

The cost of anadromy: marine and freshwater mortality rates in anadromous Arctic char and brown trout in the Arctic region of Norway

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Abstract: It is hypothesized that in diadromous fish, migrations may occur because of differences in the availability of food in marine and freshwater habitats. The benefits of migration to sea may be increased growth opportunities and reproductive output, while the costs may be increased mortality and increased energy use. Here we examine mortality rates of anadromous Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in fresh water and at sea over a 25-year period to test these hypotheses. Daily mortality rates were 5–15 times higher at sea than in fresh water, with highest rates for first-time migrants, inferring a clear trade-off between increased mass gain and mortality risk during the sea migration. Descending smolts were caught in a trap at the outlet of the river, individually tagged, and thereafter recorded each time they passed through the trap on their annual migration between the river and the sea. Brown trout females seemed to benefit to a higher degree from migrating to sea than did female Arctic char, probably because of the higher growth rate at sea, and hence higher reproductive output.

Résumé : Il est postulé que, chez les poissons diadromes, des migrations peuvent avoir lieu en raison de différences de disponibilité de nourriture entre les habitats marins et d'eau douce. Les avantages de la migration vers la mer pourraient inclure des occasions de croissance accrues et une meilleure efficacité de la reproduction, alors que les coûts peuvent comprendre une mortalité et une consommation d'énergie accrues. Nous examinons les taux de mortalité d'ombles chevaliers (*Salvelinus alpinus*) et de truites brunes (*Salmo trutta*) en eau douce et en mer sur une période de 25 ans afin de vérifier ces hypothèses. Les taux de mortalité journaliers étaient de 5 à 15 fois plus élevés en mer qu'en eau douce, les poissons migrant pour la première fois présentant les taux les plus élevés, indiquant un compromis évident entre un plus grand gain de masse et un risque de mortalité accru durant la migration vers la mer. Des saumoneaux en dévalaison ont été pris dans un piège à l'emboucheur de la rivière et marqués individuellement, puis chacun de leurs passages subséquents dans le piège durant leur migration annuelle entre la rivière et la mer a été enregistré. La migration vers la mer semblait plus bénéfique aux truites brunes femelles qu'aux ombles chevaliers femelles, probablement en raison de leur taux de croissance plus grand en mer et donc d'une plus grande efficacité de la reproduction. [Traduit par la Rédaction]

Introduction

Migratory behaviour can vary within species across a wide variety of taxa (Alerstam et al. 2003; Dingle and Drake 2007). The fitness consequences of different migratory strategies within the same populations may give special insight into the trade-offs between migration and alternative strategies (Dingle and Drake 2007). Fish that migrate across salinity barriers between seawater and fresh water (diadromous fishes) provide good opportunities for studying the fitness consequences of migration between different habitats. There are latitudinal differences in the worldwide distribution of anadromous (spawn in fresh water, grow to maturity in the sea) and catadromous (spawn at sea, grow to maturity in fresh water) fish species. Gross et al. (1988) hypothesized that diadromous migrations may occur in fishes because of differences in the availability of food in marine and freshwater habitats. Anadromous species are more prevalent in Arctic and temperate latitudes where oceans are more productive than freshwater habitats, while catadromous species tend to occur in tropical latitudes where productivity shows the opposite trend (Gross et al. 1988). Diadromous life histories may evolve through natural selection only when migration between fresh water and salt water

provides a gain to individual lifetime fitness that exceeds the costs of this behaviour (Gross 1987). These costs may include physiological adjustments, energy allocation to swimming, and increased probability of mortality during migration (Gross et al. 1988; Hinch et al. 2006).

Among anadromous salmonids, the residence time at sea varies considerably among species, from a few weeks to several years (Klemetsen et al. 2003; Behnke 2010). Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) are two species with short residence time at sea in parts of their range, including northern Norway. In that area, anadromous individuals usually spend a rather short time (some weeks or months) at sea each summer to feed (Jensen et al. 2018b). The residence time at sea appears to be greater in the south than in the north (Klemetsen et al. 2003; Thorstad et al. 2016). In southern Europe, some individuals of brown trout may stay at sea also during winter (Nall 1932; Pemberton 1976; Jonsson and Jonsson 2009). In northern Europe, however, overwintering in fresh water is almost obligatory for both species (Klemetsen et al. 2003; Jensen et al. 2015), except for some pure riverine populations (Jensen and Rikardsen 2008; Jensen et al. 2014). Both species are iteroparous, with individuals spawning more than once. They may also exhibit partial migration, where males may mature

