The growth of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) from the river Etneelva, Norway. A comparison of the periods 1976-1982 and 2000-2007.

Vekst hjå laks (*Salmo salar*) og sjøaure (*Salmo trutta*) frå Etneelva. Ei samanlikning av periodane 1976-1982 og 2000-2007.

Helene Børretzen Fjørtoft

Norwegian University of Life Sciences
Department of Ecology and Natural Resource Management (INA)
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Preface

This is my master's thesis in natural resource management at the Institute of Ecology and Natural Resource Management (INA) at the University of Life Sciences (UMB).

First and foremost I would like to thank my supervisor at INA, Professor Reidar Borgstrøm, for his patience, support and good advice. Thanks are also due to my other supervisor, Øystein Skaala at the Norwegian institute of Marine Research (IMR), for his help with providing the study material and constructive comments on the work.

In Etne I owe thanks to the fishermen who provided scale samples from the river in 2008 and to Nick Jacobsen who organized the sampling. Steinar Grindheim in the local river stake holder association helped with providing and facilitating statistical data from the river fishery. Erik Kvalheim, Etne municipality, also contributed with information. Thanks are also due to Dr. Eero Niemelä at the Finnish Game and Fisheries Research Institute for his information on the summer growth checks in Finnmark. For the statistical work I would like to thank Ellen Sandberg at UMB for her guidance and comments.

My family and family-in-law have been a constant support and have been babysitting countless hours so that I could work in quiet. Thank you. Especially I would like to thank my father, Vidar Børretzen, for sharing his knowledge and interest in the river Etneelva and its wild salmonids. Together with my mother Ingebjørg he is responsible for my love of and curiosity about nature. My friends have also been there at need. Hanne Henriksen has been a good help both as a voluntary lab assistant and with comments on the drafts, and, together with Solveig Karin Eriksen, by just being there.

Last, but not least, I would like to thank my husband and daughter for always loving me and encouraging me. I love you too.

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Summary

The populations of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) are declining in Europe. For both species the key seems to be found in the saltwater stage of their life cycle. Two major changes have occurred in this stage over the last thirty years; the rise of aquaculture and climate change. For sea trout the main problem is believed to be aquaculture, with associated epizootics of salmon lice (*Lepeophtheirus salmonis*). For Atlantic salmon the problem seems to be a changing ecosystem in the North Atlantic, probably due to climate change.

The focus of this study is growth of Atlantic salmon and sea trout caught in the river Etneelva, Western Norway, in 1983 and 2008. The growth of 1+ Atlantic salmon parr was positively correlated with river temperature. In the river, Atlantic salmon displayed a slight increase in growth between 1978-1981 and 2003-2005, but it was marginally not significant. The growth of sea trout parr was not significantly different between 1976-1981 and 2000-2006. There was a significant negative correlation between the size of 1+ Atlantic salmon parr at the beginning of the growing season and the growth of the 1+ sea trout parr. In the fjord, the sea trout post smolt growth has been reduced from 1979-1982 to 2002-2007. The growth during the second sea summer was also reduced for the sea trout, as was Fulton's condition factor when the fish were caught. For the Atlantic salmon post smolt the growth was increased from 1979-1982 to 2004-2007, while the growth was significantly reduced for the 2 SW. Fulton's condition factor for the spawners was also reduced. The weight of the MSW caught in 2008 was lower than expected. 65 % of the Atlantic salmon caught in 2008 displayed summer growth checks during their first year at sea, whereas only 4.5% of the fish caught in 1983 had this. Also the sea trout caught in 2008 had a higher occurrence of summer growth checks, with 12 % against 3.6 % in 1983.

In the river, the Atlantic salmon 1+ parr seem to benefit from the higher temperatures at the cost of the sea trout parr. High infection rates of salmon lice in the fjords are believed to be behind the reduced growth of sea trout, both because of stress and premature river run. Improved growth in spite of high occurrence of growth checks during the Atlantic salmon post smolt year might indicate that good habitats in the nursery area are more patchily distributed than before. Reduced 2 SW growth and condition factor for the returning spawners indicate that the conditions for the mature Atlantic salmon in the ocean also are less optimal.

Samandrag

Bestandane av laks (*Salmo salar*) og sjøaure (*Salmo trutta*) er i nedgong over store delar av Europa. Nykelen synest å finnast i sjøfasen for båe artar. To store endringar har skjedd der dei siste tretti åra; framvekst av akvakultur og klima endringar. For sjøaure er hovudproblemet truleg oppdrettsnæringa, med tilhøyrande oppbløming av lakselus (*Lepeophtheirus salmonis*). For laksen er årsaken truleg å finne i endringar i økosystemet i Nord-Atlanteren, som kan skuldast klimaendringar.

Fokus for denne oppgåva har vore vekst hjå laks og sjøaure fanga i Etneelva, Hordaland, i 1983 og 2008. Veksten til 1+ lakseungar var korrelert med vasstemperaturen. Veksten i elva viste ein auke hjå lakseungane frå 1978-1981 til 2003-2005, men den var så vidt ikkje signifikant. Det var ingen signifikant skilnad på veksten til aureungane mellom 1976-1981 og 2000-2006. Det var ein negativ samanheng mellom storleiken på 1+ lakseungane på byrjinga av vekstsesongen og veksten til 1+ aureungane. I fjorden har veksten til sjøaure postsmolten vorte redusert mellom perioden 1979-1982 og 2002-2007. Veksten var og redusert andre året i sjøen, det same var Fultons kondisjonsfaktor når auren vart fanga. For postsmolten til laksen auka veksten frå perioden 1979-1982 til 2004-2007, medan den minka signifikant for det andre året i havet. Fultons kondisjonsfaktor for gytefisken var dårlegare i den siste perioden. Vekta på fleirsjøvintringar tatt i 2008 var lågare enn forventa. Heile 65 % av laksane tatt i 2008 hadde falske vintersoner i løpet av postsmoltåret, mot berre 4.5 % i 1983. Og sjøauren hadde ein auke i falske vintersoner, frå 3.6 % i 1983 til 12 % i 2008.

I elva synest det at lakseungane er betre enn aureungane til å utnytte den auka temperaturen. I fjorden er truleg høge infeksjonsratar med lakselus skuld i den dårlege overlevinga og veksten hjå sjøaure. Dette skuldast både stress og at auren må gå tidlegare attende til ferskvatn. Den betra veksten til postsmolt av laks til trass for den høge førekomsten av falske vintersoner kan tyda på at dei gode oppvekstområda i Nord-Atlanteren er meir spreidd enn før. Den låge vekta og kondisjonsfaktoren på gytefisken tydar og på at tilhøva for dei vaksne laksane i havet er mindre gunstige.

Contents

Introduction

The abundance of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) are declining in Norway, as well as in other European countries (Friedland et al. 2009). In Norway the combined total annual catches of Atlantic salmon and sea trout in coastal and river fisheries have declined from 1900 tonnes in 1979 to 900 tonnes in 2008 (StatisticsNorway 2009). The more or less synchronised declines are making researchers and managers look for common causes over a large geographical area (Friedland et al. 2005; Todd et al. 2008). The problem does not appear to be in the freshwater stage, as most rivers still seem to be producing sufficient smolts to uphold the populations (Friedland et al. 2000). However, the smolts increasingly fail to return to the river, thus focus is put on the conditions in the sea stage of these anadromous fishes (Friedland et al. 1998; Jonsson & Jonsson 2009a; Todd et al. 2008). The mechanism behind the increased at-sea mortality for both Atlantic salmon and sea trout is believed to be partly growth related and mainly located in time to the first year in salt water (Jonsson & Jonsson 2009a). When growth is reduced, the post smolts stay longer inside what can be called the predation window. As the size of the post smolts increases there are fewer possible predators, thus rapid growth is essential (Brabrand 2000; Friedland et al. 1998).

During the last thirty years, one of the most important changes for the Northern European wild salmonids is the establishment of aquaculture. A study on the effect of aquaculture found significantly higher mortalities of wild salmonids in areas where aquaculture is present (Ford & Myers 2008). The increased mortalities are believed to be caused by interbreeding between farmed and wild salmonids, especially for Atlantic salmon, and increased risk of disease and parasite transfer from the fish farms to the wild fish (Jonsson & Jonsson 2009b; McGinnity et al. 2003; McVicar 1997). Unnatural high densities of hosts over unnatural long time periods have for example led to a dramatic increase in salmon lice (*Lepeophtheirus salmonis*) densities in areas with salmonid farming (Costello 2009). For post smolts of sea trout, high infection rates of salmon lice can lead to an early return to estuaries and rivers, and in turn to reduced growth (Birkeland & Jakobsen 1997). For the Atlantic salmon post smolts, the salmon lice will normally not reach a detrimental stage until the fish have reached the open ocean (Finstad et al. 2000; Sivertsgård et al. 2007). Whether the fish survives will then be determined by how heavy the infection is, and whether the salmon is reinfected at sea (Grimnes & Jakobsen 1996; Jacobsen & Gaard 1997). In general, sea trout are believed to be most affected by salmon lice infections because they remain in the fjord areas throughout their sea stage (Costello 2006).

Another factor that has been changing over the last thirty years is the climate. Norway and the Norwegian sea are now experiencing higher mean temperatures both in the air and in the water compared to the early 1980s (Guiot & Corona 2010; Todd et al. 2008). As fish are poikilotherms, the ambient temperature directly affects their metabolic rates. It appears that Atlantic salmon parr experience maximum growth at higher temperatures than sea trout parr, and that it is better at converting food to growth at higher temperatures (Forseth et al. 2001) In rivers where the two species compete for food and habitat, increased temperatures can give Atlantic salmon parr an advantage. The relationship between sea surface temperature, survival and growth of Atlantic salmon is complex. The increased mortality of post smolts after 1980 has been linked with water temperatures below the range 8-10 ^{o}C when they enter the ocean in May (Friedland et al. 1998; Friedland et al. 2000; Friedland et al. 2005). The reason is that changes in ocean currents have led to colder water along the Norwegian coast and the Norwegian sea early in the summer (Friedland et al. 2000). Increased mean summer temperatures might reduce the problem of the 8-10 ^{o}C thermal habitat for the post smolts, but too high sea surface temperatures seem to be causing a new problem (Friedland et al. 2005). The salmonids are located relatively high in the food chain, meaning that they are dependent on primary and secondary production, which is partly regulated by temperature (Beaugrand & Reid 2003). For European Atlantic salmon there now appears to be a negative correlation between higher temperatures in the ocean and growth and survival during the post smolt year (Todd et al. 2008). This could be an indirect effect of the climate driven changes in the North Atlantic ecosystem (Beaugrand & Reid 2003; Friedland et al. 2009; Todd et al. 2008). Another indirect effect of increased temperatures is higher virulence of diseases and parasites (Jonsson & Jonsson 2009b).

The present study has analysed growth of Atlantic salmon and sea trout from the river Etneelva, located in the Hardangerfjord system on the west coast of Norway. Both growth in the river and after entry to saltwater is considered. Two periods, with a span of 25 years between, are studied. The earliest period concerns fish caught in the river in 1983, and reaches from 1976 to 1982, while the most recent period involves fish caught in 2008, covering the years 2000 to 2007. Temperatures both in the river and in the saltwater habitats of the Atlantic salmon and sea trout are expected to have increased due to climate change. The magnitude of the temperature changes are tested here. The primary goal of this study is to test whether the growth of Atlantic salmon and sea trout from the river Etneelva has changed from 1976-1982 to 2000-2007, both in the river and in saltwater. The study will also test whether a link between growth at the different life stages and the ambient temperature can be found. In the river, water discharge will also be considered, as increased precipitation is expected due to climate change.

Material and methods

Location

The river Etneelva is located on the south western coast of Norway, in Etne municipality, Hordaland county (UTM zone 32, 331719 east, 6619892 north) (Fig. 1). The catchment area of the watershed is 250 km^2, of which 60 % is mountainous (Bjerknes & Waatevik 1985). The river is about seven km long, from the lake Stordalsvatnet to the fjord, Etnefjorden (Fig. 2). About halfway, a large tributary, Sørelva, enters the river. This tributary origins from the lake Litledalsvatnet, and makes a total river stretch of 13 kilometres available to salmonids (Bjerknes & Waatevik 1985). Etneelva is also called Nordelva above the river merging. Only the name Etneelva will be used in this paper for simplicity.

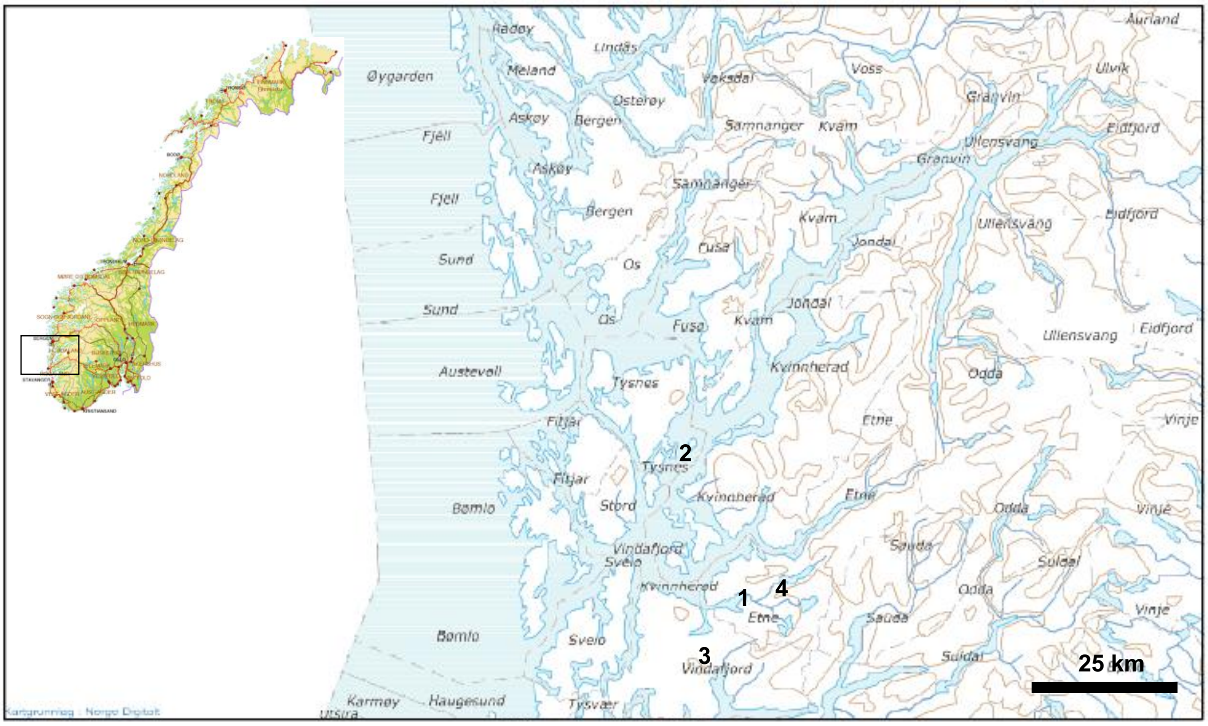

Fig. 1. Overview of the area around the river Etneelva. 1: The entrance of the river Etneelva to the fjord Etnefjorden. 2. Hardangerfjorden. 3. Weather station at Nedre Vats. 4. NVE river data station. (Map from www.gislink.no)

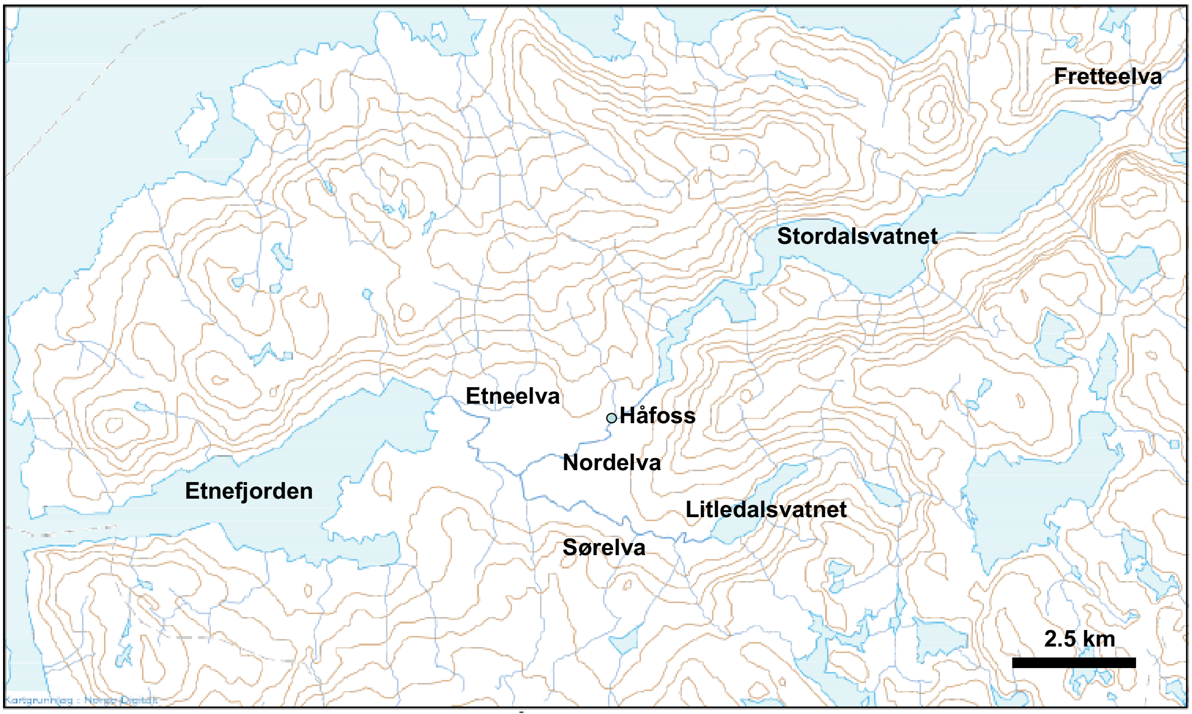

Fig. 2. Overview of the river Etneelva, with its tributary Sørelva and the lakes Stordalsvatnet and Litledalsvatnet. (Map from www.gislink.no)

The river has a low gradient, with a fall of only 51 meters from the lakes to the fjord (Fig. 3). Salmon ladders are built at Håfoss, one of the few obstacles for the salmonids (Bjerknes & Waatevik 1985). To protect agricultural land, channelization has been performed since the 1950s. In the 1980s, weirs, mainly Syvde weirs, were constructed in some parts of the river. The salmonids spawn in all parts of the river, while the trout also spawn in small inlets to the two lakes. It is believed that Atlantic salmon also can spawn in the main inlet river to the lake Stordalsvatnet, which would increase the Atlantic salmon river stretch by two kilometres (Bjerknes & Waatevik 1985). In the river, Atlantic salmon and sea trout is found along with European eel (*Anguilla anguilla*), while three-spined stickleback (*Gasterosteus aculeatus*) and arctic char (*Salvelinus alpinus*) are found in the lakes (Bjerknes & Waatevik 1985). The river has a longstanding reputation among sports fishermen as a good salmon river. Production of Atlantic salmon fry started as early as the 1880s in backwaters, and a hatchery for Atlantic salmon was built already in the 1920s (Vidar Børretzen, pers. comm.). A new hatchery was built in the 1970s. The hatchery has not been operating continually. The fishing season has recently been between the 1st of June and the 15th of September, but the river is closed in 2010 because of declining spawning populations. In 2008 a bag limit of two fish per rod per day was introduced, of which only one could be sea trout. Figure 4 shows the catch statistics in kilogram for the last thirty years. It should be noted that released individuals are only included in the 2009 numbers, but that farmed Atlantic salmon have not been excluded from the material. It is suspected that the unusually high numbers for 1990 and 1991 are fabricated to lure more fishermen to the river (Erik Kvalheim, pers. comm.).

