clay 1995). In Norway, fish ladders have opened approximately 3700 km of new river to anadromous fish (DN 2002). In the River Vefsna the building of 14 ladders has opened 97 km of new river stretch to Atlantic salmon (Johnsen & Jensen 1988).

In the River Umeälven, the first dam, Stornorrfors, located 32 km upstream from the coast, blocks the passage of anadromous fish (Lundquist *et al.* 2008). A 240 m-long fish ladder at the base of the dam allows fish to migrate upstream to the largest tributary, the River Vindelälven. The annual results obtained from a 10-year study of adult Atlantic salmon passing through the flow-regulated lower part of the river demonstrate that migratory success from the coast to the fish ladder varied between zero and 47%. The discharge from the turbines attracted the salmon away from the bypass route. The average migration duration was 44 days from the estuary to the top of the fish ladder, with large variation among individuals within the same year. In the River Emån in Sweden there are 41 hydropower plants and only the lowermost 25 km have been available for anadromous species for the last 100 years. Two new nature-like fishways built in 2000 have now increased the spawning and nursery area by 24 km (20%) (Calles & Greenberg 2005). Between 90% and 100% of the salmonids that entered these fishways actually passed through them. The fishways also functioned as a passage for downstream post-spawning migrants (Calles & Greenberg 2005).

Fish ladders may have a negative effect on the population because they may favour smaller individuals and trout. Ladders may therefore have a negative impact in rivers with large salmon. The River Lærdalselva offers one example: as many as 90% of the salmon ascending the lowermost fish ladder were grilse or 1SW. In this river most of the 1SW fish are males (80%). The lack of females therefore limited the natural reproduction above the fish ladder (Saltveit 1993).

Downstream fish-passage facilities

The trade-off between the use of water to protect salmon from turbine-induced mortality and the use for power production has led to the development of different water-efficient fish-passage outlets. The design of these outlets takes into account two fundamental behavioural patterns of salmon smolts approaching dams: they are surface-oriented and they generally follow the maximum flow patterns (Coutant & Whitney 2000; Scruton *et al.* 2003).

Johnson & Dauble (2006) have reviewed the primary passage route for different types of surface-flow outlets and the efficiency of 69 of such installations. The available data indicated an average of 53% fish-collection efficiency (Johnson & Dauble 2006). Scruton *et al.* (2007) have reported a guidance efficiency of 63% for Atlantic salmon smolts and kelts at a hydropower dam in Canada.

The efficiency of downstream fish-passage facilities for Atlantic salmon smolts at four consecutive small hydroelectric plants located on a diversion structure on the River Ariege (southwest France), varied significantly between sites. The highest efficiency (greater than 65%) was obtained with two entirely new downstream passage facilities (Croze 2008).

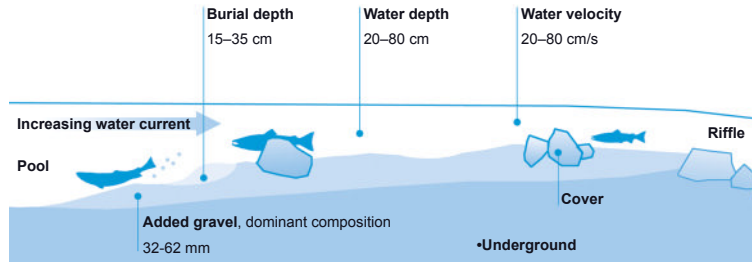


Figure 14.5 Gravel addition to establish a new spawning area for Atlantic salmon at an outlet of a pool. Typical characteristics of spawning area are shown. Modified from Barlaup *et al.* (2008).

Habitat adjustments

One way of adjusting the habitat is to add gravel. The addition of gravel can be effective for restoring spawning habitats. One study of five regulated Norwegian rivers has found that the fish spawned at all sites where gravel had been added (Barlaup *et al.* 2008). Other studies (White 1942; Rubin *et al.* 2004) have found similar results that demonstrate that fish respond quickly by utilising gravel additions for spawning. For gravel additions to be successful, it is important to consider the gravel size, the water depth and the water velocity relative to the size of the spawning fish. Figure 14.5 gives a schematic presentation of a typical substrate addition and preferred hydraulic conditions.

The benefits of enhancing habitats can, however, be limited. One study on the effects of habitat enhancements in the River Dalåa, central Norway, illustrates this point. The water discharge in the River Dalåa fell by 80% owing to hydropower development in 1994. As a compensatory effort, the tail-water habitats have since been used as nursery areas for stocked, start-fed juvenile 0+ Atlantic salmon (Arnekleiv *et al.* 2006). Habitat enhancements were implemented on the basis of hydrophysical simulations, including the construction of pools, deflectors and changes of the riverbed material with the introduction of blasted stones and natural cobbles. The Atlantic salmon densities were significantly higher at all sites with habitat improvements compared to the reference sites in spring during the first five years after the enhancement work. Shallow, riffle-run-type mesohabitats with blasted stones and cobbles were especially favoured over both pool habitats and riffle-run habitats with natural gravel and pebbles. However, in 2004–2005, 12 years after the constructions, the densities at the enhanced areas had declined, and the differences in densities between the reference sites and enhanced sites were no longer so high. This finding was probably a result of increased clogging of the substrate in the habitat-enhanced areas (Arnekleiv *et al.* 2006).

In situ monitoring during the winters of 2004–2006 in the same river showed that areas with solid anchor ice became inaccessible for salmon parr while areas with patchy anchor were used throughout the winter. The results indicated that the surface ice created conditions that allowed salmon parr to use areas that otherwise provided only a limited amount of cover (Linnansaari *et al.* 2008).

Use of water reserved for environmental purposes

Most aquatic organisms have evolved characteristic biological traits adapted to the natural flow regime of free-flowing rivers (Lytle & Poff 2004). For example, the Atlantic salmon

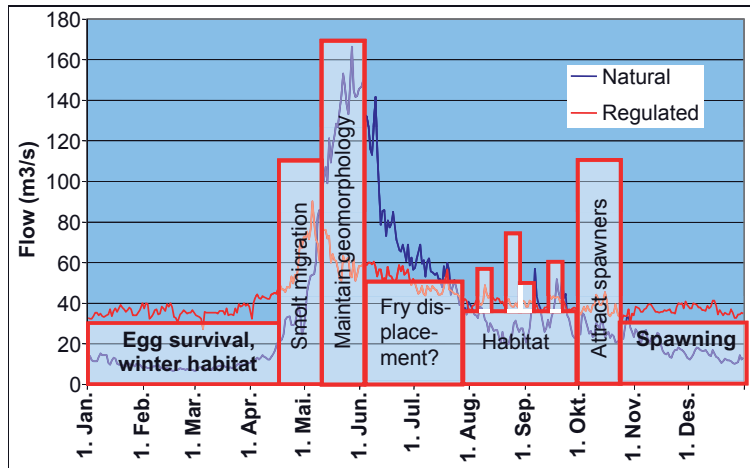


Figure 14.6 Schematic flow requirements of Atlantic salmon based on the Building Block Method (with permission from A. Harby, SINTEF Energy Research, 7465 Trondheim, Norway).

has different environmental-flow requirements during its lifespan to complete its life cycle and to increase individual fitness. The water discharge during the spawning migration is important for securing the salmon run to the spawning areas and the smolt migration is often linked to various phases of the spring flood (Fig. 14.6).

River regulation often alters the natural variability of abiotic factors, especially water discharge, water quality and related factors, which in turn may influence fish behaviour, energetics and mortality.

Artificial freshets

Research on artificial freshets as a mitigatory measure is equivocal. Artificial freshets have been used to stimulate Atlantic salmon to pass power station outlets and weirs, to find fishways and to pass river sections with reduced water flow (Baxter 1961; Thorstad *et al.* 2003; Lundquist *et al.* 2008). However, Thorstad *et al.* (2008) have concluded that small artificial freshets in large regulated rivers may be a waste of both water and money. Still, longer-lasting and larger artificial freshets may stimulate the upstream migrations of salmon.

Artificial freshets have also been employed to initiate the smolt run in periods of low flow. The effects of freshets seemed to be positive when a surplus of water was released in periods with rain (Hvidsten *et al.* 2004; Arnekleiv *et al.* 2007).

Altered flow regime and artificial floods

In order to simulate a natural flow regime, artificial floods are induced in regulated rivers to improve their ecological integrity (Robinson & Uehlinger 2008; Rader *et al.* 2008). Robinson and Uehlinger (2008) have evaluated the long-term effects of 15 floods over 8 years on the periphyton and macroinvertebrates in a regulated river. The floods reduced the fauna richness and biomass and they have concluded that the flood caused a shift in the ecosystem regime that took three years to unfold.

In a long-term study of floods in the Colorado River, Rader *et al.* (2008) have found that the community structure at the regulated site returned to pre-flood levels without increasing to reference conditions. They concluded that occasional floods did not restore biodiversity in that system.

Minimum water flow

Minimum water flow has been one of the oldest mitigatory actions for compensating for the damage to Atlantic salmon populations in regulated rivers. The Spanish water authorities have defined an 'ecological flow' as 10% of the mean annual flow. However, this definition is only a theoretical consideration because in most cases irrigation, urban and industrial supply or hydroelectrical needs have priority over environmental requirements. Rivers below reservoirs consequently suffer periods of being completely dry or having ridiculously low flows in relation to their bed size (Garcia de Jalón 1987). In some rivers, the main factor affecting trout fisheries seems to be the cold water released from the bottom outlets for summer irrigation. This cold water, especially because of its high dissolved oxygen requirements related to temperature, has allowed the trout to invade lower reaches in which they would otherwise be unable to live (Garcia de Jalón 1984).

Several studies have documented a positive correlation between winter discharge and the survival of juvenile salmon in winter (Gibson & Meyers 1988; Hvidsten 1993; Cunjak *et al.* 1998; Hvidsten *et al.* 2004; Næsje *et al.* 2005). River regulations resulting in a higher water discharge in winter have in some cases resulted in a higher smolt production (Hvidsten 1993). However, if increased water discharge leads to higher water temperature and reduced ice cover, the juveniles might experience increased energy-dependent winter mortality (Finstad *et al.* 2007).

Hydro-peaking operations of power plants may increase the juvenile mortality considerably (Salveit *et al.* 2001; Halleraker *et al.* 2003; Scruton *et al.* 2005) and lead to suboptimal water quality (see Section 14.2.1). The environmental release of water may be used to reduce the amplitude of the discharge variations in order to reduce stranding of juveniles. With hydro-peaking power operations, a high minimum water flow will create a refuge for macroinvertebrates and fish during the up- and down-ramping of water flow.

14.5 Conclusion

Hydropower development – the conversion of the potential energy of water into electrical energy – has taken place in different countries since the 1880s. Different types of hydropower facilities, depending on the landscape and the amount of water, have been developed in Atlantic salmon rivers throughout the world. This development has resulted in serious negative effects for Atlantic salmon populations in some countries while the effects have been negligible in other countries.

Hydropower development may change the physical, chemical and biological factors in rivers and fjord systems and may affect the different life stages of Atlantic salmon in several ways. River regulations often change the hydrological scheme in rivers and one common effect is a reduction of large floods in rivers. Changes in water discharge impose primary changes on flow and sediment transfer. River regulation also often changes water velocity, water temperature and ice conditions – all of which may affect macroinvertebrates, such as a decline in species diversity, increases or decreases in abundance and alteration in com-

munity composition. In rivers with bad water quality in parts of their catchment area, hydropower development may negatively affect the survival of salmon both directly and indirectly. The effect of downstream migration of smolts and kelts through hydropower turbines is of great concern. Large dams may impair the upstream migration of Atlantic salmon and thereby seriously affect the salmon population. A run-of-river type of regulation may affect salmon migration because the fish are attracted to the water flow from the power plant rather than to the reduced water flow in the river. In a glacial river system in Iceland, a change in the flow pattern through water regulation and lower turbidity has improved the conditions for upstream migration and has significantly increased the salmon catch and fry production in the mid-section of that system. In the Norwegian River Orkla, high minimum discharge during winter has increased winter survival of parr and thereby smolt production. Rapid reductions in flow have a direct effect on the mortality of fish owing to stranding or an indirect effect owing to desiccation or drift of the benthos.

There are examples of hydropower development in rivers which have led to the complete extinction of the Atlantic salmon population. But there are also examples of hydropower developments in rivers which have resulted in an increase in the Atlantic salmon population. These results mean that there are indeed ways of conducting hydropower development that effectively take the local salmon population into consideration.

There are different measures for compensating for the negative effects of hydropower development. The measures are divided into two main categories: the use of biological and physical measures and the use of water reserved for environmental purposes.

Important measures for compensating for possible negative effects in regulated rivers are fish stocking, weirs, fish ladders, downstream fish-passage facilities and different kinds of habitat adjustments. The general conclusion from reviews on fish stocking is that the effects vary greatly depending on the species, population and environmental conditions. Weirs are common constructions in rivers with strongly reduced flow, but they drastically reduce the water current. Atlantic salmon are vulnerable due to their having strong and defined preferences for different physical habitat parameters such as current, substrate and depth. A fish ladder is another mitigatory measure, an artificial bypass that enables fish to ascend a regulation dam or a natural hindrance for upstream migration. The trade-off between the use of water to protect salmon from turbine-induced mortality and the use for power production has led to the development of different water-efficient fish-passage outlets.

The Atlantic salmon has different environmental-flow requirements during its lifespan to complete its life cycle and to increase individual fitness. River regulation often alters the natural variability of water discharge. In order to simulate a natural flow regime, artificial floods are induced in regulated rivers to improve their ecological integrity. Artificial freshets have been used to stimulate Atlantic salmon to pass power station outlets and weirs, to find fishways and to pass river sections with reduced water flow, but small artificial freshets in large regulated rivers may be ineffective. However, longer-lasting and larger artificial freshets may stimulate the upstream migrations of salmon. Several studies on the practice of minimum water flow, one of the oldest mitigatory actions for compensating for the damage to Atlantic salmon populations in regulated rivers, have documented a positive correlation between winter discharge and the survival of juvenile salmon in winter. In recent years, there has been a better understanding of the need for a broader use of water for environmental purposes. In some cases this expanded knowledge has resulted in, for example, new manoeuvring rules for power plants that emphasise that the hydrological conditions must improve the environment for the salmon population.

Comprehensive studies have been conducted in regulated rivers and they have resulted in a bank of knowledge both on effects from different types of hydropower development and on mitigatory measures. In the future it will be especially crucial to identify the bottlenecks that may cause high mortality in regulated rivers.

The protection of the Atlantic salmon at both the species and population level is a goal for those countries with populations of Atlantic salmon. The objective must be to maintain the unique characteristics of each genetically distinct population. A major task for the future management of regulated rivers will be to maintain river-specific populations at levels that ensure natural reproduction and recruitment. It is particularly essential to identify and mitigate bottlenecks that may cause high mortality. Future efforts should focus on the improvement of environmental conditions for the sake of natural reproduction and survival.

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15 Lessons from Acidification and Pesticides

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Abstract

Salmon populations are on the decline on both sides of the Atlantic Ocean. The cause for this decline varies within and between regions and can be due to various contaminants acting on individual populations. While many contaminants are known to be highly toxic, knowledge regarding physicochemical factors affecting chemical speciation and bio-availability, cause–effect relationships, and response mechanisms are crucial for the identification of the chemical critical limits that have population effects. Anthropogenic acidification of waters has had severe effects on salmon stocks across the Atlantic. While acidification implies a pH reduction, it is the combined effect of reduced pH and the mobilising of aluminium (Al) that harms fish. Al binds to the fish gill, where high doses will kill the fish in fresh water, but low doses can have the same ecological effect on seawater survival. The protection of seawater traits is currently included in the water quality guidelines in Norway. Other contaminants, for example pesticides, are equally toxic and are known to affect many of the same traits as Al. Based on this, we may reasonably assume that pesticides can have severe population effects, long before the dose becomes lethal. Water quality monitoring is, however, often lacking, which reduces our ability to identify correctly the cause–response relationships.

Key words

Atlantic salmon, smolt, contaminants, acidification, aluminium, pesticides

15.1 General water quality of Atlantic salmon rivers

Some salmon populations might have been affected by anthropogenic activities that have exposed them to toxic contaminants since the start of the ‘industrial revolution’, but the awareness of cause–effect relationships and the identification of critical limits are more recent. The water quality in the individual streams and rivers housing Atlantic salmon is, however, crucial in determining whether a specific pollutant will cause an effect or not.

The water quality in lakes and rivers depends on several factors, including catchment geology (chemical composition and weathering rates), rainfall and rainfall pattern (chemical weathering and dilution), climatic zone (snow in winter and snowmelt episodes in spring), temperature (weathering rates), degree of influence from sea water (ion contribution), the level of local pollution (industry, agricultural, and sewage etc.), and long-range transported air pollutants ('acid rain' and various persistent organic micropollutants (POPs)) (Wright 1984; Gregoire & Champeau 1984, Brydsten *et al.* 1990; Skjelkvåle *et al.* 2007).

The rivers supporting Atlantic salmon can have a water chemistry composition ranging from ion-rich with a high alkalinity (often lowland rivers located in agricultural areas) to ion-poor with low alkalinity (located in areas with slow-weathering bedrock). Furthermore, water quality will vary with organic content (total or dissolved organic carbon, TOC/DOC), where water colour can range from clear blue to deep brown. This variation in chemical composition has a major effect on how severely a given concentration of a contaminant will affect fish. For most toxic metals, a high calcium (Ca) and magnesium (Mg) concentration will reduce the toxicity. Rivers with high alkalinity are not sensitivity to acid rain. Organic matter can bind metals and reduce toxicity, but organic-bound metals can also be released and be bio-available if the pH is reduced or the ion strength increases to high levels. The actual water quality depends, then, on a suite of chemicals acting in concert. To our knowledge, relevant water chemistry data has only been compiled and analysed with respect to effects on Atlantic salmon in a few countries.

15.2 Major classes of pollutants

One definition of a pollutant and an environmental contaminant is: 'A chemical or a metal which exists at a level judged to be above those that would normally occur in any particular component of the environment'. This definition regards the elements in question to be relative to the on-site natural background concentration (*Water Framework Directive: guidelines for Ecological Quality Ratio*), and implies that all man-made chemicals are contaminants!