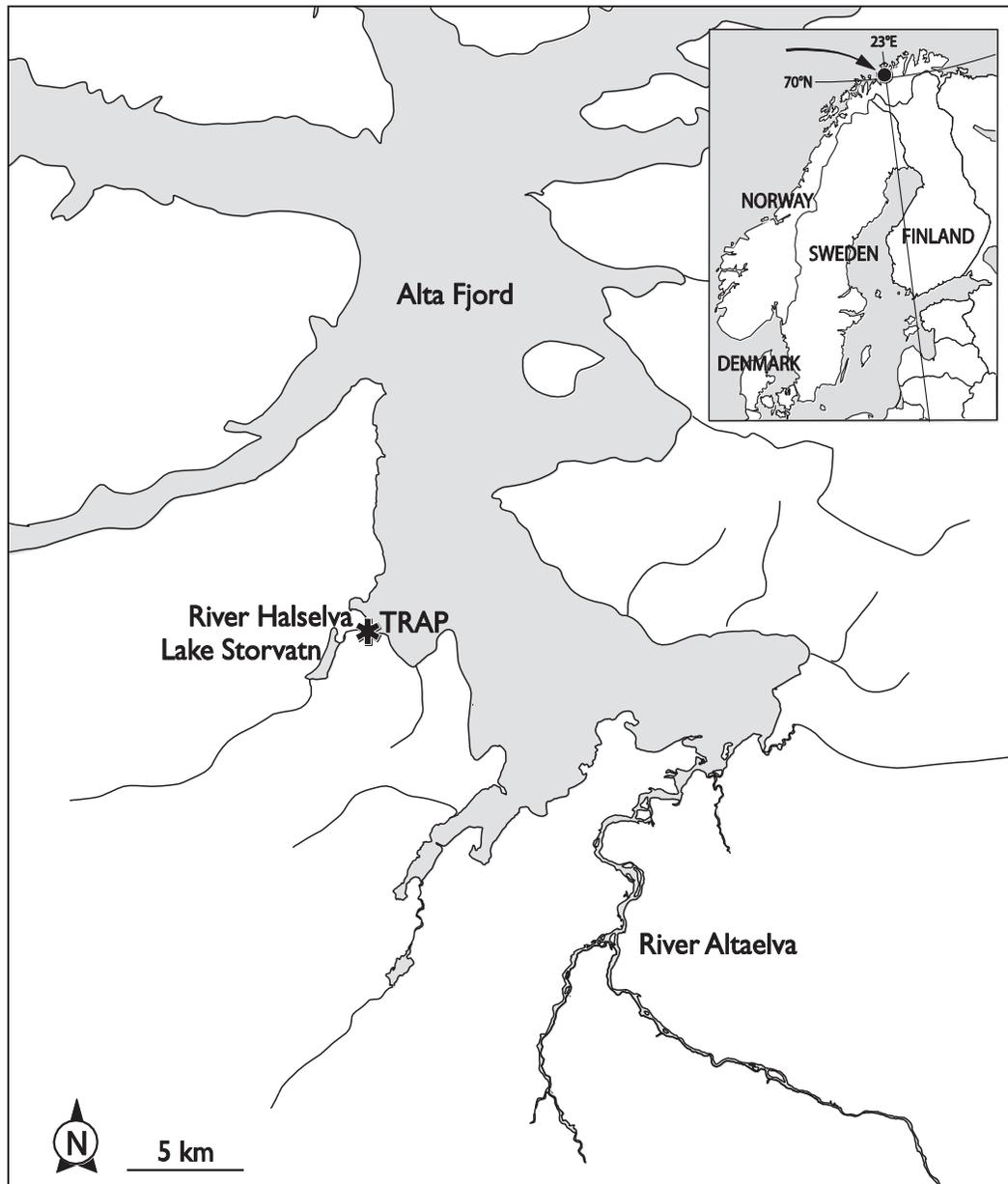
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Fig. 1. Map of the study area, with the location of the fish traps in the River Halselva for catching all ascending and descending fish (Jensen et al. 2015).



in their natal rivers without migrating to the sea for feeding (Jonsson and Jonsson 1993; Chapman et al. 2012).

The benefits of migration to sea may be increased growth opportunities and reproductive output, while the costs may be increased mortality and increased energy use (Klemetsen et al. 2003; Hendry et al. 2004). The mortality of both species is expected to be especially high immediately after the smolts enter salt water, mainly because of osmotic challenges (Finstad et al. 1989; Jørgensen and Johnsen 2014) and predation (Parker 1971; Ward and Hvidsten 2011; Thorstad et al. 2016). Size-selective mortality may also occur in individuals older than smolts, suggesting that mortality caused by predation may also be considerable for later developmental stages (Jensen et al. 2018a, 2018b).

In the present study, we present the results of a 25-year study of descending smolts of anadromous Arctic char and brown trout captured in the Hals watershed, Norway. The fish were trapped 200 m upstream from the sea, individually tagged using Carlin tags, and thereafter recorded each time they passed the trap on

their annual migrations between the river and the sea for the rest of their lives. Marine growth rates, duration of the marine migration, and survival rates between each time the fish passed the trap were estimated, as well as daily mortality rates in these two environments. In accordance with general life history theory (Gross 1987), we hypothesize that daily mortality rates are higher at sea than in fresh water at this high latitude, both for first-time and veteran migrants. Furthermore, we expect daily mortality rates to be highest for first-time migrants because of osmotic challenges and size-selective mortality.