Fig. 3. The river Etneelva. a) Close to the river mouth. b) Channelized river bend. c) Stretch with Syvde weir. d) Riffle-pool stretch. e) Håfoss. Salmon ladders on the left side. f) Upper reaches of the tributary Sørelva.

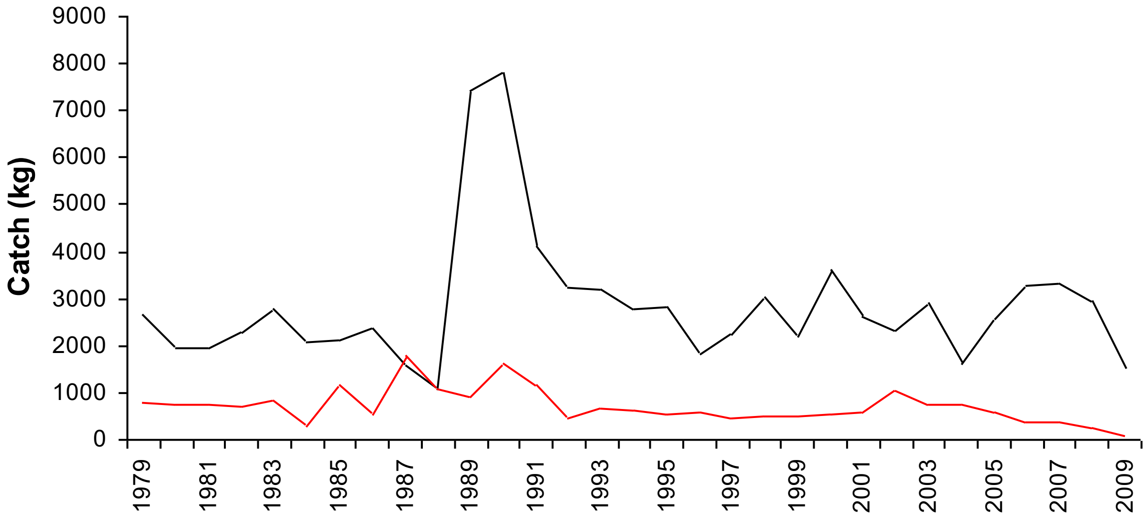

Fig. 4. Catches of Atlantic salmon (black) and sea trout (red) in the river Etneelva the last thirty years. (After data from Statistics Norway)

Figure 5 illustrates the growth of the fish farm production in the county of Hordaland until 2009. In 2009 Hordaland was responsible for 17 % of the total Norwegian production of farmed salmon (StatisticsNorway 2010). Because of the high density of Atlantic salmon farms in the area, a proportion of escapees have been present in the catches at least the last twenty years (Fig. 6). As has been noted in other rivers, the farmed Atlantic salmon often does not ascend the river until late in the season (Carr et al. 1997). The proportion of farmed salmon is thus higher in catches after the normal fishing season, for example in the fishery for stock fish to the Atlantic salmon hatchery. However, it should be noted that individuals of uncertain origin or certain farm origin might be overrepresented in the samples sent for species determination (Steinar Grindheim, pers. comm.).

The bag net at the mouth of the eight kilometres long Etnefjorden has caught both post smolts and older sea trout, indicating that the sea trout may enter the outer fjord systems already in the first sea summer. The fjord systems that the post smolts of both sea trout and Atlantic salmon have to manoeuvre through have a very high density of salmon farms and corresponding high densities of salmon lice (Fig. 7). The Hardangerfjord system, which Etnefjorden is part of, is known to have one of the highest infection rates of salmon lice in Norway (Fig. 8) (Kålås et al. 2010). The situation in the Hardangerfjord has been monitored since the early 1990s (Kålås et al. 2010).

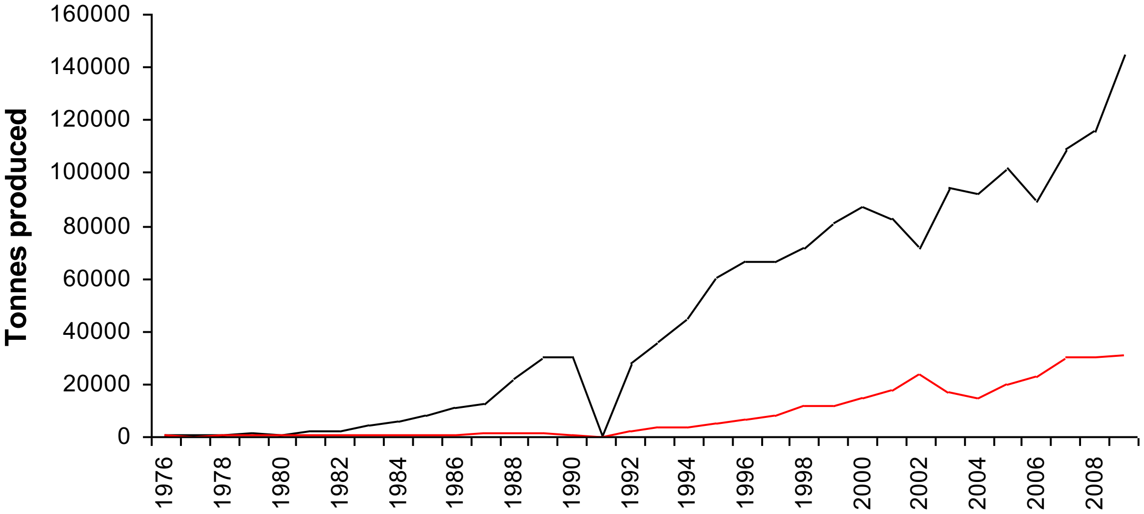

Fig. 5: Yearly production of Atlantic salmon (black) and rainbow trout (*Oncorhynchus mykiss*) (red) in the county of Hordaland, Norway. The production is reported in tonnes after the fish have been slaughtered. No data on farmed Atlantic salmon were available for 1991. (After data from Statistics Norway 2010)

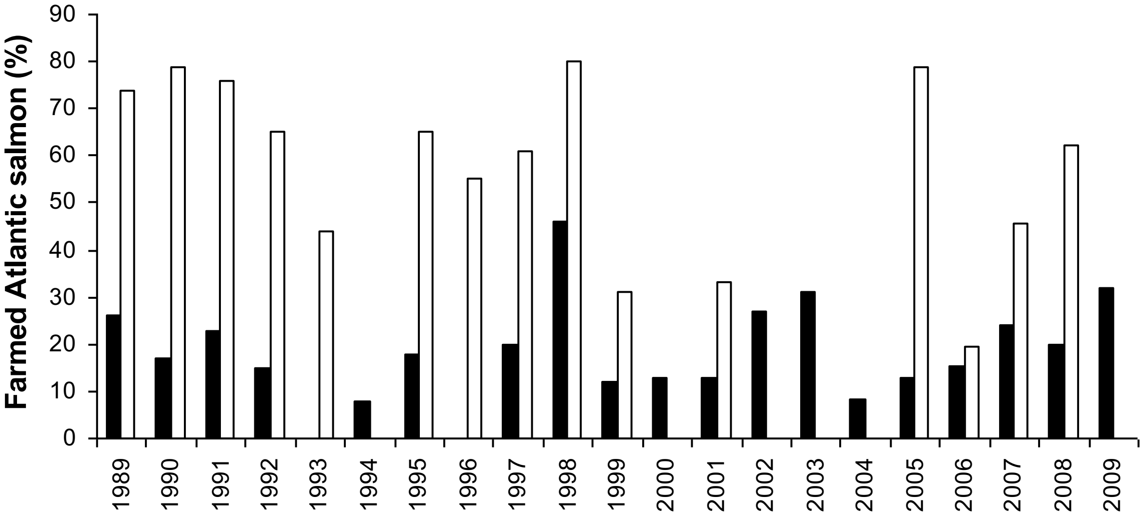

Fig. 6. Proportion of farmed Atlantic salmon in the sport fishery (black) and the catches of spawners for the hatchery (white) in the river Etneelva. From 1989-1994 sport fishery lasted until the 18th of August, while it is extended until the 1st of September from 1995. (Based on data from Fiske et al. (2001) and yearly scale sample analyses from 2001-2009 by the Norwegian Institute for Nature Research)

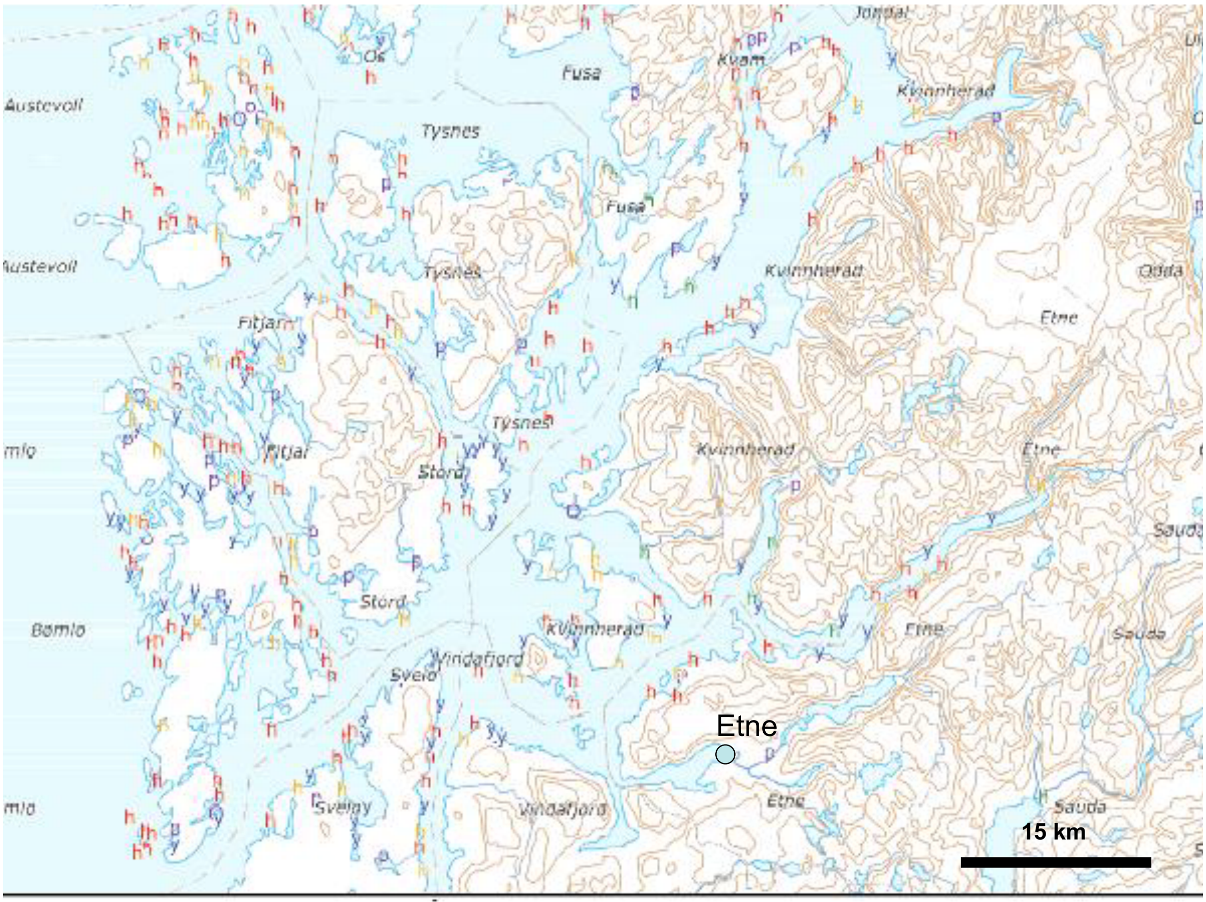

Fig. 7. Overview of aquaculture around Etne. h: Atlantic salmon or rainbow trout farm. h: Broodstock production of Atlantic salmon or rainbow trout. o: Fish slaughtery. p: Hatchery/fry production/smolt production of Atlantic salmon or raibowtrout. y: shellfish production. h: other species. (Map from www.gislink.no)

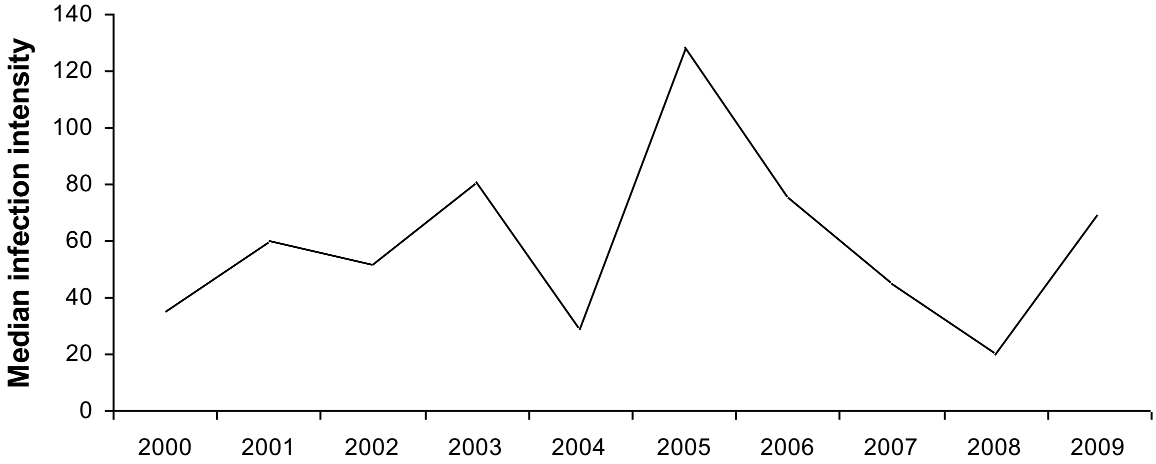

Fig. 8. Median number of salmon lice on prematurely returned sea trout in the fjord system Hardangerfjorden. (Based on data from Kålås et al. 2010)

Data collection

Age and growth of the fish were determined by scale readings. Scale samples of Atlantic salmon and sea trout caught in the river in 1983 originate from a study of the river conducted in 1983 and 1984, while samples from 2008 were obtained partly from local sport fishermen in the river, partly from research catches by a bag net in the fjord (Bjerknes & Waatevik 1985). For the 1983 datasets, scale samples of 175 Atlantic salmon and 112 sea trout were used. For the 2008 Atlantic salmon dataset scale samples of 41 individuals were used, of which 31 were caught in the river and ten in the bag net. Four individuals that were marked as Atlantic salmon by the fishermen were identified as sea trout after scale reading. For the 2008 sea trout dataset 40 individuals were included, of which only four were caught in the river, the rest in the fjord. The reason for the low number of sea trout samples from the river is probably partially because of the bag limit. The distribution of the individuals according to which year they were 1+ parr and post smolts is illustrated in table 1. A minimum of n=3 was required to make an average for each year.

Table 1. Distribution of individuals according to species and year as 1+ parr and post smolt

	Atlantic salmon		Sea trout	
Year	1+ growth	Post smolt	1+ growth	Post smolt
1976			3	
1977	1		4	
1978	13		19	
1979	61	4	41	4
1980	87	53	35	11
1981	15	25	10	71
1982		93		20
2000			3	
2001			2	1
2002			3	3
2003	11		8	
2004	19	3	12	6
2005	11	17	9	7
2006		19	3	10
2007		2		11

All scales were sampled from the area above the side line, behind the dorsal fin. In the laboratory, impressions of the scales were made in strips of cellulose acetate by a scale press, and finally analysed on a screen in a Minox micro film reader. By using a strip of paper on the screen, each of the circuli in the freshwater stage and the first year at sea were transcribed (Fig. 9). All annuli were also marked on the paper. The freshwater growth zone of both sea trout and Atlantic salmon were identified by relative short spacing between the circuli, while the sea stage was identified by a marked increase in circuli spacing (Borgstrøm 2000) (Fig. 10). The annuli were identified by a relative decrease in circuli spacing, and often also by forking of the circuli.(Borgstrøm 2000).

