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THE WORKING PARTY ON CHEMICALS, PESTICIDES AND BIOTECHNOLOGY

CONSENSUS DOCUMENT ON THE BIOLOGY OF ATLANTIC SALMON (Salmo salar)

Series on Harmonisation of Regulatory Oversight in Biotechnology
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No. 64

Consensus Document on the Biology of Atlantic Salmon (*Salmo salar*)

Environment Directorate

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ABOUT THE OECD

The Organisation for Economic Co-operation and Development (OECD) is an intergovernmental organisation in which representatives of 35 industrialised countries in North and South America, Europe and the Asia and Pacific region, as well as the European Commission, meet to co-ordinate and harmonise policies, discuss issues of mutual concern, and work together to respond to international problems. Most of the OECD's work is carried out by more than 200 specialised committees and working groups composed of member country delegates. Observers from several countries with special status at the OECD, and from interested international organisations, attend many of the OECD's workshops and other meetings. Committees and working groups are served by the OECD Secretariat, located in Paris, France, which is organised into directorates and divisions.

The Environment, Health and Safety Division publishes free-of-charge documents in eleven different series: **Testing and Assessment**; **Good Laboratory Practice and Compliance Monitoring**; **Pesticides; Biocides**; **Risk Management**; **Harmonisation of Regulatory Oversight in Biotechnology**; **Safety of Novel Foods and Feeds; Chemical Accidents; Pollutant Release and Transfer Registers; Emission Scenario Documents;** and **Safety of Manufactured Nanomaterials.** More information about the Environment, Health and Safety Programme and EHS publications is available on the OECD's World Wide Web site (http://www.oecd.org/ehs/).

This publication is available electronically, at no charge.

For the complete text of this and many other Biosafety publications, consult the OECD's World Wide Web site (www.oecd.org/biotrack/)

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FOREWORD

Consensus Documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, these are being published on information on the biology of certain plant species, selected traits that may be introduced into plant species, and biosafety issues arising from certain general types of modifications made to plants.

This document addresses the biology of Atlantic salmon *(Salmo salar)*.

Finland, Norway and the United States served as the co-leads in the preparation of this document, and the draft has been revised based on the input from other member countries and stakeholders.

This document is published under the responsibility of the Joint Meeting of the Chemicals Committee and the Working Party on Chemicals, Pesticides and Biotechnology.

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PREAMBLE

The environmental risk/safety of transgenic organisms are normally based on the information on the characteristics of the host organism, the introduced traits, the environment into which the organism is introduced, the interaction between these, and the intended application. The OECD's Working Group on Harmonisation of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on identifying parts of this information, which could be commonly used in countries for environmental safety/risk assessment to encourage information sharing and prevent duplication of effort among countries. Biosafety Consensus Documents are one of the major outputs of its work.

Biosafety Consensus Documents are intended to be a "snapshot" of current information on a specific host organism or trait, for use during regulatory assessments. They are not intended to be a comprehensive source of information on everything that is known about a specific host or trait; but they do address the key or core set of issues that member countries believe are relevant to risk/safety assessment. This information is said to be mutually acceptable among member countries.

To date, 54 Biosafety Consensus Documents have been published. They include documents which address the biology of crops, trees and micro-organisms as well as those which address specific traits which are used in transgenic crops. This is the first Biosafety Consensus Document to specifically address an animal other than a micro-organism, in this case a commonly cultured, domesticated fish that is reared for food production, Atlantic salmon, but which also occurs in the wild in undomesticated form, often in the very same geographical region. Thus in this document the biology and ecology of wild Atlantic salmon are described in addition to that of the domesticated form. Currently used production and rearing practices are also described at length for domesticated Atlantic salmon because these practices may influence the ability of, and locations where, wild and domesticated forms of Atlantic salmon might interact in the environment and the types of interactions that may occur if they co-occur. This information is intended to benefit potential risk assessors that may need to consider these potential interactions and their effects, and in assessing the risks that they might pose.

In reading the Biosafety Consensus Documents, it may be useful to consult two additional texts. The first, entitled "An Introduction to the Biosafety Consensus Document of OECD's Working Group for Harmonisation in Biotechnology" explains the purpose of the Biosafety Consensus Documents and how they are relevant to risk/safety assessment. The second text is "Points to Consider for Consensus Documents on the Biology of Cultivated Plants". Although this document is specifically for cultivated plants, it contains a structured checklist of "points to consider" for authors when drafting or for those reviewing a Consensus Document the may relevance to the biology of domesticated animals used in agriculture. Amongst other things, this text describes how each point is relevant to risk/safety assessment.

The Biosafety Consensus Documents are of value to applicants for commercial uses of transgenic organisms, regulators in national authorities as well as the wider scientific community. The Consensus Documents are not intended to be a substitute for a risk/ safety assessment, because they address only a part of the necessary information. Nevertheless, they should make an important contribution to environmental risk/ safety assessment.

As each of the documents may be updated in the future as new knowledge becomes available, users of Consensus Documents are encouraged to provide any information or opinions regarding the contents of this document or indeed, OECD's other harmonisation activities.

PART I – BIOLOGY AND ECOLOGY OF WILD ATLANTIC SALMON

1. Classification and nomenclature

1. Scientific name of Atlantic salmon: *Salmo salar* LINNAEUS, 1758

English: Atlantic salmon
French: Saumon atlantique
Spanish: Salmón Atlántico
Russian: Semga
German: Atlantischer Lachs, Salm
Phylum: Chordata

- Class: Osteichthyes (bony fishes)
  - Order: Salmoniformes
    - Family: Salmonidae (Salmon and trout)
      - Subfamily: Salmoninae
        - Species: *Salmo salar* Linneaus

2. Atlantic salmon belongs to the family *Salmonidae* (Teleosts) (Nelson, 1984). The family comprises seven genera:

a. Salmo (includes *Salmo salar* – Atlantic salmon and *Salmo trutta* – brown trout and other endemic trout species)
b. Hucho (taimen)
c. Oncorhynchus (Pacific salmon)
d. Salvelinus (charr)
e. Salmothymus (endemic Balkan/Adriatic)
f. Brachymystax (lenok)
g. Salvethymus (S. svetovidovi)

3. The most closely related species to Atlantic salmon is the brown trout, *Salmo trutta*. Low rates of hybridisation between the two species are common in the wild throughout Europe, where they are native (Youngson et al., 1993); the F1 generation can be fertile. Brown trout is not native to North America and where it has been introduced it is known to hybridise with Atlantic salmon (Verspoor, 1988a).

4. Atlantic salmon occurs naturally only in the northern hemisphere and can be divided genetically into two major lineages, a North American (west-Atlantic race) and a European. Both the North American and European lineages again can be separated into smaller regional groupings. For example, in North America, there is regional distinction among the populations of the Gulf of Maine, Outer Bay of Fundy, Inner Bay of Fundy, Labrador/Ungava, Gulf of St. Lawrence, Southern Uplands of Nova Scotia and Newfoundland (excluding Gulf Rivers; Verspoor, 2005). In Europe, there is a major division between

Atlantic salmon of the Baltic and other European populations, as well as a division between the East-Atlantic and North-Atlantic in the Barents Sea region.

- Atlantic salmon is a genetically substructured species, even at the inter- and intra-watershed scales.
- Genetic differentiation is based on homing to natal rivers (isolation of populations).
- Genetic differences have been demonstrated between populations in protein-coding genes, nuclear and mitochondrial DNA markers and genetically based performance traits.

Genetic markers:

5. Identification of Atlantic salmon can be made through the use of genetic markers: chromosome numbers, allozymes, DNA analyses (see part III).

Table 1. **Terminology: Stages in the life cycle of Atlantic salmon**

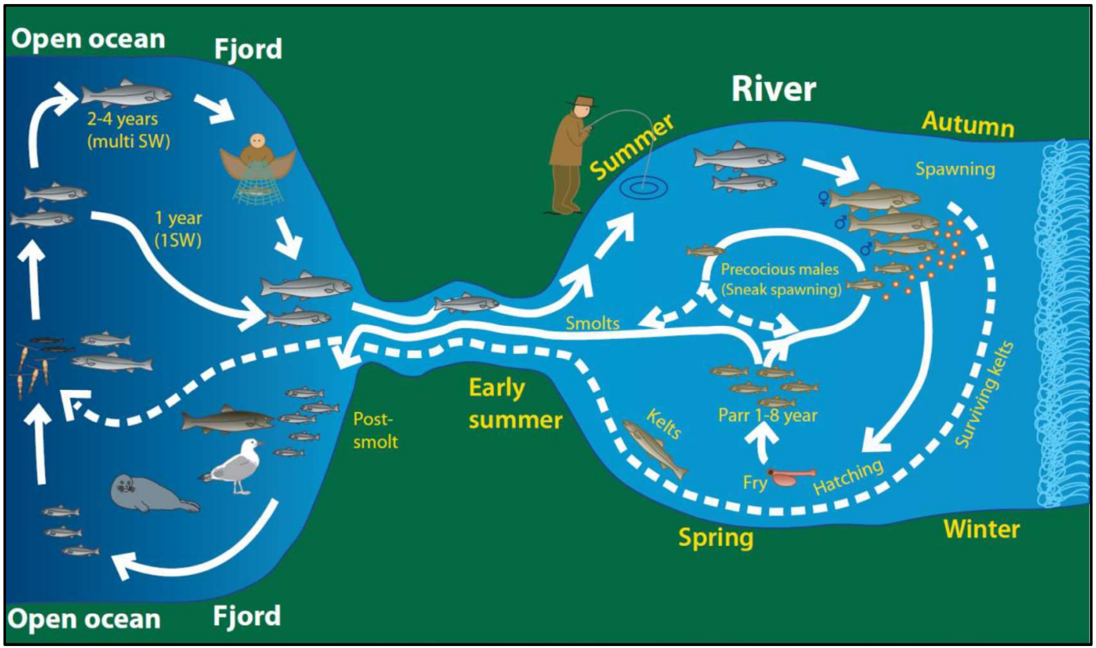
Stage	Definition
Alevin	Hatched fish still dependent on the yolk sac nutrition
Fry	Short transitional stage where the fish emerge from the redd and start to feed exogenously and disperse
Parr *Precocious parr*	Stage between full absorption of the yolk sac and smoltification *Sexually mature parr (mostly males)*
Smolt	Stage when seaward (landlocked: lakeward) migration occurs
Post-smolt	Stage from departure from the river (usually in spring / early summer) to the end of the first winter in the sea (sea-winter) or lake
Adult *Grilse (1SW)* *MSW*	Fish after the end of the first winter in the sea / Mature fish which returns to river to spawn A fish that returns to breed after one sea-winter A fish that returns to breed after multiple sea-winters
Kelt	Adult fish after spawning (spent), until it reaches the sea

2. Life history and characterisation

2.1. Characterisation

6. Atlantic salmon is anadromous typically: the young migrate from the river to the sea for feeding and at sexual maturation return to their natal river to spawn as adults (Figure 1). There are, however, populations, particularly in North America, but also in Northern Europe that complete their entire life cycle in freshwater and are known as landlocked. Freshwater resident salmon populations are more often separated by some geographical barrier from anadromous salmon populations (Klemetsen et al., 2003; Sandlund et al., 2014), but they also exist in sympatry with anadromous salmon in North America (Hutchings and Myers, 1985; Verspoor and Cole, 1989). Landlocked populations generally have lower genetic variation within populations, but larger genetic differences between populations, compared to anadromous populations (Bourret et al., 2013a; Sandlund et al., 2014). This is because of lower effective population size in some populations, and a lack of gene flow between populations because of geographical barriers. Resident salmon populations in sympatry with anadromous populations have been shown to be genetically different from anadromous populations in some watersheds but not in others (Adams et al., 2016).

Figure 1. **Schematic outline of the anadromous Atlantic salmon life cycle**



Source: courtesy of Audun Rikardsen

7. Atlantic salmon requires a freshwater environment for spawning and the development of the early life stages. Smolts leave the rivers in spring and/or early summer. As they prepare to do so, they undergo physiological (e.g. increase Na^+K^+ ATPase production), morphological (e.g. become more streamlined and take on a silvery body colouration) and behavioural changes for salt water. (Some landlocked populations may have abandoned key elements of the parr-smolt transformation associated with marine life – Nilsen et al., 2003).