Materials and methods

Study area

The Hals watershed in the Arctic region of Norway (70°2'N, 22°57'E) has a catchment area of 143 km² and drains into the Alta Fjord (Fig. 1). Approximately 20 km of the watercourse, including a 1.2 km² lake located 2.1 km inland and 30 m above sea level (Lake

Storvatn; Fig. 1), is accessible to the anadromous salmonids Arctic char, brown trout, and Atlantic salmon (*Salmo salar*) (Jensen et al. 2018b). Both bodies of water are ice-covered from December to March or April, a period characterized by low waterflow. A pronounced increase in waterflow then occurs during the snowmelt period (May–June), followed by a decrease during July and August, yielding a mean annual waterflow of 4.3 m³·s⁻¹. The outlet of the River Halselva empties directly into the sea without any distinct estuary, resulting in limited freshwater areas for fish to overwinter downstream of the fish traps (see below). The minimum water temperature in the outlet — River Halselva — is around 0 °C during the ice-covered period; the temperature then rises steadily until reaching a maximum of ~13 °C in early August. Minimum and maximum sea temperatures are ~2.5 °C in late March and ~11 °C during late July – early August, respectively (Jensen et al. 2018b).

Fish sampling

During 1987–2012, Arctic char and brown trout smolts were sampled via permanent fish traps placed 200 m upstream from the sea. All fish larger than 10 cm were trapped with a Wolf trap (apertures 10 mm, inclination 1:10; Wolf 1951) for descending fish and a fixed box trap for ascending fish (Jensen et al. 2012, 2018b). The Arctic char and the brown trout were the dominant species in the watershed, but Atlantic salmon and European eels (*Anguilla anguilla*) were also present. The traps were operated during the ice-free period (i.e., late April to October–November) and were emptied twice a day (at 0800 and 2000 h) to record morphological data before release. Body length (L , in mm; i.e., total length of the fish with the tail fin in its natural position; Ricker 1979) and mass (M , in g) were measured for all fish. The fish were externally inspected to determine sexual maturity and the sex of individuals classified as mature (Jensen et al. 2018b).

In general, Arctic char smolts in this watershed migrate before brown trout, with median dates of descent of 25 June and 4 July, respectively, although some smolts of both species leave the river throughout most of the ice-free period of the year (Jensen et al. 2012). Mean age and length were 5.04 years and 173.2 mm and 4.88 years and 195.2 mm for Arctic char and brown trout smolts, respectively (Jensen et al. 2012). The annual descent of naturally produced Arctic char and brown trout smolts were 500–3600 individuals (mean = 1350 individuals) and 300–1400 individuals (mean = 950 individuals), respectively (Jensen et al. 2012). Equal numbers of females and males were detected among first-time migrants of Arctic char, while females constituted 63% of the brown trout smolts (Jensen et al. 2012).

Brown trout and Arctic char smolts (i.e., first-time migrants; see definition by Allan and Ritter 1977) larger than 18 cm were tagged with individually numbered Carlin tags (Carlin 1955), while smaller individuals were tagged by removing a flap on one or both maxillary bones in a systematic manner to enable future identification of year of decent (Jensen et al. 2012). In this study, Carlin-tagged individuals with a length of 18–28 cm that migrated to sea before 1 August in the period 1988 to 2012 were included (in total, 11 900 Arctic char and 15 220 brown trout). Individuals migrating after 1 August (6.1% of brown trout and 1.7% of Arctic char) were omitted because of an increasing proportion of parr during the autumn and overall low marine survival of late migration individuals (A. Jensen, B. Finstad, and P. Fiske, unpublished data).

Return rates to the fish traps were used as proxies for finite survival rates (S) during the sea migration in the summer and the freshwater stay in the winter. Some individuals that left the River Halselva as first-time migrants (2.2% of Arctic char and 39.6% of brown trout) overwintered up to four times in other watersheds before most of them eventually returned to the river on reaching maturity (Jensen et al. 2015), and these individuals were included when estimating survival of first-time migrants.

Apparent survival rates S were estimated as

$$S = N_t/N_0$$

where N_0 is the number of individuals alive at the start of time period t , and N_t is the number of individuals alive at the end of the time period (Krebs 1989). If the time interval is 1 year, this would give an apparent annual survival rate.

Daily survival rates (DSR, i.e., the proportion of animals alive on day d that were still live at day $d + 1$) were estimated according to Krebs (1989) as

$$\text{DSR} = S^{1/t}$$

where S is the apparent survival rate between two observations, and t is the time period between the two observations.

