

## REVIEW PAPER

# A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow

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The present paper reviews the effects of water temperature and flow on migrations, embryonic development, hatching, emergence, growth and life-history traits in light of the ongoing climate change with emphasis on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*. The expected climate change in the Atlantic is for milder and wetter winters, with more precipitation falling as rain and less as snow, decrease in ice-covered periods and frequent periods with extreme weather. Overall, thermal limits for salmonids are species specific. Scope for activity and growth and optimal temperature for growth increase with temperature to an optimal point before constrain by the oxygen content of the water. The optimal temperature for growth decreases with increasing fish size and varies little among populations within species, whereas the growth efficiency may be locally adapted to the temperature conditions of the home stream during the growth season. Indirectly, temperature influences age and size at smolting through its effect on growth. Time of spawning, egg hatching and emergence of the larvae vary with temperature and selective effects on time of first feeding. Traits such as age at first maturity, longevity and fecundity decrease with increasing temperature whilst egg size increases with temperature. Water flow influences the accessibility of rivers for returning adults and speed of both upstream and downstream migration. Extremes in water flow and temperature can decrease recruitment and survival. There is reason to expect a northward movement of the thermal niche of anadromous salmonids with decreased production and population extinction in the southern part of the distribution areas, migrations earlier in the season, later spawning, younger age at smolting and sexual maturity and increased disease susceptibility and mortality. Future research challenges are summarized at the end of the paper.

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Key words: activity; climate; embryonic development; growth; life-history traits; migration.

## INTRODUCTION

This review examines effects of water temperature and flow on anadromous salmonids with emphasis on the Atlantic trouts (*sensu* Nelson, 1994), Atlantic salmon

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*Salmo salar* L. and brown trout *Salmo trutta* L. The literature on effects of climate change on various organism groups is growing rapidly (e.g. Gilman *et al.*, 2006; Parmesan, 2006; Portner & Farrell, 2008), and has described possible future effects on issues such as global fish production (Brander, 2007), fisheries in Britain and Ireland (Harrod *et al.*, 2009), threats to the relict fish fauna in central Sahara (Trape, 2009), and the ecology of Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) and sockeye salmon *Oncorhynchus nerka* (Walbaum) of the Columbia River (Crozier *et al.*, 2008). *Salmo salar* and *S. trutta* are iconic, well-studied species of the North Atlantic area which is likely to be strongly affected by the predicted climate change of the region.

Climate, defined as the meteorological conditions, including temperature, precipitation, solar radiation and wind that prevail in a particular region (Harrod *et al.*, 2009), determines water temperature and flow of watercourses. Climate changes continuously; there are long-term trends over the centuries and besides these, short-term variation over decennia, years and seasons. The main scenario for climate change in northern Europe and North America in the near future is milder, wetter and stormier winters (IPCC, 2007). Summers could be warmer and dryer, although the climatic effect is expected to be less than in winters. More precipitation is expected to fall as rain instead of snow in locations where the historical air temperature has been near freezing. Periods with extreme weather are likely to become more frequent, and the prevalence and severity of extreme events such as floods and droughts are expected to increase. Hydrological systems are likely to be affected by increased runoff and earlier spring peak discharge in many glacier and snow-fed rivers. The climate change will be stronger over land than over the ocean, meaning that the temperature effect could be more profound on fresh water than the marine stage of the salmonid life cycle. A more detailed account of relevant, expected climatic changes in this century is given by Harrod *et al.* (2009).

North American *S. salar* abundance has fluctuated in parallel with the Atlantic multidecadal oscillation (AMO), a basin-wide, low-frequency climate mode that has influenced sea-surface temperatures over the last century (Condrón *et al.*, 2005). During the AMO warm (cool) phase *S. salar* abundance is low (high). Changes in sea-surface temperatures associated with the AMO are most pronounced in the winter season near the Grand Banks of Newfoundland, a known overwintering area for salmon and an important time for determining survival. In the short term, the abundance of European *S. salar* has decreased gradually since the middle of the 1970s in parallel with increasing sea-surface temperatures (Beaugrand & Reid, 2003; Jonsson & Jonsson, 2004a; Todd *et al.*, 2008). Population responses to short-term climatic changes are chiefly phenotypic variations in behaviour, physiology and life history (Wootton, 1998), influencing ecological variables such as time of spawning, egg hatching and fry emergence, rate of embryonic development and growth, age and size at migration and sexual maturation, and life span (Crozier *et al.*, 2008). Indirectly climate affects populations through, effects on their competitors, pathogens, predators and water quality, and has consequences for population viability and geographical distributions (Lehodey *et al.*, 2006).

Water temperature affects ectothermic animals, through effects on the rate of biochemical reactions (Angilletta *et al.*, 2002). Thus, it influences physiological characteristics such as rates of development and growth and traits associated with these (Jonsson & L'Abée-Lund, 1993). Temperature can also serve as an ecological

timer initiating behavioural reactions such as migration from one habitat to another (Jonsson, 1991). Water flow can have a timer effect (Tetzlaff *et al.*, 2005), and influence populations through effects on the area and connectivity of habitats (Bowen *et al.*, 2003), and variables related to these such as migration, feeding and spawning, important for population recruitment, and the carrying capacity of rivers. Together, these two variables are of major importance for the ecology of salmonid species (Heggenes *et al.*, 1999; Mather *et al.*, 2008).

Populations respond to climatic variables by phenotypic changes (L'Abée-Lund *et al.*, 1989; Crozier *et al.*, 2008). The phenotypic expression of environmental variables is called the reaction norm (Angilletta *et al.*, 2003). The degree of plasticity varies among populations, and over longer time spans it can change through natural selection (Angilletta *et al.*, 2002; Nussey *et al.*, 2005). Thus, the distinction between genetic and plastic responses is simplistic (Crozier *et al.*, 2008). Furthermore, ecological changes in one life stage can have extensive consequences for later life stages, because the various life-stage transitions are finely tuned to conditions in very different environments (Jonsson & Jonsson, 1993; Fleming *et al.*, 1997).

Anadromous salmonids (those that spawn in fresh water and whose offspring make feeding migrations to marine habitats) are affected by climatic factors (Jonsson & Jonsson, 2004b; Battin *et al.*, 2007; Todd *et al.*, 2008). Salmonid embryos incubate in the gravel substratum until hatching. After hatching, the larvae (alevins *sensu* Allan & Ritter, 1977) remain in the gravel where they feed on their yolk for several weeks, before they emerge and commence external feeding. The juveniles (called parr) spend days to years in habitats ranging from small streams to rivers and lakes, depending on the species and habitat opportunities. The alevins of the Pacific salmon, *e.g.* pink salmon *Oncorhynchus gorbuscha* (Walbaum) and chum salmon *Oncorhynchus keta* (Walbaum) can move almost directly into sea water. Other Pacific salmonids such as masu salmon *Oncorhynchus masou* (Brevoort), *O. tshawytscha*, *O. nerka* and steelhead (rainbow) trout *Oncorhynchus mykiss* (Walbaum) spend one or more years in fresh water before migrating to sea for feeding.

Parr of *S. salar* spend 1–8 years in fresh water before they smolt and move to sea, by which time their body length is between 10 and 30 cm (Fig. 1). Most males can attain maturity before smolting; the proportion varies among populations and years (Österdahl, 1969; Jonsson *et al.*, 1998a). The smolt transformation pre-adapts the fish for a marine, pelagic life style (Hoar, 1988). Post-smolts spend 1–4 years at sea before attaining sexual maturity and returning to fresh water for spawning (Klemetsen *et al.*, 2003). They spawn in the autumn or in the early winter. Postspawners (kelts) can return to sea for feeding soon after spawning or wait until the subsequent spring, before returning to sea for feeding (Jonsson *et al.*, 1990). The same individual can spawn in up to at least four different years. Small adults spawn annually, large adults are biennial spawners (Jonsson *et al.*, 1991b). The life cycle of anadromous *S. trutta* (Fig. 2) differs from that of *S. salar* in that parr of both sexes frequently mature and become freshwater resident instead of migrating to sea (Jonsson, 1985; Dellefors & Faremo, 1988). Post-smolts feed in estuaries and coastal waters rather than migrating into the ocean, but immature *S. trutta* can spend the winter in fresh water similar to mature fish. The duration of the sea sojourn is more variable than that of *S. salar* (Jonsson & Jonsson, 2002, 2009).

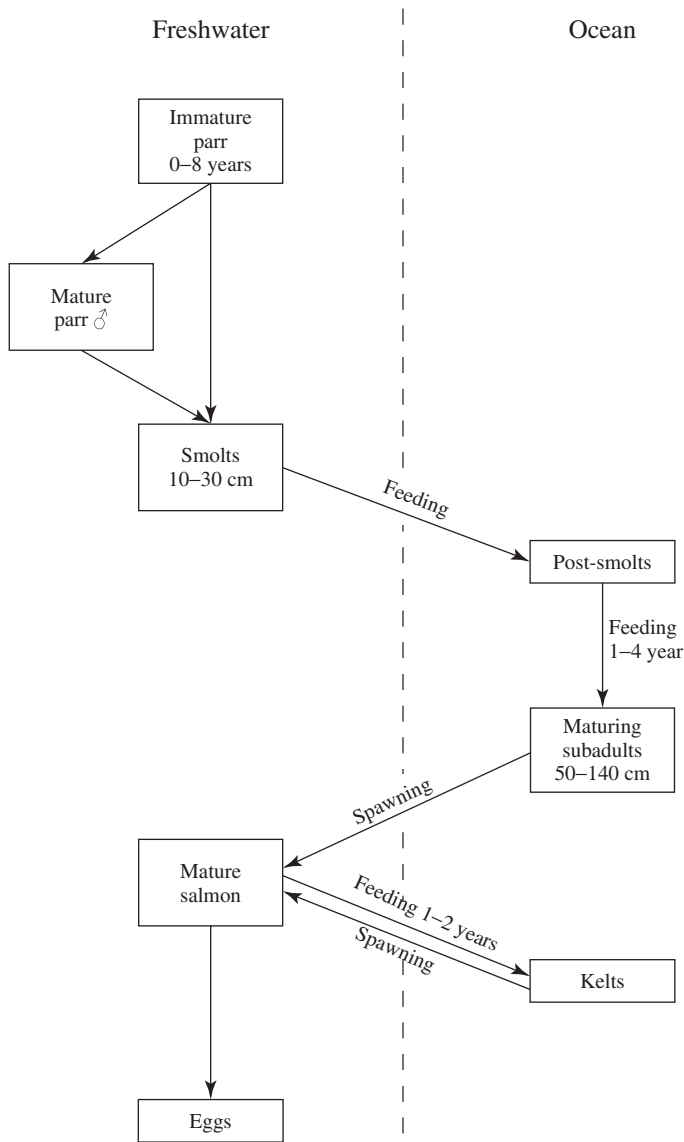
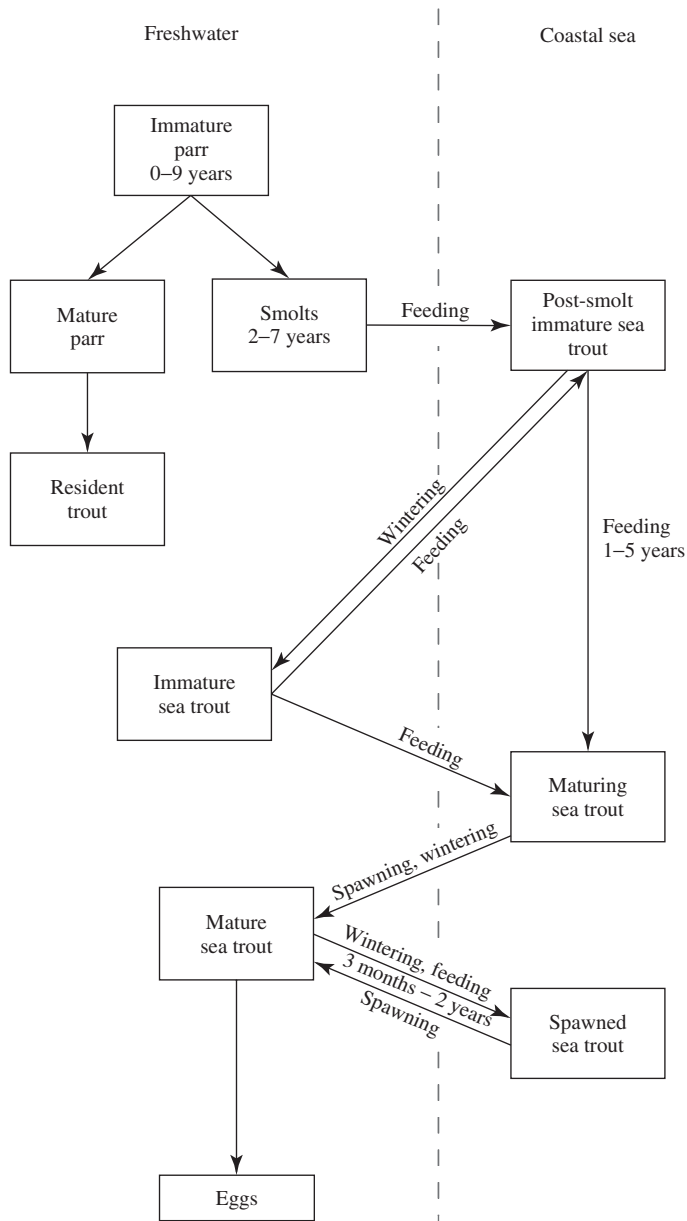


FIG. 1. Life history of *Salmo salar* (based on original data in Österdahl, 1969, Jonsson *et al.*, 1990, 1991, 1998a). For further details, see text.

*Salmo salar* and *S. trutta* are autumn spawners and the eggs incubate in the gravel substratum during winter. The effects of water temperature and flow on the ecology and behaviour of Salmonidae have been studied extensively (*e.g.* Jonsson *et al.*, 2001a, 2007), at least partly because of studies on ecological effects of hydropower regulations in rivers (Jensen, 1990, 2003; Angilletta *et al.*, 2008). The salmonids are coldwater species with high oxygen demands, and the expected rise in temperature may extirpate populations, especially at the southern end of their distribution range where small populations face the greatest risk (Bürger & Lynch, 1995). In



all these anadromous fish species, individual fish acquire the bulk of their energy reserves whilst at sea, which is used for subsequent reproduction (Jonsson & Jonsson, 2003). Charr *Salvelinus* spp., Atlantic trout *Salmo* spp. and Pacific salmon and trout *Oncorhynchus* spp. are iteroparous, whereas Pacific salmon *Oncorhynchus* spp. are semelparous and die after spawning (Scott & Crossman, 1973).

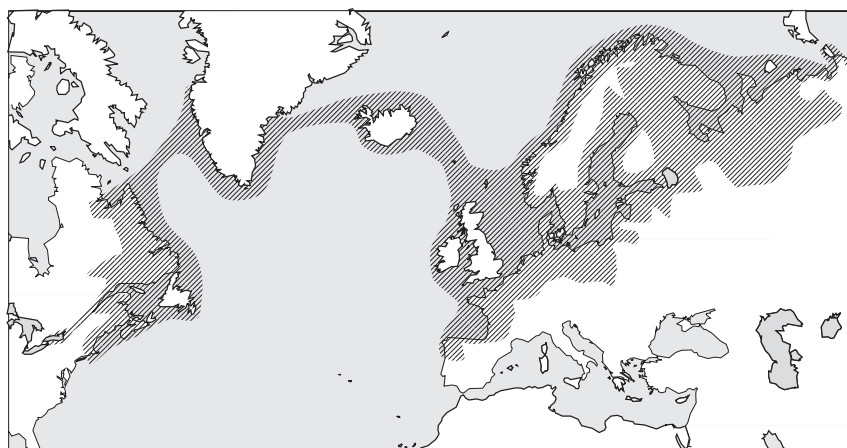


FIG. 3. Endemic range of *Salmo salar*. Distribution in the ocean is approximate (after MacCrimmon & Gots, 1979; reproduced with permission from the Minister of Public Works and Government Services, Canada).



FIG. 4. Endemic distribution of *Salmo trutta*. Broken line gives the distribution of anadromous populations (after Elliott, 1989; reproduced with permission from Wiley-Blackwell).