A contaminant will only be a problem to biota if it is in a bio-available form; that is, a form that can be absorbed or consumed by the organism and thereby have a negative effect on it. Many of the contaminants bio-concentrate (i.e. have higher concentration in the organism than in the water), bio-accumulate (i.e. increase in concentration with time of exposure, size and age) and bio-magnify (i.e. increase in those organisms higher up the food chain). With regard to the last effect, many of the POPs magnify, but only mercury (Hg) of the heavy metals has this property. Some pollutants can have a direct and acute effect, typically acting directly on the fish gill and interfering with osmoregulation or respiration, thereby causing mortality within minutes and hours (Evans *et al.* 2005). Others act over time, often by interfering with hormonal systems, for instance reducing immune defence and reproductive capability, and increasing morbidity and mortality ('umbrella endpoints'). Environmental pollutants such as trace metals, organics and radionuclides rarely occur alone. Sources contributing to contamination often contain a mixture of contaminants. Information on processes affecting ecosystem behaviour, mobility, biological uptake, metabolism and accumulation are, therefore, equally relevant for all contaminants. It is internationally recognised that there are critical gaps in the basic knowledge of biological responses to multiple-stressor exposures. The identification of biological responses to low-dose chronic

exposure calls for early warning biomarkers that utilise modern molecular and genetic tools (Salbu *et al.* 2005).

Local pollution that causes extensive fish kills is often linked to episodic releases of heavy metals from various sources, for example smelters, mining activities or industries that use metal salts in their production (direct toxicity related to the individual metal), or by industries and farming activities that release organic or nutrient waste, or both (directly or indirectly causes problems with oxygen content of the water), or a toxicity linked to an organic contaminant directly (direct toxicity related to the individual organic contaminant).

In the following sections, we concentrate on two sets of pollutants that have the largest ecological relevance to Atlantic salmon populations. One of these sets has caused the largest losses of Atlantic salmon worldwide (acidification), and the other, we believe, is a hitherto underestimated type of pollutant which will attract significant attention in the future (Organic Compounds (OCs), especially pesticides). The potential negative effects due to the current use of personal-care products, drug residues and nanotechnology remain to be investigated.

15.3 Acidification

While reductions in Atlantic salmon catches were recorded in many southern Norwegian rivers more than 100 years ago, the cause–effect link between acid rain and salmon kills were not made until the late 1950s. During the next two decades, the pH (H^+) was regarded as the main toxic component in acid water until aluminium was discovered as the ‘driver’ late in the 1970s. During the 1980s water quality standards and mitigation methods were defined, but were seriously revised during the 1990s when delayed responses on, for instance, seawater tolerance of smolts were documented. By 1999, 18 populations of Atlantic salmon and more than 9600 inland populations of fish (mainly salmonides) had been lost in Norway (Hesthagen & Hansen 1991; Hesthagen *et al.* 1999), and more than 30 rivers have reduced salmon catches most likely caused by acidification (Kroglund *et al.* 2002). Acid precipitation has killed the fish populations of 14 rivers in Nova Scotia’s southern upland region, 20 rivers have only 10% of their Atlantic salmon left, and another 30 are threatened (ASF 2009). In the northeastern United States, 14 out of 25 rivers known to have Atlantic salmon have lost their populations (Fay *et al.* 2006). Acidification has also been the cause for salmon population effects in both the United Kingdom (Harriman *et al.* 1995) and Sweden (Degerman & Appelberg 1992; Serrano 2005).

In areas exposed to long-range transported air pollution, the catchment receives a significant amount of hydrogen ions (H^+), sulphate (SO_4^{2-}), nitrate, and ammonium ions through wet (rainfall) and dry deposition, which historically has led to the acidification of freshwaters in large parts of the world (Steinberg & Wright 1994) and has had a major impact on aquatic biota (Rosseland & Staurnes 1994; Gensemer & Playle 1999). Together with the acids, heavy metals and POPs (including pesticides) are important parts of the long-range transported air pollutants.

In the early phase of an acidification, the soil bicarbonate buffering system will neutralise the acids and release Ca^{2+} and Mg^{2+} . As the process of acidification continues and pH decreases, the bicarbonate buffer system is depleted and the aluminium buffer system takes over. The reduction in pH will then mobilise Al from the catchment, where Al is the prime

toxicant for gill-breathing biota in fresh water. As for other metals, the toxicity of Al is related to the bio-available metal species that can interact with a biological membrane. Because the body surface of an Atlantic salmon is covered with mucus with negatively charged properties in acidic waters, only inorganic positively charged aluminium (mainly low molecular forms of Al, called inorganic (Ali) or labile aluminium (LAl)) will bind and cause negative effects on Atlantic salmon and other aquatic biota (Exley *et al.* 1991; Rosseland & Staurnes 1994; Gensemer & Playle 1999). Because humic substances can bind cationic (positively charged) substances, the concentration of positively charged Al in acidified waters will be related to the total concentration of Al, pH, and TOC (Lydersen 1998). The Al toxicity is also moderated by other water constituents where toxicity is reduced by increased Ca^{2+} and ion strength, and increased with increasing temperature. In the low TOC and low Ca waters of Scandinavia, the toxicity of Atlantic salmon is directly linked to Al, while in the humic-rich and low Ca rivers of Nova Scotia, Canada, it is the low pH more than Al that is critical (Lacroix & Townend 1987; Lacroix *et al.* 1990; Magee *et al.* 2003). While a pH value of five is regarded as satisfactory in Canada, Atlantic salmon would become extinct in Norwegian rivers at this pH level (Kroglund *et al.* 2002). The Canadian guidelines have their basis on smolt abundance in rivers, while the Norwegian guidelines are based on adult salmon catches together with data from salmon-exposure experiments (Kroglund *et al.* 2008). The seawater tolerance of salmon smolt is not included as target response in the Canadian guidelines, but it is in the Norwegian ones. Recent studies from the US strongly indicate that, contrary to common belief, Al also has a negative effect on seawater tolerance in US rivers (McCormick *et al.* 2009).

Not only 'acid rain' but also 'clean rain' connected to ocean storms can cause episodes that release toxic Al. After big storms, even high mountain lakes can have an increased Na^+ and Cl^- concentration that originates from the seasalt spray. Such 'seasalt episodes' can also have an important impact on river and stream chemistry (and in some cases lakes), because the seasalts, especially Na^+ , will be ion exchanged in the soil for Ca^{2+} (in areas not exposed to 'acid rain') or H^+ (in areas affected by acid rain). In the latter case, an increased H^+ will lower the pH and release aluminium (Al) in its toxic form, thus creating an episodic event which can lead to fish kills (Hindar *et al.* 1995; Barlaup & Åtland 1996; Teien *et al.* 2005; Teien *et al.* 2004).

In acidified waters low in TOC, Ali react with the gill of the fish (and gill-breathing invertebrates), which can lead to osmoregulatory and respiratory failure and rapid mortality (Rosseland & Staurnes 1994; Kroglund *et al.* 2008). The response depends on the life-history stage being exposed (Rosseland & Hindar 1991; Kroglund *et al.* 2008; Monette & McCormick 2005). Unfavourable water quality caused by acidification may directly affect the youngest life-history stages in various ways. It may affect the egg quality prior to spawning (Sangalang *et al.* 1990), reduce spawning activity (Kitamura & Ikuta 2001; Ikuta *et al.* 2003) and fertilisation, negatively affect embryo development through suboptimal swelling water quality (Keinänen *et al.* 2003), and increase day-degrees to hatching, thus reducing hatching success and increasing mortality until swimup (Rosseland & Skogheim 1984; Skogheim & Rosseland 1984; Rosseland *et al.* 1986a, b; Skogheim & Rosseland 1986). The smolt stage of Atlantic salmon is the most vulnerable stage (Rosseland & Skogheim 1984; Leivestad *et al.* 1987; Rosseland *et al.* 2001; Monette & McCormick 2005), especially during the last two weeks prior to seaward migration (Rosseland & Staurnes 1994; Staurnes *et al.* 1995; Kroglund *et al.* 2007; Kroglund *et al.* 2008). Although there are differences in

tolerance to acidic water among strains of Atlantic salmon at the fry and parr stage, the increased and similar sensitivity at time of smoltification makes stocking of more tolerant strains a non-effective tool for a mitigatory strategy (Rosseland *et al.* 2001).

There is a close relationship between Al accumulated onto the fish gill and certain physiological responses when fish and chemistry is determined *in situ* (Figs. 15.1 and 15.2). The low pH acts to increase the permeability of the gill (McWilliams *et al.* 1980). Much lower gill-Al concentrations than those affecting blood-plasma values on the freshwater stages of salmon interfere with ionoregulation in seawater and smolt to adult survival (Fig. 15.3). Even low concentrations of Al will reduce the activity of the major enzyme for ion regulation in seawater, Na/K⁺-ATPase in smolt (Staurnes *et al.* 1993; Rosseland *et al.* 1992; Kroglund *et al.* 2007), imposing stress responses when gill Al >25 µAl/g gill tissue dry weight (dw) corresponding to >5–7 µg LAI/L in the water (Kroglund *et al.* 2007; Kroglund *et al.* 2008). A gill-Al of 30 µg Al/gill dw is proposed as a water-quality (WQ) indicator that distinguishes moderate WQ from marginal water in the EU Water Framework Directive (Lyche 2008).



Figure 15.1 *In situ* exposure of salmon smolt (left). In the setup, water quality will vary with increased water age, where age increases as water passes from one tank to the next. Water age affects aluminium speciation and hence toxicity. To determine these changes, aluminium is fractionated *in situ* (right). Photos: Bjørn Olav Rosseland.

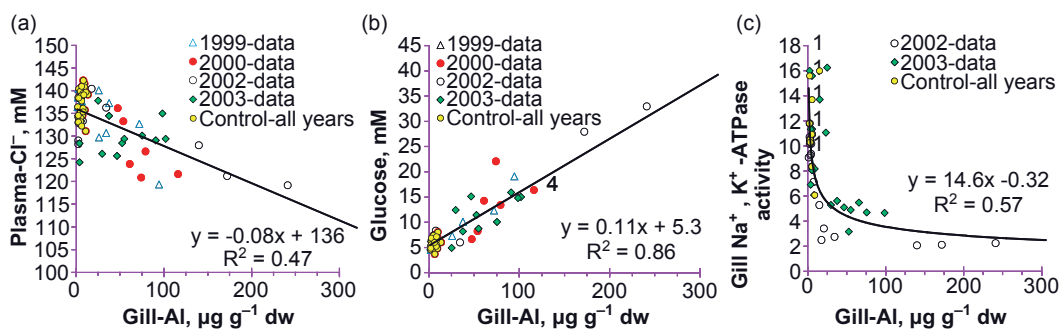


Figure 15.2 Relationship between average gill-Al and average a) plasma Cl⁻, b) glucose, and c) gill Na⁺/K⁺-ATPase (µmol ADP mg protein⁻¹ h⁻¹) for all samples from all treatments, all years. Sample year can be identified by the legend. Samples from the Control tanks are marked by the yellow dots. The regression lines are based on pooled data from all years. Reproduced from Kroglund *et al.* Copyright (2007), with permission from Elsevier.

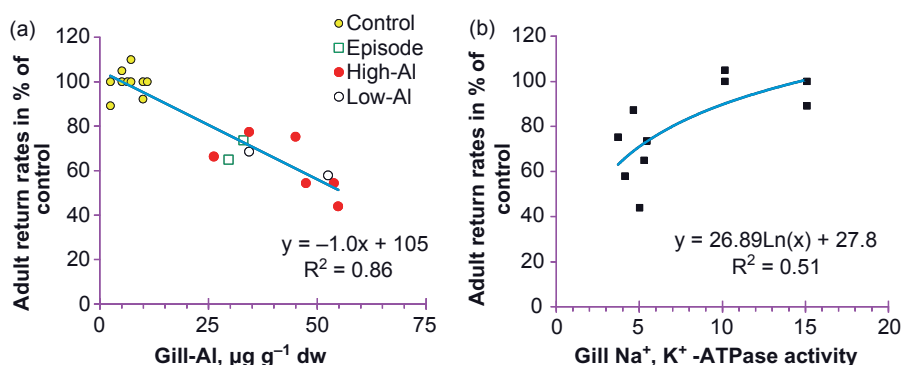


Figure 15.3 a) Relationship between gill-Al measured at exposure termination and the adult return rate in % of Control. The four treatments are identified by the legend. b) Relationship between gill Na⁺/K⁺-ATPase (µmol ADP mg protein⁻¹ h⁻¹) and adult return rate in % of Control. Reproduced from Kroglund *et al.* Copyright (2007), with permission from Elsevier.

Exposure-release studies of Carlin tagged smolt have shown that episodic exposure to moderately low pH and elevated levels of Al for only three days can lead to reduced seawater tolerance, increased vulnerability to sea lice, and reduced return rates of salmon adults by 50% compared to reference groups (Finstad *et al.* 2007; Kroglund *et al.* 2007). A smolt that is not physiologically fit entering seawater will have a poor fright-and-flight response, a reduced ability to detect danger, and will be more susceptible to predation (Jaervi, 1989; Madsen *et al.* 2004; Scholz *et al.* 2000; Tierney *et al.* 2006a, b). Thus, even short episodes of acid water during the period of downward migration of Atlantic salmon smolts might have an ecologically relevant impact on wild salmon stocks (Kroglund *et al.* 2008). Following such a sublethal episode, smolt will recover physiological health, but this process takes weeks (Kroglund *et al.* 2001b).

In a river, the water quality of the main river stem will vary with the water qualities present in the tributaries. Downstream, where there is the confluence of acid with less acidic water, Al present in the acid source will change speciation with increased pH. Similar processes also occur downstream a lime doser. In these 'mixing zones', a chemical Al-inequilibrium can create an extreme Al-related toxicity (Rosseland *et al.* 1992; Lydersen *et al.* 1994; Poléo *et al.* 1994; Teien *et al.* 2006; Kroglund *et al.* 2001a, Kroglund *et al.* 2001b), in extreme cases killing Atlantic salmon smolts within only six hours (Rosseland *et al.* 1992). The rationale behind the Norwegian pH targets for limed rivers are based on Al detoxification rates with respect to pH (Kroglund *et al.* 2008; Sandøy & Langåker 2001). Analyses of Al precipitation on olfactory tissue have shown a linear relation to gill-Al (Salbu *et al.* unpublished), which probably explains the loss of olfactory response to the amino acid L-Serine when aluminium was added to low pH water (Klaprat *et al.* 1988; Moore, 1994).

Owing to the short duration of such an episode, normal fish surveys often miss their effects. The documentation of the presence of toxic Al in mixing zones is also often faulty, because the toxic forms of Al are transformed into non-toxic forms as the water sample is transported to the laboratory. Today, the liming activity of Norwegian fresh waters has its basis in a continuous scientifically based research-and-development strategy, which includes the implementation of strategies that handle the complex Al chemistry phenomenon that



Figure 15.4 An old (left) and a new lime doser (right) in use on Norwegian salmon rivers. In all newer dosers, the storage tanks and dosing equipment are concealed inside a house. Acknowledging the fact that these dosers will need to operate for many decades, the Norwegian environmental authorities take care to ensure that they blend in with the environment. Photos: Frode Kroglund.

occurs when the pH increases (Fig. 15.4). The water quality has improved for more than 2500 inland populations of fish and more than 20 Atlantic salmon rivers (Sandøy & Langåker 2001), where salmon catches from affected and mitigated rivers have increased from levels of less than five tonnes a year to levels exceeding 50 tonnes a year (Hesthagen & Larsen 2003).

In all rivers, the water quality in the salmon-producing areas will reflect the natural water quality of the main river catchment area, as well as the input from the side tributaries along the river stretch from the upper catchment to where the river mouth meets the sea. In regulated rivers (see Johnsen *et al.* 2011 [Chapter 14]), several factors can either improve or reduce the water quality for wild salmon (Wright 1984). In rivers where reservoirs have been built for storage water, the water quality in the reservoir might improve the general water quality through increasing the retention time and thus the contact time with sediments, etc., which can increase the buffer capacity of a normal, low-ionic freshwater quality. When water is retained in the reservoir, however, tributaries downstream the reservoir will be the (main) source for water. If these tributaries are acidic, acidification episodes will occur (Skogheim *et al.* 1984; Kroglund *et al.* 2008), see also Johnsen *et al.* 2011 [Chapter 14]). As reservoir water is normally used during winter, the 'good' water is often used up long before the smolt run. In the spring the reservoirs need to be filled, which deprives the river of the good water, thus causing water quality episodes that adversely affect smolt quality. In late autumn and winter, a reduced water level caused by filling of reservoirs will increase the influence of groundwater. Increased groundwater increases the risk of CO₂ supersaturation, which can reduce the pH and mobilise Al and other metals (Norton & Henriksen 1983; Rosseland & Hindar 1991) and can reach levels of CO₂ as high as >12–15 mg CO₂/L, which is suboptimal to salmonides (Stefansson *et al.* 2007a, b). Water reservoirs and hydropower regulation can thus have a major impact on water quality.

As river waters enter fjords, large chemical changes occur in the brackish waters in the estuaries and the upper fjord waters of reduced salinity. Fresh water contains colloids and particulate matter, like humics (TOC) that have bound metals, especially aluminium and

iron. These forms of the metals are not toxic in fresh water. As fresh water meet salt water and the salinity increases above 1–3 psu, aluminium bound to humics and colloids will be released as low molecular mass forms of the metal. Because these are highly reactive to fish gills, as in freshwater ‘mixing zones’, they can impose huge mortality on fish exposed to the ‘estuarine mixing zones’ (Teien *et al.* 2006; Rosseland *et al.* 1998; Rosseland, 1998). Net-pen rearing of salmonides in fjord systems with freshwater layers originating from rivers during high flow have experienced huge mortalities caused by Al-deposits on gills, where control situations with $<10\mu\text{Al/g}$ gill tissue d.w. increases to 200–400 $\mu\text{Al/g}$ gill tissue d.w., resulting in major fish kills (Bjerknes *et al.* 2003). As poor water quality in fjords is linked to TOC, the current increase in TOC measured on both sides of the Atlantic (De Wit *et al.* 2007; Evans *et al.* 2007) could increase the possibility of toxic metals in fjords affecting salmon.

Atlantic salmon smolts from acidified rivers having problems with seawater tolerance during their outward migration to sea tend to stay in the estuaries (Magee *et al.* 2001) or to migrate in the more isoosmotic brackish layers in the fjords. They can thus be exposed to the additional stress of this phenomenon of the estuarine mixing zone and die from physiological stress, become more infected by sea lice or become easier prey for marine fish or seabirds (see also Ward & Hvidsten 2011 [Chapter 8]).

The estuarine mobilisation of toxic Al from organic matter and metal colloids is a potential problem in fjords and outer regions that in the past were or currently are affected by acid rain. It depends, however, on the inflow of such river waters along the migration route of the smolts.

15.4 Pesticides and Atlantic salmon

In most cases, a pesticide is a man-made compound or a mixture of compounds mostly of organic origin that is used to kill or reduce a ‘pest’. The term ‘pest’ includes a variety of microbes and organisms that do harm mainly to crops, and includes, for example, insects, plant pathogens, weeds, snails and other molluscs, nematodes, and even such higher organisms as fish, birds, and in some cases mammals.