Daily mortality rates (DMR, i.e., the proportion of animals alive on day d that died before day $d + 1$) were estimated as

$$\text{DMR} = 1 - \text{DSR}$$

Estimated smolt fitness (ESF) was quantified by the summation of an individual's probability p_x of survival from the smolt stage to reproduce at any sea age x multiplied by its fecundity at that sea age (b_x):

$$\text{ESF} = \sum p_x \times b_x$$

Fecundity (b) at a specific size was estimated according to Power et al. (2005) for Arctic char and Jonsson and Jonsson (1999) for brown trout. Power et al. (2005) estimated b in relation to fish length for 15 populations of anadromous Arctic char from eastern North America as

$$b = 0.625L^{2.224}$$

where L is fork length (cm) of the fish. To convert our length measurements to fork length, we used the factor 0.980 (A. Jensen, B. Finstad, and P. Fiske, unpublished data). Jonsson and Jonsson (1999) analysed the relationship between b and mass (W) of first-time and repeat spawners of anadromous brown trout from south Norway as follows, respectively:

$$\ln b = 0.800 \ln W + 2.366$$

and

$$\ln b = 1.009 \ln W + 0.695$$

Fish surveys with benthic and pelagic gill nets were carried out in Lake Storvatn on two occasions, with the objective of studying length and age distributions of mature resident Arctic char and brown trout individuals. Gill net surveys were conducted during three successive nights, 3–6 July 1989 and 8–11 August 1994, at the time of the year when most anadromous individuals of Arctic char and brown trout stayed at sea. The benthic gill nets used were three standard series consisting of six nets (27 m × 1.5 m) with mesh sizes of 12, 16, 19.5, 24, 29, and 35 mm. The nets were placed at right angles to the shoreline in panels of three nets each. The pelagic gill nets used were a panel of five nets (each 25 m × 6 m) with mesh sizes of 12, 16, 19.5, 24, and 29 mm. The benthic nets were used for about 12 h overnight, while the pelagic nets stayed in the water for 24 h, and were harvested each day at about 0800 h. In each 24 h sampling period, the pelagic nets were placed at different depths. The first night, they were placed at a depth of 12–18 m, the next night at a depth of 6–12 m, and the third night

Table 1. Catch of Arctic char and brown trout during gill net surveys in Lake Storvatn in the Hals watershed in 1989 and 1994.

	1989		1994	
	Arctic char	Brown trout	Arctic char	Brown trout
Anadromous	26	0	59	4
Mature resident	38	18	59	19
Untagged, immature	106	77	191	150

Note: For each species, the catch is separated between anadromous individuals (individuals which have been to sea and were tagged when passing the trap), mature resident individuals (untagged mature individuals), and untagged immature individuals (which may be either anadromous individuals still too young to migrate to sea or resident individuals).

at the surface (0–6 m). All anadromous individuals were previously tagged and hence could be distinguished from resident mature and untagged immature individuals. Age, length, sex, and sexual maturity were analysed in the laboratory. Age was determined from the scales of brown trout and from the otoliths of Arctic char. Altogether, 170 Arctic char and 95 brown trout were caught in 1989, and 309 Arctic char and 173 brown trout in 1994 (Table 1).

Occurrence of mature individuals in running water was examined by electrofishing. Fish densities were estimated by three-pass electrofishing trials in late summer (August) for 11 years during the period 1992–2002. Densities in ten sampling sites (70–240 m² each, six in the main tributary and four in the outlet river) were estimated with a backpack electrofishing equipment (Paulsen, Trondheim) using the removal method (Bohlin et al. 1989). All fish were stored in alcohol, and age, length, sex, and sexual maturity were analysed in the laboratory.

Results

During the 25-year study period, the between-year variation in mean residence time at sea of first-time migrants of anadromous Arctic char was 23.2–44.6 days (with a mean (±SE) duration of 34.0 ± 1.2 days), and that of brown trout was 47.3–64.0 days (mean 55.2 ± 0.9 days). Moreover, the mean residence times at the second to fifth sea migrations were 32.8–35.5 days for Arctic char and 54.5–62.3 days for brown trout (Table 2). All values for brown trout were significantly higher than those for Arctic char (pairwise *t* tests, *P* < 0.001).

The mean (±SE) survival rate of Arctic char smolts during the first sea migration was 33.6% ± 2.5%, and among those fish that ascended the trap the same summer as they returned to the river, 44.1% ± 3.0% migrated to the sea the subsequent spring (Fig. 2a). Correspondingly, 28.1% ± 2.0% of the brown trout smolts survived the first summer at sea, and among those ascending again the same summer, 62.3% ± 2.9% descended the subsequent spring (Fig. 2b). In both species, survival was higher for veteran migrants than for first-time migrants, and from the third sea migration onwards, usually 60%–80% of the individuals survived each interval between passing the trap on their way to and from the sea (Fig. 2).

Annual survival rates were higher for veteran migrants than for first- and second-time migrants (Fig. 3). In the first 3 years after smoltification, annual survival rates were roughly similar for the two species (Fig. 3), with mean (±SE) survival rates of 15.5% ± 1.8% and 13.6% ± 1.4% in the first year and 42.6% ± 2.6% and 38.1% ± 2.4% in the second year after smoltification for Arctic char and brown trout, respectively.