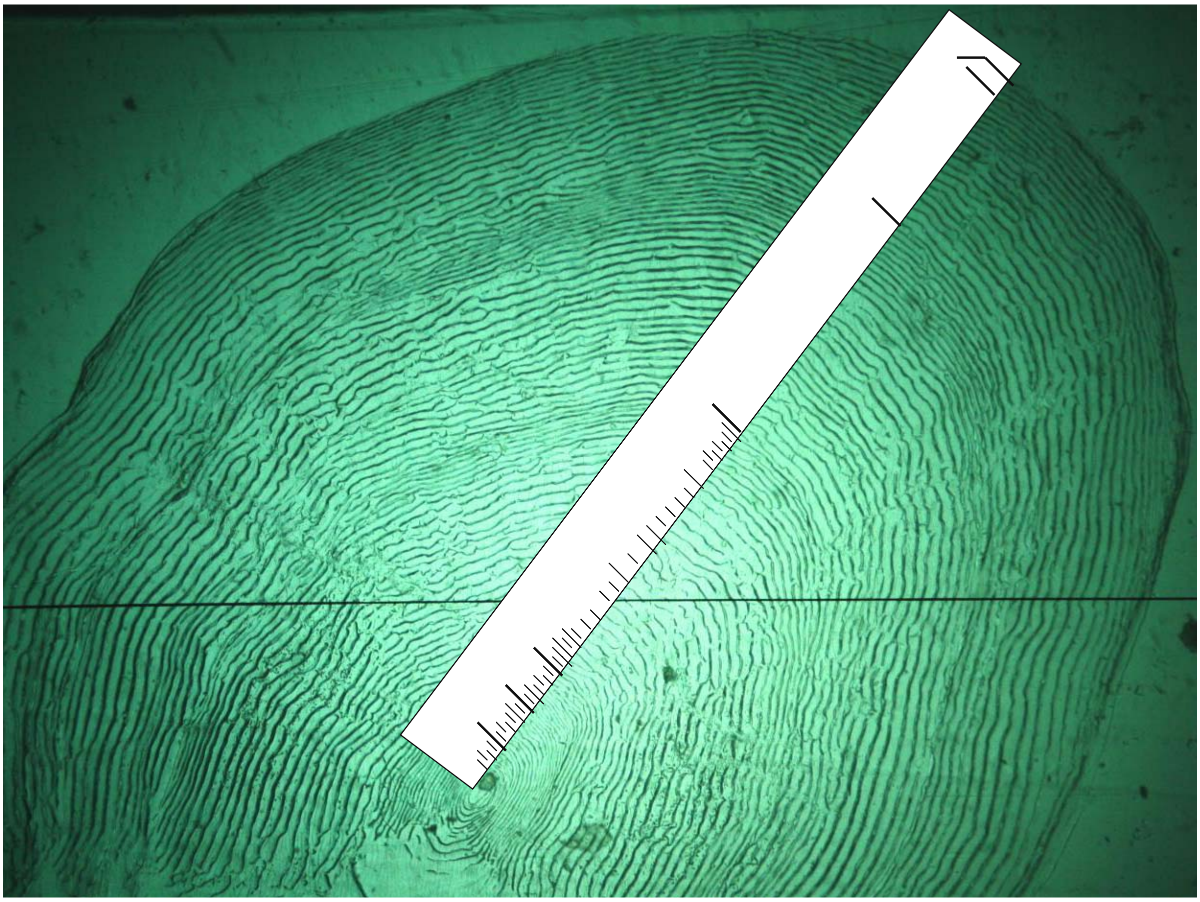

Fig. 9. Reading of scale. All circuli during the freshwater and post smolt stages, along with all annuli, were transcribed from the micro film reader screen to a strip of paper.

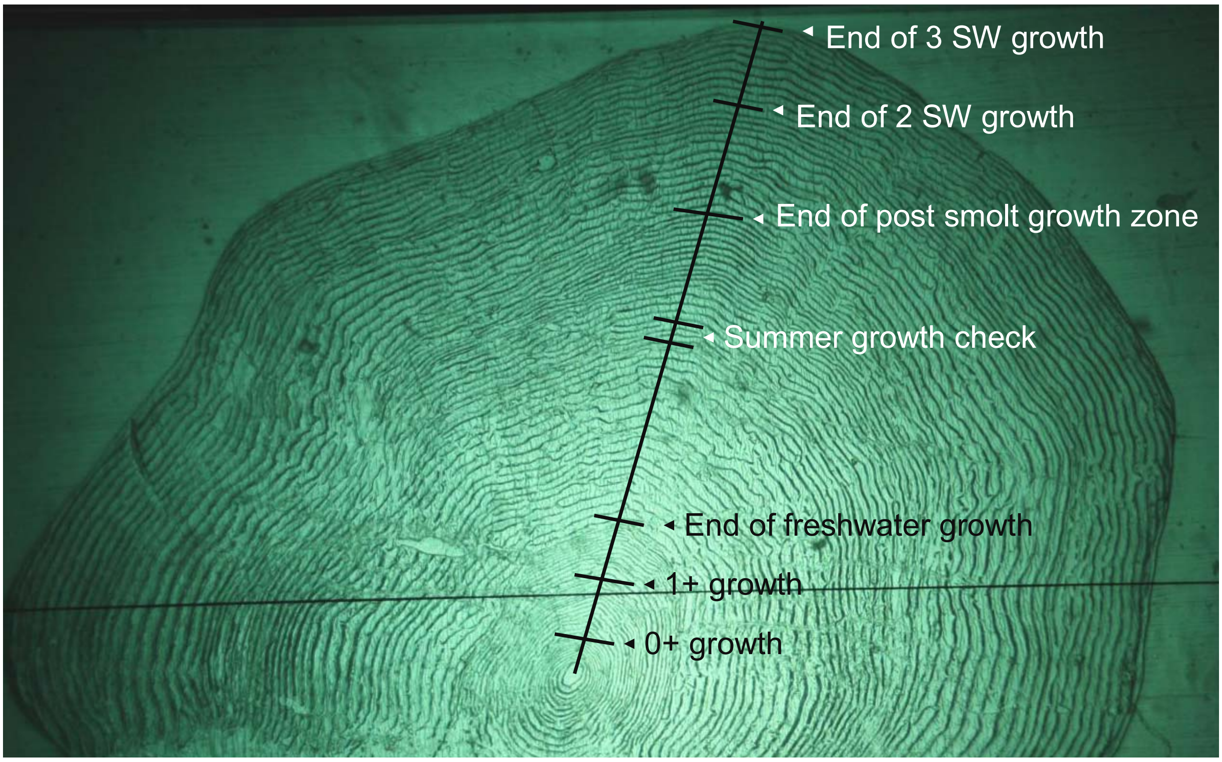

Fig. 10. Example of Atlantic salmon scale. The fish has spent three years in the river and three years in the ocean. There is a summer growth check during the post smolt year.

Summer growth checks that were not annuli were identified by a shortening of circuli spacing that lasted shorter than the normal annuli, before the spacing increased again (MacLean et al. 2000). The relative position of the growth check was found by dividing the number of circuli before the growth check on the total number of circuli in the post smolt growth zone (MacLean et al. 2000). The scale thus ranged from 0 to 1, with the relative position of the growth check somewhere between. In Atlantic salmon, the weight and age at landing were consulted before a summer growth check was identified (MacLean et al. 2000). The same magnification was used for all scale samples. Scale length, and the annual length increments marked on the strip of paper was later measured in mm. The formula of Lea-Dahl was used to back calculate the annual length increments of the individual fish (Borgstrøm 2000). The total number of circuli deposited in the post smolt year of both Atlantic salmon and sea trout were also used as a measure of growth (Peyronnet et al. 2007). Fulton's condition factor was used to study the general condition of the fish (Ricker 1975). To identify and localise the period of maximum growth during the post smolt stage, the four successive circuli deposits in the post smolt growth zone that covered the largest distance on the paper strip were chosen. The position was found by counting the number of circuli from the beginning of the post smolt zone to the start of the maximum growth period and dividing the number found on the total number of circuli in the post smolt growth zone, resulting in a relative position.

Temperature and water discharge data for the river were obtained from the Norwegian Water Resources and Energy Directorate (NVE), which has a station just below the outlet of the lake Stordalsvatnet (UTM zone 32 W, 331719 east, 6619892 north) (Fig. 1). Sea surface temperatures at the weather station Mike in the Northeast Atlantic (UTM zone 33 W, -86617 east, 7381055 north) were used to represent the temperature conditions experienced by the Atlantic salmon post smolt (Fig. 11). For the temperature in the fjord, no sea temperature was available for the entire period, thus data from the closest air temperature station, at Nedre Vats (UTM zone 33 W, -22808 east, 6630422 north) were used (Fig. 1). Both the sea surface and fjord air temperature data were obtained from the weather service eKlima (available at http://sharki.oslo.dnmi.no). Data on temperatures and water discharge were collected for the three summer months of June, July and August, because these are the warmest months and thus considered to be important for growth (Elliott 1975; McCarthy et al. 2008). Because the data were incomplete, especially for the period 1975-1982, average temperatures for each month and the whole summer (June-August) are used instead of degree days.

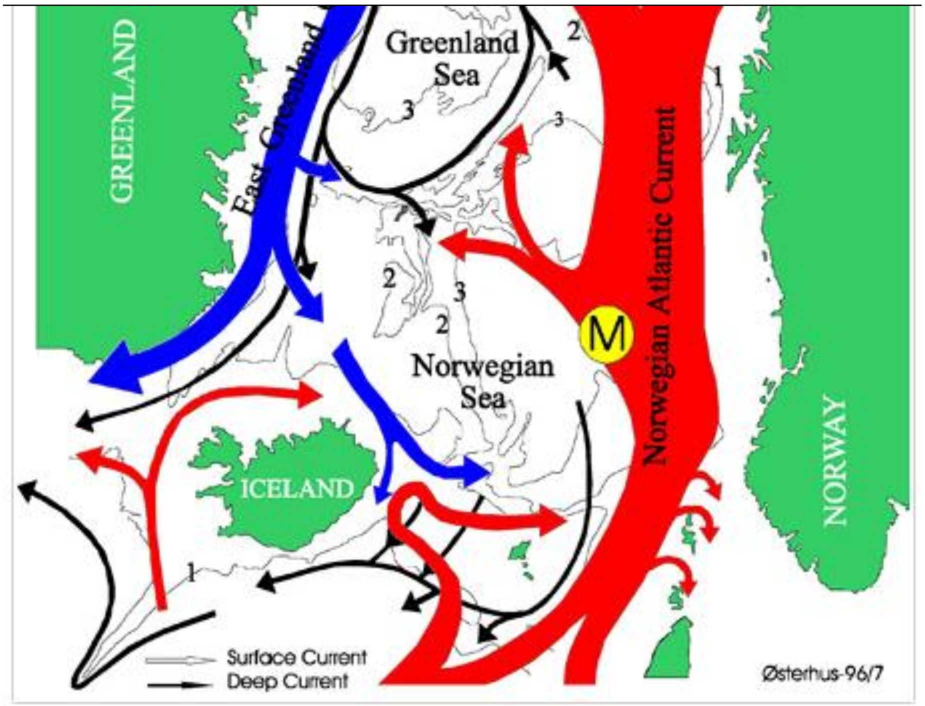

Fig. 11. The location of the weather station Mike (M), with main ocean currents (From http://outreach.eurosites.info/outreach/DeepOceans/station.php?id=3)

Statistical methods

The statistical program Minitab 15 was used to analyse the data. T-tests were used to see whether two datasets were significantly different. Some of the datasets were not normally distributed, in which cases Mann-Whitney tests were used in stead of t-tests. To look for relationships between datasets regression was used. For all statistical tests, a significance level of $\alpha=0.05$ was used.

Results

Temperature, water discharge and growth in freshwater

The mean river temperature in the river Etneelva for June, July and August during the period 2000-2007 is significantly higher than the temperature during the period 1975-1982 (t-test; $p<0.05$ for all three months) (Fig. 12). The June temperatures increased 0.6 ^{o}C on average, while the increases in July and August were 1.2 ^{o}C and 0.9 ^{o}C, respectively. When comparing the two periods, especially the most recent August temperatures are more fluctuating (Fig. 13). It should be noted that 1979 was a very cold summer, with an August mean temperature of only 13.6 ^{o}C. No significant change was detected in water discharge during the three summer months (t-test; $p>0.05$ for all three months).

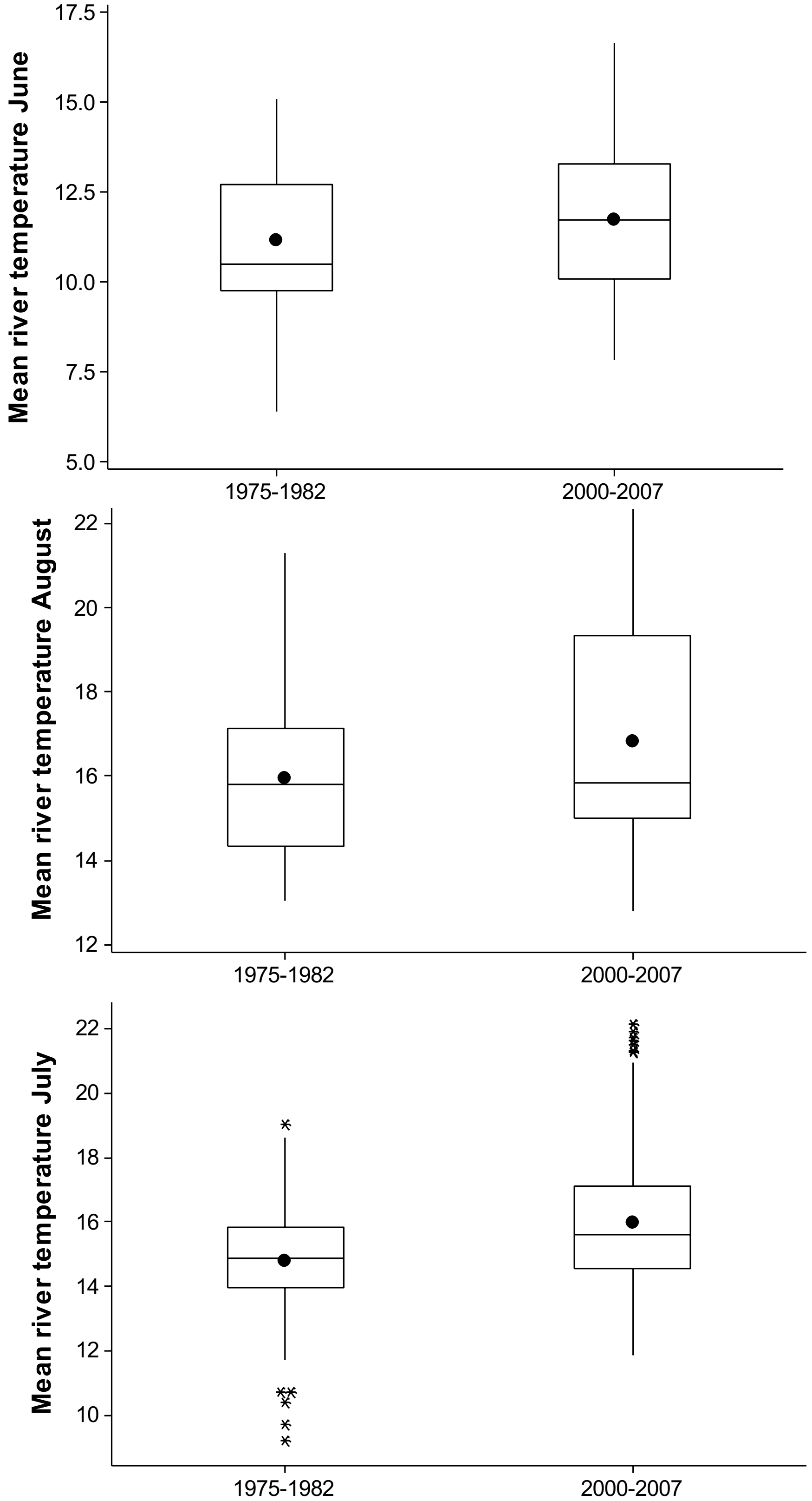

Fig. 12. Mean temperature in the river Etneelva in June, July and August for the two periods 1975-1982 and 2000-2007. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

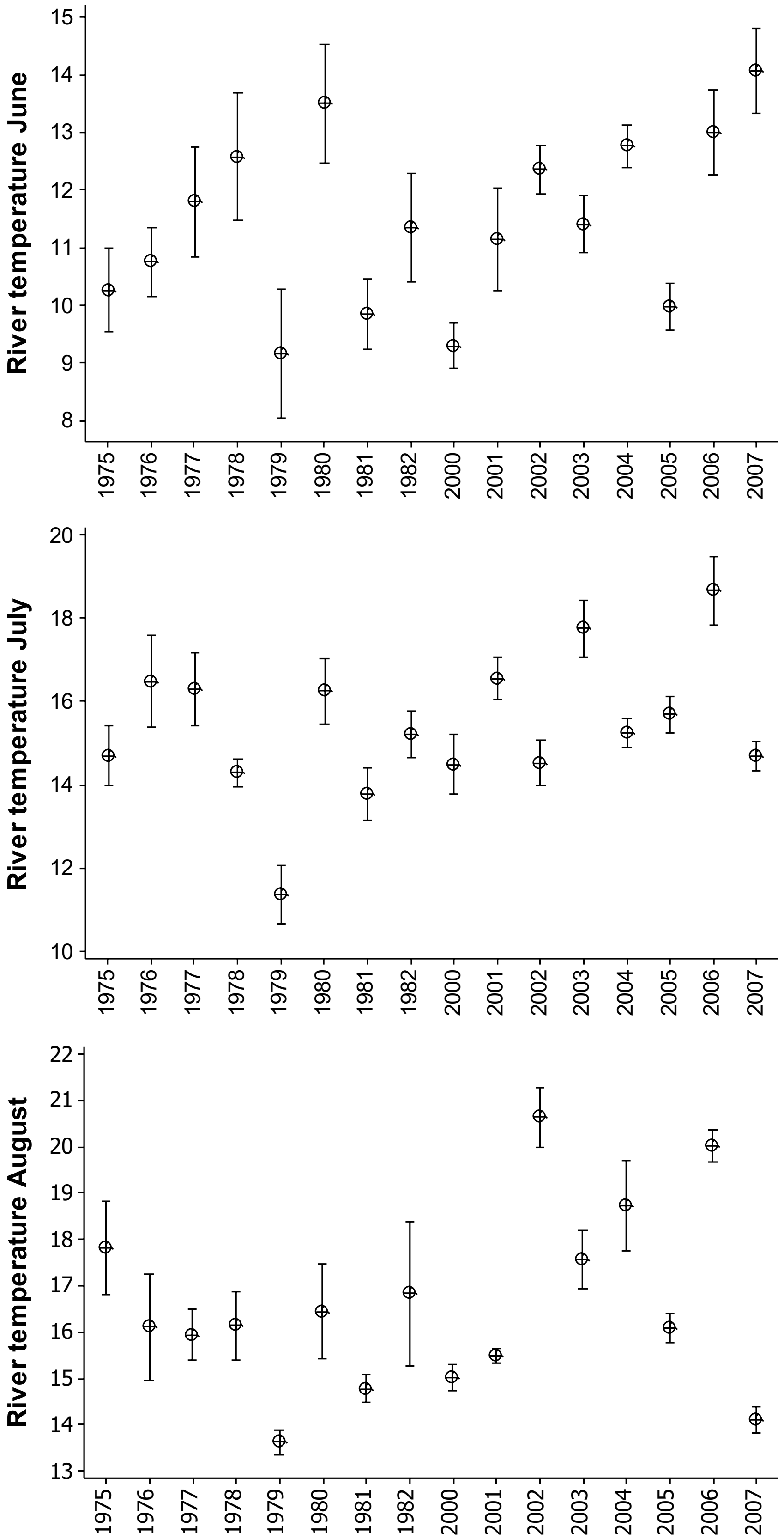

Fig. 13. Mean annual temperature in the river Etneelva in June, July and August in the years 1975-1982 and 2000-2007, with 95% confidence intervals.