The documentation on the effects of pesticides on fish and other aquatic organisms over the past few decades is thorough. As for all pollutants, the physiological and population responses vary with the species and with the life-history stage. The various pesticides can cause responses ranging from lethal to sublethal to having ‘no appreciable’ effect (Johnson, 1968; Scott & Sloan, 2004).

Pesticides can roughly be defined according to four groups:

Organophosphate Pesticides (OP) – These pesticides affect the nervous system by disrupting the enzyme that regulates acetylcholine, a neurotransmitter. Most organophosphates are insecticides.

Carbamate Pesticides (CP), like organophosphate pesticides, affect the nervous system by disrupting an enzyme that regulates acetylcholine, a neurotransmitter. The enzymatic effects are usually reversible.

Organochlorines (OC) are insecticides that were commonly used in the past, but many have been removed from the market owing to their deleterious health and environmental effects and their persistence (e.g. DDT (Dichlorodiphenyltrichloroethane) and chlordane).

Pyrethroid Pesticides (PP) were developed as a synthetic version of the naturally occurring pesticide pyrethrin, which is found in chrysanthemums. Synthetic pyrethroids are toxic to the nervous system.

The problem arises when the pesticide either enters non-target areas or affects non-targeted species. For Atlantic salmon, when pesticides are used directly in water or are brought to the waterway by heavy rain and flooding of treated ground or by polluted groundwater, they can cause harm. Many of the pesticides of organic origin will over time be degraded into other compounds, and in many cases the breakdown products may also have a negative effect on organisms (Pehkonen & Zhang 2002). Some are extremely persistent, like the chlorinated compound dioxin (polychlorinated dibenzodioxins) that is used to fight forest growth, or DDT where the breakdown products DDD and DDE (often given as sum DDTs) can be found in recipients decades after their use, as well as being spread worldwide through the atmosphere, even reaching areas like the high mountains or the Arctic where they definitely were not intended to be used (Wania & Mackay 1993; Grimalt *et al.* 2001; Vives *et al.* 2004; Vives *et al.* 2005).

Despite existing policies and legislation, the actual consumption and use of pesticides in the EU did not fall between 1992 and 2003. In 2003, approximately 300 000 tonnes of active substances were sold in the EU. According to the European water suppliers' organisation, pesticide contamination of raw water is very severe in lowland rivers (Anon 1). About 450 000 tonnes of conventional pesticides were used each year in the United States between 1992 and 2001. Pesticides or their degradates were detected in one or more water samples from every stream sampled ($n = 4380$) (Gilliom *et al.* 2006). Currently, there are 497 active substances registered within the EU Pesticides database (Anon. 2). The number of pesticides in use worldwide is, however, much larger (<http://www.pesticideinfo.org/>).

Pesticide concentrations in stream water, either singly or in mixtures, will vary throughout the year. The total combined toxicity of pesticides in water may be greater than that of any single pesticide present (Greene & Kocan 1997; Laetz *et al.* 2009). The concentration can be low or undetectable for most of the year, but punctuated by seasonal pulses or episodes. The timing and magnitude of episodes correlate with the timing and intensity of pesticide applications, the frequency and magnitude of runoff from rainstorms or snowmelt, and the timing and distribution of land management practices such as irrigation and artificial drainage (Black *et al.* 2000; Gilliom 2007; Gilliom *et al.* 2006). An episode can last from hours to weeks. Depending on the timing and duration of an episode and whether sensitive life stages of Atlantic salmon are present or not, an episode can, but will not necessarily, have detrimental effects. However, like AI effects on seawater tolerance, Atlantic salmon smolts exposed to pesticides might experience a 'multiple-stressor' effect which can be critical for survival at a later stage in their life-history.

Despite the vast literature (e.g. 4501 articles on pesticide and fish in PubMed as of 7 June, 2010), the definition of the ecological impacts of pesticides are poor for most fish species, including Atlantic salmon. Of the 556 articles on pesticide and salmonides, 72 articles are on Atlantic salmon (PubMed as of 7 June, 2010). The mechanistic understanding of dose-response relationships and the effects pesticides can have on population health remains unsatisfactory, however. There are several reasons for this assertion. The large number of chemicals in use (both singly and in combination) and the large number of fish species in question mean that the knowledge is scattered. The ecological effects can, however, often be derived through the identification of the active ingredients in the pesticide and through

the application of knowledge of the target organs or physiological processes affected. From this approach, viable suggestions on the mechanistic responses and ecological effects are possible. In addition, other water-quality constituents (both chemical and physical) have an effect on dose-response relationships and hence toxicity (Scott & Sloan 2004; Heath 1995). Generally, water quality limits derived for 'hard' water types may not protect fish in waters low in calcium and organic matter, which is more typical for rivers supporting Atlantic salmon. General water chemistry is surprisingly often omitted in the literature, and this gap makes generalisations difficult. In addition, the episodic occurrence of pesticides in a stream makes monitoring difficult. A single sample taken in spring or fall gives only a 'snapshot picture' of possible exposure concentrations. *In situ* exposures are, therefore, rare, and the more mechanistic studies are normally based on fish exposed under controlled conditions in a laboratory, and seldom examine the most sensitive life-history stage.

A pesticide can affect a fish through numerous pathways. A fish can ingest it with food or absorb it through the water and through skin and gills. Many of the pesticides have bio-magnifying properties, which affect the prey of Atlantic salmon. We have not made tables of the various pesticides and their individual ecological relevant responses, but have drawn on more general results in order to suggest how pesticides can affect Atlantic salmon. However, where data are lacking, we have included data on other salmonids and occasionally non-salmonids if we determined that the data was relevant.

Although there are a number of reported fish kills in the literature, these are fairly rare compared to the number of rivers supporting Atlantic salmon. Mortality is normally associated with 'accidental' spills. Pesticides used in agriculture have killed salmon in the US (Saunders 1969). Documentation of salmonid kills related to pesticides (potato industry) is available from Prince Edward Island, Canada (Gormley *et al.* 2005). Exposure studies and cause-effects evaluations have been the basis for the assumption that pesticides are the cause of some of the catch reductions of Atlantic salmon in Canada (Brown & Fairchild 2003; Fairchild *et al.* 1999). Salmon kills have also been reported following spraying of DDT (Kerswill & Edwards 1967). In addition to these studies, pesticides used on blueberry fields, sheep-dips, and in the potato industry have killed fish in the USA, Scotland and Wales. Few of these incidences have been scientifically documented, but have been reported mainly through the news. Pesticides are suspected to have been the cause of several fish kills in Norway, but a lack of funding has halted further research (Kroglund pers med.). Most pesticides are lethal if the dose is sufficiently high and if the exposure duration is long enough (Locke & Havey 1972; Vianta *et al.* 2006). Water-criteria limits based on mortality are generally higher than the limits based on sublethal responses (Scholz *et al.* 2000). A sublethal response can, however, have as large a population effect as direct kills, though less conspicuous. Even if animals are not overtly harmed by a contaminant, they may be unable to function in an ecological context if their normal functions are altered. Ecologically sound criteria imply that all individual traits important for population health must be protected.

It is well documented that pesticides can affect the physiological status of fish, where the responses differ with species and chemical and exposure duration. Sublethal doses can affect population health by weakening the immune system, reducing growth (smolt size), adversely influencing predator avoidance, prey detection, smoltification, imprinting, timing of seawater entry, seawater survival, and spawning and reproduction. Physiological responses include ionoregulatory status, increased cortisol secretion, glycogen mobilisation, reduced cell viability, decreased antioxidant defence, and lipid peroxidation. These responses affect growth,

act as an immunosuppressant, affect neurotransmission, and reduce the individual's health and susceptibility to diseases if the water quality does not return to acceptable levels (Beauvais *et al.* 2001; Bradbury 1994; Davies *et al.* 1994; Dorval *et al.* 2003; Eder *et al.* 2008; Moore & Waring 1996, 2001; Moore *et al.* 2003, Waring & Moore 1997, 2004; Clifford *et al.* 2005).

Reduced swimming performance and behavioural responses that affect fright-and-flight ability, predator avoidance, feeding and shoaling have been reported for several salmonids (Beauvais *et al.* 2000; Brewer *et al.* 2001; Little *et al.* 1990; Little *et al.* 1993; Sandahl *et al.* 2005; Ward *et al.* 2006; Ward *et al.* 2008). Chemical cues are of enormous importance in mediating the behaviour of animals because they enable them to navigate throughout their habitats, to detect the presence of predators or prey, and to facilitate social recognition. In this way olfactory-based behaviours play a significant role for the successful completion of the salmonid life history (Graham & Sloman 2004; Olivier *et al.* 2006; Rehnberg *et al.* 1985; Rehnberg & Schreck 1986). In many species of freshwater fish, social recognition and the recognition of conspecifics are known to be based primarily on chemical cues, where such recognition mechanisms are vulnerable to disruption by organic contaminants (Brown & Brown 1992; Moore *et al.* 2007; Ward *et al.* 2008; Brown *et al.* 1997).

The exposure of salmon to a range of environmentally relevant pesticides, which routinely occur in spawning tributaries, has been shown to inhibit olfactory-mediated reproduction, fertilisation and embryo survival and emergence. Pesticides affect olfactory-mediated behaviours by, for instance, blocking synaptic transmission because they inhibit neuronal acetylcholinesterase in salmonids. Short-term sublethal exposures to insecticides may cause significant behavioural deficits that have negative consequences for survival and reproductive success (Hidaka & Tatsukawa 1989; Jaensson *et al.* 2007; Tierney *et al.* 2006; Moore *et al.* 2007; Moore 1996; Waring & Moore 1997). Baltic salmon suffer from maternally transmitted yolk-sac fry-mortality syndrome: M74. The cause of this syndrome is unresolved, but it may relate to oxidative stress that is possibly associated with pollutants, either directly or through the prey (Vuori & Nikinmaa 2007).

There is a great deal of evidence that a suite of chemicals can significantly affect smolt by affecting growth (smolt size), migration (time and speed), and hypo-osmoregulatory capacity (SW-challenge test and measurement of Na^+/K^+ -ATPase activity). Migration occurs during the 'smolt window', a period when the individual is ecologically and physiologically adapted to sea water (Hansen & Jonsson 1989; McCormick *et al.* 1998) and when a delayed migration will reduce the probability of smolt-to-adult survival. Pollutants like pesticides (and Al) that affect smolt quality will, if present in relevant concentrations, reduce smolt quality and hence the chances of smolt-to-adult survival (Bangsgaard *et al.* 2006; Arsenault *et al.* 2004; Brown & Fairchild 2003; Fairchild *et al.* 1999; Johnson *et al.* 2007; Larsson *et al.* 1996; Madsen *et al.* 1997, Madsen *et al.* 2004; McCormick *et al.* 2005; Moore *et al.* 2007; Moore *et al.* 1995; Moore *et al.* 2003; Spaulding 2005; Waring & Moore 2004; Wedemeyer *et al.* 1980). During the seaward migration, the smolts undergo imprinting to their natal stream; that is, the olfactory imprinting for the last phase of the migration when the Atlantic salmon return to the home river to spawn (Hasler & Scholz 1983). Pesticides are known to affect olfaction (Moore *et al.* 2007; Morin *et al.* 1989; Rehnberg *et al.* 1985).

The finding that even low levels of aluminium, which have only minor physiological effects in smolt while in fresh water, have major effects on adult salmon return rates (Kroglund & Finstad 2003; Kroglund *et al.* 2007; Staurnes *et al.* 1996) supports other observations that

suggest there may be a causal link between Atlantic salmon decline and the use of pesticides in Canadian forests and in Maine, USA (Arsenault *et al.* 2004; Brown & Fairchild 2003; Fairchild *et al.* 1999; McCormick *et al.* 1998; McCormick *et al.* 2005). Similar responses for Pacific salmon species have been reported (Arkoosh *et al.* 1998; Arkoosh & Collier 2002; Cox & Hinch, 1997; Johnson *et al.* 2007).

15.5 Conclusion

Salmon populations on both sides of the Atlantic and Pacific oceans are on the decline. This reduction has arisen because of numerous drivers that act upon an individual population. The drivers can have clear local causes (habitat destruction), regional causes (salmon lice) or even affect populations that are geographically separate (marine climate) (Beamish & Bouillon 1993; Friedland *et al.* 2000; Lehodey *et al.* 2006; Friedland *et al.* 2005; Friedland *et al.* 2009; Parrish *et al.* 1998). Falls in population can also be due to contaminants that affect fish health within the freshwater habitat. While smolt production can be normal, smolt-to-adult survival is reduced. Salmon researchers and managers should not only focus on the individual drivers when seeking out the cause for declining salmon densities, but should also look for cause–effect relationships that act in concert to reduce population health. Although the correlation in population changes on both sides of the Atlantic point to factors working at regional levels (e.g., oceanic climate), it is important not to ignore freshwater-related factors because many of the contaminants are widely used, and their use has increased over the past few decades. In this respect, the reported decline in Atlantic salmon stocks can also be affected by xenobiotic (man-made) contaminants entering salmonid rivers. As water quality monitoring is often lacking, as well as relevant fish studies and the understanding of dose-response mechanisms, there is an urgent need for greater knowledge on contaminants and their ecological impact. The literature has demonstrated that both acidification (aluminium) and pesticides affect the spawning activity and spawning success of adult salmonides, as well as the survival of eggs and larvae, both of which have a direct impact on population recruitment. Furthermore, freshwater contaminants can have delayed effects, for example, by affecting smolt quality, and thereby smolt-to-adult survival in sea water. Here, the fish experiences the dose while in fresh water, but the ecologically relevant responses to that dose first emerge after the individual has entered sea water, which misleadingly might suggest marine causes. The end result stubbornly remains: there are fewer salmon surviving to spawn because they are under threat from chemicals at all life stages.

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16

Getting into Hot Water? Atlantic Salmon Responses to Climate Change in Freshwater and Marine Environments

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Abstract

Recent and projected climate changes – both in the freshwater and marine environments exploited by Atlantic salmon – present considerable adaptive challenges to many populations. In assessing the predictions and possible impacts of overall climate change, we focus in fresh water on precipitation, river discharge and temperature, whilst for the marine environment we highlight the interactions between temperature, size/growth-mediated predation and shifts in prey assemblages. Changes in seasonal temperature and flow regime will probably exert complex or conflicting interactions for particular river stocks in terms of freshwater survivorship, growth, smoltification and timing of emigration. Ocean temperature changes will directly affect early post-smolt survivorship and indirectly influence prey availability and hence longer-term survivorship, growth, maturation and spawning run-timing. It is of immediate concern that most salmon stock abundances presently are at historical lows, but perhaps the greatest uncertainty in projecting their future health lies in our poor understanding of the genetic and ecological adaptability of populations in relation to the likely rate(s) of environmental change. Against the backdrop of a rapidly changing environment, a precautionary approach to managing salmon populations should be holistic and integrative of both the marine and freshwater environments, and should include the maintenance of their genetic variability and integrity.

Key words

Salmo salar, precipitation, river discharge, ‘top-down’ control, ‘bottom-up’ control, condition factor, regime shift, ocean climate, Atlantic Multidecadal Oscillation, North Atlantic Oscillation

16.1 Introduction

There can be little doubt of the recent and marked climate changes in the terrestrial and ocean areas exploited by Atlantic salmon (*Salmo salar* L.). The consequences of climate

change since the 1970s have been especially well documented in Europe and Menzel *et al.* (2006) have shown an advancement of spring (by ~2.5 days per decade) and delay of winter (by ~1 day per decade), resulting in an increased terrestrial growing season. In terms of year-on-year change in the marine environment, the most obvious indicators are the increasing extent of summer melting of Arctic sea ice (e.g. Lindsay *et al.* 2009) and sea surface temperature (SST) anomalies, which have recently and consistently been high in some ocean areas exploited by Atlantic salmon. Climate impacts on Pacific *Oncorhynchus* spp. (e.g. Beamish & Bouillon 1993; Hinch *et al.* 1995; Finney *et al.* 2000; McFarlane *et al.* 2000) and Atlantic salmon (e.g. Narayanan *et al.* 1995; Beaugrand & Reid 2003; Friedland *et al.* 2003a; Lajus *et al.* 2007) have frequently been observed and ocean climate variation can clearly have major impacts on fisheries productivity (e.g. Lehodey *et al.* 2006; Castro-Ortiz & Lluch-Belda 2007). Because climate impacts comprise only part of an interacting hierarchy (e.g. Armstrong *et al.* 1998) it becomes problematic to attribute cause and effect to perceived or observed climate-related changes in the salmon environment (Parrish *et al.* 1998). But of even greater relevance to the complexity of revealing the underlying mechanisms and processes are that these multi-decadal patterns may show teleconnections and synchrony over large distances and even across separate ocean basins.

Richardson & Schoeman (2004) report on 'bottom-up' control of herbivorous zooplankton driven by ocean warming, and the general implications for top consumers are clear: warm seas with reduced primary production will exert predictable negative impacts upon fisheries. In addressing the generic problem of climate impact and the likely responses of Arctic fishes, Reist *et al.* (2006a, b) proposed a three-level approach to the prediction and amelioration of positive and negative impacts on Atlantic salmon. First is coupling climate predictions to known physiological limits and responses of the various life-history stages. Second is the linkage to population dynamics, and third is the focus on biogeographic shifts. The major difficulties in progressing this problem lie in the very complexity and diversity of salmon stocks and genetic populations – and how their responses will vary differentially to the same challenge – the paucity of knowledge of ecosystem-level interactions, and distinguishing changes in annual means (e.g. of precipitation or temperature) from the occurrence of exceptional, perhaps very brief, abiotic disturbance events of over-riding ecological significance. Whilst qualitative statements can be made with some confidence, for example that precipitation or temperature changes will increase or decrease parr growth, it is not yet possible to quantify that change at either the species or the population level. Atlantic salmon populations are characterised by a diversity and plasticity of life-history strategies and maturity schedules, and a high degree of population genetic structuring and variability, all of which are thought to be adaptive (e.g. Youngson *et al.* 2003; Leaniz *et al.* 2007). The immediate concern for their future health is that, as far as can be judged, most salmon populations remain at historical lows and there is little or no sign of concerted improvement or recovery for most stocks.