In the East Atlantic, anadromous *S. salar* is distributed from northern Portugal ( $42^{\circ}$  N) to Petjorskoye in northern Russian. In the West Atlantic, *S. salar* is distributed from the Connecticut River to the Ungava region of northern Quebec (MacCrimmon & Gots, 1979) (Fig. 3). *Salmo trutta* is native to Europe and Asia where anadromous populations are found from Portugal to the White Sea (Fig. 4). The species has, however, been released in rivers in other continents since the middle of the 19th century (MacCrimmon & Marshall, 1968; MacCrimmon *et al.*, 1970) where anadromous populations sometimes have been formed (Rounsefell, 1958; Frost & Brown, 1967).

The present paper reviews the thermal tolerance of salmonids. It summarizes thermal and flow effects on activity, migrations and spawning, embryonic development,

hatching, emergence, growth and life-history traits. Thereafter, possible effects of the ongoing climate change on salmonid populations in their endemic range are considered before pointing to future research needs. Possible effects of changed coastal currents and shifts in large-scale ocean current systems and production are not addressed, nor are synergistic effects of climate change and the growing *S. salar* farming industry examined, although the problems resulting from fish farms and escaped *S. salar* most probably will continue to exist. A review paper on interactions between escaped and wild *S. salar* was recently published (Jonsson & Jonsson, 2006). Although the focus is on *Salmo* spp., information on other salmonids such as *Salvelinus* spp. and *Oncorhynchus* spp. are included when relevant. Most examples are from the authors' own studies in the River Imsa, a 1 km long stream in south-west Norway supporting populations of anadromous *S. salar* and *S. trutta* which have been monitored since 1975 (e.g. Jonsson *et al.*, 1998; Jonsson & Jonsson, 1998, 2009).

## THERMAL TOLERANCE

### THERMAL LIMITS

Temperature limits the geographical distribution boundaries of species (Parmesan & Yohe, 2003; Reist *et al.*, 2006). They survive over a range of temperatures

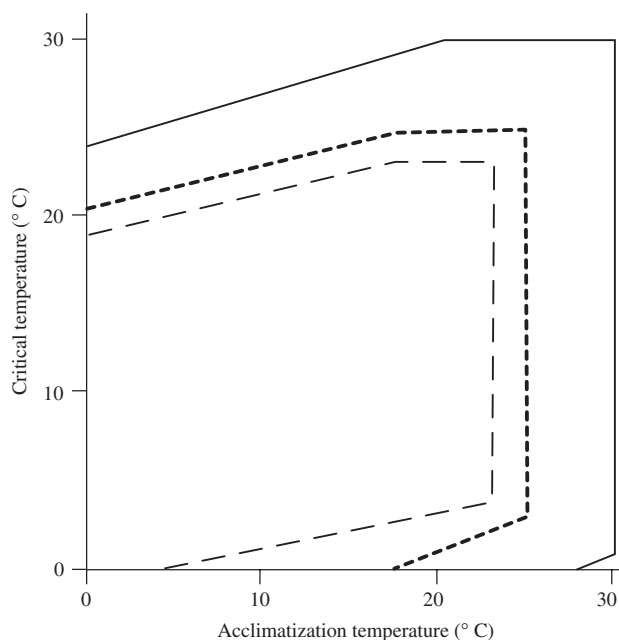


FIG. 5. Temperature tolerance polygon for *Salmo trutta* showing growth zone (inside the thin broken line, — — —), tolerance zone inside incipient lethal level (thick broken line, — — —) within which *S. trutta* feed, and ultimate lethal level where death is almost instantaneous (solid line, —). Growth at temperatures below 4°C can occur during winter but usually not from spring to autumn [based on original data in Elliott (1981) and Forseth *et al.* (2009)].

TABLE I. Upper and lower critical temperature ranges, upper incipient lethal temperatures and indices of thermal tolerance for 10 salmonid species (after Elliott, 1994)

| Species                       | Lower critical range (° C) | Upper critical range (° C) | Upper incipient lethal temperature | Thermal tolerance (° C <sup>2</sup> ) |
|-------------------------------|----------------------------|----------------------------|------------------------------------|---------------------------------------|
| <i>Salmo salar</i>            | 0–7                        | 22–33                      | 27.8                               | 708                                   |
| <i>S. trutta</i>              | 0–4                        | 20–30                      | 24.7                               | 583                                   |
| <i>Salvelinus alpinus</i>     | 0                          | 20–27                      |                                    |                                       |
| <i>S. fontinalis</i>          | 0–7                        | 20–29                      | 25.3                               | 625                                   |
| <i>Oncorhynchus gorbuscha</i> |                            | 21–28                      | 23.9                               | 450                                   |
| <i>O. keta</i>                | 0–7                        | 22–28                      | 23.8                               | 468                                   |
| <i>O. nerka</i>               | 0–7                        | 22–28                      | 24.4                               | 505                                   |
| <i>O. kisutch</i>             | 0–6                        | 23–28                      | 25.0                               | 528                                   |
| <i>O. tshawytscha</i>         | 0–7                        | 22–28                      | 25.1                               | 529                                   |
| <i>O. mykiss</i>              | 0–9                        | 19–30                      | 26.2                               |                                       |

bounded by the upper and lower incipient lethal temperatures (Fig. 5). In ectothermic organisms such as fishes, critical temperatures are probably set by the transition from aerobic to anaerobic metabolism (Klok *et al.*, 2004). In fishes, these boundaries are not defined by fixed temperatures as hypoxia will elicit metabolic depression and thereby widen the thermal window, especially when the rate of change is low (Portner *et al.*, 2004). The incipient lethal levels define the tolerance zone within which the fish can survive for a considerable length of time. The degree of thermal stress outside the tolerance zone is a function of the exposure time and the rate at which the temperature changes. The lethal temperature levels are higher for conspecifics acclimated at a high rather than low temperature, and high and abrupt temperature changes may be lethal even within their tolerance zone (Elliott, 1994). For salmonids, the lower incipient lethal temperature in fresh water is at 0° C or slightly below, whereas the upper incipient lethal limits are between 23.8° C for *O. keta* and 27.8° C for *S. salar*. Upper and lower critical temperature ranges and upper incipient lethal temperatures of 10 salmonid species are given in Table I.

Thermal requirements for feeding are at or close to the critical limits for survival, whereas the limits for growth are narrower (Fry, 1947). For instance, *S. trutta* may feed at or just above 0° C, but they do not have positive growth below c. 4° C. Growth ceases at c. 23° C whereas the fish still take food at 25° C (Forseth *et al.*, 2009).

To predict responses to changes in thermal conditions, thermal performance curves can be constructed. Such curves are continuous norms of reactions describing the relationships between animal performance and temperature (Huey & Kingsolver, 1989; Gilchrist, 1995; Kingsolver *et al.*, 2004). Based on the pioneering works of Brett (1971, 1979) and Elliott (1975a, 1976), thermal performance curves for juvenile growth of salmonids in fresh water have been established for >20 salmonid populations from the salmonid family such as *S. trutta* (Elliott *et al.*, 1995; Forseth *et al.*, 2009), *S. salar* (Elliott & Hurley, 1997; Jonsson *et al.*, 2001a) and *Salvelinus alpinus* (L.) (Larsson *et al.*, 2005). Such curves control for variation in temperature and body size and represent baseline models from which animal performance in nature or experiments can be compared (see Growth Models).



## INTRASPECIFIC VARIATION IN THERMAL TOLERANCE?

There is little, if any, potential for local adaptation in heat tolerance among populations within a species (Elliott, 1994). Populations are extirpated if the water temperature exceeds the ultimate upper lethal temperature, given that the fish have no access to a suitable coldwater refuge (Berman & Quinn, 1991). For instance, in cases where Pacific salmonids have been found in exceptionally warm localities, there are refuges with colder water to which the fish escape (Kaya *et al.*, 1977; Goniea *et al.*, 2006). If salmonids exhibit thermal adaptations to particularly cold or warm localities, extreme environments such as glacier-fed or geothermal rivers should be places to look for (Elliott, 1994). Beacham & Withler (1991) found heritability for heat tolerance in *O. tshawytscha* populations from cool but not warm streams, indicating that there was no further potential for increased heat resistance, and this appears to be common for salmonids (Brett, 1956; Konecki *et al.*, 1995a, b; Jensen *et al.*, 2000). Evidence indicates that there are species-specific upper and lower ultimate temperature tolerance limits.

Within populations, thermal tolerance is influenced by the size, age and physiological state of the fish. For instance, youngest life stages are most susceptible to both highest and lowest temperatures (Brett, 1952), as well as to fluctuations in temperature (Elliott, 1994). The upper incipient thermal limit for *S. alpinus* alevins from Windermere varied between 18.7° C and 20.8° C, whereas it was estimated at 22.7° C for underyearling parr (Baroudy & Elliott, 1994). A similar difference was found in the studies by Elliott & Klemetsen (2002) and Lyytikäinen *et al.* (1997), 19.3–21.0° C v. 23–24° C for alevins and underyearling *S. alpinus* from Fenoscandian lakes, and there are similar differences among life stages of other salmonids such as *S. trutta* (Elliott, 1994; Ojanguren & Braña, 2003) and *S. salar* (Jensen *et al.*, 1989b; Elliott, 1991).

Salmonids have low tolerance to high water temperatures because warm water has low solubility of oxygen. Hence, it is difficult to disentangle effects of high temperature from effects of low oxygen concentrations (Wootton, 1998). For instance, the scope for activity of *O. nerka* is maximal at 15° C, but the optimal temperature for activity increases above this with supplementary oxygen (Brett, 1952). This illustrates that the activity of fish often can be oxygen constrained in warm water.

## ACTIVITY AND MIGRATION

### ACTIVITY

Fishes are typically poikilothermic [but see Block & Finnerty (1994) for exceptions], and their metabolic energy costs increase with water temperature (Glebe & Leggett, 1981a; Fried, 1985; Enders *et al.*, 2005). The scope for activity and swimming speed also increases with temperature to an optimal point before they are constrained by the oxygen content in the water and start to decline (Brett, 1964; Svendsen *et al.*, 2004; Salinger & Anderson, 2006). Water temperature thus influences the opportunities for activity and fishes adjust their movements accordingly (Wootton, 1998). There have also been observations that maximum swimming speed and reaction time of fishes increase with temperature up to a certain optimal point

(Webb, 1978; Wardle, 1980; Claireaux *et al.*, 2006), and parr activity decreases with a change in temperature below and above that point (Roussel *et al.*, 2004).

## PARR MOVEMENTS

### *Refuges against high water temperature*

Water temperature influences the movements of parr. For instance, during periods of extremely high water temperature, parr in rivers may seek cool water sources as found for *O. mykiss* and parr of *O. tshawytscha* (Kaya *et al.*, 1977; Torgersen *et al.*, 1999; Goniea *et al.*, 2006). Breau *et al.* (2007) studied this for *S. salar* in New Brunswick, Canada. They found that 1 and 2 year-old parr aggregated in cool water sites when the water temperature exceeded 23° C. Age 0 fish, on the other hand, did not increase in abundance in the cooler water indicating that this behaviour may be linked to the size of the fish and previous experience from the habitat. Thus, the youngest fish can be more exposed to high temperatures than older ones, at the same time as they are more susceptible to high temperatures and rapid fluctuations in temperature (Elliott, 1994).

### *Daytime concealment at low temperature*

Parr of *S. salar* are usually day-active during early summer, but more nocturnal in late summer and autumn (Gries *et al.*, 1997; Johnston *et al.*, 2004). Young-of-the-year fish are less nocturnal than older parr (Imre & Boisclair, 2004). The activity of *S. trutta* appears bimodal (crepuscular), with a major peak at dawn and a lesser one around dusk (Bachman *et al.*, 1979). The activity pattern is governed by shifting light intensity, but changes with temperature, presence of predators and food availability (Ovidio *et al.*, 2002).

In winter *S. salar* parr prefer water temperatures below 10° C (Morgan & Metcalfe, 2001). The preferred temperature increases from winter to spring, coincident with increases in natural food availability and endogenous seasonal increases in appetite and growth rates. A similar difference in temperature preference was found for *S. alpinus* (Mortensen *et al.*, 2007). During winter, parr of *S. salar* and *S. trutta* exhibit negative relationships between tendency to seek shelter and water temperature (Valdimarsson *et al.*, 1997). When the water temperature falls below 7–11° C, they become photo-negative (Cunjak, 1988; Rimmer & Paim, 1990; Fraser *et al.*, 1993, 1995), leave their territories in riffles and find daytime concealment in pools or crevices in the river bottom substratum (Allen, 1940; Gibson, 1978; Rimmer *et al.*, 1984, 1985; Heggenes *et al.*, 1993) (Table II). Their behaviour changes in the presence of light with increasing tendency to seek shelter with increasing light intensity. This was also demonstrated for other species such as *O. mykiss* (Contor & Griffith, 1995), although the tendency was less conspicuous under ice cover and in turbid than in clear open water (Gregory & Griffith, 1996).

A proximate reason why young salmonids leave riffled areas at low water temperature is that their ability to retain their position is weak in cold water (Rimmer *et al.*, 1985; Graham *et al.*, 1996). The ability to swim against strong currents decreases rapidly as the water temperature falls below 6–8° C and their metabolic rate becomes low. The ability to swim against the current decreases with time during winter, probably due to gradually decreasing lipid reserves (Berg & Bremset, 1998; Jonsson & Jonsson, 2003; Næsje *et al.*, 2006) and decreased glycogenic reserves in muscles

TABLE II. Summary of responses by life stages of *Salmo salar* and *Salmo trutta* to increased environmental temperature based on available literature (see text)

| Character                   | Eggs | Embryos | Alevins | Parr | Smolts | Post-smolts |        |
|-----------------------------|------|---------|---------|------|--------|-------------|--------|
|                             |      |         |         |      |        | subadults   | Adults |
| Number                      | —    |         |         |      |        |             | +/-    |
| Size                        | +    |         | +/-     |      | -/+    |             | —      |
| Developmental rate          |      | +/-     | +/-     | +/-  | +      | +           | +      |
| Food consumption            |      |         |         | +/-  |        | +/-         |        |
| Growth efficiency           |      |         |         | +/-  |        | +/-         |        |
| Day activity                |      |         |         | +    | +      | +           |        |
| Time in season of migration |      |         |         |      | +      |             | +      |
| Time in season of spawning  |      |         |         | —    |        |             | —      |
| Mortality                   |      | -/+     | -/+     | +    | -/+    | +           | +      |

+, increase or earlier; —, decrease or later; +/-, maximum at intermediate value, -/+, minimum at intermediate value.

and liver and post-exercise recovery is poor due to elevated muscle lactate (Wendt & Saunders, 1973; Wilkie *et al.*, 1997; Jain & Farrell, 2003). The ultimate reason for seeking shelter during daytime in cold water may be to escape endothermic predators, as their activity is not slowed down in cold conditions unlike fishes (Valdimarsson *et al.*, 1997).

#### *Effects of flow*

During winter, increased water flow usually has little effect on the habitat use of *S. salar* parr, although the night-time activity may be reduced during periods of very high flow (Robertson *et al.*, 2004; Stickler *et al.*, 2007). Many parr remain in shallow riffles during reduced flows, which may cause mortality (Armstrong *et al.*, 1998; Berland *et al.*, 2004). In summer, flow decreases can cause emigration of *S. salar* parr into deeper pools, and Huntingford *et al.* (2001) found that parr tended to find shelter in the upstream direction at low and decreasing water flow. Landergren (2004), on the other hand, observed that parr of *S. trutta* in the Baltic survived droughts by moving downstream into brackish water. The smallest underyearling parr tended to move sooner than larger ones and the largest underyearlings retained their territories in the stream the longest. It is likely that population-specific differences exist in the direction the fish move, as experimentally shown with *S. trutta* in the River Imsa, Norway (Jonsson *et al.*, 1994). There, offspring of outlet spawners tended to move upstream whereas those of inlet spawners moved chiefly downstream. Northcote (1981) tested the current response of parr of *O. mykiss* from above and below a waterfall. He found that trout from below the waterfall exhibited more downstream movement during darkness in the autumn than those from above the waterfall.