For sea trout parr there appears to be a slight decrease in 1+ growth from the period 1976-1981 to 2000-2006, but it is not significant (t-test; p= 0.15) (Fig. 14). During the period 2003-2005, there is a slight increase in growth, although not as clear as that observed for Atlantic salmon parr (Fig. 15). The smolt size has not changed significantly between 1979-1982 and 2001-2007 (Mann-Whitney; p=0.6) (Fig. 16). There is no change in median smolt age either (Mann-Whitney; p=0.92). The growth of 1+ Atlantic salmon parr has increased, but not significantly (Mann-Whitney; p = 0.06) from 1978-1981 to 2003-2005 (Fig. 17). The mean increase is 12 mm. Within the period 2003-2005 the growth increment is also increasing, whereas growth between years is quite stable for the early period, except a very low growth rate in 1980 (Fig. 18). The length of the smolts has increased from 1979-1982 to 2004-2007 by a mean of eight mm, but the change is only barely significant (t-test; p=0.05) (Fig. 19). The median smolt age in the period has decreased from three to two years, but the change is not significant (Mann-Whitney; p=0.17).

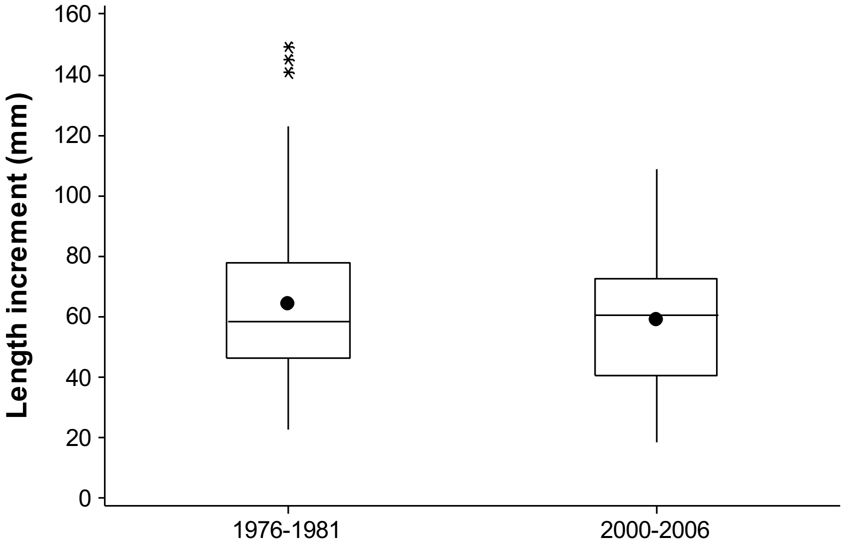

Fig. 14. Mean 1+ sea trout growth increment (mm) in the periods 1976-1981 and 2000-2006 in the river Etneelva. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

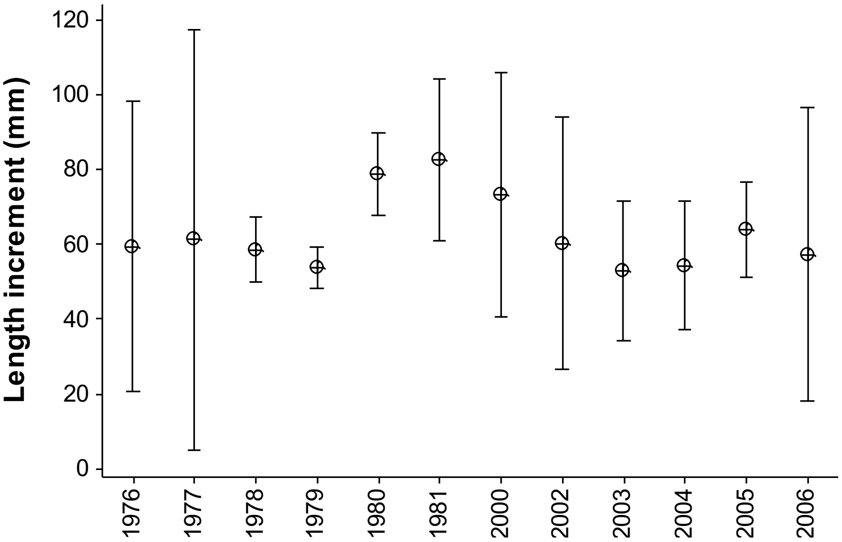

Fig. 15. Annual mean length increment (mm) of 1+ sea trout in the river Etneelva in the years 1976-1981 and 2000-2006, with 95% confidence intervals. Data from 2001 are missing.

Fig. 16. Mean back calculated length of sea trout smolts in the river Etneelva in the periods 1979-1982 and 2001-2007. In the study material there were no sea trouts smolting in 2003. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

Fig. 17. Mean 1+ Atlantic salmon length increment (mm) in the river Etneelva for the period 1979-1983 and the period 2003-2005. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean.

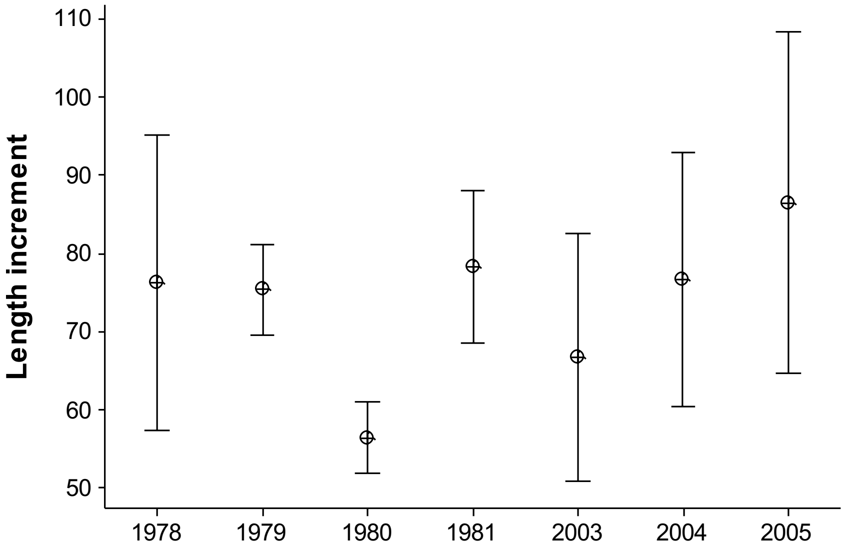

Fig. 18. Annual mean length increment (mm) of Atlantic salmon 1+ in 1978-1981 and 2003-2005 in the river Etneelva, with 95% confidence intervals.

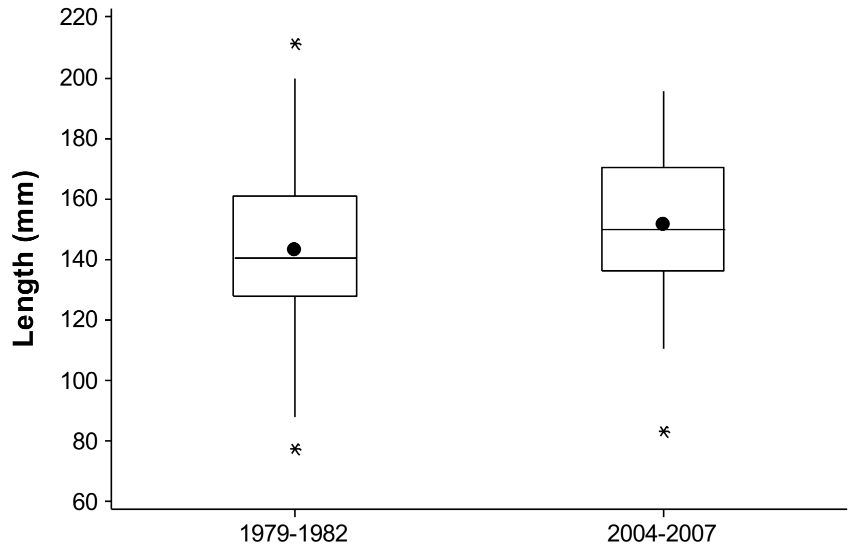

Fig. 19. Mean back calculated length (mm) of Atlantic salmon smolt in the river Etneelva in the periods 1979-1982 and 2004-2007. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

The growth of 1+ sea trout parr was negatively correlated to the length of 1+ Atlantic salmon parr at the start of the growing season (regression; R^2=76,8, p=0,01) (Fig. 20), but there was no correlation between the growth of 1+ Atlantic salmon and 1+ sea trout (regression; R^2=3.8 p=0.67). The size of the 1+ sea trout at the beginning of the growing season did not affect the growth of 1+ Atlantic salmon (regression; R^2=7.9, p=0.54). Nor did the growth as 0+ affect the growth as 1+ for neither Atlantic salmon nor sea trout (regression; R^2=7.9, p=0.54 and R^2=17.6, p=0.18, respectively). Length at smolting for sea trout was explained by age at smolting (regression; R^2=31.8, p= 0.00). There was also a significant relationship between length at smolting and age in Atlantic salmon smolt, but age did not explain much of the variation in smolt length (regression; R^2=3.3, p=0.01).

The mean summer river temperatures did not have a significant effect on the growth of 1+ sea trout (regression; R^2=6.1, p =0.44). Neither did the mean summer water discharge have any significant effect on 1+ sea trout growth (regression; R^2=8.6, p =0.35). For Atlantic salmon, however, there was a positive relationship between the growth of 1+ parr and mean summer temperature (regression; R^2=86.1, p =0.00) (Fig. 21). There is a negative relationship between the mean water discharge during the summer months and the Atlantic salmon 1+ growth, but the relationship is not significant (regression; R^2=55.8, p=0.054) (Fig. 22). Together, mean summer river temperature and mean summer water discharge in the river could explain 83.6%

of the variance in 1+ Atlantic salmon length increment (Multiple regression; R^2 adjusted=83.6, p =0.01).

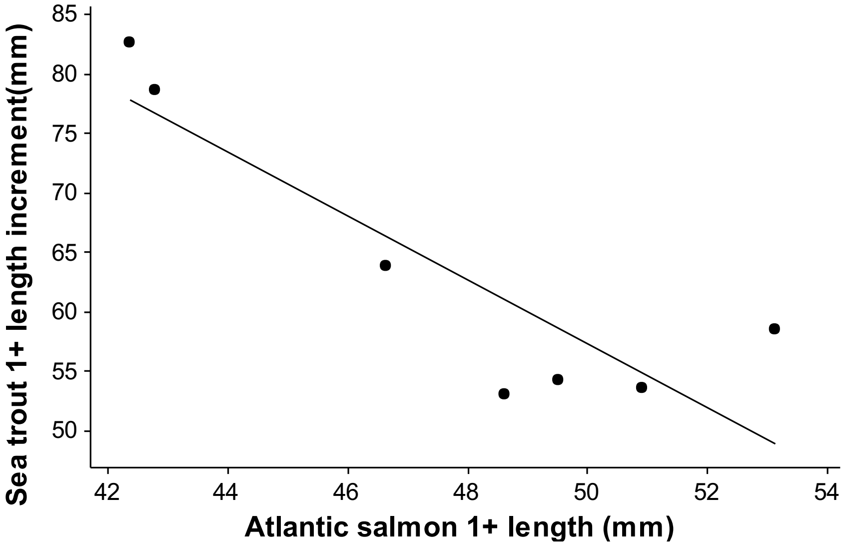

Fig. 20. The relationship between length increment (mm) of 1+ sea trout and the length of 1+ Atlantic salmon at the beginning of the growth season in the river Etneelva.

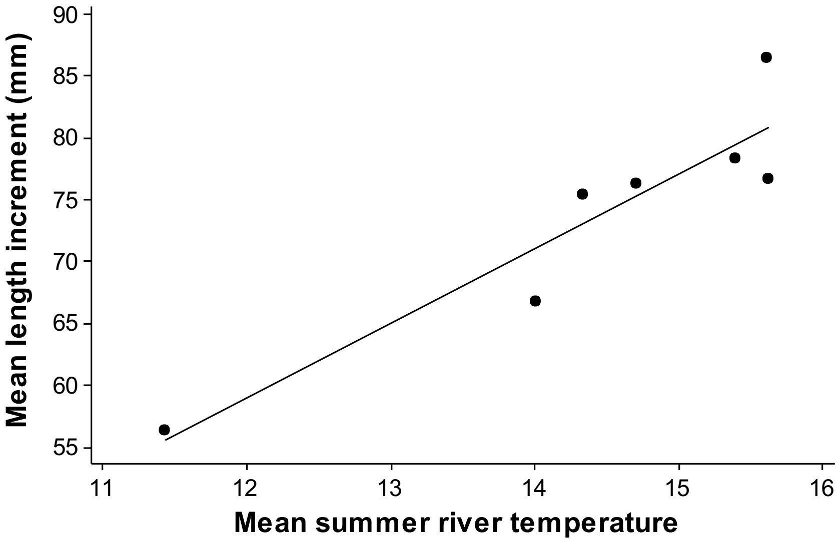

Fig. 21. The relationship between the mean summer temperature in the river Etneelva and the mean length increment (mm) of 1+ Atlantic salmon.

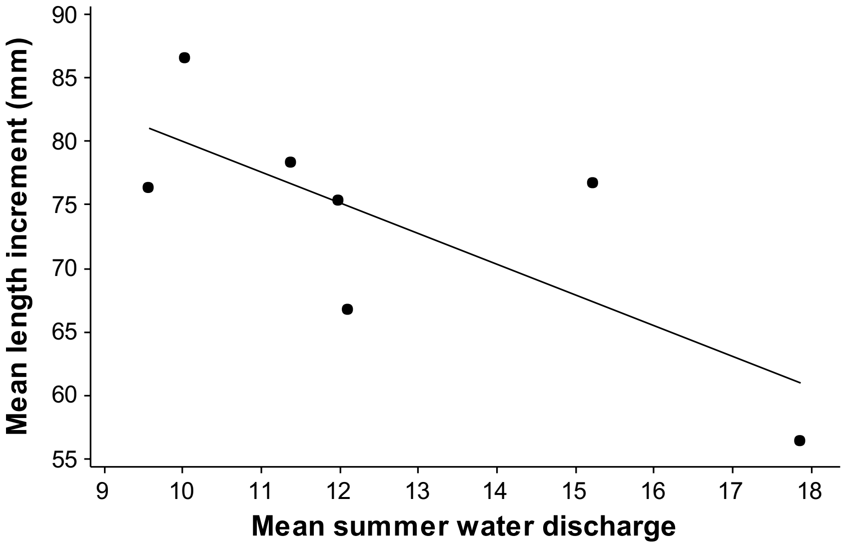

Fig. 22. The relationship between mean summer water discharge in the river Etneelva and the mean length increment (mm) of 1+ Atlantic salmon.

Temperature and growth in saltwater

The fjord temperatures have increased significantly for July and August, but not for June (t-test; p= 0.00, 0.00 and 0.33 respectively) (Fig. 23). The mean increment from 1975-1982 to 1999-2007 was 1.33 °C in July and 1.52 °C in August. The temperatures during the last period are more fluctuating (Fig. 24).Sea temperatures have risen significantly in June, July and August from 1975-1982 to 1999-2007 (t-test; $p<0.05$ for all three months) (Fig. 25). The mean increases in sea surface temperatures were 0.7 °C in June, 1.3 °C in July and 1.2 °C in August. The trend for all months is that the temperatures are more unstable in the period from 1999 to 2007 compared to the period 1975-1982 (Fig. 26). In 2002, the mean June temperature was 11.9 °C while the mean for the period 1999-2007 was 9.6 °C.