At a sea age of 3 years, annual survival rates exceeded 50% for both species (52.5% ± 3.1% for Arctic char and 54.4% ± 2.1% for brown trout). After that, annual survival rates of Arctic char increased to about 60%·year⁻¹, while for brown trout annual survival rate decreased to 40%–50%·year⁻¹ (Fig. 3). This deviation between the two species may be connected to differences in allocation of

energy for reproduction after maturity, which usually occurs after two to four sea migrations in both species (Fig. 4). The number of sea migrations until maturity was not significantly different between sexes (Arctic char: males 3.03 ± 0.17 (±95% CI) sea migrations, females 3.15 ± 0.11 sea migrations, *F*_[1,399] = 1.69, *P* = 0.194; brown trout: males 3.38 ± 0.07 sea migrations, females 3.42 ± 0.07 sea migrations, *F*_[1,1060] = 0.522, *P* = 0.470).

Daily mortality rates were considerably higher at sea than in fresh water for both species. In both environments, the daily mortality rates were highest for first-time migrants, decreasing with sea age (Table 2). The daily mortality of Arctic char was 13 and 10 times higher at sea than in fresh water for first- and second-time migrants, respectively, and five to seven times higher for older individuals. For brown trout, daily mortality rates both at sea and in fresh water were significantly lower than that for Arctic char the first year after smolt migration and the second year after smoltification in fresh water, while no significant difference between the two species was detected for older fish (Table 2). As for Arctic char, mortality rates of brown trout decreased with the number of sea migrations and was 14–15 times higher at sea than in fresh water for first- and second-time migrants and six to eight times higher for older fish.

About 6% of Arctic char and 10% of brown trout survived the period from their first migration to sea as smolts until maturity 3 years later, and between 0.5% and 1% of both species were still alive after seven sea migrations (Fig. 5). Up to 13 sea migrations were observed for Arctic char and 11 for brown trout.

The body mass (g) of both species increased with the number of sea migrations until about seven migrations, with a greater increase in brown trout than in Arctic char (Fig. 6). The mean body mass after three migrations (i.e., at the predominant age at maturity) was 503 g (corresponding to a fecundity of 1813 eggs) for Arctic char and 985 g (corresponding to 2645 eggs) for brown trout. At that time, 10.2% of the brown trout and 6.4% of the Arctic char that migrated to sea for the first time as smolts were still alive.

Estimated smolt fitness (ESF, i.e., the summation of a smolt's probability of survival to reproduce at any sea age multiplied by its fecundity at that sea age) was estimated for female smolts of both species. For a female smolt reaching maturity at a sea age of 3 years (i.e., the predominant sea age at maturity for both species), ESF was estimated as 250 eggs for Arctic char and 973 eggs for brown trout (Table 3).

During the gill net survey in Lake Storvatn in 1989, 38 mature resident individuals of Arctic char and 18 of brown trout were captured, and in 1994 the corresponding numbers were 59 and 19 individuals (Table 1). Of the 37 brown trout captured, only one individual was female. Except for two larger individuals, the length distribution of brown trout was between 120 and 265 mm (Fig. 7) and age was between 3 and 8 years (Fig. 8). The length and age distributions of mature resident Arctic char were wider, the former between 127 and 440 mm (Fig. 7) and the latter between 4 and 17 years (Fig. 8). Among the mature Arctic char, 35% were females (Fig. 8).

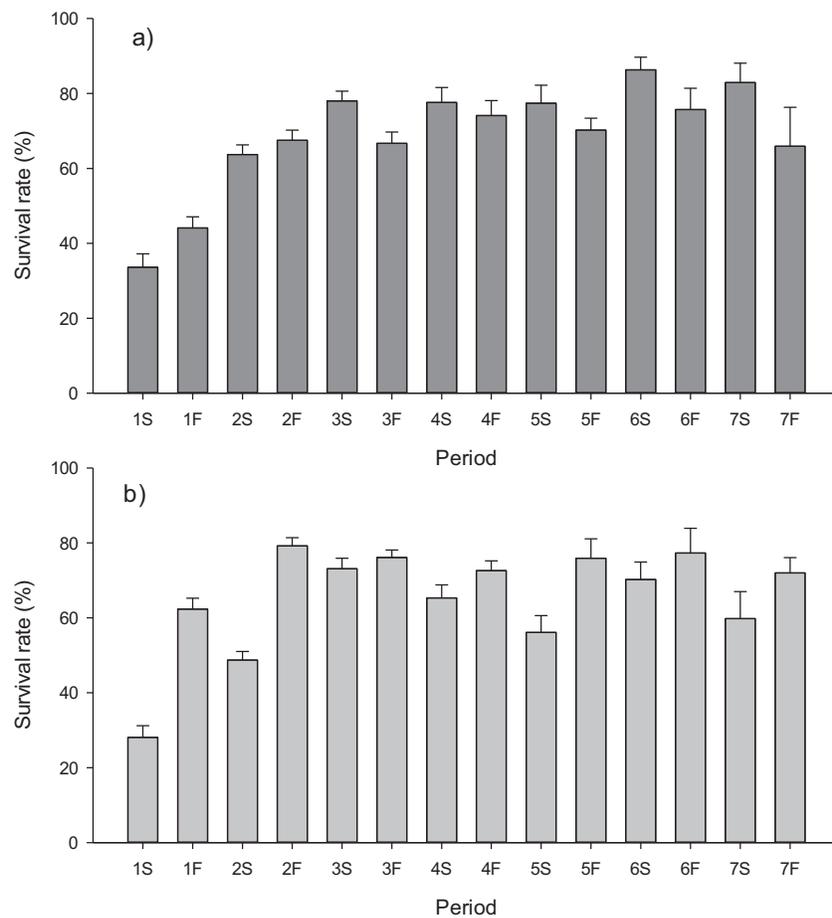
Fish densities in the main tributary were low, with brown trout and Arctic char as the predominating species (mean (±SD) densities 8.7 ± 5.8 and 6.1 ± 3.8 individuals per 100 m² for brown trout and Arctic char, respectively). Altogether, two mature individuals were caught during these 11 years: one brown trout and one Arctic char. Both were males. In the outlet river, brown trout (49.1 ± 12.9 individuals per 100 m²) and Atlantic salmon (28.0 ± 15.2 individuals per 100 m²) predominated, while Arctic char were fewer in numbers (3.5 ± 1.5 individuals per 100 m²). Most of the catch in the river were immature individuals at ages of 0–4 years. However, during the 11 years of sampling, altogether 54 mature individuals were captured, divided between 23 brown