16.2 Past and present climate for Atlantic salmon

According to the Fourth Assessment Report from the Intergovernmental Panel on Climate Change (IPCC), average global temperature has risen 0.74°C over the past century, and may increase by 1.1–6.4°C over the next century if greenhouse gas emissions are not con-

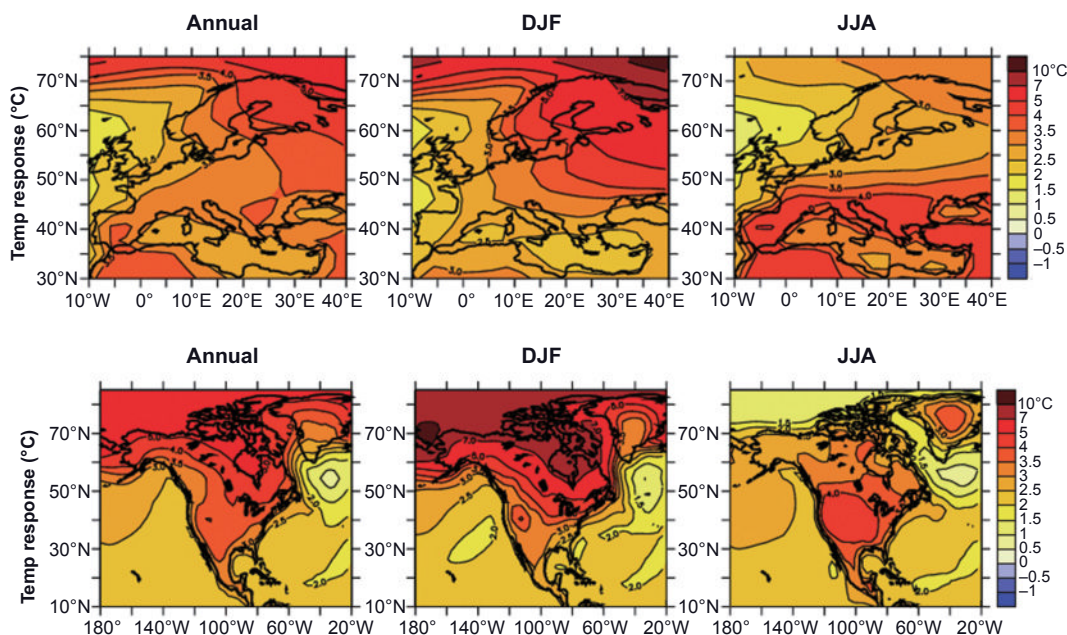


Figure 16.1 Air temperature changes over Europe (upper panel) and North America (lower panel) from the MMD-A1B simulations. Annual mean, DJF (December, January, February), and JJA (June, July, August) temperature change between 1980–1999 and 2080–2099, averaged over 21 models (from Fig. 11.5 and Fig. 11.12 in Christensen *et al.* 2007).

trolled (Solomon *et al.* 2007). Weather patterns are likely to become more extreme and throughout most of the distributional area of Atlantic salmon air temperatures will increase more over land than sea; this will be most pronounced in summer along the east coast of North America (Fig. 16.1). According to the SRES A1B scenario (IPCC 2007; Fig. 16.2), winter precipitation is likely to increase 10–20% across most of the salmon range. In the northern range, a 5–10% increase in summer precipitation is forecast, but there may be a considerable (perhaps >20%) reduction in the southern part of Europe (IPCC 2007; Fig. 16.2). Concomitant with these predictions are projections for increased annual runoff for northwestern Europe, but decreases for central Europe. Thus, above 47°N, annual average runoff may increase by ~9–22% up to the 2070s, whereas south of 47°N this may decrease by 6–36% (Bates *et al.* 2008). For eastern North America, annual mean precipitation is projected to rise up to 2100, with changes in Canada in the range of +20% for the annual mean and +30% for the winter months (Bates *et al.* 2008).

The annual duration of snow cover will also decrease across the whole salmon range, and freshwater and air temperatures will most likely increase in concert throughout most of the ice-free season. Changes in flow and temperature will, in turn, affect biotic communities in rivers and lakes (Bates *et al.* 2008), and will affect salmon.

A robust finding for rivers on both sides of the North Atlantic is that projected warming would lead to changes in flow seasonality in catchments where much of the winter precipitation presently is snow (Bates *et al.* 2008); spring flows will decrease because of reduced or earlier snowmelt, and winter flows will increase. In regions with little snowfall, runoff

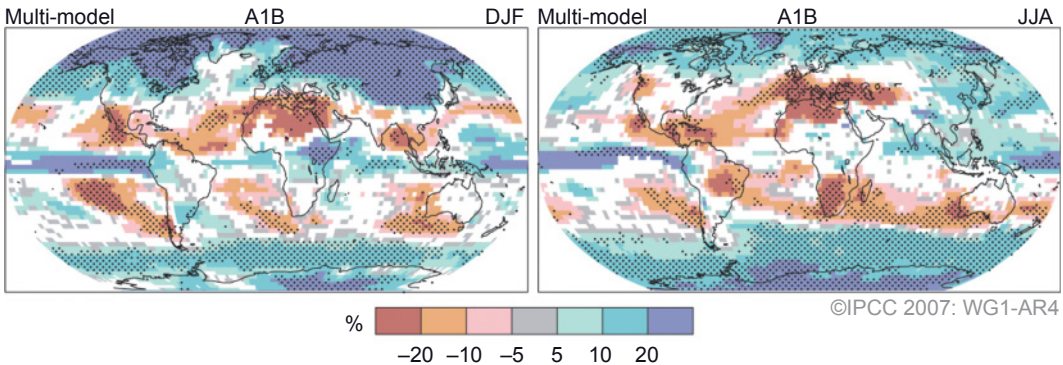


Figure 16.2 Relative changes in precipitation (in percent) for the period 2090–2099, relative to 1980–1999. Values are multi-model averages based on the SRES A1B scenario for December to February (left) and June to August (right). White areas are where less than 66% of the models agree in the sign of the change and stippled areas are where more than 90% of the models agree in the sign of the change (Figure SPM.7 in IPCC 2007).

changes are much more dependent on rainfall than temperature. Most studies in such regions project increased seasonal amplitude of flow regime, exacerbated perhaps by extended dry periods (Bates *et al.* 2008).

16.3 Upstream river migration and spawning

With the onset of sexual maturity, Atlantic salmon migrate back from the oceanic feeding areas to their natal river to spawn. Most re-enter fresh water between May and October but in the British Isles, for example, and especially Scotland, salmon return in all months (Klemetsen *et al.* 2003; Thorstad *et al.* 2011 [Chapter 1]), and some multi-sea-winter (MSW) ‘spring’ salmon may spend up to a year in fresh water before spawning. Most adults therefore will spend at least the autumn and perhaps also the summer months in fresh water prior to spawning, and accordingly are likely to encounter increased temperatures and decreased flows associated with climate warming. These changes will be most severe at the present southern limits of salmon distribution in the USA, France and the Iberian Peninsula.

River flow is the most frequently reported factor controlling upstream migration rates, but its effects are often modulated by water temperature, cloud cover, atmospheric pressure, turbidity and water quality, as well as wind and tide (Banks 1969; Thorstad *et al.* 2011 [Chapter 1]). Increased water discharge stimulates river entry of salmon (Banks 1969; Thorstad *et al.* 2008) but, once they are ascending the river, discharge effects seem generally limited in the main stems of relatively large rivers (Thorstad *et al.* 2008). Flow is still an important stimulant to upstream migration in relatively small rivers (Solomon *et al.* 1999), but adults can show plastic responses to suboptimal hydrological events as spawning time approaches (e.g. Tetzlaff *et al.* 2005). For natural or artificial physical obstacles, flow may have to be within a certain and site-specific range to allow salmon to ascend (Huntsman 1948; Banks 1969; Jensen *et al.* 1986; Thorstad *et al.* 2008) so migratory progression may be delayed by several weeks.

Temperature also influences adult ascent. Elliott & Hurley (2003) reported the thermal growth maximum for Atlantic salmon as 24.6°C and the upper incipient lethal temperature

(survival over 7d) is 27.8°C (Garside 1973; Elliott 1991), with energy expenditure during migration increasing rapidly with temperature. Swimming capabilities are reduced both at lower and higher suboptimal temperatures (Beamish 1978; Booth *et al.* 1996) and below ~5–8°C even small obstacles may prove difficult or impossible to ascend (Pyefinch 1955; Jensen *et al.* 1989a; Thorstad *et al.* 2008). Where fish are temporarily confined below obstacles, temperature- and/or flow-related hindrance of migration may enhance disease transmission (e.g. furunculosis; Johnsen & Jensen 1994). Excessive temperatures may also decrease the intensity of upward migration of the population. Elson (1969) showed ascent in the Miramichi River (eastern Canada) to increase with river temperature up to 22°C, and then decrease, whilst for the River Dee, Wales, Alabaster (1990) estimated the rate of migration to be halved at a mean weekly maximum of 19.5°C, and reduced to about a quarter at 25.5°C.

Model predictions are that earlier springtime snowmelt will probably be accompanied by reduced peak spring flow and warmer rivers, both of which might facilitate ascent of obstacles in early summer. This apparently beneficial seasonal advance in migration might, however, be countered by low summer flows and/or excessive temperatures. Moreover, fish which have progressed early in the season to shallower upper reaches may run excessive mortality risk if they lack access to deeper refuge pools during summer drought. This may pertain throughout the distributional range, but is likely to be most pronounced in southern Europe. The potential is therefore very real, in specific rivers, for seasonally variable flow and temperature to compromise survivorship, or prevent fish from reaching suitable spawning areas in time in the autumn (Thorstad *et al.* 2008; but see also Tetzlaff *et al.* 2005). In small rivers with average annual discharge of <40 m³ s⁻¹, body length and sea-age at maturity increase with discharge (Jonsson *et al.* 1991). This may be due to flow regime comprising an intense selection against large fish in small rivers with reduced flow during the migration and spawning seasons.

16.4 Eggs and alevins

Fry emergence time is effectively set by spawning date and the temperature-dependent rate of embryo and alevin development (Crisp 1981, 1988; Elliott *et al.* 1987; Jensen *et al.* 1989b; Beacham & Murray 1990). Spawning dates are probably adapted to present thermal and flow regimes such that emergence timing is optimised by intense selection (Morrison & Smith 1986; Heggberget 1988; Jensen *et al.* 1991). Marked changes in either flow or temperature during early development may therefore cause a mismatch between emergence and environmental conditions, resulting in increased egg and early juvenile mortality (Jensen *et al.* 1991). Nonetheless, ecologically important within- and between-year variability in hydrological and thermal regime can be overlooked when focusing on annual averages (e.g. Tetzlaff *et al.* 2005; Mather *et al.* 2008). Brief, intense abiotic disturbances (e.g. exceptional temperatures or spate events) may have cascading, even catastrophic, long-term consequences for multiple year-classes of juveniles, but their incidence or likelihood cannot yet be formally incorporated into future climate predictions based upon seasonal or annual averages.

Notwithstanding these facts, a general increase in winter temperatures would accelerate development and perhaps result in earlier emergence from the gravel. Increased metabolic demands on yolk sac reserves by higher winter temperatures may, however, result in smaller

or poorer-quality alevins at a particularly vulnerable phase in the life cycle (Einum & Fleming 2000). The net result of such shifts in optima for juvenile emergence might be increased mortality, and because of elevated winter flows this could be exacerbated by more frequent and intense episodes of gravel erosion and transport (Jensen & Johnsen 1999).

16.5 Parr life

Atlantic salmon typically undergo smoltification after 1–4 years in fresh water though in some locations a proportion of male parr mature precociously and may fertilise adult eggs (e.g. Gage *et al.* 1995; Martinez *et al.* 2000). Moreover, precocious male parr may be iteroparous by reproducing again either as parr or as anadromous adults. Parr life duration tends to increase both with latitude and elevation and these probably are, respectively, direct and indirect responses to the interactive effects of freshwater temperatures and prey availability. Parr survival and growth will similarly be influenced by hydrology-related changes in the aquatic community. Given sufficient egg deposition, freshwater survival is usually density-dependent (Symons 1979), and the carrying capacity to produce smolts varies from river to river depending on quantity and quality of habitat and parr growth rates.

Atlantic salmon are remarkably eurythermal (Elliott 1991) and feeding and growth typically are constrained to 4.9–26.7°C, but this narrows as food availability declines and growth therefore is determined primarily by prey, temperature and fish size (Brett *et al.* 1969; Elliott & Hurley 2003; Elliott 1994). At maximum ration, parr grow optimally at 16–20°C (Jonsson *et al.* 2001; Elliott & Hurley 2003; Forseth *et al.* 2011 [Chapter 6]); but growth is also seasonally constrained with, for example, higher rates at the same temperature in early summer (Jensen 2003; Bacon *et al.* 2005). Climate effects on juvenile growth are therefore complex and vary with latitude, elevation, prey availability, and the overall riverine thermal (e.g. Fig. 16.3) and hydrological regime. It is especially at the southern and northern

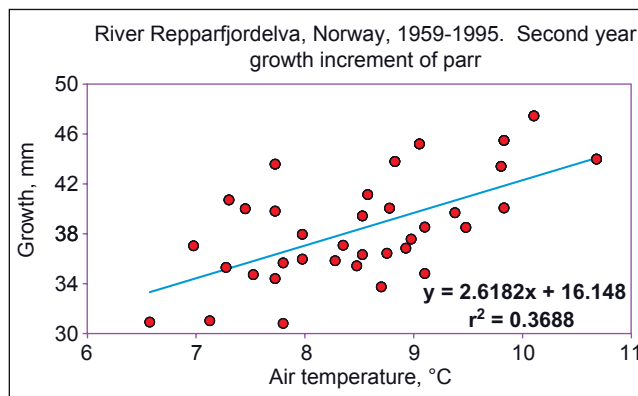


Figure 16.3 Relationship between summer (June–September) air temperature at Helnes Fyr (71° 4' N, 26° 9' E) and growth increment of Atlantic salmon parr in their second year in fresh water from the River Repparfjordelva in northern Norway (70° 27' N, 24° 20' E). Data derived from scale samples ($n = 5305$, $p < 0.001$) collected in the river over the period 1959–1995.

distributional limits that parr growth may be retarded and mortality increased because of increased periods of seasonally unfavourable temperatures, and the consequential seasonal loss of habitat and/or reduction in benthic production (Elliott 1994). Increased water temperatures also may reinforce both 'bottom-up' (resource availability) and 'top-down' (predator) population control, and interact with increases in competitor populations as more southern species extend northwards. By the same token, at the poleward limits, new habitat could be opened to salmon as temperature regimes become more amenable and benthic productivity increases; parr growth rate there is expected to increase because of more favourable summer temperatures and an extended growing season.

Under a warming scenario, parr winter survivorship might increase because of elevated flow and water temperatures. In northern rivers with winter snow cover, discharge is usually lowest in winter, and the area covered by water is probably limiting for benthic invertebrate production, as well as restricting juvenile refuges. Parr typically become photonegative and hide beneath rocks during winter and refuge availability is important for survival (Rimmer *et al.* 1983; Hvidsten 1993). But because parr energetic deficiencies are also assumed to be an important cause of winter mortality, climate-driven changes in ice-breaks or ice removal may significantly affect survivorship, particularly for northern populations (Cunjak *et al.* 1998; Finstad *et al.* 2004). For North American stocks, Friedland *et al.* (2003a) examined changes in temperature and precipitation patterns relevant to the freshwater rearing areas, but failed to find any pattern that could be related to adult abundance. It is difficult to generalise, however: for example, winter and summer floods in small streams can result in major re-distributions of gravel and Cunjak *et al.* (1998) found positive correlations between winter stream discharge and egg/juvenile survivorship. Thus, despite these negative winter impacts, summer abundances of juveniles generally were correlated positively with winter streamflow and habitat availability under ice. Notwithstanding negative density-independent impacts of extreme flows and severe icing on survivorship (e.g. Cunjak *et al.* 1998), over-winter survival of parr typically is strongly size- and growth-dependent, just as for post-smolts in the marine environment (Section 16.11).

On balance, and except for southernmost populations, freshwater growth of parr might increase, and average age at smoltification, which is clearly growth-related (Section 16.8), might reduce. Returning adult 1SW fish in the North Esk River, Scotland, have shown a steady and recent reduction in mean river age (Fig. 16.4) which may be a response of juveniles to milder recent winters in fresh water, or to seasonal changes of return migration timing of 1SW adults of contrasting river age. Because these data are temporally constrained by the legal netting season (31 August close), a reduction in overall river age over time might arise from 1SW adults of older smolt age returning later, after the netting season has closed. The shift is from three- to two-year-old smolts, and is not due to an increase in frequency of one-year-olds; if the downward progression in river age is due to changes in smoltification, this perhaps indicates the strength of environmental constraints on parr at this latitude growing sufficiently rapidly to undergo smoltification within only one year of emergence. Temperature effects on smoltification may be exerted in a narrow time window: for the River Imsa, southern Norway, winter (February–April) freshwater temperatures and flow during the embryonic phase explained a significant proportion (>30%) of the variance in subsequent parr growth rate and age at smoltification (Jonsson *et al.* 2005). Notwithstanding density-dependent effects, mild and wet winters there led to faster parr growth and earlier age at smolting.

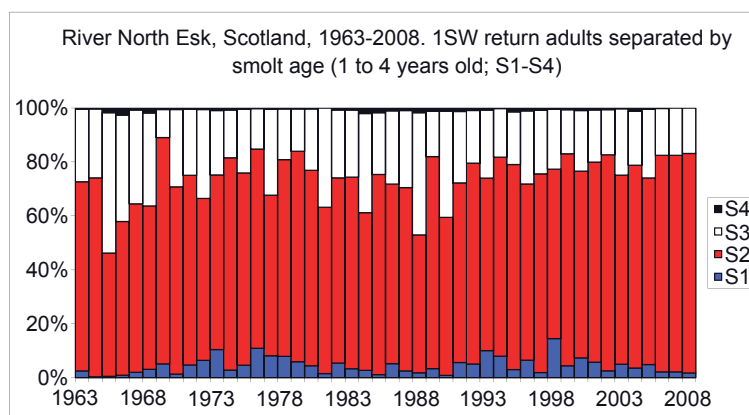


Figure 16.4 Proportionality of smolt ages (1–4 years old; S1–S4) of returning adult 1SW salmon, River North Esk, Scotland (56° 45' N, 2° 26' W), May–August inclusive. Data derived from scale readings (annual 1SW sample sizes ranging from 226 (1983) to 1589 (1998) fish). S3 smolts show a significant decline ($r = -0.389$, $p = 0.007$) in relative frequency over the 46 years.

Annual mortality of parr is estimated at 40–60% (Elson 1975; Symons 1979) and both temperature and alevin density have significant, but largely independent, effects on parr densities and ultimate smolt output (Power & Power 1994). Smolt population production is inversely related to smolt age (Symons, 1979), and it is important to emphasise that smoltification is a strictly seasonal, annual event: the ‘decision’ to not undergo smoltification commits the parr to another year in fresh water and its associated growth opportunities and mortality risks. Similarly, the ultimate fitness of parr undergoing younger smoltification is dependent largely upon their size and ability to osmoregulate and feed effectively on entering sea water (Sections 16.6, 16.11). Overall, our expectation is that parr and smolt production will increase in most northern rivers as freshwater opportunities improve and productivity increases. Furthermore, a northward distributional expansion might compensate, or even exceed, the predicted reductions and extinctions of populations in the south.