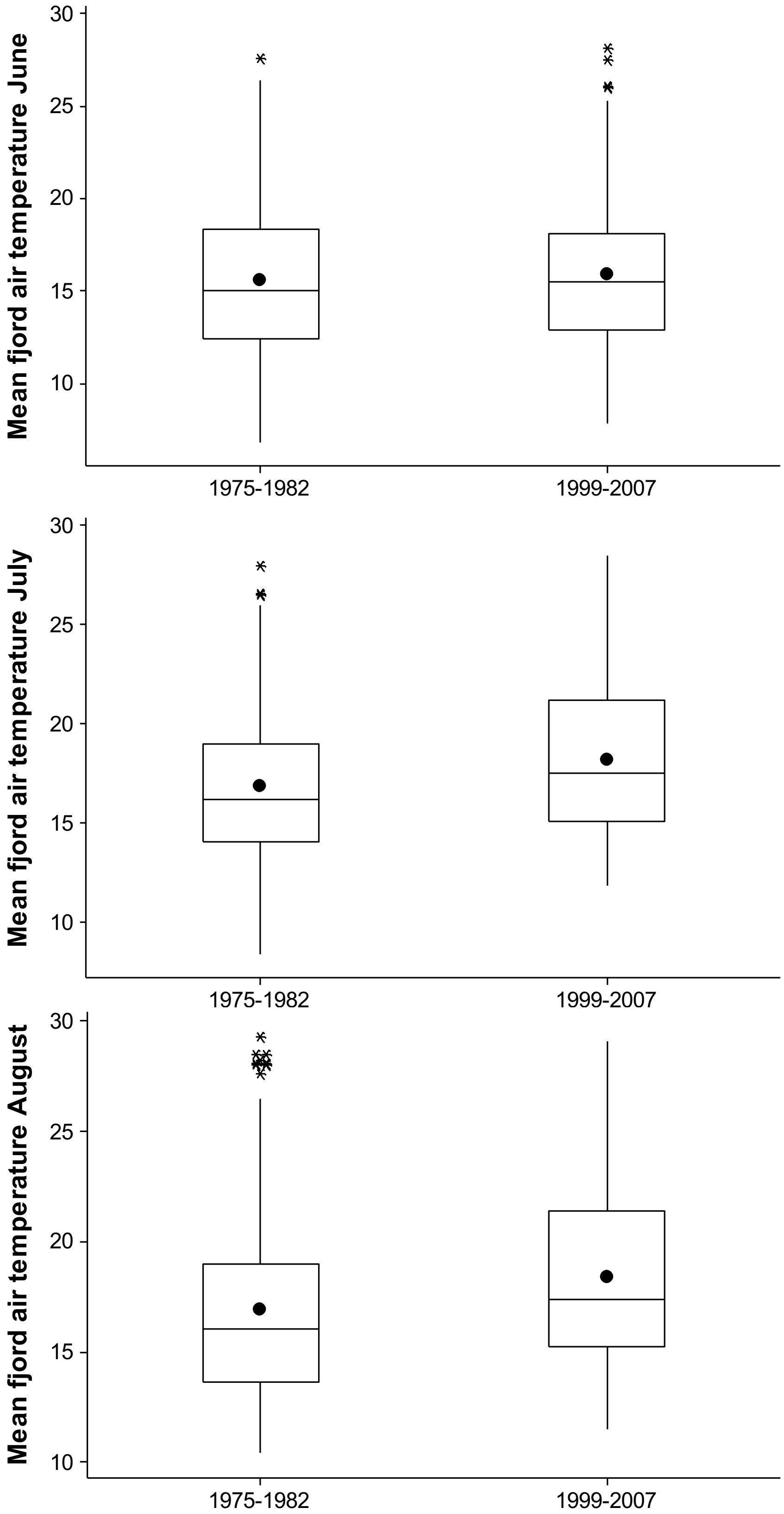

Fig. 23. Mean air temperatures in June, July and August for the periods 1975-1982 and 1999-2007 at the location Nedre Vats. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

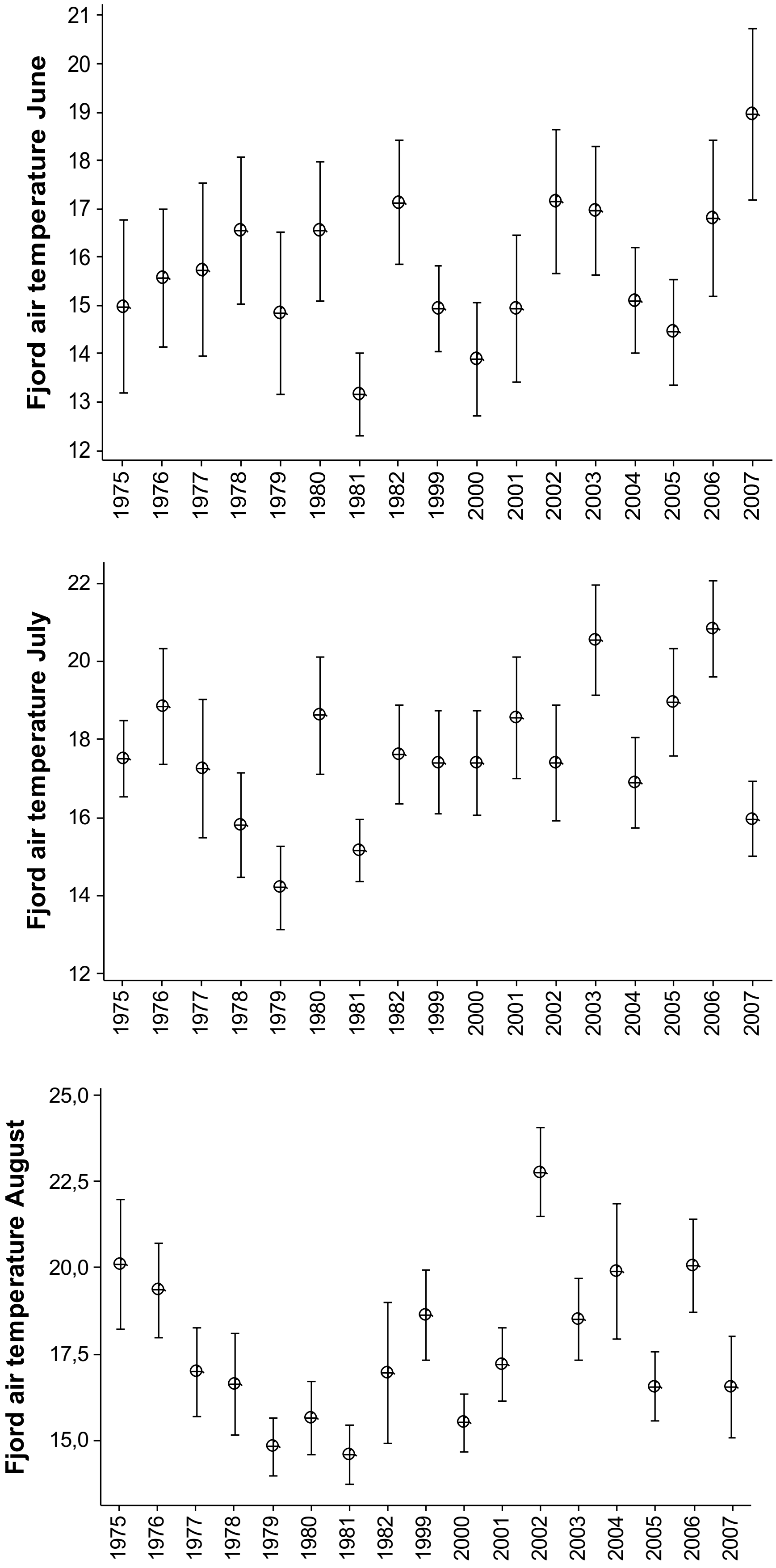

Fig. 24. Annual mean air temperatures in June, July and August in the periods 1975-1982 and 1999-2007 at the location Nedre Vats, with 95% confidence intervals.

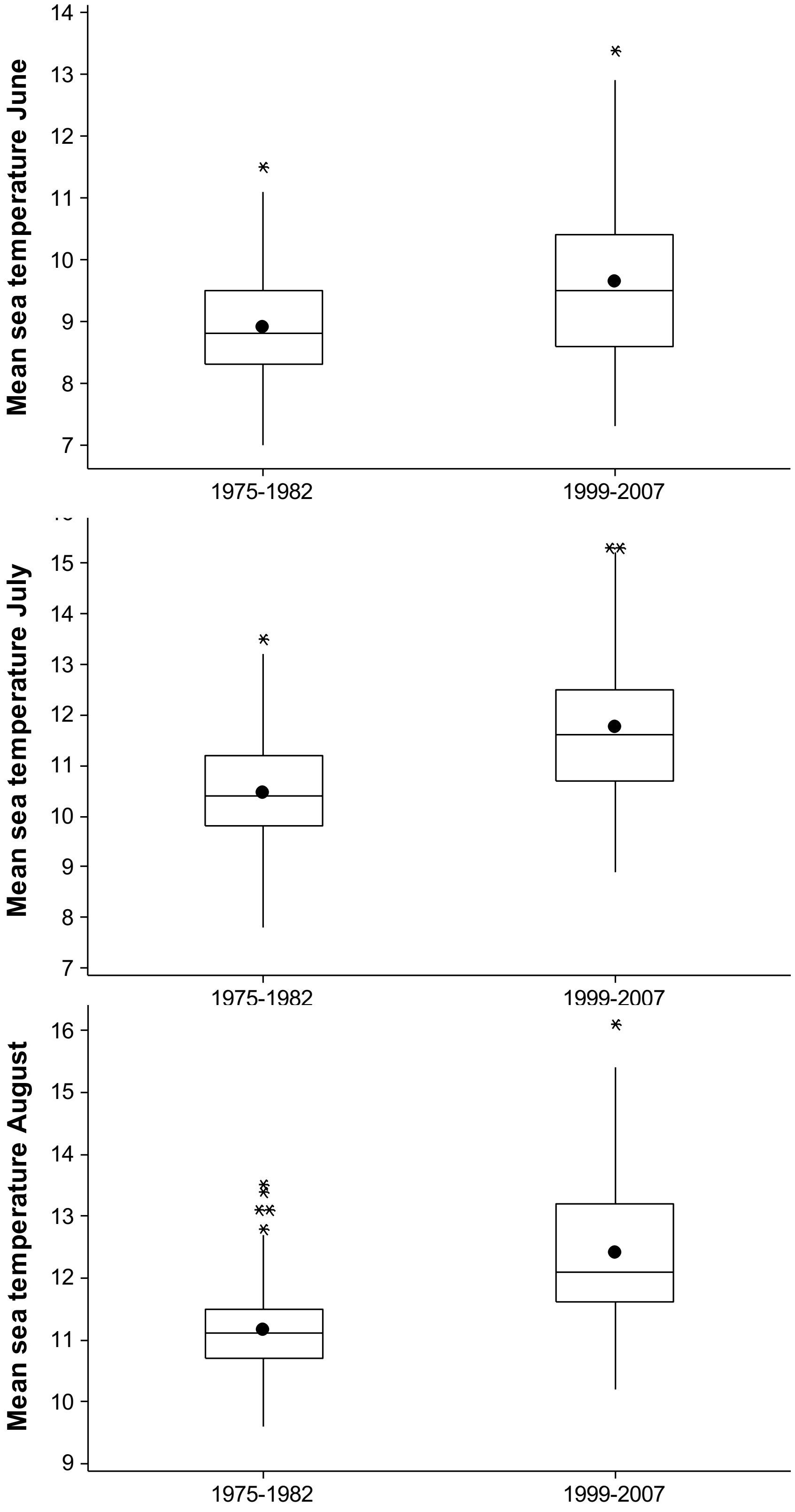

Fig. 25. Mean sea surface temperatures in June, July and August for the period 1975-82 and the period 1999-2007 at the weather station Mike. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

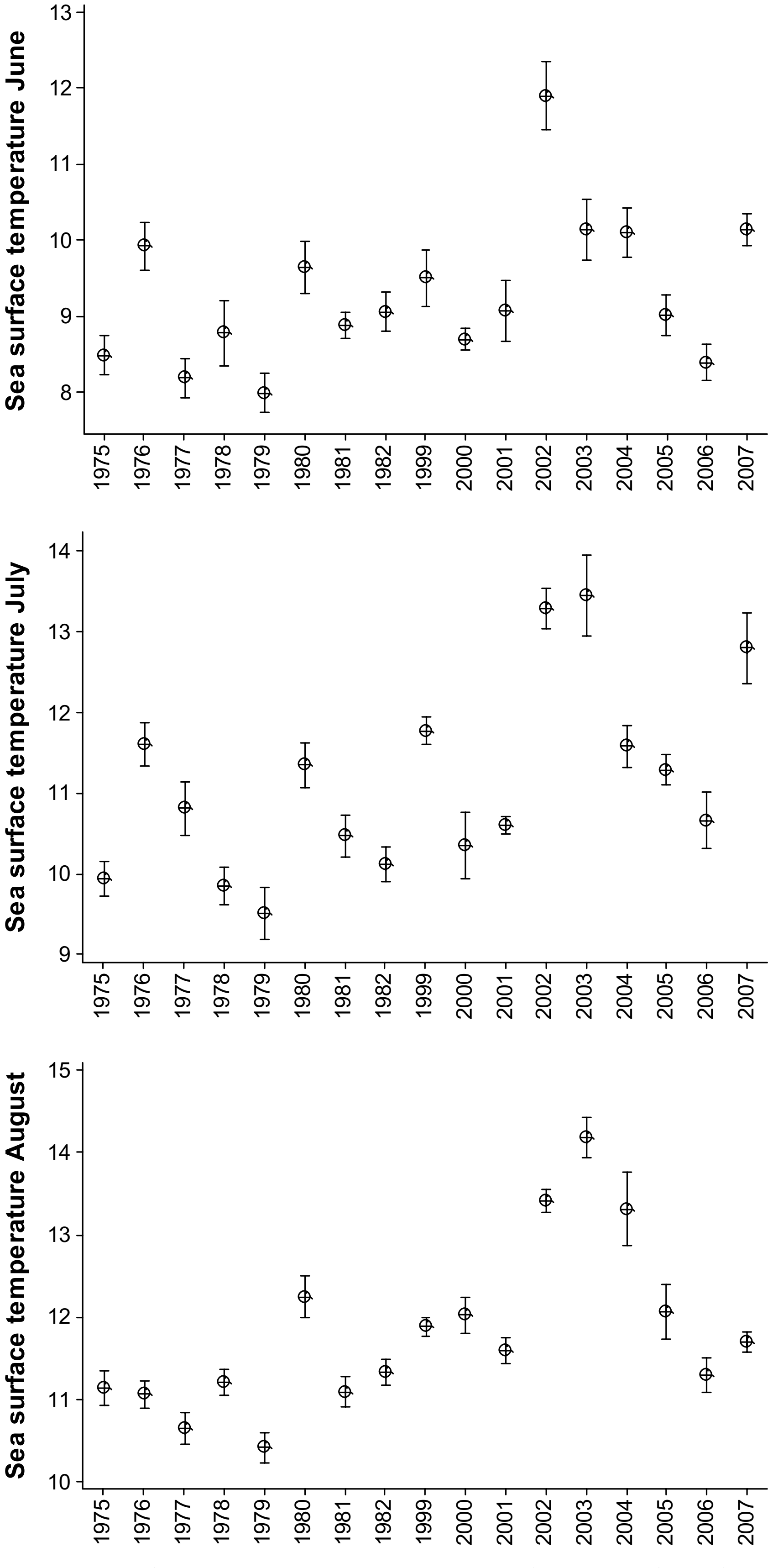

Fig. 26. Annual mean sea surface temperatures in June, July and August in the periods 1975-82 and 1999-2007 at the weather station Mike, with 95% confidence intervals.

There is a significant decrease in the growth of sea trout post smolts (Mann-Whitney; p = 0.00) during the first year in the fjord from the period 1975-1982 to 2004-2007 (Fig. 27). While the mean length increment of sea trout during the first summer in the fjord was 129 mm in 1979-1982, the mean length increment in 2004-2007 was 91 mm. There is also a negative trend in the last period (Fig. 28).The relative maximum length increments have also been reduced, from ten to eight (t-test; p=0.00). However, the relative location of the maximum growth period has not changed (t-test; p=0.63). The period of maximum growth is located relatively early in the post smolt growth zone (Fig. 29). There is no difference in total number of circuli deposited during the post smolt year between the two periods (t-test; p=0.48). Nor was there any correlation between the number of circuli deposited and the length increment during the post smolt year (regression; R^2=0.1,p=0.71). The growth during the second growth season in sea water is also reduced from the period 1979-1982 to the period 2004-2007 by a mean of 2.5 cm (Mann-Whitney; p=0.00) (Fig.30). For the third and fourth growth season at sea there is a negative development, but the differences are not significant (Mann-Whitney; p=0.37 and p=0.46 respectively). As a result, the mean accumulated length of a sea trout caught in 2008 is shorter than the mean accumulated length of a sea trout caught in 1983 that have spent the same number of years at sea (Fig. 31). Fulton's condition factor for sea trout has also decreased significantly from 1983 to 2008 (T-test; p=0.00) (Fig. 32). The mean decrease is 0.18.