8. The main feeding-grounds of anadromous Atlantic salmon are the Northern Atlantic, with European populations being found principally on the eastern side and North American populations on the western side. However, the two groups frequently overlap off Greenland. Baltic populations restrict their migrations to the Baltic Sea.

9. Once the returning salmon have entered the river, they migrate upstream until a suitable spawning site is reached. Their homing instinct brings the salmon back not only to their natal river, but also potentially to the same river section from whence they were born. This allows for geographic and genetic isolation, which are the key factors leading to river-specific adaptation (genetic differentiation) and ecological variability. Substantial genetic structuring is found both between and within watercourses throughout the species' distribution range.

2.2. Identification

10. All salmonids possess an adipose fin and an axillary process at the base of each pelvic fin. Wild anadromous Atlantic salmon have a body shaped like a torpedo, but old males can have a rather deep body. There are few spots below the lateral line and 2-4 spots on the operculum. The pectoral fins are long in comparison with other salmonids. The upper jaw reaches only the posterior of the eye, unlike that of the brown trout, which extends further. The caudal peduncle is also rather narrow and the caudal fin shallowly forked (V-shaped) in comparison with brown trout.

11. Atlantic salmon have a silvery colouration during ocean life and turn brownish during maturation, with males also developing reddish hues. Anadromous males develop a characteristic hooked jaw (kype) that is thought to be important during breeding competition.

12. Farmed Atlantic salmon have a plump body form, with numerous spots and scales may be missing. Fins are commonly worn and may be crippled. Sometimes fin rays grow together or fuse, particularly in the dorsal and pectoral fins. Scales, which are a good indicator of age and growth, can be used to distinguish wild from farmed salmon. The scales of wild salmon demonstrate the characteristic narrow annuli of the freshwater phase and wide bands representing the fast marine growth. Farmed salmon have a rather steady growth and lack the clear difference of freshwater and marine phase annuli.

13. Juveniles in the parr stage have 7-13 dark "parr marks" on each side. Red spots occur mainly along the lateral line. The adipose fin is grey. Smolts turn silver as a sub-cutaneous deposit of guanin is laid down, concealing the parr marks, and the pectoral and caudal fins turn black. At this stage the juveniles establish the characteristic torpedo-shape.

14. Smoltification (i.e. process of preparing for the transition from fresh to salt water) is size dependent and may occur from ca. 10 cm fork length. This, however, varies among populations and among individuals within populations, with fast growing parr smolting at younger ages and smaller sizes than slower growing parr (Jonsson and Jonsson, 2011). Older smolts can reach up to 22-25 cm. The maximum size of adults depends strongly on the time spent at sea. Female Atlantic salmon reach a length of 120 cm, and males reach a length of up to 150 cm. Maximum weight is 40 kg. Very large fish are commonly repeat spawners in their second or third migration. Survival to repeat breed is generally low (11%, ranging from <1% to 43%), and more so, for males than females (Fleming, 1998).

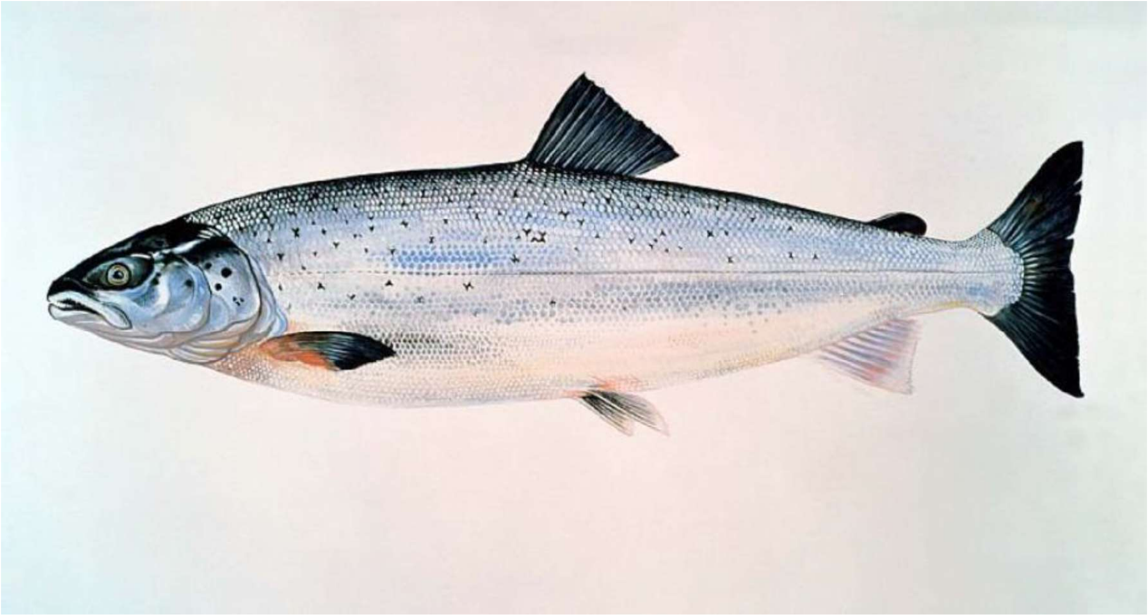
15. The scale count between the base of the adipose fin and the lateral line and the length of the upper jaw bone or maxilla in relation to the eye are two of the most reliable external features for distinguishing *Salmo salar* and the trout *Salmo trutta*.

Table 2. **Distinguishing features of species of the genus Salmo and the genus Oncorhynchus**

	Salmo salar	*Salmo trutta*	*Oncorhynchus kisutch*	*Oncorhynchus gorbuscha*
Upper jaw bone	Extends to the level of the rear of the eye	Extends well beyond the level of the eye	Extends beyond the level of the eye	Extends beyond the level of the eye
Scale count between base of adipose fin and lateral line	10-13	13-16	-	-
Number of dorsal fin rays	10-12	12-14	9-12	10-15
Number of anal fin rays	8-11	10-12	12-17	13-19
Number of gill rakers on first arch	15-20 (slender)	14-17 (short and stubby)	18-25 (coarsely toothed)	24-35
Number of scales in the lateral line	-	-	121-148 (scales moderately large)	147-205 (scales small)
Other distinguishing features	Caudal peduncle narrow; Caudal fin shallowly forked	Caudal peduncle deep and rather flat; Caudal fin square-cut or slightly concave to slightly convex	A long scaly process in axil of pelvic fin; Adipose fin well-developed	Breeding males have a pronounced humpback

Source : Mills, 1991

Figure 2. **Image of Atlantic salmon (*Salmo salar*)**



Atlantic salmon (*Salmo salar)*

Source : Pål Thomas Sundhell

3. Life stages and generation Time

3.1. General aspects

16. The full life cycle of Atlantic salmon ranges from three to twelve years. The generation time in wild and domesticated Atlantic salmon strains has a genetic component, but it is strongly modified by environmental factors such as temperature, food abundance (cultivation: feeding regime) and density. Environmental determinants (temperature and flow regimes, predation, and food availability) also provide the potential for population-specific adaptation of juvenile salmon to natal streams. The combination of genetic and environmental determinants allows for the wide diversity found in naturally occurring Atlantic salmon populations throughout their native range.

17. The generation time varies among rivers and even between river sections, mostly as a result of variation in the mean age at smolting. Variation in growth rate results in variation in size and age at smolting and an association between an index of growth potential (combination of degree-days and day length) and mean age at smolting has been shown for Atlantic salmon throughout its range (Metcalfe and Thorpe, 1990).

3.2. Incubation

18. A spawning nest known as a redd is formed by the female in the gravel at the bottom of the river. Hatching usually occurs after 400-450 day-degrees (i.e. the sum of daily temperatures [^{o}C]), but this can be shorter for populations in the northern range of the distribution, where temperatures are consistently low for long periods. Incubation time correlates closely with climate, i.e. water temperature during incubation.

In warmer regions (southern range of the distribution) it may be only eight weeks, with spawning occurring late (December–February) and emergence of the fry occurring early (March–April). In cold rivers (northern range) the incubation period can be up to 8 months, with spawning occurring early (September–October) and emergence occurring as late as June due to the slow incubation process. The optimal temperature for incubation is between 1 - 10° C; below and above this range incubation success is generally reduced. Survival during this period can correlate positively with egg size, particularly if oxygen conditions in the gravel nest become stressful for the embryos (Einum et al., 2002a).

3.3. Alevin stage

19. After hatching, alevins live off their yolk sac, which is attached to their under surface. At this stage, which takes place in and around the gravel of the redd (15-30 cm below the river bottom), alevins become increasingly mobile. During the first days, alevins are positively geotactic and negatively phototactic, but as yolk sac absorption progresses they become negatively geotactic (movement towards the surface of the redd) and positively phototactic and rheotactic. The duration of the alevin stage depends on temperature and ranges from ca. 20 to 120 days. The time from fertilisation to emergence also varies with egg size, but the effect is small with large eggs taking a few days (ca. 3 days) longer than small eggs (Einum and Fleming, 2000a).

3.4. Fry stage

20. As yolk sac absorption nears completion the fry stage begins with emergence of fry from the gravel and the start of active feeding (mostly on invertebrates). Fry then begin to disperse from the area around the redd. Most of the fry disperse downstream (though the highest concentrations often remain near the spawning grounds), with pools being avoided. The fry stage ends when the fish settle and establish small territories, which they defend against conspecifics of the same year-class. Evidence suggests that both earlier emergence (prior residency) and body size can afford fry success in competing to establish a territory (Brännäs, 1995; Cutts et al., 1999; Harwood et al., 2003) and in subsequent survival (Einum and Fleming, 2000a; 2000b).

3.5. Parr stage and age at smoltification

21. Effective foraging and anti-predator behaviours correlate positively with survival (Einum and Fleming, 2001). The duration of the parr stage again depends on productivity, temperature, density, and on the social status of the individual (i.e. dominant individuals often attain faster growth than subordinate individuals; Harwood et al., 2003; Nislow et al., 2011). Faster growing juveniles generally go to sea at a younger age. Smoltification normally occurs at a minimum size of 10 cm fork length, but this varies among populations. As part of the population continues to grow through winter, juvenile salmon develop a bimodal length distribution. The upper modal group (UMG) is composed of larger fish likely to smolt the following spring. The lower modal group is composed of smaller fish likely to spend *at least* one more year before smolting; older smolts are usually larger at smolting than UMG-smolts. In productive rivers older smolts, which spend one or more extra years in freshwater, can reach a size of more than 20 cm. Bimodality in length frequencies is a phenomenon mainly observed in wild populations that produce 1 year old smolts.

22. Because smoltification is mainly size dependent, the proportion of early smolts correlates with temperature, density and productivity of the stream. Thus there is a general tendency for smolt age to increase with latitude, though the pattern differs between the European and North American continents (Metcalfe and Thorpe, 1990). Smolt age can vary between 1 and 8 years. In the southern range, the vast majority of a year class reaches the threshold size of 10 cm in the first year and most smolts are one year old. Smolts older than two years seldom occur. Generation time is therefore short. In central Europe

(e.g. Rhine, Loire), and in the other regions with a moderate climate like Ireland and southern British Isles, around 50% of the parr reach 10 cm after one year and emigrate as smolts. Age-one smolts measure usually between 10 and 15 cm. Two year old smolts reach 12–22 cm. Three-year smolts are rare (<1%). In the Gulf of Maine and Canadian Maritimes, Scotland and southern Scandinavia the majority of smolts are two and three year olds; one-year and four-year smolts are rare. In central Scandinavia, in parts of the Russian federation and parts of Canada (e.g. Quebec and Newfoundland) smolts age varies between 2 and 5 years. There are essentially no 1-year smolts produced naturally. In northern Scandinavia and northern Canada (Labrador and Ungava Bay) parr commonly need 4-8 years to reach the critical size for smoltification. Smolts of ages one and two rarely occur in these regions.

23. Atlantic salmon smolts emigrate from freshwater nursery areas during spring and early summer (March - August) to feed and grow in the North Atlantic Ocean. The timing of the transition from the freshwater ('parr') stage to the migratory stage ('smolt') is cued by photoperiod and water temperature, with photoperiod as the dominant cue (McCormick et al., 1998; 2002). For Atlantic salmon, the timing of the smolt migration has an important role in determining smolt survival in the marine environment, and it is believed that Atlantic salmon smolts are adapted to use environmental cues in rivers that may predict favourable ocean conditions for them to initiate downstream migration (Hvidsten et al., 1998, Thorstad et al., 2012, Otero et al., 2014). Hence, the timing of the freshwater emigration has likely evolved to meet environmental conditions in the ocean as these affect growth and survival of the post-smolts.