Table 2. Residence time (days) of Arctic char and brown trout in the sea and in fresh water in the first 5 years after smoltification, daily mortality rates (%) during the same periods, and test of equality (paired samples *t* test) of daily mortality rates between the two species at each period.

Period	Arctic char		Brown trout		<i>t</i> test		
	Duration (days)	Daily mortality rate (%)	Duration (days)	Daily mortality rate (%)	<i>t</i>	df	<i>P</i>
1st summer	34.0±1.2	3.52±0.29	55.2±0.9	2.43±0.16	-5.755	24	<0.001
2nd summer	35.5±1.0	1.34±0.13	62.3±1.6	1.13±0.07	-1.06	21	0.301
3rd summer	34.9±0.8	0.76±0.11	57.1±1.6	0.54±0.07	-1.476	19	0.156
4th summer	34.8±1.4	0.69±0.12	54.5±1.6	0.79±0.09	-0.051	12	0.960
5th summer	32.8±0.9	0.58±0.11	55.8±1.8	0.90±0.12	-1.312	8	0.291
1st winter	331.3±1.3	0.262±0.020	310.0±0.9	0.161±0.016	-6.019	23	<0.001
2nd winter	329.7±1.0	0.130±0.014	302.7±1.7	0.080±0.010	-2.499	20	0.024
3rd winter	330.2±0.8	0.130±0.014	308.2±1.7	0.091±0.009	-1.906	18	0.073
4th winter	330.2±1.4	0.098±0.019	311.1±1.6	0.100±0.011	-0.110	12	0.914
5th winter	332.2±0.9	0.11±0.015	309.7±1.9	0.110±0.029	0.130	8	0.900

Note: Mean values (±SE) are given for the period from 1988 to 2012.

Fig. 2. Survival rates (%) of the (a) Arctic char and (b) brown trout populations in the River Halselva after migration to sea (S) in spring and return to freshwater (F) in summer each year in the first 7 years after smoltification. The data are mean values (+SE) for the period from 1988 to 2012.



trout and 31 Atlantic salmon. All of them were males. The catch of mature brown trout was about 0.5 individuals per 100 m², corresponding to ~100 individuals in total in the outlet river.

Discussion

For the Halselva populations of Arctic char and brown trout, daily mortality rates were 10–15 times higher at sea than in fresh water during their first two sea migrations, decreasing to five to eight times higher the following years. Despite these high differences, results of fish surveys with gill nets in Lake Storvatn and

electrofishing in lotic habitats suggest that most female brown trout migrate to sea. Although a larger part of the Arctic char population was resident, freshwater residents were smaller at each age than were anadromous individuals, owing to the reduced growth potential in fresh water in this region (Strand and Heggberget 1994). Hence, females of brown trout seem to benefit to a higher degree from migrating to sea than do female Arctic char, probably because of the higher growth rate at sea, and hence higher reproductive output. This is in accordance with the ESF estimates, which suggest that a female brown trout smolt has the

Fig. 3. Estimated annual survival rates of the Halselva populations of Arctic char and brown trout in the first 7 years after smoltification. The estimates are based on the number of individuals of a cohort observed in the fish trap in the River Halselva at descent to the sea and the fraction of the same group observed in the trap again at descent 1 year later. The data are mean values (\pm SE) for the period from 1988 to 2012.