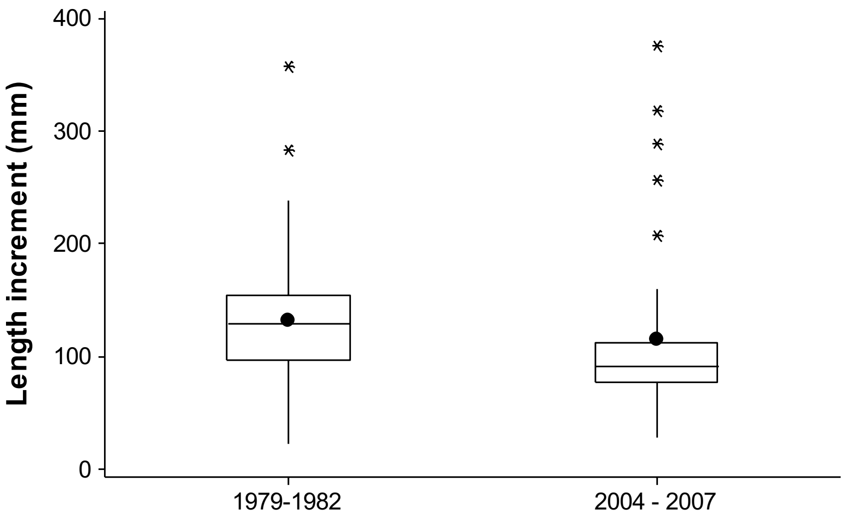

Fig. 27. Mean growth increment (mm) of sea trout from the river Etneelva during the first summer in the fiord for the period 1979-1982 and the period 2004-2007. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

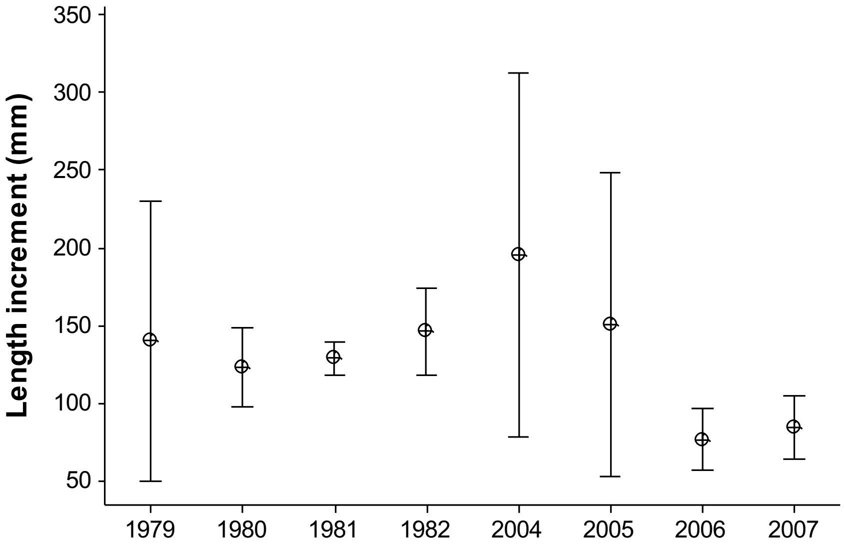

Fig. 28. Annual mean length increments (mm) of sea trout from the river Etneelva during the first summer in salt water, with 95% confidence intervals.

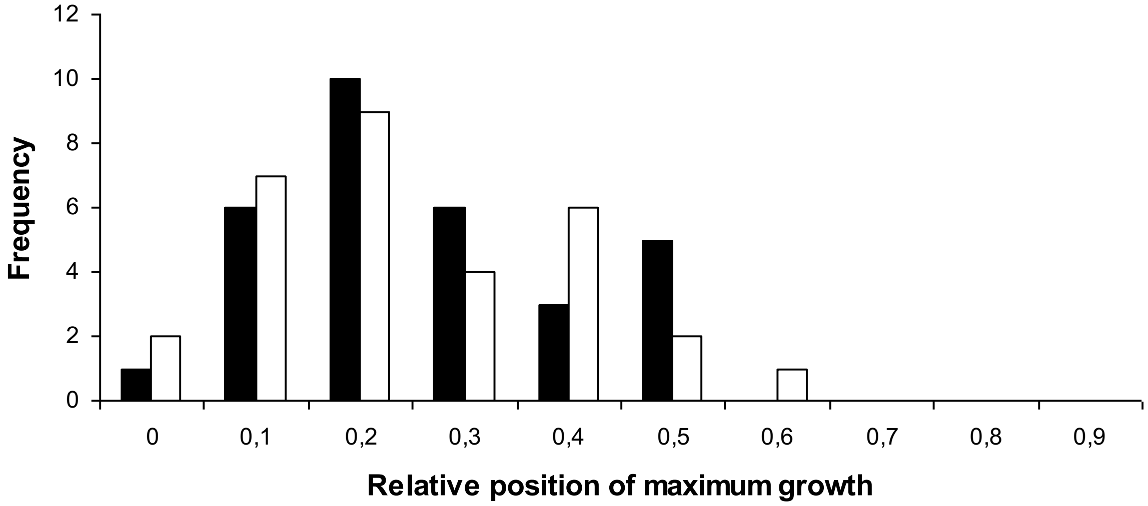

Fig. 29. Relative location of the period of maximum growth on the post smolt growth zone for sea trout caught in the river Etneelva in 1983 (black) and 2008 (white).

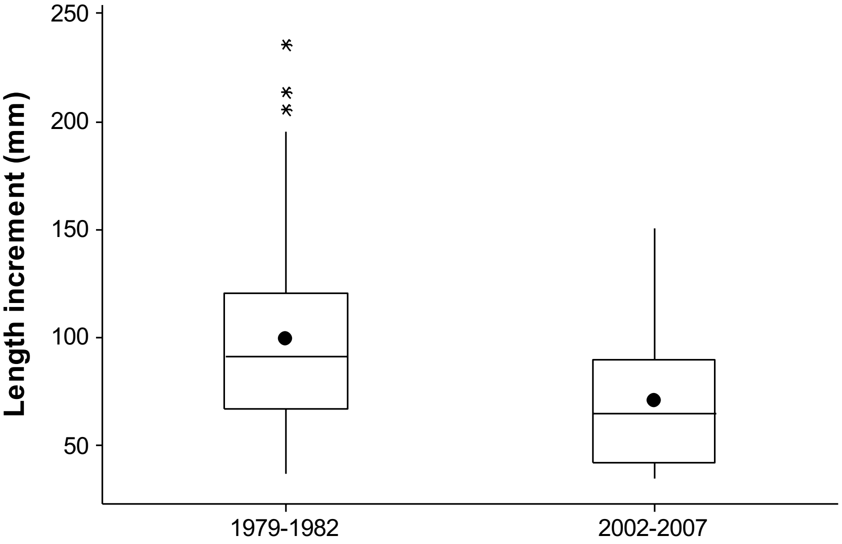

Fig. 30. Mean length increment (mm) during the second season at sea for sea trout from the river Etneelva in the periods 1979-1982 and 2002-2007. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

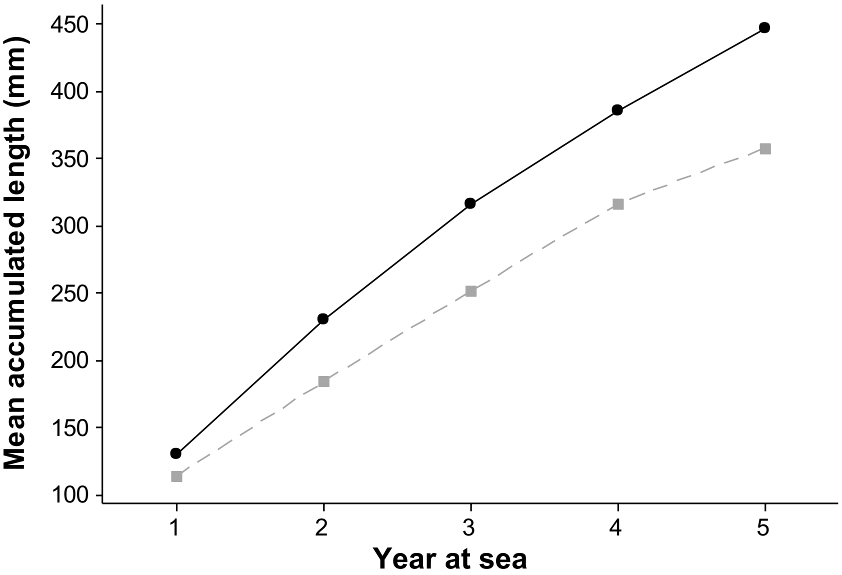

Fig. 31. Mean accumulated length of sea trout from the first to the fifth sea year, back calculated from scales of fish captured in the River Etneelva in 1983 (black) and 2008 (grey).

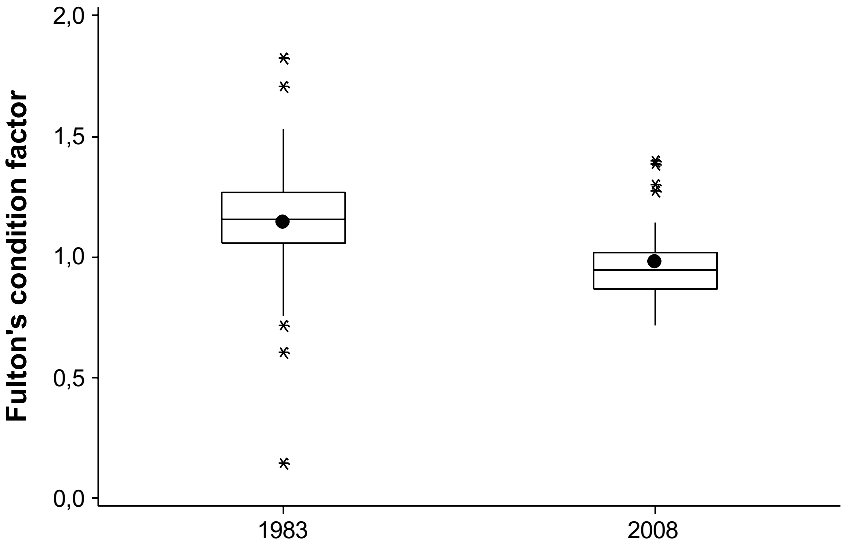

Fig. 32. Fulton’s condition factor for sea trout caught in the river Etneelva in 1983 and in 2008. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

For Atlantic salmon there is a negative trend in the length increment during the first year at sea during the period 1979-82 (Fig. 33). In comparison, the length increment of the post smolt is significantly higher in the period 2004-2006 (t-test; p= 0.01), with a mean increase in growth between the two periods of 41 mm (Fig. 34). The period of maximum growth has been slightly skewed towards the earlier part of the post smolt growth zone (Mann-Whitney; p=0.00) (Fig. 35). The relative length of the maximum growth zone has been increased significantly between the two periods, from 16 to 17.7 (t-test; p=0.00). There is a correlation between the total length increment during the post smolt growth season and the number of circuli deposited in the same period, but the correlation does not explain much of the variance in length increment (regression; R^2=6.2, p=0.00).The number of circuli deposited during the post smolt year has increased from 1979-1982 to 2004-2006 by a mean of nine circuli (t-test; p=0.00). The length increments during the second year at sea has been significantly reduced from 1979-1982 to 2004-2006 by a mean of five cm (t-test; p=0.00) (Fig. 36). There is no significant difference between the third sea year growth of the two periods (t-test; p=0.61). When the mean accumulated growth of each sea year is summed, there is little difference in length of a MSW of equal age caught in 1983 or 2008 (Fig. 37). Fulton’s condition factor has decreased significantly from the Atlantic salmon caught in the river Etneelva in 1983 to the salmon caught in 2008 (t-test; p=0.00) (Fig. 38).

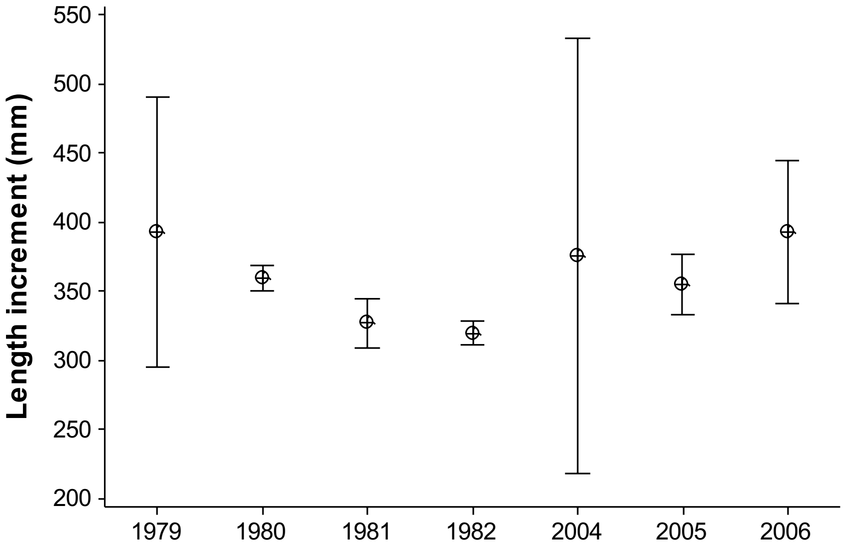

Fig. 33. Annual mean length increment (mm) of Atlantic salmon post smolts from the river Etneelva during the first year in the ocean, with 95% confidence intervals.

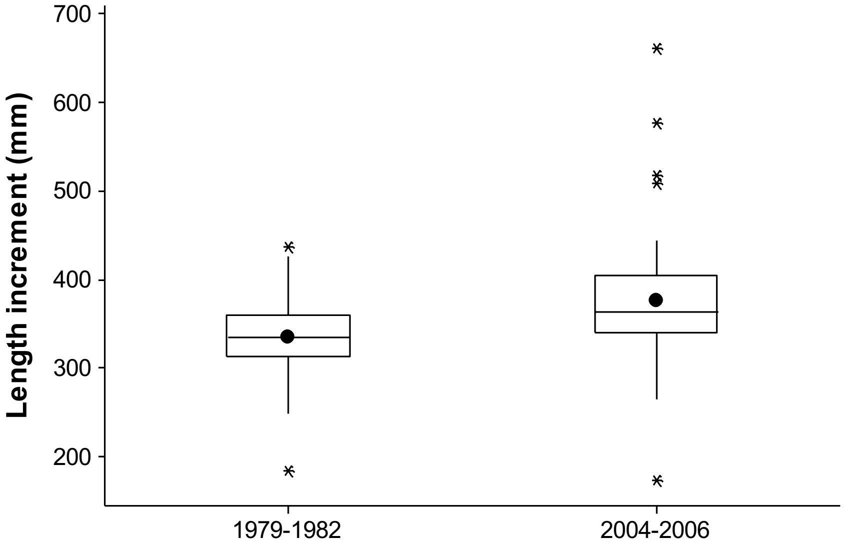

Fig. 34. Mean Atlantic salmon post smolt length increment (mm) for the periods 1979-1982 and 2004-2007 back calculated from fish caught in the river Etneelva. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

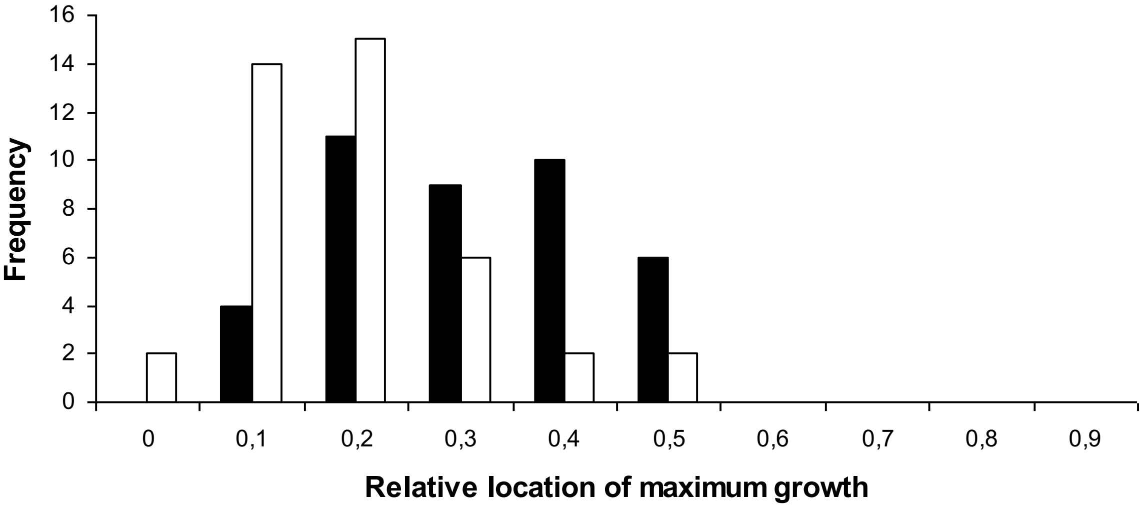

Fig. 35. Relative position of the period during the post smolt growth zone displaying maximum growth for Atlantic salmon post smolts caught in 1983 (black) and 2008 (white) in the river Etneelva.

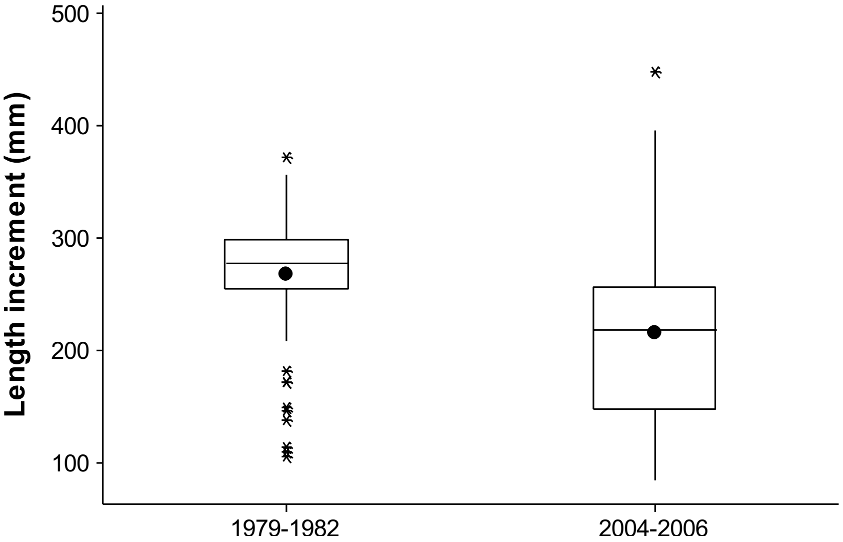

Fig. 36. Mean length increment during the second year at sea for the periods 1979-1982 and 2004-2006 for Atlantic salmon caught in the river Etneelva. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

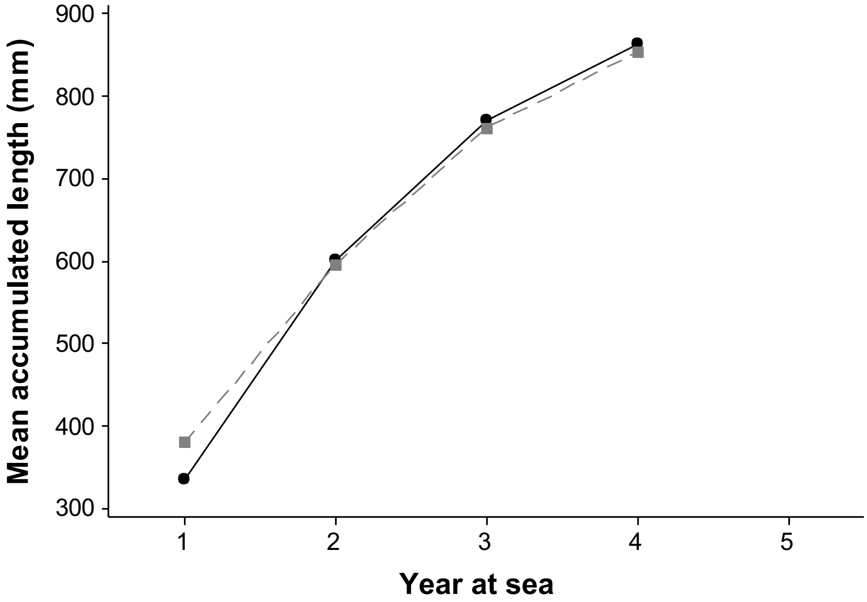

Fig. 37. Mean accumulated length of Atlantic salmon during the sea stage for fish caught in 1983 (black) and 2008 (grey) in the river Etneelva.