24. A recent analysis of spatio-temporal variations in the dates of downstream smolt migration in 67 rivers throughout the North Atlantic show that in addition to a latitudinal cline with southern populations migrating earlier than northern ones (e.g. Hvidsten et al., 1998) - the timing of migration differed strongly between the East and West Atlantic, with western populations migrating to sea at later dates than eastern populations at corresponding latitudes (Otero et al., 2014). After accounting for this spatial effect, the initiation of the downstream migration among rivers was positively associated with freshwater temperatures, up to about 10°C and levelling off at higher values, and the timing was also positive associated with sea-surface temperatures. Earlier migration occurred when river discharge levels were low but increasing (Otero et al., 2014). On average, the initiation of the smolt seaward migration has occurred 2.5 days earlier per decade throughout the basin of the North Atlantic. This shift in phenology matches changes in air, river, and ocean temperatures, suggesting that Atlantic salmon emigration is responding to the current global climate changes (Otero et al., 2014).

3.6. Post-smolt stage and sea age

25. Atlantic salmon spend one, two, three and sometimes four winters at sea. Those that spend more than one are known as MSW (multiple sea winters) fish. Five-sea-winter (5SW) fish are very rare, as well as 0SW fish. Individual fish within a population that grow faster prior to smoltification tend to have younger sea ages than those with slower pre-smolt growth rates (Einum et al., 2002b). The duration at sea is also stock-dependent and in part, genetically controlled. Recently, a study of 1SW and MSW Atlantic salmon populations from the three phylogeographic lineages of Atlantic salmon in Europe, based on using a 220,000 SNP-chip, has identified a gene that strongly affects sea age at maturity in salmon (Barson et al., 2015), Some populations consist mainly of grilse (1SW fish), others are dominated by 2SW fish (e.g. most populations in the river Rhine, French Loire-Allier, Danish Skjern, and Gulf of Maine, and many Norwegian, Scottish and Canadian Maritime populations). In some populations 3SW fish are lacking completely (e.g. many Irish populations). Long/large rivers frequently have multiple-sea-winter populations and shorter/smaller rivers less frequently so (Jonsson et al., 1991). Grilse populations dominate in small rivers, though there are exceptions. Thus migration distance alone does not explain the variability observed among populations. There are suggestions that changes in the grilse/MSW ratio can be explained by changes in oceanic temperature or feeding conditions at sea (Gudjonsson et al., 1995; Otero et al., 2012).

26. Growth in the marine environment is rapid. After one sea-winter, adult Atlantic salmon usually reach 50-75 cm total length. After two sea-winters, the fish reach 65-90 cm. 3SW salmon can measure more than 100 cm.

3.7. Lake age

27. The duration of feeding in lakes is also stock-dependent and growth tends to relate to the size of the lake (faster in larger lakes). Atlantic salmon spend from 1 to 9 winters in lakes (Klemetsen et al., 2003). Post-spawning mortality is low among resident individuals (dwarf forms are an exception) and repeat spawning common (one individual had 5 "spawning marks" (Smirnov, 1979)).

3.8. Age at sexual maturity

28. Sexual maturity is variable between sexes. In productive streams, males frequently reach sexual maturity at the parr stage during their second or third autumn. Maturity may be reached even during the first year at a size of less than 7 cm fork length. The frequency of males maturing as parr varies widely (range 2-100%), and appears to decrease with latitude (reviewed in Fleming, 1998). Females rarely mature as parr in anadromous populations. Females in landlocked/ouananiche populations, however, frequently mature at sizes smaller than that found in anadromous populations, and occasionally at sizes similar to that of mature male parr of anadromous populations.

29. In anadromous salmon populations having MSW fish, males often tend to mature at younger ages than females (i.e. males dominant numerically within the grilse component). However, some of the oldest and largest fish in these same populations may be males.

30. The persistence of a single year class in a stream (or the maximum age of a salmon) is generally shorter in the southern range than in the northern range. Repeat spawners are generally infrequent; however, in some populations over 40% of the spawners may be repeat breeders (e.g. historically Inner Bay of Fundy). The maximum life span in the wild is around 15 years.

Age structure:

1. In all salmonids, the life span of fish of northern populations is longer than in southern populations.
2. Males and females differ in the rate of sexual maturation; the early maturing age classes mostly comprise males.
3. Atlantic salmon males can reach sexual maturity in freshwater at the parr stage (as early as 0+ fish); some may subsequently stay in freshwater as resident parr, while others may migrate to the ocean to undertake an anadromous life cycle.
4. The age structure of different populations is not identical; the freshwater phase can last 1-2 years in southern populations and up to 8 years in far northern populations.
5. In the same population, age structure varies slightly from one generation to another, but one or two age groups usually remain dominant.

4. Reproduction

31. Salmon are known for their ability to return to the rivers in which they were born (usually more than 94-97 % accuracy; Stabell, 1984; Jonsson et al., 2003), a trait that segregates populations and leads to a variety of local adaptations. The low level of straying that does occur to neighbouring rivers may in some cases result in a *metapopulation* structure (i.e. a set of local breeding populations connected by exchange

of some individuals). The resulting network of local populations provides a balance between local adaptation and the evolutionary flexibility that results from exchange of genetic material among populations (NRC, 2004).

32. The return to freshwater to breed may occur from spring until fall, and in some cases as much as a year in advance of spawning (e.g. in Ungava Bay, northern Norway and Russian federation). Migration timing is a characteristic of individual populations (e.g. MSW fish entering before grilse) and environments (e.g. hydrological and temperature regimes, and length and physical difficulty of ascent). Upon entry, Atlantic salmon in some river systems remain for several months in the lower reaches of the river before ascending to the spawning grounds. In large river systems, it appears that those that enter earliest migrate the furthest upstream to spawn.

33. Spawning time, which is heritable, appears to be an adaptation to favourable conditions for spawning, embryo incubation, and juvenile emergence and subsequent feeding (Jensen et al., 1991). A female's spawning time will dictate the thermal regime her embryos experience during development and to a large extent, their hatching and emergence time from their gravel nest. Peak spawning times vary among populations from September to February (most common period is late fall), reflecting differences in water temperature regimes during incubation (Heggberget, 1988). Thus, northern populations frequently spawn before more southerly populations, and upstream populations may spawn significantly earlier than downstream populations in the same river system (Webb and McLay, 1996). Spawning within populations spans several weeks and can last as long as 10 weeks.

34. On the spawning grounds, the behaviour of the two sexes differ markedly, with female behaviour being shaped principally by natural selection for offspring production and survival, and male behaviour by sexual selection for access to matings (Fleming, 1996; Fleming and Einum, 2011). Females choose spawning locations within the river that provide favourable incubation environments for eggs (i.e. often the upstream end of riffles, having low concentration of fines and high oxygen permeability). She deposits her eggs within dedds that she creates by digging actions with her caudal fin. Once fertilised, the female covers the eggs immediately with gravel and begins preparation of the next nest. A female will construct 5-8 nests typically, and up to as many as 14, to deposit all her eggs in. The number of nests constructed increases with female size, as does their depth. Nest depth reduces susceptibility to destruction from superimposition by later spawning females, gravel shifts caused by flooding, and freezing. Once females have completed nesting, which takes a median of five to six days from start to finish, they do not overtly defend their site(s) in contrast to Pacific salmon, which do so until death. After spawning, female Atlantic salmon simply descend from the spawning grounds to a nearby pool or back to the mainstem river.

35. Female fecundity varies considerably both within and among salmon populations, as both egg number and size increase with body size (reviewed in Fleming, 1996). However, relative fecundity (i.e. eggs per kilogram body weight) varies much less (typically 1 200–2 000) and inversely with fish size (i.e. smaller fish have more eggs per kg than larger fish).

36. Male Atlantic salmon do not participate in nest acquisition or construction, but rather seek out and compete for access to spawning females. As a consequence, males spend considerably more time on the spawning grounds than females seeking breeding opportunities. While absolute sex ratio of anadromous fish (i.e. excluding mature parr) within spawning populations may vary from 20% to over 90% female (Fleming, 1998), the operational sex ratio on the spawning grounds (i.e. the number of sexually active males to females at any one time) is frequently male biased. This is because each female breeds for only 5-6 days, while each male has the capability to spawn rapidly and repeatedly over the several weeks of the spawning season. As a consequence, there is intense competition among males for access to spawning females, which has resulted in the evolution of specialised breeding traits in males, such as the hooked jaw or kype and an alternative male reproductive strategy (see next paragraph).

37. The intense competition among large anadromous males for access to breeding females (i.e. courting and fighting, with large size being advantageous), provided the opportunity for an alternative reproductive strategy to evolve. A proportion of males (2-100%) may mature precociously as parr, at less than a hundredth the weight of the anadromous males, and use their small size to sneak access to spawning females (i.e. rather than court and fight). The expression of the alternative strategy appears to have both a genetic and environmental (i.e. growth rate) component. Such males may also subsequently migrate to sea and return as a large anadromous male.

38. The larger size of anadromous males, and consequently greater ejaculate volume of sperm, typically affords them greater individual fertilisation success during spawning (averages 9-70% of the eggs) than mature parr (averages 3-14%; Fleming and Reynolds, 2004). However, mature male parr, as a group, can be responsible for fertilising a considerable proportion of the eggs within populations (11-65%; Fleming and Reynolds, 2004). As a result, they can increase the genetically effective size of the population and partly compensate for low returns of anadromous fish (males). The younger age at maturity compared to anadromous males also means that mature parr shorten generation times. However, they can also be vehicles for promoting genetic introgression (e.g. by escaped farm salmon; Garant et al., 2003), because they breed prior to migration to sea, where mortality can be high and selective.

39. Hybrids of Atlantic salmon and brown trout are found in all the regions where Atlantic salmon and brown trout are sympatric. The main factors contributing to the inter-specific hybridisation are thought to include sneaking by mature male parr, natural breeding by escaped and released cultured salmon, unstable river discharges, and overfishing. Experimental crosses suggest that the survival of F_1 hybrids can vary widely from little or no viability to full viability. The usual consequence of post-F1 hybridisation is the wastage of gametes.

5. Centres of origin and geographical distribution

5.1. Centres of origin

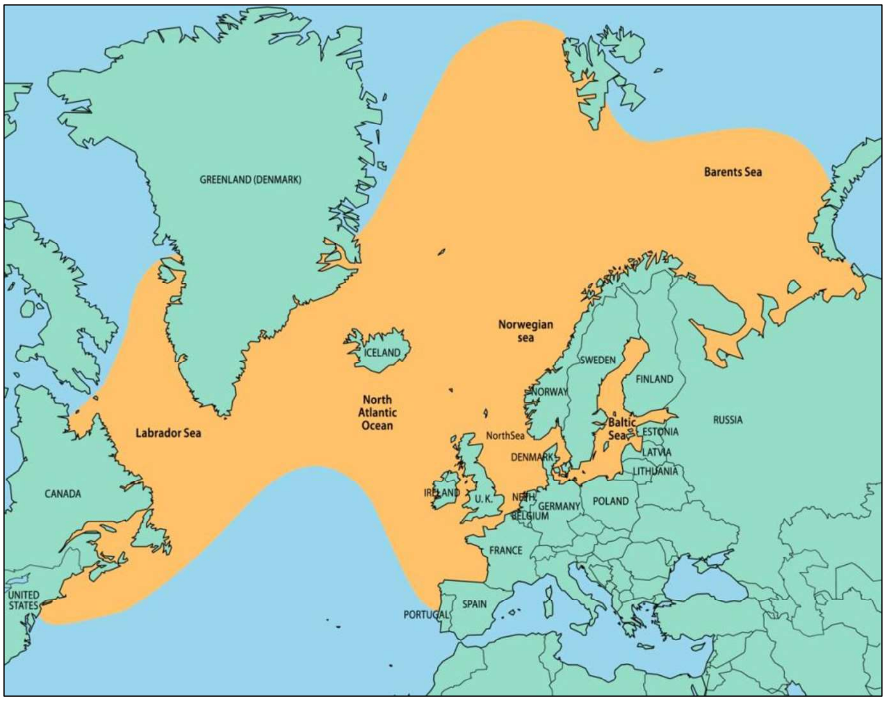
40. There is conclusive palaeontological evidence that the existing salmonid species appeared in the late Tertiary period, in the Pliocene, and became widespread in the Pleistocene, i.e. several million years ago. Most studies agree that salmonids originated in fresh water, but the evidence is sparse. There is some morphological and genetic data suggesting that Atlantic salmon evolved from brown trout (Dorofeeva, 1998), which would imply that the species appeared first in Europe where brown trout is widespread. Modern populations of the British Isles have the highest mitochondrial DNA (mtDNA) haplotype diversity (Verspoor et al., 1999), with the Kola peninsula being a secondary center of genetic diversity. The latter is an area of post-glacial mixing of Atlantic salmon from three refuges: “British”, “Baltic” and “North American” (Makhrov et al., 2005).