16.6 Smolt migration

Smoltification is a size-related, endocrine-controlled developmental event that physiologically pre-adapts salmon for migration to sea water (McCormick *et al.* 1998) in spring and early summer, generally between April and June. Although both photoperiod (Bjornsson 1997) and temperature (Staurnes *et al.* 1994) have been proposed as the primary stimulus for smoltification, the consensus is that photoperiod is the major cue determining the broad ‘window’ for smolt development, with temperature modulating the rate (Handeland *et al.* 2004). This is likely to be because of the invariance of seasonal photoperiod at a given locality as a predictor of environmental change year-on-year (Bradshaw & Holzapfel 2007) for any such critical life cycle ‘go/no go’ events. Spring arrives later at higher latitudes and temperatures often change less rapidly than photoperiod; hence, for springtime migration, photoperiod provides the more reliable indicator of season and smoltification typically occurs later the further north.

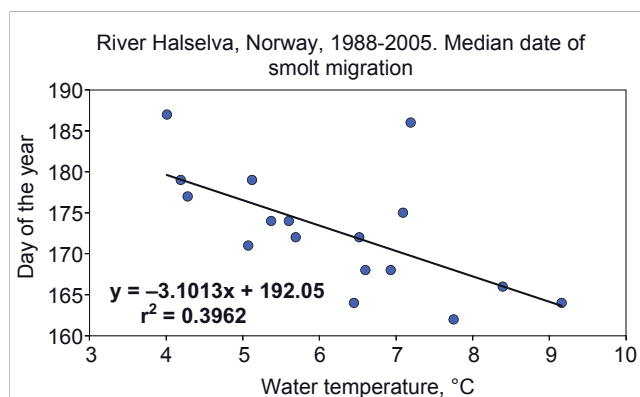


Figure 16.5 Relationship between average water temperature in June in the River Halselva in northern Norway (70°N, 23°E) and the median date (Day of the year) for Atlantic salmon smolts descending the smolt trap (just above the head of tide). Data from the period 1988–2005 ($n = 18\,168$, $p < 0.01$).

Timing of seaward migration is modulated by temperature and flow, and perhaps the lunar cycle (Wedemeyer *et al.* 1980; McCormick *et al.* 1998; Jutila *et al.* 2005; Thorstad *et al.* 2011 [Chapter 1]; Fig. 16.5). However, these may vary in importance and stimulate migration differentially, perhaps reflecting population adaptations to ensure optimal timing of migration in terms of both subsequent marine survival and growth. A key issue concerning predicted climate is the potential for smolts to encounter severe phenotype/environment mismatch if sea temperatures at first migration deviate significantly from the optimum for physiological adaptation to a hypersaline environment. The most important physiological change is the development of salinity tolerance manifest in the key osmoregulatory organs – the gills, kidney and gut. Growth hormone (GH) and cortisol are the primary hormonal control mechanisms governing smoltification (Bjornsson 1997), although insulin-like growth factor (IGF-1), prolactin and thyroid hormones have also been implicated. These may show interactions (McCormick *et al.* 2000, 2007), modulated by photoperiod and temperature, which potentially have critical effects both on smoltification itself and migration timing (Hvidsten *et al.* 1995; Zydlewski *et al.* 2005).

Smolts are subject to heavy mortality in the river and estuary (Ward & Hvidsten 2011 [Chapter 8]), and to avoid predation they typically descend in shoals and often at night (Hvidsten *et al.* 1995; McCormick *et al.* 1998). High water discharge at experimental release of smolts improves survival to adulthood, probably because of reduced early mortality (Hvidsten & Hansen 1988). Delayed downstream migration can also result in decreased survival to adulthood, and successive smolt releases have demonstrated that only a brief period was optimal for emigration (Hansen & Jonsson 1989). Increased post-smolt mortality due to low salinity tolerance occurs at low sea temperatures (Sigholt & Finstad 1990) and populations seem adapted to enter the sea when temperatures reach 8 °C or higher (Hvidsten *et al.* 1998). On entry to sea water there is a rapid reversal of the osmotic and ionic gradients, resulting in increased water loss and a gain in ions across the gills (osmotic shock). A temperature-dependent response has been reported both for acute hyperosmotic shock and

the longer stabilisation period associated with seawater acclimation (Handeland *et al.* 2000, 2003). These changes have been associated with decreased post-smolt growth performance (Handeland *et al.* 1998, 2000, 2003, 2004), and increased mortality (Sigholt & Finstad 1990), and therefore have clear implications for ultimate adult return rates. If smolts are prevented from migrating, a partial re-adaptation to fresh water occurs – a process known as desmoltification or parr revision. Relatively little is known of its control in Atlantic salmon but high temperatures accelerate the loss of hypo-osmoregulatory capacity in fresh water (Duston *et al.* 1991; Stefansson *et al.* 1998; Handeland *et al.* 2004). Temperature influences both the development and loss of smolt characteristics, and post-smolt growth performance in sea water is markedly affected by even relatively small differences in the extent and timing of smolt development caused by environmental manipulation (Handeland *et al.* 2004). Nonetheless, Atlantic salmon smolts are rather eurythermal, with high growth rates at 10–18 °C (Handeland *et al.* 2008), although it should be noted that the inflection of the temperature curve is based on only the one data point at a high temperature (18 °C).

Predictions of earlier spring snowmelt and temperature rise in most high-latitude rivers will result in stable but low freshwater temperatures in early spring, followed by a more rapid rise in mid to late spring. Higher temperatures may advance the smolt run timing but photoperiod will presumably also restrict advancement. Jutila *et al.* (2005) reported the main smolt run in a northern Baltic river to be abbreviated in years when migration was delayed by freshwater conditions, and they also showed that early summer SST which is either too low (<9 °C) or too high (>12 °C) at entry was detrimental to post-smolt survival. Because very early post-smolt mortality is typically high (Klemetsen *et al.* 2003), the implications are that timing of seawater entry has consequences for metabolic costs, physiological stress, prey availability and the likelihood of predation (Hansen & Quinn 1998). All will be impacted by climate change and reflected ultimately in year-class survivorship and subsequent return of spawning adults.

Irrespective of temperature, the other important modulator of smolt migration in some rivers is water flow (Klemetsen *et al.* 2003). Where peak spring flows decrease, the run may become more dispersed over time and shoals smaller in size. Either of these occurrences will result in increased exposure to predation. Any marked change in coastal SST having an additional and detrimental effect on early post-smolt survival will, therefore, have severe impacts on marine survivorship and adult abundances. It is important to emphasise that thermal buffering of the oceanic environment generally results in a comparatively slow rate of spring warming (cf. fresh water), and coastal waters may therefore remain conducive to smolts later in the spring. If, however, for given populations or geographic regions, freshwater and coastal temperatures become non-optimal for smolt migration and post-smolt survival then salmon are confronted with major selective and adaptive challenges. That salmon populations have successfully adapted to climate change over past glaciation cycles is not in doubt (e.g. Verspoor *et al.* 2002; Saisa *et al.* 2005; Tonteri *et al.* 2005), and under present scenarios smoltification and migration might have to advance. Of immediate concern for stock conservation is the rate of evolvability of change in the fish response to photoperiod and temperature *versus* the rate of climate-driven environmental change. Naish & Hard (2008) concluded that the critical rate of population adaptation to a shifting optimum (such as time to smoltify) is restricted by: (1) the effective population size (N_e), (2) genetic variability, and (3) the rate of environmental change that determines the selection differential. Of

course, not all smolts within a population migrate on the same day and a key issue is just how much of the smoltification process and its timing is under genetic control and how much is an expression of between-individual variation in behaviour or phenotypic plasticity.

This particular problem may be most acute in North America, because of the cooling effects of the Labrador Current. Rivers there are usually much warmer than the sea in springtime and a striking response is the production of smolts up to eight years old and much larger (typically >20 cm) than elsewhere (Klemetsen *et al.* 2003): this is most pronounced at the northernmost limit of salmon at Ungava Bay, Quebec (Power 1969). The full plasticity of salmon life-history is displayed there, with freshwater resident populations, individuals migrating to estuarine conditions only, and others undertaking estuary-to-sea and the typical large-scale marine migrations all being represented (Power *et al.* 1987). A critical factor here is that temperatures as low as 1°C may be encountered during smolt emigration, and these are well below the optimum for feeding and growth. Along the Labrador and Newfoundland coasts, temperatures are predicted to increase more in fresh water than in the marine environment (Fig. 16.1), perhaps resulting in earlier smolt emigration, and possibly into even lower SSTs than at present.

16.7 Geographical distribution and recent trends in adult stock abundance

The extent to which salmon populations can show short-term and multi-decadal fluctuations is amply illustrated for a single Scottish river population by Martin & Mitchell (1985; their Figs. 1 & 2), and by Lajus *et al.* (2007) for multiple locations in the region of the White and Barents seas. Understanding the relative importance of freshwater and marine influences and their potential interaction is central to managing salmon populations. In acknowledging that these environments are intimately linked by climate, and that marine conditions ultimately determine returning adult abundances, Bisbal & McConnaha (1998) urged an integrated and holistic approach to salmon management, and specifically so in response to ocean climate change.

Atlantic salmon occur naturally on both sides of the North Atlantic (MacCrimmon & Gots 1979), but genetic analyses (e.g. Wennevik *et al.* 2004; Verspoor *et al.* 2005) indicate that European and North American stocks are sufficiently diverged to be designated as subspecies. The North American native range was northward from the Hudson River (41°N, New York State) to the Leaf River, Ungava Bay (60°N, Quebec) (Lee & Power 1976; MacCrimmon & Gots 1979). However, salmon now are extinct in several southern rivers, and the present US range is limited to Gulf of Maine rivers (WWF 2001; Saunders *et al.* 2006). In Greenland, salmon run the Kapitsigdlit River at the head of Godthåp Fjord (64°N). The rivers of James Bay and eastern Hudson Bay (Canada) include freshwater habitats and temperature regimes similar to Ungava Bay, but Hudson Strait and Hudson Bay SST attain only 4.5 and 7.0°C, respectively; this probably explains the absence of salmon populations further north. In Europe, the distribution originally ranged from the Douro River (41°N 8°W; Portugal) to the Pechora River (69°N 65°E; northwest Russia), but includes rivers as far north as 71°N in northernmost Norway. However, some southernmost European populations are now lost, with only one of eight Portuguese populations (River Minato) remaining and only 14 of 43 historic populations extant in Spain and several of those in critical

condition (WWF 2001). Salmon also are widely distributed in Iceland, the British Isles, and in regions draining to the Baltic Sea (MacCrimmon & Gots 1979).

Given expectations of climate change and its impact on freshwater temperatures (Solomon *et al.* 2007), salmon distribution is likely to shift northwards. Over the next century, river temperatures at the southern limits on both sides of the Atlantic are expected to occasionally exceed the 27.8°C upper incipient lethal temperature. Extinction of the southernmost European populations – as far north as southern England – has to be considered likely because of summer temperature increases and more frequent summer droughts (Bates *et al.* 2008); the remaining southern European populations are expected to be diminished. Similarly, populations will probably establish further east in northern Russia. For North America, it is likely that the southernmost populations will be under the greatest threat of extinction (Reist *et al.* 2006b) but because the present northerly extent in Canada seems to be limited by cold sea water, and sea temperatures there will probably stay low (Fig. 16.1), it is not expected that the northern range will increase to any notable extent. Nonetheless, Reist *et al.* (2006b) have predicted an increase in productivity of Ungava Bay rivers as the extent and duration of sea-ice cover diminishes.

The oceanic distribution of Atlantic salmon is still not well known, but the limited information indicates that salmon are not evenly distributed (Hansen & Quinn 1998). North American fish generally remain in the western North Atlantic, including the Bay of Fundy, Labrador Sea and coasts of southern Greenland, although some may migrate to the eastern North Atlantic (Ritter 1989; Narayanan *et al.* 1995; Holst *et al.* 2000). A relatively large proportion of European MSW salmon range as far as the western North Atlantic (Hansen & Quinn 1998). Moreover, European salmon, especially from the more southerly rivers, are found at some stage of their marine migration throughout wide areas of the Norwegian Sea and the eastern North Atlantic (Holst *et al.* 2000; Holm *et al.* 2004). Less information exists about the populations from northern Norway, Finland and Russia (Holm *et al.* 2004), but contrasting growth patterns indicate that populations from the White Sea basin may utilise feeding areas quite distinct from those that migrate directly into the Barents Sea and Atlantic Ocean (e.g. Jensen *et al.* 1999).

Recent analyses of scale readings, survivorship and growth history for 1SW adults from eastern Canada indicate possible population shifts in migration destination (open western North Atlantic *versus* inner Bay of Fundy) since the turn of the millennium (Hubley *et al.* 2008). Similarly, there are recent indications from untagged captures (Berge *et al.* 2005) and tag retrievals in the eastern North Atlantic (Rikardsen *et al.* 2008) that the marine distribution of salmon might be expanding northwards. These may be harbingers of more general northward extensions of salmon migrations, and this trend is expected to develop with increasing SST and concomitant changes in the biogeographic distribution of epipelagic prey. Additional eastward expansions, further into the Barents Sea and into the Kara Sea or even beyond, also can be predicted. There are historical precedents for the latter: during the 1930s salmon were present in the Kara Sea for some years, apparently as a consequence of gradual warming over the period 1919–38. This was enhanced by a strong inflow of warm Atlantic water, and salmon spawned in the Kara River for several years from 1932 onwards (Jensen 1939; Berg 1948).

One major environmental factor which will not change with climate warming, and which is critical to the success of salmon in their marine environment, is the seasonally varying photoperiod. Atlantic salmon are generalist, opportunistic predators of zooplankton and

nekton at the ocean surface (Hansen & Quinn 1998; Jacobsen & Hansen 2000; Sturlaugsson 2000; Haugland *et al.* 2006; Rikardsen & Dempson 2011 [Chapter 5]). But they are also visual predators, and perhaps the greatest weakness in our understanding of salmon diet lies in the quantification of the abundance and local availability of particular prey species and the extent to which salmon actively choose or prefer given taxa at a particular place or time. Whilst at very high latitude salmon at sea will encounter 24-hour daylength during summer months, in winter they confront the opposite challenge. Even if zooplankton prey populations shift much further to the north, but still remain within the migratory potential of salmon, the ability of fish to forage effectively at very low ambient light levels may well constrain the latitudinal extent of salmon migration. Climate-driven poleward shifts in epipelagic prey may, therefore, result in salmon food resources effectively moving beyond their reach at least through late autumn to early spring.

16.8 Ocean climate influences on run-timing and adult abundance/recruitment

Studies of climate variability on marine survivorship and abundances of Atlantic salmon have used both direct measures of temperature and derived variables representing the dynamics of ocean thermal conditions. Direct physiological effects of temperature have often been inferred, especially for smolts first entering sea water (e.g. Narayanan *et al.* 1995; Kallio-Nyberg *et al.* 2004; Jutila *et al.* 2005; Section 16.6), and the importance of indirect effects – perhaps manifest as ‘bottom-up’ impacts through alterations in prey availability – has long been suspected or observed (e.g. Todd *et al.* 2008). For example, Rose (2005) showed how small keystone forage fish species such as herring (*Clupea harengus*) and capelin (*Mallotus villosus*), which can be important prey for Atlantic salmon (e.g. Mills 1989; Kallio-Nyberg *et al.* 2004; Haugland *et al.* 2006; Rikardsen & Dempson 2011 [Chapter 5]), may respond strongly and rapidly to changes in ocean climate because of their broad physiological limits and potential for rapid population growth.

Long-term variation, both in run-timing and the relative strengths of the 1SW and MSW maturity groupings, are characteristic of Atlantic salmon populations (e.g. Narayanan *et al.* 1995) and may comprise a fundamental population response to climate change. For example, over the past 60 years in the River Dee, Wales, Aprahamian *et al.* (2008) showed that most adults now re-enter between August and October as opposed to prior to June. This coincided with a shift from MSW domination prior to the 1980s to the present prevalence of the 1SW maturity grouping. Furthermore, River Dee juveniles now are larger and smolts younger, with average river age having declined from ~2 years prior to the 1980s to ~1.6 years (see also Fig. 16.4). For three catchments in Ireland, Quinn *et al.* (2006) analysed catch records dating back 3–7 decades and reported a similar pattern to the River Dee, and most notably a reduction in the abundance of early-running MSW fish. Notwithstanding the difficulties in using catch records as measures or indicators of population abundance (e.g. Thorley *et al.* 2005) it is clear that major changes both in the freshwater and marine habitats are implicated in these patterns, and such responses are widespread among the European stock (ICES 2008).

The main derived oceanic parameter used in analyses of marine survivorship and abundance has been ‘thermal habitat’ – the area of sea surface associated with a specific

temperature range. The first attempt to relate ocean climate to European salmon focused on adult recruitment and spring thermal habitat. That analysis was seasonally restricted due to the inadequacy of temperature databases and our limited understanding of post-smolt nursery habitats (Friedland *et al.* 1993). A relationship was, however, detected between a catch-based index of recruitment and springtime thermal habitat of 7–13 °C (Friedland *et al.* 1993). Because this index represented such a large portion of the eastern North Atlantic it was not clear whether the variation reflected a direct effect of temperature on European post-smolts, or simply climate co-variation with the recruitment pattern. Subsequently, Friedland *et al.* (1998) compared an age-disaggregated set of survival indices with a range of thermal habitat indices. They concluded that recruitment was related to eastern North Atlantic Ocean climate variation, but this offered only limited insight into the possible mechanisms of adult recruitment control. Direct analyses of SST, as opposed to thermal habitat, have been far more illustrative of the effect of change in ocean climate on adult abundances. Friedland *et al.* (2009) analysed the relationship between recruitment of European Atlantic salmon, as indexed by two river stocks, and monthly SST throughout the post-smolt year. Summer and early autumn SST for the post-smolt year correlated negatively with adult return rate, with the greatest correlative density within the same region of the Norwegian Sea identified as the post-smolt nursery by Holm *et al.* (2000).

A similar progression of analyses for the North American stock complex was less congruous. Early studies utilising derived thermal habitat variables, or variables indicating the spatial distribution of habitat, suggested the winter following smolt migration to be the critical period of survival (Reddin 1988; Ritter 1989). Post-smolt migration patterns were apparently changing in response to ocean temperature and, as a result, predation pressure on post-smolts varied (Ritter 1989). Reddin & Friedland (1993) computed the winter thermal habitat by relating catch rate at temperature to the temperature fields of the western North Atlantic and found that North American stock size was positively correlated. A systematic search for correlates to a stock index revealed winter thermal habitat variation as the strongest candidate (Friedland *et al.* 1993): when thermal habitat in the Labrador Sea was constricted then over-winter survival was poor. Atlantic salmon attain a relatively large size by their first winter and have outgrown vulnerability to most predators that affect them earlier in the post-smolt year (e.g. Allen *et al.* 1972; Narayanan *et al.* 1995). Thus, although winter SSTs appeared to provide the most robust correlates to stock size, the actual survival mechanisms were not obvious and moreover these environmental correlates have not held because survival of North American salmon has continued to be poor over the past decade.

