Ecology of Freshwater Fish 2003: 12: 1–59
Printed in Denmark · All rights reserved

ECOLOGY OF
FRESHWATER FISH
ISSN 0906-6691

Review

Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories

Klemetsen A, Amundsen P-A, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen E. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories.
Ecology of Freshwater Fish 2003: 12: 1–59. © Blackwell Munksgaard, 2003

Abstract – Among the species in the family Salmonidae, those represented by the genera *Salmo*, *Salvelinus*, and *Oncorhynchus* (subfamily Salmoninae) are the most studied. Here, various aspects of phenotypic and life-history variation of Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L., and Arctic charr *Salvelinus alpinus* (L.) are reviewed. While many strategies and tactics are commonly used by these species, there are also differences in their ecology and population dynamics that result in a variety of interesting and diverse topics that are challenging for future research. Atlantic salmon display considerable phenotypic plasticity and variability in life-history characters ranging from fully freshwater resident forms, where females can mature at approximately 10 cm in length, to anadromous populations characterised by 3–5 sea-winter (5SW) salmon. Even within simple 1SW populations, 20 or more spawning life-history types can be identified. Juveniles in freshwater can use both fluvial and lacustrine habitats for rearing, and while most smolts migrate to sea during the spring, fall migrations occur in some populations. At sea, some salmon undertake extensive oceanic migrations while other populations stay within the geographical confines of areas such as the Baltic Sea. At the other extreme are those that reside in estuaries and return to freshwater to spawn after spending only a few months at sea. The review of information on the diversity of life-history forms is related to conservation aspects associated with Atlantic salmon populations and current trends in abundance and survival. Brown trout is indigenous to Europe, North Africa and western Asia, but was introduced into at least 24 countries outside Europe and now has a world-wide distribution. It exploits both fresh and salt waters for feeding and spawning (brackish), and populations are often partially migratory. One part of the population leaves and feeds elsewhere, while another part stays as residents. In large, complex systems, the species is polymorphic with different size morphs in the various parts of the habitat. Brown trout feed close to the surface and near shore, but large individuals may move far offshore. The species exhibits ontogenetic niche shifts partly related to size and partly to developmental rate. They switch when the amount of surplus energy available for growth becomes small with fast growers being younger and smaller fish than slow growers. Brown trout is an opportunistic carnivore, but individuals specialise at least temporarily on particular food items; insect larvae are important for the young in

A. Klemetsen[1], P.-A. Amundsen[1], J. B. Dempson[2], B. Jonsson[3], N. Jonsson[3], M. F. O'Connell[2], E. Mortensen[4]

[1]Norwegian College of Fishery Science, University of Tromsø, Breivika, N-9037 Tromsø, Norway, [2]Fisheries and Oceans Canada, Science, Oceans and Environment Branch, PO Box 5667, St. John's, Newfoundland, Canada A1C 5X1, [3]Norwegian Institute of Nature Research, Dronningensgt 13, PO Box 736 Sentrum, N-0105 Oslo, Norway, [4]Ørnsøvej 15, DK-8600 Silkeborg, Denmark

Key words: Arctic charr; Atlantic salmon; brown trout; cannibalism; feeding; freshwater residence; habitat; life history; migration; phenotypic plasticity; phylogeography; polymorphism; research challenges

A. Klemetsen, Norwegian College of Fishery Science, University of Tromsø, Breivika, N-9037 Tromsø, Norway; e-mail: andersk@nfh.uit.no

Dempson and O'Connell reviewed the Atlantic salmon, Jonsson and Jonsson the brown trout and Amundsen and Klemetsen the Arctic charr. Mortensen initiated the review and gave constructive criticism to the manuscript.

Accepted for publication September 22, 2002

streams, while littoral epibenthos in lakes and fish are most important for large trout. The sexes differ in resource use and size. Females are more inclined than males to become migratory and feed in pelagic waters. Males exploit running water, near-shore and surface waters more than females. Therefore, females feed more on zooplankton and exhibit a more uniform phenotype than males. The Arctic charr is the northernmost freshwater fish on earth, with a circumpolar distribution in the Holarctic that matches the last glaciation. Recent mtDNA studies indicate that there are five phylogeographic lineages (Atlantic, Arctic, Bering, Siberian and Acadian) that may be of Pleistocene origin. Phenotypic expression and ecology are more variable in charr than in most fish. Weights at maturation range from 3 g to 12 kg. Population differences in morphology and coloration are large and can have some genetic basis. Charr live in streams, at sea and in all habitats of oligotrophic lakes, including very deep areas. Ontogenetic habitat shifts between lacustrine habitats are common. The charr feed on all major prey types of streams, lakes and near-shore marine habitats, but has high niche flexibility in competition. Cannibalism is expressed in several cases, and can be important for developing and maintaining bimodal size distributions. Anadromy is found in the northern part of its range and involves about 40, but sometimes more days in the sea. All charr overwinter in freshwater. Partial migration is common, but the degree of anadromy varies greatly among populations. The food at sea includes zooplankton and pelagic fish, but also epibenthos. Polymorphism and sympatric morphs are much studied. As a prominent fish of glaciated lakes, charr is an important species for studying ecological speciation by the combination of field studies and experiments, particularly in the fields of morphometric heterochrony and comparative behaviour.

Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

> "There is no group or family of fishes that supplies better materials for the study of the effects of geographic or physiologic isolation, or which presents more curious and interesting facts in their life histories than do the various species of Salmonidae." (Evermann 1925)

The salmonid subfamily Salmoninae comprises about 30 species of fish in seven genera (Behnke 1991; Nelson 1994) of which *Salmo* and *Salvelinus* (along with *Oncorhyncus*) are the best studied. In the present contribution, we review aspects of the biology of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). For brevity, we will usually refer to them as salmon, trout and charr in the text. The three species have wide but different natural distributions that overlap extensively in Europe. The salmon and trout are both Atlantic species but the trout occurred natively only on the eastern side of the ocean. Man has, however, introduced it across the Atlantic as well as to many other parts of the world (Elliott 1994). The salmon is found in river systems on both sides of the Atlantic and migrates over most of the northern part of the ocean during anadromy (Hansen & Quinn 1998). In contrast to the other two, the charr is a circumpolar species. It is also the northernmost of all anadromous and freshwater fishes.

These three species range among the best-studied fish species in the world. The literature on all three is very large, as is evident for instance from the six volumes of references to the Arctic charr complex up to 1996 issued by Canada Fisheries and Oceans (Marshall 1977, 1981; Marshall & Layton 1985; Heuring et al. 1991; Marshall et al. 1994, 1998). Also, there are several recent books (Balon 1980; Mills 1989, 1993; Shearer 1992; Elliott 1994), reviews (Johnson 1980; Jonsson & Jonsson 2001) and symposium proceedings (Johnson & Burns 1984; Kawanabe et al. 1989; Klemetsen et al. 1995; Mather et al. 1998; Prévost & Chaput 2001; Magnan et al. 2002) that cover important parts of the ecology and population dynamics of each of the three species considered here. We therefore will not necessarily give extensive reviews of all, or even most sides of their biology. Rather, we focus on aspects that we find interesting, diverse, currently topical, and also challenging for future research. As it turned out, these aspects proved to be quite different for the three species.

Atlantic salmon, *Salmo salar* L.

Introduction

Atlantic salmon occur naturally along both east and west coasts of the North Atlantic Ocean where it exists in both anadromous and non-anadromous freshwater resident forms. In the northwest Atlantic, salmon occur from approximately the Connecticut River in the south to Ungava Bay in the north, while in the Northeast Atlantic, salmon range from northern Portugal to rivers emptying into the Barents and White Sea areas of northern Europe (MacCrimmon & Gots 1979) occupying a diverse array of physical and biological environments (Elliott et al. 1998). In contrast with Arctic charr, there is no increase in prevalence of the anadromous form with latitude. Freshwater resident populations are common throughout the entire distributional range in North America (Power 1958; MacCrimmon & Gots 1979), while in Europe they are normally associated with larger lakes including Ladoga, Onega, Vänern and Saima (MacCrimmon & Gots 1979; Berg 1985; Kazakov 1992), although several resident riverine populations exist in the River Namsen, Norway (Berg & Gausen 1988).

Both within and among populations, salmon display variability in freshwater habitat use (Gibson 1993, 2002; Heggenes et al. 1999), length of freshwater residence (Randall et al. 1987) and sea-age at maturity (Meerburg 1986; Power 1986; Riddell 1986; Randall et al. 1986; Jonsson et al. 1991a). Indeed, the diverse life history of salmon has been suggested as the mechanism that enables small populations to persist (Saunders & Schom 1985). Such diversity is exemplified by comparing populations in Northeast Brook, Trepassey, a 21-km^2 drainage located in southeastern Newfoundland, with the enormous River Tana (Finnish: Teno) in northern Europe which has a drainage area of over 16,000 km^2. The former has an average run of 104 predominately 1 sea-winter (1SW) fish (range = 59–188, 1983–2001) (O'Connell et al. 2001a) compared with 3–5SW salmon in the latter system where annual in-river harvests can range between 100 and 200 mt (Erkinaro et al. 1997), equivalent to a catch of about 20,000–40,000 fish. Furthermore, the structure of populations is made more complex by the presence of sexually mature parr (e.g., Myers et al. 1986). In most systems, mature parr consist of males only, although mature female parr have also been reported in some instances (e.g., Power 1969; Prouzet 1981).

The information published on Atlantic salmon is immense with an abundance of individual papers, books, and journal supplements, as acknowledged recently by Chaput & Prévost (2001), devoted to all aspects of its ecology. In recent years, themes associated with many publications (e.g., Mills 1993, 2000; Hutchinson 1997; Whoriskey & Whelan 1997; Dempson et al. 1998; Mather et al. 1998; Jonsson & Waples 1999; Prévost & Chaput 2001) often relate, in whole or in part, to the reality that numerous salmon populations are in decline. Here, we present aspects of phenotypic and life-history variation in salmon, in particular highlighting the inherent variability in life-history forms both within and among populations. We emphasise the importance and utilisation of lacustrine habitat to the ecology, production, and conservation of salmon, in the context of current information regarding trends in abundance and survival. The latter is an area of particular interest especially in recent years as some populations in both US (Maine) and Canada (inner Bay of Fundy, Nova Scotia, New Brunswick) are now listed as endangered (Maine: US Endangered Species Act; Canada: Committee on the Status of Endangered Wildlife in Canada) continuing the decline observed in many areas of North America as well as Europe even in the absence of, or great reduction in directed marine fisheries (Parrish et al. 1998). We also acknowledge the wealth of suggested research recommendations from various sources and comment on avenues for future direction.

Phenotype and life-history variation

Anadromous salmon display considerable phenotypic plasticity and variability in life-history characters (Riddell & Leggett 1981; Saunders & Schom 1985; Thorpe 1986, 1989, 1994, 1998; Northcote 1988; Fleming 1996; Hutchings & Jones 1998; Thorpe et al. 1998). The Atlantic salmon is iteroparous, meaning it may spawn repeatedly, as opposed to most species of Pacific salmon (*Oncorhynchus*), which are semelparous and die after only one spawning (Schaffer 1974). Anadromous fish may mature as parr, 1–3 sea-winter fish, and in rare instances, at older sea ages. All these ages at maturity may occur in the same population, constituting a 'bet hedging' strategy (Stearns 1976; Lacey et al. 1983; Orzack & Tuljapurkar

1989; Roff 1992; Ellner & Hairston 1994), maximising survival and population stability.

Models to estimate and evaluate growth of salmon parr have recently been developed by Elliott & Hurley (1997) and Forseth et al. (2001). These studies were experimental, but built on earlier investigations of growth of salmon parr where it has been shown that parr may segregate into two or more groups at the end of the first growth season. Parr in the upper modal group may smoltify at 1+ years compared to older ages for the lower modal groups (Metcalfe et al. 1988). In the River Imsa, Norway, the older smolts are chiefly 2 or 3 years of age (Jonsson et al. 1998a). Smolt size increases with age and 1 year before smolting, parr destined to become the oldest smolts can be larger than the youngest smolts (Økland et al. 1993). Within populations, therefore, smolt length is flexibly dependent on growth rate. Smolt size can also vary widely among populations. For example, large smolts tend to occur in rivers draining into a cold ocean such as Ungava Bay, northern Quebec, where mean smolt lengths are typically greater than 200 mm (Power 1969), while small smolts, averaging 120–130 mm, can occur in cold rivers flowing into a relatively warm ocean, such as glacier fed rivers along the west coast of Norway (Jensen & Johnsen 1986), but are also characteristic of other rivers in Atlantic Canada (see Chadwick et al. 1986; O'Connell & Ash 1993).

The minimum smolt age reported for populations of wild anadromous salmon in North America is 2 years (Saunders & Schom 1985), while smolts as old as 8 years have been encountered in rivers in Ungava Bay, northern Quebec (Power 1969; Robitaille et al. 1986). Smolt age has been shown to increase with increasing latitude in North America, and concomitantly decreasing with length of growing season (Power 1981), but deviations from this general trend can occur on a local scale for various reasons (Power 1986). For instance, modal smolt age for Northeast Brook, Trepassey, the small watershed in southeastern Newfoundland referred to above, is 4 years (range of 2–6 years), similar to that characteristic of more northern populations, such as found in Labrador (Anderson 1985). Latitudinal variation in smolt age also occurs in Europe (Metcalfe & Thorpe 1990). One-year-old smolts occur in the UK, France, and Spain (Saunders & Schom 1985; Nicieza & Braña 1993) and smolts as old as 5 and 6 years have been reported for the Kola Peninsula, Russia and northern Norway, respectively (Jensen et al. 1997).

Adult salmon in North America mature for the first time after 1–3 winters at sea and the relative proportions and biological characteristics (smolt age, sex ratio, fecundity, etc.) of these age groups vary among stocks and with geographic location (Porter et al. 1986). With respect to European populations, maiden 3SW and older salmon have been reported for rivers in Scotland (Shearer 1992) and 5SW salmon are found in the River Tana in northern Europe (Erkinaro et al. 1997). Compared to other areas throughout North America, Newfoundland is unique in that with the exception of one small area on the southwest corner of the island (Bay St. George), stocks are comprised almost exclusively of 1SW salmon (Dempson et al. 1986; Porter et al. 1986). Even within populations with such a simple sea-age structure as this, there can be a multiplicity of individuals with different spawning histories contributing to egg deposition in a given year. Conne River (Dempson et al. 2001a) and Gander River (O'Connell et al. 2001b) are two Newfoundland systems where long-term information on life-history variation is available. In addition to maiden fish corresponding to the various smolt-age groups, which constitute the bulk of spawning escapements, there are significant numbers of consecutive and alternate spawners present. Salmon spawning consecutively up to four to five times have been reported in these rivers and there have been instances where consecutive spawners switched to alternate spawning (Conne River) and vice versa (Gander River). Collectively over the years, as many as 20 spawning types have been encountered for Conne River and 26 for Gander River. There can be considerable variation among populations in the relative proportions of consecutive vs. alternate spawners (Ducharme 1969; Saunders & Schom 1985; Jonsson et al. 1991a; Fleming 1996). All sea age groups possess repeat spawners and this obviously greatly increases the potential for additional spawning types depending on the population.

In Norway, mean sea age and size at maturity increases with river size for systems with a mean annual water flow of 40 $m^3 \cdot s^{-1}$. For larger rivers there is no such relationship (Jonsson et al. 1991a). One sea-winter salmon spawn usually every year, older sea-age salmon are chiefly biennial (alternate) spawners, and within populations, the proportion of biennial spawners increases with the size of fish at first maturity. The proportion of repeat spawners decreases with size of fish. This may be related to energy expenditure due to spawning. One sea-winter salmon may allocate 50% of their energy for spawning (Jonsson et al. 1991b) compared to 70% for older salmon (Jonsson et al. 1997) such as found in the River Drammen, Norway, only 2% of which spawn a second time.

In Ungava Bay, at the northern extremity of the North American distribution, a form referred to as 'estuarine' salmon occurs, in addition to 1SW and 2SW salmon (Robitaille et al. 1986). Unlike 1SW and older salmon, which undergo extensive oceanic migrations (Hansen & Quinn 1998), these fish can reach maturity and return to fresh water after only a few months in the estuary. While this form has also been encountered sporadically over the years in low numbers in Newfoundland, it has become more prevalent in recent years in certain rivers (Downton et al. 2001). In eastern Hudson Bay (Nastapoka River), there is also a northern form that migrates to the estuary for a brief time, but this one differs from the estuarine salmon of Ungava Bay in that it does not undergo smoltification and growth rates are lower (Morin 1991). In addition to the 'estuarine' type and more extensive oceanic migratory forms of salmon, there are other populations such as those originating in the Baltic Sea (Karlsson & Karlström 1994) and Inner Bay of Fundy (Amiro 1998) areas, that do not undertake long distant migrations but rather tend to stay within the geographical confines of these respective areas.

Fecundity is another trait that varies considerably both within and among salmon stocks. Egg number and size increase with body size (Thorpe et al. 1984; Jonsson et al. 1996). In a dwarf or stunted freshwater resident population from Newfoundland, mean fecundity was 33.0 eggs (SD = 7.95) (Gibson et al. 1996). In contrast, 2SW salmon from the Varzuga River, Kola Peninsula, had individual fecundity ranging as high as 17,892 (Lysenko 1997), while for the Restigouche River, New Brunswick, Randall et al. (1989) reported mean fecundity of 3SW and previous spawning salmon of 12,606 and 16,585 eggs, respectively. Although absolute fecundity varies greatly among individuals, as expected owing to high variability in adult body size, relative fecundity (eggs kg^{-1} total egg mass) as a measure of reproductive effort, varies much less. At Miramichi River, New Brunswick, relative fecundity ranged from 1331 eggs kg^{-1} in previous spawning salmon (mean length 82.1 cm) to 2035 eggs kg^{-1} in 1SW fish (Randall 1989). Similarly, relative fecundity of salmon at Varzuga River varied from 1953 to 3084 eggs kg^{-1} (Lysenko 1997). In a survey of 2440 specimens from 10 Newfoundland rivers, mean relative fecundity varied from 1278 to 2500 (O'Connell et al. 1997). Situations where mean relative fecundity varies among years by a factor of 1.5 to almost 2.0 within a population, coupled with annual variation in sex ratio and corresponding size of female spawners, contributes to the high degree of variation in estimated egg deposition rates relative to conservation goals as well as the variability observed in subsequent smolt production.

Jonsson et al. (1996) reported there can be a trade-off between egg size and fecundity. Fish may either spawn large and few eggs or small and many eggs. The faster the parr grow in fresh water before smolting, the smaller their relative egg size becomes when they attain maturity. This phenotypic response has been explained as an adaptation to the potential growth opportunities in their nursery river. This assumes that feeding opportunities that the parents experienced as juveniles in rivers is a good predictor of what their offspring experience. Usually, both egg size and fecundity increase with size of fish. Thorpe et al. (1984) cited instances of both negative and positive correlation between egg size and egg number and one study showing no correlation.

Large smolts move to sea earlier in the season than small smolts (Jonsson et al. 1990a) and water temperature often appears to be the factor stimulating river descent (Jonsson & Ruud-Hansen 1985; McCormick et al. 1998; Antonsson & Gudjonsson 2002). Support for temperature dependence is also revealed by the fact that fish move to sea earlier in southern than in northern rivers, and in Europe, sea temperature is close to 8 °C when smolts enter the ocean whether the river is southern or northern. Water flow may also have a stimulating effect as reported for smolts in the River Orkla, Norway (Hvidsten et al. 1995), as well as others in Iceland (Antonsson & Gudjonsson 2002), but the relative significance of different factors likely varies among populations, locations and years (Høgåsen 1998). McCormick et al. (1998) suggested that there is both a physiological and ecological 'smolt window', both of which act to influence subsequent survival of smolts.

Downstream migration and smolting in Atlantic salmon is further complicated in some populations where fall rather than spring migrations occur (Youngson et al. 1983; Cunjak et al. 1989; Huntingford et al. 1992). In addition, estuaries are often used by Atlantic salmon parr for rearing prior to smolting (Cunjak et al. 1989; 1990; Cunjak 1992). Cunjak (1992) reported that growth of estuarine parr was highly variable but was faster than in riverine habitat and could be due, in part, to greater feeding opportunities in estuarine areas. Cunjak (1992) concluded that estuarine rearing by juvenile salmon represented an alternate life-history tactic demonstrating further the plasticity and adaptiveness of the species.

Run timing in adult Atlantic salmon is also highly variable. It differs within stocks over time but can also vary considerably within the same year depending on the life-history stage in question. Run timing is an adaptation to local environmental conditions (Leggett & Whitney 1972) but has also been shown to be a heritable trait in salmon (Hansen & Jonsson 1991).

In Norway, most salmon enter the rivers from May to October, with a general tendency for large, multi-sea-winter salmon to enter earlier than 1SW fish (Jonsson et al. 1990a,b). While this pattern is somewhat consistent with that observed in eastern Canadian rivers (Saunders 1967), there are also exceptions where some rivers are characteristically 'early', some 'late', and others, such as the Miramichi River that have both early and late run components (Belding & Kitson 1934). These early and late runs may also differ in their respective sea-age characteristics and corresponding sex ratios. Salmon runs in Scotland demonstrate yet another example of great variability in life-history characteristics. Here, salmon can enter the rivers at any time of the year with some individuals entering over a year prior to when they will spawn (Nordqvist 1924; Webb & Campbell 2000).

The sexual maturation of wild anadromous male parr is widespread throughout the distribution of the species (Dalley et al. 1983; Myers et al. 1985) and they successfully mate with adult female salmon both in the presence and absence of adult males (Myers & Hutchings 1987), playing an important role in increasing the effective population size in small populations (L'Abée-Lund 1989). In contrast, there have only been isolated reports of the maturation of wild anadromous female parr in fresh water (Power 1969; Prouzet 1981; Baglinière & Maisse 1985; Hindar & Nordland 1989; Moore & Riley 1992). There have been cases where anadromous females that were stocked into ponds as swim-up fry have reached sexual maturity in fresh water (Harris 1973; Morrison 1983; O'Connell & Gibson 1989). These fish were subject to rapid growth and outlet configurations of the ponds prevented them from going to sea.

As pointed out earlier, nonanadromous or land-locked salmon, which complete their life cycle entirely in fresh water, are found on both sides of the Atlantic Ocean. Isolation of nonanadromous from anadromous salmon appears to have occurred during isostatic rebound of coastal regions following the last ice age, approximately 10,000 years ago (Sutterlin & MacLean 1984; Berg 1985). In contrast to the voluminous material published on the anadromous form, there is comparatively little information available on nonanadromous salmon. Nonanadromous salmon occur not only above impassable physical barriers (e.g., Andrews 1966), but are also found in sympatry with anadromous salmon in river systems that are fully accessible to the sea (Scott & Crossman 1964). For some sympatric occurrences, there is evidence to suggest the forms are reproductively isolated (Verspoor & Cole 1989; Birt et al. 1991a,b). Hutchings (1985) however, also viewed the occurrence of both forms in sympatry as phenotypic polymorphisms within a single population, as alternative evolutionarily stable strategies (ESSs) in the game theoretic context of Maynard Smith (1982). In North America, there have been reports of nonanadromous salmon measuring up to 56 cm in length for Labrador (Bruce 1974) and weighing as much as 3.9 kg for Newfoundland (Scott & Crossman 1964), 20.4 kg for Lake Ontario (Scott & Crossman 1998), and in excess of 12.2 kg for Maine, USA (Warner & Havey 1985). These are sizes comparable to those attained by anadromous salmon and are not dissimilar from those reported from some European lakes (Kazakov 1992). At the opposite end of the size spectrum, populations of small nonanadromous salmon occur in North America in both fluvial (Gibson et al. 1996) and lacustrine (Bruce 1976; Barbour et al. 1979; Sutterlin & MacLean 1984) habitats and have also been reported for both lacustrine (Dahl 1928) and riverine (Berg & Gausen 1988) habitats in Norway. In the North American fluvial situation mature females ranged in length from 84 to 123 mm (mean = 102 mm) (Gibson et al. 1996), while those from the River Mellingselva, a tributary of the River Namsen, Norway, varied from 136 to 228 mm (mean = 176 mm) (Berg & Gausen 1988).

The role of lacustrine habitat

Beginning in the mid-1970s, it became apparent that juvenile anadromous salmon use lacustrine habitat for rearing purposes to a considerable degree in Newfoundland rivers and over the years varied studies of this aspect of life history have continued (Pepper 1976; Pepper et al. 1984, 1985; Chadwick & Green 1985; Hutchings 1986; Ryan 1986; O'Connell & Ash 1989, 1993; Ryan et al. 1993; Dempson et al. 1996; O'Connell & Dempson 1996; Erkinaro & Gibson 1997a,b). Subsequent to the pioneering Newfoundland studies, evidence of rearing in lacustrine habitat has been reported for Iceland (Einarsson et al. 1990), Norway (Halvorsen & Jørgensen 1996; Halvorsen & Svenning 2000), Finland (Erkinaro et al. 1995, 1998a,b; Jørgensen et al. 1999) and Ireland (Matthews et al. 1997).

Habitats other than fluvial, including lacustrine, have been considered as marginal or secondary for juvenile anadromous salmon, occupied by individuals displaced from preferred stream habitat

(Pepper et al. 1985; Gibson 1993), which is consistent with the traditional view that they are stream dwellers (Keenleyside 1962; Gibson 1966, 1988, 1993; Marschall et al. 1998). The widespread use of lacustrine habitat by parr is believed to be due to the relative lack of predators and competitors (Hutchings 1986; Gibson 1993; Gibson et al. 1993). Growth of parr occupying lakes and ponds has been shown to be higher than for those in fluvial habitat (Hutchings 1986; O'Connell & Ash 1993; Erkinaro et al. 1995; Dempson et al. 1996; Halvorsen & Svenning 2000). Hutchings (1986) considered the use of lacustrine habitat to be nonrandom and resultant enhanced growth and survival relative to fluvial habitat to be of adaptive significance. O'Connell & Ash (1993) demonstrated that juvenile growth rate and smolt size in rivers in Newfoundland dominated by lacustrine habitat was greater than in those comprised mainly of fluvial habitat. Compared to lacustrine systems, the incidence of male precocity was lower for fluvial systems with correspondingly more anadromous males. Mean smolt age for lacustrine systems (3.2 years) was similar to that of fluvial systems (3.1 years) as was the modal age (3+ years, 69.9 and 69.3%, respectively). Adults matured almost exclusively as 1SW salmon in lacustrine systems while in fluvial systems (in Bay St. George) there was a significant component maturing at older sea ages. Overall generation time for lacustrine systems, therefore tended to be lower than for fluvial systems, consistent with the view that given environmental conditions conducive to rapid growth, fish will mature as soon as developmentally possible (Policansky 1983; Thorpe 1986, 1998). The dominance of 1SW salmon in many Newfoundland rivers therefore could be related to the preponderance of lacustrine habitat. Nicieza & Braña (1993) also found that faster growing juveniles and larger smolts favoured earlier age at first maturity for salmon in northern Spain and suggested that large smolts tend to maintain their size advantage up to the end of the first sea winter. Erkinaro et al. (1997) showed that juveniles rearing in the tributaries of the River Teno (=Tana) in northern Scandinavia grew faster that those in the main stem and tended to mature as 1SW salmon.

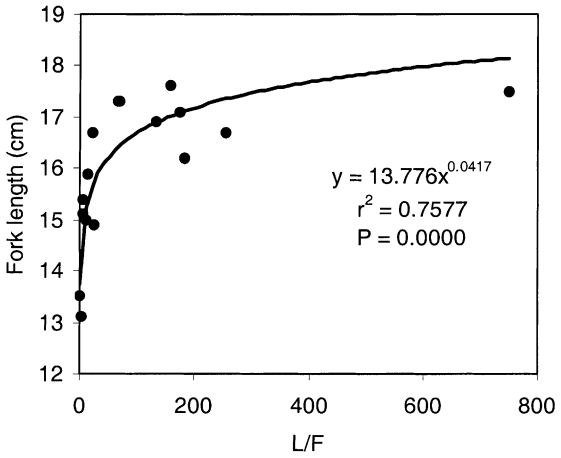

Fig. 1. Relationship between mean smolt length (cm) and the ratio of lacustrine to fluvial (*L/F*) habitat (expressed as m^2) for 16 river systems in Newfoundland.

The importance of lacustrine habitat in determining smolt size in Newfoundland rivers is further illustrated in Fig. 1. An analysis of available data for 16 river systems, with watershed areas varying in size from <100–6400 km^2, shows a significant positive relationship between mean smolt length and the ratio of lacustrine to fluvial (*L/F*) habitat (expressed as m^2). Furthermore, for six of these rivers there is some evidence that mean sea survival of smolts to adult small salmon (those <63 cm in fork length and including repeat spawners) increases with *L/F* ratio (Fig. 2) suggesting that sea survival increases with smolt size. Lundqvist et al. (1994) reported higher recapture rates for larger Baltic salmon smolts released into the Ume River in northern Sweden while Ward & Slaney (1988) found that survival of steelhead trout was positively correlated with smolt length and weight for a coastal stream in British Columbia, Canada. For coho salmon in British Columbia and Baltic salmon, Holtby et al. (1990) and Salminen et al. (1995) suggested that growth rates in the marine environment, and consequently post-smolt size, affected susceptibility to size-selective predators. Higher sea survival of larger smolts has also been reported for sockeye salmon (Koenings et al. 1993).

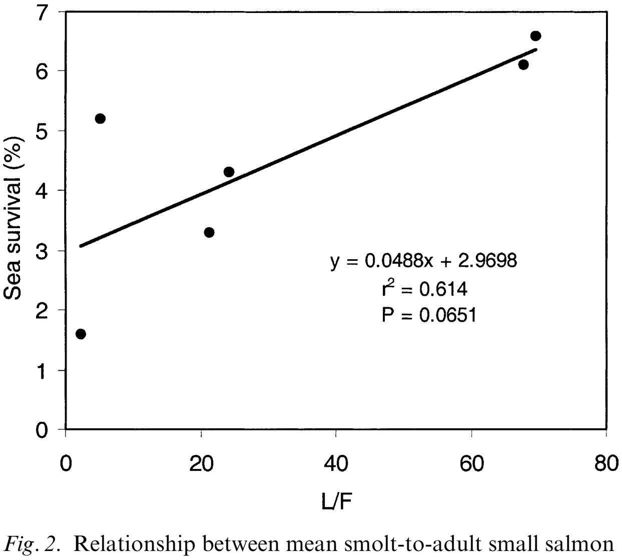

Fig. 2. Relationship between mean smolt-to-adult small salmon (<63 cm in length) survival and the ratio of lacustrine to fluvial (*L/F*) habitat (expressed as m^2) for six river systems in Newfoundland.

Lacustrine habitat may also confer better survival for parr compared to stream habitat as indicated by Hutchings (1986). Support for this comes from examining egg-to-smolt survival rates for several Newfoundland or New Brunswick rivers. Egg-to-smolt survival for Northeast Brook, Trepassey ($L/F = 5.2$) averaged 0.52% (minimum = 0.36; maximum = 1.09) over 12 year-classes (O'Connell et al. 2001a). This compares to 1.22% (0.45–2.55) for Conne River, which has an L/F-value of 24.1, for virtually the same time period (Dempson et al. 2001a). At Western Arm Brook, Newfoundland, another lacustrine system ($L/F = 69.6$), egg-to-smolt survival averaged 1.7% (Chadwick 1982), but was only 0.38% at Catamaran Brook, a fluvial tributary of the Little Southwest Miramichi River (Cunjak & Therrien 1998). In contrast, egg-to-smolt survival for the River Bush, a predominantly fluvial system in Northern Ireland, averaged 1.02% (0.16–2.02%) (Potter & Crozier 2000), and thus is comparable to that recorded for Conne River but also illustrates the variability that can occur among rivers. There is a negative relationship between egg deposition and egg-to-smolt survival for both Conne River and Northeast Brook, Trepassey, indicating that both systems might be experiencing signs of density dependence. The relationship for Conne River is shown in Fig. 3.

Biological reference points

Abundance of salmon is influenced both by density-dependent and -independent factors. Density-dependent factors are most important in fresh water whereas density-independent factors dominate the mortality in the ocean (Jonsson et al. 1998b). Recently, Elliott (2001) provided a detailed account of the relative role of density in regulating juvenile survival in fresh water. Density-dependent effects are often modelled by stock–recruitment (SR) relationships that also have utility in defining appropriate reference points for establishing conservation goals (Chaput et al. 1998). Reference points provide the means by which advice relative to the status of stocks can be evaluated and, if necessary, management strategies initiated to try and ensure conservation of the resource (reviewed by Potter 2001), an aspect of increasing importance throughout the North Atlantic as a whole.

In Newfoundland, the frequency and extent that salmon utilised lacustrine areas required the incorporation of lake habitat into initial attempts at defining conservation spawning requirements (O'Connell & Dempson 1995). Systems characterised largely by fluvial habitat could have L/F ratios of less than 10 while in lacustrine dominated systems, ratios may be 10–70 times higher. Consequently, it was important to consider the contribution of both habitats in establishing conservation requirements. However, the absence of river-specific SR relationships resulted in a broad-based approach to define conservation, using different egg-to-smolt survivals for fluvial versus lacustrine habitat. Requirements in terms of egg deposition were converted into numbers of adults

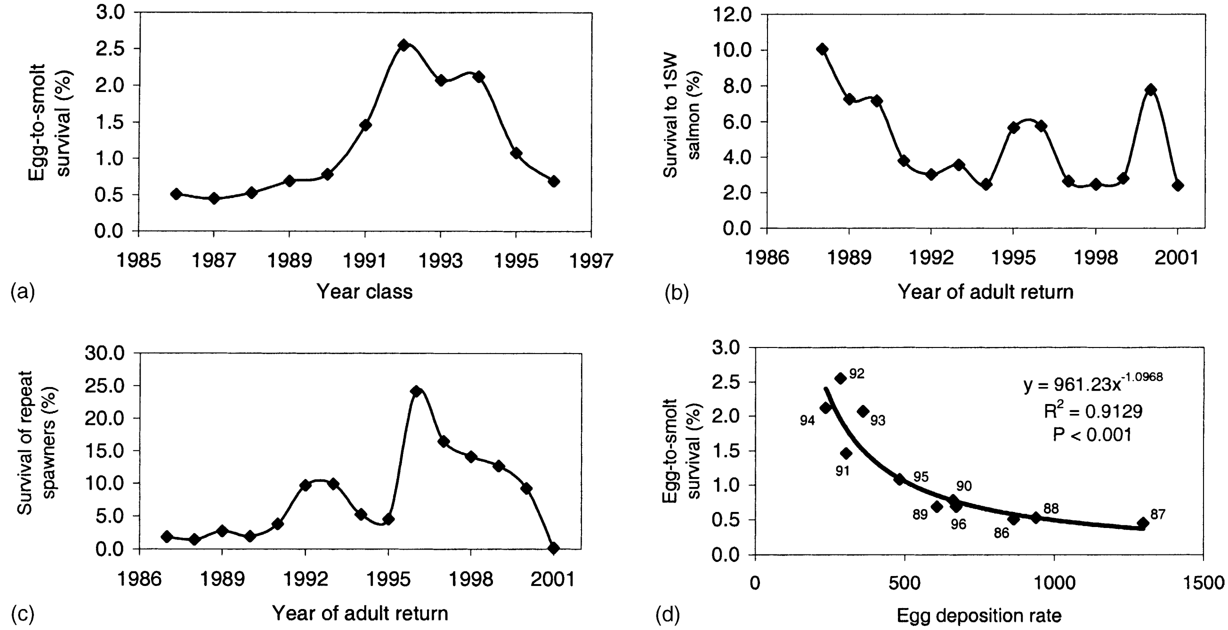

Fig. 3. Trends in survival to various life-history stages in Conne River, Newfoundland, Atlantic salmon: (a) egg-to-smolt survival; (b) smolt-to-1SW survival; (c) 1SW to consecutive spawner survival; and (d) egg-to-smolt survival relative to the estimated egg deposition spawning rate expressed as the number of eggs deposited per 100 m^2 of fluvial habitat.

based on information on size-specific fecundity and sex ratio, when available for individual rivers (O'Connell & Dempson 1995). These authors noted that in systems dominated by lacustrine habitat, sufficient fluvial spawning habitat could be limiting.

Chaput et al. (1998) described an alternate approach to define conservation requirements for salmon using egg depositions, smolt production and biological characteristics of adults from 10 rivers by modelling egg-to-smolt and egg-to-egg production. The approach differed from that presented by O'Connell & Dempson (1995), but was consistent in determining the importance of including lacustrine habitat for Newfoundland rivers and demonstrated a method of transporting SR relationships across rivers. New approaches and recommendations for transporting SR relationships are described by Prévost et al. (2001) while Koljonen (2001) has demonstrated how genetic information can be applied in the context of defining conservation goals and developing management strategies for Baltic salmon stocks.

Trends in abundance and survival

Despite the wealth of information available on Atlantic salmon, concern is increasing over the continued decline of wild stocks in the North Atlantic (Mather et al. 1998; Parrish et al. 1998; Potter & Crozier 2000). In general, it is commonly believed that factors responsible for the decline operate in the marine environment (Friedland et al. 1998; Jacobsen & Hansen 2000; Potter & Crozier 2000; Montevecchi et al. 2002), although others acknowledge impacts could be initiated in freshwater with resultant consequences when fish are at sea (e.g., Randall et al. 1989; Walters & Ward 1998; Fairchild et al. 1999).

Marine exploitation rates estimated for various Newfoundland stocks for the period 1984–1991 averaged 45.3% (range: 29.6–57%) on small (<63 cm) salmon and 74.2% (57.7–83.7%) on large salmon (≥63 cm) (Dempson et al. 2001b). Yet, closure of the Newfoundland commercial salmon fishery beginning in 1992 and the establishment of conservation requirements to assist in managing the resource has not resulted in consistent gains in overall productivity, contrary to that expected when directed marine exploitation was curtailed (Dempson & O'Connell 1993). Indeed, 5 years after the closure of the commercial fishery, during which time some stocks doubled or tripled in their spawning escapements (Dempson et al. 2001b), many Newfoundland stocks experienced substantial declines in abundance (Dempson et al. 1998). In the 5-year interval 1997–2002, a number of stocks have now experienced 4 out of 6 years with relatively low abundance. Some stocks have returns that are lower on average than in years prior to the closure of the commercial fishery (Dempson et al. 2001b) with marine survival rates less than that experienced when marine fisheries were in existence (DFO 2002a). Similarly, salmon returns throughout the Maritime Provinces of Canada have fallen short of expectations, despite the restrictive management measures introduced in both distant- and home-water areas over extended periods of time (DFO 2002b). Marine survival of salmon stocks in the northeast Atlantic was also generally lower during the 1990s than in the 1980s (Potter & Crozier 2000). Interestingly, the generalised results summarised above for salmon parallel those of various marine fish populations that have similarly shown little or no recovery despite large reductions in exploitation, implying factors other than exploitation are contributing to lack of stock recovery (Hutchings 2001).