At high autumn flow, emigration of pre-smolts into brackish waters can occur as observed in the Girnock Burn, Scotland (Youngson *et al.*, 1983) and River Imsa (Jonsson & Jonsson, 2002). In the River Imsa, relatively more pre-smolt of *S. trutta* than *S. salar* move downstream during the autumn flood (Jonsson & Jonsson, 2009), probably because *S. salar* defend fast current velocities at low temperature better than *S. trutta* due to their more streamlined body form and larger pectoral fins,

which are morphological adaptations to life in stronger water current. Survival of *S. trutta* pre-smolts emigrating early into brackish water in the autumn can be very low, as found in the River Imsa (Jonsson & Jonsson, 2009). This may be because they have poor ability to regulate their ionic concentration in sea water (Hoar, 1988; Zydlewski *et al.*, 2005). Riley *et al.* (2008) reported that *S. salar* parr that move to the estuary in autumn are not sufficiently physiologically adapted to sea water. In the River Imsa, juvenile hatchery *S. salar* released in autumn and winter exhibited poor survival and homing ability (Hansen & Jonsson, 1989, 1991), and the same may hold true for *S. trutta*. The main mortality factor for smolts is probably predation (Hvidsten & Lund, 1988; Koed *et al.*, 2006). Potential *S. trutta* predators, such as gulls *Larus* spp., cormorants *Phalacrocorax carbo* harbour seals *Phoca vitulina* and gadoid fishes, are present outside the river outlet at the time of seaward migration. There is no estimate of the effects of their predation, however, in the River Imsa system.

Thus, salmonid parr tend to escape droughts, but the direction of movement may vary among populations and appears to depend on stock-specific adaptations and the life stage of the fish. At very high autumn and winter flows, pre-smolts can be moved downstream to sea although they are unable to properly regulate their ionic concentration in sea water. In such cases, their sea survival can be very low.

## SMOLT MIGRATION

### *Regulating factors*

Anadromous salmonids smolt and move to sea in spring, and they adapt to sea life through a smolting process that takes place prior to the seaward migration. Byrne *et al.* (2004) divided factors influencing the seaward smolt run into regulating and controlling factors. Regulating factors operate before, whilst controlling factors act during the smolt run. Regulating factors affect the physiological smolting process, whereas controlling factors influence the physical process of migration such as downstream movement velocity.

The primary regulating factors of the smolting process are photoperiod and temperature. Day length is a timer, and increasing and decreasing photoperiods are major predictive, proximate factors indicating the season (Wootton, 1998). Temperature, on the other hand, affects the rate of development (McCormick *et al.*, 2002), and low water temperature such as 2° C, limits the response of *S. salar* parr to increased day length (McCormick *et al.*, 2000). Furthermore, since day length is similar on the same date and place each year, photoperiod does not cause annual population variation in smolting times.

Other cues such as water temperature are responsible for annual variation. To smolt successfully, fish need a certain amount of heat, which can be measured as number of degree-days [number of days  $\times$  mean temperature (° C)]. Zydlewski *et al.* (2005) showed that the temperature experienced over time determines the behavioural and physiological changes associated with smolting as well as the onset and termination of the smolt migration in *S. salar* (Table II). Smolt migration starts earlier and takes place over a shorter period in mild compared to cold years. For instance, *S. salar* reared at 12.0° C exhibited maximum gill  $\text{Na}^+$ ,  $\text{K}^+$ -ATPase activity, an indicator of the time of smolting, in late April compared with late May in a comparable group reared at 8.9° C (Handeland *et al.*, 2004). Similarly, temperature is found to influence

time of smolting in other salmonids such as *O. tshawytscha* (Negus, 2003), *O. mykiss* (Wagner, 1974), *S. alpinus* (Jørgensen & Arnesen, 2002) and others (Hoar, 1988).

### Controlling factors

The chief factors controlling the smolt run are water temperature, water flow and changes in water temperature and flow. Most studies indicate a pervasive effect of the temperature and temperature increases for the initiation of the seaward migration in salmonids (e.g. McCleave, 1978; Jonsson & Ruud-Hansen, 1985; Veselov *et al.*, 1998; Whalen *et al.*, 1999; Jutila *et al.*, 2005). For instance, by using the water temperature curve in spring, Jonsson & Ruud-Hansen (1985) modelled the time of smolt migration of *S. salar* in the River Imsa with a high degree of accuracy. Furthermore, the commencement of the smolt migration of *S. alpinus* in the Vesteurdalsa River, Iceland, correlated positively with water temperature (Jonsson & Antonsson, 2005). In *O. nerka* and *S. salar*, Foerster (1937) and Melnikova (1970) observed that the smolt run started earlier if the average water temperature were higher than normal in the preceding months. Similarly, smolts of *O. tshawytscha* move to sea earlier when the preceding water temperature is higher, as e.g. found in some Idaho and Oregon rivers (Roper & Scarnecchia, 1999; Achord *et al.*, 2007). Smolt migration appears not to be triggered by a specific water temperature or a specific number of degree-day during spring, but is controlled by a combination of the actual temperature and temperature increase in the water during spring. This result is also in accordance with studies on smolt migration of *S. salar* in the Burrishole system, west Ireland (Byrne *et al.*, 2004), and in the Finnish–Norwegian Rivers Utsjoki and Tana (Zydlewski *et al.*, 2005; Orell *et al.*, 2007). Holtby *et al.* (1989) studied the *Oncorhynchus kisutch* (Walbaum) smolt migration during nine consecutive years in Carnation Creek, British Columbia, Canada. They found that variability in stream temperatures accounted for 60% of the variability in the mean date of smolt emigration in that river. Investigations of *S. trutta* smolts indicated that the day number of the river descent correlated negatively with the increase in water temperature during spring (Bjorn, 1971; Solomon, 1978). Still, other evidence indicates an intermediate role of temperature. Where temperature does not have a significant effect on the initiation of the smolt migration, it may control the subsequent decrease in migratory activity as found for *O. mykiss* by Zaugg & Wagner (1973). The duration of the period when salmonid smolts tolerate the transfer from freshwater to sea water is temperature dependent. In *S. salar*, it is c. 280–350 degree-days at 10° C and 12° C and 450 degree-days at 14° C (Stefansson *et al.*, 1998). Smolts which remain in fresh water past the time of seaward migration desmolt (Mortensen & Damsgård, 1998).

In some rivers, however, the downstream migration of salmonid smolts can be initiated by increased water flow, as shown in *S. salar* from the River Rikleån, Sweden (Österdahl, 1969) and the River Orkla, Norway (Hesthagen & Garnås, 1986; Hvidsten & Johnsen, 1993). Furthermore, in the Snake River, Oregon, high water flow in March stimulated the smolt migration of *O. tshawytscha* (Connor *et al.*, 2003a). In the River Hals (northern Norway), the number of downstream migrating smolts of *S. alpinus*, and *S. salar* increased with increasing water level and decreased with increasing water temperature, whereas the abundance of *S. trutta* correlated significantly with increasing water temperature only (Carlsen *et al.*, 2004). The increase in



number of migrants correlated positively with the increase in water level the following day, indicating that fish movements represent an early response to a subsequent spate. This indicates that the fishes may also sense cues other than the water flow. Furthermore, Hartman *et al.* (1982) found a relationship between downstream movement of *O. kisutch* fry and spring flood in Carnation Creek, British Columbia. During seaward movement daily numbers fluctuated widely during the 10 year study period. Peak of movements coincided with or appeared slightly before freshet peaks. Thus, although day length and water temperature control the smolting process, their relative importance for the smolt migration varies among rivers, depending on local environmental conditions indicating population-specific adaptations to cues stimulating the onset of the salmonid smolt migration (Jonsson, 1991).

*Active migration or passive displacement by the water flow?*

Are migrating smolts carried passively downstream with the water flow? Thorpe & Morgan (1978) hypothesized that downstream migration of smolts is related to a smolting-associated reduction in swimming stamina. Their results indicated that *S. salar* smolts would not swim at speeds greater than two body lengths (BL) second<sup>-1</sup> (c. 0.3–0.4 ms<sup>-1</sup>). Tytler *et al.* (1978) and Thorpe *et al.* (1981) proposed that *S. salar* smolts were unable, or unwilling, to maintain their position in spring runoff currents and were therefore passively displaced downstream to the ocean. Peake & McKinley (1998), however, re-examined the swimming capacity of *S. salar* smolts. They found that smolts swam indefinitely against the current up to 1.26 ms<sup>-1</sup>, maintained speeds as high as 1.64 ms<sup>-1</sup> for 2–10 min, and made short bursts at speeds up to 1.95 ms<sup>-1</sup> which is c. 10 BL s<sup>-1</sup>. The huge difference between these results may be because Thorpe & Morgan (1978) used hatchery smolts that had previously not been exposed to high-current speeds and were therefore not behaving adequately when challenged by fast currents (Youngson *et al.*, 1989b).

Evidence indicates, however, that the water flow provides downstream movement of the juvenile fish. Hansen & Jonsson (1985) found that *S. salar* smolts actively move out into the main current of the river to avoid being caught by backwaters and sloughs. Moreover, Svendsen *et al.* (2007) showed that smolts migrated in a non-random spatial pattern independently of stream discharge distributions. Vertically, *S. trutta* and *S. salar* smolts demonstrated a preference for bottom-orientated positions in the river. Horizontally, all smolts preferred the mid-channel positions. These discharge-corrected preferences for certain spatial positions suggested that smolt emigration is not a matter of passive displacement. Moore *et al.* (1998) followed *S. salar* smolts downstream the River Test, England. They found that the smolts moved close to the surface, and within the fastest moving section of the water thalweg. Furthermore, smolts migrate more quickly during high than low water flows (Youngson *et al.*, 1989a). Raymond (1968) compared the migration rates of yearling *O. tshawytscha* in Snake and Columbia Rivers during periods of low and moderate discharges. The rate of migration was directly related to the current speed, *i.e.* 21 km day<sup>-1</sup> at low and 37 km day<sup>-1</sup> during moderate river discharges. A similar result was found in *O. tshawytscha* and *O. mykiss* yearlings in the lower Snake River, where the travel time was strongly correlated with water flow (Smith *et al.*, 2002; Connor *et al.*, 2003b). Thus, seaward migration is not passive, but current speed has major influence on the speed of river descent.

## SPAWNING MIGRATION

### *Timing*

The return migration of adult *S. salar* from the ocean begins early in spring. For instance, *S. salar* in the Norwegian Sea commence their return to Norwegian rivers in March (Hansen *et al.*, 1993), and angler catch data reveal that the first fish enter rivers in early April even though spawning commences in October, half a year later. In the River Dalälven, Sweden, *S. salar* enter fresh water in spring although they do not spawn before late autumn (Dahl *et al.*, 2004). Thus, despite favourable growing conditions at sea, many populations leave the ocean several months prior to spawning instead of continued feeding and growth in sea water. Large individuals often approach the coast earlier in the migratory season than smaller individuals do (Jonsson *et al.*, 1990). They appear to behave according to the 'asset-protection-principle' (Clark, 1994), which states that the larger the current reproductive asset, the more important it becomes to protect it. Thus, the larger they become they should be more unwilling to stay in the ocean and accept the risk for the same size increment because of their higher current reproductive value (defined as the expected reproduction of an individual from its current age onwards (Fisher, 1930)). Thus, large salmonids enter fresh water a long time before spawning. The river entry is also linked to the current habitat condition. For instance, in the River Dalälven, Sweden peak migration of *S. salar* was strongly correlated with both mean monthly sea and river temperatures during spring. Salmon arrived earlier when temperatures were higher and later when temperatures were lower, indicating a phenotypically plastic response to the water temperature encountered by the salmon (Table II). Often, early migratory fish are from large rivers where they perform long, time and energy-consuming migrations, which would be even more stressful during warm summer months. Conversely, in short, small rivers, adult anadromous salmonids often enter the river only shortly before spawning due to restricted water flows (Jonsson *et al.*, 1990). In such cases, the time of river entry seems independent of the water temperature (Jonsson *et al.*, 2007). Thus, the timing of the return migration appears adapted to the temperature and flow conditions of the home river, and the fish tend to enter the rivers when expected migratory conditions are favourable.

In Pacific salmon, sea-surface temperatures can influence migratory timing (Hodgeson & Quinn, 2002; Hodgeson *et al.*, 2006). The timing of the return migration may be a consequence of the fish avoiding high summer temperatures as reported for *O. nerka* (Robards & Quinn, 2002). But the timing varies among populations: when temperatures are lower than 19° C, *O. nerka* tend to approach the spawning grounds c. 1 month prior to spawning, regardless of the length of the spawning migration. For populations which have to pass areas with higher water temperature, some populations enter fresh water before the warmest period, months before spawning. Others migrate after the highest temperatures have passed. Hodgeson *et al.* (2006) reported that following a spring and summer with relatively high sea-surface water temperature, *O. nerka* returned early to the rivers in south-west Alaska and late to the Fraser River in British Columbia, Canada. In the rivers between these extremes, they found no consistent pattern. Their findings support the hypothesis that interannual variations in *Oncorhynchus* spp. distributions at sea reflect temperature conditions and that the date when the *Oncorhynchus* spp. initiate homeward migration is a population-specific trait, largely unaffected by the location of the fish at sea.

*Temperature extremes influences the river ascent*

At low water temperatures *S. salar* migrating upstream can have problems passing obstacles such as waterfalls (Jensen *et al.*, 1989a, 1998), and high temperatures can also delay upstream migration. In the River Dee, Scotland, *S. salar* remained in the sea when water temperature exceeded 20° C (Hawkins, 1989). For *O. tshawytscha* in the Columbia River, Salinger & Anderson (2006) reported maximum migratory speed at 16° C, whilst migration speed was reduced at both higher and lower temperatures. The colder the water *O. mykiss*, on the other hand, moved faster, indicating that they studied the migration at temperatures above the optimum for migration. *Oncorhynchus tshawytscha* in the Snake River, migrate up to 1500 km inland. They spawn in mid to late August, but migrate prior to the peak temperatures during summer. This is necessary to complete their long migration. Late migrants have high mortality during the migration or experience delays while they seek thermal refugia (Crozier *et al.*, 2008). Thus, temperature extremes can have an effect on the timing of the upstream migration due to selection against migration during stressful temperature conditions when the oxygen content in the water limits activity of the fish (Brett, 1964), and the temperature-dependent metabolic costs are high, quickly exhausting their energy reserves (Glebe & Leggett, 1981a).

*Population-specific variation*

The initiating effect of day length on migratory timing appears in most cases to be population specific, meaning that each population is adapted to enter fresh water at a time of the year when the migratory opportunities in the long run have been best for spawning in their home stream (Jonsson *et al.*, 2007). Although some migratory fish feeding close to the river mouth such as *S. trutta* can have a wide migratory period and may enter the spawning river most months of the year (Jonsson & Jonsson, 2002), most species and particularly the semelparous Pacific salmon, access the river within a restricted time period. For instance, in all the *O. nerka* rivers investigated by Hodgeson *et al.* (2006), the fish entered the spawning area c. 1 month prior to spawning irrespective of where they fed in the ocean. Likewise, Keefer *et al.* (2004) reported that migration date was the primary factor influencing the timing of the upstream migration of *O. tshawytscha* in the Columbia River, and that the migratory speed of adults observed at a specific point on their migratory route, increased with the progression of the migration period.

*Discharge is a controller*

Water flow is often the primary factor controlling when the salmonids enter rivers, whereas increases or decreases in river flow appear to be important for the timing of the ascent (Banks, 1969; Jonsson, 1991 and references therein). For example, in the small River Imsa (mean annual water flow of 5.1 m<sup>3</sup> s<sup>-1</sup>), the number of adult *S. salar* per day ascending a trap at the river mouth increased with increasing water discharge (Jonsson *et al.*, 1990, 2007). Saunders (1960) observed in the Ellerslie Brook, Prince Edward Island, Canada, that adult *S. salar* entered the river during autumn freshets, and remained at the head of the estuary during periods of low flow. Potter (1988) reported that *S. salar* entered the River Fowey, England, during periods of increasing freshwater discharge, and that low river flow delayed the migration of *S. salar* into the river.



For anadromous *S. trutta* in River Imsa, Jonsson & Jonsson (2002) reported that the effect of water flow changed during the year. Relatively high water flow stimulated the river ascent early in the migratory period, but gave no significant effect closer to spawning. The early effect may be related to the fact that the water level in this stream is at its minimum during summer, and the fish may ascend during occasional freshets, but close to spawning time, the fish enter the river almost irrespectively of the level of the water flow. Tetzlaff *et al.* (2005) reported that adult *S. salar* movement in the Girnock Burn, a tributary to the Aberdeenshire River Dee, Scotland, was increasingly triggered by suboptimal flow increases as spawning time approached, in dry but not in wet years, lending support to this contention.