5.2. Geographical distribution of native populations

41. The native range of Atlantic salmon extends along both sides of the North Atlantic Ocean (Figure 3). In North America, it occurs from the Connecticut River in the south (a re-introduced population, completely dependent on artificial supplementation) to Sango Brook (55°53’N) in Labrador and into Ungava Bay (58°N). Historically, Atlantic salmon were likely present as far south as the Hudson River, but have since been extirpated from watersheds south of Maine. Similarly, Atlantic salmon once extended as far west as Lake Ontario, but were extirpated in the late 1800s, and are now confined to areas east from the Jacques Cartier River (71°45’W) near Quebec City. The Atlantic salmon distribution extends eastwards to Greenland (1 population), Iceland, the British Isles and continental Europe. In Europe, Atlantic salmon occur from the Kara River (Kara Sea, Russian federation) to the Douro River (northern

Portugal) and into the Baltic Sea basin. The northern distribution limit in Europe extends to just above 70°N.

Figure 3. **Geographic marine distribution of the Atlantic salmon in the North Atlantic Ocean**



Source: courtesy of Eva Thorstad and Kari Sivertsen

5.3. Naturalised populations

42. Introduced and free-living (i.e. self-sustaining) anadromous populations of Atlantic salmon are known only within their broad native range (i.e. North Atlantic). Most such introductions have involved the removal of migratory barriers (e.g. impassable waterfalls) that restricted access to watersheds or river sections within watersheds. However, in the 1950s Atlantic salmon were introduced to the Faeroes and have since become established in five rivers. Attempts to introduce Atlantic salmon to west Greenland rivers failed because of the low water temperatures. Greenland has only one river system in the south with an indigenous Atlantic salmon population.

5.4. Introduction efforts outside the natural distribution area

43. During the early 1900s attempts were made to introduce Atlantic salmon to some British Columbia (Canadian Pacific coast) watersheds in a deliberate attempt to establish runs for sport fishing. Nearly 200 introductions were made into 52 different water bodies and a total of 13.9 million eggs, alevins, fry or smolts were introduced. None of these introductions was successful in terms of establishing runs of Atlantic salmon on the British Columbia coast. In the United States there have been at least 170 attempts in 34 different states where Atlantic salmon were not native, including Washington, Oregon, and California (MacCrimmon and Gots, 1979). None of these efforts was successful. For example, in Washington State attempts were made from 1904 to 1991 by U.S. agencies to introduce and establish Atlantic salmon and not a single self-sustaining population was established.

44. Similar results have occurred with Atlantic salmon introductions in Australia, New Zealand, South Africa, Chile and many other countries. There has never been a documented successful introduction (i.e. resulting in a self-sustainable population) of *sea run* Atlantic salmon outside of their natural territory where other native salmon species were present. There is a successful introduction reported from New Zealand, although the Atlantic salmon releases resulted only in non-migratory populations (Waiau system). However, incipient feral Atlantic salmon populations (i.e. presence of juveniles from natural spawnings) have been reported from rivers in British Columbia, South America and the sub-Antarctic Kerguelen Islands (MacCrimmon and Gots, 1979; Ayllon et al., 2004).

6. Habitats, migration, and ecological niche

45. The physical habitat requirements of the Atlantic salmon vary from life stage to life stage. Three major stages can be identified: (1) spawning and incubation; (2) juveniles in freshwater; and (3) post-smolts and pre-adults at sea.

6.1. Spawning habitat

46. Habitat requirements for spawning and incubation can vary among regions and populations. The major requirement for adult salmon is an accessible spawning area, which is of adequate size for digging nests and provides a safe location for these large fish. Shelter nearby is also important for salmon as they wait to spawn (e.g. undercut banks, overhanging and submerged vegetation, submerged objects like logs and rocks, floating debris, deep water, turbulence and turbidity; Bjorn and Reiser, 1991). The gradient of spawning rivers usually is 3 per cent or less. The preferred spawning site is a transitional area between pool and riffle where the flow is accelerating and the depth decreasing, and where gravel of a certain coarseness is present (Petersen, 1978; Bjorn and Reiser, 1991). In such a location, downwelling water fluxes through the gravel are typical, providing a certain level of dissolved oxygen in the immediate vicinity of the eggs. However, wide ranges of water flow and depths are reported. In the Russian river Varzuga, Atlantic salmon spawn at depths of 2 m. Minimum depth seems to be 10-15 cm (depending on the size of the spawning fish). Areas with upwelling groundwater may also be selected as spawning sites. Spawning by Atlantic salmon in lakes is rare, but has been documented in the non-anadromous ouananiche (Cowan and Baggs, 1988).

47. The particle size distribution of the sediments at the spawning sites is normally dominated by gravel in the 32 -128 mm range but varies within and between rivers, dependent on local- and catchment-scale characteristics (Petersen, 1978; Greig et al., 2005; Miller et al., 2008). During the incubation of ova and the emergence of fry, the intergravel physio-chemical environment is critical, and adequate flow of water through the gravel is especially important. The proportion of fine sediment/sand in the gravel must, therefore, be low, i.e. < 10-20% by weight (Petersen, 1978; Chapman, 1988; Crisp and Carling, 1989) to facilitate oxygen availability (Greig et al., 2007). Incubation, hatching and absorption of the yolk sac takes place some 10 - 30 cm deep in the gravel (De Vries, 1997). Under normal conditions mortality at this stage is low (< 20 %) but there is a risk of additional mortality through scour and dewatering. When absorption of the yolk sac is almost complete, the fry emerges from the gravel bed to start feeding. Mortality rates are very high (68-88 % in the first 17-28 days; Einum and Fleming, 2000b) due to displacement, starvation and predation. Emergence from the gravel and first-feeding are thus periods of intense selection.

48. During the incubation of ova and the emergence of fry, the intergravel physio-chemical environment is critical, and adequate flow of water through the gravel is especially important. The proportion of fine material in the gravel must, therefore, be relatively low. Petersen (1978) found that if the content of sand (i.e. grain size less than 2 mm) exceeded 20 per cent by weight, the permeability was reduced to zero. Other authors state that productive, good quality spawning gravel contains less than 5 per

cent fines (grain size less than 0.8 mm) while unproductive gravel sites are characterised by more than 30 per cent fines (reviewed in Fleming, 1996).

49. Incubation, hatching and absorption of the yolk sac takes place some 10-30 cm deep in the gravel. Under normal conditions mortality at this stage is low (< 20 %). When absorption of the yolk sac is almost complete, the fry emerges from the gravel bed to start feeding. Mortality rates are very high (68-88 % in the first 17-28 days; Einum and Fleming, 2000b) due to displacement, starvation and predation. Emergence from the gravel and first-feeding are thus periods of intense selection.

6.2. Juvenile freshwater habitat

50. For the interpretation of spatio-temporal distribution patterns of juvenile Atlantic salmon within freshwater, it is necessary to distinguish between habitat preference, which is based on the habitat requirements of the individual (looking for its optimal micro-habitat), and habitat utilisation, which is a compromise (trade-off) between the innate requirements and how these can be met by availability within the habitat.

51. Freshwater habitat use includes fluvial, lacustrine and estuarial environments. Often individual fish will utilise several habitat types during thier freshwater residency. For example, parr may use small tributaries to spawning rivers as feeding areas during their first summer of life and as they get older move to the mainstem river or even into small lakes. The highest population densities are frequently associated with rivers that have moderate temperatures and flows. Such rivers contain riffle, run and pool sections in lower stream orders (i.e. tributaries and smaller rivers) and are dominated by moderate size "cobble" stones. Parr are highly territorial and territory size depends on food abundance, substrate coarseness (instream cover, visual isolation) and social status. Heggenes (1990) considered water depth, water velocity, and streambed sub-stratum cover to be the principal physical variables for juvenile salmon *in situ*. Most relevant studies refer to one or more of these variables in discussions of habitat characteristics. Connectivity between a variety of habitats will also be important for providing alternative shelter/feeding opportunities seasonally and for providing a conduit to pass from one habitat to another (e.g. rearing stream to estuary).

52. Atlantic salmon inhabits cool temperature streams and can tolerate freshwater temperatures ranging from 0 to 28°C. Under laboratory conditions (given food in excess), summer acclimatised juvenile salmon generally show positive growth from 5-7 to 24-26°C and grow fastest at 16-20°C. The thermal range for growth declines with reduced food consumption, whereas the temperature for maximum growth appears not to change. Winter acclimatised salmon can under laboratory conditions however obtain positive growth in temperatures at least as low as 1°C (Forseth et al., 2011). Feeding and growth rates are highest in spring and early summer. Feeding rates decrease with falling temperatures in autumn, but juveniles also feed during winter (Johansen et al., 2011). At high temperatures, juveniles may cease feeding and seek refuge from thermal stress. Temperature, food availability, river discharge, season, and density are the factors correlated most strongly with growth of juvenile salmon in fresh water. Growth is also state-dependent, with growth being accelerated or depressed according to physiological needs or life-history stages (Forseth et al., 2011).

53. Atlantic salmon have a minimum pH tolerance level between pH 5.0–5.4 depending on other river variables (e.g. aluminium levels); pH tolerance may be population-specific (Donaghy and Verspoor, 1997).

54. Fry and parr densities vary considerably in natural streams. The availability of suitable habitat is often considered the limiting factor. Mean salmon densities (m^2) for a number of river systems in Great Britain and Ireland have been reported to range from 0.036 to 2.06 for young-of-the-year and 0.027

to 0.334 for one-year-old parr (Kennedy, 1988). The highest reported density of fry was more than 30 per 1 m^2, whereas the corresponding density of parr after the first summer can be 4-5 per 1 m^2 (Veselov and Kalyuzhin, 2001). These values come from salmon habitat of high quality. Conversely poor habitats support fewer fish.

55. Fry and underyearling parr have been found to occupy locations other than those occupied by older and larger parr. For some areas, significant differences between summer and winter microhabitats have been reported (Cunjak, 1988). Juvenile salmon have been observed in water flow velocities from 0 to 80 cm/s, with the highest densities in areas of 10-75 cm/s velocity. Pebbly riffles without boulders are considered to be prime nursery habitat for salmon less than 7 cm long (reviewed by Gibson, 1993).

56. The proportion of 0+ to 1+ age-group parr decreases as depth increases between 20 and 40 cm; yearling or older parr are rarely observed in riffles of less than 20 cm depth and without boulders (particle size > 256 mm) (Heggenes, 1990; Gibson, 1993; Schneider, 1998).

57. Experiments indicate that as parr grow there is an increasing preference for deeper and swifter parts of riffles. At 8-9 cm in length, 80-90 per cent of underyearlings prefer cobble/boulder habitats (particle size > 6.4 cm) of more than 30 cm depth. In general, juvenile salmon occupy shallow fast flowing water with a moderately coarse substrate combined with overhead cover provided by surface turbulence. In summer, fry occupy shallower and faster flowing sections of rivers with slightly smaller sized gravel than that selected by parr (reviewed by Heggenes, 1990; Gibson, 1993).

58. Most studies on the microhabitats of juvenile salmon describe the distribution and location of the fish during the summer months. However, the habitat utilisation changes when the water temperature falls in the autumn. In Scottish rivers, juvenile salmon tend to leave the shallow riffle habitats during the autumn and move to deeper water in pools, reappearing in the shallow water when the temperature rises to 6-7° C in spring (Mills, 1989). Generally, salmonids prefer shelter and low water velocities during winter and movement out of summer habitats may not occur in autumn if summer habitats provide appropriate overwintering conditions (reviewed by Huusko et al., 2007).