Marine mortality on salmon is commonly believed to be highest in the initial periods that smolts are at sea (Hansen & Quinn 1998; Potter & Crozier 2000) and is consistent with observations on timing of mortality of wild Conne River smolts that were transferred to an estuarine aquaculture grow-out facility at Roti Bay, Newfoundland (Dempson et al. 1999a). Nonetheless, the early life-history of salmon at sea is one area where there is a virtual lack of information by comparison with, say, efforts directed at catching salmon on the high seas.

Over the past several decades much has been learned from studies in the marine environment (e.g., Reddin 1988; Hansen et al. 1993; Friedland 1998; Hansen & Quinn 1998; Mills 2000). Despite this, we are unable to explain with certainty why stocks, such as Conne River and Western Arm Brook, Newfoundland, can experience substantial fluctuations in marine survival often in successive years (Conne River: 1999, 3.4% survival; 2000, 8.1%; 2001, 2.4%; and Western Arm Brook: 1999, 6.1%; 2000, 11.1%; 2001, 4.4%). Marine environmental temperature conditions have been linked in various studies with salmon abundance and survival, but as stated by Potter & Crozier (2000), none have demonstrated clear causal relationships. The lack of causal relationships between abundance and environmental conditions was similarly reported by Lindroth (1965) in an examination of factors influencing variation in abundance of Baltic salmon. Potter & Crozier (2000) also noted the apparent breakdown of thermal habitat indices and abundance of North American origin salmon, as the latter has remained low while the apparent thermal habitat indices have increased in recent years, and suggest additional research into other potential contributory factors. A similar situation has been observed for Conne River, Newfoundland, where there had also been an environment–survival association, but survival has for the most part remained low throughout most of the past decade despite improved ocean temperature conditions (Dempson et al. 1999b). Elliott (2001) citing Summers (1995), noted that other associations have not held up when longer time series are examined. Similarly, Crozier & Kennedy (1999) have shown that the postulated growth/survival model apparent in some populations (Friedland et al. 1993), was not apparent in analyses of marine growth and survival of River Bush salmon. In the absence of information on underlying mechanisms and causal relationships, simply catching additional salmon at sea and recording temperatures will yield limited new information over that which is already known.

Cold sea temperatures alone, are likely not directly responsible for low survival of salmon after they have passed the 'post-smolt' stage in late fall and winter of the year in which they migrated to sea, but can be a critical factor during the initial smolt phase of their migration (McCormick et al. 1998), as well as altering distribution and behaviour (Drinkwater 2000). In the Conne River smolt rearing experiment (Dempson et al. 1999a), salmon had attained approximately 70% of their subsequent adult 1SW size by the end of October (mean length = 374 mm; mean weight = 780 g). During winter, temperatures at Roti Bay are typically less than 2.5 °C with salinities varying from 20 to 28 (PSU) at depths from 2 to 6 m based on observations in other years. The upper level of water ranged from 0 to 5 PSU and surface ice can persist for several months (Sutterlin & Stevens 1992). Aquaculture salmon have been maintained in this environment for a number of years, and over-winter survival of the wild Conne River reared salmon was similarly high (72% survival from December 31 to May 15) (Dempson et al. 1999a).

Evidence exists for differential survival between 1SW and 2SW life-history stages of salmon, and while at times patterns in survival appear coherent among stocks, it is not consistent among regions (Potter & Crozier 2000). Previously it was also stated that marine survival is more variable than survival in freshwater (Chadwick 1987) with the former largely responsible for influencing changes in population abundance. However, a total life-cycle approach has been advocated by Crozier & Kennedy (1999) and Potter & Crozier (2000) as the variability in natural survival in freshwater of River Bush, Northern Ireland, salmon has been found to exceed that associated with marine survival. A similar situation is observed at Conne River where variability in fresh water survival (mean = 1.22%, C.V. = 63.6%) exceeds that of smolt to 1SW (mean = 4.77%, range = 2.41–10.04%, C.V. = 52.1%), with survival of consecutive repeat spawners showing the greatest variation (mean = 7.85%, range = 0.16–24.16%, C.V. = 86.5%) (Fig. 3). Thus, comments such that freshwater production has been maintained in the face of variable marine survival are correct in terms of numbers of smolts produced (smolt production: C.V. = 18.8% at Conne River), but not if overall egg-to-smolt survival is considered. The interannual variability in fresh water survival has been linked with environmental conditions, in particular, discharge and break-up events during the critical winter period (Cunjak & Therrien 1998; Cunjak et al. 1998). However, as cautioned by Northcote (1988), despite decades of research devoted to understanding functional processes affecting survival of salmon, it has been difficult to identify and quantify fluctuations in abundance of even small monitored populations.

Future direction

Atlantic salmon have existed in the north Atlantic for thousands of years. As summarised above, they have a highly diverse and plastic life history that rivals that of other salmonid species, including Arctic charr. They have a decidedly variable maturation schedule spreading their reproductive potential from a single spawning over many years, and, as stated by Hansen & Quinn (1998), are adapted to the prevailing environmental conditions they encounter. Indeed, McCormick et al. (1998) state that smolts are not only physiologically adapted to surviving in the marine environment, but to thrive there. Thus, salmon should have the capability to survive in variable fluctuating environments, and in the past at least, displayed a high resilience in many areas where various stressors have challenged their continued survival and productivity. Unfortunately, despite the wealth of information accumulated, especially over the past several decades, and for reasons that are not always entirely clear, their continued existence and persistence is increasingly being threatened.

Parrish et al. (1998) posed the question 'Why aren't there more Atlantic salmon?' in a review of the current status of salmon throughout its native range. They also acknowledged problems associated with linking cause and effect to what is likely a result of multiple factors contributing to the decline of many salmon populations, and suggested how scientists and managers should respond to these challenges. Indeed, interested readers and researchers need go no further than a number of the publications cited earlier (e.g., Mills 1993, 2000; Whoriskey & Whelan 1997; Mather et al. 1998; Jonsson & Waples 1999; Prévost & Chaput 2001) to find a multitude of recommendations for future research covering a vast assortment of ecological and population dynamics issues. Numerous recommendations are also provided in the proceedings of a recent workshop convened explicitly to review and solicit insight into developing research strategies associated with causes for the continuing decline in survival and abundance of salmon (O'Neil et al. 2000; Cairns 2001). Thus, we refrain from providing a specific list of similar recommendations but rather comment in general on avenues for future direction. In reviewing many of the various recommendations that have been made, we also note that at times, some are frequently repeated, for example, the requirement for additional studies on salmon in the marine environment. This could be due, in part, to a lack of resources from which to initiate directed research, or a lack of insight as to how to address the specific questions tabled.

Earlier, we acknowledged the paucity of information on the early life history of salmon at sea, and highlighted it as a specific knowledge gap requiring attention. This, and the acknowledgement by Elliott (1994), Marschall et al. (1998), Crisp (2000), Potter & Crozier (2000) as well as others, for the need to maintain or initiate long-term monitoring of populations, are also areas of fundamental importance. Interestingly, given the high degree of emphasis on problems associated with the marine survival of salmon, there are decidedly few stocks where both smolt and adult salmon are enumerated from which to monitor, and model trends in marine survival either from the northwest or -east Atlantic region. The potential impacts of escaped farmed salmonids on wild populations is another controversial area requiring additional research given the widespread concern raised in many areas (e.g., Hutchinson 1997; Noakes et al. 2000).

Complementing additional marine research is the need for a better understanding of factors influencing the production of salmon in freshwater habitats. Recent examples of specific recommendations can be found in Heggenes et al. (1999) and include obvious links to fundamental questions concerning the productive capacity of habitats including the influence of extreme events such as floods or droughts, both of which have been shown to effect abundance of juvenile salmonids (e.g., Armstrong et al. 1998; Jensen & Johnsen 1999; Weng et al. 2001). The potential impacts of the latter two phenomena are highlighted given the current interest and concern as to how climate change, particularly climate warming in general, will ultimately influence and affect salmonid populations in various ways (e.g., Jensen 1992; Turrell & Shelton 1993; Mangel 1994; Power & Power 1994; Minns et al. 1995; McCarthy & Houlihan 1997; McCormick et al. 1997; Dempson et al. 2001c). In any event, focused rather than generalised approaches are required to address specific research questions or hypotheses, and scientists should expect only small incremental steps at improving our understanding of factors influencing the survival and abundance of salmon, both in freshwater and marine habitats.

Application of electronic technology, such as the use of telemetry and various data storage (archival) tags, provide opportunities to explore aspects of the ecology of salmon not feasible in past decades to the degree possible today (e.g., Lacroix & McCurdy 1996; Moore et al. 2000), and with the rate this technology is developing, should provide even more insight into the distribution and migrations of salmon in near-shore and off-shore areas in the future. This could be of value when examining stocks that, apparently, are still quite 'healthy', or stable. Inferences obtained from these stocks could possibly assist in understanding better those where conservation problems exist. Finally, we note that salmonid species other than salmon may provide better opportunities to examine early life-history in near-shore areas and the influence of marine environmental conditions on distribution, growth, and survival. One example would be anadromous Arctic charr; their localised migrations in coastal areas for comparatively brief periods of time, coupled with their greater longevity and tolerance for handling, by comparison with, say, salmon, lend themselves ideally in situations where the likelihood of tracking and recovering fish would greatly exceed that of salmon. Knowledge gained could be transferable, at least in part, to provide better insight into understanding the dynamics of salmon during their early marine life phase.

Brown trout, *Salmo trutta* L.

Introduction

This chapter reviews life-history variation in brown trout (Fig. 4). After a brief outline of the life cycle and habitat use, we give more detailed

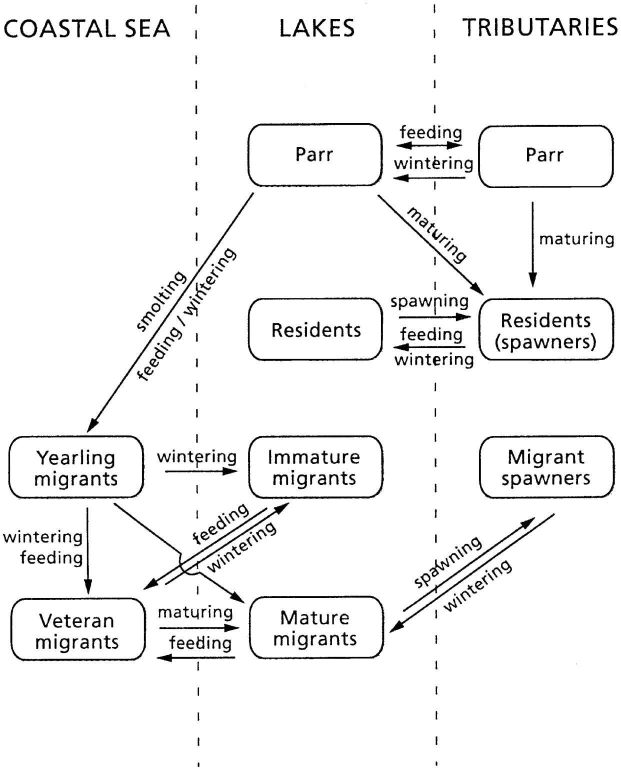

Fig. 4. Life history of brown trout.

information on distribution, feeding, growth, migration, maturation and longevity. In conclusion, we summarise some specific life-history traits of this ecologically variable species.

The review emphasises the most recent work on brown trout life history. The detailed knowledge on the species is growing rapidly, and we feel that this research reveals how the life history of a species is adapted to survival under different environmental conditions.

The population dynamics and production of brown trout were recently reviewed by Elliott (1994). Therefore, we have highlighted other aspects of the life history such as resource use and ecological variability within this species, which we find particularly interesting.

Geographical distribution

Brown trout is indigenous to Europe, North Africa and western Asia (MacCrimmon et al. 1970). In Europe, its northern limits are Iceland, northern Scandinavia and Russia (Elliott 1994). Western limits are defined by the European coastline and the southern limits by the northern coastline of the Mediterranean Sea at the islands of Corsica, Sardinia and Sicily, and the Atlas mountain of North Africa. Its eastern limits are probably the Ural Mountains in the north and the AmuDar'ya River Drainage of the Aral Sea in the south. The isolated population in the Aral Sea and its tributaries is now probably extinct (Williams & Aladin 1991).

Anadromous trout are not as extensively distributed as inland populations of brown trout but are found in Iceland and Scandinavia, in rivers flowing into the White Sea and Cheshkaya Gulf in the north, as well as the Baltic and North Sea and as far south in the Atlantic as the Bay of Biscay to northern Portugal (Frost & Brown 1967), at least to the Rio Miño (Lobón-Cerviá, personal communication). Anadromous trout are absent from the Mediterranean Sea, but may occur in the Black Sea and Caspian Sea (Elliott 1994). Throughout the range, sea trout and freshwater resident trout appear to inhabit the numerous river basins in varying proportions.

Brown trout have been introduced into at least 24 countries outside Europe and have now a world-wide distribution (Elliott 1994). The earliest introductions occurred in 1852 in eastern Russia, New Zealand 1867–1885, USA and Canada 1883 and 1887, respectively, Australia 1888, South Africa 1890, Japan 1892, and South America between 1904 and 1938. During less than 90 years (1852–1938), the brown trout changed from an European to a global species.

The reasons for the wide geographical distribution of this species are its ecological variability, excellent ability to spread and colonise new water courses, and its reputation as fine food and good sport. The species varies in size, growth rate, feeding niche and habitat use within and among water courses. The phenotypic appearance varies largely with the habitat, and to some degree also its ecology (Pakkasmaa & Piironen 2001). Given that it has suitable spawning substratum, proper temperature conditions and sufficiently good water quality, it occupies habitats from very small brooks to the largest rivers, from small tarns to fjords and coastal waters within its range. It is so variable that about 50 species have been described for varieties of brown trout (Behnke 1986), all grouped together in one polymorphic species. The species appears evolved through five different evolutionary lineages in geographical isolation during the Pleistocene and have remained largely allopatric since then (Bernatchez 2001).

Life cycle and habitat use

The trout spawn on stone and gravel bottoms, usually in running waters, although lake spawning populations occur occasionally (Klemetsen 1967; Scott & Irvine 2000; Sneider 2000; Brabrand et al. 2002). The species reproduces in autumn or

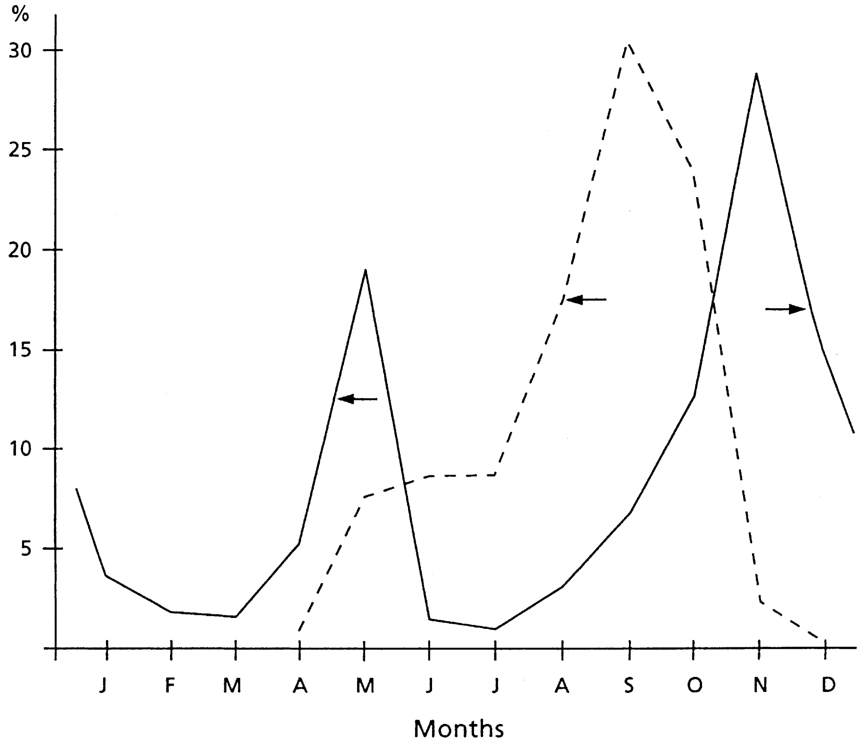

Fig. 5. Monthly percentage of brown trout descending (solid line) and ascending (broken line) the River Imsa between 1976 and 1999. The arrows indicate the distribution of large relative to smaller trout.

winter; the earlier the higher the latitude and altitude because of lower water temperature and longer egg incubation period.

Brown trout females dig their nests in the bottom substratum (Haury et al. 1999), and large females will often spawn on coarser gravel and bury their eggs deeper than small ones (Fleming 1996). One female is often courted by several competing males, but one large male may fertilise the majority of the eggs (Jones & Ball 1954; Largiander et al. 2001). Smaller, subordinate males may contribute to the fertilisation of the eggs of females primarily spawning with a large dominant male (Garcia-Vazquez et al. 2001). Within minutes after spawning, the female covers the fertilised eggs with stones and gravel.

Females spawn only a portion of their eggs at the time. The second portion may be placed in a new nest right in front of the first one, or it may be spawned at a proper place elsewhere in the river. A series of nests spawned by one female in front of each others is called a redd. One female may be reproductively active over a few days. She does not defend her redd after the spawning period is finished. Usually, she abandons the area as soon as the spawning is finished, while the males stay longer and if possible, spawn with more females. Male spawners are often present on the spawning grounds for a long time after all the females have disappeared from the area.

The eggs are incubated whilst buried in the gravel for 1 to several months, and hatch in the subsequent spring. Thereafter, the larvae, called alevins, feed for weeks on yolk which they carry in a sac underneath their belly. The length of the periods for egg incubation and endogenous larval feeding are temperature dependent, and longer the lower the temperature (Crisp 1988; Elliott & Hurley 1998a). The water temperature is higher in the bottom sediment than in the water above, so hatching may occur earlier than expected from the stream temperature above (Acornley 1999). Eggs may also hatch earlier as a consequence of environmental disturbance and stress (Næsje & Jonsson 1988).

The alevins, *c.* 20 mm in total length, swim up from the gravel when most of the yolk is consumed, and they start feeding in or near the spawning area. The young are aggressive, defend territories, form dominance hierarchies and compete intensively for resources (Kalleberg 1958; Héland 1999; Lahti et al. 2001). Individuals which are unable to catch food, may drift downstream and most of these will probably die within a short period (Elliott 1994). Those, which start to feed will disperse as they grow larger with expanded needs for food and space.

Sometimes brown trout may be quite sedentary in rivers, but often they appear to move about frequently (Crisp 1993; Gowan et al. 1994), so the turnover rate within a restricted area may be considerable (Rodriguez 2002), not the least if the environmental conditions such as food availability, current velocity and fish density, change

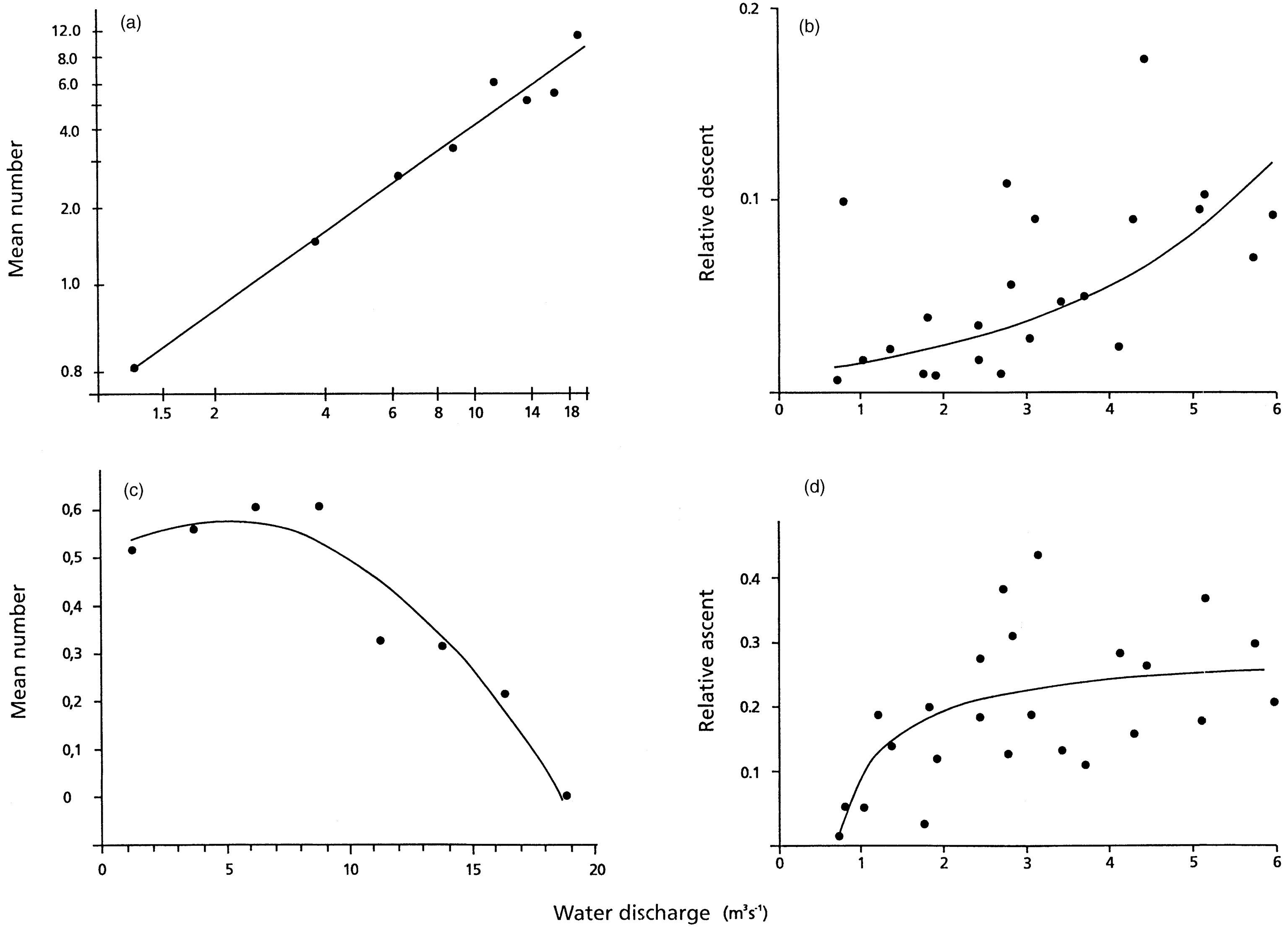

Fig. 6. The relationship between flow and (a) mean number of descending brown trout per day at different median flows (1.25, 3.75, 6.25, 8.75, 11.25, 13.75, 16.25 and 18.75 $m^3 \cdot s^{-1}$) in the River Imsa for fish <30 cm in body length (b) relative river descent (number of trout <30 cm in body length per month/number per year) over mean monthly water flow in between August 1976 and 1999 (c) mean number of ascending brown trout per day at different median flows (as in (a)) between April and December (d) relative ascent in August (number of ascending trout in the month/number in the year) over mean water flow between 1976 and 1999. (Redrawn from Jonsson & Jonsson 2002)

(Kalleberg 1958; Jenkins 1969; Nordwall et al. 2001). Furthermore, individuals with different foraging status make use of foraging areas sequentially (Alanara et al. 2001). Dominant fish feed mainly at the most beneficial times of the dusk and the early part of the night, whereas more subordinate individuals feed at other times. The motivation of a fish to defend a territory increases with residence time, which will influence the outcome of territorial contests (Johnsson & Forser 2002).

If the fish have access to a lake, many of them will gradually move there for feeding (Jonsson 1989). This movement may start shortly after the young emerge from the gravel bottom, but the trout may also stay in the nursery area longer, and some even become stream resident in systems with access to richer feeding areas such as a lake or a coastal fjord (Jonsson 1985).

The variability and quality of the habitat will strongly influence fish density in a river (Heggenes et al. 1999; Jutila et al. 2001; Rincón & Lobón-Cerviá 2002). During their first year in the river, the young dwell largely in shallow areas (<30 cm deep), often located along the river bank with moderately fast flowing water ($0.2–0.5\,\mathrm{m \cdot s^{-1}}$) (Roussel & Bardonnet 1999). As they grow older and larger, they prefer deeper, more slowly flowing parts of the stream (Heggenes 2002), but their habitat use in nature is flexibly dependent on habitat availability and time of the day (Elso & Greenberg 2001; Greenberg et al. 2001; Heggenes et al. 2002). They are more inclined to exploit pools in the river during night than during day time. Trout prefer stony bottoms where they can hide under cover, but are also found on fine grained substratum like gravel, sand, silt and mud (Heggenes et al. 1999).

In summer, feeding is the dominant behaviour during the day, and they are most active during twilight and night (Bunnell et al. 1998; Young 1999), but sometimes they feed continuously during day and night (Lobón-Cerviá, personal communication). During winter when the water temperature is low, the activity drops, and the species seek shelter in interstitial spaces in the substratum during daylight, but may hold position on or close to the bottom in slow flowing water during dark, and may feed down to temperatures of 0 °C (Bremset 2000). The species exploits more slow flowing water in winter than during summer, and the switch from summer to winter activity occurs when the water temperature drops below *c.* 8 °C (Heggenes & Dokk 2001). In southern populations, where in particular the water temperature in winter is higher, the seasonal difference in activity is smaller (Rincón & Lobón-Cerviá 1993).

In lakes, trout exploit mainly near-surface waters, and few individuals feed deeper than 1–2 secchi-disc depths (Haraldstad & Jonsson 1983; Jonsson & Gravem 1985; Schei & Jonsson 1989; Langeland et al. 1991).

Brown trout occurring in rivers or lakes with free access from the sea often form anadromous populations. These fish live in fjords and coastal waters during summer, and are seldom found far offshore in the Atlantic. Tagging experiments show, however, that individuals sometimes migrate as far as across the North Sea from France to Scandinavia (Anon 1994; Euzenat 1999) and from southern to northern Norway (Jonsson et al. 1995). Chiefly, they occur in shallow waters (Lyse et al. 1998; Knutsen et al. 2001), and most individuals are found within 100 km of the mouth of the home river. There are differences in migratory distance among populations, due both to heredity and environment (Jensen 1968; Svärdson & Fagerström 1982; Jonsson 1985; Berg & Berg 1987; Jonsson et al. 1995).

The migration to sea may be for the summer only, or the fish may stay at sea for 2 or more years before returning to their river of origin for spawning (Jensen 1968; Went 1962; Jonsson & Jonsson 2002). Both growth and mortality rates are high at sea (Berg & Jonsson 1990). Sea trout are eaten by mammals such as seals and otter, piscivorous fish like cod (*Gadus morhua*) and different kinds of sea birds (Lyse et al. 1998; Dieperink et al. 2001).

Anadromous brown trout can be found in very small brooks (Jonsson et al. 2001; Landergren 2001). There, they survive because they can abandon the brook and move to brackish water during periods of hostile conditions such as in periods of drought. In the Baltic Sea, the species may also spawn directly in brackish water where eggs and young appear able to survive at salinities up to 4–5‰ salt (Limburg et al. 2001). In this way, the species has expanded its habitat beyond that of freshwater resident populations. In small brooks, the significance of migration for the survival of populations is frequently demonstrated, as there is often no resident fish above the barrier limiting the upstream movement of sea trout.

Feeding

As young stream living parr, insect larvae, chironomids in particular, are the main food item, but they can also take surface arthropods like flying insects. With increasing fish size, they gradually take larger food items such as insect larvae of the groups Ephemeroptera, Plecoptera, Simulidae and Trichoptera (Jonsson & Gravem 1985; Haraldstad et al. 1987; Neveu 1999; Rincón &

Lobón-Cerviá 1999; Steingrimsson & Gislason 2002).

In lakes, zoobenthos in shallow waters are the major food, but the importance of pelagic food such as chironomid pupae and zooplankton as well as surface insects, increases with increasing size and age. Apparently, the particle size eaten by similar sized fish is smaller in lakes than in streams (Keeley & Grant 2001). In lake-living populations, brown trout sometimes feed almost exclusively on zooplankton (Klemetsen 1967; Schei & Jonsson 1989). In fresh waters, brown trout may start fish feeding from a body length of *c.* 15 cm (L'Abée-Lund et al. 1992). In piscivorous populations, the trout change gradually to fish feeding with increasing size, fast growers change feeding habit when smaller and younger than slow growers. In Lake Femund, for instance, mean age and length of the youngest fish feeders are 4 years and 17.5 cm, whereas the oldest invertebrate feeders are 9 years and 36 cm (Jonsson et al. 1999). According to Keeley & Grant (2001) salmonids are predominantly fish feeding from a length of 31 cm. The size of fish eaten increases gradually with the size of the predator (L'Abée-Lund et al. 1992; Næsje et al. 1998).

Brown trout is a visual feeder, and the water transparency appears to be an important determinant for its vertical distribution, i.e., they exploit deeper waters in clear than turbid lakes (Langeland et al. 1991). Often, young and small fish feed closer to the surface and shore line than older and larger individuals which also move about more (Ovidio 1999) and are more inclined to feed in the pelagic zone. Allopatric populations may have a wider habitat use than those living together with other fish species such as Arctic charr or whitefish (*Coregonus lavaretus*), which both are better adapted to feeding along deep bottoms and in the pelagic zone. Brown trout distribute themselves deeper during the spring and autumn circulation periods than in summer, although the summer water temperature in the surface layer may be quite high for the species at that time of the year. Under ice in winter, the young fish stay close to the bottom in shallow waters, whereas larger fish stay generally deeper. In spring, the fish appear to move frequently even well before the ice break-up (Haraldstad & Jonsson 1983; Jonsson & Gravem 1985; Schei & Jonsson 1989; Langeland et al. 1991).

As a species, brown trout is known as an opportunistic feeder, and the diet varies with habitat, season, fish size and age (Bridcut & Giller 1995). At the individual level, on the other hand, the fish may exhibit dietary specialisation, rather than opportunism, meaning that some individuals at least for periods of time, feed chiefly on one food item such as chironomid larvae whereas others chiefly take zooplankton (Grey 2001).

In northern populations, the feeding activity of brown trout is most intense as the temperature increases in spring and early summer. The period of maximum feeding in spring coincides with that of minimum fat content in the fish (Jonsson & Jonsson 1997, 1998; Berg et al. 2000). This seasonal difference is smaller in southern Europe (Rincón & Lobón-Cerviá 1993).

Anadromous brown trout may also feed quite heavily in early autumn in the sea and shortly after they arrive in fresh water, but the feeding activity drops rapidly during the autumn to the winter minimum when many individuals appear to live primarily on previously stored energy reserves (Jonsson & Gravem 1985). Females feed more in fresh water than males (Elliott 1997).

Anadromous brown trout feed on marine crustaceans, polychaetes, fish and surface insects (Pemberton 1976a; Fahy 1983; Grønvik & Klemetsen 1987; Lyse et al. 1998; Knutsen et al. 2001). Polychaetes are most important in spring whereas fish dominate by weight in the autumn. Most of the prey taken are typical for shallow and brackish waters, and as for freshwater living trout, the seasonal change is probably a reflection of the changes in prey availability (Knutsen et al. 2001). The trout may start fish feeding earlier at sea than in fresh water (Keeley & Grant 2001). The diet change from marine to freshwater and terrestrial foods as they move upstream from the sea (Elliott 1997)

The quantity and quality of the food eaten are very important for the growth rate of the fish (Wootton 1998), and the ability to grow continuously during the entire life span depends heavily on whether the fish have opportunities to change to larger sized food items as they grow larger (Gorman & Nielson 1982). If not, the growth rate will usually stagnate.

Development, growth, and production

Developmental rate is affected by temperature, and the time required for egg incubation and from hatching to the end of endogenous feeding period increases with increasing temperature in a hyperbolic way, so that the number of degree days needed increases with water temperature (Crisp 1988; Elliott & Hurley 1998a). Larval size at hatching decreases with increasing incubation temperature, but the relative amount of yolk is higher at high temperatures. The reason may be that the efficiency of yolk conversion to body tissue decreases with increasing temperature (Fleming & Gross

1990; Jonsson & Jonsson 1999). The main determinant of amount of yolk and larval size, however, is female size (Elliott & Hurley 1998b). Egg size increases positively with the size of the mother, which is at least partly due to environment and lipid contents (Lobón-Cerviá et al. 1997; Jonsson & Jonsson 1999).

Brown trout growth and size vary considerably among individuals and populations where 4-year-old fish may vary in size from about 20 g in slow growing fish in small brooks to between 0.5 and 1 kg in fast-growing piscivorous and anadromous populations (e.g., Jonsson & Sandlund 1979; Jonsson 1985; Swales 1986; L'Abée-Lund et al. 1989; Lobón-Cerviá et al. 1997; Champigneulle et al. 1999; Landergren 2001). Variation in food consumption and temperature are probably the main reasons for this vast variation (Alm 1959; Elliott et al. 1995), but also food particle size is important (Wootton 1998). With increasing size the fish need and can exploit gradually larger food items to grow. Such food items may previously be inaccessible whereas previously used resources may become unavailable (Rincón & Lobón-Cerviá 2002). Furthermore, Lobón-Cerviá (2000) reported that slow growing adults spawned fewer but larger eggs that result in larger offspring, which may also contribute to size variation among populations. One reason why anadromous brown trout grow faster than resident fish may be that they start fish feeding earlier (Keeley & Grant 2001). Therefore, the relationship between per capita resource available and body size is likely to depend on local conditions and may not be directly predictable only from scaling the needed amount of food with body size (Rincón & Lobón-Cerviá 2002).

High population density also has a negative effect on growth. This is found both in streams (Jenkins et al. 1999) and lakes (Jensen 1977). This is at least partly because high numbers of fish reduce food abundance, but there may also be a negative effect of intensified competition and aggressive encounters as fish abundance increases decreasing food or habitat availability. Furthermore, the individual variation in growth rate decreases with fish density in streams. This effect on growth is established in the first month after emergence of the alevins from the gravel, probably as a consequence of intraspecific competition (Elliott 1994).

The lower critical temperature for growth is 3–6 °C and the upper critical temperature is 25–26 °C. The optimal temperature for growth is between 13 and 18 °C, and it increases with increasing food consumption (Elliott & Hurley 2000; Ojanguren et al. 2001). The feeding rate parallels that of the growth rate, and the temperature at maximum feeding is only slightly higher than the optimal temperature for growth. The temperatures of commencement, termination and maximum growth decrease with decreasing feeding rate and stomach fullness. There is little evidence of a genetic variability in the thermal performance of growth rates in populations from geographically different areas, and populations appear not to be genetically adapted to the temperatures of their natural habitats (Elliott 1994) although the growth rate of the fish in some very cold glacier fed rivers is surprisingly high (Jensen et al. 2000). Furthermore, Lobón-Cerviá & Rincón (1998) studying brown trout in the Spanish River Chabatchos observed growth rates consistently higher than those predicted by the Elliott et al. (1995) growth model, and they suggested that this may be a local adaptation of the thermal regulation of growth. An alternative explanation may be that the growth model is underestimating the growth rate because the optimal temperature for growth is higher than estimated by Elliott et al. (1995). This will be the case if the fish feed more than they expected (Elliott & Hurley 2000).

The trout grow in size with age so that they maximise their number of viable offspring. Somatic investments increase competitive and defence abilities and the volume of the body cavity where the sexual products are stored. The fish store energy reserves which are used to develop primary and secondary sexual characters and perform reproductive activities, and metabolised during critical periods when feeding is low. Thus, the reproductive success of organisms depend on both somatic and gonadal allocations. Natural selection is expected to favour the energy partitioning and use which maximise fitness (Brown et al. 1993, 1996). Reproductive success should increase with the size of the fish, and fitness maximised as a trade-off between the rate of energy acquisition and survival (Kozlowski 1996). Therefore, life-history decisions, such as time of switching to a new feeding habitat or when to mature sexually, depend on the energetic state of the organism, and should occur at a time (or size) when the fitness will be less relative to competitors if the decision is delayed (Jonsson & Jonsson 1993). Thus, the relationship between expected chances of survival and growth before and after the decision appears important for when life-history decisions are being made (Werner & Gilliam 1984).

The production rate of a population is defined as the total elaboration of fish tissue during a known time interval (Ivlev 1966; Chapman 1978), and is the product of mean biomass and specific growth rate. These factors governing growth and mortality rates of populations are those influencing the production rate. In streams, the annual production of brown trout ranged from 0.14 to $54.70\,\mathrm{g \cdot m^{-2}\,year^{-1}}$ (Elliott 1994 and references therein). This range reflects variation found in 38 studies. The main reason for the observed differences is variation in growth rate. However, most data series are based on data collected over relatively short periods of time, usually less than 5 years, and may therefore provide little information on temporal variation in production rates in natural ecosystems. Such information is essential before meaningful comparisons can be made between streams. However, in Black Brows Beck the production of brown trout was studied in detail for more than 20 years (Elliott 1985, 1993, 1994). The annual production of migratory trout in this stream for the period between emergence from the gravel as alevins and migration to the sea ranged from 8.86 to $33.9\,\mathrm{g \cdot m^{-2}\,year^{-1}}$ between 1967 and 1990. The lowest values were in drought years 1983 and 1984. However, production in other drought years 1976 and 1989, was not unusually low. The production for individual cohorts varied from $7.59\,\mathrm{g \cdot m^{-2}\,year^{-1}}$ for 1983 to $33.88\,\mathrm{g \cdot m^{-2}\,year^{-1}}$ for the 1970 cohort. Examples of high values comparable to those for Black Brows Beck are from 12.2 to $36.0\,\mathrm{g \cdot m^{-2}\,year^{-1}}$ in a North American stream (Brynildson & Brynildson 1984) and between 14.1 and $33.1\,\mathrm{g \cdot m^{-2}\,year^{-1}}$ in different sections of a Danish stream (Mortensen 1978, 1985). Accurate assessment of production and consumption of fish in natural populations is essential for the understanding of environmental factors that regulate and limit fish populations and efficient fishery management.