Early analyses of thermal habitat did not include areas such as the Gulf of St Lawrence, and perhaps did not adequately test the effect of coastal environmental variability on post-smolts during their first months at sea. Using improved data sources, Friedland *et al.* (2003a, b) found that the abundance of North American stocks is indeed associated with climate variability in the Gulf of St Lawrence and that post-smolts are subject to differing mortality risks associated with variation in SST during the first month at sea. As for Europe, increasing SSTs in the post-smolt nursery habitats are associated with declining survivorship. The main contrast between the thermal effects on European and North American stocks appears to be one of timing; the negative correlation between SST and survival appear to be focused during spring in North America and during summer in Europe.

16.9 Migration, diurnal behaviour and changes in the epipelagic food web

Because salmon are generalist, opportunistic predators any long-term trends – or climate-driven responses – in survivorship, population size or individual condition factor are not likely to be attributable simply to fluctuations in a single, key prey species but probably are more broadly indicative of major perturbations of ocean conditions, such as the regime shifts reported for the north Pacific (e.g. Beamish *et al.* 1999; Mantua & Hare 2002; Section 16.10). Sturlaugsson & Thorisson (1997) found that tagged salmon were located primarily at the surface during daytime and underwent their deepest dives (to >100 m) at night, but whether or not night-time dives relate to diurnal patterns in foraging behaviour remains unknown. By contrast, from data storage tag (DST) records recovered from post-smolts, Reddin *et al.* (2006) deduced that they avoided avian predators by positioning themselves deeper in the water column by day. Notwithstanding these contradictions, and assuming that tagged smolts behave in a representative manner, salmon evidently spend most time at the ocean surface and variation in SST and epipelagic prey availability will be key influences on their growth and survivorship. There have been changes in the food web dynamics of the oceanic nursery habitats supporting European Atlantic salmon that are concordant with the observed changes in the physical habitat. Furthermore, changes in North Atlantic secondary production are reflected in dominance shifts in zooplankton species (e.g. Reid & Beaugrand 2002; Taylor 2002; Beaugrand *et al.* 2002; Beaugrand & Ibañez 2004). The distribution of marine fishes has also changed, with most exploited and unexploited species undergoing a shift in mean latitude or in depth (Perry *et al.* 2005).

Beaugrand & Reid (2003) correlated change in the plankton community to the abundance of European salmon, which suggests a specific linkage between diet and growth, although any linkage would most likely be related to conditions specifically affecting the preferred forage of salmon post-smolts (Haugland *et al.* 2006). The trophic shifts in the Norwegian Sea do show some level of complementary change in prey taxa directly utilised by salmon *versus* those affecting other species upon which salmon may feed. Friedland *et al.* (2009) reported a positive correlation between salmon survival and the summer abundance of euphausiid krill in the Norwegian Sea, a taxon directly utilised by post-smolts (Jacobsen & Hansen 2000). But they also found both positive and negative correlations with other taxa that would not be directly utilised by post-smolts. In the western North Atlantic there have also been marked ecosystem shifts. Patterns of primary production and the structure of continental shelf food webs have changed in association with thermal conditions (Zwanenburg *et al.* 2002), and changes in water column stability associated with Arctic ice melt (Choi *et al.* 2004). Notably, what previously were gadoid-dominated ecosystems are now dominated by varying communities of pelagic and invertebrate species (Frank *et al.* 2005). There have, however, been no studies examining the possible impact of this ecosystem change on the potential forage base or the predator fields that are likely to impact Atlantic salmon in North America.

Salmon stocks both in Europe and North America have experienced declines in recent decades (e.g. Jonsson & Jonsson 2004a; but see also Niemelä *et al.* 2004 for northern Finland) that support the contention that marine survival is to some degree a response to a

shared set of climate drivers. The historical pattern for European (Friedland *et al.* 2009) and North American (Friedland *et al.* 2003a) stocks is characterised by a peak in marine survival during the 1970s, followed by three decades of progressively lower abundances. The nature of any climate-related teleconnections between the two stock complexes has yet to be studied, but emerging hypotheses of recruitment control tend to focus on temperature impacts on epipelagic community structure and phenology. Abundance trends within the respective stock complexes also suggest that climate effects are not uniform over the latitudinal range of the species (ICES 2008).

16.10 Do changes in North Atlantic zooplankton communities comprise regime shifts?

Large-scale ecological regime shifts occur when the ecosystem ‘flips over’ from one apparently stable state to another. Such changes can be rapid and comprise a non-linear response to key variables (e.g. temperature) exceeding a threshold level (e.g. Scheffer & Carpenter 2003). A central feature of these phenomena is that the initial ecosystem state is not necessarily re-attained as the key variable reverts to its previous level. The possibility of recent regime shifts in the epipelagic ecosystem, which may be driving indirect responses of salmon stocks, is perhaps best assessed from zooplankton and nekton studies not necessarily focused on salmon. For example, Frederiksen *et al.* (2006) emphasised the primary importance of ‘bottom-up’ regulation (which itself is largely under climate control) over ‘top-down’ (natural and fishery predation) control of the North Sea pelagic ecosystem. Their analysis centred on the abundance of keystone species, such as sandeel (*Ammodytes marinus*), which is itself a key prey organism for higher consumers (including salmonids), and this clearly has regulatory effects on predatory seabird and fish populations. Beaugrand *et al.* (2002) and Reid & Beaugrand (2002) related large-scale recent changes in calanoid copepod distributions in the eastern North Atlantic to the increasing trends in Northern Hemisphere temperatures and the North Atlantic Oscillation (NAO; Section 16.14). Although no suitably comprehensive or long-term zooplankton data are available for the entire salmon post-smolt habitat throughout the Norwegian Sea, these and other studies of both the eastern and western North Atlantic (e.g. Beaugrand & Reid 2003; Beaugrand 2004; Beaugrand *et al.* 2008) have shown that major ecological changes have occurred in recent decades.

As a generalisation, in the western North Atlantic Arctic zooplankton species have spread southwards, whereas in the warmer water of the eastern North Atlantic, southern species have spread further north. For the North Sea, Beaugrand *et al.* (2008) report that the high sensitivity of biome boundaries has led to a recent plankton regime shift and these fundamental changes appear to correspond also with changes in fishery populations. These shifts have influenced the coupled benthic and pelagic foodwebs and, depending upon the specific indicator (Beaugrand 2004), 1984–85 and 1987–88 were the key periods of North Sea ecosystem transition. Although the topic is not without controversy (e.g. Taylor 2002), the weight of evidence does support the contention of these biotic changes comprising a regime shift (Beaugrand 2004), and these are very likely to be linked to the deteriorating performance of salmon populations at sea (Friedland *et al.* 2009).

16.11 Change in size and growth in the marine environment

Smolt size and post-smolt growth rates have been variously identified as influencing marine survival and adult recruitment (sections 16.6, 16.8), and both are likely to be influenced by climate change. In precedent, and largely influenced by data for hatchery stocks, researchers have considered that post-smolt mortality may be punctuated at first entry to sea water (McCormick *et al.* 1998), and hence critical to ultimate recruitment of maturing adults. Alternatively, if growth has a role to play, it may be manifest as size-mediated predation over a more protracted period; more rapid growth may result in lower mortality due to the ability of faster growing post-smolts to outgrow predation-vulnerable size ranges (e.g. Sogard 1997), especially in relation to seabirds (e.g. Narayanan *et al.* 1995). However, Friedland *et al.* (2006) could show no relationship between smolt size and initial marine growth, and for this reason perhaps size at ocean entry and post-smolt growth should be considered separately.

Size clearly is important in determining hatchery smolt survival (e.g. Kallio-Nyberg *et al.* 2004; Lacroix & Knox 2005), but its influence for wild smolts has been poorly studied and remains unclear. In the Baltic Sea, Jutila *et al.* (2005) and Kallio-Nyberg *et al.* (2004) found that the typically larger size of hatchery individuals may, to some extent, compensate for their origin in comparison to wild smolts. Friedland *et al.* (2009) report on data for two wild stocks monitored over a period of highly contrasting survival rates: for the River North Esk (Scotland), smolt size clearly had no influence on resultant survival rate, whereas for the River Figgjo (Norway), survival rate was correlated with size at sea entry.

The critical importance of post-smolt growth to survival emerged from an analysis of back-calculated growth increment data for the North Esk (Friedland *et al.* 2000); but its role in the marine survival of North American stocks remains unknown. Growth during the first year at sea apparently influenced adult return rates, but that analysis shed little light on the biological mechanism involved. Subsequent and more detailed analyses of post-smolt growth increment included seasonal disaggregation to allow for inferences about different parts of the post-smolt year. Similar multi-decadal patterns in post-smolt growth to those reported for the River North Esk were shown for stocks in Ireland (Peyronnet *et al.* 2007), Norway (McCarthy *et al.* 2008) and multiple locations across Europe (Friedland *et al.* 2009). These higher-resolution data now suggest that the first few summer months at sea define the critical period of growth-mediated post-smolt survival (McCarthy *et al.* 2008; Friedland *et al.* 2009; Section 16.8) and perhaps future analyses of climate impacts should focus on this period.

For North American stocks a rather different picture has emerged. For example, for the Margaree River stock (Nova Scotia, Canada), early marine growth had apparently increased over an extended period of stock decline (Friedland *et al.* 2005), whilst for the Miramichi River (Canada) smolt years of 1956–2003 there was no mirroring of the situation established for European stocks (Friedland *et al.* 2009). Specifically, the Miramichi River showed a negative correlation between post-smolt growth during the second month (5th–7th weeks) at sea and subsequent adult recruitment. Mortality which ultimately dictated return adult abundances was therefore apparently confined to a narrow time window and may be independent of ocean climate or early post-smolt growth conditions.

Because salmon populations are genetically structured, the likelihood is that not all stocks will respond in an identical manner to even marked environmental change. For example,

Jonsson & Jonsson (2007) found that different sea-age/maturity groupings in northern Norway showed differing post-smolt growth responses to ocean climate. That was in marked contrast to 1SW and 2SW fish studied by Friedland *et al.* (2000), which showed no differences in growth-mediated survival; but this may be explicable simply by these stocks representing 'northern' and 'southern' European components, which themselves typically exploit differing areas of the Norwegian Sea (Hansen & Jacobsen 2003). Given that post-smolt marine growth – perhaps focused during the first summer at sea – repeatedly emerges as a crucial correlate with survival and recruitment for European populations, the question arises as to whether salmon are displaying compensatory growth. Rapid, and compensatory, increase in growth rate clearly is possible for opportunistic generalist predators if their behaviour is sufficiently plastic to enable them to exploit locally variable prey resources (e.g. Kaeriyama *et al.* 2004 for *Oncorhynchus* spp.). This may, for example, be manifest in the deep dives periodically recorded for post-smolt Atlantic salmon with implanted DSTs (Section 16.9). Small increases in size during the early growth phase also provide opportunities for post-smolts to prey on a wider range of planktonic species. Thus early post-smolts may be restricted primarily to invertebrate zooplankton and fish larvae, but perhaps the transition to piscivory is crucial here (e.g. Haugland *et al.* 2006).

16.12 Adult somatic condition and lipid reserves: indicators of ocean climate deterioration?

Two independent time series of southern European 1SW adults (Todd *et al.* 2008) have shown a steady, marked and concordant decline in average somatic condition factor since the late 1990s. SST anomalies in the Norwegian Sea over the study period (1993–2006) showed a strong increase from the mid-1990s onwards, and fish mean length fluctuated but remained broadly stable. 2006 was, however, exceptional in showing adults returning at a significantly shorter length and disproportionately low weight. Analyses of SST implicated midwinter (January) anomalies in the Norwegian Sea as driving the final somatic condition of entire year-classes of 1SW adults returning to fresh water over the following summer months. The conclusion was that recent excessive ocean warming had exerted consistent and progressively detrimental indirect effects on body mass and lipid reserve accretion during those final months at sea. There have been pronounced changes in SST anomalies in the eastern North Atlantic since the 1970s (Beaugrand & Reid 2003) and marked changes in plankton communities over the past two decades (e.g. Beaugrand *et al.* 2002, 2008; Beaugrand & Reid 2003; Beaugrand 2004). These factors all point to radical and profound changes both in ocean climate and prey availability for post-smolt salmon. That mean length had more or less been maintained, yet overall somatic condition had progressively fallen since the late 1990s, is indicative of 1SW salmon presently being severely growth-compromised, to the extent that many essentially starve, during their final months at sea. Poor condition individuals appear to have been catabolising their lipid energy reserves before completion of their marine migration and ocean warming seems indirectly responsible in mediating changes in 'bottom-up' control of variation in salmon growth success. These findings are quite distinct from those discussed above in relation to growth-mediated survival of post-smolts during their first summer at sea, in that no connection has been sought between somatic condition and population survivorship or abundances.

16.13 Maturity schedules

Maturation control of Atlantic salmon is influenced both by genetic and environmental factors and their interaction (e.g. Friedland & Haas 1996; Thorpe *et al.* 1998; Jonsson & Jonsson 2007; Wright 2007), but their relative importance remains unclear. Feeding ceases during migratory return and the general evidence is that salmonid maturation is growth-related (e.g. Hutchings & Jones 1998; Morita & Fukuwaka 2007), is ultimately determined by successive hormonal inhibition, and that the ‘decision’ is linked to the individual’s energy status (lipid reserves) during critical periods of the year. From experimental analyses of juvenile maturation in fresh water, and observations of cultured salmon in aquaculture pens, Thorpe (1994, 2007) and Thorpe *et al.* (1998) formulated maturation as a genotype x environment interaction in which maturation has priority over somatic growth; the latter can be arrested annually, at critical times of year, in response to photoperiod and to stored energy reserves. If, in springtime, the individual’s lipid reserves exceed the threshold, or the current energy accretion rate exceeds a critical level, then the ‘decision’ is made to mature and return to fresh water. Should those conditions not be met then Thorpe’s model would dictate the fish remains at sea for at least a further year and becomes or remains part of the MSW stock component. From analysis of growth rate thresholds for multiple populations, Hutchings & Jones (1998) found that increased growth generally favoured earlier, but never delayed, maturity and that earlier maturity was favoured in response to reduced survival at sea. By contrast, Jonsson & Jonsson (2007) found for a range of river populations, spanning 11 degrees of latitude in Norway, that high growth rates in the early part of the first year at sea tended to lead to a relatively high age of maturity. Considerable among-population variation therefore exists in the determination of size and sea-age at maturity, and predicting climate change-related impacts inevitably will be complex.

It is of interest, however, that Thorpe’s endocrine/photoperiod/energy threshold model does not appear to conform to the above time series observations of declining condition factor and lipid reserves for 1SW salmon (Todd *et al.* 2008). Since the mid to late 1990s, southern European 1SW fish have continued to initiate maturation and return to spawn despite showing annually decreasing average somatic condition and exceptionally low lipid reserves. The individuals in the poorest condition were up to 30% underweight and had lipid reserves reduced by as much as 80% compared to full condition fish. Notwithstanding the possibly intense selective pressure in favour of early maturity in response to high marine mortality (Hutchings & Jones 1998), that such energetically impoverished individuals should continue to mature and return as 1SW fish can be reconciled with the above energetic model only if catabolism of reserves had occurred in the few weeks prior to summer return to coastal waters, and following Thorpe’s critical spring photoperiod ‘window’. But this seems unlikely, given that Kadri *et al.* (1995) recorded a daily weight loss rate of only 0.1% per day for 1SW cultured salmon held in tanks during the summer weeks following their cessation of feeding. The available evidence for these time series of wild 1SW adults points to an extended period of months of food limitation or starvation perhaps dating to midwinter, and almost certainly prior to a spring photoperiod maturation window.

Our understanding of abiotic and biotic factors influencing post-smolt marine growth and survivorship is now considerable and multi-decadal in extent (Friedland *et al.* 2003a, 2009). More important, analyses now include periods of high abundances (1960s–1970s), of marked stock declines (1970s–present) and accelerated ocean warming (1990s–present).

Specifically for the southern European stock component, the paradigm is one of survivorship showing significant linkages to ocean climate and these being manifest during the first summer of the marine migration (Friedland *et al.* 2009). As a generalisation, warmer summer SSTs correlate negatively with survivorship to return as adults. But, irrespective of ocean climate impacts on abundances, recent excessive warming of the North Atlantic appears also to have detrimental indirect effects on the quality (condition) of 1SW adults surviving to return. Thus, ocean temperatures may be having both direct and indirect effects on growth, survivorship and condition factor manifest through changes in prey availability. Changes in prevailing climate, and alterations in the distribution and abundance of appropriate prey at different stages of the post-smolt marine migration, clearly are not simple (Reist *et al.* 2006a, b) and overall climate impacts may also contrast markedly between the freshwater and marine habitats.

16.14 Large-scale indicator indices of ocean climate change and impacts on salmon

Dunbar & Thomson (1979) assessed records dating to the seventeenth century and were the first to draw a connection between variation in Atlantic salmon catches and the NAO, in the context of this atmospheric index providing a broad-scale indicator of ocean climate variation. It was perhaps the realisation that patterns of fish abundance can show teleconnections over very large oceanic distances that drew the attention of fishery biologists to the likely importance of such large-scale climate indices as environmental drivers (Lehodey *et al.* 2006). In the Northern Hemisphere, both the Pacific Decadal Oscillation (e.g. Mantua & Hare 2002) and the NAO have featured prominently in analyses of pelagic ecosystem regime shifts and of changes in abundances of target fish species. The winter NAO index has shown a strong pattern of change from intensely negative values during the 1960s to increasingly positive values toward the turn of the millennium (Fig. 16.6a). This coincided with high catches for salmon stocks exploiting the North Atlantic during the 1960s and early 1970s and the steady declines in abundance up to the present (but cf. Niemelä *et al.* 2004, 2005 for Barents Sea).