Likewise, upstream migration studies based on telemetry show that water discharge influence salmonid river ascent. For instance, studies of radio-tagged *S. salar* entering the River Dee, Scotland support this (*e.g.* Hayes, 1953; Allen, 1966; Webb & Hawkins, 1989; Laughton, 1991). *Salmo salar* started to enter the spawning grounds in the Girnock Burn early and the fish entry continued throughout the pre-spawning period in wet years. In dry years, the fish were delayed (Tetzlaff *et al.*, 2008). Also in the Rohden Stream, Denmark, initiation of the upstream migration is positively correlated with stream discharge (Svendsen *et al.*, 2004), and in the River Tana (along the border between northern Norway and Finland), increasing discharge is associated with enhanced swimming activity of *S. salar*, especially late in summer (Erkinaro *et al.*, 1999).

Very high water discharges can decrease (Jonsson & Jonsson, 2002; Jonsson *et al.*, 2007), and even temporarily halt upstream fish migrations (Davidson *et al.*, 1943; Sørensen, 1951; Stuart, 1957; Jensen *et al.*, 1989a). For instance, in the River Mistassini, Quebec, Trepanier *et al.* (1996) found that the ascent of landlocked *S. salar* correlated negatively with water flow, suggesting that the fish preferred falling water phases for ascent. This is supported by findings from north European *S. salar* (Jensen *et al.*, 1998; Lilja & Romakkaniemi, 2003) and *S. trutta* rivers (Svendsen *et al.*, 2004). Keefer *et al.* (2004) reported that *O. tshawytscha* in Columbia River moved more slowly when the water discharge was high. Other studies, however, have indicated that the flow has no effect on the upstream migration of adult *S. salar* (Thorstad & Heggberget, 1998; Lilja & Romakkaniemi, 2003; Thorstad *et al.*, 2003; Karppinen *et al.*, 2004), or *S. trutta* (Rustadbakken *et al.*, 2004). Salinger & Anderson (2006) maintained that water flow was of minor importance for the migratory speed of the homing *O. tshawytscha* in the Columbia River. Possibly, water flow does not constrain the upstream migration in these latter cases because the streams are large relative to the amount of water required by the fish, and the current speed is not particularly high.

#### *Direct and indirect population effects of low discharge*

The migratory effect on the adult spawners of high water flow is size and age specific (Table III). At low flow in small streams, the ascent of large salmonids is delayed relative to that of smaller ones (Jonsson *et al.*, 1990, 2007; Jensen & Aass, 1995). This may be because the fish are vulnerable to predation during the river ascent, as well as they may be more adverse to risk taking according to the asset-protection-principle (Clark, 1994). Freshets decrease the vulnerability of the fish

TABLE III. Increased water discharge affects salmonid migration and population characteristics of anadromous *Salmo salar* and *Salmo trutta*

| Character  | Species          | Sources  |
|--|------------------|--|
| Stimulates river entry from the sea at suboptimal flow early in the migration season | <i>S. trutta</i> | Jonsson & Jonsson (2002)   |
|  | <i>S. salar</i>  | Jonsson <i>et al.</i> (1990, 2007)<br>Jensen & Aass (1995)   |
| Positive effect on fish size and sea-age at maturity in small streams                | <i>S. trutta</i> | Jonsson <i>et al.</i> (2001b)  |
|  | <i>S. salar</i>  | Schaffer & Elson (1975)<br>Scarnecchia <i>et al.</i> (1991)<br>Jonsson <i>et al.</i> (1991b)<br>Mitchell & Cunjak (2007) |
| Positive effect on population size   | <i>S. salar</i>  | Mitchell & Cunjak (2007)<br>Tetzlaff <i>et al.</i> (2008)  |

because of increased turbidity, deeper water and higher water speed, making predation more difficult (Abrahams & Kattenfield, 1997). For instance, in the small River Imsa, large *S. salar* were delayed more in their ascent from the sea than smaller individuals (Jonsson *et al.*, 1990, 2007). Similarly, in the Catamaran Brook, a third-order tributary to the Miramichi River, New Brunswick, the proportion of one-sea-winter *S. salar* in the run and female body size were negatively correlated with stream discharge. The low-flow years were very influential in the correlation (Mitchell & Cunjak, 2007). For *O. kisutch* in the Deer Creek Junior, large females entered the creek at peak discharge and progressively smaller ones entered as water level receded (van den Bergh & Gross, 1989). The upstream migration of the smaller males, on the other hand, was independent of high flows.

As an evolutionary consequence, river flow influences population structure and abundance (Table III). As low flow constrains the entry of large individuals, adult size of anadromous salmonids increases with stream flow in small but not in large rivers (Schaffer & Elson, 1975; Scarnecchia *et al.*, 1991). In Norway, it was found that water flow constrains the sizes of *S. salar* and *S. trutta* in streams with annual mean water discharge less than *c.* 20 m<sup>3</sup> s<sup>-1</sup> and 0.2 m<sup>3</sup> s<sup>-1</sup>, respectively (Jonsson *et al.*, 1991b, 2001b).

Water flow may also restrict the size of the spawning stock. In the Gironck Burn, fewer *S. salar* spawners entered the spawning grounds in dry than wet years (Tetzlaff *et al.*, 2008). In Catamaran Brook, Mitchell & Cunjak (2007) found a strong relationship between the total number of adult *S. salar* returning within a year and maximum water discharge during the migration period. Thus, reduced water flow during the upstream spawning migration has a significant effect on adult return. In the long term, the evolutionary effects will probably be decreased population abundance, smaller size at maturity and changed time of river ascent in adults. The return migration will either change to a period with more water or be delayed to close before spawning as seen in small rivers with restricted water flow.

## SPAWNING

### *Strong selection for spawning date*

The accuracy, with which salmonids return to their natal stream for spawning makes it reasonable to assume that salmonid populations exhibit specific adaptations regarding spawning time, and the adaptations depend heavily on water temperature (Henderson, 1963). Up to a certain temperature, instream biological rates, such as that of gonadal development, should follow Van't Hoff's rule which states that the biological activity doubles for every 10° C increase of water temperature (Caissie, 2006). For instance, adult *S. salar* spawning in the coldest uppermost tributaries of the River North Esk enter the river early in the year and the lowest tributaries late in the year (Summers, 1996). Similarly, in the Scottish River Dee, early-running fish home to the upper parts of the catchment to spawn, whereas the late-running fish tend to spawn lower down the catchment (Webb & McLay, 1996). Such differences appear to be adaptive and selection effects may continually modify these populations. Differential exploitation of the various population components of such rivers can adversely affect the diversity, abundance and long-term survival of the entire stock (Thorley *et al.*, 2007).

Evidence for strong heritability for spawning time is seen both in wild and farmed *S. salar*. Lura & Sægrov (1993) studied the spawning time of escaped farmed and native *S. salar* in the River Vosso, western Norway. The escapees attained maturity 21–26 days earlier than the native fish. River Vosso is relatively mild during winter, and the native fish were probably adapted to this thermal regime and spawned late. The Norwegian farmed *S. salar* originated from colder, more northern rivers, and have been subjected to artificial selection for several generations in culture (Gjedrem *et al.*, 1991). Thus, farmed fish lack an adequate response to the water temperature in the River Vosso. Other studies have also revealed significant differences in spawning time between native and escaped farmed *S. salar*. Webb *et al.* (1991) found that wild *S. salar* spawned before the hatchery fish did in Scotland. Furthermore, the mean spawning dates of *O. kisutch* and *O. tshawytscha* of the University of Washington Hatchery is earlier in the year now than in the 1950s and 1960s, apparently owing to artificial broodstock selection in the hatchery, contrasting an expectancy of later spawning due to higher autumn temperature (Quinn *et al.*, 2002). Thus, spawning time partly reflects river temperature, partly the origin and genetic adaptation of the fish.

The reason for the temperature dependence of spawning time is probably that it influences the duration of embryonic development (Elliott & Hurley, 1998a), and thereby the time of hatching (Crisp, 1981). Larval growth and survival depend on appropriate food resources (Frank & Leggett, 1986), predator protection (Shepherd & Cushing, 1980) and benign abiotic conditions (Elliott & Elliott, 2006). Natural selection favours commencement of external feeding at a time when the survival and growth opportunities are maximal (Cushing, 1982). Fry survival will be low if emergence is either too early or too late (Einum & Fleming, 2000; Letcher *et al.*, 2004).

### *Intraspecific variation in spawning temperature and time*

Spawning temperature varies among populations within species. Peterson *et al.* (1977) reported that *S. salar* in the Miramichi River, New Brunswick spawned at

a water temperature of 6° C and less, whereas Heggberget (1988) observed temperatures varying between 1.0° C and 4.7° C during peak spawning in Norwegian *S. salar* populations. He found that the day of commencement of spawning was positively correlated with mean water temperature from December through April in the river, a time period when the eggs were buried in the gravel substratum. Spawning time was earlier in rivers where the mean winter temperature was low (<1.5° C) than in the streams with higher water temperature.

There are also population-specific variations in spawning time. According to Heggberget (1988), peak spawning time of Norwegian *S. salar* varied between 20 October and 10 January. In the northern streams (63–70° N), peak spawning occurred between 20 October and 5 November, in the southern rivers (59–63° N) it occurred between 25 October and 10 January. Spawning occurred later in the autumn in rivers where the winter temperature was relatively warm (2–4° C) than cold (0–1° C), but the local variation was large probably because other factors also influence spawning time such as habitat accessibility at a particular time (Tallman & Healey, 1991) and energy demands on the adults (Jonsson *et al.*, 1997). In the River Dee, Scotland, *S. salar* spawned earliest at high-altitude sites in the upper reaches and progressively later at sites farther downstream (Webb & McLay, 1996). Probably, the optimal time of fry emergence varies among different parts of the river, and is the reason for this. Similarly, Sheridan (1962) observed that *O. gorbuscha* spawned earlier in relatively cold than warmer streams in Alaska. Spawning time of *O. tshawytscha* transplanted from North America to New Zealand have changed substantially since their introduction 80 years ago, with later spawning in populations where the embryos develop in warmer water (Quinn *et al.*, 2000, 2001; Unwin *et al.*, 2000). This means that spawning time may change quickly if the environmental conditions change, as shown by the high heritability estimates (Carlson & Seamons, 2008).

## EMBRYONIC DEVELOPMENT, HATCHING AND EMERGENCE

### INCUBATION TEMPERATURE

Most anadromous salmonids are autumn or early winter spawners, with Pacific trouts as exceptions. They reproduce chiefly in spring or summer (Scott & Crossman, 1973). The majority of the species bury their eggs in gravel substratum of rivers, where they hatch in spring when a particular heat-sum is accumulated. The heat-sum required from fertilization to hatching and swim-up differs among populations and species, as reported for Atlantic and Pacific salmon by Berg & Moen (1999), Beacham & Murray (1987, 1990) and Konecki *et al.* (1995a, b). Hendry *et al.* (1998) reported an adaptive divergence in developmental biology of *O. nerka* in Lake Washington, Seattle, U.S.A. during the last 50 years. A somewhat contrasting result was found by Wallace & Heggberget (1988) who compared the temperature sum requirement for hatching of five *S. salar* populations from the north and south of Norway. They were unable to detect any difference in the duration of incubation time between *S. salar* from south-west and north Norway when they were retained at a constant water temperature, and concluded that the populations revealed no local adaptation to the temperature conditions of their home rivers. The main reason for Wallace & Heggberget's (1988) result may have been a too small climatic variation between the

localities chosen for the population comparison. The climate along the Norwegian west coast is governed by the North Atlantic Gulf Stream.

There appears to be an optimal temperature for egg development. Ojanguren & Braña (2003) found maximal embryo survival of *S. trutta* between 8 and 10° C and no survival at 16° C or higher. They suggested an upper thermal limit for embryonic development between 14° C and 16° C. Pankhurst *et al.* (1996) reported that the success of the egg development in *O. mykiss* varied with temperature. They found that all adult females they held at 9° C and 12° C ovulated, whereas only a fraction of those held at 15° C and 18° C ovulated. Almost no fish ovulated when kept at 21° C. These results indicate that elevated autumn temperatures can have a deleterious effect on ovulation and offspring production at the southern edge of the current range. There has been a gradual increase in river temperatures during recent years (Webb, 1996; Jonsson *et al.*, 2005), a trend which is expected to continue (IPCC, 2007). According to McCarthy & Houlihan (1997), there will be a northward shift in the geographic distribution of *S. salar*, and higher river temperature during gonadal maturation may be one of the possible reasons for local extinction at the southern edge of the current range.

## INCUBATION TIME

A number of studies provide estimates of degree-days required for the egg incubation time for various salmonid species. For instance, Crisp (1981) maintains that *S. salar* require (on average) 63 days from fertilization to 50% hatching at 8.0° C and 37.8 days at 12.0° C. From fertilization to 50% swim-up, 99 days and 62 days are needed at the same temperatures, respectively (Gunnes, 1979). Beacham & Murray (1985) reported that the corresponding values for *O. keta* were 67.5 and 45 days from fertilization to 50% hatching and 108.5 and 77.4 days from fertilization to 50% swim-up. The heat-sum required is lower when water temperature approaches 0° C than in warmer water (Wallace & Heggberget, 1988). Crisp (1981) on the other hand reported that the heat-sum from incubation to hatching was 10% lower when the eggs were incubated at 12° C than at 8° C for *S. salar*. Thus, the heat-sum required from fertilization to hatching may be highest at an intermediate temperature (Table II).

Incubation time depends also on other factors such as the temperature level and degree of environmental stress. If the eggs are mechanically disturbed, *e.g.* during a freshet, or stressed by lack of oxygen they can hatch sooner (Hamor & Garside, 1976; Næsje & Jonsson, 1988). Hatching is stimulated because of increased activity of the embryo within the egg as a response to hostile environmental conditions (Hamor & Garside, 1976; Ciuhandu *et al.*, 2005).

The emergence period of a fish stock varies among years. Elliott & Hurley (1998a) studied the interannual variations in the emergence period exhibited by *S. trutta* of the Black Brows Beck, Lake District, England. During 1967–1996, the dates of emergence varied between 11 March to 4 April 1989 and 15–20 May 1979. Most of the variation in median emergence date was due to variation in water temperature, with spawning dates as a secondary factor; the latter, however, had a greater effect on the length of the emergence period. Furthermore, there may be a general trend that fish originating from cold rivers have higher developmental rates and require fewer degree-days at the same temperature (Brannon, 1987; Brannon *et al.*, 2004), but this may not always be the case as shown for Pacific salmon (Beacham & Murray,

1987), and Hebert *et al.* (1998) found little heritability of embryo developmental rate in *O. gorbusha*.

In all, tables giving the duration of the embryonic development are approximations, and as such a useful first step. They, however, may not give the exact hatching time as they are based only on the effect of temperature and there can be local adaptations in developmental rate as well as confounding factors that influence time of hatching.

## EMBRYO SIZE

Incubation temperature influences the rate and efficiency of the yolk absorption (Kamler, 1992) as well as alevin size (Beacham & Murray, 1990) (Table I). According to Atkinson (1994), size at a given ontogenetic stage decreases with increased rearing temperature. In support of this, Ojanguren & Braña (2003) found that the *S. trutta* embryo size at 50% cumulative hatching increased with decreasing water temperature from 16° C to 4° C. These temperatures are, however, very different, and Beacham & Murray (1990) found that *O. kisutch* alevins and fry were larger when developed at 4° C than at 1° C and 8° C, and in *O. gorbusha* and *O. keta*, alevins and fry were largest when the eggs were incubated at 8° C. Thus, Atkinson's (1994) general rule may be too simple, and that the embryo size is largest when incubated at an intermediate temperature.

## EARLY MORTALITY AND RECRUITMENT

### POPULATION REGULATION

Salmonid populations are often regulated by density-dependent mortality, typically during the early stage after fry emerge from spawning gravel (Milner *et al.*, 2003). This early regulatory period may occur on spatial scales much smaller than that of the whole population, such as the area used for spawning (Einum & Nislow, 2005). Density-dependence appears most important for recruitment in high-density populations (Elliott, 1987; Jonsson *et al.*, 1998b), whereas density-independent factors are of prime importance when the density is below the carrying capacity of the habitat (Elliott & Hurley, 1998b; Lobón-Cerviá, 2007). After the early regulatory phase, mortality appears controlled mainly by density-independent factors, and stream flow may be such a factor (Elliott & Elliott, 2006), and mortality can be particularly high during winter. For instance, Letcher *et al.* (2002) reported that the survival of *S. salar* parr in West Brook, Massachusetts, was approximately two-fold lower during winter as compared with summer and was higher for parr in their first winter than for fish in their second winter. Much of this mortality is attributed to the transition phase of late fall and early winter (Carlson & Letcher, 2003).