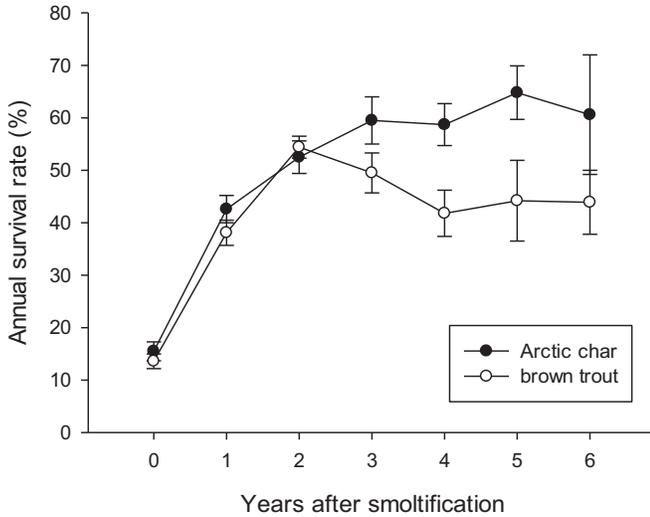
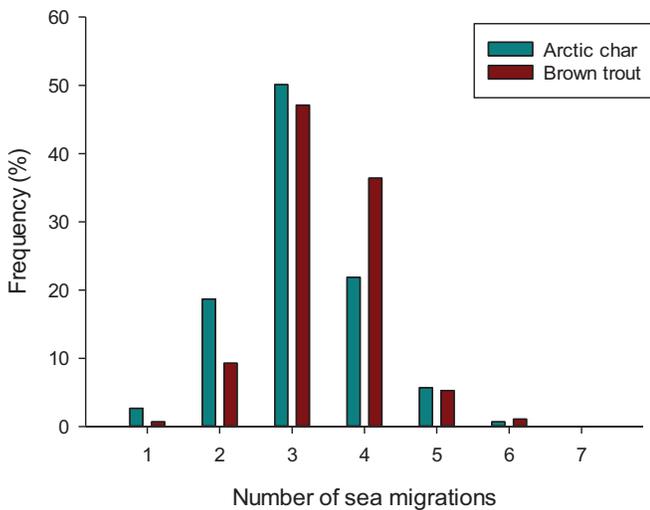


Fig. 4. Sea age distribution (i.e., number of sea migrations) of the Halselva populations of Arctic char and brown trout at maturity. The data are mean values for the period from 1988 to 2012. [Colour online.]



potential during her lifetime to produce several times as many eggs as a female Arctic char smolt.

To our knowledge, this is the first study comparing daily mortality rates of anadromous salmonids in marine and freshwater habitats. Gross (1987) tried to get some insight into the cost and benefits of anadromy from existing data by comparing anadromous and nonanadromous forms within seven different species of *Salmo* and *Salvelinus*. Egg production by anadromous forms was on average threefold greater than that of their nonanadromous conspecifics. Therefore, he concluded that anadromous fishes may have as much as threefold higher mortality than nonanadromous fishes and still be favoured in evolution. He also pointed out that differences in productivity between marine and freshwater habitats are important, and in cases with high differences in pro-

Fig. 5. Survival (% \pm 95% CI) of Arctic char and brown trout after the first migration to sea as smolts and in the following 13 years. The arrow indicates the predominant age at maturity for both species (see Fig. 4).

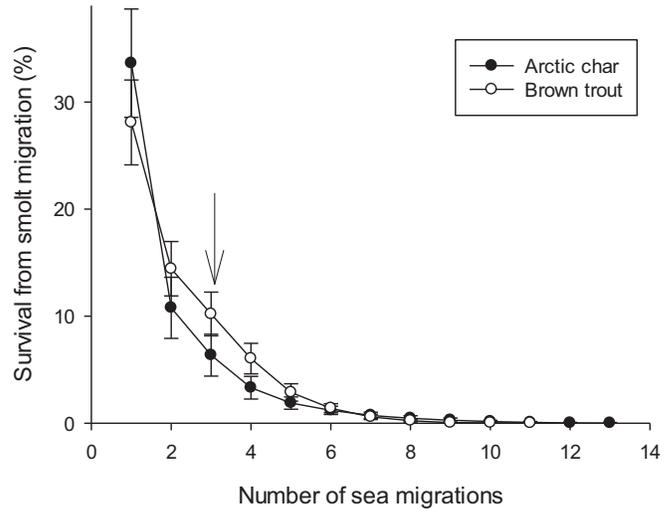
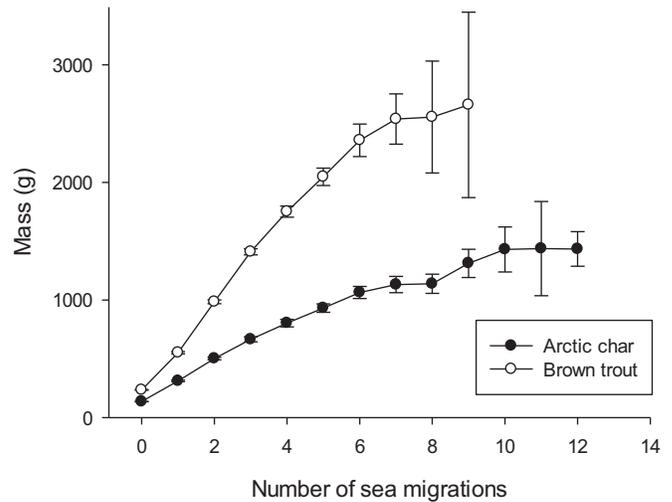