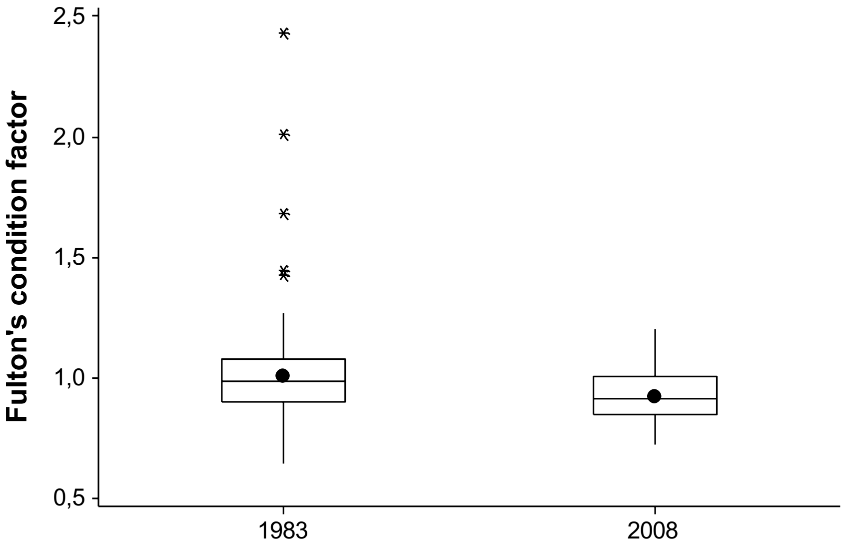

Fig. 38. Fulton's condition factor for Atlantic salmon caught in the river Etneelva in 1983 and 2008. The box contains the middle 50% of the data with the median marked with a horizontal line and the mean with a dot. Upper and lower whiskers include data points up to1.5 box lengths from the mean. Observations outside the whiskers are marked with *.

Mean summer fjord temperatures did not affect the growth of sea trout post smolts (Fig. 39) (regression; R^2=12.9, p =0.34). Nor did mean sea surface temperatures during the summer months have any significant effect on the growth of Atlantic salmon post smolts (regression; R^2=0.3, p =0.91) (Fig. 40).

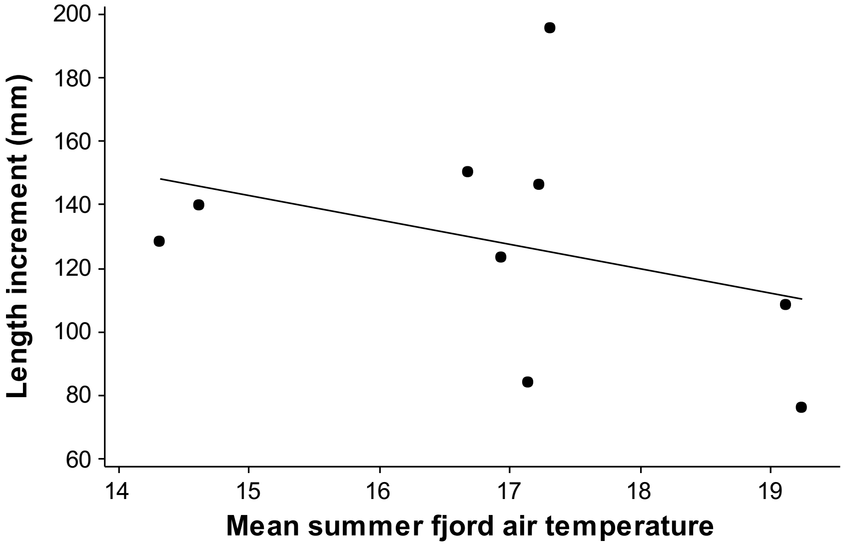

Fig. 39. The relationship between mean summer air temperatures at the location Nedre Vats and the length increment (mm) of sea trout from the river Etneelva during their first year at sea.

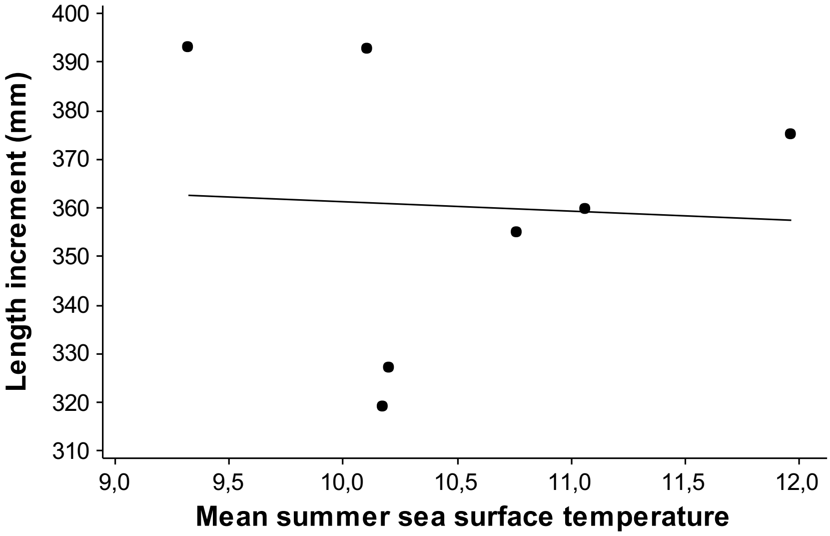

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Fig. 40. The relationship between mean summer sea surface temperatures at weather station Mike and the length increment (mm) of Atlantic salmon from the river Etneelva during their first year at sea.

Of the Atlantic salmon caught in 2008, 65 % of the fish showed signs of growth checks that were not annuli during their first year at sea. The trend seems to have started in 2005, as none of the fish that were post smolts in 2004 displayed growth checks, whereas 53 % of the 2005 post smolts, 84 % of the 2006 post smolts and 100 % of the 2007 post smolts had summer growth checks. There also appears to be a trend of the growth checks appearing relatively earlier in the growth season (Fig. 41). For the Atlantic salmon caught in 1983 only 4.5 % of the fish had summer growth checks. The sea age of the Atlantic salmon caught in 1983 was divided into 2.3 % 4 SW, 30.3 % 3 SW, 14.3 % 2 SW and 53.1 % 1 SW (Fig. 42). For the 2008 study material, the proportions were 7.3 %, 41.5 %, 46.3 % and 4.9%, respectively. Of the Atlantic salmon caught in 2008 that were more than one sea winter old, 53.8 % had spawned earlier. For the Atlantic salmon that returned to the river in 1983 the proportion was 20.2 %.

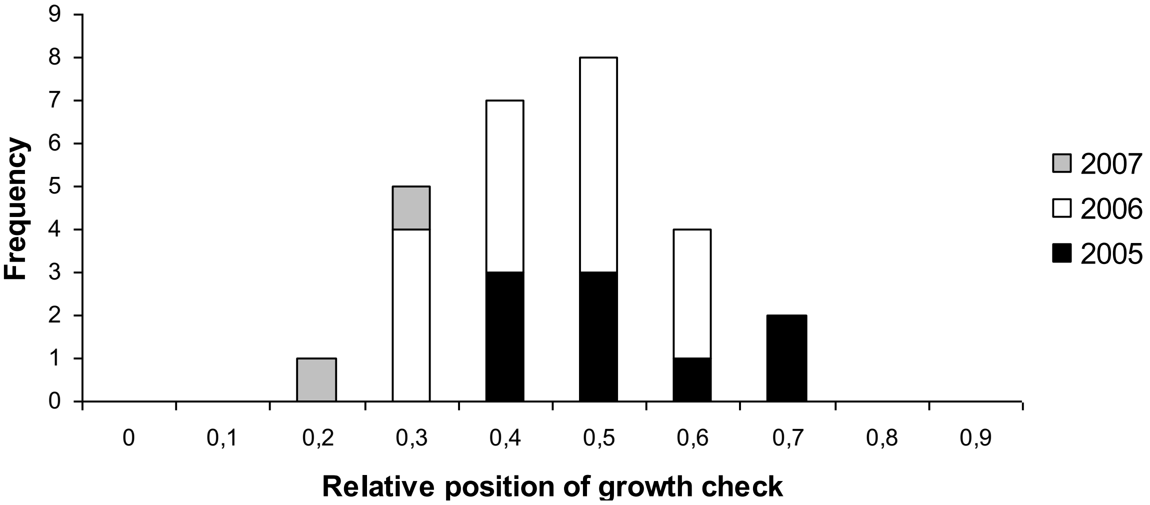

Fig. 41. Distribution of relative position of summer growth check on the post smolt growth zone for the smolt years 2005-2007 for Atlantic salmon caught in the river Etneelva.

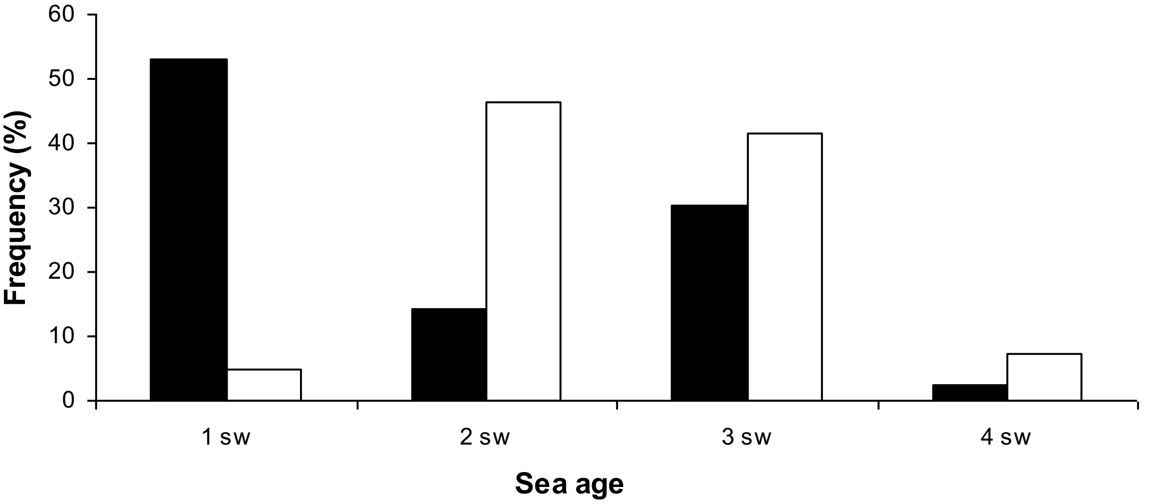

Fig. 42. Distribution of sea age for returning Atlantic salmon to the river Etneelva in 1983 (black) and 2008 (white).

Traditionally, sea age has been determined roughly by weight classes in cases where scale samples have not been available. Atlantic salmon under 3 kg have been determined as 1 SW, individuals between 3 kg and 7 kg have been determined 2 SW, and those above 7 kg have been determined to be more than 2 SW. However, if this classification had been used on the 2008 material from the river Etneelva, the 1 SW proportion would have been greatly overestimated, while both the 2 SW and >2 SW groups would have been underestimated (Fig.

43). The 1983 material shows a relatively good fit between actual sea age and sea age determined by weight, except a slight overestimation of 2 SW salmon.

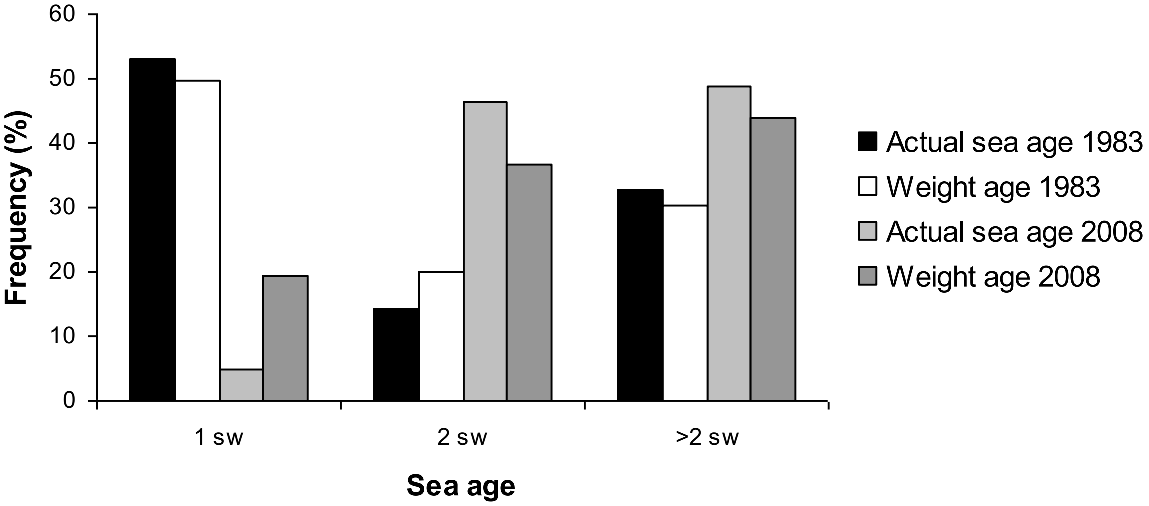

Fig. 43. Distribution of actual sea age and sea age determined by weight classes for Atlantic salmon caught in the river Etneelva

In 12 % of the sea trout caught in 2008, a growth check was observed in the scales, while the same was observed in only 3.6 % of the 1983 catch. One of the five growth checks occurred in the second summer at sea, while the others occurred during the post smolt year. The growth checks occurring during the post smolt year were located relatively early in the growth season (Fig. 44). Of the sea trout caught in 2008, 23.7 % of the fish that had spent more than one season at sea had spawned earlier, and of these, 66.6 % had spawned more than once. The corresponding numbers for sea trout caught in 1983 were 26.4 % and 37.9 %, respectively.

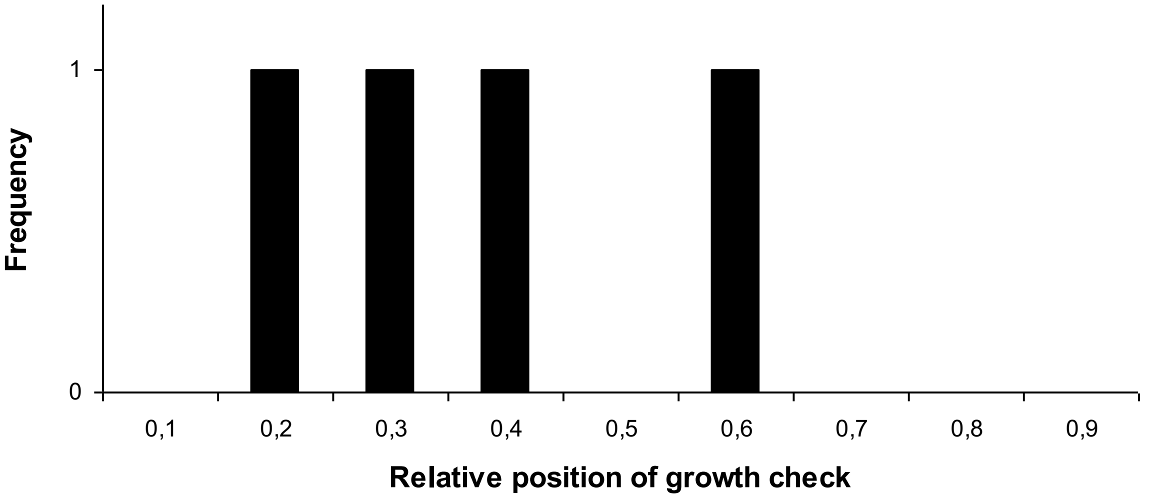

Fig. 44. Distribution of relative position of summer growth checks on the post smolt growth zone for sea trout caught in the river Etneelva in 2008.

Discussion

Conditions in the river

Only Atlantic salmon 1+ parr growth was correlated with temperature and water discharge in the river Etneelva. The summer river temperature has increased from 1983 to 2008 and the Atlantic salmon 1+ parr seem to have shown a positive response to increased temperatures. However, the difference between the two periods was marginally not significant (p-value=0.06). In a study where the temperature has risen because of hydro power manoeuvring, the increased temperature has led to increased growth and earlier smolting in Atlantic salmon parr (Saltveit & Bremnes 2004). Similarly, the parr in a river experiencing lower temperatures after regulation displayed poorer growth and later smolting compared to unaffected parts of the river (Saltveit 1990).This indicates that Atlantic salmon parr respond positively to increased river temperatures, thus improved growth in Atlantic salmon parr in the river Etneelva should be expected as a result of increased summer temperatures.