Summary:

- Underyearling parr (< 7 cm TL) are most common in shallow (< 15 cm) pebbly riffles with broken water surface
- Larger parr prefer riffles deeper than 20 cm with coarse substrate and some will migrate to lacustrine habitats (a niche shift commonly observed in some regions, e.g. Newfoundland)
- Depth preference and preference for coarse substrate increase with body size
- Below temperatures of 6-7 ˚C small parr shelter among coarse substrate or move to pools

(review by Gibson, 1993).

6.3. Marine habitat

59. The transition from freshwater to marine environments for Atlantic salmon can be a critical period affecting survival. It is generally believed that water temperature is the main proximate variable controlling the onset of smoltification (i.e. process of preparing for the transition from fresh to salt water), though photoperiod is also considered important. While the time spent in the estuary or inshore areas near the natal river is thought to be brief (hours to a few days), it can be critical for postsmolt survival.

60. In Europe, the fish appear to leave their natal rivers and head northwards with the shelf edge current towards the Norwegian Sea, where they appear to be distributed over large areas. Evidence suggests that a relatively large proportion of the European MSW salmon move into the west Atlantic.

Grilse spend the winter mostly in the Norwegian Sea east of Iceland. Populations from northern Europe may move as far north as Spitsbergen and far eastwards into the Barents Sea.

61. Baltic populations are restricted to the Baltic Sea, where they live in brackish waters and an environment very different from the oceanic conditions of the North Atlantic.

62. Western Atlantic populations tend to stay in the western Atlantic. In late summer and autumn, non-maturing salmon are found inshore along the northeast Newfoundland and Labrador coasts, at West Greenland, in the Labrador Sea and in the Irminger Sea including the east Greenland coast. Most salmon destined to be MSW fish range over much of the Northwest Atlantic, while those 1SW (grilse) salmon do not, staying closer to home. At Greenland, for instance, only salmon that would mature as 2SW and older are caught.

63. The distribution of Atlantic salmon in the sea appears to reflect environmental factors such as surface temperature and currents, and food availability. The marine environment can have a strong influence on survival and thus recruitment to, and the dynamics of Atlantic salmon populations.

6.4. Migration

6.4.1. Smolt migration

64. Salmon are flexible and variable in their migration patterns - temperature and season (spawning time) seem to be the governing factors.

65. After the onset of smoltification when young salmon start their seaward migration, their displacement in the rivers is largely nocturnal at low water temperatures and affected by factors influencing water currents. At higher temperatures and at high latitudes with 24 h daylight, smolts may migrate at all times of the day (Davidsen et al., 2005; Ibbotson et al., 2006). The downstream migration was previously believed to result from passive transportation by the currents, but several studies have now documented that active migration also occurs, with smolts swimming faster than the currents. Progression rates of smolts in freshwater may vary considerably with reported speeds of 0.2 to 60 km/day (Thorstad et al., 2012). The seaward migration often starts in cool temperatures in spring, but the temperature varies among populations and also among years in the same river (Jonsson and Jonsson, 2011). Depending on the geographical factors (temperature, day-length, discharge, feeding opportunity), smolt migration can take place between March (southern range) and August (northern range). Timing of seaward migration appears adapted to favourable temperature and feeding conditions at sea (Hvidsten et al., 1998) and smolts from northern rivers generally migrate later than smolts from southern rivers.

6.4.2. Post-smolt migration

66. In contrast to the relative uniformity of the riverine environment, the post-smolts encounter a complexity of environmental conditions in the estuaries, fjords and coastal waters, where the tides and/or winds influence the speed and directions of the surface currents, as well as the distribution of different water layers and any fronts that may evolve between these waters. The Atlantic salmon post-smolt migration is an active process with an overall seaward vector, but the migration pattern shows great individual variability with some post-smolts taking a direct route towards the sea whereas others show more irregular movement patterns. Progression rates (how fast the post-smolt travels between two points on their route) vary among sites, years and groups of fish studied (Thorstad et al., 2012). Progression rates of wild Atlantic salmon post-smolt in coastal areas range from less than 2 km/day up to more than 30 km/day. True swimming speeds are usually higher as post-smolts do not always take the shortest possible route. Progression rates may also depend on the movements of the water currents. In Norwegian fjords (which are up to 200 km long) most fish may spend from < 1 week and up to 4 weeks before they enter the

open ocean (Thorstad et al., 2012), whereas the residence period in the 230 km long Bay of Fundy in Canada may be more than a month (Lacroix, 2008). Migration of post-smolt Atlantic salmon in coastal waters occurs during both day and night. Post-smolts usually swim close to the surface during the early marine migration (0-3 m depth), but make irregular dives down to about 6.5 m depth. They have been shown to swim closer to the surface at night than during the day (Thorstad et al., 2012).

67. Post-smolts have the capacity to travel rapidly over long distances. Ocean recaptures of post-smolts, that were individually tagged leaving their rivers as smolts, show minimum progression rates of between 6 and 26 km/day (Shelton, 1997; Holm et al., 2003).

68. Europe: The observed distribution of post-smolts considered in relation to the prevailing hydrographic regime suggests a close correlation between strong northerly or north-easterly surface currents, temperature, salinity and post-smolt migrations in the north-east Atlantic (reviewed by Holm et al., 2003 and Hansen et al., 2003). Also, tidal streams are used. The general patterns indicate that the use of currents enables the post-smolts to reach their northern feeding grounds with the least expenditure of energy. These currents may act as a “food-stream” as well, with a high concentration of potential prey (sand-eels and invertebrates in coastal areas; herring, blue whiting, amphipods and other pelagic species in oceanic areas), which post-smolts feed on opportunistically. European Atlantic-going Atlantic salmon migrate north along the Norwegian Coast. Atlantic salmon of Iberian, French, and German origin have been recaptured in Irish coastal waters. There is evidence that post-smolts from southern Europe (Iberian peninsula, France, Germany, Denmark and British Isles) use a migration route along the Faroe-Shetland Channel and western sector of the Norwegian Sea. A larger proportion of post-smolts from northern Europe (principally Norway) migrate through the eastern sector of the Norwegian Sea. Far north populations (Norway, Russian federation) migrate westwards through the Barents Sea, or may use the Barents Sea as a rearing area.

69. Baltic sea: Baltic populations are restricted to the Baltic Sea and rarely migrate into the Atlantic ocean. The main feeding areas of Baltic salmon are the Baltic Main Basin and the Gulf of Finland in the south and the Bothnian Sea in the north.

70. The United States and Canada: Postsmolts in the northwest Atlantic Ocean tend to move up into the Labrador Sea during their first year at sea for feeding. An exception is thought to be salmon of the Inner Bay of Fundy, which may remain within the Bay and surrounding area. Because many postsmolt salmon are found in the Labrador Sea within four months of leaving their home rivers, this area is thought to be an important nursery habitat for salmon during their early marine life. Water temperatures during this period have been shown to influence postsmolt survival and growth, through effects on the salmon themselves and on the ecosystem they inhabit. Salmon in this region are found most abundantly in regions where sea surface temperatures range from 4 to 10 °C. They also tend to inhabit mostly the upper part of the water column, but do make deep dives probably in search of prey.

6.4.3. Spawning migration

71. The salmon's homing ability is the basis for the classification of the populations. Over the generations these populations have developed different inherited characteristics and have thus become adapted to their watercourse through natural selection.

- The time of entry of the main runs of salmon varies from river to river and runs peak at different times in different rivers.
- The spawning migration peak may correlate with mean monthly sea and river temperatures during spring: salmon arrive earlier when temperatures are higher and later when temperatures are lower (Dahl et al., 2004).

- MSW-fish often enter rivers in spring. Grilse (1 SW) runs are often recorded in summer and autumn.
- Some fish enter rivers up to 13 months before spawning (reasons unclear).
- Particularly in large river systems (e.g. Connecticut, Loire, Rhine), salmon enter all year round - but all year return patterns are reported from many small rivers as well.
- In Arctic regions (Canada, Russian federation) constraints to movement of salmon are imposed by sea and river temperatures (=> peak run in late summer).
- Few fish enter rivers for overwintering, without spawning (Berg, 1964).

72. The upriver spawning migration of wild Atlantic salmon takes place in three phases: (1) a migratory phase consisting of direct or step-wise movement to or close to the position that will be held at spawning; (2) a (short) search phase with repeated movements both up- and downstream at or close to the position held at spawning; and (3) a holding phase with little or no movement until the spawning. After spawning the fish move down into pools of the river, where they hold before exiting the river that fall or more often, the following spring.

73. Farmed salmon escapees are "homeless" and usually stray to rivers nearby. In the eastern Atlantic, escaped smolts are usually transported north by marine currents, so straying normally occurs north of the escape sites.

6.5. Ecological niche (limiting environmental conditions)

74. Phenotypic plasticity bespeaks the great ability of this species to adapt to variable conditions and rigorous environments that are characteristic of northern latitudes. The life history of a local Atlantic salmon population can vary dependent upon water temperatures, photoperiod length, stream productivity, ocean productivity, and a host of other environmental factors. One genotype may display a variety of phenotypic life histories, depending on environmental conditions (reviewed in Hutchings, 2011). Additionally, there is evidence that Atlantic salmon populations have evolved local and regional adaptations that are genetically based, due to the relative breeding isolation of populations returning to home streams or even stream segments for mating (reviewed in King et al., 2007).

75. Atlantic salmon may be exposed to widely differing environmental conditions across the species range. At some point, one or more physical, chemical, or biological factors likely become limiting and adversely affect a critical fitness trait such as survival, growth or reproduction. As discussed earlier in Sections 6.1-6.4, optimal and limiting environmental conditions may differ considerably with lifestage and/or life history phase, geographic location and habitat (e.g. such as whether the immediate environment is a freshwater river or the open ocean), and season.

76. Potentially limiting environmental conditions may be of a physical, chemical, or biological nature. Examples of these include:

- Physical – water temperature, turbidity, substrate type, flow
- Chemical – water chemistry (e.g. pH, dissolved oxygen, salinity) and contaminants
- Biological – food availability, competition, predators, pathogens

77. Water temperature is perhaps the most important single factor controlling the overall natural distribution of Atlantic salmon and affecting this species' life history either directly or indirectly. Water temperature affects embryo development, fish growth and survival directly, but may also influence migratory behaviour (e.g. emigration of smolts), habitat utilisation, and other aspects of life history which may indirectly affect growth, reproduction and survival. For example, water temperature may indirectly

affects salmon growth and survival by influencing the distribution of plankton assemblages and the prey associated with them, which in turn influences food availability for the salmon.

78. In Atlantic salmon, like other salmonid fishes, the efficiency of the conversion of yolk to body tissue is temperature dependent (Heming, 1982; Petersen and Martin-Robichaud, 1995) and declines noticeably at temperatures of 12°C and above (Gunnes, 1979; Beacham and Murrary, 1990). The optimum temperature for Atlantic salmon embryo development is near 6°C (Petersen et al., 1977) and the upper thermal limit near 16°C (Ojanguren et al., 1999). As noted in section 6.2, Atlantic salmon can tolerate temperature extremes as great as 0 to 28ºC, but depending on the lifestage, the optimal temperature can be much narrower. Upper lethal temperatures in Atlantic salmon may vary by as much as 3ºC among individuals (Elliott, 1991) and the upper temperature limit for feeding in fresh water by juveniles is 22.5 ± 0.3°C (Elliott, 2006). Maximum growth occurs at 16-20ºC (Elliott, 1991; 2006; Forseth et al., 2011). Low flow conditions caused by summer droughts in combination with high water temperatures, may be particularly limiting. In northern regions, low temperature may be the limiting environmental factor, with a cessation of growth normally below 4-7ºC in juveniles (Jonsson et al., 2001; Elliott, 2006). In the marine environment, postsmolts seem to prefer a range of 9-11ºC (Todd et al., 2011) and can achieve high growth rates at 10-18ºC (Handeland et al., 2008). There is widespread evidence that the marine distribution of Atlantic salmon is dependent on temperature (Reddin and Shearer, 1987) and that marine mortality is temperature-related (Hansen et al, 2003); however, as pointed out by Potter and Crozier (2000), none of the studies to date has demonstrated a clear causal relationship.