### EFFECTS OF FLOW

One of the anticipated effects of climate change is an increase in both frequency and intensity of extreme weather events, such as floods and droughts (Milly *et al.*, 2002; Palmer & Raisanen, 2002). The warming of Earth may fuel interactions between the ocean and atmosphere which will amplify the frequency and intensity of extreme weather events. According to IPCC (2007), extremes such as higher



maximum land temperatures and more intense precipitation are projected to have a 90–99% chance of occurring, and can lead to drought and flooding.

There is a positive relationship between water discharge and the survival of eggs and underyearling *S. salar*, both during winter and summer (Gibson & Myers, 1988). Extremes in flow can, however, affect fry survival negatively. In years with high discharge during the alevin stage of *S. salar*, mortality can be elevated as found in the River Saltdalselva, northern Norway (Jensen & Johnsen, 1999). High discharge during the egg stage seemed to be less important. *Salmo trutta* had highest mortality in years with low water temperature at emergence as well as high discharge during the alevin stage. Low flow at the time of or just after emergence can also decrease the survival rate of the young fish (Elliott, 1985). It is significant especially in areas often experiencing droughts such as *S. trutta* populations in Spain (Lobón-Cerviá & Rincón, 2004; Lobón-Cerviá & Mortensen, 2005; Nicola *et al.*, 2008).

The annual mortality of *S. trutta* population in Spruce Creek, Pennsylvania, was best explained by water discharge during spring (Carline, 2006). Density of age 1 fish was inversely related to spawner density and positively related to discharge during the fall spawning period. Interactive effects of discharge and *S. trutta* density accounted for most of the annual variation in mortality, recruitment and growth during the first year of life. There was a negative association between growth and mortality. Droughts that prevent adult fish from reaching their spawning grounds may have a similar constraining effect on recruitment. In the regulated River Orkla, Norway, increased water flow in winter has increased the production of *S. salar* parr. Low flow may also restrict recruitment in *O. tshawytscha*. Connor *et al.* (2003a) reported that flow augmentation in the Snake River, Idaho, increased the cohort survival of subyearling fish. When flow is low, the individual growth of young fish may decline, as reported for *O. mykiss* (Harvey *et al.*, 2006).

## TEMPERATURE AND ACCOMPANIED EFFECTS

Gibson & Myers (1988) found a positive relationship between temperature and survival of underyearling *S. salar* in Newfoundland and New Brunswick rivers, but also noted that extreme temperatures could reduce recruitment. Connor *et al.* (2003a) reported that water temperature correlated negatively with the survival of subyearling *O. tshawytscha* in the Snake River British Columbia. The negative effect of particularly high or low water temperature seems strongest during embryonic development, at hatching, just before emergence and when the alevins commence external feeding. For instance, mortality of *S. salar* in the Norwegian River Saltdalselva increased significantly in years with high discharge during the alevin stage as well as in the first week after emergence. High discharge during the egg stage and >1 week after emergence seemed to be of minor importance. Mortality of *S. trutta* was highest in years with low water temperatures at emergence and high discharge during the alevin stage (Jensen & Johnsen, 1999).

An effect of high water temperature is low oxygen content in the water. In oxygen saturated water, dissolved O<sub>2</sub> content decreases by *c.* 2% per 1° C increase in temperature at 18° C and a barometric pressure of 760 mm Hg, a little more in colder and less in warmer waters (Atkins, 1998). Oxygen deficits accompanied by pollutants can cause egg mortality. With low water flow, gravel interstices can be clogged by fine sediment which reduces the intragravel oxygen supply to eggs and alevins (Merz

*et al.*, 2004; Merz & Setka, 2004). Thus, low flow and high temperature in synergy with low oxygen supply and pollution can restrict salmonid recruitment. Embryos and alevins are most threatened by these abiotic factors at the southern edge of their distribution range where the water temperature is critically high.

## GROWTH

### GROWTH MODELS

Temperature affects metabolic processes and growth in fishes (Wootton, 1998). It influences the timing and duration of most life-history stages. Not only fry emergence, as discussed above, but also growth to parr size and smolt emigration (Connor *et al.*, 2002), indicate the strong effect of water temperature. As poikilotherms, they are sensitive to changes in temperature and the gills act as effective heat exchangers. Most heat transfer, however, is by conduction directly through the body wall (Elliott, 1981). Because of the allometric relationship between the volume and the surface of a fish, small fish are more susceptible to fluctuations in water temperature than larger ones (Elliott, 1994).

A useful model linking temperature to growth was developed by Elliott *et al.* (1995). This model relates specific growth rate of *S. trutta* parr to water temperature, and initial mass of the fish. The parameters are estimated from laboratory experiments over a range of water temperatures, and the parameters are upper, lower and optimal temperature for growth as well as growth rate at the optimal temperature (Elliott & Hurley, 1997).

The Elliott *et al.* (1995) growth model forms a triangular curve with temperatures at beginning, end and maximum growth forming the triangle's corners. The effect of a temperature increase depends on whether the temperature is above or below the point for optimal growth. To the left of this point, an increase in temperature results in increased growth given adequate food intake (*e.g.* Connor & Burge, 2003); to the right, growth will decrease (*e.g.* Brown, 2004). A reason for the triangular shape may be that the scope for growth increases with temperature until constrained by the oxygen content in the water (Brett, 1952, 1964).

The triangular relationship between temperature and growth appears to hold for a number of salmonid populations (Elliott, 1994; Larsson *et al.*, 2005; Forseth *et al.*, 2009), and it explains why growth rate decreases at high temperatures (Marine & Cech, 2004). There are, however, differences in maximum growth among individuals of the same population, meaning that for populations a rounded top may be more appropriate than the strict triangular shape (Elliott & Hurley, 2003). One such model is the Ratkowsky *et al.* (1983) model, a four-parameter model developed for the dependence of bacterial culture growth rate on temperature. The model was re-parameterized for *S. salar* growth by Forseth *et al.* (2001) and consists of four biologically meaningful parameters: temperatures at maximum, upper and lower limits for growth and maximum specific growth rate, *i.e.* the same four biologically interpretable parameters as the Elliott *et al.* (1995) generic model for fish growth.

The Elliott and the Radkowsky models can be used to control for differences in body size and temperature, and therefore facilitate direct comparisons of growth performance among individuals or groups of fishes. This was applied by Einum &



Fleming (1999, 2000), who explored effects of variable egg size and Vøllestad *et al.* (2002) who studied density effects of *S. trutta*. Furthermore, Nislow *et al.* (2004) accounted for effects of between-site and between-year differences in temperature by using the *S. salar* growth models of Jonsson *et al.* (2001a), in their test for effects of variation in hydrological regime on summer growth of juvenile *S. salar*.

As maintained by Nicola & Almodóvar (2004), the Elliott growth model appears to underestimate growth in the coldest rivers, and several other models to fish growth testing effects of temperature and fish size have been developed. Most of these models, however, do not use biologically meaningful parameters as *e.g.* the polynomial model developed by Ojanguren & Braña (2003). An analytic growth model presented by Bacon *et al.* (2005) described the growth rate (in body mass and length) of *S. salar* parr as a function of ambient temperature, body length, condition factor (mass  $\times$  L<sup>-3</sup>), day of the year and interaction between these and lifestyle variables (parr maturation and smolting). Bacon *et al.* (2005) estimated the importance of season (18% of total variation) by including day number as an explanatory variable. Their regression model comprised 23 estimated parameters, including polynomials up to the fifth order, and was developed without *a priori* biological prediction of shape. The model predicted complex and multiple peak growth patterns when visualizing the growth performance of one population living under natural conditions in the Girnock Burn, Scotland. Growth models similar to the one suggested by Bacon *et al.* (2005) can accurately describe seasonal growth patterns. One may be sceptical to the generality of such models and the predictive value for other populations and rivers. They, however, pinpoint that time of the year may influence the growth performance of the fish. For instance, winter-acclimatized *S. salar* parr maintain positive growth at water temperatures as low as 1° C (Finstad *et al.*, 2004b; Murphy *et al.*, 2006), which is much lower than during summer (4–5° C) (Jonsson *et al.*, 2001a). Winter-acclimatized parr outgrow summer acclimatized fish at low temperatures. Furthermore, fish often experience a compensatory growth rate in spring which may be two to three times higher than that of conspecifics tested later in summer and autumn (Larsson & Berglund, 2006). Also, the loss of body mass is larger in winters with warmer, more variable temperatures than in cold winters (Murphy *et al.*, 2006).

## DO SALMONIDS EXHIBIT THERMAL GROWTH ADAPTATIONS?

Optimal temperatures for parr growth of most salmonid species are close to 15° C and equally high for *S. alpinus* as *S. trutta* and the *Oncorhynchus* species investigated (Table IV). This temperature is similar to the temperature for maximum activity (Brett, 1964). At higher temperatures the scope for growth and activity are constrained by water oxygen content. The optimal temperature for growth of *S. salar* in fresh water is a little higher than the others, and *O. mykiss* has an intermediate optimal temperature for growth. *Salmo salar* is the only anadromous salmonid that has been tested for optimal temperature in sea water (Handeland *et al.*, 2003). The results indicate that optimal temperature for growth decreases with size of the fish as also found for Atlantic cod *Gadus morhua* L. by Björnsson & Steinarsson (2002). Bioenergetic simulations have likewise shown numerically that the optimal temperature for growth decreases with increasing body size (Ursin, 1967; Cuenco

TABLE IV. Optimal temperatures for growth of parr of eight anadromous salmonid species. For *Salmo salar*, optimal temperature for post-smolt growth in sea water is also given

| Species               | Life stage  | Optimal temperature for growth (° C) | Sources  |
|-----------------------|-------------|--------------------------------------|--|
| <i>S. salar</i>       | Parr        | 16–20                                | Elliott, 1991; Jonsson <i>et al.</i> (2001a)   |
|                       | Post-smolts | 13                                   | Koskela <i>et al.</i> (1997); Handeland <i>et al.</i> (2003)   |
| <i>S. trutta</i>      | Parr        | 13–17                                | Jensen (1990); Forseth & Jonsson (1994); Elliott & Hurley (1997, 1999); Ojanguren <i>et al.</i> (2001); Forseth <i>et al.</i> (2009) |
| <i>S. alpinus</i>     | Parr        | 14–17                                | Lyytikäinen <i>et al.</i> (1997); Larsson <i>et al.</i> (2005)   |
| <i>S. fontinalis</i>  | Parr        | 14.4–16                              | Dwyer <i>et al.</i> (1983)   |
| <i>O. kisutch</i>     | Parr        | 12–15                                | Brett (1952); Edsall <i>et al.</i> (1999)  |
| <i>O. nerka</i>       | Parr        | 15                                   | Brett (1952)   |
| <i>O. tshawytscha</i> | Parr        | 15                                   | Banks <i>et al.</i> (1971); Brett <i>et al.</i> (1982)   |
| <i>O. mykiss</i>      | Parr        | 15–19                                | Hokanson <i>et al.</i> (1977); Wurtsbaugh & Davis (1977); Myrick & Cech (2000)   |

*et al.*, 1985). Furthermore, the growth performance curve is less sharply pointed at the optimal temperature in large than smaller *S. trutta* (Elliott, 1975a).

There are adaptive differences in growth rate among populations as indicated by the heritability for growth in fresh and salt waters (Table V). Heritability, which is a measure of the phenotypic variation for a trait that is attributable to additive genetic variation, ranges from 0 (no genetic basis at all to the variation) to 1 (all variation has a genetic basis). Furthermore, maximum growth rates vary among populations within species as illustrated by Jonsson *et al.* (2001a) who established and compared growth models for *S. salar* from five Norwegian rivers in an experiment performed during late summer-early autumn. They also compared the established growth curves for Norwegian *S. salar* with similar curves for two British populations (Elliott, 1991), and found that the populations exhibited similar growth performances.

The geographical distribution of species is expected to vary due to climate change (Davis & Shaw, 2001; Root *et al.*, 2003), and most attempts to understand how climate will affect spatial distributions rely on correlations between the current species area and ambient temperature (Parmesan & Yohe, 2003), either alone or in combination with laboratory-based thermal performance models (Chown & Gaston, 2008; Portner & Farrell, 2008). Most studies predicting distributional effects of climate change, however, implicitly assume that the species' thermal performance is related to the experienced temperatures, either as general geographical trends in temperature performance (Bradshaw *et al.*, 2000), or as specific adaptations to the prevailing temperatures in their local environment (Gilman *et al.*, 2006). The present literature, however, indicate that there is little adaptive variation in intraspecific thermal performance in *S. salar* and *S. trutta*, and most variation observed is phenotypically plastic (Jonsson *et al.*, 2001a; Forseth *et al.*, 2009).

TABLE V. Heritability ( $h^2$ ) estimates for life-history character of *Salmo salar* and *Salmo trutta*

| Character   | Species          | $h^2$     | Sources   |
|---|------------------|-----------|---|
| Rates and patterns of growth in fresh water   | <i>S. salar</i>  | 0.10–0.40 | Bailey & Loudenslager (1986); Jonasson (1997); Garant <i>et al.</i> (2003)                      |
|   | <i>S. trutta</i> | 0.28–0.45 | Vandeputte <i>et al.</i> (2004); Blanc (2005)   |
| Rates and patterns of growth at sea   | <i>S. salar</i>  | 0–0.36    | Ryman (1972); Gunnes & Gjedrem (1978); Jonasson <i>et al.</i> (1997); Jonasson & Gjedrem (1997) |
| Age-at-smolting   | <i>S. salar</i>  | 0.08–0.25 | Refstie <i>et al.</i> (1977)  |
| Age-at-maturity   | <i>S. salar</i>  | 0.10–0.48 | Glebe & Saunders (1986); Gjerde <i>et al.</i> (1994); Wild <i>et al.</i> (1994)                 |
| Return rate to home river   | <i>S. salar</i>  | 0.04–0.12 | Jonasson <i>et al.</i> (1997)   |
| Susceptibility to <i>Lepeophtheirus salmonis</i> and <i>Caligus elongatus</i>                                     | <i>S. salar</i>  | 0.22–0.26 | Mustafa & MacKinnon (1999); Kolstad <i>et al.</i> (2005)  |
| Susceptibility to <i>Aeromonas salmonicidae</i> , <i>Renibacterium salmoninarum</i> and <i>Vibrio salmonicida</i> | <i>S. salar</i>  | 0.13–0.23 | Gjedrem & Gj  en (1995)   |

Maximum food consumption increases with temperature, and the temperatures for both maximum growth and food consumption are similar or even slightly higher for the latter (Jonsson *et al.*, 2001a). In *S. trutta*, Elliott (1975b) found that the optimal temperature for growth increases with increasing food ration and quality. Because of this, piscivorous *S. trutta* exhibit 3–4° C higher optimal temperature for growth than *S. trutta* feeding on invertebrates (Forseth & Jonsson, 1994; Elliott & Hurley, 2000). For other species such as *S. salar*, smaller food rations appear not to have a similar reducing effect on the optimal temperature for growth (Jonsson *et al.*, 2001a).

There is little, if any, support for the hypothesis that variation in salmonid growth rates reflects thermal adaptations to their home stream. Jonsson *et al.* (2001a) found no significant correlation between thermal conditions in the rivers of origin and the limits for growth or maximum growth rates. Similarly, Larsson *et al.* (2005) compared growth performance curves for *S. alpinus* from 11 European watercourses between 54 and 70° N and found no geographical or climatic trend in growth performance among populations. Maximum growth rate in different *S. alpinus* populations, however, correlated positively with their size-at-maturity in the wild (Larsson *et al.*, 2005), and the same appears to hold for *S. trutta* (Forseth *et al.*, 2009) and probably also for *S. salar* (Jonsson & Jonsson, 2007). Thus, the adaptive variation in growth potential appears related to life-history characteristics influencing reproductive success rather than their thermal conditions.