The NAO is a measure of the atmospheric pressure gradient between Iceland and either Portugal (Hurrell's index) or the Azores (Rogers' index), and dominates the climate over Europe as far east as Siberia. Hurrell's winter (December–March) index appears the better ocean climate indicator for the eastern North Atlantic and Rogers' index (December–February) for the western North Atlantic. In essence, high NAO index winters are characterised by (1) low pressure, strong westerlies and high air temperatures in continental Europe, and (2) the North Atlantic Current (NAC) penetrating high into Nordic seas, with deep convection active in the Greenland Sea but minimal in the Labrador Sea. Low index years show the converse, with high pressure, cold dry Arctic air stretching further south in Europe, weak NAC penetration into Nordic seas, and warmer waters extending into the high Arctic (Reid & Beaugrand 2002). The winter NAO indices therefore provide indicators of ocean climate dynamics in being strongly negatively correlated with winter SST and they are perhaps particularly relevant to salmon overwintering at sea. Over the period 1960–1997, Dickson & Turrell (2000) noted that the multi-decadal evolution of the NAO showed a pattern of earlier low index years corresponding with high catches (1960s), followed by

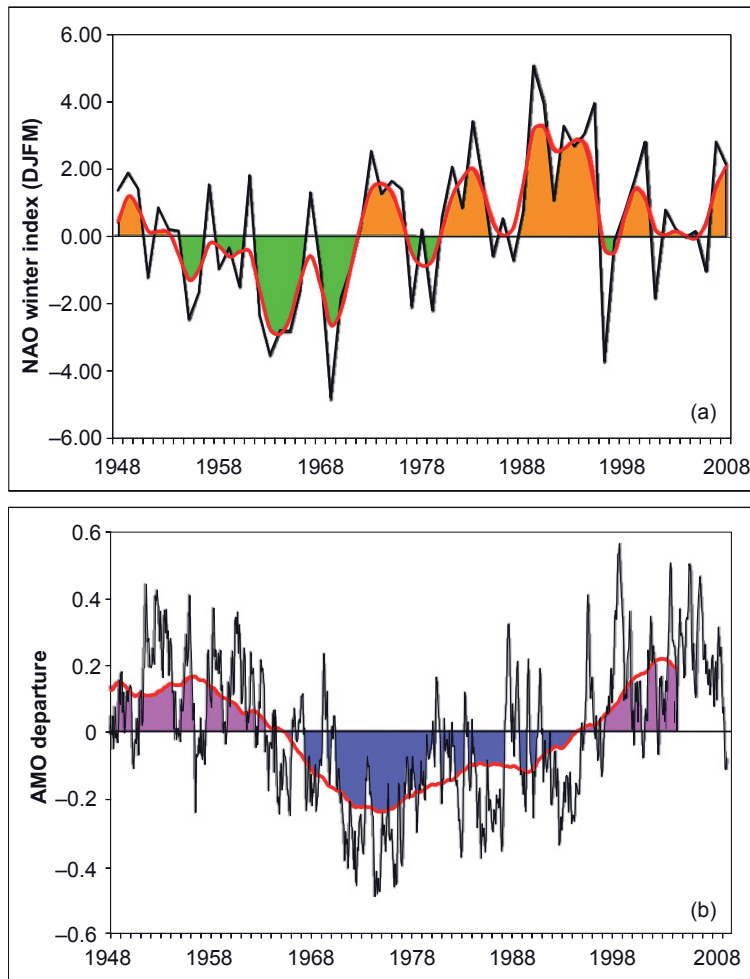


Figure 16.6 (a) Hurrell's winter (December–March) North Atlantic Oscillation (NAO) index for the years 1948–2008 (NAO Index Data provided by the Climate Analysis Section, NCAR, Boulder, USA, Hurrell (1995), <http://www.cgd.ucar.edu/cas/jhurrell/Data/naodjfmindex.xls>). The smooth curve is a weighted running mean (s.d. ± 1 year). (b) The Atlantic Multi-decadal Oscillation (AMO) for the years 1948–2009. (AMO index data and smoothed curve provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their website at <http://www.cdc.noaa.gov/data/timeseries/AMO/>.)

a progressive period of generally positive indices and low catches since the 1970s (see also Boylan & Adams 2006). But Dickson & Turrell (2000) also reported a deterioration of this apparent correlation in later years; despite the NAO evolving towards seemingly more favourable low indices, from the mid-1990s salmon catches did not recover.

For North American stocks, Friedland *et al.* (1993, 2003a) found that abundances were correlated with the NAO. However, Friedland *et al.* (2003a) also considered the Gulf Stream North Wall (GSNW) index: this reflects the position of the Gulf Stream and is indicative of SST distribution in the western North Atlantic. GSNW indices are characterised as monthly and annual means of the first principal component of the position of the north wall of the

Gulf Stream, 1966–2000 (Taylor & Stephens 1980), and provided much higher correlations than the NAO, suggesting that the distribution of SST may be of greater importance to the recruitment process than forcing associated with atmospheric variability. In Europe, Jonsson & Jonsson (2004b) reported a positive correlation over the period 1976–2001 between (1) the sea-age at maturity, and (2) body mass increment from smolt to adult salmon and the February–April NAO (note, not Hurrell's winter index) for the post-smolt year. For higher index years they observed increased proportions of fish maturing and returning as 1SW adults. But significant correlations with the NAO have not always been the outcome. For example, for hatchery-reared and wild Baltic post-smolts, Kallio-Nyberg *et al.* (2004) found no correlation between the NAO and survivorship of wild smolts, but did note a positive correlation between year-class survivorship and July SST – immediately after smolt entry to sea water – perhaps indicating a detrimental effect of cold summers. Similarly, Niemelä *et al.* (2004) found no correlation between the NAO and salmon catches in the rivers Teno and Naatamojoki (northern Finland), the stocks of which migrate to the Barents Sea and show large natural fluctuations. Those catch time series date from the 1970s and are especially important because they run counter to the general pattern of recent stocks declines of Atlantic salmon (Niemelä *et al.* 2004, 2005). Juvenile abundances increased over the period 1977–2003 and strong smolt years were reflected positively in subsequent returns of spawning adults, perhaps because of warmer oceanic conditions (Niemelä *et al.* 2004).

In a detailed regional analysis of southern European salmon survival in relation to the NAO, Peyronnet *et al.* (2008) assessed two wild and nine hatchery populations from rivers in western Ireland since the early 1980s. They showed the importance of the NAO to adult survival and recruitment, and especially the intense impact of the winter NAO prior to the spring smolt migration to sea. Overall, the recent positive NAO phase and increasing SSTs were linked to the general decrease in salmon survival (cf. Dickson & Turrell 2000, and discussion above), with SST explaining most of the deviance. In a further analysis of the winter NAO and an Irish catchment, Boylan & Adams (2006) found this to be a highly significant predictor of the five-year running mean of salmon catches over the past five decades. Their Fig. 1 shows a striking pattern of negative correlation between the NAO and annual commercial catches dating back to 1875, but especially notable is the breakdown of that association since the early 1990s. This could be interpreted in two ways: either the historical correlations observed between the NAO and salmon catches are spurious, or major recent changes (sections 16.10, 16.12) have occurred in the oceanic environment of salmon which led to a breakdown in that association.

Whilst the atmospheric NAO has proven to be of variable, or questionable, utility, an explicitly oceanic climate indicator that may well assist our further understanding of both past and future dynamics of salmon abundances is the Atlantic Multidecadal Oscillation (AMO; Sutton & Hodson 2005; Fig. 16.6b). This index is thought to be driven by the thermohaline circulation and is derived from the de-trended annual mean SST over the area 0°N–75°N, 75°W–7.5°W (Enfield *et al.* 2001; <http://www.cdc.noaa.gov/data/timeseries/AMO/>); during the twentieth century the index showed both cool (1905–1925; 1965–1990) and warm (1931–1960; 1995–present) periods, with the greatest SST anomalies just east of Newfoundland. The present warm AMO phase should dictate warmer and drier summers in North America, perhaps together with warmer and wetter summers in Western Europe. However, the utility of the AMO in forecasting climate may alter as interactions with anthropogenic effects become apparent (Sutton & Hodson 2005). In their analysis of the

European stock complex, Friedland *et al.* (2009) found adult abundances to be more closely associated with the AMO than the NAO, suggesting that processes related to water temperature are of greater importance to recruitment than atmospheric forcing. Over the period 1948–2008, whilst the AMO has recently strengthened the NAO has been weak and variable since the late 1990s (Fig. 16.6). Note that it has been particularly in these more recent years that the apparent correlation between salmon abundances, plankton abundances (e.g. Reid & Beaugrand 2002) and the NAO has broken down and this might reinforce the contention that the AMO (although a crude measure of North Atlantic SST) is a more relevant indicator of ocean climate impacts on marine ecosystems and salmon populations.

16.15 Management issues and responses to changes in ocean climate

Bisbal & McConnaha (1998) highlighted the dichotomy between (1) those who consider that the oceanic environment is well buffered and stable, and that detrimental changes in freshwater production underlie salmon declines, and (2) those of an opposite view, that oceanic influences primarily control salmon abundance. Under the latter circumstances it is understandable that in responding to climate change impacts freshwater managers might question the utility or value of efforts to address seemingly overwhelming ‘marine’ problems; this is perhaps all the more acute given the common perception that freshwater production of smolts generally is being maintained and yet marine survivorship continues to decline (e.g. Friedland *et al.* 2003a; Jonsson & Jonsson 2004a; McCarthy *et al.* 2008).

If one accepts that salmon populations are genetically structured and show local adaptation then it is imperative to incorporate genetic perspectives into any strategy for managing salmon populations in response both to present pressures and future challenges (Youngson *et al.* 2003). Naish *et al.* (2007) reviewed the success and effects of hatchery-reared juveniles on wild populations, and hatchery-reared juveniles clearly have lower survivorship and return rates than wild juveniles. Whilst acknowledging the benefits in maintaining endangered populations, the consensus is that hatchery releases can be detrimental to wild populations, including the conservation target (Naish *et al.* 2007). The genetic risks of inbreeding depression, loss of genetic diversity, reduction of N_e , introgression and outbreeding depression are all prominent, and they highlighted the particular genetic risks of introgression presented by permanent, conservation-based hatcheries for rivers in which the wild and hatchery populations can interact. ‘Supportive breeding’ (bringing a fraction of the wild spawning population into a hatchery and releasing their offspring to mix with wild conspecifics) can markedly alter the variance in family size, and for small populations this can significantly reduce N_e (Ryman & Laikre 1991).

The census size (N_c) for most breeding populations of Atlantic salmon adults is probably typically rather low – perhaps a few hundred up to a few thousand adults surviving to reach the spawning redds. N_e is related to the total population size but may be surprisingly low in marine fish populations (e.g. Hauser & Carvalho 2008) and this is perhaps a salutary warning to managers to give close consideration to the genetic benefits and costs of any future conservation strategies that may be adopted in tackling climate change impacts on wild Atlantic salmon. Reduction of N_e can radically alter the rate of loss of genetic heterozygosity in any population and for salmon this may be especially pertinent for small river stocks. Nonetheless, the estimation of N_e in salmon populations is very complex; the flexibil-

ity and variability in age at maturity (1SW vs. MSW), population age structure, incidence and prevalence of iteroparity – as well as the occurrence of precocious male parr – can all influence N_e in salmon populations (Palstra *et al.* 2009). Martinez *et al.* (2000) assessed the frequency of precocious male parr fertilisations in three small threatened river stocks at the southern distributional limit in Europe. They found frequent multiple paternity within redds, and that precocious parr had significant effects in increasing N_e , whereas Palstra *et al.* (2009) found a rather lesser effect in larger Canadian populations. Palstra *et al.* (2009) concluded that N_e was more influenced by age-structure related variation in anadromous (adult) male reproductive success.

It remains a prime concern in salmon management that there is presently no means of predicting change in local selection pressure, or adaptive response, for any population (Youngson *et al.* 2003). The precautionary approach in a rapidly changing environment is to assume both genetic structuring and local adaptation, to minimise transplants and introductions, and thereby to conserve population genetic variability and integrity. Management strategies maximising natural smolt production through riparian habitat improvement, and control of the fishery, might well be beneficial even if the major problem facing the population is at sea. This might be viewed as treating wild smolt production as ‘lambs to the slaughter’, but from a genetic standpoint it might well be best to allow populations to respond to, and recover from, climate change as naturally as possible. Certainly, Leaniz *et al.* (2007) contend that the risk of salmon mismanagement through acting under the assumption that they are displaying local adaptations is far less than the risk of mismanaging salmon under the assumption that they are not locally adapted. From the wider perspective, the need for predictive models to underpin and inform fishery management and conservation strategies in response to climate change is clear (e.g. Lassalle *et al.* 2008). While Atlantic salmon biologists and oceanographers have made substantive progress in interpreting major and recent biological changes in terms of indicator indices, it could be argued that the more informed approach in the future might be to apply modern ecosystem modelling as exemplified by Wells *et al.* (2008). Other research priorities include improving our knowledge of the oceanic migratory routes and destinations of the various salmon stock complexes, and of the spatial and temporal variations in availability of salmon forage species in addition to active prey choice. Intimately linked to this requirement is a better understanding of climate-driven dynamics of those potential forage species for salmon at sea. We have highlighted the current paradigms concerning growth-mediated survival of post-smolts, and the benefit from perhaps focusing future research efforts especially on the earlier periods of the ocean migration. But that should not detract from the need also for integrated predictive models of climate impacts on freshwater growth, survivorship and smoltification. Especially prominent in that context is our present inability to reach beyond the analysis of predictions of changes in seasonal and annual means, and to incorporate into models the brief and extreme abiotic disturbances that are likely for freshwater temperatures and flow discharges as the climate changes.

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17

Salmon Ecological Research and Conservation

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Abstract

This chapter highlights contemporary challenges in Atlantic salmon research, and discusses the relationship between research and conservation. The myriad ecological and genetic studies of salmon that have been undertaken around the Northern Hemisphere over the past century and more have powerfully advanced our understanding of salmon biology. However, knowledge alone will not save salmon; only actions will. Indeed, we know enough now about salmon ecology and genetics to reverse or at least reduce the decline of many populations or protect those that have not declined. Nonetheless, we still lack important knowledge related to several aspects of salmon ecology and life-history strategies, particularly in the sea. In addition, we do not know to what degree increasing smolt production in fresh water can compensate for problems salmon face in the marine phase of their lives. Better cooperation, improved methods and technology and more carefully designed studies will help to enhance our knowledge. Salmon declines are not likely to be reversed without changes in market structures, human attitudes, institutions and political will. It would therefore be negligent of us not to emphasise the importance of interdisciplinary studies, involving our colleagues in the social sciences. With improved understanding of the interplay between humans and salmon and the environments we share, sustainable management of Atlantic salmon might be achieved.

Key words

Atlantic salmon, research strategies, research needs, cooperation, multidisciplinary research, conservation

17.1 Introduction

Salmon are unique among commercially important species in that their life-histories and demography are exceptionally well studied. It is hard to think of another group of fish species whose populations can be assessed so accurately, because of their anadromous habit: almost

all the sexually mature adults swim up rivers each year, and hence they can be counted. We know an enormous amount about their movements and habitat use, interactions with other species (competitors, prey, predators, parasites), growth and reproduction, and mechanisms of population regulation, as described in the many excellent contributions to this volume, and often we know more about their genetic structure than we know about many economically important mammals (Verspoor *et al.* 2007).

But the anadromy that in some ways makes salmon so easy to study exposes them to double jeopardy. Not only do they have to survive the rigours of ocean life, they and their offspring have to run the gauntlet of rapids and falls; nets; dams; hydropower turbines; residential, commercial, and industrial development; climate change; pesticides; anglers and fishermen; and other natural and human-caused dangers in freshwater environments. It is a wonder they ever could survive. The numerous interactions between salmon, at all stages of their life-history, and human activities have caused global declines of salmon populations. Only in a few low-impact regions, such as Alaska and Iceland (e.g., Policansky 2009 for Pacific salmon, Hindar *et al.* 2011 [Chapter 12] for Atlantic salmon), do populations appear to remain more robust. What, then, should we do as scientists? Would more detailed, comprehensive, extensive and expensive studies help reverse the declines? If so, what should we study? If not, should we abandon salmon science in favour of something else, and what should that something else be? These are difficult questions, discussed in more detail below, but in summary our answers are first that the myriad ecological and genetic studies of salmon that have been undertaken around the Northern Hemisphere over the past century or so have powerfully advanced our understanding of salmon biology, and second that knowledge alone will not save salmon; only actions will. Indeed, we know enough now about salmon ecology and genetics to reverse or at least reduce declines of many populations or protect those that have not declined (see Box 17.1).

Yet science still has important contributions to make. Much of the scientific understanding of salmon ecology is described in this volume; without those studies, we would be helpless to manage salmon declines. We would not be able to design effective measures to restore populations and prevent further declines, because we would not understand population dynamics and salmon ecology as we do. But many of the anthropogenic factors that threaten salmon are economically important and crucial for modern society, such as hydropower, agriculture, aquaculture, fishing, transportation, and use of land for commercial, residential and industrial development. Those activities will not easily be abandoned for the sake of saving salmon. Therefore, we need additional, focused ecological studies that identify efficient management measures; and focused socioeconomic studies that identify what actions societies might accept. Indeed, such studies – and actual conservation efforts like Norway's

Box 17.1 Heritage rivers and fjords: A Norwegian approach to salmon conservation

Atlantic salmon are divided into numerous populations and sub-populations that are subjected to density-dependent and stochastic mortality. We know that populations in more pristine environments perform better, and that interaction with humans causes many of the problems. We also know that a major threat in several regions is the combination of declining wild populations, degradation of habitat, and the increase in farmed salmon escapees. This implies that conservation interest is diminishing and commercial farming interest is

increasing. How can we meet this challenge? In Norway, a system of National Atlantic Salmon Rivers and Fjords has been adopted (Fig. B17.1.1). These include the more productive populations that are more resilient to genetic drift, an approach that is different from classic conservation strategies focusing on the most threatened populations. In addition, it is easier to protect good habitats than to restore degraded ones (Policansky 2009). Such a system, perhaps World Heritage Salmon Rivers and Fjords, throughout the distribution area of salmon, may be necessary to protect salmon populations. It would increase conservation and management effort in these localities and also include the valuable cultural aspects of salmon. Here, salmon interests must have a higher priority than other economic interests, and counteract the current situation in which market structures value wild salmon less than the many activities that threaten them. These rivers could form a stronghold for the future of Atlantic salmon, a stronghold that is badly needed in view of continued human activities and development.



Figure B17.1.1 The River Gaula near Trondheim, currently one of the most productive salmon rivers in the world. The fjord outside this river and several others draining to the same fjord comprise one major element in the 'Norwegian Salmon Heritage Rivers and Fjords' conservation system. Photo: Øystein Aas.

system of National Atlantic Salmon Rivers and Fjords (Box 17.1) – could develop knowledge relevant to other conservation challenges. Similarly, those who would conserve salmon could learn from other examples, such as Brazil's Project Tamar, which has involved local communities in developing local businesses and providing incentives to protect sea turtles and their habitats (Project Tamar's web page is at <http://www.tamar.org.br/ingles/>). Finally, salmon researchers need close communication with managers and policy makers to help develop scientifically sound and politically feasible approaches.