79. The concentration of dissolved oxygen (DO) in water is inversely related to temperature, and as such, is an additional stress that may be associated with high temperature conditions. The incipient oxygen level where juvenile Atlantic salmon begin to show stress affecting swimming ability is 4.5 mg L^{-1} O_s (Davis, 1975). It is suggested that oxygen concentrations not fall below a single-day mean of 8 mg L^{-1} for spawning fish, while levels of 5.0–6.5 mg L^{-1} are acceptable for adult fish when not spawning (Binkley and Brown, 1993). For embryos, critical levels to meet 0_2 demands depend on temperature and life stage, ranging from ca. 0.8 to 7.0 mg L^{-1} O_s, with higher demands during the later stages of embryo development just prior to hatching (Davis, 1975). Survival during embryogenesis and during the hatching period appear to be limited primarily by oxygen supply and secondarily by water exchange, both having highly significant effects (Hamor and Garside, 1976). Availability of oxygen for embryos is tied directly to water flow through the incubation gravel and as such, is affected by the presence of fines in the gravel (Petersen, 1978; reviewed in Fleming, 1996).

80. Embryos and alevins are highly sensitive to acidification and are affected detrimentally by pH lower than 5.5 and cannot tolerate a pH of much less than 4.5 (Petersen et al., 1980; Lacroix, 1985). Increased acidity increases the mobility of toxic metals, particularly aluminium and as such, is affected by local geology. Older freshwater life stages are also quite susceptible. For instance, low pH during the smoltification process can have subsequent detrimental effects resulting in mortality during the ocean migration (Magee et al., 2003; Rosseland and Kroglund, 2011). Little is known about the effects of pH in marine waters (7.9-8.3 in open ocean surface waters), which are typically much higher than those in fresh water, though pH have been decreasing (ocean acidification) in recent decades.

81. Salinity tolerance in Atlantic salmon is size dependent and the capability of tolerating full strength marine waters does not occur until after smoltification (physiological preparation) from ca. 10 cm in body length. Earlier life stages, however, can tolerate brackish waters (Cunjak, 1992).

82. Salmon are susceptible to deteriorating water quality as a result of both direct point-source discharges and diffuse or non-point-source pollution such as heavy metals and organic chemicals arising from land-use practices or industrialisation (reviewed by Hendry and Cragg-Hine, 2003).

83. Salmon can be affected by prey availability at all life stages where they feed exogenously, and prey availability will be affected by environmental conditions, such as temperature, water chemistry and photoperiod, and both intra- and interspecific competition for such resources.

84. Similarly, predators (other fishes, birds and mammals; reviewed in Ward and Hvidsten, 2011), parasites (e.g. sea lice and *Gyrodactulus salaris*; reviewed in Finstad et al., 2011; Harris et al., 2011) and pathogens (bacterial and viral; reviewed in Harris et al., 2011) have considerable potential to affect Atlantic salmon populations. Their effects will be modulated by environmental conditions, both directly and indirectly, through any associated stress the fish may be under.

85. When this document was initially conceived it was assumed that the ecological niche of locally-adapted wild Atlantic salmon could be defined, at least in broad terms. The genetic basis for the phenotypic traits of locally-adapted wild Atlantic salmon is elucidated through the genome projects (Part III), and this body of data and information may provide a basis for comparing wild Atlantic salmon to genetically engineered lines of Atlantic salmon.

86. Despite the extensive current and growing body of knowledge on Atlantic salmon, there is still insufficient information to adequately describe the critical or limiting environmental conditions controlling the survival and distribution of this species. In addition, the underlying genetics that allow for phenotypic adaptations to those limiting environmental conditions has not been adequately characterised.

87. Clear correlations of adaptive phenotypes with specific genes do not yet exist and may be available only partially in the future, due to the complications of the genetic heterozygosity and resultant phenotypic plasticity present and essential in wild populations of this species (Part III). See Devlin et al. (2006) for a discussion of environmental risk assessment of transgenic fish with a recognition of these complications. It is extremely difficult to make a convincing case that specific genes are ‘for’ a given, relatively well-defined, trait (Kaplan and Pigliucci, 2001). In addition, determining the genetic underpinnings of many traits may be difficult, if not impossible, because some of the variation among individuals, populations and species is traceable to a certain number of regulatory elements (generically defined as any gene producing a product whose function is to turn on or off the action of other genes), or to the regulatory regions upstream of genes known to play important roles in development (Pigliucci, 2003).

7. Population dynamics

88. Populations of Atlantic salmon vary in size over time, and year-to-year variation in environmental conditions is likely to be causing variation in survival rates both in freshwater and at sea (Hutchings and Jones, 1998; Einum and Nislow, 2011). 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 of Atlantic salmon, and such compensatory mechanisms exert a strong regulatory effect on populations (Einum and Nislow, 2011). Competition among individuals for limited resources such as food or space (e.g. for access to feeding territories or shelters) increases with fish density. Such competition can influence fish survival either directly (by increasing fish mortality) or indirectly due to density effects on growth rates and thus fish size-at-age. However, several environmental factors may also influence population growth rates directly through density-independent mortality. Such factors have constant *per capita* effects, and operate independent of the population density. For example, large-scale climate oscillations in the marine environment appear to have such strong but density-independent effects on adult Atlantic salmon stock size (Todd et al., 2011).

89. There is considerable evidence for density dependence in the freshwater life stages of Atlantic salmon (Milner et al., 2003), which implies that there is an upper limit to the number of smolts produced in

a given river system (Einum and Nislow, 2011; Hindar et al., 2011). Results from a number of recent studies support the idea that competition for food and space among similar aged fish, especially age-0 fish, is an important mechanism underlying population dynamics and population regulation in Atlantic salmon (Nislow et al., 2011). Studies from Canada indicate that the timing of population regulation varies among populations (Gibson, 2006). Density-dependent effects appear to be manifested rapidly in single age-classes in some populations, but to extend over multiple age-classes in other populations. The reasons for these differences among populations is poorly understood.

90. Density dependence in Atlantic salmon populations in the marine environment is relatively unstudied, but thought not to be strong if it exists at all. Density-dependent mortality at sea is not likely because the population density is assumed to be far below the assumed carrying capacity for Atlantic salmon in that habitat (Jonsson and Jonsson, 2004), an assumption that is supported by empirical evidence from some populations (e.g. Jonsson et al., 1998). Other density-dependent effects are however possible, such as density-dependent predation on migrating smolts in estuaries or adults prior to upstream migration for spawning.

91. Variability in freshwater survival may appear to be less than that in marine survival because of compensatory process in freshwater that can potentially buffer some of the variability (Milner et al., 2003). That is, decreased survival at certain freshwater life stages can result in increased survival at others due to density-dependent processes. Compensatory survival in fresh water results from competition for limited resources, including food and space. Thus, populations are regulated more strongly by density dependent processes in freshwater than in marine environments and variability in marine survival (due to density-independent factors) appears to be more important for determining overall population size.

92. Egg-to-smolt survival rates in Atlantic salmon have been observed to range from as low as 0.1% to as high as 6.5% (Klemetsen et al., 2003). Estimates of survival during the marine phase have often been more difficult to obtain because adults are enumerated back to the river and have been exposed to both natural and fishing mortality factors. There are a limited number of stocks for which the return rates of smolts to adults have been measured (Chaput, 2012). In a few instances, the return rates can be inferred to represent survival rates at sea, because the adults are almost entirely 1SW maturing salmon. In all other cases, where there are two or more ages at maturity, the return rates of smolts to 1SW are the product of the proportion of the smolts destined to mature as 1SW salmon and the first year survival at sea. In the North Atlantic, return rates of 1SW salmon are generally higher than those of 2SW salmon (Chaput, 2012). The highest measured return rates of 1SW salmon in predominantly 1SW stocks are generally in the range of 6–12%, whereas in MSW salmon stocks, return rates of 1SW salmon are in the range of 1–6% and for 2SW salmon, in the range of 1–3%. The return rates of European stocks are generally higher than for North American stocks, with return rates to the coast for smolts from the River Bush (1SW stock) being as high as 35% (Crozier and Kennedy, 1994) and return rates to the coast for 1SW fish from other stocks generally being > 10%. There is evidence from hatchery smolts that body size is an important determinant of survival, but its influence for wild smolts has been poorly studied and patterns appear equivocal, with evidence for a role in some populations but not others (Friedland et al., 2009; reviewed in Todd et al., 2011).

8. Population status and trends

8.1. Status of populations (by country)

93. The status of Atlantic salmon worldwide was assessed by Parrish et al. (1998) and by World Wildlife Fund (WWF) (2001). Parrish et al. (1998) 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. Generally, stable populations (no consistent decline in returns) were

found in northern areas of the distribution range, whereas more southerly populations showed declining trends or were extirpated (no returns for at least 10 years). WWF (2001) collated information on 2600 rivers from national representatives in all countries holding self-reproducing populations of wild salmon. Information was considered sufficient for a rough classification in 2005 rivers. Atlantic salmon populations are considered extinct from 309 rivers worldwide (15%), 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. On the other hand, Atlantic salmon populations are considered healthy in 867 rivers (43%), most of which are located in Iceland, Scotland, Norway and Ireland (WWF, 2001). The WWF classification may, however, provide misleading information at smaller scales (Hindar et al., 2011) as the proportion of rivers with unknown status in this survey was rather large in the Russian federation and Canada.

94. The North Atlantic Salmon Conservation Organization (NASCO) has defined the conservation limit in Atlantic salmon fishery management as the spawning stock level below which recruitment starts to decline significantly (NASCO, 1998, see Hindar et al., 2011). The precautionary approach then dictates that the populations should be maintained above the conservation limit by use of a management or spawning target, that is the spawning stock level that ensures population viability. Such conservation limits are regularly applied in assessing status of Atlantic salmon by the International Council for the Exploration of the Sea (ICES) and national authorities. The assessments differ in detail from assessments of whole stock-complexes down to assesments for stocks in individual rivers, and are mainly used as a basis for catch advice for mixed-stock marine fisheries and catches in individual rivers.

95. ICES perform yearly assessments of several stock-complexes in the North East Atlantic Ocean that form the basis for catch advice for mixed-stock marine fisheries (ICES, 2012a). For each stock-complex assessments are made for both 1SW- and MSW-salmon. In the latest assessment, the number of spawners of 1SW- and MSW-salmon from the northern North East Atlantic stock-complex (populations from Russian federation, Finland, Norway, North & East Iceland, and west-coast Sweden) are considered to be at full reproductive capacity and so is MSW-salmon from the southern North East Atlantic stock-complex (populations from United Kingdom, Ireland, France, South & West Iceland), while 1SW-salmon from the southern North East Atlantic stock-complex is considered to be at risk of suffering reduced reproductive capacity. Assessment at the stock-complex level can, however, mask the regional and river-specific situations of Atlantic salmon populations (Chaput, 2012). In some parts of the North Atlantic the abundance of Atlantic salmon has declined by much greater amounts than suggested by stock-complex assessments, and the abundance of spawners is much lower than interpreted by such (Chaput, 2012). This poses particular threats to stocks that are at low abundance and subject to other threats unrelated to fishing, such as freshwater habitat degradation.

96. ICES also provides updated status for salmon stocks at the national level and/or compliance with river-specific conservation limits for individual river stocks for the countries where such limits are established. In 2011, Russian federation, Norway (for 2010), Iceland, UK (North Ireland & Scotland) met national conservation limits (CLs) for both 1SW- and MSW-salmon (ICES, 2012a). Ireland and UK (England & Wales) were below national CLs for MSW- and 1SW-salmon, respectively, whereas France, Sweden and Finland/Norway (the large River Teno/Tana) did not meet such national CLs for either 1SW- or MSW-salmon.

97. Assessment for individual rivers in the North East Atlantic showed that salmon in 7 of 8 (88 %) rivers in Russia met their river specific conservation limit in 2011. The figures for other countries were: 162 of 211 (77 %) rivers in Norway (for 2010), 11 of 28 (39 %) rivers in France, 58 of 141 (41 %) rivers in Ireland, 2 of 7 (29 %) rivers in UK (N. Ireland), and 41 of 64 (64 %) rivers in UK (England & Wales).