Migration and habitat shifts

Habitat shifts in brown trout occur on different spatial scales at different stages of development. The first habitat shift takes place at the end of the embryonic period, when the larvae migrate through several centimetres or even metres of gravel to the open stream bed (Thorpe 1988). Shortly after hatching, newly emerged fry move away from the nest. According to some authors, they are mainly moving downstream with the water current, but many may also stay in the area or move upstream (Elliott 1966; Mortensen 1977). In Black Brows Beck, Elliott (1986) found that the moribund fry drifted downstream after emergence. Many of those were probably going to die, and their density increased with the number of eggs in the redd. Similar moribund fry were not found by Crisp (1993). This early movement of fry from the nest reduces the clumped distribution, and as a consequence, the habitat use is optimised.

During the first summer, the fry often stay in their natal stream (Elliott 1986), roaming around for food and shelter against predators and high water currents (Heggenes & Traaen 1988; Héland et al. 1995). The habitat used during the subsequent developmental stages vary among populations. Three different versions of the life cycle are illustrated below (Fig. 4). In the first, the juveniles migrate from the natal river to a larger river for feeding. This was for instance observed in the Søre Osa river system, eastern Norway (Jonsson & Sandlund 1979). There, the trout use the small tributary, Østre Æra, as spawning and nursery grounds and migrate to the larger River Søre Osa for feeding. Lake feeding trout spawning in inlets and outlets perform an alternative movement when the young trout migrate from their natal stream into the lake as they grow older (Arawomo 1981; Haraldstad & Jonsson 1983; Schei & Jonsson 1989; Forseth et al. 1999; Jonsson et al. 1999). For instance, Näslund (1993) describes such a life history from Lake Storvindelen, northern Sweden. This lake supports a population of freshwater migratory brown trout (Näslund 1993). Spawning and early rearing take place in the main river, Vindelälven, whereas most growth occurs in the lake. The third life-history type is found in anadromous trout (sea trout), where the juveniles migrate to the estuary or coastal areas for feeding and return to freshwater for spawning or wintering (Jensen 1968; Jonsson 1985; Berg & Berg 1987; Jonsson & Jonsson 2002). A fourth type is isolated river populations where the fish cannot migrate to richer feeding habitats (Jonsson & Sandlund 1979; Rincón & Lobón-Cerviá 2002).

Age and size at migration. Brown trout disperse extensively during their first years of life. Bagliniére et al. (1994) reported migratory 0+ trout from the nursery streams to the larger River Scorff in France, whereas Thorpe (1974) observed the displacement of 0+ and 1+ trout from the tributaries into Loch Leven, Scotland. Brown trout living in afferent streams of Lake Femund, eastern Norway, were older (1–8 years) when they moved from the natal stream and into this mountain lake, with most of them descending as 2 (40%)- and 3 (27%)-year-olds (Jonsson et al. 1999). Furthermore, the trout in Windermere, the largest natural lake in UK, emigrated from the streams into the lake at 1 (16%), 2 (70%) and 3 years of age (14%; Craig 1982).

In anadromous brown trout, the young may smolt and move to sea for feeding when the fish have reached a certain length and age (L'Abée-Lund et al. 1989; Økland et al. 1993). However, not all individuals of a particular year-class smolt at the same age. From the British Isles, six different age-groups of smolts have been recorded (Fahy 1978) and from Norway eight different age-groups (L'Abée-Lund et al. 1989). Field observations show that mean smolt age varies with latitude, probably as a consequence of differing water temperatures. Fahy (1978) found that mean smolt age was higher in Scotland (range = 2.4–3.4 years) than in Irish and Welsh rivers (range = 2.1–2.8 years). Furthermore, Jonsson & L'Abée-Lund (1993) reviewed the clinal variation in mean smolt age from 102 European rivers between 54°N and 70°N, and found that it ranged from 2.1 years at 54°N to 5.6 years at 70°N. On the other hand, they found no correlation between smolt size and latitude. Rivers with small and large smolts were found both in southern and northern parts of the distribution area.

Parr living in streams draining to brackish water may migrate to sea very young and small (Titus & Mosegaard 1989, 1992; Järvi et al. 1996). In the small stream Arån on the Swedish island Gotland, the parr migrate to the Baltic Sea as 3 months old and *c*. 30 mm in length (Landergren 2001). The water in the Baltic Sea is brackish (salinity 6–7‰) and smolting appears not essential for survival (Landergren 2001; Limburg et al. 2001). Landergren (2001) found no difference in survival and growth between parr raised in fresh and brackish waters. He concluded that the brackish water around Gotland island is not a physiological obstacle for the survival of early out-migrating parr, and imposes no cost in terms of growth reduction.

There is a segregation in body size and age among migrants. The earliest trout migrating from the nursery streams to Loch Leven were of a smaller size range (6–9 cm) than the later migrants consisting of trout up to 21 cm in length (Arawomo 1981). However, in sea trout, larger and older individuals descended to sea earlier in the year than smaller and younger ones (Fig. 5). This is observed in smolts (Rasmussen 1986; Bohlin et al. 1993a, 1996), sub-adults and adults (Jonsson & Jonsson 2002). Bohlin et al. (1996) tagged wild 1- and 2-summer-old sea trout parr with PIT-tags in late autumn and recaptured them in a smolt trap during the following spring. They found that one-summer-old smolts migrated smaller and later than older ones. They concluded that the difference in timing between the age-classes was an effect of body size rather than age. Furthermore, in the River Imsa, trout larger than 30 cm (two or more sea sojourn) descended earlier in spring than smaller fish (Jonsson & Jonsson 2002).

There are several possible reasons for this size and age segregation in anadromous trout. The seaward migration includes salinity regulatory problems and increased risk of predator encounters. The general ability to survive in sea water increases with body size of the fish (Wagner et al. 1969; Finstad & Ugedal 1998). Experiments with hatchery-reared smolts show that large individuals (mean = 199 mm, range = 172–228 mm) established seawater tolerance about 2 weeks earlier than smolts from a smaller size group (mean = 180 mm, range = 143–210 mm). Also, the osmoregulatory capacity of fish from the large size group was better when compared to that of smaller fish. The better hypo-osmoregulatory capacity is partly due to the decline in exposed surface area relative to mass as animals grow in size (Handeland et al. 1998; Claireaux & Audet 2000). Moreover, larger individuals may be less vulnerable to predation than smaller individuals (Dill 1983). Therefore, the expected sea survival increases with the size of the fish.

Why migrate? One reason for the habitat shift in younger parr may be that their ability to utilise resources and to avoid predation change during the ontogeny, and by that the profitability of exploiting different niches will also change. Another reason is that the ability to avoid adverse environmental conditions such as icing-up of streams or low water flow, changes with age (Nikolskii 1963). In the small stream Årungselva in southeastern Norway, the growth of the young trout is fast and smolting occurred at a short length (Borgstrøm & Heggenes 1988). One-year-old parr larger than 8 cm in the autumn smolted during the subsequent spring. Jonsson et al. (2001) found even smaller smolts in small streams (mean annual water discharge above $0.04\,\mathrm{m}^3 \cdot \mathrm{s}^{-1}$) in southern Norway. There, the trout moved to sea from a length of approximately 6 cm onwards. Such a small smolt size may be an adaptation to drought and low water levels during summer. In small trout streams the water levels may be so low that the feeding opportunities for large parr are poor. In these streams it might be advantageous to smolt young and leave the stream already at a small body size.

Jonsson et al. (2001) found that the smolts were on average larger and older in large than small brooks, and that the individual variation in size and age decreased with increasing stream size. A more heterogeneous smolt size in the smallest streams may reflect a more variable success for large smolts in small than large streams. Larger streams have probably enough water to reduce the importance of flow variation for the size when the trout should leave for feeding in the sea, and factors influencing the sea survival may become more important for the size at smolting (L'Abée-Lund et al. 1989).

The time of smolting in trout has been related to, e.g., body size, growth rate, developmental rate and physiological state of the fish. Fahy (1985) claimed that the parr has to attain a specific body length (10 cm) in the autumn, to smolt during the subsequent spring. This was tested by Økland et al. (1993). They found no such threshold size regulating size or age at smolting, but that the smolt age was negatively correlated with parr growth, and positively correlated with smolt size.

Forseth et al. (1999) studied the time of migration in relation to growth rate and metabolic rate in juvenile brown trout migrating from the Litjåa stream into Lake Femund. The energy budgets of the migratory fish were compared with individuals that remained one or more years longer in the stream. They found that fast-growing individuals migrated to the lake earlier and at a smaller body size than slower-growing individuals. The 2+ migrants were larger than those that remained in the stream, and 3+ migrants were larger than 2+ migrants. Furthermore, the food consumption and the energy budgets of 2+ migrants were more than four times higher than those of the resident 2+ fish. Total energy allocated to growth was also higher among migrants than among resident fish. The proportional energy allocation to growth among the 2+ migrants, however, was much lower than that of those remaining longer in the stream. The reduction in the proportion of energy available for growth from age 1+ to 2+ was larger among migrants (88%) than among resident fish (68%). Therefore, they concluded that fast-growing individuals shift their niche earlier and at a smaller body size than slower-growing individuals because they maintain higher metabolic rates and were energetically constrained at a younger age by limited food resources in the river, than slow growers.

Environmental factors such as water temperature, are important for the timing of the smolting process. Smolt age has been related to parr growth rate, and faster-growing parr smolt usually at an earlier age than slower-growing siblings. Elliott (1975) showed that the weight gain by trout fed on maximum rations was related to water temperature and the length of the growing season. From field observations, Egglishaw & Shackley (1977) found that trout growth was related to the number of degree days over 0 °C and the length of the growth season. Thus, the variation in mean smolt age with latitude appears mainly to be a temperature effect (L'Abée-Lund et al. 1989). Mean water temperature is generally lower at more northerly latitudes in Europe, hence the juvenile trout grow more slowly and have higher mean smolt age than in streams farther south.

Down- and upstream migration. The time of seaward migration varies among rivers and the developmental stage of the fish. The downstream migration takes place during two periods, a feeding migrating in spring and an over-wintering migration in autumn and winter (Fig. 2). In spring, smolts and larger fish spending the winter in fresh waters migrate to the estuary for feeding. In general, the smolt migration takes place from March towards June, although downstream movement of pre-smolts can occur earlier, particularly at low latitudes were water temperatures during winter are relatively high (Le Cren 1985). At high latitudes, such as at 69°N in northern Norway, the migration comes later (Berg & Berg 1987; Berg & Jonsson 1989). Bohlin et al. (1993b) found that 90% of the downstream migrating smolts in Norumsån, southern Sweden occurred during 29 days, with median times ranging from 26 April to 17 May. In Stjørdalselva, mid-Norway, the main smolt run takes place during 7–10 days in the middle to second half of May (Hembre et al. 2001). Rasmussen (1986) found that the smolt migration extended from early March into June in a Danish sea-trout stream. Furthermore, spent trout (kelts), which have over-wintered in fresh water, migrate to sea for feeding in spring. In the River Vardnes, northern Norway, veteran migrants descended downstream earlier in spring than the smolts (Berg & Jonsson 1989), whereas in the River Istra, western Norway, the kelts arrived in the sea at the same time as the smolts in May (Jensen 1968).

Trout descend to sea for wintering during autumn and winter. In sea lochs on the west coast of Scotland, Pemberton (1976b) found that sea trout could move to sea in August and stay there to late spring. Furthermore, small numbers of kelts were caught at sea from December onwards. In the River Imsa, immature and mature migrants also move to sea from September throughout January (Fig. 5; Jonsson & Jonsson 2002).

Anadromous trout feed in fjords and coastal waters during summer. The duration of the sea sojourn increases with increasing water temperature during summer. Sea trout from mid-Norway stay at sea for about 90 days before ascending to fresh water (Jensen 1968), whereas trout from northern Norway stay shorter, between 45 and

70 days (Berg & Jonsson 1990). Females stay at sea for a slightly longer time period than the males, 69 versus 66 days, respectively (Berg & Berg 1989b).

After feeding in fjords and coastal waters, immature and mature trout return to fresh water for spawning and wintering in summer and autumn, most return to their river of origin (Jensen 1968; Jonsson 1985). The fish move quickly against the current (Armstrong & Herbert 1997), and the oldest trout appear to move upstream earlier than the younger ones (Jonsson & Gravem 1985; Le Cren 1985; Jonsson & Jonsson 2002). The timing of the run varies considerably, from a peak in May in the southwest UK, to June and July in Cumbrian rivers and in the Burrishoole system in Ireland, although it is sometimes as late as October on the River Coquet in northern UK.

In the Norwegian river, Gudbrandsdalslågen, eastern Norway, lake feeding brown trout ascended the river from late June to mid-October (Jensen & Aass 1995), and in the River Istra, mid-Norway, most anadromous trout ascended during August and September, although the migration actually began in July and extended until October or November (Jensen 1968). In the River Imsa, southern Norway, the trout ascended in all months from April to December, but the main upstream migration (72%) occurred between August and October (Fig. 5; Jonsson & Jonsson 2002).

The time of freshwater ascent appears to depend on river size. Sea trout spawning in large rivers, ascended fresh water some 6 months before actually arriving at the spawning areas (Campbell 1977), whereas trout spawning in small streams often ascend in a short period of time just prior to spawning.

The movement of sea trout in rivers have been studied by use of acoustics or radio-tags. Sea trout migrating up the Afon Glasly in Wales, moved between 4 and 8 km over 1–10 days without any pause in the lower 4 km of the semi-tidal zone (Le Cren 1985). After this, the fish held up for long periods of between 3 and 79 days near the confluences of tributaries. Furthermore, in the River Fowl, it was found that sea trout move at night at low to medium discharges, covering about 3 km each night at speeds up to $2\,\mathrm{km}\cdot\mathrm{h}^{-1}$ (Le Cren 1985). Armstrong & Herbert (1997) found that the homing of trout was directed and rapid and up to 1.22 body lengths s^{-1} against the flow. Ovidio et al. (1998) studied the mobility of trout in the River Ourthe, Belgian Ardennes. In the first part of the migratory period (August until October) the daily journeys never exceeded 300 m and corresponded to displacements by high floods or to routine home range movements. When the spawning time approached, the spawners migrated into tributaries and sub-tributaries and the distance travelled increased. The migratory speed was fast during the early days, when trout travelled up to more than 5 km per night, then progressively decreased as they approached putative spawning redds.

Environmental factors. Changes in environmental factors such as water temperature and water flow appear to induce the up- and downstream migration in trout (Jonsson 1991). Migration of fry into Loch Leven was associated with increased water discharge caused by the onset of floods, whereas increased water temperature accelerated the pace of migration into the loch in spring (Arawomo 1981). The smolt migration, however, may be initiated by a combination of environmental factors. In the Norumsån (58°N), a small stream in southwestern Sweden, 47% of the variation in daily smolt descent was explained by the number of degree-days, change in water level, temperature change during the preceding week, and mean annual fish length. Hembre et al. (2001) studied the effects of water discharge and temperature on timing of the smolt run in River Stjørdalselva (63°N), mid-Norway. They found support for the hypothesis that high water discharge and temperature triggered the run. Few smolts descended at low water discharges ($<50\,\mathrm{m}^3\cdot\mathrm{s}^{-1}$) and at water temperatures below 4 °C. However, maximum number of smolts were caught when the discharge was moderate (70–$150\,\mathrm{m}^3\cdot\mathrm{s}^{-1}$) and the water temperature high (6–8 °C). The relative importance of these factors on smolt migration varied during the 3 years study. The smolts seem to react to both discharge and temperature in combination.

The downstream migration of brown trout in the River Imsa in spring was influenced by water temperature, but not flow (Fig. 6; Jonsson & Jonsson 2002). About half of the trout smaller than 30 cm moved downstream at water temperatures between 7.5 and 12.5 °C, whereas most large trout (larger than 30 cm; 87%) moved at temperatures below 7.5 °C. During autumn (September–January), both water temperature and flow influenced the trout descent.

The spawning run of trout is influenced by increased water flow, but sometimes water temperature or a combination between flow and temperature appears important. For instance, in Great Lake, Tasmania, the spawning migration occurred predominantly at low flow when the temperature was 6–10 °C, with peak migration at 7.6 °C (males) and 7.8 °C (females) (Davies & Sloane 1987). Ovidio et al. (1998) radio-tagged brown trout in the Belgian Ardennes and found that a combination of high variations of water temperature and water level between consecutive days within a thermal range of 10–12 °C triggered the upstream migration. In the Kirk Burn, River Tweed, however, sudden increases in water level appeared to stimulate the upstream migration of both brown trout and sea trout (Campbell 1977). In the River Imsa, the majority of the spawners ascended at low to medium high flows, maximum ascent was between 7.5 and 10 $m^3 \cdot s^{-1}$, and no fish ascended at the highest flow rates (>20 $m^3 \cdot s^{-1}$) (Jonsson & Jonsson 2002). There was a significant correlation between water temperature and trout ascent. Furthermore, to some degree, increased flow appeared to stimulate the upstream migration, but too much water decreased the upstream migratory activity, probably because it is energy demanding to swim against strong currents (Fig. 6).

Benefits and costs of migration. The benefits of migration are increased growth opportunities and reproductive output (Jonsson 1985; Jonsson & Jonsson 1997, 1998), whereas the costs are increased mortality and increased energy use. Bohlin et al. (2001) provided a direct test on the meaning of this cost for the distribution of anadromous fish in water courses. They studied anadromous and nonanadromous populations on the southern coast of Sweden that varied in elevation (as an index of migratory difficulty). At low elevations, juvenile density (as a measure for population productivity) was higher for migratory than for nonmigratory populations, showing that migration was beneficial because it increased the production of juveniles. Juvenile density then decreased with increasing elevation in anadromous but not nonanadromous brown trout. At an elevation of about 150 m, juvenile density was similar for the two, suggesting that the cost of migration had reached the point where it offset the benefits. As expected, the presence of anadromous fish also disappeared at higher elevations. This evidence suggests that costs of migration in addition to impassable barriers like water falls limit the distribution of anadromous fish inland.

Females surplus among migrants. Females are generally more migratory than males (Campbell 1977; Jonsson 1985; Dellefors & Faremo 1988; Elliott 1994). Male is the sex that typically shows reduced migratory tendency in populations with partial migration, i.e., the local deme is environmentally split between migratory and resident individuals (Jonsson & Jonsson 1993). For brown trout in 17 coastal streams of Norway, on average 48.9% of the males but only 3.7% of females spa- wned as residents, the rest spawned as anadromous trout (Jonsson et al. 2001). The incidence of females will however, vary with the feeding conditions in fresh water relative to the sea, and in south Swedish populations, Pettersson 2002) found *c.* 10% stream resident and 90% anadromous females, and according to Lobón Cerviá (personal communi- cation), all migratory brown trout analysed from the Cantabrian Sea are females. Thus, there may be a latitudinal effect as growth conditions in fresh relative to salt waters increase towards the south on the northern hemisphere (Gross et al. 1988).

This sexual dimorphism indicates that the benefits of migration are larger in female than male sea trout, and a similar difference is common in freshwater living trout as well (Jonsson & Sandlund 1979; Crisp et al. 1984; Baglinière et al. 1989). Among many anadromous trout populations, the female/male ratio appears to be close to 1.5 (Jonsson 1985). One proximate explanation is that this reflects an inherited differences in life-history tactics between the two sexes (Jonsson 1989). The ultimate explanation is that female more than male fitness depends on growth rate and size of the fish.

The reproductive success of females should increase linearly with body mass (Wootton 1998). Because anadromy increases the egg production (fecundity and egg size) in females (Jonsson 1985; Jonsson & Jonsson 1999), its benefits are obvious. Furthermore, large females are better able to acquire high-quality territories for spawning and egg development and have higher success in nest defence than smaller females (van den Berghe & Gross 1989). The benefits of a large female size are to a certain extent absolute (bigger females produce more eggs, regardless of the number of other females).

For males, the benefits of anadromy are less obvious. A male's reproductive success is determined by the number of eggs he fertilises in competition with other males. This may not be a linear function of body size, as small males may adopt an alternative reproductive tactic where they do not compete directly for access to females but rather hide near the female and dart in to fertilise eggs when the female begins oviposition (Gross 1985; Hutchings & Myers 1985, 1988; Jonsson 1985; Fleming 1996). Thus males, subordinate according to size and fighting ability, may fertilise some of the eggs of females primarily spawning with larger, dominant males

(Gross 1985; Hutchings & Myers 1985, 1988). Furthermore, resident males may become principal spawners when migratory males are absent (Jonsson 1985). These males can have substantial reproductive success, they do not pay the costs of migration, and they are often younger at maturity. Thus, the male reproductive success is relative to size and condition of other males, and the benefits of migration appears less for males than for females in accordance with their lower tendency to migrate.

Sexual maturation

Smolting and maturation: competing processes? In partly migratory species, such as brown trout, the populations are split into migratory and freshwater resident individuals (Jonsson & Jonsson 1993). The migrants attain maturity after a period of growth at sea, whereas the residents mature in fresh water, often at a small body size early in the life, and they seldom smolt later.

Migration and sexual maturation thus appear to be competing processes (Thorpe 1986, 1987). The parr either mature or smolt before attaining maturity. In this way, sexual maturation appears usually to inhibit smolting later (Jonsson 1985; Dellefors & Faremo 1988). This is in contrast to Atlantic salmon, where mature parr often smolt and migrate to sea (Jonsson et al. 1998a). In a few cases, however, mature trout smolt. If so, they do not seem to spawn again the same year but wait at least 1 year before spawning again. Other major niche shifts appear to have a similar delaying effect on maturation, as seen when brown trout switch from benthivorous to piscivorous feeding (Jonsson 1977; Jonsson et al. 1999).

Age and size at maturity. Freshwater resident populations of brown trout mature sexually at an age between 1 and 10 years. The fish mature older in cold localities such as in mountain lakes and rivers far north (Jonsson et al. 1991c). In the southern part of the distribution area of anadromous trout, many fish reproduce after only 1 summer at sea. In the north, most first-time spawners spend 2–3 summers at sea before attaining maturity (Jonsson & L'Abée-Lund 1993). A part of the spawners survive and spawn again, but many die as a consequence of the reproduction. In anadromous brown trout, it has been found that about 60% spawn repeatedly in southern rivers whereas the corresponding figure is about 30% in northern rivers.

Age and size of maturity vary among the sexes. Males usually mature younger and at a more variable size than females (Jonsson 1989). Often, males mature early in life as parr in the nursery stream, or they mature at a larger body size after a period of growth in a lake or at sea. Mature parr males constitute a large part of the populations of anadromous trout. In Norumsån and Arödsån, in southwestern Sweden, the proportion of mature parr males varied between 17.9 and 57% (Dellefors & Faremo 1988), and in Norwegian rivers the proportion varied between 0.6 and 62% (L'Abée-Lund et al. 1990). However, in females the maturity may be associated with the attainment of a certain length in resident and sea trout (Jonsson 1977, 1985). Females living in systems freely accessible from the sea, often mature sexually after one or more growth seasons at sea (Jonsson et al. 2001). Resident females in these systems are sparse. In Kirk Burn, the male:female ratios of spawners were 1 : 1.4 in sea trout and 6 : 1 in residents (Campbell 1977). In 17 small sea trout streams in Norway, only 3.7% of the spawning females were residents (Jonsson et al. 2001). Resident females appear common only when the growth and feeding conditions in fresh water are good, as in systems with nutrient-rich lakes (Jonsson 1985). Similarly, L'Abée-Lund et al. (1990) found that male brown trout tended to mature more as residents in nutrient-rich than in nutrient-poor systems.

Do age and size at maturity differ between the sexes? Males may attain maturity from less than 10 cm in length and 1 years of age (Jonsson & Sandlund 1979; Dellefors & Faremo 1988; L'Abée-Lund et al. 1990). Anadromous males can mature as 'finnock' or 'whitling', i.e., the same years as their first migration into the sea (Elliott 1994; Le Cren 1985; Maisse et al. 1991). In the River Eriff, Ireland, 13% of the male finnock was mature at the end of summer (Le Cren 1985). In the coastal stream Tverrelva in northern Norway, males matured at ages between 2 and 8 years (Hesthagen 1989) and in Vangsvatnet lake, anadromous males matured from 2 years and residents from 1 year onwards (Jonsson 1989). Mean body lengths at maturation in males from 17 streams in south Norway ranged between 19 and 40 cm in anadromous and between 16 and 24 cm in residents (Jonsson et al. 2001). Females can also mature as finnock, and in the River Eriff, 8% matured during their first year at sea (Le Cren 1985).

In south Norway, mean lengths (pooled sexes) at maturity in 17 small stream (annual mean water discharge $<1\ \mathrm{m}^3 \cdot \mathrm{s}^{-1}$) were between 33 and 37 cm (Jonsson et al. 2001), whereas ages at maturity varied between 2 and 4 years (Hesthagen 1989; Jonsson 1989). In larger rivers, the size at maturity is often larger (L'Abée-Lund et al. 1989).

Furthermore, in the two Norwegian rivers, Gaula and Namsen, mean length and sea age at sexual maturity increased with increasing altitude of the spawning area and with migration distance in fresh water (L'Abée-Lund 1991). Among rivers, mean sea-age at sexual maturity increases with latitude (between 54°N and 70°N; Jonsson & L'Abée-Lund 1993). In the southern-most populations, sea-age at 50% maturity was 0.5 years, half of the fish attained maturity the same year as they smolted and moved to sea. In the north (70°N), sea age at 50% maturity approached 3 years.

The difference in age at maturity between sexes appears to be genetic, and independent of growth rate (Jonsson 1989). Under the same artificial rearing conditions, immature females and male brown trout grew at the same rate, but the females matured on average older than males. The differences in size at maturity between males and females, appear not to be due to differences in growth rate between the sexes. In nature but not in the laboratory, however, Jonsson (1989) found that the youngest mature females were larger than immature and mature males of the same age. This seems to be because males compared to females show a tendency to exploit less risky habitats where the growth rate is also lower. This differences indicates that there is a higher selective premium on higher growth rate for females than males.

Fecundity and egg mass. The reproductive potential of females is determined by the number and quality of their eggs. Large eggs give large offspring which grow and compete well for food resources (Elliott 1994, 1995; Einum & Fleming 1999), and experiments show that there is trade-off between egg size and egg number (Jonsson & Jonsson 1999). There are several factors which influence egg size, among which the size of the mother is the most important. Mean egg mass in anadromous females weighing 300 and 500 g are 0.047 and 0.058 g, respectively. Offspring of freshwater trout reared under similar conditions were larger; 0.069 and 0.074 g in 300 and 500 g large trout, respectively. Furthermore, mean fecundity in anadromous trout with body masses of between 100 and 500 g are *c.* 300 and 1500 eggs. The corresponding fecundity in residents are 270 and 1100 (Jonsson & Jonsson 1999).

Why do fecundity and egg size increase with the size of the mother? Fecundity increases with body size because the amount of energy available for egg production and the body cavity accommodating the eggs increase with fish size (Jonsson & Jonsson 1997). But why egg mass increases with fish size is not clear, although environment appears important (Lobón-Cerviá et al. 1997). Rearing experiments indicated that heavy feeding as sub-adults gave large eggs even in small females, evening out the variation due to size (Jonsson & Jonsson 1997). Furthermore, a high water temperature during the yolk absorption may select for large egg sizes (Jonsson & Jonsson 1999). This means that it is favourable for individuals that spawn late in the season to have relatively larger eggs than those spawning early, because they hatch later and the alevins will develop at a relatively high water temperature.

There is a trade-off between egg mass and fecundity as females have limited energy resources available for egg production and limited body cavity for accommodation of the eggs. A female's decision to produce a few large or many small eggs may depend on, e.g., environmental variation, energetic resource of the female, morphs and number of spawning (Bagenal 1969; Duarte & Alcaraz 1989; Berg et al. 1998; Jonsson & Jonsson 1999; Olofsson & Mosegaard 1999). In an experiment where trout was offered surplus feeding, most of the increase in egg mass with fish size disappeared (Jonsson & Jonsson 1999). This means that a large part of the variation in egg mass within and among populations is due to environment. Studies of body composition of brown trout in nature have shown that the fat concentration of the fish increases with size (Jonsson & Jonsson 1997, 1998). In hatcheries, a common strategy is to feed all fish to satiation. Thus, small trout may also have had somatic fat reserves, which they allocated in producing relatively large eggs. This finding may appear contradictory to Bagenal (1969). He found that brown trout spawned more, but smaller eggs if they were fed 9 months prior to spawning, relative to unfed conspecifics.

Water temperature may influence egg production. Jonsson & Jonsson (1999) found smaller, but more numerous eggs in trout caught at 63° than 58°N. This trend was found in resident as well as sea run trout spawning in similar brooks in the two areas. Moreover, there appeared not to be large differences in feeding, as the growth rate of the fish was similar between the two areas. In Pacific salmon (sockeye, chinook, chum and coho) also egg mass decrease and fecundity increase with increasing latitude (Fleming & Gross 1990; Beacham & Murray 1993). Fleming & Gross (1990) postulated that selection favours increasing egg mass with increasing water temperature and therefore, size would decrease with latitude because higher water temperature reduces the efficiency of yolk conversion to body tissue. Thus, egg mass should vary according to the prevailing water temperature during the yolk absorption period of the alevins. In contrast to these findings, L'Abée-Lund & Hindar (1990) found no latitudinal gradient in egg mass in anadromous trout between 58° and 65°N in Norway, and we see no obvious reason for this differing result.

In partially migratory populations, residents spawn relatively large but few eggs compared with similarly sized anadromous trout (Jonsson & Jonsson 1999; Olofsson & Mosegaard 1999). This appears contrary to the hypothesis that egg mass increases with the fat content of the fish, because the fat content in residents is lower than that of anadromous trout (Jonsson & Jonsson 1997). Thus, large eggs of resident trout may be a specific adaptation of this morph. Selection for this may be competitive ability of the young towards anadromous offspring. After swim-up, the offspring of the two morphs compete for the same food resources. Because of the large body size of their mother, most anadromous offspring have large yolk sacs. To compensate, the smaller resident females may produce large eggs for their own body size. If this is correct, resident trout co-occurring with anadromous trout, should have larger eggs than corresponding residents competing only among themselves. This is observed in sympatric trout in Jördalsån stream in southwestern Sweden (Olofsson & Mosegaard 1999). In this stream, resident trout living in sympatry with anadromous trout had larger eggs (65.9–108.5 mg) than both sympatric migratory trout (76.8–84.2 mg) and allopatric resident trout (23.7–80.1 mg) or migratory populations (44.5–121.9 mg). Furthermore, the sympatric resident population had a low absolute fecundity compared to migratory trout. Larger eggs were also found in brown trout population living in sympatry with alpine bullhead *Cottus poecilopus* compared to allopatric populations living above a waterfall (Olsen & Vøllestad 2001). Mean dry weights of the eggs were 26.84 and 20.80 mg, respectively.

In brown trout, egg size is strongly correlated with size of the offspring (Elliott 1984; Einum & Fleming 1999; Olsen & Vøllestad 2001). Larger offspring have improved competitive ability and higher survival relative to offspring from smaller eggs (Elliott 1984; Hutchings 1991; Wootton 1998). Repeat spawners produced larger and fewer eggs than similar sized first-time spawning trout (Jonsson & Jonsson 1999). This is not only caused by an increase in fish size or energy content, but a general tendency for repeat spawners to invest relatively more energy into each offspring than first-time spawners (Jonsson 1985).

Longevity

Although brown trout as old as *c.* 20 years of age have been caught (Sømme 1941), most brown trout die much younger, and in anadromous populations few fish live longer than 10 years. For anadromous brown trout, it has been found that the longevity increases with latitude and is approximately 8 years in northern Norway and 3–5 years in Britain. This decrease in longevity towards the south is closely correlated with increasing water temperature (Jonsson et al. 1991a).

In addition to low water temperature, a slow but steady growth and large body size are factors correlated with late maturity and a long life span (Jonsson et al. 1991a). This appears to hold for both resident and anadromous trout. As for growth rate, there is also correlation between age at maturity and longevity. Often, the fish attain maturity as the growth rate levels off (Jonsson & Jonsson 1993; He & Steward 2002), and fish which mature early tend to die early as a cost of reproduction (Wootton 1998). Furthermore, fast growers may die early because they may be more susceptible to infectious diseases than slow growers (Snieszko et al. 1959), and they may be more vulnerable to predators, fishing included (Ricker 1975), because they are more active, more exposed to enemies and exploit more risky habitats (Jonsson & Gravem 1985; Jonsson 1989).

Life-history characteristics: concluding remarks

Brown trout is found in both fresh and salt waters over most of its original area. It mainly uses running water as spawning habitat, but lake spawning populations occur. Possibly, the species also spawn successfully in brackish water. It feeds in streams, lakes and at sea. There are few other European fish species exploiting this huge variation in habitats. This is made possible both by a wide environmental tolerance and the migratory behaviour so that adverse conditions during sensitive stages can often be avoided.

Brown trout feed usually close to surface and shore. However, quite large individuals appear to move far offshore. The species shows ontogenetic habitat shifts, which partly is related to size, partly to developmental rate. Fast growers switch habitat and diet younger and smaller than slow growers. The time and size of the habitat switch appear largely influenced by the rate of energy acquisition in the habitat. When the amount of surplus energy available for growth becomes small, the fish will leave for a richer feeding habitat.

Brown trout is an opportunistic carnivore, although individuals appear to specialise at least temporarily on particular food items. The food eaten depends on availability. Insect larvae appears especially important for the young in streams. Littoral zoobenthos are the main food for lake living populations, whereas fish are most important for large trout. As for the habitat switch, the time of diet changes appear influenced by developmental rate and size of the fish.

The species exhibits sexual dimorphism not only in secondary sexual characters but also in size and habitat use (Table 1). Males less than females are inclined to become migratory. Many remain in running waters near the spawning area. Females are more lake living, more inclined to exploit pelagic waters as well as becoming anadromous and move to sea. Therefore, they may feed more on pelagic food such as zooplankton and be more heavily infested by cestode cysts having copepods as intermediate host. Females often become larger and exhibit a more uniform phenotype than males. The size differences obtained are not only due to differential habitat use, but also different age at maturity which is lower and more variable in males than females. The ultimate reason is probably that female fitness is increasing with female size except if there are environmental constraints such as lack of water. Males, on the other hand, may be reproductively fit both as small and large fish.

The life history varies with habitats exploited. For instance, the tendency to migrate varies among populations from resident ones in isolated streams and lakes to open systems where the fish may migrate among habitats serving different purposes (feeding, spawning, wintering). Populations are often partially migratory, i.e., one part of the population leave and feed elsewhere, while another part stay as residents (Table 2). In large, complex systems, the species is polymorphic with different size morphs in the various parts of the habitat. The largest, most fast growing fish are found in the richest habitat. Fish from different feeding habitats meet and spawn together on the same spawning grounds in the autumn.

Table 1. Ecological differences between male (M) and female (F) brown trout.

Trait	Difference
River use	M > F
Lake use	M < F
Relative lake use	
Littoral zone	M > F
Pelagic zone	M < F
Anadromy	M < F
Mean adult body size	M < F
Sexual mature parr	M > F
Longevity	M < F
Phenotypic variability	M > F

Table 2. Differences between anadromous (A) and resident (R) brown trout in partially migratory populations.

Trait	Difference
Growth rate	A > R
Adult body size	A > R
Relative lipid content	A > R
Age at maturity	A > R
Male/female ratio	A < R
Egg number	A > R
Total egg size	A > R
Egg size relative to body size	A < R

Complex systems may thus have populations consisting of river resident, lake resident and sea run migratory individuals, all occurring together on the same spawning grounds. The body size of those exploiting small brooks is smaller and the life cycle shorter than of those living in large rivers in the same area. But also anadromous fish exhibits special adaptations when exploiting marginal habitats such as very small streams. There, the spawners are young and small and the offspring move early to sea at a very small body size. Furthermore, egg size varies differently with fish size in resident and migratory fish from the same populations which may be also adaptations to differing incubation temperatures and competitive climate for the young. The variation observed appears partly to be the result of phenotypic plasticity, partly an effect of genetic selection. To reveal the relative importance of these two mechanisms, however, will be one of the objective of future brown trout research.

Arctic charr, *Salvelinus alpinus* (L.)

Introduction

The review by Johnson (1980) covers most aspects of Arctic charr biology and still is an excellent reference text to the species. In the present contribution we will first give an overview of phenotype and life-history variation and then focus on some fields of research that has attracted much interest since Johnson's review. Cannibalism in lacustrine systems and anadromy are two such fields. Polymorphism and speciation in charr were recently reviewed by Jonsson & Jonsson (2001). This is a field of rapid development. Here, we want to bring the discussion in Jonsson & Jonsson (2001) forward with a special focus on recent publications but also with a retrospective view because there has been much interest and debate in this field for several decades. Schluter (1996; 2001) pointed to recently glaciated lakes as important arenas for speciation in fishes. As a dominant fish in the northern post-glacial lakes, the Arctic charr is of particular importance in their evolutionary history. The recent demonstration of five Holarctic evolutionary lineages within the *S. alpinus* complex by Brunner et al. (2001) by mtDNA analysis sets the discussion of Arctic charr evolution in an interesting Pleistocene perspective.

Salvelinus is a genus of the Northern Hemisphere, with several species and with several problems in systematics and taxonomy (Behnke 1989). All species except *S. alpinus* have restricted distributions within the Holarctic region. *S. alpinus* is the only species with a circumpolar distribution. It is also the northernmost of all *Salvelinus* species, and indeed of all freshwater and anadromous fish. To cite Johnson (1984), it has a capacity to explore the unknown waters left by the receding icecap. It is a valuable sport and household fish, not the least for indigenous peoples of the North (Balikci 1980; Johnson 1984; Boivin et al. 1989; Power et al. 1989). Important commercial fisheries are developed in Canada (Kristofferson et al. 1984; Dempson 1995; Dempson & Shears 1998) and the species has a potential in aquaculture (Jobling et al. 1993).