In *S. trutta*, Jensen *et al.* (2000) found slight indications of growth adaptation to cold water. This was revealed in a field study on 42 European anadromous populations of *S. trutta*. They found variation in annual growth rates related to environmental variability. This adaptation may, however, be a phenotypic response to the water temperature experienced by the alevins. This contention appears supported by the physiological findings of Rungruangsak-Torrissen *et al.* (1998). They found different trypsin isozymes in comparable groups of *S. salar* hatching at 6 and 10° C. Trypsin is a key digestive protease which is sensitive to environmental changes and influences feed utilization and growth of the entire life cycle (Rungruangsak-Torrissen & Male, 2000). The various trypsin isozyme variants influence maintenance ration differently and the capacity for protein synthesis in white muscle, with effects on growth, size and other life-history traits. Changes in phenotypic expression of trypsin are induced by temperature during the egg incubation and the beginning of feeding period of alevins. Furthermore, trypsin secretion and the relative amount of trypsin are modified by temperature. This may explain the findings of Alvarez *et al.* (2006) who demonstrated that the standard metabolic rate of *S. trutta* changed in response to the temperature experienced by the fish during the yolk-absorption period. Changes in metabolic rate affect the growth rate of the fish. For instance, Cutts *et al.* (1998) demonstrated a significant association between the standard metabolic rate and the growth rate of *S. salar*. Thus, when comparing the growth rates among populations, early experienced temperature conditions may affect later performance with probable effects on the optimal temperature for growth.

Salmonid growth exhibits little, if any, support to the counter-gradient hypothesis that populations adapted to cold environments perform better than those from warmer water when tested in a common environment whether this is warm or cold (Conover & Present, 1990). There appears to be no evidence of a geographic pattern of genotype influences which oppose environmental influences minimizing phenotypic changes in thermal gradient as hypothesized by Conover & Schultz (1995). Nicieza *et al.* (1994a,b) maintained that their results on growth bimodality and digestive performance of *S. salar* from Spain and Scotland lend support to this hypothesis, but the statistical power of these two studies is weak since only two populations were used. This population variation can be environmentally plastic and not genetically fixed. Furthermore, phenotypic effects of early thermal experiences as discussed above, may be easily confused with support for a genetic counter-gradient variation hypothesis. The reason why salmonids do not show thermal growth adaptations may be that they have evolved and they live in environments with seasonally, annually and spatially variable temperatures where phenotypic plasticity is more advantageous than genetic fixation.

## FOOD CONSUMPTION AND GROWTH EFFICIENCY

There is little support for the view that temperature for maximum food consumption is significantly higher than the optimal temperature for growth as suggested by Elliott (1975a). The reasons for such a discrepancy could be that the fish cease feeding below their maximum rations (Forseth & Jonsson, 1994; Elliott & Hurley, 2000), or that the water is not oxygen saturated and limits the growth of the fish (Brett, 1952).

The temperature for maximum growth efficiency [*sensu* Brett (1979)] (the increase in mass in a defined time interval divided on mass of food consumed during the interval) was lower (1.5–4.5° C) than the corresponding temperature for maximum growth and food consumption in *S. salar* parr (Jonsson *et al.*, 2001a), and no distinct peak in the growth efficiency was observed at the maximum point. Jonsson *et al.* (2001a) reported maximum growth efficiencies between 42 and 58% estimated for moderately growing *S. salar*. For *S. trutta*, it is lower probably because of higher activity and aggression levels. The temperature for maximum growth efficiency of *S. alpinus*, which is between 45 and 55%, is below 10° C, and suggests an adaptation to cold environment in this species (Larsson & Berglund, 2005). Thus, *S. alpinus* seems to exhibit a metabolic adaptation to life in cold water. The low temperature at maximum growth efficiency is probably important for the northern distribution of *S. alpinus* relative to other anadromous salmonids which have similar optimal temperature for growth (Table IV).

The relationship between growth and the quantity of food consumed differs somewhat with temperature and among population origins (Jonsson *et al.*, 2001a). Jonsson *et al.* reported that the growth efficiency of *S. salar* parr was higher among fish originating from cold rivers with poor growth opportunities than for fish coming from rivers with benign growth conditions, after fish were experimentally reared and tested in a common environment. Furthermore, the growth efficiency reached maximum at lower temperature (12° C) for populations originating from cold than warm rivers. Larsson & Berglund (2005) reported a similar association between temperature and growth efficiency in *S. alpinus*. Although phenotypically plastic, the temperature for maximum growth efficiency also appears to be adapted to local temperature conditions (Jonsson *et al.*, 2001a).

There is a phenotypic association between growth efficiency and growth rate of salmonids. Forseth *et al.* (2001) reported maximum growth efficiency at 14° C for *S. salar* parr growing at a maximum rate, and that the growth efficiency increased to 17° C for slow-growing fish from the same population. In *S. salar*, there is also correlation between growth efficiency and the efficiency of retention of the synthesized proteins (Carter *et al.*, 1993). Thus, the temperature of maximum growth efficiency is also flexibly dependent on the growth rate of the fish.

## GROWTH AT SEA

The mass increment of salmonids increases rapidly after entering sea water (Jonsson & Jonsson, 2003), and temperature appears to be one of the major abiotic factors influencing growth. Investigations of *O. tshawytscha* in the Gulf of the Farallones, central California, revealed that post-smolts grew better and had higher energy storage in a warm year with reduced salinity and elevated zooplankton productivity than in colder years with higher salinity (Macfarlane *et al.*, 2005). Similarly, the growth increment of the one-sea-winter *S. salar* was higher in years with large areas with relatively high water temperature and high North Atlantic Oscillation index (NAOI) in May, the month when the smolts moved to sea (Friedland *et al.*, 2000; Jonsson & Jonsson, 2004b). Conversely, Todd *et al.* (2008) reported that the growth rate of *S. salar* in the North Atlantic has fallen as sea-surface temperature has risen, especially during winter. The reason for this is unknown, but may be related to poor feeding opportunities in recent years associated with particularly low abundance of

*Calanus finmarchicus*, a key species in the marine food web in the North Atlantic (Beaugrand & Reid, 2003).

Handeland *et al.* (2003) found that the optimal temperature for growth of *S. salar* post-smolts was 13.0° C, whereas maximum growth efficiency was 10.5° C. Reddin *et al.* (2006), on the other hand, reported that *S. salar* post-smolts selected waters of *c.* 12° C during their first months at sea, between the estimated temperatures for maximum growth and maximum growth efficiency. Thus, *S. salar* appear not to maximize growth rate or growth efficiency in nature, but prefer a temperature in between. The reason may be that *S. salar* maximize fitness and not growth *per se*. Fitness also depends on the probability of survival which generally increases with decreasing temperature in *S. trutta* (Jonsson *et al.*, 1991a), and many other fish species (Pauly, 1980).

## LIFE-HISTORY VARIABLES

### SMOLT AGE AND SIZE

There are population-specific variations in age at smolting as also indicated by the heritability of this trait (Table V). Most of the variability observed, however, is a phenotypic effect of differing growth rate and temperature. Climatic conditions encountered during the embryonic development influence later life-history traits such as smolt size in anadromous salmonids. Correlation studies in the River Imsa, Norway indicated that the warmer and wetter the winter before hatching is, the better the offsprings grow in the subsequent first year of life, and the higher the proportion of the cohort smolted as 1 year olds (Jonsson *et al.*, 2005). Strothotte *et al.* (2005) reported a similar association between first year's growth and smolt age in Canadian *S. salar*. Owing to high water temperature during embryonic development, the eggs hatch early, extending the first growth season, as found for *S. trutta* (Elliott *et al.*, 2000). Furthermore, feeding opportunities may be good after mild, wet winters with large water-covered areas. Thus, the parr may become large at the end of the first growth season resulting in more 1 year-old smolts.

Age at smolting is influenced by parr growth and size. Fast growers tend to smolt at an earlier age and a smaller size than more slow-growing individuals from the same population (Ricker, 1938; Økland *et al.*, 1993; Strothotte *et al.*, 2005). The effects of water temperature on smolt age and size are mediated through variation in growth rate (Edmundson & Mazumder, 2001). Smolt size, however, may also be more directly associated with water temperature. For instance, *S. salar* parr growing in rivers emptying into relatively warm sea water smolt at a smaller size relative to those from rivers emptying into colder sea water (Power, 1981; L'Abée-Lund *et al.*, 1989; Jensen *et al.*, 1989b). This appears related to the fact that ionic regulation in cold sea water is easier for large than for small fish, at least partly because of the decreasing relationship between surface and volume of the fish with increasing size (Finstad *et al.*, 1988; Hoar, 1988).

Contrary to expectation, the time series (1976–2000) from the River Imsa did not reveal any significant relationship between water temperature from spring through autumn and first-year parr growth or age at smolting. As growth rate is temperature dependent, there may be confounding factors acting in rivers such as variable



fish density and feeding opportunities. Whatever the reason, latitudinal clines in growth rate and smolt age of *S. salar* and *S. trutta* in northern Europe (Metcalf & Thorpe, 1990; Jonsson & L'Abée-Lund, 1993) are indications of a thermal effect on early growth. In the southernmost part of their distribution area such as Spain, juvenile growth can be constrained by very high water temperatures during summer (Ojanguren *et al.*, 1999; Forseth *et al.*, 2001). Therefore, smolt age may be higher than expected from the clinal variation farther north. Another reason may be that parr from southern systems often grow up in relatively cold water (for the latitude) such as high-altitude sites. *Salmo salar* in the Miramichi River, New Brunswick are located towards the southern edge of their range in North America, and fork lengths of Miramichi parr are negatively correlated with water temperature (Swansburg *et al.*, 2002). This may be a result of increased metabolic costs at higher temperatures, resulting in less energy being devoted to growth, or younger smolt age and thereby smaller size (Økland *et al.*, 1993).

## RESIDENT OR MIGRANT?

To some degree, smolting and sexual maturation as parr are competing processes (Hansen *et al.*, 1989; Berglund *et al.*, 1991). Sexual maturation at the parr stage reduces the chance of subsequent smolting as found in *S. alpinus* (Nordeng, 1983) and *S. trutta* (Jonsson, 1985). These species are partially migratory, i.e. the populations are split into migratory and resident individuals. The migrants move to richer feeding areas in the sea whereas the residents remain in fresh water throughout life. This phenomenon is also known from a number of species, e.g. Dolly Varden charr *Salvelinus malma* (Walbaum), brook charr *Salvelinus fontinalis* (Mitchill), *O. nerka* and threespined stickleback *Gasterosteus aculeatus* L. (McDowall, 1987; Foote *et al.*, 1989; review in Jonsson & Jonsson, 1993). In these species, the resident individuals usually attain maturity in the parr stage (as a neotenic life history), whereas the anadromous ones mature later. Parr maturity is linked to growth rate and thereby indirectly to temperature. Furthermore, anadromy tends to increase towards the north within the species range, possibly due to improved productivity and growth opportunities in marine habitats relative to freshwater habitats with increasing latitude (Gross *et al.*, 1988), relationships which could be influenced by a future climate change (Jonsson & Jonsson, 2009). Anadromy in *S. alpinus* also declines or ceases towards the extreme northern geographic limits, probably because access to and time at sea are limited (Svenning & Gullestad, 2002). Generally, individuals of a population that exhibit anadromous behaviour grow faster and have a larger maximum size, indicating some benefit to seaward migration and feeding.

## PARR MATURITY

In many fishes, including *S. salar* and *S. trutta*, fast juvenile growth is associated with decreased age at maturity (Thorpe, 1986; Day & Rowe, 2002; Piché *et al.*, 2008). Thus, the probability of parr maturation is linked to environmental factors influencing early growth (Jonsson & Jonsson, 1993). If under future climatic conditions, growth and survival in fresh water improve more than those at sea, one would expect a higher proportion of freshwater resident compared to anadromous individuals (Gross *et al.*, 1988). Whether a partially migratory population will become more

or less migratory will depend on both short and long-term changes in the growth opportunities of their habitats in fresh water and salt water.

There are links between environmental temperature and parr maturity (Table I). Duston & Saunders (1997) reported that the incidence of sexual maturity at age 1 among male parr was positively related to winter rearing temperature, body size and condition factor in spring. Conversely, Baum *et al.* (2005) found no effect of elevated water temperature on the incidence of parr maturity in *S. salar* relative to parr living upstream in colder water. They suggested that this may be because there was a higher growth threshold for attaining parr maturity among fish living in heated water than those from the upstream site. Probably, the different associations between growth rate and maturation reflect different norms of reaction due to different relationships between growth and survival at the two sites and may therefore be a phenotypically plastic effect (*cf.* Jonsson & Jonsson, 1993, 2004a).

### POST-SMOLT MATURITY

Although there is heritability for age at maturity in *S. salar* (Table V), the abundance of multi-sea-winter fish (maturation after 2 or more years at sea) in North America is directly scaled to the sea temperature in the north-west Atlantic (Friedland, 1998). This suggests a link between post-smolt maturation and environment. Furthermore, Friedland & Haas (1996) reported that the fraction of post-smolt cohorts attaining maturity after 1 year at sea correlated positively with growth during late summer. In the north-east Atlantic, sea age at maturity decreased with decreasing sea growth and increasing values of the seasonal North Atlantic Oscillation Index (NAOI) from February to April indicative of mild springs (Jonsson & Jonsson, 2004b). This appears largely to be a phenotypic response to reduced growth rate. Similarly in Pacific salmon, the size at maturity has decreased during recent years. In these species, however, the age at maturity has increased during the same period. Morita & Fukuwaka (2007) reported that for Japanese *O. keta*, this appeared largely to be a phenotypically flexible response to the reduced growth rate caused by changed environmental conditions; although fishery-induced evolution cannot be ruled out. Overall, it is not clear whether reduced sea growth is associated with increased or decreased sea age at maturity.

### EGG SIZE AND FECUNDITY

Egg size increases with increasing mean annual temperature and is negatively correlated with environmental productivity (Johnston & Leggett, 2002) (Table II). Most variation among populations within species is probably environmental (see Heath *et al.*, 2003 for alternative view), as found in *S. salar* (Jonsson *et al.*, 1996). Jonsson & Jonsson (1999) reported that the egg size of anadromous *S. trutta* decreased and fecundity increased with increasing latitude through a trade-off mechanism. Most of the observed variation disappeared when the fish were experimentally reared in a common environment, indicative of an environmental influence. Similarly, Fleming & Gross (1990) reported that egg mass decreased and fecundity increased with latitude in *O. nerka*, *O. keta* and *O. tshawytscha*. They postulated that selection favoured increased egg mass with increasing water temperature, because higher water temperature reduces the efficiency of the yolk conversion to body tissue. Thus, egg mass



should vary according to the prevailing water temperature during the yolk-absorption period of the alevins.

Jonsson *et al.* (1996) showed experimentally that early parr growth of *S. salar* influenced egg size and fecundity when they attained maturity. The faster the young fish grew early in life, the smaller eggs they produced as adults. A similar effect was reported for *O. masou* (Tamate & Maekawa, 2000), but not for *S. trutta* (Jonsson & Jonsson, 1999) and *O. kisutch* (Quinn & Vøllestad, 2003). In these latter cases, adult size was the main factor regulating egg size. Thus, the main effects of temperature on egg size and fecundity may be its influences on yolk-absorption rate, early growth rate and adult size.

## MORTALITY AND SEA SURVIVAL

Fish mortality is related to water temperature. Pauly (1980) showed that there is significant correlation between the natural instantaneous mortality rate and water temperature. He investigated 175 different populations of 84 species from freshwater and marine environments. A study by Jonsson *et al.* (1991a) indicated that this also applies to salmonids. They found that the longevity of Norwegian anadromous *S. trutta* increased with decreasing water temperature in fresh water. The reason for the observed effect of temperature may be that it increases the metabolic rate which increases mortality and shortens the life span (Glebe & Leggett, 1981a, b) (Table II).

The causes of marine mortality are poorly known. Coherent patterns among regional and continental stock groups, however, suggest broad-scale environmental effects on survival during the post-smolt period at sea. Most probably, growth-mediated survival determines stock abundance during early weeks at sea (Friedland, 1998). Correlations between sea-surface temperatures and survival have been reported from the north-east Atlantic suggesting that temperature may affect growth directly or indirectly through changes in food abundance or distribution (Friedland *et al.*, 2000; Beaugrand & Reid, 2003).