17.2 Ecological research that contributes to conservation

Salmon research and mitigation efforts have evolved over a long period, from early naturalist and fisherman observations in the Age of Enlightenment, via enhancement work such as the building of fish ladders in the 1800s and the development of artificial hatcheries toward the end of the 1800s, the problem-oriented and applied investigations related to pollution and damming after the Second World War, up to current more ecologically inspired research. Thus, salmon ecology (research and management) has evolved from a practical, applied tradition, rooted in a context of enhancement and maximum sustainable yield (MSY), to one serving resource conservation, biodiversity and ecosystem structure and functioning. It is indeed important for salmon ecologists to understand their scientific heritage (Bottom 1997), and how earlier research and management focused on mitigation, such as stocking and fish ladders, to attempt to compensate for lost production following loss or degradation of habitat. Atlantic salmon have probably been the subject of more research than any other commercially important fish species. How do we navigate and make use of the huge amount of existing knowledge? If we do not believe that all studies of salmon are a waste of money and time in terms of reversing salmon declines and restoring their populations – and we emphatically do not – what studies are most likely to be effective?

Salmon live in complex, dynamic, and stochastic environments, which exhibit large variation in production and 'yield'. Therefore, the crucial questions to answer for research to sustain Atlantic salmon are: What factors decide the size of the spawning populations in naturally reproducing stocks? How can we predict and decide harvest strategies and levels? What are the habitat requirements for salmon?

Addressing these questions requires an understanding of population dynamics. Detailed studies of single factors are obviously required, but eventually they need to be linked together in a comprehensive understanding that covers both freshwater and marine environments. Given current knowledge, salmon ecologists should be able to build generic models that capture the essence of salmon population dynamics, although responses to environmental conditions in the oceans remain a challenge. However, applying such models to specific populations requires site-specific data. Thus, the main challenge is to construct models that capture the essential processes, and that can realistically be applied given constraints in data access.

A starting point for such a model, and a conceptual framework that is important to understand for management and conservation even in the absence of models, is that we now know that the processes occurring in freshwater and marine environments are fundamentally different in one crucial aspect: the operation of density-dependent processes. Whereas density-dependent processes strongly influence salmon growth and survival rates in rivers,

at sea, density-independent processes most likely dominate (Einum & Nislow 2011 [Chapter 11]). So what does this tell us? For a start, it is important to recognise that the temporal order of these two processes has major ecological significance. If density-dependent processes affecting salmon are largely confined to fresh water, the expectation is that no compensatory processes would occur in the sea to counteract negative environmental conditions and their effect on the size of the spawning population. Thus, different sources of mortality from the smolt stage to the adult stage at sea will act in an additive manner. The negative environmental influences that we are aware of during these stages are either relatively easy (e.g. fishing mortality, Hindar *et al.* 2011 [Chapter 12]; sea lice, Finstad *et al.* 2011 [Chapter 10]), difficult (e.g. predation, Ward & Hvidsten 2011 [Chapter 8]) or impossible (ocean temperatures, Todd *et al.* 2011 [Chapter 16]) to react to. Due to the lack of density dependence, any rise in the number of individuals entering the sea or increase in the sea survival will have an obvious positive effect on the spawning stocks. Thus, for some of the environmental challenges, and given sufficient political will, it seems possible to implement management measures that can prevent or reduce further declines in the size of spawning populations.

There is agreement that increased mortality and reduced growth at sea from 1980 to the present is a major factor for the reduction in overall salmon productivity and abundance (ICES 2009), at least in parts of their range (the US National Research Council (2004) concluded that dams were the biggest threat to salmon in Maine, for example). Despite many studies indicating correlations between salmon production and environmental factors on a larger scale, there are also clear regional differences (Vøllestad *et al.* 2009).

No matter whether the marine or the freshwater environment poses bigger challenges for salmon, we still lack a full understanding of the mechanisms acting on salmon at sea. The contributions by Todd *et al.* 2011 [Chapter 16] and Rikardsen & Dempson 2011 [Chapter 5] are eloquent testimony to the impressive body of knowledge that has been generated about salmon in marine environments. At the same time these and others point out what we do not yet understand about salmon at sea. Therefore it is not surprising that many have called for intensified research on salmon at sea. The Norwegian Research Council gave high priority to this in the Wild Salmon Research Programme that started in 2001; Hutchinson *et al.* (2002) emphasised the need for studies of salmon at sea, and the US National Research Council (2004) also emphasised this research area for Atlantic salmon in North America, along with a focus on the transition to saltwater and freshwater chemistry that could affect that transition. The National Research Council (2005), in advising on the development of a research and restoration plan for Pacific salmon in western Alaska, advised obtaining better information on marine survival and productivity of salmon. Also, within NASCO and ICES, efforts of financial and organisational character have been given priority to boost international cooperation about research on the marine phase of Atlantic salmon. Climate change is a frequently discussed topic, and is likely to affect salmon productivity and survival both at sea and in freshwater environments.

Technological advancements have been very helpful in providing better platforms for marine research (see for instance Thorstad *et al.* 2011 [Chapter 1]). In particular, improvements in tags, especially in data storage tags, that have made such equipment both more advanced, and cheaper, are a major step forward. Catching salmon at sea for research purposes has been a challenge, which has now been largely overcome by improved surface trawls, at least regarding post-smolts. Also, new genetic investigations are now used to assign

salmon caught in a feeding area at sea to different rivers (or regions) of origin (<http://www.nasco.int/sas/salseamerge.htm>).

However, while improved methods and technologies are a blessing in many cases, they cannot by themselves provide a better understanding of the mechanisms acting upon salmon at sea. In addition, some factors potentially act at a local or regional level, such as farm-escalated parasitism on post-smolts from sea lice (Finstad *et al.* 2011 [Chapter 11] and pollution in fresh water (Rosseland & Kroglund 2011 [Chapter 15]). What probably is true is that all these processes and factors can act together at times and to varying degrees. This again underlines the urgency of ranking the importance of factors acting in coastal waters and at sea as a guide for prioritising research and conservation efforts.

If there is a lack of political will to address problems faced by salmon at sea, or if the problems are beyond our control, we might think that we can retain productivity, or at least save populations from extirpation, by focusing even more on the rivers. For rivers with particular problems such as loss of access to habitat by blocking of streams (Thorstad *et al.* 2011 [Chapter 1]), hydropower operations (Johnsen *et al.* 2011 [Chapter 14]), the parasite *Gyrodactylus salaris* (Harris *et al.* 2011 [Chapter 9]), siltation or pollution of streams (Rosseland & Kroglund 2011 [Chapter 15]), or extensive land use impacts (Ugedal & Finstad 2011 [Chapter 13]) this clearly is relevant and urgent (e.g., NRC 1996). However, in the absence of such obvious issues, as is the case for many rivers, the course of action is less clear. For one thing, density dependence, being caused by competition for resources among the juveniles (Nislow *et al.* 2011 [Chapter 7]), is responsible for much of the variation in growth and survival rates in such rivers. This means that a focus on the potential limiting resources (spawning sites, shelter or other aspects of the physical environment, food) would be the best approach to increase smolt production for a given spawning population size. But if those resources are not limiting – if the spawning population size is small – competition among juveniles may be negligible, and the response to increasing resources available to the resulting juveniles may be modest.

Given such an apparent constraint on what we can achieve by improving conditions in fresh water in such relatively unaffected rivers, it would seem that saving the salmon in the face of a continuing negative trend in sea survival is an impossible task. However, and fortunately, things are more complicated than this. The view expressed above is based on the perspective obtained from stock-recruitment relationships. These are highly valuable tools in management (Hindar *et al.* 2011 [Chapter 12]), and further developments and applications of these are crucial for management of fisheries. They do, however, contain inherent limitations due to the need for simple and useful models. In particular, they often ignore spatial factors and changes in habitat use, behaviour and resource requirements with increasing body size. Recent studies (Einum & Nislow 2011 [Chapter 11]) suggest high intensity of competition and intense density-dependent mortality over small spatial scales for early juvenile stages following emergence from nests. If so, and if the competition intensity is relaxed during later juvenile stages (see discussion of ‘self-thinning’ in Einum & Nislow 2011 [Chapter 11]), we may still see pronounced responses in terms of smolt production by ensuring sufficient dispersion of spawners (Fleming & Einum 2011 [Chapter 2]), and by providing good abiotic habitat (Finstad *et al.* 2011 [Chapter 3]) with sufficient access to food (Johansen *et al.* 2011 [Chapter 4], Forseth *et al.* 2011 [Chapter 6]) for the sensitive emerging juveniles. We have made significant progress in understanding these processes in

fresh water. However, much remains to be learned about the processes shaping salmon growth and survival throughout the freshwater stage, and that knowledge will be important in managing the freshwater stage of salmon. Any successful conservation efforts in fresh water would counteract the many negative processes occurring in the less manageable ocean environment.

17.3 Environment, genetics, and changes in life-history

In this book we have aimed to maintain a strong focus on the ecology of Atlantic salmon, and consequently readers interested in issues relating to contemporary evolutionary and phenotypic responses to environmental changes should consult other texts. Hendry & Stearns (2004), Verspoor *et al.* (2007), and Waples & Hendry (2008) and accompanying papers in the special issue of *Evolutionary Applications* give insights into this field.

In short, the relationship between growth, maturation, environment, and genetics in fishes is a complicated one. Alm (1959) recognised its importance over 50 years ago, but in the absence of genetic information, he could not untangle the problem. Even with genetic information, the problem is difficult: we are in essence trying to solve a differential equation with several variables, not all of which are adequately characterised. The problem is made worse if fishing (e.g. Policansky 1993) or hatcheries (e.g. NRC 2004) are involved. Contemporary trends in salmon populations include changes in absolute sizes of mature adults, in the proportion of multiple spawners, in the proportion of salmon less than 3 kg that have spent more than one winter at sea, and other life-history changes (e.g., Todd *et al.* 2011 [Chapter 16], Anon. 2009, Box 17.2). Thus, there should be no doubt that environmental changes influence salmon populations beyond the numerical changes that managers and scientists commonly focus on. Environmental changes that may affect the salmon include changes in the populations, or at least infestation rate, of sea lice; local enrichment of the sea water by salmon farms; changes in the flow patterns of rivers and the temperature regimes in the ocean and in rivers associated with larger-scale climate change; changes in populations of predators on or competitors with salmon; changes in fishing mortality; and so on. These changes may produce both phenotypic (plastic) and genetic (evolutionary) changes in salmon. Such changes can occur surprisingly fast, and often genetic responses are very difficult to disentangle from environmentally mediated responses (e.g. Policansky 1993), although genetic changes probably could not have occurred fast enough to account entirely for differences observed only in the past decade or less. Thus, an important research question exists for understanding, managing and restoring salmon populations: To what degree are observed changes in aspects of salmon life-histories the result of phenotypic adaptation to environmental changes, and to what degree are they the result of genetic adaptation (evolution) to environmental changes? The answer(s) to that question can help answer the management question, i.e., to what degree, and how, can those environmental changes be reduced, mitigated, compensated for, or – in cases where the changes in life-history lead to increased productivity – enhanced?

It is beyond our scope here to propose a specific research agenda to address this problem. But we do strongly suggest that it receives focused attention from researchers and managers in regions where Atlantic salmon live. In an era of increasingly rapid environmental changes, this is one of the most important problems to understand.

Box 17.2 Life-history variations on the Alta River

It is late October 2008, and together with my colleague Audun Rikardsen and our PhD student Elina Halttunen, we are drifting down the River Alta, checking acoustic signals from tagged salmon, and trying to catch more fish for research purposes. The pools are filled with spent salmon of all sizes, and on the banks we can see the occasional dead fish. Spawning season is just over, and huge areas of the riverbed are turned upside down – the spawning stock has been tremendous this year. What a life – no wonder some are envious that we not only get to spend time on this river, but that we even get paid for it!

Down on Granstrømmen, a famous pool on the river, I can see a white-tailed eagle (*Haliaeetus albicilla*) depart from a huge salmon carcass on the cobblestone beach, as we slowly approach the bank. While Audun and Elina take up fishing, in search of an immature autumn salmon to implant and tag, I walk down to the carcass. It is a huge male, 117 cm long, meaning the salmon was close to 20 kg when it entered the river sometime in June or July. The fish probably drifted ashore not long ago, and the eagle has started its feast on the skull. Its side is starting to fade, yet the intense colours of spawning are still recognisable.

As I look at the fish in admiration and awe, I start to think. ‘How did you live, and where have you been?’ Alta salmon are dominated by males that have spent one winter at sea (1SW), and females that have spent three winters at sea. This is definitely not a 1SW male, and besides the Alta is famous for salmon above 20 kg. These biggest fish are often males, having spent four or even five winters at sea (Ugedal *et al.* 2006). Studies have revealed that the large salmon in the Alta River also include a high percentage of repeat spawners (Elina Halttunen pers. comm.). The now seemingly more common 12–16 kg females are typically fish in for their second spawning, having spent three winters at sea before their first spawning, then one winter in the river, before entering the sea for their fourth season, prior to the second spawning run. The big salmon of the Alta migrate over enormous areas. Pop-up satellite tags have documented that some go at least as far as the north-east of Novaja Zemlja in Russia, while others have left their tags near Jan Mayen Island; one fish even reached north of Spitsbergen at 78 degrees north (Audun Rikardsen pers. comm.).

My reflection over the dead male is suddenly interrupted. Elina is shouting, having hooked a fish as strong as an express train (Fig. B17.2.1). The salmon is definitely no worn-out kelt. After a while we can net, tag, and release a female immature salmon around 11 kg, fresh run, with sea lice attached. Tagging studies have shown that these fish stay one year in the river before they spawn together with the ‘normal’ summer running mature salmon, but why they do this instead of feeding one more year at sea is not known. These immature salmon, often labelled ‘autumn running’ salmon (see Thorstad *et al.* 2011, [Chapter 1]) display yet another fascinating life-history strategy of Atlantic salmon in the Alta.

Øystein Aas



Figure B17.2.1 PhD- student Elina Halttunen displays a fresh ‘autumn’ salmon, likely to spawn in 12 months. The fish was caught, tagged and released in the river Alta, Norway, October 2008. Photo: Audun Rikardsen.

17.4 Enhanced cooperation

Salmon research has changed a lot in the past few decades, and we are proud to salute the genuinely international author groups of most of the chapters in this book. Despite long-term cooperation among salmon researchers in such fora as ICES Working Group on Atlantic salmon, through different NASCO efforts, we cannot emphasise the importance of continued and strengthened cooperation enough. Cross-national cooperation has advanced our field, and systematic cooperation between scientists working with Atlantic and Pacific salmon has brought us even further forward (Hutchinson *et al.* 2002; Lynch *et al.* 2002). However, we believe that strengthened strategic cooperation between groups of scientists of different qualifications also is a potential success factor. Not surprisingly, much of the previous and existing cooperation is between salmon ecologists from different regions and with somewhat different approaches, yet with many of the same strengths and interests. We think new teams could be more complex and complementary. Salmon ecologists and general ecologists; ecologists and geneticists; ecologists and physiologists, ecologists and biostatisticians – these are just some examples of types of cooperation that might bring us forward (Box 17.3).

17.5 Multidisciplinary science

This is a book about salmon ecology, and so we have focused here primarily on ecological studies. However, salmon declines will not be reversed without changes in market structures, human attitudes, institutions and political will. We therefore wish to emphasise the importance of interdisciplinary studies, involving our colleagues in the social sciences. We have learned a great deal about how humans interact with their environment and how their various cultures and institutions in various societies influence those interactions, although a great deal remains unknown. The call for such research is not novel. For example, the [US] National Research Council (1996) concluded that ‘the social structures and institutions that have been operating in the [United States] Pacific Northwest have proved incapable of providing a long-term future for salmon, in large part because they do not operate at the right time and space scales’. Such an understanding is also clearly reflected in both the organisation and the priorities of the Norwegian Research Council Programme ‘Environment 2015’, which is now responsible for salmon research in Norway. However, such research has already pointed out that solutions will be complex, expensive and difficult, and it will require political courage to undertake them. Current market structures value wild salmon less than many activities that threaten them. Lackey (2009) has reached even more pessimistic conclusions, suggesting that to save wild salmon, we will need to reverse many rules of commerce, reduce competition with salmon for natural resources, somehow manage the continually increasing aggregate demands of humans for habitats and resources, persuade individuals and groups that salmon really are worth saving, persuade elected and appointed officials to confront difficult truths and make hard decisions, and persuade scientists to be more explicit in setting forth those difficult ecological truths. Although both Lackey and the US NRC were writing about Pacific salmon, we cannot see how the case of Atlantic salmon is significantly different: similar conclusions apply as well (e.g. NRC 2004), although the scale of Atlantic salmon populations is smaller, and perhaps for those reasons, there is more hope

Box 17.3 Planning research programmes for Atlantic salmon

Ecological research makes progress through a combination of theory, field studies and controlled experiments. Today, we have most likely identified most of the factors that limit and adversely affect wild salmon stocks. However, much still remains in order to understand their relative importance in time and space. Studies of population dynamics in salmon would still benefit a great deal from taking a stricter, more mechanistic approach towards quantitative population modelling, where the understanding of the magnitude of the different factors and how they act in concert are key issues. To extract and identify cause–effect relations and not only correlations is a very demanding, yet crucial challenge that acts as a major bottleneck for Atlantic salmon research.

Careful and creative planning of studies, with an active interplay between theory, field studies, and controlled experiments is essential for progress in our understanding (Morin 1998; Werner 1998; Fig. B17.3.1). Traditionally, field studies and empirical findings have dominated salmon ecology; more recently we have seen more experiments, especially for the freshwater phase, and even a purposely planned interplay between experiments in laboratory, semi-natural environments, and in the field (see Einum & Nislow 2011 [Chapter 11] and Fleming & Einum 2011 [Chapter 2] for examples). Through creative and original research designs, better cooperation, advances in technology and more active use of theory, we hope to see even further growth in such studies, despite the huge practical challenges of ecological research at sea. In addition, the extensive statistical and biological data that have been collected over the past 150 years should not be neglected. Additional cooperation, better sharing of data between scientists, institutions and countries, perhaps a common international database, will increase the potential for making use of old as well as new data.

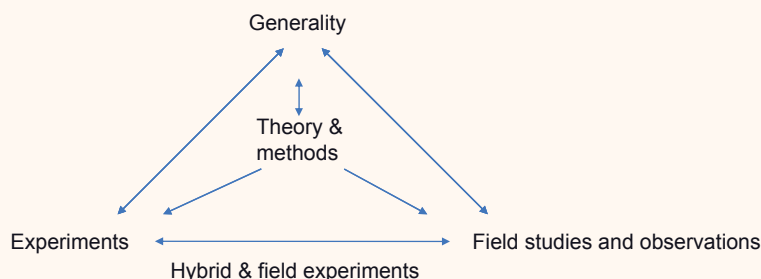


Figure B17.3.1 Careful design and interplay between field studies and observations, field experiments and ‘true’ experiments is imperative for increased general understanding of key ecological processes regulating Atlantic salmon.

of arresting their declines, at least for the more northerly populations. It is therefore our hope that this book can help lead to more focused salmon research, a more urgent ranking of important research and conservation topics, and better communication with policy makers and managers.

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