Geographical distribution

Arctic charr are found throughout the arctic, subarctic, boreal and temperate climate regions of the Holarctic. Maitland (1995) estimated that there are 50.000 populations world-wide. Most are found in Scandinavia with 30.000 in Norway and 13.000 in Sweden but the estimates for Canada (about 3500) and Russia (1000) are probably too low. Iceland and Greenland have about 1000, USA about 500, UK about 200 and other countries below 100 populations. It is typically found in cool or cold lakes with depauperate fish communities. In alpine or northern lakes, it is often the only fish species. Extreme northern populations live in lakes where the ice does not disappear in the summer in some or most years. Examples are the large Lake Hazen on Ellesmere Island, Canada (Reist et al. 1995; Guiguer et al. 2002), Char Lake, Cornwallis Island, Canada (Schindler et al. 1974; MacCallum & Regier 1984) and Arkvatn, Svalbard, Norway (Hammar 1982; Svenning 2001). Arkvatn holds the northernmost charr population in Europe (Hammar 1989) and has both resident and anadromous charr (Svenning 2001). The most northern record of a sea charr is at 82°34′N on Ellesmere Island (Günther 1877; Johnson 1980). The southernmost populations in Europe are found in the Pyrenees but all are introduced by man (Machino 1995). The original post-glacial distribution in the Alps region was restricted to the Rhine and Danube catchments (Pechlaner 1987) but charr have been extensively introduced to many lakes in central Europe (Pechlaner 1984b; Brunner et al. 1998). In the Alps, it occurs both in deep pre-alpine lakes (Bohl et al. 1989; Brenner 1980; Hartmann 1984; Ruhlé 1984, 1987; Jagsch 1987; Bohl et al. 1989) and high altitude lakes (Balon & Penczak 1980; Pechlaner 1984b, 1987; Cavalli et al. 2002). All high altitude populations are probably introduced by man, some of them in mediaeval times (Pechlaner 1984b). On the American continent, the southernmost native populations occur in woodland lakes in Maine, US (Kircheis 1980, 1989). According to Brunner et al. (2001) these populations belong to a separate lineage (Acadian) in the evolution of charr.

The native distribution matches the last (Weichsel–Wisconsin) glaciation in the Holarctic closely. The species probably occurred over most of the glaciated areas in early post-glacial times but is today absent from many lakes in the southern part of these areas; probably for climatic reasons (too warm), because of eutrophication (Hartmann 1984; Ruhlé 1984; Champigneulle & Gerdeaux 1995; Maitland 1995) or from negative interactions with increasingly complex fish assemblages (Hammar 1998). About 1300 populations (Maitland 1995) migrate to full strength sea-water as anadromous fish, and the charr has found its way to remote islands such as the Faeroes (Gydemo 1983), Jan Mayen (Skreslet 1973) and Bear Island (Klemetsen et al. 1985). It can tolerate slightly brackish lakes as in Nordlaguna, Jan Mayen (Skreslet 1969) and Arresjøen, Svalbard (Svenning 1993). Some northern populations are riverine (Curry-Lindahl 1957; Power 1973), but the typical environment of the charr is oligotrophic and ultraoligotrophic lakes.

Phenotype and ecology

In this section, we will discuss the view that phenotypic expression and ecology of the charr is more variable than in most, if not all, fishes.

Size and maturation. The size at maturation varies greatly between charr populations. Mature fish are known from 3 g to 12 kg or more. Exceptionally small sexually mature fish of both sexes are described in a few cases. In Thingvallavatn, Iceland, mature females of the small benthivorous morph were 73–310 mm long

(Sandlund et al. 1992). In the Zackenberg area, NE Greenland, Riget et al. (2000) found nearly ripe females as small as 7 and 7.5 cm total length in two small lakes. In Fjellfrøsvatn, northern Norway, spawning females of the profundal morph were 7–14 cm long and weighed 3–17 g (Klemetsen et al. 2002a). Mature males were of the same sizes. Nyman (1987) describes four populations of very small charr that live allopatrically in small habitats (rock crevices, brook pools) in middle Sweden. Mean sizes were 91–116 mm and maximum sizes were 117–166 mm. These cases indicate that the minimum body size for mature female charr is about 70 mm fork length, or about 3 g body weight.

The number of eggs that can be produced by a small body probably sets the limit. The lowest number observed was 13 in Thingvallavatn (Sandlund et al. 1992) and 18 in Fjellfrøsvatn (Klemetsen et al. 2002a). For a given fish size, fecundity could be increased by decreasing the egg size. In brown trout, Jonsson & Jonsson (1999) found a negative correlation between egg mass and fecundity when the effect of body size was removed. In salmonids, individuals with too small yolk reserves would have low probability of survival because the eggs are left without parental care for a long time and the start of exogenous feeding is a bottleneck with a high mortality risk. Therefore, a minimum egg size is probably selected. Johnson (1980) gives a range of 3.6–5.0 mm for lacustrine charr. Brenner (1980) found an average diameter of 3.8 mm in Atteresee, Austria, Baroudy and Elliott (1994) found 3.4 mm for the spring spawning morph in Windermere and Klemetsen et al. (unpublished results) found 3.8 mm for the profundal morph in Fjellfrøsvatn. The Fjellfrøsvatn profundal eggs weighed only 39% of eggs from the littoral morph. In Thingvallavatn, eggs from the small benthivorous morph were smaller than eggs from the planktivorous morph (Eiriksson et al. 1999). These findings indicate that there is a lower size of about 3.5 mm for charr eggs. Two populations (Windermere spring morph and Fjellfrøsvatn profundal morph) spawn exceptionally late (February–March) and have very small eggs. The females in Windermere are much larger than the profundal Fjellfrøsvatn females. This could indicate that late spawning rather than body size selects for small eggs because of their short development time.

Some cases of charr maturing between 10 and 15 cm body lengths are known, for example in the Alps (Balon & Penczak 1980; Brenner 1980), in Norway (Klemetsen et al. 1972; Hesthagen et al. 1995), Iceland (Sandlund et al. 1992) and the Arctic (Klemetsen et al. 1985; Parker & Johnson 1991; Svenning 1993; Riget et al. 2000). Spawning sizes of 15–20 cm in lacustrine charr are very common in both temperate, subarctic and arctic areas (see for instance Johnson 1980; Nyman et al. 1981; Hindar & Jonsson 1982; Hammar 1984; Sparholt 1985; Riget et al. 1986; Walker et al. 1988; Griffiths 1994; Alekseyev et al. 2000; Klemetsen et al. 2002b). In sympatry, such populations are often called ‘dwarf charr’ while the other morph is called ‘normal charr’. We agree with Adams (1999) that these terms place indefensible anthropocentric value judgements on the fish. The terms should therefore be avoided. As noted by Pechlaner (1984a) and others, slow growth and small body size are mostly phenotypic traits. In Takvatn, northern Norway individual growth and size was greatly improved when intensive fishing reduced the density of charr (Amundsen et al. 1993; Klemetsen et al. 2002b). Laboratory experiments, however, indicate differently with respect to genetic control of growth in charr. Hindar & Jonsson (1993) found indications of a genetic influence in 2+ fish but concluded that growth differences between sympatric charr morphs of Vangsvatn, western Norway are largely under environmental control. Eliassen et al. (1998) found that hatchery raised charr of the small-sized morph from Båtsvatn, northern Norway (Klemetsen & Grotnes 1980) grew well and became large. Offspring of the small profundal morph from Fjellfrøsvatn grew twice as fast as the littoral morph in experiments (Klemetsen et al. 2002a). In contrast to these results, Svedäng (1990), Skulason et al. (1996) and Eiriksson et al. (1999) concluded that different phenotypic growth performance between sympatric morphs (respectively from Rösjön, Sweden and Thingvallavatn, Iceland) had some genetic basis. These studies support the view that growth difference between sympatric Arctic charr morphs are strongly influenced by the environment, but that there may also be genetic differences in the growth potential of sympatric morphs.

Most commonly, lacustrine charr mature at 20–40 cm. Mature anadromous charr are from 30 to 70 cm, with a tendency to be larger towards the North in Arctic Canada (Johnson 1980). The mean length of charr in commercial catches on the Labrador coast varied from 49 to 53 cm in 1980–93 (Dempson 1995). In contrast to the low number of eggs produced in small lacustrine charr, larger anadromous charr in Labrador have been found to contain more than 9200 eggs (Dempson & Green 1985). Anadromous charr in northern Norway are often quite small. Svenning et al. (1992) recorded a median length of about 30 cm in ascending fish and Kristoffersen et al. (1994) found that most mature fish were 30–40 cm long and that males were frequently below 30 cm. Populations with larger sea charr are however, found (Rikardsen et al. 1997). Populations in the European Arctic have large fish (Svenning 1993; Gulseth & Nilssen 2000; Svenning & Gullestad 2002). According to Johnson (1980), the largest anadromous charr on record (15.9 kg) was caught near Novaja Zemlya. Piscivorous charr in lakes also grow to several kg (Alm 1951; Seppovaara 1969; Ruhlé 1984; Klemetsen et al. 1985; Riget et al. 1986; Sandlund et al. 1992; Reist et al. 1995; Svenning & Borgstrøm 1995; Gullestad & Klemetsen 1997) and in rare cases even above 10 kg (Johnson 1980). Vøllestad & L'Abée-Lund (1994) analysed data from 44 charr populations in Europe and Canada. Despite the large variation, they found that the life history of Arctic charr can be accurately described by a number of dimensionless indices based on common life-history descriptors.

The size variation of sexually mature fish of both sexes is *c.* 3–12 000 g in charr. A difference of three orders of magnitude, or 4000 times, between the smallest and the largest adults is found in very few, if any, other species of fish or any other vertebrate. The large size variation in the Arctic charr matches the large variation in habitat, niche shifts, migration and other ecological traits of the species. It probably reflects a very high flexibility in its genetic constitution that may be a basic adaptation to the extreme and unpredictable environment of the far north.

Coloration. In addition to size, coloration is a phenotypic expression that varies very much in charr. Along with the Dolly Varden charr *S. malma* (named after the blacksmith's daughter in Dickens' novel 'Barnaby Rudge', famed for her colourful pink dress, see Kipling (1991)), the Arctic charr is possibly the most colourful of all northern fishes. Spawning dresses may, however, vary from almost colourless to strong carmine red bellies and bright white fin margins. Both sexes can have strong colours but males are often more ornamented than females. The variation is large both within and between populations and all shades of red, orange and yellow are found. Colour plates that show striking differences between sympatric morphs are given by Hindar & Jonsson (1982) and Sandlund et al. (1992). Also, Alexander & Adams (2000) show a nice collection of coloured pictures of Irish and Scottish charr. Sandlund et al. (1992) found significant differences in ornamental traits between the Thingvallavatn morphs. Coloration probably depends very much on growth, condition, fat contents and access to carotenoid-rich crustacean food, but colour differences of sympatric morphs may be adaptive. Offspring of the two morphs from Fjellfrøsvatn maturing in 2001–2002 have colour differences that match the colours of their wild parents closely (A. Klemetsen et al. unpublished). This indicates that the spawning dresses of these sympatric morphs are under genetic control. This may be of importance in assortative mating. Skarstein & Folstad (1996) found that the red coloration in both sexes of the littoral morph was negatively correlated to lymphocyte counts and discusses this in relation to sexual selection and immunocompetence.

Habitat. The charr is a habitat generalist like no other northern fish. It is found in streams, at sea and in all habitats of oligotrophic lakes. Lacustrine populations are by far the most common. Entirely riverine populations are found in the North (Curry-Lindahl 1957; Power 1973) but few are studied in detail. Most are probably allopatric and quite stationary. Like riverine brown trout, they often grow slowly and mature as small fish (Nyman 1987). The charr is found in all sizes of lakes, from very small, almost ponds, often with very little water under the ice in the winter (Nyman 1987; Riget et al. 2000) to very large lakes such as Constance, Ness, Vättern, Saimaa, Onega, Thingvallavatn and Hazen. Within lakes, the charr can use all major habitats and depth zones. In several, now classical, studies of salmonids in Sweden, Nilsson (1955, 1961, 1965, 1967) inferred from analyses of stomach contents that there is interactive segregation between lacustrine charr and trout. The charr prefers the littoral zone in allopatry but shifts flexibly to the pelagic or the profundal under competition in sympatry. Habitat segregation between trout and charr has since then been studied several times, see for instance Langeland et al. (1991) and Hesthagen et al. (1997). Langeland et al. (1991) suggested that differences in habitat use between sympatric and allopatric charr were largely (but not entirely) selective in contrast to the hypothesis of Nilsson that mainly focused on the interactive element. Halvorsen & Jørgensen (1996) and Halvorsen et al. (1997) found that parr of trout and salmon occupied the littoral habitat in several north Norwegian lakes while the charr were found in the deeper parts or the pelagic zone. Salmon and trout had close habitat choices and the charr had the same habitat segregation in competition with both *Salmo* species as with one (*S. trutta*). Similarly, in a Newfoundland pond with four salmonids (brook charr *S. fontinalis* in addition to charr, trout and salmon), O'Connell & Dempson (1996) found that the Arctic charr segregated to pelagic and deep benthic habitats except in spring and late autumn when it also occurred in the littoral habitat. In two rivers with anadromous populations of the three species, however, Heggberget (1984) found that pre-smolt charr and trout preferred close habitats in shallow water while the salmon were found in deeper and swifter water.

Intraspecific competition because of high densities can give pronounced ontogenetic habitat shifts. In Takvatn, northern Norway Klemetsen et al. (1989) found that the adults occupied the littoral. They returned to their home area when marked and moved 2–7 km away (Svenning & Grotnes 1991). The youngest fish were found in the profundal zone but shifted to a pelagic mode of life at 3–4 years of age when they became food-limited in the profundal (Klemetsen et al. 1985). Bjøru & Sandlund (1995) found similar ontogenetic and seasonal niche shifts in a monomorphic population in Store Rennen, middle Norway. When the density was reduced by heavy fishing in Takvatn (Amundsen et al. 1993), the charr stopped using the pelagic zone and the whole population re-distributed along the bottom profile (Klemetsen & Dahl-Hansen 1995).

Charr live very deep in some lakes, as in Attersee (Brenner 1980) and Bodensee (Hartmann 1984) in the Alpine region. They have been recorded down to 220 m in Loch Ness, Scotland (Shine et al. 1993; A. Shine pers. comm.). In Gander Lake, Newfoundland, they were caught in gill nets at 200 m (O'Connell & Dempson 2002), and recently as deep as 280 m (M.F. O'Connell, unpublished observation). The very deep Tinnsjøen (max. depth 460 m) in Norway has a deep-living morph that may live very deep, although there are no reliable records below 140 m (L. R. Flå, pers. comm.). The profundal zone of very deep lakes offers a habitat that the charr, with its ability to push ecological barriers, can use like few other northern freshwater fish. The 'Tiefseesaibling' in the deep lakes in the Alpine region has an extreme degree of differentiation within the genus, and Behnke (1972, 1980, 1984, 1989) recognises it as a separate species, *S. profundus*. Lake Elgygytgyn in Chukotka, northeast Russia is a deep and probably very old (3.5 Ma) lake in a meteorite crater (Chereshnev 1996, 1998) that holds three forms of charr recognised as *S. boganidae*, *S. elgyticus* and *Salvethymus svetovidovi* by Russian workers (Chereshnev & Skopets 1990, 1999; Chereshnev 1996, 1998). All live partly in deep water, and *S. svetovidovi* normally deeper than 50 m (Chereshnev 1996), although it was recently also found in shallower water (Chereshnev & Skopets 1999). The very special case of Lake Elgygytgyn shows that endemic species of charr can evolve when the time span is long and where profundal habitats are available for the development of niches in very deep water.

Pelagic charr usually stay in epipelagic waters. A depth limit of about 40 m was found in Jonsvatn and Atnasjøen, Norway (Brabrand 1991; Næsje et al. 1991) and Loch Ness, Scotland (Winfield et al. 2002). Brabrand (1994), however, found pelagic fish that were probably deep-living charr morph down to about 80 m in Tinnsjøen and Jensen et al. (1997) had registrations as deep as 140 m in Limingen, Norway. Elliott et al. (1996) found considerable densities of pelagic fish, mostly charr, both above and below 20 m depth in Windermere. The densities increased at night. In cases of sympatric morphs, one, often a small-sized morph, commonly lives deeper than the other (Nyman et al. 1981; Hindar & Jonsson 1982; Hammar 1984; Klemetsen et al. 1997), but the small-sized morph can also occupy the shallow littoral (Klemetsen & Grotnes 1975).

The shift to the pelagic habitat for feeding on plankton and surface insects found by many authors was discussed by L'Abée-Lund et al. (1993). They concluded that there is a trade-off between food demand and predator presence in charr and that the habitat distribution depends on food availability and predation risk, especially from brown trout. Klemetsen et al. (1992) found that 2+ and 3+ charr had the same food intake rates in the profundal zone of Takvatn. This gave scope for growth for the 2+ but not the 3 + 0. The 3+ shifted to the pelagic zone in late summer. The conclusion was that the profundal is a marginal feeding habitat only suitable for very small fish. In a study of energy budget, niche shift and maturation, Forseth et al. (1994) found that young charr fed successfully on plankton but that the energy intake levelled off in 3–4-year-old fish and decreased in older fish. This coincided with a niche shift to benthos predation that also gave reduced feeding costs because benthic prey are larger. They developed a model where the timing of the niche shifts and sexual maturation was a function of metabolic rate. In an experiment with transfer of charr fry to a small lake without fish, Langeland & L'Abée-Lund (1998) concluded that the size when charr perform the habitat shift to the pelagic zone is not under genetic control, but is a trade-off between feeding and predation risk.

Charr survive and feed very close to 0 °C (Brännäs & Wiklund 1992). Hammar (1998) found littoral benthos in the stomachs of charr under the ice at different times of the winter in several Swedish lakes. He concluded that the charr reoccupy the littoral in frozen lakes with a competitive edge over the brown trout because they can feed in the cold littoral water under the ice. High temperatures can limit the habitat choice in southern lakes. There are no indications that southern populations are selected to tolerate higher temperatures. On the contrary, recent findings indicate negligible geographical variation in the thermal limits for alevins and 0+ parr (Baroudy & Elliott 1994; Lyytikäinen et al. 1997; Thyrel et al. 1999; Elliott & Klemetsen 2002). Larsson & Berglund (1998) found that the growth rates of 1+ charr were high in the range 13–18°. Langeland & L'Abée-Lund (1996) found that charr moved to relatively warm littoral water (17°) when the density of trout (and charr) had been reduced. In another study, Langeland & L'Abée-Lund (1998) found that charr avoided littoral temperatures of 16–20°. There is thus somewhat conflicting information about the influence of high temperatures on the habitat choice of charr, but it appears that warm epilimnic water can be the reason why charr often move to the hypolimnion during the summer. Apart from this constraint, high habitat flexibility is characteristic for the charr. This makes it well suited for occupying vacant niches, especially in glacial lakes with low diversities of fish.

Feeding. Lakes have four animal communities with potential prey animals for predatory fish: pleuston, plankton, benthos and nekton. Except for nekton, these communities are habitat specific, pleuston at the lake surface, plankton in the pelagic zone and benthos at the bottom in the littoral and profundal zones. Nekton (mostly fish) move between two or more habitats. The adaptations in form (body, fins, mouth), senses (especially vision), behaviour and habitat tolerance that a predator needs differ with prey guilds and their habitats. The charr seems to have the adaptations that are needed to take all four types of lacustrine prey in their typical habitats. The same applies to anadromous charr at sea where they mainly feed on plankton and pelagic fish, but also can take littoral hyperbenthos and even surface insects (Moore & Moore 1974; Grønvik & Klemetsen 1987; Rikardsen et al. 2000; Dempson et al. 2002). Little is known on feeding in streams, but charr are probably able to take both surface and mid-water drift as well as benthos.

Apart from very young fish (alevins, 0+), the diet of lacustrine charr is well studied. Diet segregation between sympatric charr populations is repeatedly demonstrated. The grand example is Thingvallavatn, Iceland where two distinct types, one limnetic and one benthic, each consisting of a small and a large morph (Malmquist 1992), gives four distinct morphs termed small benthivorous, large benthivorous, planktivorous and piscivorous charr (Sandlund et al. 1992). There was clear diet segregation between the benthic and limnetic morphs (Malmquist et al. 1992) and also between the two limnetic morphs because the larger morph turns to piscivory. The segregation between the benthics and limnetics was confirmed by experiments with wild-caught fish (Malmquist 1992). The two benthic morphs overlapped more in their diet. Both fed extensively on gastropods but there was a size-related segregation between them (Malmquist et al. 1992). Other examples of diet differences between sympatric charr morphs are from Sweden (Henricson & Nyman 1976), Greenland (Riget et al. 1986), Scotland (Adams et al. 1998), Canada (Guiger et al. 2002) and western (Hindar & Jonsson 1982), northern (Klemetsen & Grotnes 1975, 1980) and Arctic Norway (Klemetsen et al. 1985).

In Takvatn, Amundsen (1995) found that the charr is able to utilise pleuston, plankton, benthos and nekton with a highly flexible feeding strategy depending on prey types, resource variation and intraspecific competition. The population niche width was wide during the open water season with the exception of June when the diet was dominated by emerging chironomids. In contrast, individual niches appeared to be narrow with extensive individual specialisation. He concluded that the individual specialisation was caused by a high intraspecific competition. Knudsen (1995) and Knudsen et al. (1996) used food-transmitted parasites as indicators of past prey selection in Takvatn and the nearby Fjellfrøsvatn. The results confirmed Amundsen's conclusion that there is a strong prey specialisation in individual charr. Strong infections of parasite species that live for long times in the fish indicate that diet specialisation's may last for a long time. Bjøru & Sandlund (1995) concluded that pelagic and benthic feeding specialisation was clearly correlated to morphometric differences.

0+ feeding. The food of young charr, especially at the critical early alevin stage but also through most of the first summer is poorly known. The main reason for this is that these small fishes are difficult to find and sample in lakes. The depth of the spawning grounds varies between lakes but is commonly shallow, often less than 5 m deep. This means that the first feeding mostly takes place among stones and gravel in the littoral. The coarse habitat also provides shelter against predation from fish and diving birds. In allopatry, the fry stay in the shallow littoral of Arctic and alpine lakes (Finstad et al. 2000). Stenzel & Power (1991) found about one to eight juvenile charr 100 m^{-2} in Alik Lake, Ungava Bay, Canada. The fishes were observed in very shallow water and close to the shore (mean depths <50 cm and mean distances from the shore <1 m). There was a clear preference for boulder and bedrock substrate. Predators are few in Arctic and alpine lakes (usually only charr and few, if any, birds) so the predation pressure is probably low enough to allow feeding in the littoral zone. Most subarctic and temperate lakes have no 0+ charr in shallow water. We know little about the time they leave the shore region and how deep they move. Lindström (1955) observed that alevins had eaten small insect larvae and crustaceans. On Baffin island, Moore & Moore (1974) found that <5 cm, riverine anadromous charr fry had eaten small (1–2 mm) chironomid larvae and pupae. Hindar & Jonsson (1982) caught 14 21–27-mm-long alevins on the spawning grounds of Vangsvatn, western Norway. All but one had resorbed the yolk sac and five had food in their stomachs. All had eaten one or more chironomid larvae and four had taken benthic copepods. In the Iterlaa lakes in Greenland, Sparholt (1985) found that charr below 5 cm had eaten equal amounts of benthic cladocerans, ostracods and chironomids. The diet of 0+ charr in the surf zone of Thingvallavatn was strongly dominated by larvae and pupae of orthocladine chironomids (Sandlund et al. 1988). Surface insects, zooplankton and benthic microcrustaceans were unimportant. In the autumn, other benthic insects and gastropods gained importance. Pelagic 0+ charr had mainly eaten planktonic copepods in September. The morphs therefore showed habitat and diet segregation already in their first season. In Jonsvatn, Central Norway, Næsje (1995) sampled 0+ charr with a fine-meshed beam trawl and got good samples in 1986 and 1991. The yearlings were distributed at the bottom from depths of 5–30 m. This was a study of the effects of introduced *Mysis relicta*, and he found that mysids were the dominant prey of 0+ charr in the spring and autumn. Crustacean plankton, both copepods and *Bosmina*, and chironomid larvae and pupae came into the diet from June and were more important than mysids in August and September. On this diet, the 0+ had a relatively poor first-year growth of 20.5 mm, but the 1+ grew much better on a similar diet.

Apart from Thingvallavatn and Jonsvatn, knowledge of the food of very small charr is based on few fish, and is therefore circumstantial rather than analytical. The surf zone in Thingvallavatn is special, with many crevices in the neo-lava that provide better shelter than in most lakes. Jonsvatn is also special because of the introduced *M. relicta*. The results from these lakes may thus not apply to other systems. Benthic microcrustaceans may for example be more important in other systems. Early feeding is generally considered to be a life-history bottleneck with a high mortality risk. We know that chironomids and microcrustaceans probably are the main prey types. But chironomids, chydorids, ostracods and harpacticoids are all groups with high species diversities. Many, if not most, species in these groups are not studied in terms of life histories, population dynamics and production. In many lakes we do not even know their names. Identification of the important prey species and studies of their life histories in relation to early feeding in charr is a challenge likely to provide good progress in charr biology.

Selective predation. Selective predation by planktivorous lacustrine fishes has been a field of special focus ever since Brooks & Dodson (1965), see review by Lazarro (1987). Nilsson & Pejler (1973) demonstrated that charr fed selectively on euphyllopods and cladocerans and found a clear connection between fish fauna and zooplankton composition in a series of Swedish lakes with increasing predation pressures from fishless to trout–charr–whitefish lakes. In 10 Norwegian charr lakes, Langeland (1978) found that charr selected cladocerans above copepods and that increasing predation had negative effects on large cladocerans and also affected the size of two important prey species. In a 6-year experimental study in one lake, Langeland (1982) found that predation from charr changed the zooplankton community from large- to small-sized species. The predation also affected body size and the production of resting eggs in cladocerans negatively. The plankton community in Takvatn, northern Norway, was dominated by two copepod species and *Bosmina longispina* when the pelagic density of charr was high (Dahl-Hansen et al. 1994). When the pelagic density of charr was reduced to zero as a result of the experimental mass removal of charr (Amundsen et al. 1993; Klemetsen et al. 2002b), the plankton biomass increased sharply and larger cladocerans returned, albeit more slowly than predicted, possibly because of a brief incidence of pelagic predation by three-spined sticklebacks in the absence of charr (Dahl-Hansen 1995). Enclosure experiments demonstrated that both charr and sticklebacks were efficient plankton predators with clear selective preferences for cladocerans (Dahl-Hansen 1998). Recent studies of sediments in Arctic lakes in Greenland by Jeppesen et al. (2001) show that selective predation by charr probably eliminated *Daphnia pulex* and the epibentic phyllopod *Lepidurus arcticus*. The benthic chydorids *Alona* and *Macrothrix* were abundant in charr lakes but not in fishless lakes with *L. arcticus*. This indicates that selective predation by charr on benthos can have cascading effects in low complexity systems. Such effects are probably also present in more complex systems but are not yet demonstrated.

Cannibalism

Cannibalism, the consumption of conspecifics, is widespread in fishes (Smith & Reay 1991) and common in Arctic charr. It is known in Arctic Canada (Johnson 1980; Hobson & Welch 1995), Greenland (Riget et al. 1986; Sparholt 1985), Jan Mayen (Skreslet 1973), Bear Island (Klemetsen et al. 1985), Svalbard (Gullestad 1975; Svenning & Borgstrøm 1995) and mainland Norway (Amundsen 1989; 1994). It is not commonly observed in temperate lakes (Amundsen et al. 1999), and Griffiths (1994) found that it increased strongly with latitude. Amundsen et al. (1995) demonstrated cannibalism experimentally with naive hatchery raised charr and found that the prey was on average 22% of the cannibal length. A specialisation developed among the experimental fish with only some individuals developing cannibalism and this individual specialisation appeared to persist over time (Amundsen et al. 1997). In a later experiment, Amundsen et al. (1999) tested the hypothesis of a latitudinal increase in cannibalism by comparing the cannibalistic response between one Arctic (Vårflusjøen, Svalbard, 79°N) and three subarctic (70°N) populations. Offspring of the Arctic population had much higher cannibalistic response than the others. The experiment therefore supported the hypothesis.

In stomach analyses, only a low per cent of the fish is usually found to be cannibals. L'Abée-Lund et al. (1992) considered 5% cannibalism to be of insignificant importance in structuring the populations. Svenning & Borgstrøm (1995) developed a simple model for a Svalbard lake that refuted this. By varying the mortality and occurrence of small charr in the diet of large charr, they found that cannibalism was important in structuring the age- and length class distribution in the population. Svenning and Borgstrøm proposed that cannibalism might be a key process in structuring the fish populations in Arctic and alpine lakes. Hammar (2000) suggested that prey shortage and slow juvenile growth induce cannibalism in Svalbard lakes. He concluded that cannibalism is an important strategy for landlocked charr in the High Arctic despite the conflicting cost of accumulation of *Diphyllobothrium* cestodes in the cannibals. In an alpine lake in central Norway, Finstad et al. (2001) estimated the biomass and production of cannibals and their prey. Depending on the food conversion factor, they found that cannibals removed 10–40% of the annual production of prey charr and that the efficiency of energy transfer between the prey and predator population was 4.4%.

Takvatn in northern Norway had a narrowly unimodal population of stunted charr in 1980. By intensive trap fishing in 6 years, the populationdensity was first reduced to about 20% (Amundsen et al. 1993). Individual growth improved and the population changed to a bimodal size structure (Klemetsen et al. 2002b). Fishes that hardly weighed over 100 g before the fishing programme now could grow to 1–2 kg or even more. Cannibalism started to occur in the population and Amundsen (1994) found that 5.3% of the fishes >20 cm were cannibals. A simple model suggested that cannibalism accounted for all the mortality of 1–4-year-old charr. This indicates that a group of large charr is essential for the long-term development of bimodality in the lake (Klemetsen et al. 2002b). Damsgård (1993) found that brown trout had larger gape sizes in relation to body size than charr. In a laboratory experiment with charr as prey and trout as predator, the observed vulnerability with body depth was lower than predicted. When brown trout were released in a small charr lake, the piscivorous predation increased growth in the remaining charr. Fewer charr, therefore were vulnerable to predation 2 years after the introduction of piscivorous trout (Damsgård & Langeland 1994). The results of these whole-lake experiments refute the suggestion by L'Abée-Lund et al. (1992) and Griffiths (1994) that cannibalism is unimportant for structuring the populations of charr lakes. Johnson (1983, 1987) found that Arctic charr populations returned quickly to the original structures after perturbations. The results from Takvatn were different, and Amundsen et al. (1993) proposed that more than one stable state is possible if the perturbation is strong enough. The prolonged time series confirms this (Klemetsen et al. 2002b). Vik (2002) developed feedback models for population regulation in charr and trout that further support the importance of piscivory.

Anadromy

As with brown trout, Arctic charr populations migrate within river systems, but since charr often spawn in lakes, most migrations take place within one lake, often as ontogenetic habitat shifts (Klemetsen et al. 1989). Some populations have regular migrations between separate lakes in a river system (Näslund 1990). Migrations between river systems and the sea (anadromy) are found in the northern part of its range, i.e., in Northern Russia, Northern Canada, Greenland, Iceland and North Norway.

Anadromy is complex in charr because both sexually mature and immature fish perform seasonal migrations between river systems and coastal areas (Nordeng 1983; Johnson 1989). It is different from anadromy in salmon because all migrants, including juvenile fish, return to freshwater every year. Similar complexity is found in brown trout, but charr return earlier to freshwater and stay there during the winter, while sea trout can make winter migrations to the sea (see the discussion under brown trout).

A trap for migrating salmonids was operated in the Vardnes River on Senja, northern Norway in 1956–1963 and 1967–1970 (Mathiesen & Berg 1968; Jensen & Berg 1977; Berg & Berg 1989b). The descent of charr started at icebreak, with repeat migrants going first. The main downstream migration took place from early May to the middle of June and the main ascent took place during July (Berg & Berg 1989b). Jensen & Berg (1977) estimated an annual survival rate of 0.50 for the exploited part of the population, but found significantly lower survival for smaller fish. Most recaptures (74%) were within 25 km from the river, but one fish had travelled 940 km. A high proportion of the freshwater recaptures were from other rivers. The growth in the sea was high in the first part of the season in spite of low temperatures (Berg & Berg 1989b).

Unexploited anadromous stocks of charr in Arctic Canada have large fish with mean lengths of 60–65 cm and weights of 3–6 kg (McGowan 1985). Migration was studied in 1974–1979, 1984 and 1988 in the Nauyuk system (Gyselman 1984; Johnson 1989). The upstream run was estimated at 11,000 fish in 1974, but declined to 3000 or less by the mid-1980s. Nonspawning fish overwinter in Nauyuk Lake, move to the sea in the spring, and return to the lake after 35–45 days. The migration to the sea started as soon as the river opened in June. The largest fish descended first, and there was a decline in size with time. The migrants had a bimodal length distribution with modal sizes of 22 and 59 cm. The youngest migrants were 6 years old. There was still ice on the sea when the migration started and the temperature of the seawater was below −1 °C. The growth at sea was rapid, with mean weight gains up to 42%. There was probably considerable straying between systems for overwintering. The Nauyuk charr spawn with 2-, 3- or even 4-year intervals. The average spawning age was 13 years. Maturing fish move upstream to Willow Lake and spend the summer there before spawning. The spent fishes overwinter in Willow Lake but join the nonspawners in their descent to the sea in the spring. The mortality of spawning fish was about 10%, but Dutil (1986) found that postspawners had 64% less energy than nonspawning fish. The recruitment was low in most years, and Johnson (1989) raised the question of whether the adult stock suppresses recruitment until a point where low density allows an upsurge of recruits.

Dempson & Green (1985) did detailed investigations on migration, fecundity and spawning in the subarctic Fraser River, Labrador in 1975–1979. The upstream counts varied from about 2300–6400 fish. Size and age varied little (mean length 44.5–45.8 cm, mean age about 8 years). Seaward migration started at ice break-up in the river. First-time migrants were 9–13 cm long and 3–7 years old. The growth at sea was 7–10 cm. No Fraser River charr made extensive coastal migrations. Annual mortality was 44–49%. About 60% of the ascending females were sexually mature. Spawning took place in October in a 8-km section of river, but redds were also observed in shallow water (1.5–2 m depth) along the side of a small lake.

Mortensen & Christensen (1983) studied the population dynamics of charr in the River Narssaq, Greenland in 1981 by electro-fishing and with a trap for ascending fish. Survival curves for 0–2+ and for a composite year-class of anadromous charr were established. The stock of anadromous charr was estimated to be 1200 fish, and the annual mortality was 0.59 for this exploited stock.

In the High Arctic Dieseth river system on Svalbard, Gulseth & Nilssen (2000) found an average sea residence of 34 days over 3 years. This is similar to results from the Nauyuk system (Johnson 1989) and the Hals system in mainland Norway (35 days, Finstad & Heggberget 1993), but lower than in the Vardnes River, also in mainland Norway (48 days, Mathiesen & Berg 1968; Berg & Berg 1989b), and Nain and Tikkoatokak, Labrador (57 and 52 days, Dempson & Kristofferson 1987). The return rate from the sea varied little between years but increased with fish size (33–75%). The average return of first-time migrants was 43%. This is higher than found in mainland Norway (Finstad & Heggberget 1993), and could reflect a lower risk of predation in the Arctic for the smolts. Svenning & Gullestad (2002) found a strong correlation between air temperatures and water flow in the same system. The persistence of the passage channel to the sea therefore varied unpredictably between years. In one year, only a few small fish returned because the stream had a low water flow in late summer. The migratory window was closed and the fish most certainly died in the sea during winter. Climate variations can thus inflict high mortality on Arctic anadromous populations. By microchemical analysis for Sr/Ca ratios in otoliths, Radtke et al. (1996) and Svenning (2001) found that individual charr abstained from migration in some years inVårflusjøen (79°N) and Arkvatn (80°25′N) further north on Svalbard. Jørgensen & Arnesen (2002) found a more rapid development and loss of hypo-osmoregulatory capacity in charr from Vårflusjøen than from the mainland, and proposed this to be an adaptation to the unpredictable variation of the time when charr can migrate in the High Arctic. Radtke et al. (1996) raised the question of whether extremely northern populations may be characterised as facultatively anadromous.

Based on a literature survey, Tallman et al. (1996) concluded that when charr display a life-history dichotomy, the migratory forms mature at older ages, have higher fecundity and greater longevity. Most river systems with anadromous charr also have resident charr that belong to the same population, as Nordeng (1961, 1983) found in the Salangen river system, North Norway. In extensive rearing experiments, Nordeng et al. (1989) always found that a fraction of the resident charr smoltified and transformed into anadromous fish. They also found that a higher proportion of the offspring from anadromous parents smoltified when released into the river than did the offspring from resident parents. This indicated that there is some genetic influence on anadromy. Nordeng's long-time studies of charr in Salangen and other systems also led to the formulation of the pheromone hypothesis for the orientation back to the native river (Nordeng 1971). The relative proportions of the two life-history types vary greatly between populations. Anadromous charr may dominate in some systems (Svenning et al. 1992; Strand & Heggberget 1994). In both these cases from North Norway (Sila and Hals river systems), it was concluded that the first-time migrating smolts had a high pre-smolt growth rate. It was also concluded that most of the slower growing parr also migrated to the sea, but at a higher age, thereby turning most of the population anadromous. In a series of North Norwegian river systems, Kristoffersen et al. (1994) scored anadromy by an index based on marine parasites, fish size and maturity. Anadromy prevailed in systems with shallow lakes and residency in systems with deep lakes. The relative volume of the profundal zone correlated negatively with anadromy scores and with parr growth. Also, there were negative correlations between anadromy scores and stream velocities and distances from the lakes to the sea (Kristoffersen 1994). The charr population of Storvatn in Hammerfest town, North Norway has been used extensively in aquaculture and in experiments (Jobling et al. 1993; Adams et al. 1995). Rikardsen et al. (1997) estimated the numbers of anadromous and resident charr in the population, and found that about two-thirds of the fish older than 5 years were anadromous. They also found that the high incidence of females among ascending fish was caused by higher mortality among male post-smolts at sea. In another study (Rikardsen & Elliott 2000) that compared Storvatn with another system, Rungavatn, it was found that the largest parr migrated for the first time as 4+, while medium sized parr went as 5 + 0. The smallest parr became resident fish. Significant differences were found in life-history characteristics of the two populations, and the results suggested that they had adapted differently due to unequal growth, energy allocations and competition in the lakes.

Finstad et al. (1989) exposed charr to water with different salinities and temperatures at different times of the year and found that an increase in day length induces a hypo-osmoregulatory capacity in the summer. In another experiment, Arnesen et al. (1992) showed that the hypo-osmoregulatory capacity in charr was induced by increased day lengths while the fish was still in freshwater. This was tested in the field by capturing descending smolts in the Å river system on Senja, North Norway, and exposing them to different salinities. The group that was transferred directly to full strength seawater had a good osmoregulatory capacity that did not differ from the groups that were first retained in fresh or brackish water to simulate estuarine conditions. Dempson (1993) found that small charr (<120 mm) could tolerate intermediate salinities (10–20 ppt) whereas survival of charr at salinities >30 ppt was size-dependent. Collectively, these experiments show that most descending charr smolts are physiologically pre-adapted for migrating directly into seawater without osmoregulatory problems.