98. In North America, ICES assesses the status of populations in six regions (Labrador, Newfoundland, Quebec, Gulf of St. Lawrence, Scotia-Fundy and the United States) and within each region individual river stocks are also assessed. The latest assessment showed that 2SW-salmon spawner estimates were above their conservation limits in Newfoundland and Gulf of St. Lawrence, marginally below in Quebec, and below the conservation limit for the other three regions, as well as overall for the North American stock-complex (ICES, 2012a). The latest assessment was somewhat higher than assessments in previous years. To date, 1082 rivers have been identified in eastern Canada and 21 rivers in eastern USA, where Atlantic salmon are or were present within the last half century. Assessments were reported for 74 of these rivers in 2011 and 45 of the rivers (61%) exceeded their river-specific conservation limit (estimated egg deposition by all sea ages combined), whereas 15 of the rivers (20%) reached less than 50% of their CLs. Individual river stocks which are failing to meet CLs were found in four of the regions, but particularly in the southern areas (Scotia-Fundy and the USA).

99. The status of Baltic salmon is assessed by evaluating the probability that individual salmon rivers have reached 50% and 75% of the potential smolt production (ICES, 2012b). In the Gulf of Bothnia and Baltic Main Basin the large, northernmost stocks have likely or very likely reached the 50 % objective, but only three rivers have likely reached the 75 % objective. Southern stocks and a few small northern stocks have variable and, on the average, much poorer stocks. In the Gulf of Finland, salmon stocks show indication of some recovery, but the status of most stocks is still poor.

100. In some countries the conservation status of stock-complexes or individual stocks is also characterised with respect to possible future status of the stocks.

101. The Committee on the Status of Endangerd Wildlife in Canada identifies and assigns conservation status of 16 distinct Designatable Units (DUs) for Atlantic salmon in Canada (COSEWIC, 2010). A Designatable Unit represents discrete and evolutionary significant units of the species that are important to its evolutionary legacy as a whole and if lost would likely not be replaced through natural dispersion. Of 15 anadromous DUs, five were classified as endangered (facing imminient extirpation or extinction), one as threathened (likely to become threatened by extirpation or extinction if no action is taken), four as of special concern (may become threatened), one as data deficient and four as not at risk. The five DUs classified as endangered are located in the southern part of Canada (Inner and Outer Bay of Fundy, Nova Scotia Southern Upland, Eastern Cape Breton and Anticosti Island). In addition, the freshwater living Lake Ontario DU was classified as extinct.

102. The Norwegian Directorate for Nature Management identifies threats and assesses the status of wild salmon stocks in Norway (http://www.miljødirektoratet.no/Villaksportalen/). The most recent update (from 2012) gives the status for 481 rivers where salmon are or were originally present. The status is based on assessments of how different human impacts affect the production of salmon with respect to the viability of the stock and its capacity to produce a harvestable surplus. In addition, the genetic status is assessed with respect to possible impacts on the viability of the stock from introgression of escaped farmed salmon. Of the 481 stocks, 54 were classified as critically endangered or lost, 44 as threatened, facing exctinction if the impacts continue or increase, 126 stocks were classified as vulnerable, potentially becoming threatened if the impacts continue or increases, 241 stocks as moderately affected with significant reductions in harvestable surplus, 16 stocks had good status, while no stocks were classified to have very good status.

8.2. Trends in abundance

103. Atlantic salmon abundance in the North Atlantic Ocean has declined the latest decades. Estimates by ICES on the development of salmon abundance in the period 1970-2009 suggest that pre-fishery abundance (PFA; defined as number of fish on 1 January of their first winter at sea) was highest in the

early 1970s at some 10 million fish (Chaput, 2012). By the mid-1990s abundance had declined considerably and has, with some variation, remained low thereafter. In the most recent 5-year period, total PFA was estimated at about 3.5 million fish. The decline in abundance has generally been larger for MSW-salmon than for 1SW-salmon. The decline in PFA of MSW-salmon has been larger in the North West Atlantic and in the southern part of the North East Atlantic than in the northern part of the North East Atlantic. In the period 1970-2009, the catches of Atlantic salmon have declined considerably, especially in marine commercial fisheries. The reduction in marine exploitation (fishing) is achieved through great reductions in effort or in some cases complete bans. As a result, the estimated number of MSW spawners has remained rather unchanged in the North West Atlantic and in the northern part of the North East Atlantic, while the number of 1SW spawners has increased in these two areas during the period 1970-2009. The estimated number of spawners has decreased over the time period for both 1SW- and MSW-salmon in the southern part of the North East Atlantic (Chaput, 2012).

8.3. Factors affecting abundance

104. Three main factors affect the abundance of adult wild Atlantic salmon; smolt production in freshwater, natural mortality in the marine environment, and exploitation in commercial (mostly marine), and recreational fisheries (mostly riverine).

105. Historically, many of the declines and extirpations of Atlantic salmon can be more or less directly attributed to human activities affecting freshwater production of salmon, such as dams, pollution (including acid rain) and dewatering of streams (Parrish et al., 1998). Today, populations are recovering in parts of the salmon distributional range due to stronger legal measures to control and reduce pollution from industry and sewage systems (c.f. Mawle and Milner, 2003). For example, reduced acid depositions combined with extensive liming of rivers affected by acid rain have led to re-establishment of several salmon populations in Southwestern Norway that were extirpated or severely reduced (Hesthagen and Larsen, 2003). However, many salmon stocks worldwide still suffer reduced smolt production due to different human impacts.

106. The reasons for the more recent decline in the abundance 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). Over the past 30 years post-smolt survival has declined in the entire North Atlantic (Chaput, 2012), and the coherence observed in the patterns of declining adult recruitment of salmon over large geographic areas suggests that recent changes in mortality have been dominated by factors operating in the marine environment. The ocean climate of the North Atlantic has undergone marked changes over the period of declining salmon abundance (Beaugrand, 2008; Beaugrand and Reid, 2012). There appears to be a close relationship between the growth, maturation, survival, and distribution of salmon at sea and ocean climate as reflected in sea temperature (Friedland et al., 2005; Todd et al., 2008). Water temperature and other abiotic environmental factors acting indirectly to cause changes in the production and availability of suitable food items reflecting large-scale ecological changes in the marine ecosystem may be the primary cause of changes in the abundance of salmon, as well as other species (c.f. Friedland et al., 2009). It has been suggested that different factors may govern the successful return of Atlantic salmon to rivers in Europe and North America, and that survival of European Atlantic salmon is linked to growth and feeding conditions whereas survival of North American Atlantic salmon may be more linked to predation (Friedland et al, 2005; 2012).

107. Marine mortality of salmon does not necessarily operate independently of factors acting in freshwater. Over recent decades, biological characteristics of Atlantic salmon smolts have changed in many rivers (Russell et al., 2012). Juvenile salmon have grown faster and migrated to sea at a younger age, so have been smaller typically than they were earlier. Over the same period, smolt run-timing across the geographic range has been earlier, at an average rate of almost 3 days per decade. How such changes in smolt characteristics and migration timing influence mortality at sea is unknown. Moreover, acidification,

contaminants and other factors operating in freshwater may also impact smolt quality with adverse consequences for sea-survival of Atlantic salmon (Rosseland and Kroglund, 2011).

108. The survival of wild and hatchery-reared Atlantic salmon post-smolts during their first year at sea has declined in the Baltic Sea from 25-40% in the late 1980s and early 1990s to 5-15% in the period 2005 - 2010 (ICES, 2011). The open-sea ecosystems in the Baltic have experienced pronounced changes in the past two decades, characterised by shifts in species composition across several trophic levels (Möllmann et al., 2009; Diekmann and Möllmann, 2010). These changes in the ecosystem have affected the abundance of both the prey (herring and sprat) and the potential predators (grey seals) of Atlantic salmon. A recent analysis showed that the declining trend in post-smolt survival could be explained by the increased number of grey seals, whereas the annual variation in survival coincides with variation in the recruitment of Bothnian Sea herring (Mäntyniemi et al., 2012). Hence, both food availability and predation could contribute in regulating post-smolt survival. However, it remains uncertain whether the observed correlations arise from direct causalities or other mechanisms (Mäntyniemi et al., 2012).

8.4. Threats to salmon populations

109. Widespread declines and extirpations of Atlantic salmon populations have occurred in Europe and North America, particularly in southern portions of the range. Many of these declines or extirpations can be attributed to human impacts, such as dams, pollution (including acid rain), dewatering of streams and overfishing. The threats, however, are often multi-factorial involving both human impacts in concert with environmental change (e.g. changing ocean conditions). In an effort to evaluate the possible factors contributing to the decline of salmon, the Department of Fisheries and Oceans Canada convened an expert panel, which in the end identified 63 such factors (Cairns, 2001). The threats were often region, or even river specific, though some were broader, such as ocean conditions.

110. The major threats to wild Atlantic salmon populations include:

- Overfishing in the sea, estuaries and rivers that reduces population sizes to below a critical level.
- Hydropower dams and other man-made river obstructions that form severe obstacles to upstream and downstream migration of salmon, inhibiting access to habitats.
- River engineering schemes (e.g. for flood defence or navigation) result in direct habitat loss (e.g. through channel deepening) and disconnection of the main river from the complex of floodplain habitats (e.g. oxbow lakes, channels and islands). Habitat degradation also occurs through the resulting changes in ecological processes such as nutrient cycling, sedimentation and flooding.
- Pollution (from industry, urban settlements and agriculture) resulting in acid rain, inputs of excessive nutrients and upstream sediments, heavy metals and other toxic substances, including endocrine disrupters. These pollutants degrade the salmon habitats and some have direct impacts on species mortality and behaviour.
- Erosion/homogenisation of the natural gene pool through interbreeding with salmon aquaculture escapes and thus disruption of local adaptations and evolutionary potential of wild stocks. Diseases and parasites (e.g. sea lice) transferred from caged salmon to wild salmon can represent a further hazard.

8.5. Conservation measures

111. The conservation and restoration of Atlantic salmon is a daunting task because of the complex and dynamic nature of the freshwater and marine ecosystems that the species exploits. It requires the identification of the units of conservation (e.g. Evolutionary Significant Units [ESU] as in the U. S. Endangered Species Act or Designatable Units [DU] in the Canadian Species at Risk Act) and then a

well-documented action plan. Such an approach is being employed with the endangered Atlantic salmon of State of Maine and inner Bay of Fundy, Canada.

112. In the European Union (EU), Atlantic salmon is listed under Annex II in the Flora-Fauna-Habitats – Directive (COUNCIL DIRECTIVE 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora). The 1992 Habitats Directive aims to protect wildlife species and habitats. Each Member State is required to identify sites of European importance and to put in place a special management plan to protect them (in special areas of conservation), combining long-term conservation with economic and social activities, as part of a sustainable development strategy. The EU - Water Framework Directive (2000/60/E) requires that all inland and coastal waters within defined river basin districts must reach at least good status by 2015 and defines how this should be achieved through the establishment of environmental objectives and ecological targets for surface waters. Anadromous species like Atlantic salmon presumably will act as indicators and should benefit from the activities in the member states.

113. NASCO is an international organisation established under the Convention for the Conservation of Salmon in the North Atlantic Ocean, which entered into force on 1 October 1983. All governments throughout the Atlantic salmon's native range are NASCO Member Countries. NASCO's main objective is to contribute to the conservation, restoration, enhancement and management of Atlantic salmon. Through the NASCO Convention, parties agreed to cooperate in the management of fisheries that exploit Atlantic salmon originating in rivers of other parties. The two principal fisheries that are regulated are the West Greenland fishery and the Faroese fishery. Both fisheries exploit a mix of salmon populations originating from broad geographical areas.

114. The North Atlantic Salmon Fund (NASF), as a non-governmental organisation (NGO), mobilises international support and persuades commercial fishermen to give up fishing for salmon, either permanently or for a period long enough to allow stocks to recover. The organisation has raised nearly $30-million to buy out netting rights to reduce excessive commercial exploitation. Another international NGO is the Atlantic Salmon Federation, which is based out of North America and promotes the conservation and wise management of wild Atlantic salmon and its environment. The Atlantic Salmon Trust is a UK-based NGO. The Trust addresses the decline of salmon stocks, as well as the need for practical research into the problems regarding the decline of salmon populations.

115. Within the natural range of salmon the following management tools contribute to the conservation efforts:

- Habitat improvement and restoration
    1. Re-establishing migration corridors by building fish-passes at obstructions (weirs, sluices, dams), regulation of hydroelectric development or catch and transport of salmon to inaccessible spawning habitats (trap and truck)
    2. Rehabilitation of spawning/nursing habitats
    3. Reduction of pollution (including effects of acid rain by liming of rivers)
    4. Regulation of land and water use
- In-river management of populations
    1. Living and frozen gene banks and hatchery supplementation programs, see NASCO[1] for more information about cultivation and stock enhancement.