It is interesting that a relatively strong correlation is found between the growth of 1+ Atlantic salmon in the river Etneelva and the mean summer river temperature, while such relationship are not seen for the same year classes of sea trout. Higher river temperatures in Black Brows Beck, England, and in the river Suldalslågen, Norway, led to increased growth of sea trout parr (Elliott 2009; Saltveit & Bremnes 2004). In the river Etneelva, however, the trend, although not significant, is a negative development in growth for 1+ sea trout parr. The long time study of Atlantic salmon and sea trout in the river Imsa, Norway, also failed to find a correlation between water temperature and the growth and age of maturation of the parr, indicating that other factors mask the correlation with temperature in some rivers (Jonsson & Jonsson 2009b). Such factors could be competition for food, either through high fish densities, or through variable food availability (Jonsson & Jonsson 2009b).

Growth studies indicate that Atlantic salmon is adapted to thrive at higher temperatures than sea trout (Forseth et al. 2001). While sea trout parr is believed to have maximum growth around 13 °C, Norwegian Atlantic salmon parr have been found to reach their maximum growth at temperatures between 16 °C and 20 °C (Elliott et al. 1995; Jonsson et al. 2001). Atlantic salmon parr also seem to converse the food more effectively to growth than sea trout at temperatures approaching optimal growth (Forseth et al. 2001). Atlantic salmon parr from the river Suldalslågen, for example, had a maximum growth at 16 °C, while the maximum growth efficiency was reached at 12 °C (Jonsson et al. 2001). For sea trout parr feeding on invertebrates, the maximum growth efficiency has been found to be 8.9 °C (Elliott & Hurley 2000). Mean temperatures in both July and August for the period 2000-2007 are above 16 °C in the river Etneelva, and mean monthly temperatures have been close to and above 20 °C. Growth of sea trout parr is modelled to be equal to zero when the water reaches 19.5 °C (Elliott 1975). This indicates that Atlantic salmon parr in the river Etneelva will benefit more from increased river temperatures than sea trout parr (Forseth et al. 2001). A study of Atlantic salmon parr and rainbow trout showed that the Atlantic salmon was a better competitor than the larger rainbow trout when temperatures were high (Coghlan & Ringler 2005). The fact that the length increment of 1+ sea trout parr is negatively correlated with the size of the 1+ Atlantic salmon parr at the beginning of the growing season could indicate that there is competition within the same cohort of salmonids in the river Etneelva. This indirect effect of temperature could thus be more determining for the growth of sea trout parr than the temperature itself. However, how well the Atlantic salmon 1+ parr grew did not affect the growth of the sea trout parr. There were also no indications of competition with older year classes, neither intra- nor interspecific.

Conditions in the fjord

The post smolt growth of sea trout from the river Etneelva has been significantly reduced with an average of 30 mm over the last 25 years, in spite of higher temperatures during June and July. There was, however, no correlation between temperature and post smolt growth, indicating that other factors are more important in determining growth. Jonsson and Jonsson (2009a) indicate that the sea trout to a certain degree can select thermal habitat in the fjords, thus making climatic conditions less important. In accordance with the reduced growth, also during the second summer at sea, Fulton's condition factor has been reduced by 0.18. At the same time, the occurrence of summer growth checks has increased, from 3.9 % in the 1983 catch to 12 % in 2008. These findings point towards harsher conditions in the fjords for the sea trout from Etneelva, and one negative factor might be sea lice infections.

The free living nauplius stages of the salmon lice are transported by the currents in the fjords, where they can infest wild salmonids (Bjorn & Finstad 2002; Krkosek et al. 2005). The early, immobile copepodid and chalimus stages of the lice are not very harmful to the salmonids, but once the mobile preadult and adult stages are reached, the host fish receives mechanical damage to the skin and fins, which in turn leads to osmoregulatory stress (Bjorn & Finstad 1998; Grimnes & Jakobsen 1996). High infection rates of salmon lice can lead sea trout post smolts to return prematurely to estuaries or freshwater (Birkeland & Jakobsen 1997). Many sea trout return to freshwater already when the salmon lice are at the chalimus stage (Birkeland 1996). The osmoregulatory stress factor in itself can reduce the fish's ability to eat and grow, and a premature return to fresh water shortens the period of good growth normally found at sea (Birkeland 1996). After a stay in fresh or brackish water, the sea trout post smolts might return to the fjord again (Birkeland 1996). A study from the river Lønningdalselva, Norway, showed that the post smolts lost almost a quarter of their body mass in the river before they reentered the fjord (Birkeland 1996). This could explain the incidences of summer growth checks and reduced growth during the first season at sea. Older sea trout did not return to the river until close to the normal time, and did not return to the fjord in the same season (Birkeland 1996). The trend of reduced growth only during the first and second fjord season which has been observed in the river Etneelva is in accordance with this observation. The reason is probably that larger individuals can tolerate higher infections of salmon lice before they become stressed (Birkeland 1996; Jacobsen & Gaard 1997). Salmon lice are also affected by temperature (Boxaspen & Naess 2000). The development time for the lice is reduced as the temperature is increased, meaning that higher temperatures in the fjords throughout the year can lead to shorter generation times and thus higher production of salmon lice (Boxaspen & Naess 2000). This means that the post smolts can receive harmful infection rates earlier in the season. However, no shift towards maximum growth earlier in the post smolt year has been observed in the river Etneelva.

Another factor that might have contributed to the reduced sea growth of sea trout from the river Etneelva is changed food availability in the fjord system. In the Hardangerfjord, a change in the seaweed community, from stable sugar kelp (*Saccharina latissima*) forests to unstable blanketweeds, might have led to a bottom up effect on the ecosystem due to reduced primary production and loss of habitat (Moy et al. 2008). However, such local changes cannot explain the declining sea trout populations over most of Norway and Europe, indicating that it is not the main driving force. On the larger scale, salmon lice is believed to be the main cause of the decline in anadromous trout (Jonsson & Jonsson 2009b). In an experiment from the river Guddalselva in the Hardangerfjord, one of two groups of descending sea trout post smolts received treatment against salmon lice before they were released into the fjord (Finstad et al. 2007). The treated group displayed fifty percent higher survival than the not treated group, indicating that mortality on sea trout post smolts due to salmon lice in the Hardangerfjord system can be as high as fifty percent (Finstad et al. 2007).

Conditions in the ocean

European stocks of Atlantic salmon, including Irish and Scottish stocks, have experienced dwindling numbers and reduced growth at sea (Friedland et al. 2000; Todd et al. 2008). This has led to the assumption that the increased at-sea mortality is growth related (Friedland et al. 2000). A strong correlation between the post smolt growth and the return of 1 SW the year after to the river North Esk, Scotland supports this hypothesis (Friedland et al. 2000). Other rivers in Norway have also experienced reduced growth during the post smolt year over the last decades (Jonsson & Jonsson 2004; McCarthy et al. 2008). However, the situation seems to be changing in the most recent years. In the river Drammenselva, post smolt length increment had a peak in the mid-1980s, before it decreased to a minimum in 1997 (McCarthy et al. 2008). However, from 1993 to 2002 the growth increment has occasionally risen again, and the length increment of the 2002 post smolt year was similar to or larger than the increment for 1980-1982 (McCarthy et al. 2008). Scale studies of wild Atlantic salmon caught in the sport fishery on the west coast of Norway also indicate large year to year variations in post smolt length increments (Urdal 2009). Over the last ten years, the smolt year 2004 revealed the best growth, while the succeeding smolt years were rather poor (Urdal 2009). The variations are synchronised for the three counties studied. Although 2006 had the highest post smolt length increment for the river Etneelva, it seems likely that the river is experiencing the same fluctuations as the rest of the rivers on the west coast and the Drammenselva. Especially since it is generally believed that the Atlantic salmon stocks of Southern Norway migrate to the same nursery areas in the north east Atlantic (Holm et al. 2000).

The Atlantic salmon post smolts from the river Etneelva displayed improved growth during the first year at sea in spite of higher occurrence of growth checks. The growth during the second year at sea, however, has been significantly reduced. This indicates that the conditions for the mature fish are less optimal compared to the early 1980s, which has been observed in several European Atlantic salmon stocks (Friedland et al. 2009; Todd et al. 2008). This observation is strengthened by the fact that the weights of the spawners caught in 2008 in the river Etneelva are less than expected regarding their sea age. Even if length increment seems to be continuing, the body mass increment is poorer, as can be observed in a significant reduction of Fulton's condition factor. However, the greatest change seems to have occurred during the post smolt year. Higher sea surface temperatures could explain the increased growth, but in this study there is no relationship between temperature and post smolt growth (Handeland et al. 2008). The increased growth is also contradicted with summer growth checks, indicating that the optimal temperature or nutritional conditions are more patchily distributed than before (Hvidsten et al. 2009; Peyronnet et al. 2008).

The temperatures for optimal growth and maximum feed conversion efficiency for Atlantic salmon post smolts are size dependent, with 12.8 ^{o}C and 13.4 ^{o}C respectively for post smolts up to 150 g, and 14.0 ^{o}C and 11.0 ^{o}C for post smolts above 150 g (Handeland et al. 2008). The growth conditions for the Atlantic salmon post smolts when regarding temperature should thus be optimal in the summer months during the last decade. However, mapping of the Atlantic salmon ocean habitat indicates that the post smolts prefer the thermal habitat of 8-11 ^{o}C, which is somewhat lower than expected regarding optimal growth (Handeland et al. 2008; Holm et al. 2000).The reason could be that the main food organisms of the post smolts are associated with temperatures around 10 ^{o}C. The 9-10 ^{o}C isotherm has been identified as an upper threshold boundary for many cold water zooplankton species, and a northward shift in the location of this isotherm has led to dramatic changes in the zooplankton community (Beaugrand et al. 2008; Friedland et al. 2009). The larger cold water zooplankton species have been replaced by smaller temperate water species, a shift which is likely to cause bottom-up effects for the fish species in this area, such as Atlantic cod (*Gadus morhua*) and Atlantic salmon (Beaugrand et al. 2008; Friedland et al. 2009; Peyronnet et al. 2008). As an example, *Calanus finmarchicus*, which has been found to have a positive correlation with post smolt survival, has been replaced by the smaller relative *C. helgolandicus* (Ellertsen & Melle 2009; Peyronnet et al. 2008). The possible cascading effect of this species displacement is given extra weight by the fact that *C. finmarchicus* spawn during spring and represent an important food source early in the summer, while *C. helgolandicus* spawn in the fall (Ellertsen & Melle 2009). If the thermal niche of many species partly overlap around 10 ^{o}C, this will be a relatively species rich area (Beaugrand et al. 2008). The hypothesis of a beneficial prey abundance around 10 ^{o}C could explain the apparent negative correlation found between growth of Scottish post smolts and higher summer temperatures (Friedland et al. 2005). When the temperature exceeds 10 ^{o}C, the cold water segment of the zooplankton become unavailable for the post smolts and the post smolt prey. In addition, higher temperatures also increases the metabolism of the post smolts, which in turn leads to an increase in food demand

(Handeland et al. 2008). The temperature range of 8-10 °C coincides with that found in the Atlantic current, bringing warm, saline water northwards (Holm et al. 2000). The post smolts have been found to follow this current, and are thus also depending on the food organisms that are transported therein (Haugland et al. 2006; Holm et al. 2000). This could in part explain the apparent link between post smolt survival and the location of 8-10 °C surface waters in May (Friedland et al. 1998). In the 1970s the thermal habitat of 8-10 °C reached the Norwegian coast earlier, and the resulting ocean survival of the Atlantic salmon was higher (Friedland et al. 2000). However, although low temperatures might cause osmoregulatory stress, the link between the 8-10 °C thermal habitat and survival is probably indirect through the availability of food organisms in this thermal habitat (Handeland et al. 2000; Hvidsten et al. 2009).

The North Atlantic is not a homogenous habitat. Currents and weather is constantly changing the thermal composition of the surface area, where the Atlantic salmon is believed to spend the most time (Holm et al. 2000; Todd et al. 2008). If the post smolts and the older Atlantic salmon prefer the thermal habitat around 10 °C because of the prey found there, the overall increase in ocean temperature might result in fewer and more scattered areas with this temperature and associated prey organisms (Hvidsten et al. 2009; Peyronnet et al. 2008). The movement of both the period of maximum growth and of growth checks towards the beginning of the post smolt growth season might be an indication that the post smolts reach the 8-10 °C thermal habitat earlier, but that it also disappears earlier. Although growth is good in these habitats, it can be energetically demanding to localise them (Friedland et al. 2000; Hvidsten et al. 2009). This could explain the occurrence of growth checks from 2005. It is, however, strange that the growth has decreased during the second year at sea, but that no growth checks are found on the scales for this period in the study material. If growth checks can be interpreted as critical periods for survival, the findings could suggest that growth conditions for older Atlantic salmon are overall poorer in the last decade, but that the growth during the second year at sea is less correlated with survival than the post smolt year (Friedland et al. 2005). This could be because larger individuals have a larger pool of potential prey than the smaller ones, meaning that they can sustain growth longer than the post smolts (Brabrand 2000).

The Atlantic salmon that return to the river to spawn represent the survivors. If growth checks indeed can be interpreted as critical periods for survival, the recent high occurrence of such episodes in post smolt scales can explain the dwindling numbers of successful returners. The increasing occurrence of growth checks has been observed in other stocks of Atlantic salmon as well (Hvidsten et al. 2009). In the North Esk, Scotland, a peak in summer growth checks was observed in 1997, when 20 % of the returning 1 SW and 2.9 % of the 2 SW had such checks (MacLean et al. 2000). In comparison, the occurrence of growth checks never exceeded 1.3 % in either group since scale sampling started in 1969 (MacLean et al. 2000). For the 1 SW Atlantic salmon, the majority of the growth checks occurred during the summer months of May to August, with a peak in July (MacLean et al. 2000). However, there was no correlation between this increase in growth checks and growth increments or return rates (MacLean et al. 2000). A sudden increase in the occurrence of summer growth checks was also observed in the coastal catches of Atlantic salmon in Finnmark, Northern Norway, and in the rivers Tana (Teno) and Neiden, also Finnmark, in 2008 (Eero Niemelä, pers. comm.). In these northern populations, the growth checks occurred in the second summer at sea for 2 SW and 3 SW, not for 1 SW (Eero Niemelä, pers. comm.).

Several studies have revealed that offspring of farmed salmon and hybrids between farmed and wild salmon have lower survival at sea than pure, wild salmons (Fleming et al. 2000; McGinnity et al. 2003). With the high incidence of farmed Atlantic salmon in the river Etneelva during spawning, it is likely that hybridization occurs, and that also pure farm offspring is produced. This could also contribute to the declining number of returning spawners (Fleming et al. 2000; McGinnity et al. 2003). In a study where farmed salmon, wild salmon and hybrids were held under equal conditions, the farmed salmon displayed much better growth than did wild salmon, with the hybrids in between (Glover et al. 2009). If sufficient farmed salmon has been included in the Etneelva stock, this could also in part explain the improved growth. However, a genetic study comparing Atlantic salmon parr from the river Etneelva in 1998 with individuals from 1983 found no significant change in the genetic composition of the stock (Skaala et al. 2006). If this has not changed markedly in the most recent years, genetic pollution from farmed Atlantic salmon is not likely to have affected the growth and survival of Atlantic salmon from the river Etneelva directly.

One possible mechanism that can lead to reduced survival in spite of improved growth in the sea is if the main mortality or reason for mortality occurs before the fish reaches its nursery areas in the North Atlantic. High infection rates of salmon lice could cause such early mortality, as well as coastal predation. Normally Atlantic salmon post smolts move very quickly through the fjord systems and into the ocean (Sivertsgård et al. 2007). This means that the most harmful stages of the salmon lice infection often are not reached until the post smolts have reached the nursery areas (Finstad et al. 2000; Sivertsgård et al. 2007). An infection with thirty salmon lice of the chalimus stage, or ten at the preadult stage will be detrimental for an Atlantic salmon post smolt (Costello 2006; Grimnes & Jakobsen 1996). Such infections and higher are commonly observed on sea trout returned to freshwater in the Hardangerfjord system (Kålås et al. 2010). Passive sentinels for salmon lice infection rates in the outer part of the Hardangerfjord display large variations in the years 2004-2006, with mean infection rates on Atlantic salmon post smolts from 0.5 to above 6 salmon lice per fish (Finstad et al. 2007). Individual post smolts are thus likely to receive infection rates that later can affect growth, and in some cases, cause death while they migrate through the fjords. If the infection is sublethal, the fish can still carry a harmful number of salmon lice to sea, and be reinfected during the ocean stage (Jacobsen & Gaard 1997). A study of salmon lice infestations in the Norwegian sea in the winter found a mean of six adult salmon lice on the 1 SW Atlantic salmon and thirty on 2 SW salmon, indicating that these are close to the upper limits of salmon lice tolerance for the two age classes (Jacobsen & Gaard 1997).

Conclusion

The changes in the environment for the wild salmonids from the river Etneelva seems to be most markedly in the saltwater stage, as has been observed in other Atlantic salmon and sea trout stocks both in Norway and other parts of Europe. Although local conditions, such as a changing sea weed ecosystem in the fjords, might contribute to the negative development in growth and survival for the sea trout, the most important change seems to be the introduction of high densities of farmed salmonids in the area, with associated high levels of salmon lice. The year round presence of hosts, together with higher temperatures in the fjords, is making salmon lice a major cause of death and decreased growth for the sea trout. The salmon lice is most probably also affecting the Atlantic salmon post smolts negatively, but the main cause of Atlantic salmon declines appears to be the changing ecosystem in the nursery area. Increased temperatures early in the sea phase seem to have reduced the early sea mortality, but later in the summer the higher temperatures appears to be affecting the food resources negatively. The improved growth occurring together with growth checks indicates that the thermal and nutritional conditions favouring high growth and survival are more patchily distributed than before. The reduced growth during the second year at sea is also indicative of reduced food availability for the larger Atlantic salmon, as can also be seen by the reduced weights and condition factor for the spawners.

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