Moore & Moore (1974) found that anadromous charr in Cumberland Sound, Baffin Island fed on planktonic amphipods, copepods and fish (polar cod, *Boreogadus saida*, and sculpins). At Senja, North Norway, Grønvik and Klemetsen (1987) found pelagic fish (herring, *Clupea harengus,* sand-eels, *Ammodytes* spp.), pelagic crustaceans (including copepods, amphipods, krill and crab megalopae), hyperbenthic crustaceans (amphipods, mysids) and surface insects in the marine diet. Adams et al. (1989) found that the charr in Ungava Bay, Québec, had eaten fish (sand eels, cottids) and a large variety of both planktonic and hyperbenthic crustaceans, especially numerous different amphipods, as well as polychaetes, molluscs and surface insects. They estimated that charr at sea consumed about 7.5% of their body weight per day. Rikardsen et al. (2000) found that the smolts of the Storvatn (Hammerfest) population fed mainly on pelagic copepods (*Calanus finmarchicus*) and krill (*Thysanoëssa* spp.) and less on fish, surface insects and benthos in the sea. Their food intake rates and growth were higher than in resident charr of the same population at the same time. This direct comparison of the two life-history types demonstrated that migration to the sea is beneficial for growth. Rikardsen et al. (2002) showed that smolts fed mostly on surface insects in the lake before migrating to sea. This indicates that smoltification not only involves changes in physiology, morphology, color and swimming behaviour, but may also change the feeding behaviour in a significant way. Based on more than 2500 stomach samples from Labrador, Dempson et al. (2002) found that sand lance (*Ammodytes* spp.), capelin (*Mallotus villosus*), sculpins (*Triglops* spp. and *Myoxocephalus* spp.) and hyperiid amphipods (*Parathemisto* spp.) were the most important prey. Capelin, sand lance and sculpins were important in southern populations, capelin, sand lance and amphipods in middle populations, while amphipods and sculpins were important in the north. The relative importance of prey varied with charr size. For one stock complex, a decline in weight with time was correlated to a decrease in the importance of capelin in the diet. This could be associated with changes in the distribution of capelin on the Labrador coast, which may be caused by changes in the ocean climate. Commercial fisheries have been developed in Northern Labrador, where 936 mt were landed from the Nain stock complex over a 20-year period (Dempson 1995). The total catch and catch rates declined, but there were no indications of a stock collapse. In an earlier study from Labrador, Dempson & Misra (1984) were able to identify discrete stocks by multivariate analysis of meristic data. Bernatchez et al. (1998) confirmed the existence of distinct anadromous populations on a microgeographic scale in Labrador by use of microsatellite analysis.

Polymorphism and speciation

In their review of polymorphism and speciation in charr, Jonsson & Jonsson (2001) describe charr morphs with emphasis on color and morphology, life-history traits and parasites and discuss the ecological significance of charr polymorphism with emphasis on trophic adaptation, camouflage, body size and parasites. An extensive table with definition of terms and another giving characteristics of sympatric charr morphs from a selection of localities are included. Jonsson & Jonsson (2001) find that morphological segregation in charr is driven by trophic adaptation. This is essentially trophic polymorphism as proposed for vertebrates by Skulason & Smith (1995) and Smith & Skulason (1996). There is a range of reproductive isolation from very low to complete among cases of sympatric morphs in charr, as shown by Gislason et al. (1999) for some Icelandic lakes. Jonsson and Jonsson point to assortative mating and trophic adaptation as responsible for reproductive isolation of sympatric morphs. Morphologically similar individuals attract each other and morphologically intermediate offspring are inferior in competition with more specialised individuals. Behavioural isolation with assortative mating based on trophic morphology and site fidelity with homing to the same spawning site are important mechanisms.

Jonsson & Jonsson (2001) concluded that similar Arctic charr morphs in different systems are not individual species because of: (1) their polyphyletic origin; (2) the young age and transient environment of their systems; and (3) the low genetic differentiation among morphs. The application of the biological species concept with recognition of similar morphs in separate systems as different species may result in chaotic systematics. Although disruptive selection may lead to incipient speciation, as suggested for African ciclids, sympatric forms of charr should be called morphs within the *S. alpinus* species complex.

Savvaitova (1995) discussed the patterns of diversity and processes of speciation in charr, based for a large part on her long experience with *Salvelinus* from Russia, especially eastern Russia. Several forms of charr are found on the Kola and Taimyr Peninsulas, in the Lena River Delta, in waterbodies of the Chukotka and Kamchatka Peninsulas, and along the coast of the Okhotsk Sea (Savvaitova 1989, 1995). In Taimyr, four endemic species have been described, and sympatric morphs are found in several lakes. Genetic differences in the frequencies of Est-2 alleles are found in some cases. Savvaitova (1995) finds it likely that the emergence of charr forms in Taimyr depends on extended spawning seasons, differences in growth and time of maturation. Three charr morphs that differed in a number of characters were found in the Pegtymel lakes in Chukotka. A deep-living morph is probably reproductively isolated. These charr morphs differ from all other described morphs in the numbers of gill rakers, pyloric caeca and vertebrae. Two morphs with completely different niches are found in Lake Nashikinskoe in Kamchatka. One of them lives only in the lake, while a small lacustrine-riverine morph prefers affluent streams. They differ in morphology, ecology and karyotype, and are reproductively isolated. Savvaitova (1995) points out that different degrees of divergence between sympatric morphs are found throughout the range of *S. alpinus*, and that reproductive isolation is frequent. Some forms can probably be considered separate species, but in general, the Arctic charr should be treated as one superspecies – the *S. alpinus* complex.

Adams (1999) discussed if the nature of charr polymorphisms differs across the species. He suggested that there are two types of polymorphism in charr; 'ontogenetic polymorphism' and 'genetic polymorphism'. In ontogenetic polymorphism, the morph expression is strongly influenced by environmental factors, particularly through growth. Individual fish can transform from one morph to another during its lifetime. Adams terms this horizontal transformation. In Salangen, northern Norway, Nordeng (1983) studied three morphs of charr termed small resident, large resident and anadromous charr. This is a good example of ontogenetic polymorphism. Genetic polymorphism is characterised by phenotypic stability that transforms vertically, i.e., over generations. Horizontal transformations do not occur and morph differences are clearly influenced by genetics. Thingvallavatn (four morphs) and Loch Rannoch (three morphs) are good examples. In both cases, genetic differences in morphological and behavioural traits between morphs are established by experiment (Skulason et al. 1993; Adams & Huntingford 2002a,b).

Skulason et al. (1999) discuss a proposal for an evolutionary process with focus on charr. They found that the relative importance of phenotypic plasticity and genetic influence on phenotypes (morphs) differ within and between systems. The relative importance of these effects depends on selective environments and developmental constraints like the cost of plasticity in behaviour, life history and morphology. After post-glacial colonisation, morph expression was primarily caused by phenotypic plasticity. The Salangen system (Nordeng 1983) is probably in this state. With increasing stability of niches, ecological segregation of morphs became stable with a noticeable genetic component. The proposal implies that the evolution of morphs, especially their increased ecological specialisation, is characterised by loss of plasticity in life history and morphology. Skulason et al. (1999) note that there is a continuum from great flexibility to considerable specialisation among charr systems. Evolutionary processes as in Thingvallavatn may take place in some systems while flexibility and phenotypic plasticity continues in other systems.

There has long been a discussion if sympatric morphs of charr have sympatric or allopatric origins. Jonsson & Jonsson (2001) summarised that a hypothesis of allopatric origin (and subsequent invasion) of sympatric morphs has little coherent empirical evidence for Scandinavian charr. On the contrary, genetic studies (Hindar et al. 1986; Hartley et al. 1992a,b; Volpe & Ferguson 1996) lend support to the alternative hypothesis of repeated sympatric diversification in Scandinavia and elsewhere. This is a view that most charr workers hold today. Jonsson & Jonsson (2001) do, however, not exclude the possibility of an allopatric origin of some sympatric morphs, especially if introduction by man is involved. In a genetic study by allozymes of charr populations in South Norway, Hindar et al. (1986) found a conspicuous branching in the dendrogram between a western and an eastern population group. This did not explain any of the sympatric pairs but indicated that separate invasions to southern Norway may have taken place. Klemetsen (1991) found a distribution of esterase allele frequencies among 61 populations of northern Norway that could be explained by opposite post-glacial invasion routes from possible Weichselian refugia in SW Europe and Siberia. These two studies are not conclusive but may be taken to suggest that Weichselian allopatry explains some of the variation we see in the Arctic charr complex. McPhail (1961) proposed opposite invasion routes of Arctic charr in North America, and Hammar (1984) proposed that three waves of charr colonised central and northern Sweden. Wilson et al. (1996) used mtDNA analyses to reconstruct post-glacial dispersal of Arctic charr in North America by, and concluded that there are three phylogeographical lineages that suggest dispersal from separate glacial refugia. In Newfoundland, microsatellite analyses suggest that charr from Gander Lake may have a post-glacial origin that is distinct from Labrador populations (Bernatchez et al. 1998). Bernatchez et al. (1998) claim that another case, Kogluktokluk Brook in Labrador, may represent a population of distinct post-glacial origin. In their microsatellite analyses, they compared the Gander Lake population with several anadromous populations in Labrador. The high divergence of the Gander Lake population was as expected, but the pronounced genetic differentiation between Kogluktokluk Brook and a nearby tributary was not expected. The divergence was greater than observed for other charr from much wider geographic areas. Bernatchez et al. (1998) emphasise that the reason for this is not clear, but indicate that the striking differences between the Kogluktokluk Brook and all other Labrador populations indirectly support a hypothesis of reproductive isolation in post-glacial refugia. With reference to several cases in North America, Europe and Siberia, Osinov 2001) found that there are grounds to suggest that the formation of sympatric pairs in charr is related both to sympatric divergence and secondary contact between allopatric populations.

The glacial history is considered important for the distribution, and sometimes also the sympatric occurrence of morphs, in several fishes. Ferguson & Taggart 1991) concluded that the sympatric populations of brown trout in Lough Melvin, Ireland probably derived in allopatry and invaded the lake in post-glacial times. Garcia-Marin et al. (1999) explained the distribution of brown trout in northern Europe by post-glacial colonisation from three refugia. Bernatchez & Dodson (1994) suggested post-glacial colonisation of northern and central Europe by *Coregonus* from two allopatric refugia. Refseth et al. (1998) and Nesbø et al. (1999) found that the genetic divergence and phylogeography of perch *Perca fluviatilis* reflect glacial refugia and post-glacial history. This has been suggested also for northern marine fishes. Jørstad et al. (1994) found that two local populations of herring *Clupea harengus* in Troms, northern Norway, were so divergent genetically from the oceanic and coastal stocks that a separate history was indicated, possibly by post-glacial invasion along the Siberian coast. For charr, Savvaitova (1995) stressed that not every case of sympatry should be treated as the result of sympatric speciation, but that processes of sympatric and allopatric divergence complement each other.

There is reason to consider the question raised by Power (2002). With reference to Hewitt's (1996) hypothesis on the effects of glaciations on evolution, he asks if we have looked the wrong way. Maybe the speciation processes we study in our time (i.e., interglacial) have no long-term importance because most of the morphs will be wiped out by the next Ice Age. Power concludes that it is more important to understand what occurred in the glacial refugia. The mtDNA analyses of Wilson et al. (1996) and Brunner et al. (2001) and the allozyme analyses of Osinov (2001) are important in this context. Wilson et al. (1996) discuss post-glacial dispersal and glacial refugia in North America. The three phylogeographical lineages they found (Arctic, Laurentian and Labrador) matches the conclusion of Brunner et al. (2001) that there are five Arctic charr lineages (Atlantic, Arctic, Bering, Siberian and Acadian) in the Holarctic. Brunner et al. (2001) included Labrador and Newfoundland in the Atlantic lineage and found the pattern of the Laurentian group of Wilson et al. (1996) almost identical to their Acadian group. They cautiously indicated that the five phylogeographic groups date back to a common ancestor in early or mid-Pleistocene, or 300 000–700 000 years ago. Osinov (2001) concluded that the southern Dolly Varden charr (*S. malma*) from Japan is the most closest related to the common ancestor of the *S. alpinus–S. malma* complex and that the centre of its origin was in the Pacific. There are several problems with the origin of *S. alpinus* in this region, but Osinov (2001) suggests that the Taranetz charr, which is found on both sides of the Bering Strait, is most closely related to the ancestral form of Arctic charr. The problem with allozyme, mtDNA and other DNA analyses has been the low levels of variation (Brunner et al. 1998). In contrast, their analyses of charr from central Europe by microsattelite DNA demonstrated high levels of genetic diversity between and among populations. This refuted the long-held view of Arctic charr being a genetically depauperate species.

Bernatchez & Wilson (1998) noted that diversification of sympatric ecomorphs has occurred in extremely short timespans (<15,000 years) in northern fishes, among them Arctic charr. More advanced cases of genetic divergence through ecological diversification have led to reproductively isolated taxa and species pairs in *Coregonus*, *Gasterosteus* and *Osmerus* (Bodaly 1979; McPhail 1993; Taylor & Bentzen 1993; Vuorinen et al. 1993). There is strong evidence, for instance in lake whitefish *C. clupeaformis*, that similar phenotypic patterns evolved in parallel in separate but closely related lineages. With reference to Schluter & Nagel (1995), Bernatchez and Wilson wrote that such cases represent the strongest nonexperimental evidence of natural selection imposed by ecological forces. Some sympatric charr morphs may constitute cases of parallel evolution imposed by ecological forces because they have reproductive isolation and ecological and genetic diversification. The Thingvallavatn studies indicate that the limnetic and benthic morphotypes are reproductively isolated and they are clearly segregated in habitat and trophic ecology (Sandlund et al. 1992). The types have different trophic morphologies (Snorrason et al. 1994) and genetic differences in feeding behaviour are demonstrated by experiment (Skulason et al. 1993). Loch Rannoch in Scotland has three morphs of charr (Adams et al. 1998). The benthivorous and planktivorous morphs are morphometrically distinct and have different food niches. Their spawning times overlap slightly but peak separately in middle October and early November. The spawning grounds are 12 km apart. The populations are probably reproductively isolated. This is confirmed by genetic analyses that concluded with differences at one mtDNA locus (Hartley et al. 1992b). Experiments with offspring concluded that there were inherited differences in head morphometry and feeding behaviour between the two morphs (Adams & Huntingford 2002a,b).

The littoral and profundal morphs of Fjellfrøsvatn, northern Norway are extraordinary segregated in time (5 months, September vs. February) and place (littoral vs. profundal) of spawning (Klemetsen et al. 1997, 2002a). They are completely reproductively isolated. Their habitats, food and parasites (Knudsen et al. 1997) are different and genetic differences in morphometry and behaviour are demonstrated by experiment (Klemetsen et al. 2002a). Vangsvatn in western Norway holds two morphs that are possibly reproductively isolated although there is a slight overlap in time and place of spawning (Hindar & Jonsson 1982). Their niches are definitely separate and although Hindar & Jonsson (1993) concluded that most of the polymorphism was environmentally induced, their experiment suggested genetic differences for growth rate and jaw morphology. The autumn spawners and spring spawners of Windermere, England are well separated in time and place of spawning (November vs. February, littoral vs. profundal) (Mills 1989; Elliott & Baroudy 1995). There is therefore reproductive isolation and Partington & Mills (1988) found slight but significant differences in the frequencies of esterase and malate dehydrogenase alleles. There are small differences in size and morphology, and fish from both spawning grounds in both basins seem to have similar pelagic niches. Baroudy & Elliott (1994) did, however, find that both eggs and alevins were larger for the autumn spawners. The survival was also higher for the progeny of the autumn spawners, and Baroudy & Elliott (1994) discuss if this difference could be responsible for the relative small proportion (4–6%) of spring spawners in the lake.

These probable cases of parallel evolution of sympatric charr morphs are all within the phylogeographic range of the Atlantic lineage of *S. alpinus* found by Brunner et al. (2001). They provide a confirmation for Arctic charr of the suggestion by Bernatchez & Wilson (1998) of parallel evolution of similar phenotypic patterns in northern fishes. The Atlantic lineage includes continental Europe west of Finland, the British Isles, Iceland, southern Greenland and Newfoundland. Recent results from Newfoundland indicate that Gander Lake holds two morphs that differ in size, meristic characters and habitat (O'Connel & Dempson 2002). There are few examples of sympatric morphs in the other lineages but Lake Hazen (Reist et al. 1995) and Lake Tasersuaq (Riget et al. 1986) in the Arctic lineage and lakes in the Svalbard archipelago, Norway (Klemetsen et al. 1985; Svenning 1993; Svenning & Borgstrøm 1995) and Lake Davatchan in Transbaikalia (Alekseyev & Pichugin 1998) in the Siberian lineage are possible cases. Lake Davatchan is particularly interesting in this context because a benthophagous morph is markedly different in morphology from a piscivorous and a planktivorous morph in the lake. The benthophage has a different spawning time and there is probably a strong reproductive isolation from the other morphs. There are also several other interesting cases of sympatric morphs in Transbaikalia (Alekseyev et al. 2000, 2002). Alekseyev et al. (2002) studied the role of trophic polymorphism by comparing the morphology and diet of sympatric morphs in a number of lakes. They concluded that sympatric morphs have diverged in sympatry, and therefore do not represent separate lineages but that the level of divergence varied between lakes.

Griffiths (1994) analysed published information on the size structure in charr lakes and found that bimodality increased with latitude and was characteristic of deep lakes with few fish species. He discarded most explanations for bimodality and suggested that much of the variation in structure be caused by increased seasonality in food supply with latitude. Parker et al. (2001) developed mathematical models to explain bimodal charr populations. Two alternatives for genetic relationships were assumed: complete reproductive isolation and facultative alternative strategies in a single stock. They proposed that there is an evolutionary significance to 'semi-speciation' within a bimodal population and speculate that there is a dynamic equilibrium whereby speciation is arrested before it becomes complete. Most charr populations will maximise individual fitness in the semi-speciated configuration by incomplete assortative mating.

Skulason et al. (1999) and Eiriksson et al. (1999) suggested that heterochrony can be the driving mechanism through which polymorphism may evolve. Benthic morphotypes are often paedomorphs that retain juvenile characters in the adult phenotype. Heterochrony could be based on simple changes in regulatory genes (Skulason & Smith 1995). Jonsson & Skulason (2000) proposed that the subtle differences found among two benthophagous morphs in the shallow Vatnshlidarvatn, Iceland could be related to heterochrony in an early ontogenetic phase. Adams & Huntingford (2002a) showed that offspring of the pelagic and benthic morphs of Loch Rannoch developed differences in some head measures that must have a genetic basis. Lower jaw length and head depth showed allometric growth that differed between offspring of the two morphs. Adams & Huntingford (2002b) found that offspring of the benthic morph developed a relatively larger gape than the pelagic morph and could handle larger food particles. The two morphs behaved differently towards pelagic and benthic prey types. These experiments support the hypothesis that heterochrony can drive the evolution of trophic polymorphism in charr.

The present review has shown that there is currently considerable research interest in ecological speciation of the Arctic charr complex. Claessen & Dieckmann (2001) concluded that Arctic charr, sticklebacks and cichlids are candidate systems for critical testing of their model for evolutionary branching in size-structured populations through ontogenetic niche shifts. A recent review by McKinnon & Rundle (2002) summarises the important work that has been done on the three-spined stickleback species complex as a natural model for speciation research. The Arctic charr is also important in this respect among northern fishes because of its extreme phenotypic variation and ecological versatility.

Future research in this field should combine modern genetic analyses with fieldwork and experiments. Microsatellite DNA opens new possibilities for genetic analyses because of its resolution power (Brunner et al. 1998). Fieldwork should concentrate on cases of sympatric morphs with emphasis on life histories, morphology and detailed studies of niche parameters, especially among very young fish. Care should be taken to include cases of both ontogenetic and genetic polymorphisms in the sense discussed by Adams (1999). Some experiments have demonstrated genetic differences in morphology and behaviour between sympatric morphs (Skulason et al. 1993; Mikheev et al. 1996; Adams & Huntingford 2002a,b; Klemetsen et al. 2002a). Skulason et al. (1999) emphasised the importance of behaviour because it is flexible, and can therefore be of major adaptive importance, especially in fluctuating environments. Jonsson & Jonsson (2001) concluded that more need to be known about the genetics behind the phenotypic plasticity. Combined field and experimental studies on sympatric morphs with focus on morphometric heterochrony and comparative behaviour are promising fields for future studies of the evolution of the complexity of Arctic charr in recently glaciated lakes.

Resumen

1. Las especies de los generos *Salmo*, *Salvelinus* y *Oncorhyncus* (Subfamilia Salmoninae) son los mas estudiadas de la familia Salmonidae. En este trabajo revisamos varios aspectos relacionados con las variaciones fenotípicas y biológicas de *Salmo salar* L., *Salmo trutta* L. y *Salvelinus alpinus* (L.). Mientras que muchas tácticas y estrategias les son comunes, aparecen diferencias en sus ecologías y dinámicas poblacionales que resultan en una variedad de tópicos desafiantes para la investigación futura.

2. *S. salar* muestra considerable plasticidad fenotípica y variabilidad en caracteres biológicos. Desde formas totalmente residentes en agua dulce donde las hembras pueden madurar a los 10 cm hasta poblaciones anádromas caracterizadas por individuos con tres, cuatro o cinco inviernos en el mar (5SW). Incluso dentro de poblaciones 1SW, mas de 20 tipos de biologías reproductivas distintas pueden ser identificadas. Los juveniles en agua dulce pueden utilizar habitats fluviales y lacustres y mientras la mayor parte de los 'smolts' migran al mar durante la primavera, tambien aparecen migraciones otoñales en algunas poblaciones. En el mar, algunos salmones realizan migraciones oceánicas extensas mientras que otras poblaciones permanecen dentro de los confines geográficos de areas tales como el mar Báltico. En el otro extremo estarían los que residen en estuarios y vuelven al agua dulce para reproducirse despues de permanecer solamente unos meses en el mar. Esta revisión sobre la diversidad de formas biológicas se enfoca sobre aspectos de conservación asociados hacia *S. salar* tanto como sobre las tendencias en abundancias y supervivencia.

3. *Salmo trutta* es indigena de Europa, del norte de Africa y de Asia occidental pero ha sido introducida en, al menos, 24 Paises fuera de Europa y en la actualidad tiene distribución mundial. *S. trutta* explota aguas dulces y salobres (no saladas) para alimentarse y reproducirse y sus poblaciones son a menudo parcialmente migratorias. Mientras que una parte de la población sale para alimentarse en otros lugares, otra parte permanece residente. En sistemas grandes y complejos, la especie es polimórfica con diferentes morfas de diversos tamaños en varias partes de un mismo habitat. Se alimenta cerca de la superficie y cerca de la orilla pero los individuos de mayor tamaño pueden moverse lejos de la orilla. Muestra cambios ontogenéticos de nicho relacionados en parte con el tamaño y en parte con la tasa de desarrollo. Esos cambios se producen cuando la cantidad de energía disponible para el

crecimiento llega a ser demasiado pequeña con individuos de crecimiento mas rápido siendo mas jóvenes y mas pequeños que los que crecen mas lentamente. *S. trutta* es carnívora oportunista pero los individuos se especializan, al menos temporalmente, en alimento particulado. Las larvas de insectos son importantes para los juveniles en rios mientras que epibentos litoral en lagos y peces son mas importantes para las truchas mayores. Los sexos difieren en el uso y en el tamaño de los recursos. Las hembras se inclinan mas que los machos a ser migradores y alimentarse en aguas pelágicas. Los machos, mas que las hembras, explotan aguas corrientes cerca de la orilla y aguas de superficie. Por ello, las hembras se alimentan mas de zooplancton y muestran fenotipos mas uniformes que los machos.

4. *Salvelinus alpinus* es la especie que ocupa las posiciones mas al norte del planeta con una distribución circunpolar en el Holartico que corresponde a la ultima glaciación. Estudios recientes sobre mtDNA indican cinco linajes filo-geográficos (Atlántico, Artico, Bering, Siberia y Nueva Escocia) que pueden tener origen pleistocénico. Tanto la ecología como la expresión fenotípica son mas variables que en ningun otro pez. Los pesos en la primera madurez varian entre 3 g y 12 kg. Diferencias entre poblaciones en la morfología y coloración pueden tener origen genético. *S. alpinus* vive en rios, en el mar y en todos los habitats de lagos olitróficos incluyendo areas profundas. Cambios ontogenéticos de habitat entre habitat lacustres son comunes. Se alimentan de todos los tipos de presas de rios, lagos y en habitats marinos cerca de la orilla pero tienen gran flexibilidad de nicho en la competición. El canibalismo se expresa en muchos casos y puede llegar a ser importante para el desarrollo y para el mantenimiento de distribuciones de tamaño bimodales. La anadromia se localiza en la región norte de su rango y envuelve 40 dias o mas en el mar. Todos los individuos hibernan en agua dulce. Migraciones parciales son comunes pero el grado de anadromía varía entre poblaciones. El alimento en el mar incluye zooplancton y peces pelágicos pero tambien epibenthos. El polimorfismo y las morfas simpátridas han sido muy estudiadas. Como especie prominente en lagos glaciales, *S. alpinus* es una especie importante para estudiar especiación ecológica a traves de estudios de campo combinados con experimentos, en particular, en los campos de la heterocronía morfométrica y el comportamiento comparado.

Acknowledgements

Elisabeth Mølbach helped with drawing the figures on brown trout. J. Malcolm Elliott and J. Lobón-Cerviá commented critically on an early draft of the paper.

References

Acornley, R.M. 1999. Water temperatures within spawning beds in two chalk streams and implications for salmonid egg development. Hydrological Processes 13: 439–446.

Adams, C.E. 1999. Does the underlying nature of polymorphism in the Arctic charr differ across the species? International Society of Arctic Charr Fanatics Information Series 7: 61–67.

Adams, C.E. & Huntingford, F.A. 2002a. Inherited differences in head allometry in polymorphic Arctic charr from Loch Rannoch, Scotland. Journal of Fish Biology 60: 515–520.

Adams, C.E. & Huntingford, F.A. 2002b. The functional significance of inherited differences in feeding morphology in a sympatric polymorphic population of Arctic charr. Evolutionary Ecology 16: 15–25.

Adams, N.J., Power, G. & Barton, D.R. 1989. Diet and daily ration of anadromous Arctic charr in Ungava Bay. Physiology and Ecology Japan 1 (spl.): 253–264.

Adams, C.E., Fraser, D., Huntingford, F.A., Greer, R.B., Askew, C.M. & Walker, A.F. 1998. Trophic polymorphism amongst Arctic charr from Loch Rannoch, Scotland. Journal of Fish Biology 52: 1259–1271.

Alanara, A., Burns, M.D. & Metcalfe, N.B. 2001. Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. Journal of Animal Ecology 70: 980–986.

Alekseyev, S.S. & Pichugin, M.Y. 1998. A new form of charr *Salvelinus alpinus* from lake Davatchan in Transbaikalia and its morphological differences from sympatric forms. Journal of Ichthyology 38: 328–337.

Alekseyev, S.S., Pichugin, M.Y. & Samusenok, V.P. 2000. Diversity of Arctic charrs from Transbaikalia in meristic characters, their position in the complex of *Salvelinus alpinus*, and the origin of sympatric forms. Journal of Ichtyology 40: 279–297.

Alekseyev, S.S., Samusenok, V.P., Matveev, A.N. & Pichugin, M.Y. 2002. Diversification, sympatric speciation, and trophic polymorphism of Arctic charr, *Salvelinus alpinus* complex, in Transbaikalia. Environmental Biology of Fishes 64: 97–114.

Alexander, G.D. & Adams, C.E. 2000.The phenotypic diversity of Arctic charr, *Salvelinus alpinus* (Salmonidae) in Scotland and Ireland. Journal of Ichtyology and Aquatic Biology 4: 77–88.

Alm, G. 1951. The tagging of char, *Salmo alpinus*, Linné, in Lake Vättern. Report of the Institute of Freshwater Research, Drottningholm 32: 15–31.

Alm, G. 1959. Connection between maturity, size and age in fishes. Report of the Institute of Freshwater Research, Drottningholm 40: 5–145.

Amiro, P.G. 1998. The mystery of the missing inner Bay of Fundy salmon. Atlantic Salmon Journal 47: 50–53.

Amundsen, P.-A. 1989. Effects of intensive fishing on food consumption and growth of stunted Arctic charr (*Salvelinus alpinus*. L.) in Takvatn, northern Norway. Physiology and Ecology Japan 1(spl.): 265–278.

Amundsen, P.-A. 1994. Piscivory and cannibalism in Arctic charr (*Salvelinus alpinus* (L.). Journal of Fish Biology 45 (Suppl. A): 181–189.

Amundsen, P.-A. 1995. Feeding strategy of Arctic charr (*Salvelinus alpinus*): general opportunist but individual specialist. Nordic Journal of Freshwater Research 71: 150–165.

Amundsen, P.-A., Klemetsen, A. & Grotnes, P.E. 1993. Rehabilitation of a stunted population of Arctic charr by intensive fishing. North American Journal of Fisheries Management 13: 483–491.

Amundsen, P.-A., Damsgård, B., Arnesen, A.M., Jobling, M. & Jørgensen, E.H. 1995. Experimental evidence of cannibalism and prey specialization in Arctic charr, *Salvelinus alpinus*. Environmental Biology of Fishes 43: 285–293.

Amundsen, P.-A., Siikavuopio, S. & Christensen, G. 1997. Significance and temporal persistence of individual specialization in cannibalistic charr, *Salvelinus alpinus*. Nordic Journal of Freshwater Research 73: 28–34.

Amundsen, P.-A., Svenning, M.-A. & Siikavuopi, S.I. 1999. An experimental comparison of cannibalistic response in different Arctic charr (*Salvelinus alpinus* (L.)) stocks. Ecology of Freshwater Fish 8: 43–48.

Anderson, T.C. 1985. The rivers of Labrador. Canadian Special Publication of Fisheries and Aquatic Sciences 81. viii + 389 pp.

Andrews, C.W. 1966. Landlocked Atlantic salmon (*Salmo salar* L.) in the Terra Nova River system, Newfoundland. The Canadian Field-Naturalist 80: 101–109.

Anonymous. 1994. Report of the study group on anadromous trout. ICES CM 1994/M4: 1–80.

Antonsson, T. & Gudjonsson, S. 2002. Variability in timing and characteristics of Atlantic salmon smolt in Icelandic rivers. Transactions of the American Fisheries Society 131: 643–655.

Arawomo, G.A.O. 1981. Downstream movement of juvenile brown trout, *Salmo trutta* L., in the tributaries of Loch Leven, Kinross, Scotland. Hydrobiologia 77: 129–131.

Armstrong, J.D. & Herbert, N.A. 1997. Homing movements of displaced stream-dwelling brown trout. Journal of Fish Biology 50: 445–449.

Armstrong, J.D., Braithwaite, V.A. & Fox, M. 1998. The response of wild Atlantic salmon parr to acute reductions in water flow. Journal of Animal Ecology 67: 292–297.

Arnesen, A.M., Halvorsen, M. & Nilssen, K.J. 1992. Development of hypoosmoregulatory capacity in Arctic charr (*Salvelinus alpinus*) reared under either continuous light or natural photoperiod. Canadian Journal of Fisheries and Aquatic Sciences 49: 229–237.

Bagenal, T.B. 1969. The relationship between food supply and fecundity in brown trout *Salmo trutta* L. Journal of Fish Biology 1: 167–182.

Baglinière, T.B. & Maisse, G. 1985. Precocious maturation and smoltification in wild Atlantic salmon in the Amorican Massif, France. Aquaculture 45: 249–263.

Bagliniére, J.-L., Maisse, G., Lebail, P.Y. & Nihouarn, A. 1989. Population dynamics of brown trout, *Salmo trutta* L., in a tributary in Brittany (France): spawning and juveniles. Journal of Fish Biology 34: 97–110.

Bagliniére, J.-L., Prévost, E. & Maisse, G. 1994. Comparison of population dynamics of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in a small tributary of the River Scorff (Brittany, France). Ecology of Freshwater Fish 3: 25–34.

Balikci, A. 1980. Charr fishing among the Arviligjuarmiut. In: Balon, E.K., ed. Charrs Salmonid Fishes of the Genus *Salvelinus*. The Hague: Junk, pp. 7–8.

Balon, E.K. 1980. Early ontogeny of the European Arctic charr – altricial form, *Salvelinus (Salvelinus) alpinus alpinus*. In: Balon, E.K., ed. Charrs Salmonid Fishes of the Genus *Salvelinus*. The Hague: Junk, pp. 607–630.

Balon, E.K. & Penczak, T. 1980. The dwarfed charr of Dösener See, an alpine lake in Austria. In: Balon, E.K., ed. Charrs Salmonid Fishes of the Genus *Salvelinus*. The Hague: Junk, pp. 773–796.

Barbour, S.E., Rombough, P.J. & Kerekes, J.J. 1979. A life history and ecologic study of an isolated population of ‘dwarf ‘ouananiche, *Salmo salar*, from Gros Morne National Park, Newfoundland. Naturaliste Canadien 106: 305–311.

Baroudy, E. & Elliott, J.M. 1994. Racial differences in eggs and juveniles of Windermere charr, *Salvelinus alpinus*. Journal of Fish Biology 45: 407–415.

Beacham, T.D. & Murray, C.B. 1993. Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). Journal of Fish Biology 42: 485–508.

Behnke, R.J. 1972. The systematics of salmonid fishes of recently glaciated lakes. Journal of the Fisheries Research Board of Canada 29: 639–671.

Behnke, R.J. 1980. A systematic review of the genus S*alvelinus*. In: Balon, E.K., ed. Charrs Salmonid Fishes of the Genus *Salvelinus*. The Hague: Junk, pp. 441–480.

Behnke, R.J. 1984. Organizing the diversity in of the Arctic charr complex. In: Johnson, L. & Burns, B.L., eds. Biology of the Arctic charr. Winnipeg: University of Manitoba Press, pp. 3–21.

Behnke, R.J. 1986. Brown trout. Trout 27: 42–47.

Behnke, R.J. 1989. Interpreting the phylogeny of *Salvelinus*. Physiology and Ecology Japan 1(spl.): 35–48.

Behnke, R.J. 1991. The ancestry of trout. In: Stolz, J. & Schnell, J., eds. Trout. Harrisburg: Stackpole Books, pp. 2–8.

Belding, D.L. & Kitson, J.A. 1934. Spring-run and fall-run Atlantic salmon. Transactions of the American Fisheries Society 64: 225–230.

Berg, O.K. 1985. The formation of non-anadromous populations of Atlantic salmon, *Salmo salar* L., in Europe Journal of Fish Biology 27: 805–815.

Berg, O.K. & Berg, M. 1987. Migrations of sea trout, *Salmo trutta* L., from the Vardnes River in Northern Norway. Journal of Fish Biology 31: 113–121.

Berg, O.K. & Berg, M. 1989a. Sea growth and time of migration anadromous Arctic charr (*Salvelinus alpinus*) from the Vardnes River, in northern Norway. Canadian Journal of Fisheries and Aquatic Sciences 46: 955–960.

Berg, O.K. & Berg, M. 1989b. The duration of the sea and freshwater residence of the sea trout, *Salmo trutta*, from the Vardnes River in northern Norway. Environmental Biology of Fishes 24: 23–32.

Berg, O.K. & Gausen, O.D. 1988. Life history of a riverine, resident Atlantic salmon *Salmo salar* L. Fauna Norvegica Series A 9: 63–68.

Berg, O.K. & Jonsson, B. 1989. Migratory patterns of anadromous Atlantic salmon, brown trout, and Arctic charr from the Vardnes River in northern Norway. In: Brannon, E. & Jonsson, B., eds. Proceedings of the Salmonid Migration and Distribution Symposium. Seattle: School of Fisheries, University of Washington, pp. 106–115.

Berg, O.K. & Jonsson, B. 1990. Growth and survival rates of the anadromous trout, *Salmo trutta* from the Vardnes River northern Norway. Environmental Biology of Fishes 29: 145–154.

Berg, O.K., Thronæs, E. & Bremset, G. 1998. Energetics and survival of virigin and repeat spawning brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 55: 47–53.

Berg, O.K., Thronæs, E. & Bremset, G. 2000. Seasonal cycle of body composition and energy of brown trout (*Salmo trutta*) in a temperate zone lake. Ecology of Freshwater Fish 9: 163–169.

van den Berghe, E.P. & Gross, M.R. 1989. Natural selection resulting from female breeding competition in Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution 43: 125–140.

Bernatchez, L. 2001. The evolutionary history of brown trout (*Salmo trutta* L.) inferred from phylogeographic, nested clade, and mismatch analyses of mitochondrial DNA variation. Evolution 55: 351–379.

Bernatchez, L., Dempson, J.B. & Martin, S. 1998. Microsatellite gene diversity analysis in anadromous Arctic charr, *Salvelinus alpinus*, from Labrador, Canada. Canadian Journal of Fisheries and Aquatic Sciences 55: 1264–1272.

Bernatchez, L. & Dodson, J.J. 1994. Phylogeographic structure in mitochondrial DNA of the lake whitefish (*Coregonus clupeaformis*) and its relation to Pleistocene glaciations. Canadian Journal of Fisheries and Aquatic Sciences 47: 533–543.

Bernatchez, L. & Wilson, C.C. 1998. Comparative phylogeography of Nearctic and Palearctic fishes. Molecular Ecology 7: 432–452.

Birt, T.P., Green, J.M. & Davidson, W.S. 1991a. Mitochondrial DNA variation reveals genetically distinct sympatric populations of anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 48: 577–582.

Birt, T.P., Green, J.M. & Davidson, W.S. 1991b. Contrasts in development and smolting of genetically distinct sympatric anadromous and nonanadromous Atlantic salmon, *Salmo salar*. Canadian Journal of Zoology 69: 2075–2084.

Bjøru, B. & Sandlund, O.T. 1995. Differences in morphology and ecology within a stunted Arctic charr population. Nordic Journal of Freshwater Research 71: 163–172.

Bodaly, R.A. 1979. Morphological and ecological divergence within the lake whitefish (*Coregonus clupeaformis*) comples in Yukon Territory. Journal of Fisheries Research Board of Canada 36: 1214–1222.