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[1] http://www.nasco.int/implementation_plans_cycle2.html and http://www.nasco.int/pdf/agreements/williamsburg.pdf

2. Fishing regulations (catch and release, biological reference points for setting allowable removal rates or escapement levels)
3. Legislation
4. Control of poaching

- Regulating marine exploitation

1. Fishing regulations, quotas (NASCO)
2. Buy-out of licenses / netting rights (NASF)

- Salmon farming, estuary management

116. In order to reduce the possible impacts of fish farming, in some countries (such as Iceland, Norway) it was decided to protect (some) wild salmon stocks by establishing fish farm exclusion zones in the coastal marine/estuary environment.

9. Interactions with other organisms

9.1. Salmon as prey

117. Atlantic salmon are vulnerable to predators at every stage of their life cycle (Mather, 1998; Ward and Hvidsten, 2011). The impacts of predation on salmon populations are likely to be particularly severe at older life stages and for populations already suppressed by other factors (Ward and Hvidsten, 2011).

118. Predation on juvenile salmon and smolts in freshwater:

- Birds: (heron, sawbill ducks, cormorant, gulls, belted kingfisher, merganser, goosander).
- Fish: (salmon, several native and introduced trout species, charr, bull head, burbot, chub, eels, pike, pikeperch, perch, grayling, catfish, smallmouth bass, striped bass).
- Reptiles (water snakes).
- Mammals: (otter, mink).

119. Predation on post-smolts in estuaries, coastal waters and sea:

- Birds: (cormorant, gannets, terns, gulls, murres)
- Fish: (gadoids, sea trout, eels, ling, sharks)
- Mammals: (otter, grey seal, harbour seal, harp seal, harbour porpoise, bottlenose dolphin, beluga whale (Middlemas et al., 2003))

120. In the Baltic sea, the number and abundance of potential predators on young salmon is low compared to that in the North Atlantic Ocean.

9.2. Salmon as predators

121. Atlantic salmon are generalist predators that feed on available prey. They are gape-limited so that prey-size usually increases as the fish grow in length. Juvenile salmon are able to feed successfully in different habitats ranging from small streams to large lakes (Johansen et al., 2011). They also feed under different light conditions and seasons. In running water, the salmon can feed on invertebrates drifting either on the surface or in the water column, as well as on invertebrates living on the streambed surface. Prey of salmon in fresh water:

- Juveniles are opportunistic predators of aquatic invertebrates, especially those difting at the surface or in the water column (e.g. Ephemeroptera, Plecoptera, Trichoptera, Chironomiidae and Coleoptera).
- Larger parr are also piscivorous, feeding on smaller trout and salmon juveniles and eggs.
- Adult Atlantic salmon are generally believed to cease feeding upon entry into fresh water.

122. Lakes can serve as nursery habitat for juvenile anadromous salmon and are the main rearing habitat for most land-locked or resident Atlantic salmon populations (Klemetsen et al., 2003). Prey of salmon in lakes:

- Invertebrates; fishes, mostly smelt, vendace and stickleback (Smirnov, 1979).

123. Atlantic salmon are opportunistic feeders, utilising a wide variety of available prey while feeding at sea (Rikardsen and Dempson, 2011). The first few months at sea are often regarded as an important feeding period in order for young salmon to rapidly enhance their size and reduce their risk of predation. Prey of salmon in marine waters:

- Postsmolts are primarily pelagic and mid-water feeders and their diet includes sand lance and other small fish, euphausiids, amphipods, copepods and crab larvae.
- Piscivory is the main feeding mode for post-smolts $\geq$ 25 cm in the northwest Atlantic Ocean and the diet frequently contains capelin, sand lance and herring.
- In the northeast Atlantic, invertebrates play a greater role in the salmon diet, which includes amphipods, euphausiids, herring, capelin, redfish larvae, blue whiting, lanternfish, sprat, cod and smelt.
- In the Baltic Sea salmon feed on marine fish species such as herring and sprat. In the northern parts (Bothnian Sea) only herring is abundant in the diet.

9.3. Competition

124. Juvenile Atlantic salmon may compete amongst themselves and with other species for critical resources such as food and space (Nislow et al., 2011). The fish assemblages of salmon river systems in the North Atlantic is generally species-poor, and salmon co-exist most frequently with resident and anadromous forms of other salmonids, such as brown trout (Europe; has been introduced into North America), brook charr (North-America), Arctic charr (Europe and North America) and grayling (Europe). Non-salmonid species that co-occur with juvenile Atlantic salmon include cyprinids (frequently demersal species), cottids (bullheads), anguillids (eels) and lampreys. For the most part, these species tend to be habitat and trophic generalists and may therefore be potential competitors for food with Atlantic salmon (Fausch, 1998; Nislow et al., 2011). In some river systems, specialised piscivores such as pike and percids also co-occur with Atlantic salmon.

9.3.1. Competition for food and space

125. The large majority of studies of interspecific interactions in Atlantic salmon ecology involve salmonid species (review in Nislow et al., 2011). Due to the general reliance of stream salmonids on aquatic invertebrates, there is opportunity for prey resource competition between Atlantic salmon and co-occurring salmonid species. Moreover, competition for space is also expected as other stream salmonids may have more or less overlapping habitat requirements with Atlantic salmon. Studies of habitat-use in rivers show that Atlantic salmon are often strongly associated with riffle habitats, whereas brown trout, Arctic charr and brook charr tend to use slower-flowing areas more extensively. Atlantic salmon are particularly well adapted to fast-flowing water due to their large pectoral fins, which may be used as hydrofoils to hold station in such environments. However, Atlantic salmon appear to prefer pool habitat

both as fry and parr. Thus, their extensive use of riffles might be seen as a displacement due to competition with other stream salmonids (Nislow et al., 2011).

126. There is evidence that brown trout tend to be more aggressive than, and socially dominant to, Atlantic salmon of similar size. However, in competition for shelter during winter, dominance depended solely on the size and not the species. Both intrinsic dominance (often related directly to relative size) and prior residence in a patch of streambed are important factors in establishing outcomes of competition between pairs of fish. Such behavioural mechanisms may be important for the outcome of inter-specific competition of Atlantic salmon and other salmonids. However, even in situations where the strength and direction for pairwise interactions can be tested, the consequences of these interactions for habitat use and population dynamics can be complex and difficult to predict (reviewed by Nislow et al., 2011).

127. Impacts of interactions between Atlantic salmon and brown trout or brook charr are thought to be highest during the first year of life when density-dependent processes are most intense (Milner et al., 2003). A combination of studies involving behavioural ecology, habitat associations and fish distributions showed that interspecific interactions between Atlantic salmon and brown trout must be viewed in the context of scale (reviewed by Westley et al., 2011). At fine spatial scales, brown trout may out-compete Atlantic salmon for many habitats, except those with relatively high water velocity. At large spatial and temporal scales, segregation of Atlantic salmon and brown trout among habitats may be apparent.

128. Quantitative studies on the effects of non-salmonid fishes on juvenile Atlantic salmon are rare. Ward et al. (2008) found no evidence of competition between re-introduced juvenile salmon and the native fish fauna in tributaries of the Connecticut River (the United States). Studies in the laboratory and field surveys, however, indicate that juvenile salmon may influence both the presence and abundance of non-salmonid species at least in certain habitat types (review by Nislow et al., 2011). At present, 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 (Nislow et al., 2011).

9.3.2. Competition for spawning sites

129. Superimposition of Atlantic salmon redds by brown trout or vice versa may occur when spawning is not segregated spatially. Atlantic salmon and brown trout tend to select similar spawning habitats, which contributes to redd superimposition. Both species were found to construct redds in areas with similar water depths, water velocities and distance to stream banks and there was a large overlap in gravel size (Heggberget et al., 1988; Louhi et al., 2008). Brown trout tend to spawn earlier than Atlantic salmon, but overlap in spawning times can be considerable. Overlap in spawning times is also evident as hybrids between Atlantic salmon and brown trout commonly occur, but usually in low frequency, in nature (review in Westley et al., 2011).

9.3.3. Other types of competition

130. Marine competition: It has been difficult to determine the extent of competitive interactions faced by Atlantic salmon in the marine environment because of the vast scale of the habitat exploited.

9.4. Pathogens

> **Rationale:** *Provided, for example, if there is a genuine possibility of increasing the importance of a disease or parasite. Critically important organisms and relationships (*e.g. *a virus disease that is a principal management issue) are covered.*

131. The total number of species of infectious agents reported from wild and domesticated (ranched/hatchery) Atlantic salmon in both marine and freshwater habitats is 225 (table 3) (Bakke and Harris, 1998).

Table 3. **Total number of species of infectious agents in Atlantic salmon**

Group	Number of species
Virus	9
Monera	21
Protoctista	27
Animalia	
Hirudinea	3
Helminths	
Monogenea	11
Digenea	41
Cestoda	35
Nematoda	29
Acanthocephala	20
Crustacea	13
Mollusca	3
Acarina	2
Fungi	11
Total number	**225**

Source: Bakke and Harris, 1998

132. Few pathogens have caused significant disease epidemics in the wild, and although parasites of returning adults are well documented, diseases among freshwater stages (parr; e.g. *Gyrodactylus salaris*) seem to be most important, in addition to infestations by the salmon louse (*Lepeophtheirus salmonis*) in sea water.

133. *Gyrodactylus salaris* is a freshwater parasite that does not occur naturally in Norway. It was probably introduced in Norwegian rivers in the 1970s by infected hatchery-reared salmon. An epizootic of this species was reported in Norway in 1975 (Johnsen and Jensen, 2003). The entire lifecycle of the parasite is in fresh water, the majority of it spent on young fish. It is less than 0.5 mm in length and attaches by hooklets to the scales and fins of the fish. *G. salaris* has a significant negative influence on the Atlantic salmon. Most often it will kill more than 90% of the young salmon in the river after being introduced. The monogenean *G. salaris* naturally occurs in the Baltic Sea drainage. The parasite was found in White Sea drainage in 1992 (Keret river) and 2002 (Pista river). The introduction in Norway has initiated an extensive program for eradication of the parasite, mainly by use of the piscicide rotenone. This strategy has also made it necessary to keep affected salmonid populations in gene banks until they can be safely returned to the treated rivers (http://www.dirnat.no/content/2475/Handlingsplan-forslag-mot-lakseparasitten-Gyrodactylus-salaris).

134. Many viruses infect salmon within aquaculture facilities, but there are no reports of disease epidemics due to viruses in wild salmon populations. However, there is increasing evidence for transfer of infectious pancreatic necrosis virus (IPNV) from farmed to wild salmon populations. (reviewed by Johansen et al., 2011). It is also likely that the newly discovered piscine reovirus (PRV) is transferred between wild and farmed fish. It is highly prevalent in both wild and escaped farmed salmon (Garseth et al., 2012).

135. Numerous bacterial pathogens may cause serious epidemics: *Renibacterium salmoninarum* causes bacterial kidney disease (BKD), a fatal systemic infection of both farmed and wild salmonids.

Furunculosis, caused by *Aeromonas salmonicida* is one of the most important diseases of wild and farmed salmonids, and most outbreaks occur when the water temperature is above 10°C.

136. Crustaceans such as sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) can be a problem for the Atlantic salmon farming industry and there are concerns about impacts on wild salmonids as well. Marine rearing pens may function as pathogen culture facilities at the crossroads for migrant salmonids moving between fresh and salt water. A recent study demonstrates that sea lice infestations may have had a large effect on wild salmon in the Northeast Atlantic Ocean (Krkošek et al, 2013), but a similar study focusing on Ireland only concludes that sea lice has a minor contribution to marine mortality of salmon (Jackson et al., 2013). Apparently, this is still a controversial issue.

137. Pearl mussel *Margaritifera margaritifera L.* larvae are a parasite of Atlantic salmon (some specialists (Ziuganov et al., 1994) speculated about salmon-pearl mussel symbiosis). The number of pearl mussel populations is decreasing. They are currently listed in the European Habitat & Species Directive Annexes II and V and in the Bern Convention Annex 3 (Geist, 2005).