Sea survival is influenced by water temperature in coastal waters at the time when the smolts enter sea water (Hvidsten *et al.*, 1998). Friedland *et al.* (2000) reported that high sea-surface temperatures along the Norwegian coast during May correlated positively with post-smolt survival of *S. salar*. There is positive correlation between sea survival and the area of the North Atlantic with water temperatures of 8–10° C in May, when the smolts at this latitude enter the sea (Friedland *et al.*, 1998). A reciprocal negative correlation was found between survival and the size of the North Atlantic surface area with water temperatures between 5 and 7° C. Probably, relatively warm water is positive for the commencement of feeding in salt water. Warm water during summer, however, may influence survival negatively. Friedland *et al.* (2003) found that *S. salar* abundance was negatively correlated with mean sea-surface temperature during June. The negative effect of warm ocean conditions in the nursery area during summer is possibly associated with poor feeding opportunities for *S. salar* (Beaugrand & Reid, 2003).

Survival of *S. salar* in the Baltic Sea appears influenced by the coastal Bothnian Sea conditions during migration to the sea and soon after (Jutila *et al.*, 2006). This supports the findings of Kallio-Nyberg *et al.* (2004) who reported that cold summers in the Gulf of Bothnia reduced the survival of *S. salar* post-smolts. Mueter *et al.* (2005) correlated sea survival of *O. gorbuscha*, *O. nerka* and *O. keta* with coastal

sea-surface temperature, sea-surface salinity, upwelling and a large-scale index of ocean climate. Survival rates of all three species correlated significantly with ocean temperatures just prior to, during and after the smolt migration to sea, supporting an influence on survival of early marine conditions experienced by the juvenile salmon. The survival of *O. nerka* was most strongly correlated with coastal seawater temperature during winter and spring prior to the emigration. Mueter *et al.* (2005) gave no explanation for this, but a plausible hypothesis is that this may be because mild winter and spring conditions permit early seaward migration which was advantageous for this fish. The survival of *O. gorbuscha* was also related to the sea-surface salinity prior to emigration. This species enters the sea whilst still very small, soon after emergence at the start of external feeding, and ionic regulation under high salinity may be problematic (Hoar, 1988). A relatively high water temperature when the fish start feeding at sea may be advantageous for ionic regulation, food consumption and growth.

North American *S. salar* abundance has fluctuated in parallel with the AMO in climate (see Introduction). Over the last century, *S. salar* abundance has been low during phases with warm sea-surface temperatures and high during cold phases. It is currently in a warm phase, and the moratorium on the fishing of north-west Atlantic *S. salar* established in 1992 has so far contributed few signs of improvement in stock size.

Favourable ocean conditions may thus be the main reason why the return of adult salmon to rivers is unusually large in some years. The climatic effect is regional and includes stocks from many disconnected rivers. For instance, the return of *O. tshawytscha* in fall Chinook rivers in the U.S. north-west appears negatively influenced by increasing sea-surface temperature during the winter of their first year in coastal waters off the coast of British Columbia (Hyun *et al.*, 2007). Rand *et al.* (2006) evaluated effects of temperature and flow on the survival of Fraser River *O. nerka*. They reported that fish of mass relative to length (lower condition factor) exhibited disproportionately higher mortality during the spawning run. Furthermore, energy use is higher in warm than in cold years meaning that fewer fish will be able to reach the spawning grounds of the water course if the water temperature is high. Conversely, reduced water flows may compensate for this. But if the ongoing decline in mean mass of adult *O. nerka* continues, their ability to migrate long distances in fresh water will decrease with the most severe effects on the longest migrating populations.

## PREDICTING THE EFFECTS OF CLIMATE CHANGE

How does this knowledge influence the thinking about effects of the ongoing climate change? As temperature increases are expected to be stronger over land than in the ocean (IPCC, 2007), the physiological changes are expected to be largest in fresh water, from the spawning migration to the smolt stage. Global warming could influence geographical distribution and disease vulnerability as well as population traits such as time of migration, spawning, hatching and emergence, growth rate, age at molting and maturity, recruitment, mortality, longevity and production of the anadromous fish. Considering recent trends and latitudinal gradients in population traits for *S. salar* and *S. trutta*, it can be predicted how these species could be affected by climate change in the near future (Harrod *et al.*, 2009).

## GEOGRAPHICAL DISTRIBUTION MOVES NORTHWARDS

A predicted warmer climate will probably exterminate salmonid populations in the southern parts of their distribution area. The distribution range of *Salmo* in North America could move northwards, in Europe it could move north- and eastwards (along the north coast of continental Russia). The predicted change in salmonid distribution areas could probably be due to a combined effect of altered temperature, rainfall and runoff. Arctic rivers, which are currently unsuitable or marginally suitable for salmonids, may become habitable, and able to sustain new anadromous salmonid populations, at the same time as salmonid production decreases in the southern part of the distribution range (Stefansson *et al.*, 2003). Climate change models for eastern Canada have predicted an overall loss of juvenile *S. salar* habitats (Minns *et al.*, 1995), a view supported by the work of Lund *et al.* (2002). For anadromous *S. trutta* the present distribution area appears highly influenced by competition from *S. alpinus*. The latter are best able to exploit marginal northern habitats because of their high growth efficiency at low water temperatures (Larsson & Berglund, 2005). With climate change, the productivity of Arctic systems could increase and the competitive advantage of *S. alpinus* relative to *S. trutta* decrease and the species could move northwards.

With a possible northward movement of the thermal niche of the Atlantic trouts, a number of competing species could also expand their range to higher altitudes and latitudes. Species which are currently limited in their northern distribution by temperature-related effects, *e.g.* northern pike *Esox lucius* L., several cyprinids and percids, would move northwards. For instance, the present northern distribution of zander *Sander lucioperca* (L.) coincides with the July 15° C isotherm and is likely to shift northward with climate change (Reist *et al.*, 2006). Successive year-class strengths and growth rates in northern environments are also likely to increase as temperatures increase. Increases in both abundance and size are very likely to have consequences for the competitiveness of resident coldwater-guild fishes if concomitant increases in lake productivity fail to yield sufficient ration to meet the needs of expanding populations of *S. lucioperca* and other percids. In northern Russia, *E. lucius*, ide *Leuciscus idus* (L.), and roach *Rutilus rutilus* (L.) have become much more numerous in the Pechora River Delta and the estuary Sredinnaya Guba (68° N) of the Barents Sea (Reist *et al.*, 2006). Furthermore, from *c.* 1980 onwards the European bitterling *Rhodeus amarus* (Bloch) has expanded its distribution in many parts of Europe and particularly in eastern Europe (van Damme *et al.*, 2007). Recently, diadromous, underyearling thinlip grey mullets *Liza ramada* (Risso) were for the first time observed in a Scandinavian stream (Jonsson & Jonsson, 2008).

Northward moving cyprinids and percids can out-compete *S. trutta* in lakes where they co-occur, as these species are trophically highly specialized. *Esox lucius* is a specialized predator that feeds on *S. trutta* and other freshwater fishes (Greenberg, 1999). Thus, a possible northward movement of competing and predatory species can decrease the success of the Atlantic trouts, but this effect of climate changes will probably be strongest in the southern part of the distribution range.

## INCREASED DISEASE THREATS

With increasing temperature due to predicted future climate change, several fish diseases may become more virulent at the same time as the salmonids become

stressed by high temperatures and their disease resistance drops (Marcogliese, 2001). Diseased fish are more susceptible to predation and less able to perform essential functions such as feeding, migration and territory defence. For instance, the myxozoan *Tetracapsuloides bryosalmonae*, causing proliferative kidney disease (PKD), instigates mortality when water temperature exceeds 15–16° C (Tops *et al.*, 2006). The virulence of *Aeromonas salmonicida* subsp. *salmonicida* causing furunculosis (McCullough, 1999; Nordmo & Ramstad, 1999), and sea lice *Lepeophtheirus salmonis* and *Caligus elongatus* killing salmonids at sea ((McVicar *et al.*, 1993; Boxaspen, 2006), also increases with water temperature.

Outbreaks of furunculosis in wild salmonids in Norwegian rivers in the late 1980s were associated with thermal stress and high density of anadromous fish beneath waterfalls. Both *S. salar* and *S. trutta* adults suffered high mortalities (Johnsen & Jensen, 1994). Declines in anadromous *S. trutta* during the last two decades in the northern Atlantic have been associated with an increase in *L. salmonis* abundance. Reasons may be the growth of the aquaculture industry with an immense increase in the number of parasite hosts in the sea (Heuch *et al.*, 2002; Todd, 2007), and higher temperatures at sea. In warmer waters *L. salmonis* decreases its life cycle and permits more generations in a season, with a potential increase in infection pressure (Heuch *et al.*, 1995). Furthermore, winter mortality of the parasite may decrease and a more rapid establishment in spring may be allowed. Also, harmful algal blooms may become more prevalent with a higher temperature in marine habitats (Edwards *et al.*, 2006). For instance, the bloom of the toxic alga *Crysochromulina polylepis* killed large quantities of fish including *S. trutta* and invertebrates along the south Scandinavian coast in May and June 1988 (Berge *et al.*, 1988). Eutrophication and higher than normal sea-surface temperature were the most probable reasons for the bloom (Rosenberg *et al.*, 1988).

Thus, with a continued climate warming together with other human effects on natural marine and freshwater ecosystems, there are good reasons to expect a continuing increase in disease pressure on anadromous salmonids. Biological effects due to global warming, however, are not predictable simply in terms of temperature response alone. To understand future effects, indirect effects on aquatic parasites of alterations in host distribution, water levels, eutrophication, stratification, ice cover, acidification, oceanic currents, ultraviolet-light penetration, weather extremes, and human interference have to be explored (Marcogliese, 2001). In the long term, climatic change may influence the susceptibility of the fish to the pathogen since there are inherited differences in disease resistance within and among populations (Table V). Due to selection, however, life-history traits affecting parasite transmission and, potentially, virulence can also change.

## WINTER MORTALITY OF PARR

The most plausible climate predictions state that the ice-covered periods of rivers and lakes will decrease possibly causing negative effects on salmonid survival. This may increase winter mortality in northern rivers. For instance, Finstad *et al.* (2004a) reported that *S. salar* parr had lower metabolic energy costs in darkness under ice than in open rivers during winter, and that winter mortality of parr is associated with the level of energy storage (Finstad *et al.*, 2004c). The increased metabolic cost was

highest for parr from a northern river which is usually covered by ice during winter, indicating a genetic adaptation to living under ice.

Linnansaari *et al.* (2008) found that surface ice created conditions that allowed salmon parr to use stream habitats that would otherwise stay unused owing to limited amount of instream cover. Mild winters are usually wetter (IPCC, 2007), and Cunjak *et al.* (1998) observed that high egg mortalities of *S. salar* were triggered by a rain on snow event that resulted in ice scouring of the stream bed and redds. Also winter flooding can increase extinction risk in some populations (Battin *et al.*, 2007). On the other hand, increased stream flow during winter can decrease density-dependent parr mortality because more habitats become available (Hvidsten, 1990; Linnansaari *et al.*, 2008), and milder winters in more southern rivers could decrease ice building and reduce ice scouring. Thus, there is good reason to expect increased egg-to-fry mortality and fry-to-parr mortality in rivers with increased winter temperature in northern rivers, although an increase in river flow and less ice building can decrease this negative effect in more intermediate parts of the distribution range.

Winter and spring droughts, which may become more frequent in the southernmost part of the distribution range, can reduce parr survival. In particular, the young-of-the-year are sensitive to extremely low flow because of low mobility and reduced ability to escape (Elliott & Elliott, 2006). During moderate flow decreases, parr of *S. salar* may remain in riffle habitats, but during severe droughts they tend to move to deep pools (Armstrong *et al.*, 1998). Also parr of *S. trutta* can escape by moving to deep pools or into brackish water in periods of drought (Landergren, 2004).

## SPAWNING AND EMBRYONIC DEVELOPMENT

Time of spawning could be delayed in autumn and winter under future climate conditions, whereas hatching eggs and alevin emergence in the water courses could be earlier since these traits are under strong selection (Hendry & Day, 2005; Carlson & Seamons, 2008). Energy consumption of the returning adults will increase with higher water temperature in rivers accessed by the spawners. Leggett & Carscadden (1978) found a gradient in repeat spawning with latitude with semelparity in the southern and iteroparity in the northern part of the area of American shad *Alosa sapidissima* (Wilson). This is probably because of higher energy costs in the warm water (Glebe & Leggett, 1981a). The same may hold true for salmonids, as spawning survival appears to decrease with increasing energy costs of *S. salar* spawners (Jonsson *et al.*, 1997) as in several other salmonid species (Glebe & Leggett, 1981b).

## LONGER GROWTH SEASONS

With predicted warmer winters and earlier springs, the feeding opportunities for the fry could improve and the growth season could be longer. Thus, the annual size increment of the fish could increase as already found for *S. salar* in the River Imsa, Norway, during recent years (Jonsson *et al.*, 2005). With increasing growth and annual size increment, smolt age and size are expected to decrease in temperate and northern latitudes (L'Abée-Lund *et al.*, 1989), but probably not in southern parts of the distribution area. Wild *S. salar* and *S. trutta* do not smolt younger than age 1. Furthermore, the distance from the southern populations to the feeding areas in the North Atlantic are long, and the smolts need large lipid reserves to survive and reach



the feeding grounds (Jonsson & Jonsson, 2005). A third point is that the temperatures in some southern rivers are very high during summer so the annual growth may be restricted (Brett, 1952, 1979). The long-term effect can be different since new norms of reactions may be selected for under changed environmental conditions.

Whether smolt production will increase or decrease depends on the location of the system. At the southern edge of the species' range, rises in summer temperature will probably be associated with a decline in smolt production. In northern rivers, smolt production could increase (Power & Power, 1994). The reason is increased metabolic costs of growth at elevated temperatures in the south and increases towards optimal temperatures for growth in the north.

## SHIFTS IN TIME OF SMOLTING AND SEAWARD MIGRATION

During smolting, salmonid parrs become pre-adapted for a pelagic life style in marine waters. Salinity tolerance increases and the fish acquire pelagic camouflage colour and a more streamlined body form. Simultaneously, they lose their positively rheotactic behaviour and move with the water current to sea (Hoar, 1988; Stefansson *et al.*, 2003). The temperature experienced by young salmonids determines the rate and timing of the transformation, and cumulative degree-days provide a proxy for this process (Zydlewski *et al.*, 2005). As a phenotypic response to predicted higher spring temperature, smolting could occur earlier in the season. Salinity tolerance increases during smolting (Duston *et al.*, 1991; McCormick *et al.*, 1997).

The initiation of smolt migration is often stimulated by high and increasing water temperature. Annual variation in the timing of the river descent is highly correlated with annual variation in water temperature pattern during spring (Jonsson & Ruud-Hansen, 1985; Jonsson & Jonsson, 2009). Furthermore, Whalen *et al.* (1999) reported that peak migration of *S. salar* occurred later in spring for tributaries with lower temperature. Zydlewski *et al.* (2005) showed that smolts that experienced an earlier and more rapid increase in spring temperatures as a phenotypic response migrated downstream earlier than fishes exposed to ambient conditions. Smolts that experienced a later and slower increase in temperature migrated over a longer period. All fish initiated and terminated downstream migration at the same number of degree-days, regardless of the temperature regimes they had experienced. Smolts experiencing cooler climates migrate downstream over a longer period than in warmer climates or early springs. There is an optimal time frame for migration in spring from a survival point of view, termed the 'physiological smolt window' (Hansen & Jonsson, 1989; McCormick *et al.*, 1999). Hansen & Jonsson (1991) showed that the homing ability of the fish was best when they entered sea water during this time window. Thus, the success of the smolt migration is strongly influenced by climate during spring, and the experiments by Hansen & Jonsson (1989, 1991) with releases of juvenile *S. salar* each month of the year indicated that the timing of the migration plays an important role in the ultimate success of migration to sea water.

In addition to high temperature, the seaward migration can be initiated by high water flow. This can be flooding due to the melting of snow or heavy rain (Hvidsten *et al.*, 1995; Hembrel *et al.*, 2001). With increased precipitation as rain in the autumn and winter and more extreme weather conditions, more fish will probably descend to sea at that time (Youngson *et al.*, 1983; Jonsson & Jonsson, 2002), but Riley *et al.*

(2008) reported that *S. salar* parr that move to the estuary in autumn are not sufficiently physiologically adapted to sea water. Thus, they survive poorly in the ocean and spend the winter in the estuary. Riley *et al.* (2008) were unable to determine if the autumn migration to the estuary influenced the winter survival of the juveniles. But findings from the River Imsa, Norway, suggest that their survival can be poor. In the River Imsa, few of the juvenile *S. trutta* descending to the estuary in autumn and winter survived till adulthood and returned to the river (Jonsson & Jonsson, 2009). Furthermore, hatchery-reared juvenile *S. salar* released every month of the year only survived well when descending to sea in spring (Hansen & Jonsson, 1989). Those released in autumn and winter exhibited poor homing ability which may hold true also for wild salmonids.