Bohl, M., Leuner, E., Legele, R.D. & Bohl, E. 1989. Reduced Growth of Arctic charr (*Salvelinus alpinus* L.) in the Lake 'Königsee', Bavarian National Park. Physiology and Ecology Japan 1(spl): 639–646.

Bohlin, T., Dellefors, C. & Faremo, U. 1993a. Optimal time and size for smolt migration in wild sea trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences 50: 224–232.

Bohlin, T., Dellefors, C. & Faremo, U. 1993b. Timing of sea-run brown trout (*Salmo trutta*) smolt migration: effects of climatic variation. Canadian Journal of Fisheries and Aquatic Sciences 50: 1132–1136.

Bohlin, T., Dellefors, C. & Faremo, U. 1996. Date of smolt migration depends on body-size but not age in wild sea-run brown trout. Journal of Fish Biology 49: 157–164.

Bohlin, T., Pettersson, J. & Degerman, E. 2001. Population density of migratory and resident brown trout (*Salmo trutta*) in relation to altitude: evidence for a migration cost. Journal of Animal Ecology 70: 112–121.

Boivin, T.G., Power, G. & Barton, D.R. 1989. Biologial social aspects of an inuit winter fishery for Arctic charr (*Salvelinus alpinus*). Physiology and Ecology Japan 1(spl): 653–672.

Borgstrøm, R. & Heggenes, J. 1988. Smoltification of sea trout (*Salmo trutta*) at short length as an adaptation to extremely low summer stream flow. Polskie Archiwum Hydrobiologii 35: 375–384.

Brabrand, Å. 1991. The estimation of pelagic fish density, single fish size and fish biomass of Arctic charr (*Salvelinus alpinus* L.) by echosounding. Nordic Journal of Freshwater Research 66: 44–49.

Brabrand, Å. 1994. Tetthet, biomasse og størrelsesfordeling av pelagisk fiskebestand i Tinnsjøen, Telemark, beregnet med hydroakustikk. LFI, Zoologisk Museum, Oslo, Rapport 148: 1–20 (in Norwegian).

Brabrand, Å., Koestler, A.G. & Borgstrøm, R. 2002. Lake spawning of brown trout related to groundwater influx. Journal of Fish Biology 60: 751–763.

Brännäs, E. & Wiklund, B.-S. 1992. Low temperature growth potential of Arctic charr and rainbow trout. Nordic Journal of Freshwater Research 67: 77–81.

Bremset, G. 2000. Seasonal and diel changes in behaviour, microhabitat use and preferences by young pool-dwelling Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. Environmental Biology of Fishes 59: 163–179.

Brenner, T. 1980. The Arctic charr, *Salvelinus alpinus alpinus*, in the prealpine Attersee, Austria. In: Balon, E.K., ed. Charrs. Salmonid Fishes of the Genus *Salvelinus*. The Hague: Junk, pp. 765–772.

Bridcut, E.E. & Giller, P.S. 1995. Diet variability and foraging strategies in brown trout (*Salmo trutta*): an analysis from subpopulations to individuals. Canadian Journal of Fisheries and Aquatic Sciences 52: 2543–2552.

Brooks, J.L. & Dodson, S.I. 1965. Predation, body size, and composition of plankton. Science 150: 28–35.

Brown, J.H., Marquet, P.A. & Taper, M.L. 1993. Evolution of body size: consequences of an energetic definition of fitness. The American Naturalist 142: 573–584.

Brown, J.H., Marquet, P.A. & Taper, M.L. 1996. Darwinian fitness and reproductive power: reply to Kozlowski. The American Naturalist 147: 1092–1097.

Bruce, W.J. 1974. The limnology and fish populations of Jacopie Lake, West Forebay, Smallwood Reservoir, Labrador. Fisheries and Marine Service Technical Report Series no. NEW/T-74–2.

Bruce, W.J. 1976. Age, growth, maturity and food habits of landlocked Salmon (*Salmo salar*) in Soldiers Pond, a Newfoundland Lake. Fisheries and Marine Service Technical Report 668. 16 pp.

Brunner, P.C., Douglas, M.R. & Bernatchez, L. 1998. Microsatellite and mitochondrial DNA assessment of population structure and stocking effects in Arctic charr *Salvelinus alpinus* (Teleostei: Salmonidae) from central Alpine lakes. Molecular Ecology 7: 209–223.

Brunner, P.C., Douglas, M.R., Osinov, A., Wilson, C.C. & Bernatchez, L. 2001. Holarctic phylogeography of Arctic charr (*Salvelinus alpinus* L.) inferred from mitochondrial DNA sequences. Evolution 55: 573–586.

Brynildson, O.M. & Brynildson, C.L. 1984. Impact of flood retarding structure on year class strength and production of wild brown trout in a Wisconsin coulee stream. Wisconsin Department and Nature Research, Technical Bulletin 146: 1–20.

Bunnell, D.B., Isley, J.J., Burrell, K.H. & VanLear, D.H. 1998. Diel movement of brown trout in a southern Appalanchian river. Transactions of the American Fisheries Society 127: 630–636.

Cairns, D.K., ed. 2001. An evaluation of possible causes of the decline in pre-fishery abundance of North American Atlantic Salmon. Canadian Technical Report of Fisheries and Aquatic Sciences 2358. vi + 67pp.

Campbell, J.S. 1977. Spawning characteristics of brown trout and sea trout *Salmo trutta* L. in Kirk Burn, River Tweed, Scotland. Journal of Fish Biology 11: 217–229.

Cavalli, L., Pech, N., Tron, L. & Chappaz, R. 2002. Growth patterns of Arctic charr in five high altitude lakes in the French Alpine massif. Journal of Fish Biology 60: 453–465.

Chadwick, E.M.P. 1982. Stock–recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. Canadian Journal of Fisheries and Aquatic Sciences 39: 1496–1501.

Chadwick, E.M.P. 1987. Causes of variable recruitment in a small Atlantic salmon stock. American Fisheries Society Symposium 1: 390–401.

Chadwick, E.M.P. & Green, J.M. 1985. Atlantic salmon (*Salmo salar*) production in a largely lacustrine Newfoundland watershed. Verhandlungen Internationale Vereinigung für Theoretische und Angewandte Limnologie 22: 2509–2525.

Chadwick, E.M.P., Randall, R.G. & Léger, C. 1986. Ovarian development of Atlantic salmon (*Salmo salar*) smolts and age at first maturity. In: Meerburg, D.J., eds. Salmonid Age at Maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89. pp. 15–23.

Champigneulle, A., Buttiker, B., Durand, P. & Melhaoui, M. 1999. Main characteristics of the biology of the trout

(*Salmo trutta* L.) in Lake Léman (Lake Geneva) and some of its tributaries. In: Baglinière, J.L. & Maisse, G., eds. Biology and Ecology of the Brown Trout and Sea Trout. Berlin: Springer-Praxis Series in Aquaculture and Fisheries, pp. 147–174.

Champigneulle, A. & Gerdeaux, D. 1995. Survey, management and recent rehabilitation of the Arctic charr (*Salvelinus alpinus*) fishery in the French-Swiss Lake Leman. Nordic Journal of Freshwater Research 71: 173–182.

Chapman, D.W. 1978. Production in fish populations. In: Gerking, S.D., ed. Ecology of Freshwater Fish Production. Oxford: Blackwell, pp. 5–25.

Chaput, G. & Prévost, E. 2001. Reference points to improve Atlantic salmon management. In: Prévost, E. & Chaput, G., eds. Stock, Recruitment and Reference Points: Assessment and Management of Atlantic Salmon. Paris: Hydrobiobiologie et Aquaculture, INRA Editions, pp. 17–24.

Chaput, G., Allard, J., Caron, F., Dempson, J.B., Mullins, C.C. & O'Connell, M.F. 1998. River-specific target spawning requirements for Atlantic salmon (*Salmo salar*) based on a generalized smolt production model. Canadian Journal of Fisheries and Aquatic Sciences 55: 246–261.

Chereshnev, I.A. 1996. Threatened fishes of the world: *Salvethymus svetovidovi* Chereshnev & Skopets, 1990 (Salmonidae). Environmental Biology of Fishes 46: 166.

Chereshnev, I.A. 1998. Threatened fishes of the world: *Salvelinus elgyticus* Viktorovskii & Glubokovskii, 1981 (Salmonidae). Environmental Biology of Fishes 51: 24.

Chereshnev, I.A. & Skopets, M.B. 1990. *Salvethymus svetovidovi* genus et species nova. A new endemic fish of the subfamily Salmoninae from the Lake Elgygytgyn (Central Chukotka). Journal of Ichtyology 30: 87–103.

Chereshnev, I.A. & Skopets, M.B. 1999. New data on the morphology and biology of charrs of Elgygytgyn Lake (Central Chukotka). International Society of Arctic Char Fanatics Information Series 7: 93–99.

Claessen, D. & Dieckmann, U. 2001. Ontogenetic niche shifts and evolutionary branching in size-structured populations. International Institute for Applied Systems Analysis, Interim Report IR-01-056: 1–33.

Claireaux, G. & Audet, C. 2000. Seasonal changes in the hypo-osmoregulatory of brook charr: the role of environmental factors. Journal of Fish Biology 56: 347–373.

Craig, J.F. 1982. A note on growth and mortality of trout, *Salmo trutta* L., in afferent streams of Windermere. Journal of Fish Biology 20: 423–429.

Crisp, D.T. 1988. Prediction from temperature of eyeing, hatching and 'swim up' times for salmonid embryos. Freshwater Biology 19: 41–48.

Crisp, D.T. 1993. Population-densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. Journal of Applied Ecology 30: 759–771.

Crisp, D.T. 2000. Trout and salmon: ecology, conservation and rehabilitation. Oxford: Fishing. News Books, Blackwell Science.

Crisp, D.T., Mann, R.H.K. & Cubby, R.P. 1984. Effects of impoundment upon fish populations in afferent streams at Cow Green Reservoir. Journal of Applied Ecology 21: 739–756.

Crozier, W.W. & Kennedy, G.J.A. 1999. Relationships between marine growth and marine survival of one sea winter Atlantic salmon, *Salmo salar* L. from the River Bush, Northern Ireland. Fisheries Management and Ecology 6: 89–96.

Cunjak, R.A. 1992. Comparative feeding, growth and movements of Atlantic salmon (*Salmo salar*) parr from riverine and estuarine environments. Ecology of Freshwater Fish 1: 26–34.

Cunjak, R.A. & Therrien, J. 1998. Inter-stage survival of wild juvenile Atlantic salmon, *Salmo salar* L. Fisheries Management and Ecology 5: 209–223.

Cunjak, R.A., Chadwick, E.M.P. & Shears, M. 1989. Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 46: 1466–1471.

Cunjak, R.A., Prowse, T.D. & Parrish, D.L. 1998. Atlantic salmon (*Salmo salar*) in winter: 'the season of parr discontent'. Canadian Journal of Fisheries and Aquatic Sciences 55: 161–180.

Cunjak, R.A., Saunders, R.L. & Chadwick, E.M.P. 1990. Seasonal variations in the smolt characteristics of juvenile Atlantic salmon (*Salmo salar*) from estuarine and riverine environments. Canadian Journal of Fisheries and Aquatic Sciences 47: 813–820.

Curry-Lindahl, K. 1957. The occurrence of the char, *Salmo alpinus*, in running waters in arctic and high boreal areas in Sweden. Kungliga Fysiografiske Sällskapet i Lund, Förhandlingar 27: 147–172.

Dahl, K. 1928. The dwarf salmon of Lake Byglandsfjord. Salmon and Trout Magazine 51: 108–112.

Dahl-Hansen, G.A.P. 1995. Long-term changes in crustacean zooplankton – the effects of a mass removal of Arctic charr, *Salvelinus alpinus* (L.) from an oligotrophic lake. Journal of Plankton Research 17: 1819–1833.

Dahl-Hansen, G.A.P. 1998. The relationship between selective feeding in Arctic charr, *Salvelinus alpinus* (L), and crustacean plankton: a study on the effects of a mass removal of Arctic charr. Dr Scient Thesis. The Norwegian College of Fisheries Science, University of Tromsø.

Dahl-Hansen, G.A.P., Rubach, S.H. & Klemetsen, A. 1994. Selective predation by pelagic Arctic charr on crustacean plankton in Takvatn, northern Norway, before and after mass removal of Arctic charr. Transactions of the American Fisheries Society 123: 385–394.

Dalley, E.L., Andrews, C.W. & Green, J.M. 1983. Precocious male Atlantic salmon parr (*Salmo salar*) in insular Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 40: 647–652.

Damsgård, B. 1993. Biomanipulation with piscivorous fish. An experimental study of prey selection, food consumption and growth of piscivorous brown trout, *Salmo trutta* L. & Arctic charr *Salvelinus alpinus* (L.). Dr Scient Thesis, The Norwegian College of Fisheries Science, University of Tromsø.

Damsgård, B. & Langeland, A. 1994. Effects of stocking of piscivorus brown trout, *Salmo trutta* L., on stunted Arctic charr, *Salvelinus alpinus* (L.). Ecology of Freshwater Fish 3: 59–66.

Davies, P.E. & Sloane, R.D. 1987. Characteristics of the spawning migrations of brown trout, *Salmo trutta* L. & rainbow trout, *S. gairdneri* Richardson, in Great Lake, Tasmania. Journal of Fish Biology 31: 353–373.

Dellefors, C. & Faremo, U. 1988. Early sexual maturation in males of wild sea trout, *Salmo trutta* L., inhibits smoltification. Journal of Fish Biology 33: 741–749.

Dempson, J.B. 1993. Salinity tolerance of freshwater acclimated, small-sized Arctic charr, *Salvelinus alpinus* from northern Labrador. Journal of Fish Biology 43: 451–462.

Dempson, J.B. 1995. Trends in population characteristics of an exploited anadromous population of Arctic charr, *Salvelinus alpinus*, stock in northern Labrador. Nordic Journal of Freshwater Research 71: 197–216.

Dempson, J.B. & Green, J.M. 1985. Life history of anadromous Arctic charr, *Salvelinus alpinus*, in the Fraser River, northern Labrador. Canadian Journal of Zoology 63: 315–324.

Dempson, J.B. & Kristofferson, A.H. 1987. Spatial and temporal aspects of the ocean migration of anadromous Arctic char. American Fisheries Society Symposium 1: 340–357.

Dempson, J.B. & Misra, R.K. 1984. Identification of anadromous Arctic charr (*Salvelinus alpinus*) stocks in coastal areas of northern Labrador based on multivariate statistical analysis of meristic data. Canadian Journal of Zoology 62: 631–636.

Dempson, J.B. & O'Connell, M.F. 1993. Impacts of the 1992 Atlantic Salmon (*Salmo salar* L.) commercial fishery moratorium – Newfoundland Region. Department of Fisheries and Oceans Atlantic Fisheries Research Document 93/11. 28 pp.

Dempson, J.B. & Shears, M. 1998. Characteristics of commercially exploited anadromous Arctic charr, *Salvelinus alpinus*, populations on northern Labrador with emphasis on the Voisey and Okak stock complex. International Society of Arctic Char Fanatics Information Series 6: 27–46.

Dempson, J.B., Myers, R.A. & Reddin, D.G. 1986. Age at first maturity of Atlantic salmon (*Salmo salar*) – influences of the marine environment. In: Meerburg, D.J., ed. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89, pp. 79–89.

Dempson, J.B., O'Connell, M.F. & Shears, M. 1996. Relative production of Atlantic salmon from fluvial and lacustrine habitats estimated from analyses of scale characteristics. Journal of Fish Biology 48: 329–341.

Dempson, J.B., Reddin, D.G., O'Connell, M.F., Helbig, J., Bourgeois, C.E., Mullins, C., Porter, T.R., Lilly, F., Carscadden, J., Stenson, G.B. & Kulka, D. 1998. Spatial and temporal variation in Atlantic salmon abundance in the Newfoundland-Labrador region with emphasis on factors that may have contributed to low returns in 1997. Department of Fisheries and Oceans, Canadian Stock Assessment Secretariat Research Document 98/114. 161 pp.

Dempson, J.B., Pepper, V.A., Furey, G., Bloom, M., Nicholls, T. & Hoskins, G. 1999a. Evaluation of an alternate strategy to enhance salmon populations: cage rearing wild smolts from Conne River. Newfoundland ICES Journal of Marine Science 56: 422–432.

Dempson, J.B., Furey, G. & Bloom, M. 1999b. Status of Atlantic salmon in Conne River, SFA 11, Newfoundland, 1998. Department of Fisheries and Oceans Canadian Stock Assessment Secretariat Research Document 99/92. 51 pp.

Dempson, J.B., Furey, G. & Bloom, M. 2001a. Assessment of the status of the Atlantic salmon stock of Conne River, SFA 11, Newfoundland, 2000. Canadian Science Advisory Secretariat Research Document 2001/030. 45 pp.

Dempson, J.B., Schwarz, C.J., Reddin, D.G., O'Connell, M.F., Mullins, C.C. & Bourgeois, C.E. 2001b. Estimation of marine exploitation rates on Atlantic salmon (*Salmo salar* L.) stocks in Newfoundland, Canada. ICES Journal of Marine Science 58: 331–341.

Dempson, J.B., O'Connell, M.F. & Cochrane, N.M. 2001c. Potential impact of climate warming on recreational fishing opportunities for Atlantic salmon, *Salmo salar* L. in Newfoundland, Canada. Fisheries Management and Ecology 8: 69–82.

Dempson, J.B., Shears, M. & Bloom, M. 2002. Spatial and temporal variability in the diet of anadromous Arctic charr, *Salvelinus alpinus*, in northern Labrador. Environmental Biology of Fishes 64: 49–62.

DFO. 2002a. Newfoundland & Labrador Atlantic salmon stock status for 2001. Department of Fisheries and Oceans Science Stock Status Report D2-01(2002). 20pp.

DFO. 2002b. Atlantic salmon Maritime Provinces Overview for 2001. Department of Fisheries and Oceans Science Stock Status Report D3-14(2002). 43 pp.

Dieperink, C., Pedersen, S. & Pedersen, M.I. 2001. Estuarine predation on radiotagged wild domesticated sea trout (*Salmo trutta* L.) smolts. Ecology of Freshwater Fish 10: 177–183.

Dill, L.M. 1983. Adaptive flexibility in the foraging behaviour of fishes. Canadian Journal of Fisheries and Aquatic Sciences 40: 398–408.

Downton, P.R., Reddin, D.G. & Johnson, R.W. 2001. Status of Atlantic salmon (*Salmo salar* L.) in Campbellton River, Notre Dame Bay (SFA 4), Newfoundland in 2000. Canadian Science Advisory Secretariat Research Document 2001/031. 73 pp.

Drinkwater, K.F. 2000. Changes in ocean climate and its general effect of fisheries: examples from the north-west Atlantic. In: Mills, D., eds. The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Oxford: Fishing News Books, Blackwell Science, pp. 116–136.

Duarte, C.M. & Alcaraz, M. 1989. To produce many small or few large eggs: a size-independent reproductive tactic of fish. Oecologia 80: 401–404.

Ducharme, L.J.A. 1969. Atlantic salmon returning for their fifth and sixth consecutive spawning trips. Journal of the Fisheries Research Board of Canada 26: 1661–1664.

Dutil, J.D. 1986. Energetic constraints and spawning interval in the anadromous Arctic charr (*Salvelinus alpinus*). Copeia 1986: 945–955.

Egglishaw, H.J. & Shackley, P.E. 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream 1966–75. Journal of Fish Biology 11: 647–672.

Einarsson, S.M., Mills, D.H. & Johannsson, V. 1990. Utilisation of fluvial and lacustrine habitat by anadromous Atlantic salmon, *Salmo salar* L., in an Icelandic watershed. Fisheries Research 10: 63–71.

Einum, S. & Fleming, I.A. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proceedings of the Royal Society of London, Series B 266: 2095–2100.

Eiriksson, G.M., Skulason, S. & Snorrason, S.S. 1999. Heterochrony in skeletal development and body size in progeny of two morphs of Arctic charr from Thingvallavatn, Iceland. Journal of Fish Biology 55 (Suppl A): 175–185.

Eliassen, R.E., Johnsen, H.K., Mayer, I. & Jobling, M. 1998. Contrasts in osmoregulatory capacity of two Arctic charr *Salvelinus alpinus* (L.) strains from northern Norway. Aquaculture 168: 255–269.

Elliott, J.M. 1966. Downstream movements of trout fry (*Salmo trutta*) in a Dartmoor stream. Journal of Fisheries Research Board of Canada 23: 157–159.

Elliott, J.M. 1975. The growth rate of brown trout (*Salmo trutta* L.) fed on maximum rations. Journal of Animal Ecology 44: 805–821.

Elliott, J.M. 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966–83. Journal of Animal Ecology 53: 327–350.

Elliott, J.M. 1985. Growth, size, biomass and production for different life-stages of migratory trout, *Salmo trutta*, in a Lake District stream, 1966–1983. Journal of Animal Ecology 54: 985–1002.

Elliott, J.M. 1986. Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a Lake District stream. Journal of Animal Ecology 55: 907–922.

Elliott, J.M. 1993. The self-thinning rule applied to juvenile sea-trout, *Salmo trutta*. Journal of Animal Ecology 62: 371–379.

Elliott, J.M. 1994. Quantitative Ecology and the Brown Trout. Oxford: Oxford University Press. xi + 286 pp.

Elliott, J.M. 1995. Fecundity and egg density in the redd for sea trout. Journal of Fish Biology 47: 8893–8901.

Elliott, J.M. 1997. Stomach contents of adult sea trout caught in six English rivers. Journal of Fish Biology 50: 1129–1132.

Elliott, J.M. 2001. The relative role of density in the stock–recruitment relationship of salmonids. In: Prévost, E. & Chaput, G., eds. Stock, recruitment and reference points: assessment and management of Atlantic Salmon. Paris: Hydrobiobiologie et Aquaculture, INRA Editions, pp. 25–66.

Elliott, J.M. & Baroudy, E. 1995. The ecology of Arctic charr, *Salvelinus alpinus*, and brown trout, *Salmo trutta*, in Windermere (northwest England). Nordic Journal of Freshwater Research 71: 33–48.

Elliott, J.M. & Hurley, M.A. 1997. A functional model for maximum growth of Atlantic salmon parr, *Salmo salar*, from two populations in northwest England. Functional Ecology 11: 592–603.

Elliott, J.M. & Hurley, M.A. 1998a. An individual-based model for predicting the emergence period of sea-trout fry in a Lake District stream. Journal of Fish Biology 53: 414–433.

Elliott, J.M. & Hurley, M.A. 1998b. Predicting fluctuations in the size of newly-emerged sea-trout fry in a Lake District stream. Journal of Fish Biology 53: 1120–1133.

Elliott, J.M. & Hurley, M.A. 2000. Daily energy intake and growth of piscivorous brown trout, *Salmo trutta*. Freshwater Biology 44: 237–245.

Elliott, J.M. & Klemetsen, A. 2002. The upper critical thermal limits for alevins of Arctic charr from a Norwegian lake north of the Arctic circle. Journal of Fish Biology 60: 1338–1341.

Elliott, J.M., Hurley, M.A. & Fryer, R.J. 1995. A new, improved growth model for brown trout, *Salmo trutta* L. Functional Ecology 9: 290–298.

Elliott, J.M., Fletcher, J.M., Elliott, J.A., Cubby, P.R. & Baroudy, E. 1996. Changes in the population density of pelagic salmonids in relation to changes in lake enrichment in Windermere (northwest England). Ecology of Freshwater Fish 5: 153–162.

Elliott, S.R., Coe, T.A., Helfield, J.M. & Naiman, R.J. 1998. Spatial variation in environmental characteristics of Atlantic salmon (*Salmo salar*) rivers. Canadian Journal of Fisheries and Aquatic Sciences 55: 267–280.

Ellner, S. & Hairston, N.G. Jr. 1994. Role of overlapping generations in maintaining genetic variation in a fluctuating environment. American Naturalist 143: 403–417.

Elso, J.I. & Greenberg, L.A. 2001. Habitat use, movements and survival of individual 0+ brown trout (*Salmo trutta*) during winter. Archiv für Hydrobiologie 152: 279–295.

Erkinaro, J., Dempson, J.B., Julkunen, M. & Niemelä, E. 1997. Importance of ontogenetic habitat shifts to juvenile output and life history of Atlantic salmon in a large subarctic river: an approach based on analysis of scale characteristics. Journal of Fish Biology 51: 1174–1185.

Erkinaro, J. & Gibson, R.J. 1997a. Interhabitat migration of juvenile Atlantic salmon in a Newfoundland river system, Canada. Journal of Fish Biology 51: 373–388.

Erkinaro, J. & Gibson, R.J. 1997b. Movements of Atlantic salmon, *Salmo salar* L., parr and brook trout, *Salvelinus fontinalis* (Mitchill), in lakes, and their impact on single-census population estimation. Fisheries Management and Ecology 4: 369–384.

Erkinaro, J., Shustov, Y. & Niemelä, E. 1995. Enhanced growth and feeding rate in Atlantic salmon parr occupying a lacustrine habitat in the River Utsjoki, northern Scandinavia. Journal of Fish Biology 47: 1096–1098.

Erkinaro, J., Niemelä, E., Saari, A., Shustov, Y. & Jørgensen, L. 1998a. Timing of habitat shift by Atlantic salmon parr from fluvial to lacustrine habitat: analysis of age distribution, growth, and scale characteristics. Canadian Journal of Fisheries and Aquatic Sciences 55: 2266–2273.

Erkinaro, J., Shustov, Y. & Niemelä, E. 1998b. Feeding strategies of Atlantic salmon *Salmo salar* parr occupying lacustrine and fluvial habitats in a subarctic river, northern Finland. Polskie Archiwum Hydrobiologii 45: 259–268.

Euzenat, G. 1999. Sea trout (*Salmo trutta* L.) in Normandy and Picardy. In: Baglinière, J.L. & Maisse, G., eds. Biology and ecology of the brown trout and sea trout. Berlin: Springer-Praxis Series in Aquaculture and Fisheries, pp. 175–203.

Evermann, B.W. 1925. In: Mcfarland, W.L., ed. Salmon of the Atlantic. New York: Parke, Austin & Lipscomb, Inc, pp. v–viii.

Fahy, E. 1978. Variation in some biological characteristics of British sea trout, *Salmo trutta* L. Journal of Fish Biology 13: 123–138.

Fahy, E. 1983. Food and gut parasite burden of migratory trout *Salmo trutta* L. in the sea. Irish Naturalists' Journal 21: 11–18.

Fahy, E. 1985. Cyclic fluctuations in the abundance of trout (*Salmo trutta* L.). Archium für Hydrobiologie Supplementband 3: 404–428.

Fairchild, W.L., Swansburg, E.O., Arseenault, J.T. & Brown, S.B. 1999. Does an association between pesticide use and subsequent declines in catch of Atlantic salmon (*Salmo salar*) represent a case of endocrine disruption? Environmental Health Perspectives 107: 349–357.

Ferguson, A. & Taggart, J.B. 1991. Genetic differentiation among sympatric brown trout (*Salmo trutta*) in Loch Melvin, Ireland. Biological Journal of the Linnean Society 43: 221–237.

Finstad, B. & Heggberget, T.G. 1993. Migration, growth and survival of wild and hatchery-reared anadromous Arctic charr (*Salvelinus alpinus*) in Finnmark, northern Norway. Journal of Fish Biology 43: 303–312.

Finstad, B. & Ugedal, O. 1998. Smolting in sea trout (*Salmo trutta* L.) in northern Norway. Aquaculture 168: 341–349.

Finstad, B., Nilssen, K.J. & Arnesen, A.M. 1989. Seasonal changes in sea-water tolerance of Arctic charr (*Salvelinus alpinus*). Journal of Comparative Physiology B 159: 371–378.

Finstad, A., Jansen, P.A. & Langeland, A. 2000. Gillnet selectivity, and size and age structure of an alpine Arctic charr (*Salvelinus alpinus*) population. Canadian Journal of Fisheries and Aquatic Sciences 57: 1718–1727.

Finstad, A., Jansen, P.A. & Langeland, A. 2001. Production and predation rates in a cannibalistic Arctic charr (*Salvelinus alpinus*) population. Ecology of Freshwater Fish 10: 220–226.

Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6: 379–416.

Fleming, I.A. & Gross, M.R. 1990. Latitudinal clones: a trade-off between egg number and size in Pacific salmon. Ecology 71: 1–11.

Forseth, T., Hurley, M.A., Jensen, A.J. & Elliott, J.M. 2001. Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. Freshwater Biology 46: 173–186.

Forseth, T., Næsje, T.F., Jonsson, B. & Hårsaker, K. 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology 68: 783–793.

Forseth, T., Ugedal, O. & Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic charr, *Salvelinus alpinus*. Journal of Animal Ecology 63: 116–126.

Friedland, K.D. 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. Canadian Journal of Fisheries and Aquatic Sciences 55: 119–130.

Friedland, K.D., Reddin, D.G. & Kocik, J.F. 1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. ICES Journal of Marine Science 50: 481–492.

Friedland, K.D., Hansen, L.P. & Dunkley, D.A. 1998. Marine temperatures experienced by postsmolts and the survival of Atlantic salmon, *Salmo salar* L., in the North Sea area. Fisheries Oceanography 7: 22–34.

Frost, W.E. & Brown, M.E. 1967. The Trout. London: Collins. 316 pp.

Garcia-Marin, J.-L., Utter, F.M. & Pla, C. 1999. Postglacial colonization of brown trout in Europe based on distribution of allozyme variants. Heredity 82: 46–56.

Garcia-Vazquez, E., Moran, P., Martinez, J.L., Perez, J., de Gaudemar, B. & Beall, E. 2001. Alternative mating strategies in Atlantic salmon and brown trout. Journal of Heredity 92: 146–149.

Gibson, R.J. 1966. Some factors influencing the distributions of brook trout and young Atlantic salmon. Journal of the Fisheries Research Board of Canada 23: 1977–1980.

Gibson, R.J. 1988. Mechanisms regulating species composition, population structure, and production of stream salmonids; a review. Poliskie Archiwum Hydrobiologii 35: 469–495.

Gibson, R.J. 1993. The Atlantic salmon in freshwater: spawning, rearing and production. Reviews in Fish Biology and Fisheries 3: 39–73.

Gibson, R.J. 2002. The effects of fluvial processes and habitat heterogeneity on distribution, growth and densities of juvenile Atlantic salmon (*Salmo salar* L.), with consequences on abundance of the adult fish. Ecology of Freshwater Fish 11: 207–222.

Gibson, R.J., Stansbury, D.E., Whalen, R.R. & Hillier, K.G. 1993. Relative habitat use, and inter-specific and intra-specific competition of brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) in some Newfoundland rivers. In: Gibson, R.J. & Cutting, R.E., eds. Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. Canadian Special Publication of Fisheries and Aquatic Sciences 118, pp. 53–69.

Gibson, R.J., Williams, D.D., McGowan, C. & Davidson, W.S. 1996. The ecology of dwarf fluvial Atlantic salmon, *Salmo salar* L., cohabiting with brook trout, *Salvelinus fontinalis* (Mitchill), in southeastern Newfoundland, Canada. Polskie Archiwum Hydrobiologii 43: 145–166.

Gislason, D., Ferguson, M.M., Skulason, S. & Snorrason, S.S. 1999. Rapid and coupled phenotypic and genetic divergence in Icelandic Arctic charr (*Salvelinus alpinus*). Canadian Journal of Fisheries and Aquatic Sciences 56: 2229–2234.

Gorman, G.C. & Nielson, L.A. 1982. Piscivory by stocked brown trout (*Salmo trutta*) and its impact on the nongame fish community of Bottom Creek, Virginia. Canadian Journal of Fisheries and Aquatic Sciences 39: 862–869.

Gowan, C., Young, M.K., Fausch, K.D. & Riley, S.C. 1994. Restricted movement in resident stream salmonids: a paradigm lost. Canadian Journal of Fisheries and Aquatic Sciences 51: 2626–2637.

Greenberg, L., Steinwall, T. & Persson, H. 2001. Effect of depth and substrate on use of stream pools by brown trout. Transactions of the American Fisheries Society 130: 699–705.

Grey, J. 2001. Ontogeny and dietary specialization in brown trout (*Salmo trutta* L.) from Loch Ness, Scotland, examined using stable isotopes of carbon and nitrogen. Ecology of Freshwater Fish 10: 168–176.

Griffiths, D. 1994. The size structure of lacustrine Arctic charr (Pisces: Salmonidae) populations. Biological Journal of the Linnean Society 51: 337–357.

Grønvik, S. & Klemetsen, A. 1987. Marine food and diet overlap of co-occurring Arctic charr *Salvelinus alpinus* (L.), brown trout *Salmo trutta* L. and Atlantic salmon *S. salar* L. off Senja, N Norway. Polar Biology 7: 173–177.

Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. Nature 313: 47–48.

Gross, M.R., Coleman, R.M. & McDowall, R.M. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239: 1291–1293.

Guiguer, K.R.R.A., Reist, J.D., Power, M. & Babaluk, J.A. 2002. Using stable isotopes to confirm the trophic ecology of Arctic charr morphotypes from Lake Hazen, Nunavut, Canada. Journal of Fish Biology 60: 348–362.

Gullestad, N. 1975. On the biology of char (*Salmo alpinus* L.) in Svalbard. I. Migratory and non-migratory char in Revvatnet, Spitsbergen. Norsk Polarinstitutt, Årbok 1973: 125–140.

Gullestad, N. & Klemetsen, A. 1997. Size, age and spawning frequency of landlocked Arctic charr *Salvelinus alpinus* (L.) in Svartvatnet, Svalbard. Polar Research 16: 85–92.

Gulseth, O.A. & Nilssen, K.J. 2000. The brief period of spring migration, short marine residence, and high return rate of a northern Svalbard population of Arctic char. Transactions of the American Fisheries Society 129: 782–769.

Günther, A. 1877. An account of the fishes collected by Capt. Fielden between 78° and 89°N Lat during the Arctic expedition of 1875–1876. Proceedings of the Zoological Society of London 1877: 293–295.

Gydemo, R. 1983. The Arctic charr in Lake Leynavatn, Faroe Islands. International Society of Arctic Char Fanatics Information Series 2: 43–46.

Gyselman, E.C. 1984. The seasonal movements of anadromous Arctic charr at Nauyuk Lake, Northwest Territories, Canada. In: Johnson, L. & Burns, B.L., eds. Biology of the Arctic charr. Winnipeg: University of Manitoba Press, pp. 575–578.

Halvorsen, M. & Jørgensen, L. 1996. Lake-use by juvenile Atlantic salmon (*Salmo salar* L.) and other salmonids in northern Norway. Ecology of Freshwater Fish 5: 28–36.

Halvorsen, M., Jørgensen, L. & Amundsen, P.-A. 1997. Habitat utilization of juvenile Atlantic salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* (L.) in two lakes in northern Norway. Ecology of Freshwater Fish 6: 67–77.

Halvorsen, M. & Svenning, M.-A. 2000. Growth of Atlantic salmon parr in fluvial and lacustrine habitats. Journal of Fish Biology 57: 145–160.

Hammar, J. 1982. Röding i Arktis. Fauna Och Flora 77: 85–92 (In Swedish with an English summary).

Hammar, J. 1984. Ecological characters of different combinations of sympatric populations of Arctic charr in Sweden. In: Johnson, L. & Burns, B.L., eds. Biology of the Arctic charr. Winnipeg: University of Manitoba Press, pp. 35–64.

Hammar, J. 1989. Freshwater ecosystems of polar regions: vulnerable resources. Ambio 18: 6–22.

Hammar, J. 1998. Interactive asymmetry and seasonal niche shifts in sympatric arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*): evidence from winter diet and accumulation of radiocesium. Nordic Journal of Freshwater Research 74: 33–64.

Hammar, J. 2000. Cannibals and parasites: conflicting regulators of bimodality in high latitude Arctic char, *Salvelinus alpinus*. Oikos 88: 33–47.

Handeland, S.O., Berge, A. & Bjørnsson, B.T. 1998. Effects of temperature and salinity on osmoregulation and growth of Atlantic salmon (*Salmo salar* L.) smolts in seawater. Aquaculture 168: 289–302.

Hansen, L.P. & Jonsson, B. 1991. Evidence of a genetic component in the seasonal return pattern of Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 38: 251–258.

Hansen, L.P., Jonsson, N. & Jonsson, B. 1993. Oceanic migration in homing Atlantic salmon. Animal Behaviour 45: 927–941.

Hansen, L.P. & Quinn, T.P. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl 1): 104–118.

Haraldstad, Ø. & Jonsson, B. 1983. Age and sex segregation in habitat utilization by brown trout in a Norwegian lake. Transactions of American Fisheries Society 112: 27–37.

Haraldstad, Ø., Jonsson, B., Sandlund, O.T. & Schei, T.A. 1987. Lake effect on stream living brown trout (*Salmo trutta*). Archievium für Hydrobiologie 109: 39–48.

Harris, G.S. 1973. Rearing smolts in mountain lakes to supplement salmon stocks. International Atlantic Salmon Foundation Special Publication Series 4: 237–252.

Hartley, S.E., Bartlett, S.E. & Davidson, W.S. 1992a. Mitochondrial DNA analysis of Scottish populations of Arctic charr, *Salvelinus alpinus* (L.). Journal of Fish Biology 40: 219–224.

Hartley, S.E., McGowan, C., Greer, R.B. & Walker, A.F. 1992b. The genetics of sympatric Arctic charr (*Salvelinus alpinus* L.) populations from Loch Rannoch, Scotland. Journal of Fish Biology 41: 1021–1031.

Hartmann, J. 1984. The charrs (*Salvelinus alpinus*) of Lake Constance, a lake undergoing cultural eutrofication. In: Johnson, L. & Burns, B.L., eds. Biology of the Arctic charr. Winnipeg: University of Manitoba Press, pp. 471–486.

Haury, J., Ombredane, D. & Baglinière, J.L. 1999. The habitat of the brown trout (*Salmo trutta* L.) in water courses. In: Baglinière, J.L. & Maisse, G., eds. Biology and ecology of the brown trout and sea trout. Berlin: Springer-Praxis Series in Aquaculture and Fisheries, pp. 37–89.

He, J.X. & Steward, D.J. 2002. A stage-explicit expression of the von Bertalanffy growth model for understanding age at first reproduction of Great Lakes fishes. Canadian Journal of Fisheries and Aquatic Sciences 59: 250–261.

Heggberget, T.G. 1984. Habitat selection and segregation of parr of Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar* L.) in two streams in North Norway. In: Johnson, L. & Burns, B.L., eds. Biology of the Arctic charr. Winnipeg: University of Manitoba Press, pp. 217–232.

Heggenes, J. 2002. Flexible summer habitat selection by wild, allopatric brown trout in lotic environments. Transactions of the American Fisheries Society 131: 287–298.

Heggenes, J., Baglinière, J.L. & Cunjak, R.A. 1999. Spatial niche variability for young Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in heterogeneous streams. Ecology of Freshwater Fish 8: 1–21.

Heggenes, J. & Dokk, J.G. 2001. Contrasting temperatures, waterflows, and light: Seasonal habitat selection by young Atlantic salmon and brown trout in a boreonemoral river. Regulated Rivers: Research and Management 17: 623–635.

Heggenes, J., Saltveit, S.J., Bird, D. & Grew, R. 2002. Static habitat partitioning and dynamic selection by sympatric young Atlantic salmon and brown trout in south-west England streams. Journal of Fish Biology 60: 72–86.

Heggenes, J. & Traaen, T. 1988. Downstream migration and critical water velocities in stream channels for fry of four salmonid species. Journal of Fish Biology 32: 717–727.

Héland, M. 1999. Social organization and territoriality in brown trout juveniles during oontogeny. In: Baglinière, J.L. & Maisse, G., eds. Biology and ecology of the brown trout and sea trout. Berlin: Springer-Praxis Series in Aquaculture and Fisheries, pp. 115–143.

Héland, M., Gaudin, P. & Bardonnet, A. 1995. First behavioural adjustments in relation to habitat use after emergence in running water salmonids. Bulletin Francais de la Peche et de la Pisciculture 337: 191–197.

Hembre, B., Arnkleiv, J.V. & L'Abée-Lund, J.H. 2001. Effects of water discharge and temperature on the seaward migration of anadromous brown trout, *Salmo trutta* L., smolts. Ecology of Freshwater Fish 10: 61–64.

Henricson, J. & Nyman, L. 1976. The ecological and genetical segregation of two sympatric species of dwarfed char (*Salvelinus alpinus* (L.) species complex). Report of the Institute of Freshwater Research, Drottningholm 55: 15–37.

Hesthagen, T. 1989. Life history variables of resident brown trout *Salmo trutta* L. in a coastal stream in northern Norway. Fauna Norvegica Serie A 10: 25–32.

Hesthagen, T., Hindar, K., Jonsson, B. & Ousdal, J.-Ø. 1995. Effects of acidification on normal and dwarf Arctic charr *Salvelinus alpinus* (L.) in a Norwegian lake. Biological Conservation 74: 115–123.

Hesthagen, T., Jonsson, B., Ugedal, O. & Forseth, T. 1997. Habitat use and life history of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in some low acidity lakes in central Norway. Hydrobiologia 348: 113–126.

Heuring, L.G., Babaluk, J.A. & Marshall, K.E. 1991. A bibliography of the Arctic charr, *Salvelinus alpinus* (L.) complex: 1985–1990. Canadian Technical Report of Fisheries and Aquatic Sciences 1775: 1–46.

Hewitt, G.M. 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. Biological Journal of the Linnean Society 58: 247–276.

Hindar, K. & Jonsson, B. 1982. Habitat and food segregation of dwarf and normal Arctic charr (*Salvelinus alpinus*) from Vangsvatnet lake, western Norway. Canadian Journal of Fisheries and Aquatic Sciences 39: 1030–1045.

Hindar, K. & Jonsson, B. 1993. Ecological polymorphism in Arctic charr. Biological Journal of the Linnean Society 48: 63–47.

Hindar, K. & Nordland, J. 1989. A female salmon, *Salmo salar* L., maturing sexually in the parr stage. Journal of Fish Biology 35: 461–463.

Hindar, K., Ryman, N. & Ståhl, G. 1986. Genetic differentiation among local populations and morphotypes of Arctic charr, *Salvelinus alpinus*. Biological Journal of the Linnean Society 27: 269–285.

Hobson, K.A. & Welch, H.E. 1995. Cannibalism and trophic structure in a high Arctic lake – insights from stable-isotope analysis. Canadian Journal of Fisheries and Aquatic Sciences 52: 1195–1201.

Høgåsen, H.R. 1998. Physiological changes associated with the diadromous migration of salmonids. Canadian Special Publication of Fisheries and Aquatic Sciences 127. viii + 128.

Holtby, L.B., Andersen, B.C. & Kadowaki, R.K. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 47: 2181–2194.

Huntingford, F.A., Thorpe, J.E., Garcia de Leaniz, C. & Hay, D.W. 1992. Patterns of growth and smolting in autumn migrants from a Scottish population of Atlantic salmon, *Salmo salar* L. Journal of Fish Biology 41 (Suppl B): 43–51.

Hutchings, J.A. 1985. The adaptive significance of lakeward migrations by juvenile Atlantic salmon *Salmo Salar* L. MSc Thesis. St. John's, Newfoundland. Memorial University of Newfoundland. 132 pp.

Hutchings, J.A. 1986. Lakeward migrations by juvenile Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 43: 732–741.

Hutchings, J.A. 1991. Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. Evolution 45: 1162–1168.

Hutchings, J.A. 2001. Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. Journal of Fish Biology 59 (Suppl A): 306–322.

Hutchings, J.A. & Jones, M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl A): 22–47.

Hutchings, J.A. & Myers, R.A. 1985. Mating between anadromous and non-anadromous Atlantic salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 63: 2219–2221.

Hutchings, J.A. & Myers, R.A. 1988. Mating success of alternative maturation phenotypes in Atlantic salmon, *Salmo salar*. Oecologia 75: 169–174.

Hutchinson, P., ed. 1997. Interactions between salmon culture and wild stocks of Atlantic salmon: the scientific and management issues. ICES Journal of Marine Science 54: 963–1227.

Hvidsten, N.A., Jensen, A.J., Vivås, H., Bakke, Ø. & Heggberget, T. 1995. Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction. Nordic Journal of Freshwater Research 70: 38–48.

Ivlev, V.S. 1966. The biological productivity of waters. Journal of the Fisheries Research Board of Canada 23: 1727–1759.

Jacobsen, J.A. & Hansen, L.P. 2000. Feeding habits of Atlantic salmon at different life stages at sea. In: Mills, D., ed. The Ocean Life of Atlantic Salmon: Environmental and Biological Factors Influencing Survival Oxford: Fishing News Books, Blackwell Science, pp. 170–192.

Jagsch, A. 1987. Arctic charr in some of the lakes of the eastern Alps (Austria). International Society of Arctic Charr Fanatics Information Series 4: 64–72.

Järvi, T., Holmgren, K., Rubin, J.-F., Petersson, E., Lundberg, S. & Glimsäter, C. 1996. Newly emerged *Salmo trutta* fry that migrate to the sea – an alternative choice of feeding habitat? Nordic Journal of Freshwater Research 72: 52–62.

Jenkins, T.M. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Animal Behviour Monographs 3: 57–123.

Jenkins, T.M., Diehl, S., Kratz, K.W. & Cooper, S.D. 1999. Effects of population density on individual growth of brown trout in streams. Ecology 80: 941–956.

Jensen, K.W. 1968. Sea trout (*Salmo trutta* L.) of the River Istra, western Norway. Report of the Institute of Freshwater Research, Drottningholm 48: 187–213.

Jensen, K.W. 1977. On the dynamics and exploitation of the population of brown trout, *Salmo trutta* L., in Lake Øvre Heimdalsvatn, southern Norway. Report of Institute of Freshwater Research, Drottningholm 56: 18–69.

Jensen, A.J. 1992. Possible effects of climatic changes on the ecology of Atlantic salmon, *Salmo salar* (L.). Norwegian Institute for Nature Research, Forskningsrapport 36: 1–21.

Jensen, A.J. & Aass, P. 1995. Migration of a fast-growing population of brown trout (*Salmo trutta* L.) through a fish ladder in relation to water flow and water temperature. Regulated Rivers Research and Management 10: 217–228.

Jensen, K.W. & Berg, M. 1977. Growth, mortality and migrations of the anadromous char, *Salvelinus alpinus* L., in the Vardnes River, Troms, northern Norway. Report of the Institute of Freshwater Research, Drottningholm 56: 70–80.

Jensen, A.J., Forseth, T. & Johnsen, B.O. 2000. Latitudinal variation in growth of young brown trout *Salmo trutta*. Journal of Animal Ecology 69: 1010–1020.

Jensen, A.J. & Johnsen, B.O. 1986. Different adaptation strategies of Atlantic salmon (*Salmo salar*) populations to extreme climates with special reference to some cold Norwegian rivers. Canadian Journal of Fisheries and Aquatic Sciences 43: 980–984.

Jensen, A.J. & Johnsen, B.O. 1999. The functional relationship between peak spring flood and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Functional Ecology 13: 778–785.

Jensen, A.J., Zubchenko, A., Hvidsten, N.A., Johnsen, B.O., Kashin, E. & Næsje, T.F. 1997. A comparative study of life histories of Atlantic salmon in two Norwegian and two Russian rivers. Trondheim: NINA-NIKU Project Report 007: 1–44.

Jeppesen, E., Christoffersen, K., Landkildehus, F., Lauridsen, T., Amsinck, S.L., Riget, F. & Søndergaard, M. 2001. Fish and crustaceans in northeast Geenland lakes with special emphasis on interactions between Arctic charr (*Salvelinus alpinus*), *Lepidurus arcticus* and benthic chydorids. Hydrobiologia 442: 329–337.

Jobling, M., Jørgensen, E.H., Arnesen, A.M. & Ringø, E. 1993. Feeding, growth and environmental requirements of Arctic charr: a review of aquaculture potential. Aquaculture Internation 1: 20–46.

Johnson, L. 1980. The Arctic charr, *Salvelinus alpinus*. In: Balon, E.K., ed. Charrs, Salmonid fishes of the genus. Salvelinus. The Hague: Junk, pp. 15–98.

Johnson, L. 1983. Homeostatic characteristics of single species fish stocks in Arctic lakes. Canadian Journal of Fisheries and Aquatic Sciences 40: 987–1024.

Johnson, L. 1984. Charr and man: the philosophy of limited interactions. In: Johnson, L. & Burns, B.L., eds. Biology of the Arctic charr: Proccedings of the International Symposium on Arctic Charr. Winnipeg: University of Manitoba Press, pp. 523–532.

Johnson, L. 1987. Changes in the Arctic charr population of Keyhole lake over a 25 year period. International Society of Arctic charr Fanatics Information Series 4: 73–87.

Johnson, L. 1989. The anadromous Arctic charr, *Salvelinus alpinus* of Nauyuk Lake, N.W.T., Canada. Physiology and Ecology Japan, 1(spl): 201–228.

Johnson, L. & Burns, B.L., eds. 1984. Biology of the Arctic Charr: Proccedings of the International Symposium on Arctic Charr. Winnipeg: University of Manitoba Press. 584 pp.

Johnsson, J.I. & Forser, A. 2002. Residence duration influences the outcome of territorial conflicts in brown trout (*Salmo trutta*). Behavioral Ecology Sociobiology 51: 282–286.

Jones, J.W. & Ball, J.N. 1954. The spawning behaviour of brown trout and salmon. British Journal of Animal Behaviour 2: 103–114.

Jonsson, B. 1977. Demographic strategy in a brown trout population in Western Norway. Zoologica Scripta 6: 255–263.

Jonsson, B. 1985. Life history pattern of freshwater resident and sea-run migrant brown trout in Norway. Transactions of the American Fisheries Society 114: 182–194.

Jonsson, B. 1989. Life history and habitat use of Norwegian brown trout (*Salmo trutta*). Freshwater Biology 21: 71–86.

Jonsson, B. & Gravem, F.R. 1985. Use of space and food by resident and migrant brown trout, *Salmo trutta*. Environmental Biology of Fishes 14: 281–293.

Jonsson, B. & Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3: 348–365.

Jonsson, B. & Jonsson, N. 2001. Polymorphism and speciation in Arctic charr. Journal of Fish Biology 58: 605–638.

Jonsson, B. & L'Abée-Lund, J.H. 1993. Latitudinal clines in life-history variables of anadromous brown trout in Europe. Journal of Fish Biology 43 (Suppl A): 1–16.

Jonsson, B. & Ruud-Hansen, J. 1985. Water temperature as the primary influence on timing of seaward migrations of Atlantic salmon (*Salmo salar*) smolts. Canadian Journal of Fisheries and Aquatic Sciences 42: 593–595.

Jonsson, B. & Sandlund, O.T. 1979. Environmental factors and life histories of isolated river stocks of brown trout (*Salmo trutta* m. fario) in Søre Osa river system. Norway Environmental Biology of Fishes 4: 43–54.

Jonsson, B. & Skulason, S. 2000. Polymorphic segregation in Arctic charr *Salvelinus alpinus* (L.) from Vatnshlidarvatn, a shallow Icelandic lake. Biological Journal of the Linnean Soceity 69: 55–74.

Jonsson, B. & Waples, R. 1999. Convenors-Theme session on diadromous fish extinction: threats on local and global scales, 1997. ICES Journal of Marine Science 56: 405–472.

Jonsson, B., Jonsson, N. & Hansen, L.P. 1990b. Does juvenile experience affect migration and spawning of adult Atlantic salmon? Behavioural Ecology Sociobiology 26: 225–230.

Jonsson, B., L'Abèe-Lund, J.H., Heggberget, T.G., Jensen, A.J., Johnsen, B.O., Næsje, T.F. & Sættem, L.M. 1991c. Longevity, body size and growth in anadromous brown trout. Canadian Journal of Fisheries and Aquatic Sciences 48: 1838–1845.

Jonsson, B., Jonsson, N., Brodtkorb, E. & Ingebrigtsen, P.-J. 2001. Life-history traits of brown trout vary with the size of small streams. Functional Ecology 15: 310–317.

Jonsson, N. 1991. Influence of water flow, water temperature and light on fish migration in rivers. Nordic Journal of Freshwater Research 66: 20–35.

Jonsson, N. & Jonsson, B. 1997. Energy allocation in polymorphic brown trout. Functional Ecology 11: 310–317.

Jonsson, N. & Jonsson, B. 1998. Body composition and energy allocation in life-history stages of brown trout. Journal of Fish Biology 53: 1306–1316.

Jonsson, N. & Jonsson, B. 1999. Trade-off between egg mass and egg number in brown trout. Journal of Fish Biology 55: 767–783.

Jonsson, N. & Jonsson, B. 2002. Migration of anadromous brown trout in a Norwegian river. Freshwater Biology 47: 1–11.

Jonsson, N., Jonsson, B. & Hansen, L.P. 1990a. Partial segregation in the timing of migration of Atlantic salmon of different ages. Animal Behaviour 40: 313–321.

Jonsson, N., Hansen, L.P. & Jonsson, B. 1991a. Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. Journal of Animal Ecology 60: 937–947.

Jonsson, N., Jonsson, B. & Hansen, L.P. 1991b. Energetic cost of repeat spawning in male and female Atlantic salmon (*Salmo salar* L.). Journal of Fish Biology 39: 739–744.

Jonsson, N., Jonsson, B. & Hansen, L.P. 1995. Brown trout *Salmo trutta* released to support recreational fishing in a Norwegian fjord. Journal of Fish Biology 46: 70–84.

Jonsson, N., Jonsson, B. & Fleming, I.A. 1996. Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? Functional Ecology 10: 89–96.

Jonsson, N., Jonsson, B. & Hansen, L.P. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. Journal of Animal Ecology 66: 425–436.

Jonsson, N., Jonsson, B. & Hansen, L.P. 1998a. Long-term study of the ecology of wild Atlantic salmon smolts in a small Norwegian river. Journal of Fish Biology 52: 638–650.

Jonsson, N., Jonsson, B. & Hansen, L.P. 1998b. The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. Journal of Animal Ecology 67: 751–762.

Jonsson, N., Næsje, T.F., Jonsson, B., Saksgård, R. & Sandlund, O.T. 1999. The influence of piscivory on life history traits of brown trout. Journal of Fish Biology 55: 1129–1141.

Jørgensen, E.H. & Arnesen, A.M. 2002. Seasonal changes in osmotic and ionic regulation in Arcic charr, *Salvelinus alpinus*, from a high- and sub-arctic anadromous population. Enviromental Biology of Fishes 64: 185–193.

Jørgensen, L., Amundsen, P.-A., Gabler, H.-M., Halvorsen, M., Erkinaro, J. & Niemelä, E. 1999. Spatial distribution of Atlantic salmon parr (*Salmo salar* L.) and bullhead (*Cottus gobio* L.) in lotic and lentic habitats of a diversified watercourse in northern Fennoscandia. Fisheries Research 41: 201–211.

Jørstad, K.E., Dahle, G. & Paulsen, O.I. 1994. Genetic comparison between Pacific herring (*Clupea pallasi*) and a Norwegian stock of Atlantic herring (*Clupea harengus*). Canadian Journal of Fisheries and Aquatic Sciences 51 (Suppl A): 233–239.

Jutila, E., Ahvonen, A. & Julkunen, M. 2001. Instream and catchment characteristics affecting the occurence and population density of brown trout (*Salmo trutta* L.) in forest brooks of a boreal basin. Fisheries Management and Ecology 8: 501–511.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout

(*Salmo salar* L. & *S. trutta* L.). Report of Institute of Freshwater Research, Drottningholm 39: 55–98.

Karlsson, L. & Karlström, Ö. 1994. The Baltic salmon (*Salmo salar* L.): its history, present situation and future. Dana 10: 61–85.

Kawanabe, H., Yamazaki, F. & Noakes, D.L.G. 1989. Biology of Charrs and Masu Salmon. Physiology and Ecology Japan 1 (spl.): 1–711.

Kazakov, R.V. 1992. Distribution of Atlantic salmon, *Salmo salar* L., in freshwater bodies of Europe. Aquaculture and Fisheries Management 23: 461–475.

Keeley, E.R. & Grant, J.W.A. 2001. Prey size of salmonid fishes in streams, lakes and oceans. Canadian Journal of Fisheries and Aquatic Sciences 58: 1122–1132.

Keenleyside, M.H.A. 1962. Skin-diving observations of Atlantic salmon and brook trout in the Miramichi River, New Brunswick. Journal of the Fisheries Research Board of Canada 19: 625–634.

Kipling, C. 1991. The chars in English books. International Society of Arctic Charr Fanatics Information Series 5: 103–107.

Kircheis, F.W. 1980. The landlocked charrs of Maine: the sunapee and the blueback. In: Balon, E.K., ed. Charrs Salmonid fishes of the Genus *Salvelinus*. The Hague: Junk, pp. 749–756.

Kircheis, F.W. 1989. History of landlocked Arctic charr management in Maine, USA. Physiology and Ecology Japan 1 (spl.): 615–623.

Klemetsen, A. 1967. On the feeding habits of the population of brown trout (*Salmo trutta* L.) in Jølstervann, west Norway. Nytt Magasin for Zoologi 15: 50–67.

Klemetsen, A. 1991. Countercurrent postglacial invasion of Arctic charr to northern Norway? International Society of Arctic Charr Fanatics Information Series 5: 103–107.

Klemetsen, A. & Dahl-Hansen, G.A.P. 1995. Disruption of the ontogenetic habitat shift pattern in a population of Arctic charr *Salvelinus alpinus* as a result of intensive fishing. Nordic Journal of Freshwater Research 71: 324–332.

Klemetsen, A. & Grotnes, P.E. 1975. Food and habitat segregation of two sympatric Arctic charr populations. Verhandlungen die Internationale Vereinigung für Limnologie 19: 2521–2528.

Klemetsen, A. & Grotnes, P.E. 1980. Coexistence and immigration of two sympatric Arctic charr. In: Balon, E.K., ed. Charrs, Salmonid fishes of the genus *Salvelinus*. The Hague: Junk, pp. 757–763.

Klemetsen, A., Grotnes, P.E. & Andersen, C. 1972. Preliminary studies of North Norwegian arctic char lakes. Verhandlungen die Internationale Vereinigung für Limnologie 18: 1107–1113.

Klemetsen, A., Grotnes, P.E., Holthe, H. & Kristoffersen, K. 1985. Bear Island charr. Report of the Institute of Freshwater Research, Drottningholm 62: 98–119.

Klemetsen, A., Amundsen, P.-A., Muladal, H., Rubach, S. & Solbakken, J.I. 1989. Habitat shifts in a dense, resident Arctic charr *Salvelinus alpinus* population. Physiology and Ecology Japan 1 (spl.): 187–200.

Klemetsen, A., Muladal, H. & Amundsen, P.-A. 1992. Diet and food consumption of young, profundal Takvatn charr (*Salvelinus alpinus*). Nordic Journal of Freshwater Research 67: 34–43.

Klemetsen, A., Jonsson, B. & Elliott, J.M., eds. 1995. Proceedings of the Third International Charr Symposium. Nordic Journal of Freshwater Research 71: 1–451.

Klemetsen, A., Amundsen, P.-A., Knudsen, R. & Hermansen, B. 1997. A profundal, winter-spawning morph of Arctic charr *Salvelinus alpinus* (L.) in lake Fjellfrøsvatn, northern Norway. Nordic Journal of Freshwater Research 73: 13–23.

Klemetsen, A., Elliott, J.M., Knudsen, R. & Sørensen, P. 2002a. Evidence for genetic differences in the offspring of two sympatric morphs of Arctic charr. Journal of Fish Biology 60: 933–950.

Klemetsen, A., Amundsen, P.-A., Grotnes, P.E., Knudsen, R., Kristoffersen, R. & Svenning, M.-A. 2002b. Takvatn through 20 years: long-term effects of an experimental mass removal of Arctic charr, *Salvelinus alpinus*, from a subarctic lake. Environmental Biology of Fishes 64: 39–47.

Knudsen, R. 1995. Relationships between habitat, prey selection and parasite infections in Arctic charr (*Salvelinus alpinus*). Nordic Journal of Freshwater Research 71: 333–344.

Knudsen, R., Klemetsen, A. & Staldvik, F. 1996. Parasites as indicators of individual feeding specialization in Arctic charr during winter in northern Norway. Journal of Fish Biology 48: 1256–1265.

Knudsen, R., Kristoffersen, R. & Amundsen, P.-A. 1997. Parasite communities in two sympatric morphs of Arctic charr, *Salvelinus alpinus* (L.), in northern Norway. Canadian Journal of Zoology 75: 2003–2009.

Knutsen, J.A., Knutsen, H., Gjøsæter, J. & Jonsson, B. 2001. Food of anadromous brown trout at sea. Journal of Fish Biology 59: 533–543.

Koenings, J.P., Geiger, H.J. & Hasbrouck, J.J. 1993. Smolt-to-adult survival patterns of sockeye salmon (*Oncorhynchus nerka*): effects of smolt length and geographic latitude when entering the sea. Canadian Journal of Fisheries and Aquatic Sciences 50: 600–611.

Koljonen, M.-L. 2001. Conservation goals and fisheries management units for Atlantic salmon in the Baltic Sea area. Journal of Fish Biology 559 (Suppl A): 269–288.

Kozlowski, J. 1996. Optimal initial size and adult size of animals: consequences for macroevolution and community structure. American Naturalist 147: 101–114.

Kristoffersen, K. 1994. The influence of physical watercourse parameters on the degree of anadromy in different lake populations of Arctic charr (*Salvelinus alpinus* (L.)) in northern Norway. Ecology of Freshwater Fish 3: 80–91.

Kristofferson, A.H., McGowan, D.K. & Carder, G.W. 1984. Management of the commercial fishery for anadromous Arctic charr in the Cambridge Bay area, Northwest Territories, Canada. In: Johnson, L. & Burns, B.L., eds. Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr. Winnipeg: University of Manitoba Press, pp. 447–462.

Kristoffersen, K., Halvorsen, M. & Jørgensen, L. 1994. Influence of parr growth, lake morphology and freshwater parasites on the degree of anadromy in different populations of Arctic charr (*Salvelinus alpinus*) in northern Norway. Canadian Journal of Fisheries and Aquatic Sciences 51: 1229–1246.

L'Abée-Lund, J.H. 1989. Significance of mature male parr in a small population of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 46: 928–931.

L'Abée-Lund, J.H. 1991. Variation within and between rivers in adult size and sea age at maturity of anadromous brown trout, *Salmo trutta*. Canadian Journal of Fisheries and Aquatic Sciences 48: 1015–1021.

L'Abée-Lund, J.H. & Hindar, K. 1990. Interpopulation variation in reproductive traits of anadromous female brown trout, *Salmo trutta* L. Journal of Fish Biology 37: 755–763.

L'Abée-Lund, J.H., Jensen, A.J. & Johnsen, B.O. 1990. Interpopulation variation in male parr maturation of anadromous brown trout (*Salmo trutta*) in Norway. Canadian Journal of Zoology 68: 1983–1987.

L'Abée-Lund, J.H., Jonsson, B., Jensen, A.J., Sættem, L.M., Heggberget, T.G., Johnsen, B.O. & Næsje, T.F. 1989. Latitudinal variation in life-history characteristics of sea-run migrant brown trout *Salmo trutta*. Journal of Animal Ecology 58: 525–542.

L'Abée-Lund, J.H., Langeland, A. & Sægrov, H. 1992. Piscivory by brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.) in Norwegian lakes. Journal of Fish Biology 41: 91–101.

L'Abée-Lund, J.H., Langeland, A., Jonsson, B. & Ugedal, O. 1993. Spatial segregation by age and size in Arctic charr: a trade-off between feeding possibility and risk of predation. Journal of Animal Ecology 62: 160–168.

Lacey, E.P., Real, L.R., Antonovics, J. & Heckel, D.G. 1983. Variance models in the study of life histories. American Naturalist 122: 114–131.

Lacroix, G.L. & McCurdy, P. 1996. Migratory behaviour of post-smolt Atlantic salmon during initial stages of seaward migration. Journal of Fish Biology 49: 1086–1101.

Lahti, K., Laurila, A., Enberg, K. & Piironen, J. 2001. Variation in agressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. Animal Behaviour 62: 935–944.

Landergren, P. 2001. Sea trout Salmo trutta L., in small steams on Gotland; the coastal zone as a growth habitat for parr. PhD Thesis. Stockholm, Sweden: Stockholm University. 6 papers + 39 pp.

Langeland, A. 1978. Effect of fish (*Salvelinus alpinus*, arctic char) predation on the zooplankton in ten Norwegian lakes. Verhandlungen die Internationale Vereinigung für Limnologie 20: 2065–2069.

Langeland, A. 1982. Interactions between zooplankton and fish in a fertilized lake. Holarctic Ecology 5: 273–310.

Langeland, A. & L'Abée-Lund, J.H. 1996. Habitat use, size and age structure in sympatric brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) stocks: resistance of populations to change following harvest. Ecology of Freshwater Fish 5: 49–58.

Langeland, A. & L'Abée-Lund, J.H. 1998. An experimental test of the genetic component of the ontogenetic habitat shift in Arctic charr (*Salvelinus alpinus*). Ecology of Freshwater Fish 7: 200–207.

Langeland, A., L'Abée-Lund, J.H., Jonsson, B. & Jonsson, N. 1991. Resource partitioning and niche shift in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. Journal of Animal Ecology 60: 895–912.

Largiander, C.R., Estoup, A., Lecerf, F., Champigneulle, A. & Guyomard, R. 2001. Microsatellite analysis of polyandry and spawning site competition in brown trout (*Salmo trutta* L.). Genetics Selection Evolution 33 (Suppl 1): 205–222.

Larsson, S. & Berglund, I. 1998. Growth and food consumption of 0+ Arctic charr fed pelleted or natural food at six different temperatures. Journal of Fish Biology 52: 230–242.

Lazarro, X. 1987. A review of planktivorous fishes: their evolution, feeding behaviours, selectivities and impacts. Hydrobiologia 146: 97–167.

Le Cren, E.D. 1985. The biology of the sea trout. Pitlochry: Atlantic Salmon Trust. 44pp.

Leggett, W.C. & Whitney, R.R. 1972. Water temperatures and the migrations of American shad. Fishery Bulletin 70: 659–670.

Limburg, K.E., Landergren, P., Westin, L., Elfman, M. & Kristiansson, P. 2001. Flexible modes of anadromy in Baltic sea trout: making the most of marginal spawning streams. Journal of Fish Biology 57: 682–695.

Lindroth, A. 1965. The Baltic salmon stock. Mitteilungen Internationale Vereinigung Für Theoretische und Angewandte Limnologie 13: 163–192.

Lindström, T. 1955. On the relation fish size – food size. Report of the Institute of Freshwater Research, Drottningholm 36: 133–147.

Lobón-Cerviá, J. 2000. Determinants of parr size variations within a population of brown trout *Salmo trutta* L. Ecology of Freshwater Fish 9: 92–102.

Lobón-Cerviá, J. & Rincón, P.A. 1998. Field assessment of the influence of temperature on growth rate in a brown trout population. Transactions of the American Fisheries Society 127: 718–728.

Lobón-Cerviá, J., Utrilla, C.G., Rincón, C.G. & Amezcua, F. 1997. Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta* L. trade-offs between egg size and number. Freshwater Biology 38: 277–288.

Lundqvist, H., McKinnell, S., Fängstam, I. & Berglund, I. 1994. The effect of time, size and sex on recapture rates and yield after river releases of *Salmo salar* smolts. Aquaculture 121: 245–257.

Lyse, A.A., Stefanson, S.O. & Fernø, A. 1998. Behaviour and diet of sea trout post-smolts in a Norwegian fjord system. Journal of Fish Biology 52: 923–936.

Lysenko, L.F. 1997. On the population structure of Atlantic salmon *Salmo salar* in the Varzuga River (Kola Peninsula). Journal of Ichthylogy 37: 431–437.

Lyytikäinen, T., Koskela, J. & Rissanen, I. 1997. Thermal resistance and upper lethal temperatures of underyearling Lake Inare Arctic charr. Journal of Fish Biology 51: 515–525.

MacCallum, W.R. & Regier, H.A. 1984. The biology and bioenergetics of Arctic charr in Char Lake, N.W.T., Canada. In: Johnson, L. & Burns, B.L., eds. Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr. Winnipeg: University of Manitoba Press, pp. 392–340.

MacCrimmon, H.R. & Gots, B.L. 1979. World distribution of Atlantic salmon, *Salmo salar*. Journal of the Fisheries Research Board of Canada 36: 422–457.

MacCrimmon, H.R., Marshall, T.L. & Gotos, B.L. 1970. World distribution of brown trout, *Salmo trutta*: further observations. Journal of the Fisheries Research Board of Canada 27: 811–818.

Machino, Y. 1995. The status of *Salvelinus* in France. Nordic Journal of Freshwater Research 71: 352–358.

Magnan, P., Audet, C., Glèmet, H., Legault, M., Rodríguez, A. & Taylor, E.B., eds. 2002. Ecology, behaviour and conservation of the charr, genus *Salvelinus*. Environmental Biology of Fishes 64: 1–351.

Maisse, G., Mourot, B., Breton, B., Fostier, A., Marcuzzi, O., Le Bail, P.Y., Bagliniére, J.L. & Richard, A. 1991. Sexual maturity in sea trout, *Salmo trutta* L., running up the River Calonne (Normandy, France) at the 'finnock' stage. Journal of Fish Biology 39: 705–715.

Maitland, P. 1995. World status and conservation of the Arctic charr *Salvelinus alpinus* (L.). Nordic Journal of Freshwater Research 71: 113–127.

Malmquist, H.J. 1992. Phenotypic-specific feeding behaviour of two Arctic charr *Salvelinus alpinus* morphs. Oecologia 92: 354–361.

Malmquist, H.J., Snorrason, S.S., Skulason, S., Jonsson, B., Sandlund, O.T. & Jonasson, P.M. 1992. Diet differentiation in polymorphic Arctic charr in Thingvallavatn. Iceland Journal of Animal Ecology 61: 21–35.

Mangel, M. 1994. Climate change and salmonid life history variation. Deep-Sea Research II: 75–106.

Marschall, E.A., Quinn, T.P., Roff, D.A., Hutchings, J.A., Metcalfe, N.B., Bakke, T.A., Saunders, R.L. & Poff, N.L. 1998. A framework for understanding Atlantic salmon (*Salmo salar*) life history. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl 1): 48–58.

Marshall, K.E. 1977. A bibliography of the Arctic char, *Salvelinus alpinus* (L.) complex to 1976. Canadian Fisheries and Marine Services Technical Report 621: 1–49.

Marshall, K.E. 1981. A bibliography of the Arctic charr, *Salvelinus alpinus* (L.) complex to 1980. Canadian Technical Report of Fisheries and Aquatic Sciences 1004: 1–68.

Marshall, K.E., Heuring, L.G. & Babaluk, J.A. 1994. A bibliography of the Arctic charr, *Salvelinus alpinus* (L.) complex: 1990–1993. Canadian Technical Report of Fisheries and Aquatic Sciences 1950: 1–36.

Marshall, K.E. & Layton, M. 1985. A bibliography of the Arctic charr, *Salvelinus alpinus* (L.) complex: 1981 through 1984. Canadian Technical Report of Fisheries and Aquatic Sciences 1345: 1–16.

Marshall, K.E., Layton, M. & Babaluk, J.A. 1998. A bibliography of the Arctic charr, *Salvelinus alpinus* (L.) complex: 1993–96. Canadian Technical Report of Fisheries and Aquatic Sciences 2194: 1–48.

Mather, M.E., Parrish, D.L. & Folt, C.L., eds. 1998. Selected proceedings of the international workshop entitled 'Integrating across scales: predicting patterns of change in Atlantic salmon'. Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl 1): 1–323.

Mathiesen, O.A. & Berg, M. 1968. Growth rates of the char, *Salvelinus alpinus* (L.) in the Vardnes River, Troms, northern Norway. Report of the Institute of Freshwater Research, Drottningholm 48: 177–186.

Matthews, M.A., Poole, W.R., Dillane, M.G. & Whelan, K.F. 1997. Juvenile recruitment and smolt output of brown trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) from a lacustrine system in western Ireland. Fisheries Research 31: 19–37.

Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge: Cambridge University Press. 224 pp.

McCarthy, I.D. & Houlihan, D.F. 1997. The effect of temperature of protein metabolism in fish: the possible consequences for wild Atlantic salmon, *Salmo salar* (L.) stocks in Europe as a result of global warming. In: Wood, C.M. & McDonald, D.G., eds. Global warming: implications for freshwater and marine fish. Cambridge: Cambridge University Press. Society for Experimental Biology Seminar Series 61: 51–77.

McCormick, S.D., Hansen, L.P., Quinn, T.P. & Saunders, R.L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55 (Suppl 1): 77–92.

McCormick, S.D., Shrimpton, J.M. & Zydlewski, J.D. 1997. Temperature effects on osmoregulatory physiology of juvenile anadromous fish. In: Wood, C.M. & McDonald, D.G., eds. Global warming: implications for freshwater and marine fish. Cambridge: Cambridge University Press. Society for Experimental Biology Seminar Series 61: 279–301.

McGowan, D.K. 1985. Data on test fisheries conducted on the Baffin and Central Arctic regions, Northwest Territories, 1980–1984. Canadian Data Reports of Fisheries and Aquatic Sciences 531.

McKinnon, J.S. & Rundle, H.D. 2002. Speciation in nature: the threespine stickleback model systems. Trends in Ecology and Evolution 17: 480–488.

McPhail, J.D. 1961. Study of the *Salvelinus alpinus* complex in North America. Journal of the Fisheries Research Board of Canada 18: 793–816.

McPhail, J.D. 1993. Ecology and evolution of sticklebacks (*Gasterosteus*): origin of the species pairs. Canadian Journal of Zoology 71: 515–523.

Meerburg, D.J., ed. 1986. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89. iv + 118p.

Metcalfe, N.B., Huntingford, F.A. & Thorpe, J.E. 1988. Feeding intensity, growth rates, and the establishment of life-history patterns in juvenile Atlantic salmon *Salmo salar*. Journal of Animal Ecology 57: 463–474.

Metcalfe, N.B. & Thorpe, J.E. 1990. Determinants of geographical variation in the age of seaward-migrating salmon, *Salmo salar*. Journal of Animal Ecology 59: 135–145.

Mikheev, V.N., Adams, C.E., Huntingford, F.A. & Thorpe, J.E. 1996. Behavioural responses of benthic and pelagic Arctic charr to substratum heterogeneity. Journal of Fish Biology 49: 494–500.

Mills, C.A. 1989. The Windermere populations of Arctic charr *Salvelinus alpinus*. Physiology and Ecology Japan 1 (spl.): 371–382.

Mills, D., ed. 1993. Salmon in the sea and new enhancement strategies. Oxford: Fishing News Books, Blackwell Science. viii+424 pp.

Mills, D., ed. 2000. The ocean life of Atlantic salmon – environmental and biological factors influencing survival. Oxford: Fishing News Books, Blackwell Science. vii+228 pp.

Minns, C.K., Randall, R.G., Chadwick, E.M.P., Moore, J.E. & Green, R. 1995. Potential impact of climate change on the habitat and population dynamics of juvenile Atlantic salmon, *Salmo salar* (L.), in eastern Canada. In: Beamish, R.J., ed. Climate change and northern fish populations. Canadian Special Publication of Fisheries and Aquatic Sciences 121: 699–708.

Montevecchi, W.A., Cairns, D.K. & Myers, R.A. 2002. Predation on marine-phase Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 59: 602–612.

Moore, A., Lacroix, G.L. & Sturlaugsson, J. 2000. Tracking Atlantic salmon post-smolts in the sea. In: Mills, D., ed. The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Oxford: Fishing News Books, Blackwell Science, pp. 49–64.

Moore, J.W. & Moore, I.A. 1974. Food and growth of arctic char, *Salvelinus alpinus* (L.), in the Cumberland Sound area of Baffin Island. Journal of Fish Biology 6: 79–92.

Moore, A. & Riley, W.D. 1992. A sexually mature female Atlantic salmon, *Salmo salar* L., smolt. Aquaculture and Fisheries Management 23: 273–274.

Morin, R. 1991. Atlantic salmon (*Salmo salar*) in the lower Nastapoka River, Quebec: distribution and origins of salmon in eastern Hudson Bay. Canadian Journal of Zoology 69: 1674–1681.

Morrison, B.R.S. 1983. Observations on the food of juvenile Atlantic salmon, *Salmo salar* L., reared in a Scottish hill loch. Journal of Fish Biology 23: 305–313.

Mortensen, E. 1977. Population, survival, growth and production of trout *Salmo trutta* in a small Danish stream. Oikos 28: 9–15.

Mortensen, E. 1978. The population dynamics and production of trout (*Salmo trutta* L.) in a small Danish stream. In: Moring, J.R., ed. Proceedings of the wild trout – catchable trout symposium. Oregon: Eugene, pp. 151–160.