### UPSTREAM MIGRATION

The effect on the run timing of a future climate change will probably vary with the local conditions of the river. In cases of extremely low river flow, the upstream migration of salmon can be delayed (Solomon & Sambrook, 2004; Jonsson *et al.*, 2007), and straying of returning salmon into other rivers may increase (Jonsson *et al.*, 2003). Studying radio-tagged salmon in four south-western rivers in England, Solomon & Sambrook (2004) noted that when water flows were relatively high, the majority of adult *S. salar* passed through estuaries and into the rivers with a minimum of delay. When river flow was low, however, most fish arriving from the sea did not pass quickly into fresh water but remained in the estuary or returned to sea for up to several months. Many fish subsequently failed to enter the river when favourable flow conditions returned, possibly as a result of lost physiological opportunity. In areas located towards the southern limit of the species' range, low summer flows are common and summer running *S. salar* are rare (Juanes *et al.*, 2004). The majority of the adults migrate upstream before June, when river flows are relatively high and estuarine temperatures are low. High water level is probably favourable because their vulnerability to predators may be reduced because of high turbidity, deep water and high water velocity, making predation difficult (Abrahams & Kattenfield, 1997). Relatively high flows may be particularly important for salmonid ascent in small rivers and for upstream migration of particularly large fish (Jonsson *et al.*, 1990, 1991b; Jensen & Aass, 1995).

Extremely high flow, on the other hand, can also delay the upstream spawning migration of adult *S. salar* and *S. trutta* as observed in the River Imsa (Jonsson & Jonsson, 2002; Jonsson *et al.*, 2007). The reason is probably that there are increased migratory costs associated with the higher current velocity (Enders *et al.*, 2005).

Variations in return timing are partly a phenotypic response to experienced local flow and temperature regimes (Webb & McLay, 1996; Lilja & Romakkaniemi, 2003). In small rivers, flow conditions strongly influence river ascent of salmonids. In many rivers, returning fish have to wait in the estuary for suitable migratory conditions to ascend and the upstream migration is adjusted according to the prevailing water discharge (Jonsson *et al.*, 2007). A predicted decrease in summer rainfall (Harrod *et al.*, 2009) can result in earlier and later runs of salmonids (spring and autumn) that are now becoming more prevalent in rivers such as the Fowey, Camel and Plym in south-west England (Solomon & Sambrook, 2004).

There are also genetic differences among populations in time of migration (Jonsson *et al.*, 2007), and in a warmer climate regime, the adult return should occur earlier in the season in rivers with good flow conditions as experienced in Sweden (Dahl *et al.*, 2004). On the east coast of North America, *S. salar* has returned earlier during recent years. In the Connecticut River, historically the southernmost extent of the North American range of *S. salar*, stocked fish have ascended the river by  $0.5 \text{ day year}^{-1}$  earlier during 23 years of study (Juanes *et al.*, 2004). The change is not unique to this stock but has also been observed in more northern populations in Maine and Canada indicating a shift to earlier peak migration dates correlated with long-term changes in temperature and flow. Furthermore, Quinn & Adams (1996) reported that the time of 50% river ascent in introduced *A. sapidissima* past a regulation dam in the Columbia River, British Columbia, occurred 38 days earlier in the 1990s than in 1938, and that the altered migration time paralleled changes in water flow and temperature during the same period. The indigenous *O. nerka* in the Columbia River returned earlier as well, but the shift was not as pronounced as in *A. sapidissima*, indicating that there are species-specific responses to changes in flow and temperature. Quinn & Adams (1996) interpret this as a response to genetic selection. Similarly, summer-run *O. mykiss* exhibited changes in migration patterns in response to changes in water temperature and flow (Robards & Quinn, 2002).

#### REDUCED POST-SMOLT GROWTH

The annual size increment of one-sea-winter *S. salar* has decreased during the recent warming period concurrently with an increase in marine surface water temperatures (Jonsson *et al.*, 2003; Peyronnet *et al.*, 2007; Todd *et al.*, 2008). Jonsson & Jonsson (2004b) found significant correlation between the May NAOI of the smolt year and the total mass increment at sea of one-sea-winter salmon. Friedland *et al.* (1998, 2000) also found a positive correlation between size increment at sea and survival, indicating a linkage between survival and growth at sea. A similar tendency has been reported for anadromous *S. trutta* in the River Imsa, Norway, where the sea survival was best in years when the winter temperature was low prior to the seaward migration in spring, and post-smolt growth was high (Jonsson & Jonsson, 2009).

#### HIGHER POST-SMOLT MORTALITY

Varying ocean climates during first entry into the marine environment are critical to *S. salar*. Mortality is highest during the first few months (Salminen *et al.*, 1995; Friedland *et al.*, 2003). Young salmonids are sensitive to variable climatic factors and to food availability (Friedland *et al.*, 2000; Beaugrand & Reid, 2003). Friedland *et al.* (1998, 2000) observed that thermal regimes during the first 2 weeks at sea were correlated with good growth and high survival patterns of two index stocks, one migrating from southern Norway and the second from the west of Scotland. In years when warm thermal regimes existed in the North Sea and southern Norwegian coast at a time coincident with the post-smolt migration, survival was good. Similar results were found in Baltic salmon post-smolts (Kallio-Nyberg *et al.*, 2004). Thus, post-smolt mortality may increase under future climatic conditions due to earlier emigration of smolts from rivers (Crozier & Kennedy, 2003). Probably, good growth



during this critical early marine period is associated with reduced predation risk, and increased survival.

Climate change will influence the time of both the smolt migration and the upstream migration in anadromous fishes. Recent observations on *S. trutta* in the River Imsa indicated that increased water temperature will cause seaward migration early in spring, a period when sea growth and survival are poor (Jonsson & Jonsson, 2009). Probably, growth and survival are best when the fish enter sea water when the temperature is relatively high (Friedland *et al.*, 1998, 2000; Jonsson & Jonsson, 2004b). Recently, Peyronnet *et al.* (2008) reported that NAOI for the winter before the smolt migration explained 70% of the deviance in marine survival of *S. salar*, and Boyle & Adams (2006) reported that the salmon catch in the River Foyle, Ireland, correlated negatively with the winter NAOI, supporting this.

In partially migratory populations such as *S. trutta* and *S. alpinus*, poor early sea survival may select for increased residency rather than for migration, especially if the productivity in fresh water increases due to longer growth season (Gross, 1987; Jonsson & Jonsson, 1993), and the geographical limit for anadromy in these species could move northwards (Gross *et al.*, 1988). The projected effects of climate change on northern freshwater systems are increased productivity due to a longer ice-free growing season and higher nutrient loads. Parr of anadromous fish populations will probably benefit with increases in survival, abundance and size, which will possibly cascade to older, normally anadromous stages. Partly anadromous populations will possibly exhibit progressively less anadromous behaviour, if over time the benefits of remaining in freshwater systems outweigh the advantages of migrating to coastal areas for summer feeding. For instance, when the freshwater food supply was experimentally increased, the incidence of anadromous migration by *S. alpinus* decreased (Nordeng, 1983). In systems where the estuarine productivity increases, however, anadromy in species such as *S. trutta* and *S. alpinus* will persist. The exact balance and circumstances of how such scenarios unfold will be ecosystem-specific and depend on productivity, accessibility and ease of migration by fish, as well as the nature and degree of any climate-related effects (Reist *et al.*, 2006).

## YOUNGER SEA AGE AT MATURITY

There are population-specific differences in the age at sexual maturity among fish (Saunders, 1981). Increasing marine temperature, however, affects growth of salmon at sea and can also affect maturation and the relative contribution of one and multi-sea-winter salmon returning to natal streams to spawn (Scarnecchia, 1983; Jonsson & Jonsson, 2004a). Saunders *et al.* (1983) showed that cold winters inhibited maturation of cage-reared salmon and significantly reduced the one to multi-sea-winter salmon ratio, and Scarnecchia (1983) showed a similar effect of smolts migrating from north Icelandic rivers into the sub-Arctic compared to southern Icelandic stocks migrating into the warmer North Atlantic. He concluded that warmer temperatures resulted in better growth and earlier maturation (Scarnecchia, 1983). The growth rate of *S. salar* in the North Atlantic, however, appears to have decreased during recent years together with a tendency to attain maturity younger (Gudjonsson *et al.*, 1995; Jonsson & Jonsson, 2004b; Friedland *et al.*, 2005, 2009). The proportion of *S. salar* returning as one-sea-winter fish to the River Imsa, Norway was positively correlated with the NAOI of the winter after smolting (milder marine winter conditions

during positive NAOI) (Jonsson & Jonsson, 2004b). The mass increment of the one-sea-winter salmon correlated positively with the NAOI during spring and early summer when the smolts first enter the marine environment. Elevated NAOI values when smolts first enter sea water promoted rapid growth and an increased number of salmon returning as one-sea-winter fish, a probable result especially because the subsequent winters were relatively mild (Saunders *et al.*, 1983).

Observations indicate that mature one-sea-winter salmon at spawning have been both in particularly poor condition (Todd *et al.*, 2008) and slow growing in recent years (Jonsson & Jonsson, 2004a), whereas the size of the multi-sea-winter fish seems to have changed less (Jonsson *et al.*, 2003). This indicates that the fish has to surpass a size threshold at the first winter at sea to remain immature and become multi-sea-winter salmon. This is supported by Spanish (Nicieza & Braña, 1993) and Norwegian studies (Jonsson *et al.*, 2003). Such a relationship between sea growth and maturity is contrary to the observation that fast juvenile growth decrease age-at-maturity of parr (Thorpe, 1986), but supports the finding that niche shifts resulting in increased growth rate delay maturation in salmonids as a norm of reaction (Jonsson *et al.*, 1999). This is probably because the fitness gained by remaining at sea is larger for large than for small individuals. In *O. kisutch*, Beamish *et al.* (2004) found a positive correlation between survival and size. The larger the fish, the better they survived. If expected sea survival is also low for small *S. salar*, selection may favour the storing of energy reserves at the cost of somatic protein growth, increasing the probability of early sexual maturation. In *O. keta*, Morita & Fukuwaka (2006) found that the influence of recent growth was more important than size in terms of whether a fish matured during the subsequent breeding season, and the same may hold for *S. salar*.

Thus, *S. salar* could probably become younger and smaller as a phenotypic plastic reaction to climate change. In the longer term also a genetic change in age-at-maturity is expected.

## REDUCED RECRUITMENT

In a future scenario with more small, less fecund females due to climate change, smolt production is likely to be reduced. There is evidence that smolt production in some rivers has decreased during recent decades, although trends are variable (Hutchings & Jones, 1998; Scott, 2001). There are several reasons for variation in smolt output, including fluctuations in water quality and temperature (Arkoosh & Collier, 2002). In some rivers, mean smolt size has decreased (Scott, 2001). This may have resulted in an increase in predation rate of post-smolts. There is, however, little knowledge about trends in post-smolt predation.

In all, survival conditions for salmon and trout will probably decrease in the southern part of their current distribution, and in the temperate, medium parts where the winter temperature historically has been close to freezing, natural populations are expected to decline. In the northern part of their current distribution, a positive effect of global warming due to improved feeding opportunities can be expected, and with that improved growth and survival conditions. The salmonids may also invade new rivers where conditions were previously too cold. The situation is dynamic and the strength and duration of the population effects depend on how the climate will change in the long run.

## SUMMARY OF PREDICTED CLIMATIC EFFECTS

(1) The thermal niche of the anadromous Atlantic salmonids will move northwards with extinction of southern populations and invasion of new spawning and nursery rivers and feeding areas north of the present species range. (2) Increased threats from parasites and contagious fish diseases due to increased transmission rates, faster development and increased virulence of the infectious agents. Infected fish have decreased activity, competitive ability and defence against predation. (3) Increased winter mortality of parr in northern and southern parts of the distribution range. In the north, the energy consumption of the parr could increase due to less stable flow and ice conditions. In the south, there is an increased probability of droughts during winter and spring. (4) Delayed time of spawning in the autumn or early winter and advanced time of egg hatching and alevin emergence in spring. Length of the growth season will probably increase, and growth rate will also increase if temperature is below the optimal temperature for growth. (5) Increased annual size increment and reduced age at smolting, especially in northern and intermediate parts of the distribution range. (6) Advanced time of smolt migrations in spring and increased early post-smolt mortality in the sea because of a higher temperature increase in rivers than in marine habitats. (7) Advanced time of spawning migrations under suitable flow conditions which augments energy uses before spawning and increases adult mortalities. Extreme flow conditions can delay upstream spawning migration in rivers which can increase straying to other rivers. Drought during the upstream migration period reduces spawning stocks and improves the reproductive success of small relative to large adults. (8) Decreased post-smolt growth, survival, age at sexual maturity, and recruitment. The effect could probably be strongest in the intermediate and southern parts of the distribution range. Parr maturation could expand. Freshwater resident individuals could be selectively favoured in partly migratory populations. (9) A large part of these changes could be an immediate, phenotypic response to the altered climate. In the longer term, however, genetic changes in traits such as smolt age, age at maturity and disease resistance can also be expected.

## FUTURE RESEARCH CHALLENGES

There is a lack of knowledge about effects of early temperature experiences on later development, growth and behaviour of salmonids. For instance, Alvarez *et al.* (2006) demonstrated that the standard metabolic rate of *S. trutta* changed in response to the temperature experienced by the fish during the yolk-absorption period, yet little is known about effects of this early temperature experience on later growth performances, life-history characters or behavioural such as the timing of migration and spawning.

How are the reaction norms among water temperature, growth rate, growth efficiency and age at sexual maturation of anadromous salmonids? There is little knowledge about optimal temperature for marine growth and growth efficiencies at different feeding rates and fish sizes, and the association between water temperature during early development and later performance. Information on effects of water temperature on food consumption, metabolism and growth has been successfully used to model growth rate from water temperature in juvenile *S. trutta*, where it is used

to forecast production (Elliott, 1994). Similar studies in salt water should be performed to investigate possible environmental influences. Furthermore, the growth efficiency influences the competitive ability of fishes and should be further investigated to better understand the competitive outcome of contests between species with similar niches in the wild, and how this will be impacted by predicted climate change.

There is lack of knowledge about mortality effects during winter of the various life stages of trout and salmon compared with that in summer. Is water flow during winter more limiting for parr production in rivers than summer flow, when activity of fish and the ability to escape hostile conditions should be higher?

The spatial distribution of *Salmo* in the ocean and environmental conditions encountered by the fish should be studied. Analysis of stable oxygen isotopes in otoliths is a promising technique for estimating the ambient temperature experienced by fish, but consistent equations relating temperature and fractionation of stable oxygen isotopes in otoliths among different fish species are lacking (Høie *et al.*, 2004). Use of data-storage tags is an alternative (Rikardsen & Thorstad, 2006). There is little knowledge about to what extent marine distribution changes with changes in climate, marine currents and sea-surface temperatures or whether fish sometimes are trapped in cold areas during winter from where they cannot escape and therefore die. The marine distribution may also affect risk of predation, as potential predators may be more common in some than other areas. Better knowledge about the geographical distribution of salmonids in the ocean can be gathered through systematic fishing.

Parasites and contagious diseases are important mortality factors, but little is known about their effects in wild populations and how this may be affected by climate change. Almost all that are known about fish diseases are from investigations on cultured fish. There is a need for more knowledge about their effects in wild populations and almost nothing is known about how serious these diseases are for post-smolt survival.

Anadromous salmonids have complex life cycles in fresh and salt waters, and effects on one life stage will affect others. It is crucial to consider climatic effects on the entire life cycle as well as that on sympatric competitors and prey to understand how future climate change will affect salmonid populations. Although salmonids often occur in relatively simple ecosystems, little is known about community interactions. A better understanding of the range of possible community interactions will be most helpful in future management and conservation efforts of anadromous salmonids.

There is a need for models predicting climatic effects on future salmon production. Recent calculations based on regression models showed a steady decrease in the production of *S. salar* in the River Imsa, Norway between 1976 and 2000 (Jonsson & Jonsson, 2004a), but there is a need for a functional model based on known relationships between water temperature and salmon production which predict future production based on climatic scenarios.

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