Mortensen, E. 1985. Population and energy dynamics of trout *Salmo trutta* in a small Danish stream. Journal of Animal Ecology 54: 869–882.

Mortensen, E. & Christensen, B. 1983. Population dynamics of Arctic charr, *Salvelinus alpinus* (L.), in River Narssaq, Greenland. International Society of Arctic Char Fanatics Information Series 2: 107–125.

Myers, R.A. & Hutchings, J.A. 1987. Mating of anadromous Atlantic salmon parr, *Salmo salar* L., with mature male parr. Journal of Fish Biology 31: 143–146.

Myers, R.A., Hutchings, J.A. & Gibson, R.J. 1985. Variation in precocious maturation within and among populations of Atlantic salmon. International Council for the Exploration of the Sea C.M. 1985/M:9. 21 pp.

Myers, R.A., Hutchings, J.A. & Gibson, R.J. 1986. Variation in male parr maturation within and among populations of Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 43: 1242–1248.

Næsje, T.F. 1995. Effects of introduced *Mysis relicta* on habitat utilisation and feeding of Arctic charr. Nordic Journal of Freshwater Research 71: 359–371.

Næsje, T.F. & Jonsson, B. 1988. Impacted stress: a causal agent of reduced whitefish egg incubation time. Canadian Journal of Fisheries and Aquatic Sciences 45: 27–31.

Næsje, T.F., Jensen, J.A., Moen, V. & Saksgård, R. 1991. Habitat use by zooplankton, *Mysis relicta*, and Arctic charr in Lake Jonsvatn, Norway. American Fisheries Society Symposium 9: 75–87.

Næsje, T.F., Sandlund, O.T. & Saksgård, R. 1998. Selective predation by brown trout (*Salmo trutta*) on polymorphic whitefish (*Coregonus lavaretus* L.). Special Issues of Advances in Limnology 50: 283–294.

Näslund, I. 1990. The development of regular seasonal habitat shifts in a landlocked Arctic charr, *Salvelinus alpinus* L., population. Journal of Fish Biology 36: 401–414.

Näslund, I. 1993. Migratory behaviour of brown trout *Salmo trutta* L. importance of genetic and environmental influences. Ecology of Freshwater Fish 2: 51–57.

Nelson, J.S. 1994. Fishes of the world. 3rd edn. New York: Wiley. 600 pp.

Nesbø, C.L., Fossheim, T., Vøllestad, L.A. & Jakobsen, S.J. 1999. Genetic divergence and phylogeographic relationships among European perch (*Perca fluviatils*) populations reflect glacial refugia and postglacial colonization. Molecular Ecology 8: 1387–1404.

Neveu, A. 1999. Feeding strategy of the brown trout (*Salmo trutta* L.) in running water. In: Baglinière, J.L. & Maisse, G., eds. Biology and Ecology of the brown trout and sea trout. Berlin: Springer-Praxis Series in Aquaculture and Fisheries, pp. 91–113.

Nicieza, A.G. & Braña, F. 1993. Relationships among smolt size, marine growth, and sea age at maturity of Atlantic salmon (*Salmo salar*) in northern Spain. Canadian Journal of Fisheries and Aquatic Sciences 50: 1632–1640.

Nikolskii, G.V. 1963. The ecology of fishes. London: Academic Press. 352 pp.

Nilsson, N.-A. 1955. Studies on the feeding habits of trout and char in north Swedish lakes. Report of the Institute of Freshwater Research, Drottningholm 36: 162–225.

Nilsson, N.-A. 1961. The effect of water-level fluctuations on the feeding habits of trout and char in the lakes Blåsjön and Jormsjön, North Sweden. Report of the Institute of Freshwater Research, Drottningholm 42: 238–261.

Nilsson, N.-A. 1965. Food segregation between salmonid species in north Sweden. Report of the Institute of Freshwater Research, Drottningholm 46: 58–78.

Nilsson, N.-A. 1967. Interactive segregation between fish species. In: Gerking, S.D., ed. The Biological basis of freshwater fish production. Oxford: Blackwell, pp. 295–313.

Nilsson, N.-A. & Pejler, B. 1973. On the relation between fish fauna and zooplankton composition in north Swedish lakes. Report of the Institute of Freshwater Research, Drottningholm 53: 51–77.

Noakes, D.J., Beamish, R.J. & Kent, M.L. 2000. On the decline of Pacific salmona and speculative links to salmon farming in British Columbia. Aquaculture 183: 363–386.

Nordeng, H. 1961. On the biology of char (*Salmo alpinus* L.) in Salangen, North Norway. Part I. Age and spawning frequency determined from scales and otoliths. Nytt Magasin for Zoologi 10: 67–123.

Nordeng, H. 1971. Is the local orientation of anadromous fishes determined by pheromones? Nature 233: 411–413.

Nordeng, H. 1983. Solution to the 'charr problem' based on Arctic charr (*Salvelinus alpinus*) in Norway. Canadian Journal of Fisheries and Aquatic Sciences 40: 372–1387.

Nordeng, H., Bratland, P. & Skurdal, J. 1989. Pattern of smolt transformation in the resident fraction of anadromous Arctic charr *Salvelinus alpinus* genetic and environmental influence. Physiology and Ecology Japan 1 (spl.): 483–488.

Nordqvist, O. 1924. Times of the entering of the Atlantic salmon (*Salmo salar* L.) in the rivers. Conseil Permanent International pour l'exploration de Mer. Rapports et Procèes-Verbaux XXXIII. 61 pp.

Nordwall, F., Näslund, I. & Degerman, E. 2001. Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. Canadian Journal of Fisheries and Aquatic Sciences 58: 298–2308.

Northcote, T.G. 1988. Catching the rise: ascent of experimental approaches in trout stream research and its challenge. Polskie Archiwum Hydrobiologii 35: 231–265.

Nyman, L. 1987. High, old and small: the dwarfs of 'chardom'. International Society of Arctic Char Fanatics Information Series 4: 107–112.

Nyman, L., Hammar, J. & Gydemo, R. 1981. The systematics and biology of landlocked populations of Arctic charr from northern Europe. Report of the Institute of Freshwater Research, Drotningholm 59: 128–141.

O'Connell, M.F. & Ash, E.G.M. 1989. Atlantic salmon (*Salmo salar*) smolt production in a Newfoundland river system characterized by lacustrine habitat. Internationale Revue der Gesamten Hydrobiologie 74: 73–82.

O'Connell, M.F. & Ash, E.G.M. 1993. Smolt size in relation to age at first maturity of Atlantic salmon (*Salmo salar*): the role of lacustrine habitat. Journal of Fish Biology 42: 551–569.

O'Connell, M.F. & Dempson, J.B. 1995. Target spawning requirements for Atlantic salmon, *Salmo salar* L., in Newfoundland rivers. Fisheries Management and Ecology 2: 161–170.

O'Connell, M.F. & Dempson, J.B. 1996. Spatial and temporal distributions of salmonids in two ponds in Newfoundland, Canada. Journal of Fish Biology 48: 738–757.

O'Connell, M.F. & Dempson, J.B. 2002. The biology of Arctic charr, *Salvelinus alpinus*, of Gander Lake, a large, deep, oligotrophic lake in Newfoundland. Canada Environmental Biology of Fishes 64: 115–126.

O'Connell, M.F. & Gibson, R.J. 1989. The maturation of anadromous female Atlantic salmon, *Salmo salar* L., stocked in a small pond in urban St. John's, Newfoundland, Canada. Journal of Fish Biology 34: 937–946.

O'Connell, M.F., Dempson, J.B. & Reddin, D.G. 1997. Inter-annual and inter-river variability in fecundity in Atlantic salmon (*Salmo Salar* L.) in Newfoundland Region Rivers. Department of Fisheries and Oceans Canadian Stock Assessment Secretariat Research Document 97/94. 33 pp.

O'Connell, M.F., Walsh, A. & Cochrane, N.M. 2001a. Status of Atlantic salmon (*Salmo salar* L.) in Middle Brook (SFA 5), Northeast Brook, Trepassey (SFA 9), and Northeast River, Placentia (SFA 10), Newfoundland, in 2000. Canadian Stock Assessment Secretariat Research Document 2001/042. 89 pp.

O'Connell, M.F., Walsh, A. & Cochrane, N.M. 2001b. Status of Atlantic salmon (*Salmo salar* L.) in Gander River, Newfoundland, 2000. Canadian Stock Assessment Secretariat Research Document 2001/041. 63 pp.

O'Neil, S., Ritter, J. & Robichaud-Leblanc, K., eds. 2000. Proceedings of a workshop on research strategies into the causes of declining Atlantic salmon returns to North American rivers. Fisheries and Oceans Canada. Canadian Stock Assessment Secretariat Proceedings Series 2000/18. 80 pp.

Ojanguren, A.F., Reyes-Gavilan, F.G. & Brana, F. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. Journal of Thermal Biology 26: 165–170.

Økland, F., Jonsson, B., Jensen, A.J. & Hansen, L.P. 1993. Is there a threshold size regulating seaward migration of brown trout and Atlantic salmon? Journal of Fish Biology 42: 541–550.

Olofsson, H. & Mosegaard, H. 1999. Larger eggs in resident brown trout living in sympatry with anadromous brown trout. Ecology of Freshwater Fish 8: 59–64.

Olsen, E.M. & Vøllestad, L.A. 2001. Within-stream variation in early life-history traits in brown trout. Journal of Fish Biology 59: 1579–1588.

Orzack, S.H. & Tuljapurkar, S. 1989. Population dynamics in variable environments. Part VII. The demography and evolution of iteroparity. American Naturalist 133: 901–923.

Osinov, A.G. 2001. Evolutionary relationships between the main taxa of the *Salvelinus alpinus – Salvelinus malma* complex: results of a comparative analysis of allozyme data from different authors. Journal of Ichtyology 41: 192–208.

Ovidio, M. 1999. Annual activity cycle of adult brown trout (*Salmo trutta* L.): a radio-telemetry study in a small stream of the Belgian Ardenne. Bulletin Francais de la Peche et de la Pisciculture 352: 1–18.

Ovidio, M., Baras, E., Goffaux, D., Birtles, C. & Phillipart, J.C. 1998. Environmental unpredictability rules the autumn migration of brown trout (*Salmo trutta* L.) in the Belgian Ardennes. Hydrobiologia 371/372: 263–274.

Pakkasmaa, S. & Piironen, J. 2001. Morphological differentiation among local trout (*Salmo trutta*) populations. Biological Journal of the Linnean Society 72: 231–239.

Parker, H.H. & Johnson, L. 1991. Population structure, ecological segregation and reproduction in non-anadromous Arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in the Canadian high Arctic. Journal of Fish Biology 38: 123–147.

Parker, H.H., Noonburg, E.G. & Nisbeth, R.M. 2001. Models of alternative life-history strategies, population structure and potential speciation in salmonid fish stocks. Journal of Animal Ecology 70: 260–272.

Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D. & Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Canadian Journal of Fisheries and Aquatic Science 55 (Suppl 1): 281–287.

Partington, J.D. & Mills, C.A. 1988. An electrophoretic and biometric study of Arctic charr, *Salvelinus alpinus* (L.) from ten British lakes. Journal of Fish Biology 33: 791–814.

Pechlaner, R. 1984a. Dwarf populations of Arctic charr in high-mountain lakes of the Alps resulting from under-exploitation. In: Johnson, L. & Burns, B., eds. Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr. Winnipeg: University of Manitoba Press, pp. 319–328.

Pechlaner, R. 1984b. Historical evidence for the introduction of Arctic charr into high-mountain lakes in the alps by man. In: Johnson, L. & Burns, B., eds. Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr. Winnipeg: University of Manitoba Press, pp. 549–558.

Pechlaner, R. 1987. Habitats of charr (*Salvelinus alpinus salvelinus* L.) at high elevations of the Alps in Austria. International Society of Arctic Char Fanatics Information Series 4: 113–119.

Pemberton, R. 1976a. Sea trout in North Agryll sea lochs. Part 2. Diet. Journal of Fish Biology 9: 195–208.

Pemberton, R. 1976b. Sea trout in North Argyll sea lochs, populations, distribution and movements. Journal of Fish Biology 9: 157–179.

Pepper, V.A. 1976. Lacustrine nursery areas for Atlantic Salmon in Insular Newfoundland. Fisheries and Marine Service Technical Report 671. xiii+61 pp.

Pepper, V.A., Oliver, N.P. & Blunden, R. 1984. Lake surveys and biological potential for natural lacustrine rearing of juvenile Atlantic salmon (*Salmo Salar*) in Newfoundland. Canadian Technical Report of Fisheries and Aquatic Sciences 1295. iv + 72 pp.

Pepper, V.A., Oliver, N.P. & Blunden, R. 1985. Juvenile anadromous Atlantic salmon of three lakes of Newfoundland. Internationale Revue der Gesamten Hydrobiologie 70: 733–753.

Pettersson, J.C.E. 2002. Migration in brown trout Salmo trutta – causes and consequences. PhD Thesis. Göteborg, Sweden: Göteborg University. 6papers + 27 pp.

Policansky, D. 1983. Size, age and demography of metamorphosis and sexual maturation in fishes. American Zoologist 23: 57–63.

Porter, T.R., Healey, M.C., O'Connell, M.F., Baum, E.T., Bielak, A.T. & Côté, Y. 1986. Implications of varying sea age at maturity of Atlantic salmon (*Salmo salar*) on yield to the fisheries. In: Meerburg, D.J., ed. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89, pp. 110–117.

Potter, T. 2001. Past and present use of reference points for Atlantic salmon. In: Prévost, E. & Chaput, G., eds. Stock, recruitment and reference points: assessment and management of Atlantic salmon. Paris: Hydrobiobiologie et Aquaculture, INRA Editions, pp. 195–223.

Potter, E.C.E. & Crozier, W.W. 2000. A perspective on the marine survival of Atlantic salmon. In: Mills, D., eds. The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Oxford: Fishing News Books, Blackwell Science, pp. 19–36.

Power, G. 1958. The evolution of the freshwater races of the Atlantic salmon (*Salmo salar* L.) in eastern North America. Arctic 11: 86–92.

Power, G. 1969. The Salmon of Ungava Bay. Arctic Institute of North America Technical Paper no. 22. 72pp.

Power, G. 1973. Estimates of age, growth, standing crop and production of salmonids in some North Norwegian rivers and streams. Report of the Institute of Freshwater Research, Drottningholm 53: 78–111.

Power, G. 1981. Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Canadian Journal of Fisheries and Aquatic Sciences 38: 1601–1611.

Power, G. 1986. Physical influences on age at maturity of Atlantic salmon (*Salmo salar*): a synthesis of ideas and questions. In: Meerburg, D.J., ed. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89, pp. 97–101.

Power, G. 2002. Charrs, glaciations and seasonal ice. Environmental Biology of Fishes 64: 17–35.

Power, M. & Power, G. 1994. Modeling the dynamics of smolt production in Atlantic salmon. Transactions of the American Fisheries Society 123: 535–548.

Power, G., Barton, D. & Bray, K. 1989. Managing the Arctic charr Resource. Waterloo, Ontario: University of Waterloo. 114 pp.

Prévost, E. & Chaput, G., eds. 2001. Stock, recruitment and reference points: assessment and management of Atlantic salmon. Paris: Hydrobiologie et Aquaculture, INRA Editions. 223 pp.

Prévost, E., Chaput, G. & Chadwick, E.M.P. 2001. Transport of stock–recruitment reference points for Atlantic salmon. In: Prévost, E. & Chaput, G., eds. Stock, recruitment and reference points: assessment and management of Atlantic salmon. Paris: Hydrobiologie et Aquaculture, INRA Editions, pp. 95–135.

Prouzet, P. 1981. Observations d'une femelle de tacon de saumon atlantique (*Salmo salar* L.) parvenu à maturité sexuelle en rivière. Bulletin Francais de la Pisciculture 282: 16–19.

Radtke, R., Svenning, M., Malone, D., Klemetsen, A., Ruzicka, J. & Fey, D. 1996. Migrations in an extreme northern population of Arctic charr *Salvelinus alpinus*: insight from otolith micrchemistry. Marine Ecology Progress Series 136: 13–23.

Randall, R.G. 1989. Effect of sea-age on the reproductive potential of Atlantic salmon (*Salmo salar*) in eastern Canada. Canadian Journal of Fisheries and Aquatic Sciences 46: 2210–2218.

Randall, R.G., Thorpe, J.E., Gibson, R.J. & Reddin, D.G. 1986. Biological factors affecting age at maturity in Atlantic salmon (*Salmo salar*). In: Meerburg, D.J., ed. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89, pp. 90–96.

Randall, R.G., Healey, M.C. & Dempson, J.B. 1987. Variability in length of freshwater residence of salmon, trout, and char. American Fisheries Society Symposium 1: 27–41.

Randall, R.G., O'Connell, M.F. & Chadwick, E.M.P. 1989. Fish production in two large Atlantic coast rivers, Miramichi and Exploits. Canadian Special Publication of Fisheries and Aquatic Sciences 106: 292–308.

Rasmussen, G. 1986. The population dynamics of brown trout (*Salmo trutta* L.) in relation to year-class size. Polskie Archiwum Hydrobiologii 33: 489–508.

Reddin, D.G. 1988. Ocean life of Atlantic salmon (*Salmo salar* L.) in the northwest Atlantic. In: Mills, D. & Piggins, D., eds. Atlantic salmon: planning for the future. Oxford: Croom Helm, pp. 79–103.

Refseth, U.H., Nesbø, C.L., Stacy, J.E., Vøllestad, L.A., Fjeld, E. & Jakobsen, K.S. 1998. Genetic evidence for different migration routes of freshwater fish into Norway revealed by analysis of current perch (*Perca fluviatilis*) populations in Scandinavia. Molecular Ecology 7: 1015–1027.

Reist, J.D., Gyselman, E., Babaluk, J.A., Johnson, J.D. & Wissink, R. 1995. Evidence for two morphotypes of Arctic charr *Salvelinus alpinus* (L.) from Lake Hazen, Ellesmere Island, Northwest Territories, Canada. Nordic Journal of Freshwater Research 71: 396–410.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populatins. Bulletin of the Fisheries Research Board of Canada 191: 1–382.

Riddell, B.E. 1986. Assessment of selective fishing on the age at maturity in Atlantic salmon (*Salmo salar*): a genetic perspective. In: Meerburg, D.J., ed. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89, pp. 102–109.

Riddell, B.E. & Leggett, W.C. 1981. Evidence of an adaptive basis for geographic variation in body morphology and time of downstream migration of juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 38: 308–320.

Riget, F.F., Nygaard, K.H. & Christensen, B. 1986. Population structure, ecological segregation, and reproduction in a population of arctic char (*Salvelinus alpinus*) from lake Tasersuaq, Greenland. Canadian Journal of Fisheries and Aquatic Sciences 43: 985–992.

Riget, F., Jeppesen, E., Landkildehus, F., Lauridsen, T.L., Geertz-Hansen, P., Christoffersen, K. & Sparholt, H. 2000. Landlocked Arctic charr (*Salvelinus alpinus*) population structure and lake morphometry in Greenland – is there a connection? Polar Biology 23: 550–558.

Rikardsen, A.H. & Elliott, J.M. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway. Journal of Fish Biology 56: 328–346.

Rikardsen, A.H., Svenning, M.-A. & Klemetsen, A. 1997. The relationships between anadromy, sex ratio and parr growth of Arctic charr in a lake in North Norway. Journal of Fish Biology 51: 447–461.

Rikardsen, A.H., Amundsen, P.-A., Bjørn, P.A. & Johansen, M. 2000. Comparison of growth, diet and food consumption of sea-run and lake-dwelling Arctic charr. Journal of Fish Biology 57: 1172–1188.

Rikardsen, A.H., Amundsen, P.-A. & Bodin, P. 2002. Feeding behaviour of Arctic charr during smolt migration in a lake in northern Norway. Journal of Fish Biology 60: 489–491.

Rincón, P.A. & Lobón-Cerviá, J. 1993. Microhabitat use by stream-resident brown trout: bioenergetics consequences. Transactions of the American Fisheries Society 122: 575–587.

Rincón, P.A. & Lobón-Cerviá, J. 1999. Prey-size selection by brown trout (*Salmo trutta* L.) in a stream in northern Spain. Canadian Journal of Zoology 77: 755–765.

Rincón, P.A. & Lobón-Cerviá, J. 2002. Nonlinear self-thinning in a stream-resident population of brown trout (*Salmo trutta*). Ecology 83: 1808–1816.

Robitaille, J.A., Côté, Y., Shooner, G. & Hayeur, G. 1986. Growth and maturation patterns of Atlantic salmon of Atlantic salmon, *Salmo salar*, in Koksoak River, Ungava, Quebec. In: Meerburg, D.J., ed. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89, pp. 62–69.

Rodriguez, M.A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. Ecology 83: 1–13.

Roff, D.A. 1992. The Evolution of Life Histories. New York, London: Chapman & Hall. xii + 535 pp.

Roussel, J.M. & Bardonnet, A. 1999. Ontogeny of diel pattern of stream-margin habitat use by emerging brown trout, *Salmo trutta*, in experimental channels: influence of food and predator presence. Environmental Biology of Fishes 56: 253–262.

Ruhlé, C. 1984. The management of Arctic charr (*Salvelinus alpinus* L.) in eutrophied Lake Zug. In: Johnson, L. & Burns, B., eds. Biology of the Arctic Charr: Proceedings of the International Symposium on Arctic Charr. Winnipeg: University of Manitoba Press, pp. 487–492.

Ruhlé, C. 1987. Status of the Arctic charr fishery in Switzerland. International Society of Arctic Charr Fanatics Information Series 4: 128–133.

Ryan, P.M. 1986. Lake use by wild anadromous Atlantic salmon, *Salmo salar*, as an index of subsequent adult abundance. Canadian Journal of Fisheries and Aquatic Sciences 43: 2–11.

Ryan, P.M., O'Connell, M.F. & Pepper, V.A. 1993. Report from the workshop on lake use by Atlantic salmon in Newfoundland, Canada. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2222. iv + 54 pp.

Salminen, M., Kuikka, S. & Erkamo, E. 1995. Annual variability in survival of sea-ranched Baltic salmon, *Salmo salar* L. significance of smolt size and marine conditions. Fisheries Management and Ecology 2: 171–184.

Sandlund, O.T., Malmquist, H.J., Jonsson, B., Skulason, S., Snorrason, S.S., Jonasson, P.M., Gydemo, R. & Lindem, T. 1988. Density, length distribution, and diet of age-0 Arctic charr *Salvelinus alpinus* in the surf zone of Thingvallavatn, Iceland. Environmental Biology of Fishes 23: 183–195.

Sandlund, O.T., Gunnarson, K., Jonasson, P.M., Jonsson, B., Lindem, T., Magnusson, K.P., Malmquist, H.J., Sigurjonsdottir, H., Skulason, S. & Snorrason, S.S. 1992. The Arctic charr *Salvelinus alpinus* in Thingvallavatn. Oikos 64: 305–351.

Saunders, R.L. 1967. Seasonal pattern of return of Atlantic salmon in the Northwest Miramichi River, New Brunswick. Journal of the Fisheries Research Board of Canada 24: 21–32.

Saunders, R.L. & Schom, C.B. 1985. Importance of the variation in life history parameters of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 42: 615–618.

Savvaitova, K. 1989. Arctic chars. The structure of population systems and prospects for economic use. Moscow: Agropromizdat. 224 pp. (In Russian). Canadian Translations of Fisheries and Aquatic Sciences 1993: N 5607.

Savvaitova, K. 1995. Patterns of diversity and processes of speciation in Arctic charr. Nordic Journal of Freshwater Research 71: 81–91.

Schaffer, W.M. 1974. Selection for optimal life histories: the effects of age structure. Ecology 55: 291–303.

Schei, T.A. & Jonsson, B. 1989. Habitat use of lake-feeding, allopatric brown trout in Lake Oppheimsvatnet, Norway. In: Brannon, E. & Jonsson, B., eds. Proceedings of the salmonid migration and distribution symposium. Seattle: University of Washington, pp. 156–168.

Schindler, D.W., Welch, H.E., Kalff, J., Brunskill, G.J. & Kritsch, N. 1974. The physical and chemical limnology of Char Lake, Cornwallis Island (75°N lat.). Journal of the Fisheries Research Board of Canada 31: 585–607.

Schluter, D. 1996. Ecological speciation in postglacial fishes. Philosophical Transactions of the Royal Society of London, Series B 351: 807–814.

Schluter, D. 2001. Ecology and the origin of species. Trends in Ecology and Evolution 16: 372–380.

Schluter, D. & Nagel, L.M. 1995. Parallel speciation by natural selection. American Naturalist 146: 292–301.

Scott, W.B. & Crossman, E.J. 1964. Fishes occurring in the fresh waters of insular Newfoundland. Ottawa: Department of Fisheries. iv + 124 pp.

Scott, W.B. & Crossman, E.J. 1998. Freshwater fishes of Canada. Oakville, Ontario: Galt House Publications Ltd. xx + 966 pp.

Scott, D. & Irvine, J.R. 2000. Competitive exclusion of brown trout *Salmo trutta* L., by rainbow trout *Oncorhynchus mykiss* Walbaum, in lake tributaries, New Zealand. Fisheries Management and Ecology 7: 225–237.

Seppovaara, O. 1969. Char (*Salvelinus alpinus* L.) and its fishing industrial importance in Finland. Suomen Kalatalous 37: 1–75. (In Finnish with an English summary).

Shearer, W.M. 1992. The Atlantic salmon. New York, Toronto: John Wiley & Sons, Inc. xvii + 244 pp.

Shine, A.J., Kubecka, J., Martin, D.S. & Duncan, A. 1993. Fish habitats in Loch Ness. Scottish Naturalist 105: 237–255.

Skarstein, F. & Folstad, I. 1996. Sexual dicromatism and the immunocompetence handicap: an observational approach using Arctic charr. Oikos 76: 359–367.

Skreslet, S. 1969. The ecosystem of the Arctic Lake Nordlaguna, Jan Mayen Island. Part I. General features and hydrography. Astarte 2: 27–34.

Skreslet, S. 1973. The ecosystem of the arctic Lake Nordlaguna, Jan Mayen Island. Part III. Ecology of Arctic char, *Salvelinus alpinus* (L.). Astarte 6: 43–54.

Skulason, S. & Smith, T.B. 1995. Resource polymorphism in vertebrates. Trends in Ecology and Evolution 10: 366–370.

Skulason, S., Snorrason, S.S. & Jonsson, B. 1999. Sympatric morphs, populations and speciation in freshwater fish with emphasis on Arctic charr. In: Magurran, A.E. & May, R.M., eds. Evolution of Biological Diversity. New York: Oxford Press, pp. 70–92.

Skulason, S., Snorrason, S.S., Noakes, D.L.G. & Ferguson, M.M. 1996. Genetic basis of life history variations among sympatric morphs of Arctic charr, *Salvelinus alpinus*. Canadian Journal of Fisheries and Aquatic Sciences 53: 1807–1813.

Skulason, S., Snorrason, S.S., Ota, D. & Noakes, D.L.G. 1993. Genetically based differences in foraging behaviour among sympatric morphs of Arctic charr (Pisces: Salmonidae). Animal Behaviour 45: 1179–1192.

Smith, C. & Reay, P. 1991. Cannibalism in teleost fish. Reviews in Fish Biology and Fisheries 1: 41–64.

Smith, T.B. & Skulason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annual Reviews in Ecology and Systematics 27: 111–133.

Sneider, B. 2000. Spawning microhabitat selection by brown trout in the Linthkanal, a mid-sized river. Journal of Freshwater Ecology 15: 181–187.

Snieszko, S.F., Dunbar, C.E. & Bullock, G.L. 1959. Resistance to ulcer disease and furunculosis in eastern brook trout, *Salvelinus foutinalis*. Progressive Fish Culturist 21: 111–116.

Snorrason, S.S., Skulason, S., Jonsson, B., Sandlund, O.T., Malmquist, H.J. & Jonasson, P.M. 1994. Trophic specialisation in Arctic charr *Salvelinus alpinus* (Pisces: Salmonidae): morphological divergence and ontogenetic niche shifts. Biological Journal of the Linnean Society 52: 1–18.

Sømme, I.D. 1941. Ørretboka. Dybwads forlag, Oslo. (In Norwegian).

Sparholt, H. 1985. The population, survival, growth, reproduction and food of Arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland. Journal of Fish Biology 26: 313–330.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51: 3–47.

Steingrimsson, S.O. & Gislason, G.M. 2002. Body size, diet and growth of landlocked brown trout, *Salmo trutta*, in the subarctic River Laxa, north-east Iceland. Environmental Biology of Fishes 63: 417–426.

Stenzel, A. & Power, G. 1991. Aspects of summer ecology of juvenile Arctic charr in the Koroc River, Quebec. International Society of Arctic Char Fanatics Information Series 5: 161–168.

Strand, R. & Heggberget, T.G. 1994. Growth and sex distribution in an anadromous population of Arctic charr in northern Norway. Transactions of the American Fisheries Society 123: 377–384.

Summers, D.W. 1995. Long-term changes in the sea-age at maturity and seasonal time of return of salmon, *Salmo salar* L., to Scottish rivers. Fisheries Management and Ecology 2: 147–156.

Sutterlin, A.M. & MacLean, D. 1984. Age at first maturity and early expression of oocyte recruitment processes in two forms of Atlantic salmon (*Salmo salar*) and their hybrids. Canadian Journal of Fisheries and Aquatic Sciences 41: 1139–1149.

Sutterlin, A.M. & Stevens, E.D. 1992. Thermal behaviour of rainbow trout and Arctic charr in cages moored in stratified water. Aquaculture 102: 65–75.

Svärdson, G. & Fagerström, Å. 1982. Adaptive difference in the long-distance migration of some trout (*Salmo trutta* L.) stocks. Report of the Institute of Freshwater Research, Drottningholm 60: 51–80.

Svedäng, H. 1990. Genetic basis of life history variation of dwarf and normal Arctic charr *Salvelinus alpinus* (L.), in Stora Rösjön, central Sweden. Journal of Fish Biology 36: 917–932.

Svenning, M.-A. 1993. Life history variations and polymorphism in Arctic charr, *Salvelinus alpinus* (L), on Svalbard and in Northern Norway. Dr. Scient. Thesis. University of Tromsø, Norway.

Svenning, M.-A. 2001. Røyeotolitten som ferdsskriver: Livshistorievariasjon i ekstremt og uforutsigbart miljø. Norsk institutt for naturforskning Temahefte 17: 107–114 (In Norwegian with an English abstract).

Svenning, M.-A. & Borgstrøm, R. 1995. Population structure in landlocked Spitsbergen Arctic charr. Sustained by cannibalism? Nordic Journal of Freshwater Research 71: 424–431.

Svenning, M.-A. & Grotnes, P. 1991. Stationarity and homing ability of landlocked Arctic charr. Nordic Journal of Freshwater Research 66: 36–43.

Svenning, M.-A. & Gullestad, N. 2002. Adaptations to stochastic environmental varations: the effects of seasonal temperaures on the migratory window of Svalbard Arctic charr. Environmental Biology of Fishes 64: 165–174.

Svenning, M.-A., Smith-Nilsen, A. & Jobling, M. 1992. Sea water migration of Arctic charr (*Salvelinus alpinus* L.): correlation between freshwater growth and seaward migration, based on back-calculation from otoliths. Nordic Journal of Freshwater Research 67: 18–26.

Swales, S. 1986. Population dynamics, production and angling catch of brown trout, *Salmo trutta*, in a mature upland reservoir in Mid-Wales. Environmental Biology of Fishes 16: 279–293.

Tallman, R.F., Saurette, F. & Thera, T. 1996. Migration and life history variation in Arctic charr, *Salvelinus alpinus*. Ecoscience 3: 33–41.

Taylor, E.B. & Bentzen, P. 1993. Evidence for multiple origins and sympatric divergence of trophic ecotypes of smelt (*Osmerus*) in northeastern America. Evolution 47: 813–832.

Thorpe, J.E. 1974. The movement of brown trout, *Salmo trutta* (L) in Loch Leven, Kinross, Scotland. Journal of Fish Biology 6: 153–180.

Thorpe, J.E. 1986. Age at first maturity in Atlantic salmon, *Salmo salar*: freshwater period influences and conflicts with smolting. In: Meerburg, D.J., ed. Salmonid Age at Maturity Canadian Special Publication of Fisheries and Aquatic Sciences 89, pp. 7–14.

Thorpe, J.E. 1987. Smolting versus residency: developmental conflicts in salmonids. American Fisheries Society, Symposium 1: 244–252.

Thorpe, J.E. 1988. Salmon migration. Science Progress, Oxford 72: 345–370.

Thorpe, J.E. 1989. Developmental variation in salmonid populations. Journal of Fish Biology 35: 295–303.

Thorpe, J.E. 1994. Reproductive strategies in Atlantic salmon, *Salmo salar*. Aquaculture and Fisheries Management 25: 77–87.

Thorpe, J.E. 1998. Salmonid life-history evolution as a constraint on marine stock enhancement. Bulletin of Marine Science 62: 465–475.

Thorpe, J.E., Mangel, M., Metcalfe, N.B. & Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 12: 581–599.

Thorpe, J.E., Miles, M.S. & Keay, D.S. 1984. Developmental rate, fecundity and egg size in Atlantic salmon, *Salmo salar* L. Aquaculture 43: 289–305.

Thyrel, M., Berglund, I., Larsson, S. & Näslund, I. 1999. Upper thermal limits for feeding and growth of 0+Arctic charr. Journal of Fish Biology 55: 199–210.

Titus, R.G. & Mosegaard, H. 1989. Smolting at age 1 and its adaptive significance for migratory trout, *Salmo trutta* L., in a small Baltic-coast stream. Journal of Fish Biology 35 (Suppl A): 351–353.

Titus, R.G. & Mosegaard, H. 1992. Fluctuating recruitment and variable life history of migratory brown trout, *Salmo trutta* L., in a small, unstable stream. Journal of Fish Biology 41: 239–255.

Turrell, W.R. & Shelton, R.G.J. 1993. Climatic change in the north-eastern Atlantic and its impact on salmon stocks. In: Mills, D., ed. Salmon in the Sea and New Enhancement Strategies. Oxford: Fishing News Books, Blackwell Science, pp. 40–78.

Verspoor, E. & Cole, L.J. 1989. Genetically distinct sympatric populations of resident and anadromous Atlantic salmon, *Salmo salar*. Canadian Journal of Zoology 67: 1453–1461.

Vik, J.O. 2002. Feedback and population regulation by piscivory in Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. Dr Scient Thesis. Agricultural University of Norway, Ås.

Vøllestad, L.A. & L'Abée-Lund, J.H. 1994. Evolution of the life history of Arctic charr *Salvelinus alpinus*. Evolutionary Ecology 8: 315–327.

Volpe, J.P. & Ferguson, M.M. 1996. Molecular genetic examiation of the polymorphic Arctic charr *Salvelinus alpinus* of Thingvallavatn, Iceland. Molecular Ecology 5: 763–772.

Vuorinen, J.A., Bodaly, R.A., Reist, J.D., Bernatchez, L. & Dodson, J.J. 1993. Genetic and morphological differentiation between dwarf and normal size forms of lake whitefish (*Coregonus clupeaformis*) in Como Lake, Ontario. Canadian Journal of Fisheries and Aquatic Sciences 50: 2023–2036.

Wagner, H.H., Conte, F.P. & Fessler, J.L. 1969. Development of osmotic and ionic regulation in two races of chinook salmon *Oncorhynchus tshawytscha*. Comparative Biochemistry and Physiology 29: 325–341.

Walker, A.F., Greer, R.B. & Gardner, A.S. 1988. Two ecologically distinct forms of Arctic charr *Salvelinus alpinus* (L.) in Loch Rannoch, Scotland. Biological Conservation 43: 43–61.

Walters, C. & Ward, B. 1998. Is solar radiation responsible for declines in marine survival rates of anadromous salmonids that rear in small streams? Canadian Journal of Fisheries and Aquatic Sciences 55: 2533–2538.

Ward, B.R. & Slaney, P.A. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 45: 1110–1122.

Warner, K. & Havey, K.A. 1985. Life History, Ecology and Management of Maine Landlocked Salmon. Maine Department of Inland Fisheries and Wildlife, vii + 121pp.

Webb, J.H. & Campbell, R.N.B. 2000. Patterns of run timing in adult Atlantic salmon returning to Scottish rivers – some new perspectives and management implications. In: Whoriskey,F.G. Jr. & Whelan, K.E., eds. Managing Wild Atlantic Salmon: New Challenges – New Techniques The Atlantic Salmon Trust, pp. 100–138.

Weng, Z., Mookerji, N. & Mazumder, A. 2001. Nutrient-dependent recovery of Atlantic salmon streams from catastrophic flood. Canadian Journal of Fisheries and Aquatic Sciences 58: 1673–1682.

Went, A.E.J. 1962. Irish sea trout, a review of investigations to date. Scientific Progresses of the Royal Society of Dublin 1: 265–296.

Werner, E.E. & Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Reviews in Ecology and Systematics 15: 393–425.

Whoriskey,F.G. Jr. & Whelan, K.E., eds. 1997. Managing wild Atlantic salmon – new challenges – new techniques. The Atlantic Salmon Trust, iii+244 pp.

Williams, W.D. & Aladin, N.V. 1991. The Aral Sea: recent limnological changes and their conservation significance. Aquatic Conservation: Marine and Freshwater Ecosystems 1: 3–23.

Wilson, C.C., Hebert, P.D.N., Reist, J.D. & Dempson, J.B. 1996. Phylogeography and postglacial dispersal of Arctic charr *Salvelinus alpinus* in North America. Molecular Ecology 5: 187–197.

Winfield, J., Bean, C.W. & Hewitt, D.P. 2002. The relationship between spatial distribution and diet of Arctic charr, *Salvelinus alpinus*, in Loch Ness, UK. Environmental Biology of Fishes 64: 63–73.

Wootton, R.J. 1998. Ecology of Teleost Fishes, 2nd edn. London: Kluwer.

Young, M.K. 1999. Summer diel activity and movement of adult brown trout in high-elevation streams in Wyoming, USA. Journal of Fish Biology 54: 181–189.

Youngson, A.F., Buck, R.J.G., Simpson, T.H. & Hay, D.W. 1983. The autumn and spring emigrations of juvenile Atlantic salmon, *Salmo salar* L., from the Girnock Burn, Aberdeenshire, Scotland: environmental release of migration. Journal of Fish Biology 23: 625–639.