Fig. 6. Mean mass (g \pm 95% CI) of Arctic char and brown trout on arrival at the fish trap in the River Halselva in the summer of the same year they migrated to sea as smolts and in the following 13 years.



ductivity, higher mortality in marine habitats may still favour anadromy. In our study, mortality rates at sea relative to freshwater were considerably higher than that proposed by Gross (1987). High marine relative to freshwater productivity may be the main reason why anadromous populations of Arctic char and brown trout are present in northern Norway, in spite of the high marine mortality rates in that area.

Mortality rates in the present study may have been overestimated because of mortality due to handling, anaesthesia, and tagging (Hansen 1988). Furthermore, a few individuals stayed more than 1 year in fresh water before they returned to sea, and others changed from a migratory to a resident life (Jensen et al. 2015). On the other hand, a sport fishery for both species takes place during summer in the sea and both during summer and winter in fresh water. These factors do not, however, change the main conclusion that daily mortality rates are several times higher at sea than in fresh water.

Table 3. Basic data used to compute estimated smolt fitness (ESF) of a female smolt of Arctic char and brown trout, which reaches maturity after three sea migrations.

Sea migrations	N	Survival (%)	Mean mass (g)	Fecundity	ESF
Arctic char					
1	3689	33.63	137	0	0
2	1001	10.79	313	0	0
3	580	6.36	503	1813	58
4	313	3.32	666	2237	49
5	179	1.89	804	2563	39
6	112	1.21	932	2879	32
7	67	0.75	1065	3164	25
8	36	0.47	1132	3321	17
9	21	0.30	1139	3443	12
10	10	0.16	1312	3738	8
11	8	0.08	1431	3871	5
12	3	0.04	1437	4373	2
13	2	0.02	1435	4498	2
14	0	0	—	—	0
Total ESF					250
Brown trout					
1	2854	28.10	236	0	0
2	1278	14.43	553	0	0
3	1041	10.21	985	2645	266
4	715	6.04	1410	3017	257
5	318	2.88	1753	3756	190
6	152	1.41	2048	4396	127
7	59	0.61	2359	5068	72
8	21	0.24	2539	5459	33
9	6	0.06	2556	5497	9
10	3	0.05	2660	5721	7
11	1	0.04	3833	8272	11
12	0	0	—	—	0
13	0	0	—	—	0
14	0	0	—	—	0
Total ESF					973

Note: EFS was calculated as the summation of a smolt's probability p_x of surviving to reproduce at any sea age x multiplied by its fecundity at that sea age. N is number of individuals returning to fresh water. Survival (%) is the probability of surviving from smolt until ascent into fresh water after x sea migrations, mass (g) is the mean mass of individuals at that time, and fecundity is the mean number of eggs produced by females of that mass.

The transition from fresh to salt water is a bottleneck in the life cycle of anadromous salmonids, with high mortality in salt water, mainly caused by osmoregulatory challenges (Sigholt and Finstad 1990) and predation from marine fishes, birds, and mammals (Hedger et al. 2011; Ward and Hvidsten 2011; Thorstad et al. 2016). Mortality from predation is size-selective, and size-selective mortality has been detected in the Halselva populations of Arctic char and brown trout also during the second and third summers at sea, suggesting severe predation from marine fishes also long after the first sea entrance (Jensen et al. 2018a). In general, there is higher predation risk at sea than in fresh water (Hendry et al. 2004; Thorstad et al. 2016), and although the estimated survival rates at sea and in fresh water are estimated at different seasons (the former survival occurred during summer and the latter during autumn, winter, and spring), the higher mortality rates estimated at sea in the present study were in accordance with what has previously been found.

The estimated survival rates in the present study are in line with other studies of anadromous Arctic char and brown trout in northern Norway (Jensen and Berg 1977; Berg and Jonsson 1990) as well as for brown trout in central Norway (Jensen 1968; Eldøy et al. 2015; Flaten et al. 2016), but higher than rates further south in Europe. In the River Imsa in southern Norway, mean sea survival of veteran migrants of brown trout was 32.7%, while sea survival

of first-time migrants was 15% or lower (Jonsson and Jonsson 2009). In the Burrishoole system in Ireland, the proportion of brown trout smolts that returned as finnock prior to 1988 ranged from 11.4% to 34.2%, with a mean of 21%. After a collapse of the population related to marine conditions in 1989, return rates decreased to a mean of 6.8% (Poole et al. 2006). In a French river, survival of postsmolts during their first summer at sea was 14%–20%, and survival of kelts from one spawning season to another was 30%–50% (Euzenat 1999).

Annual survival rates of immature individuals were similar for Arctic char and brown trout. Following maturity (i.e., after about three sea migrations), however, survival rates were higher in Arctic char than in brown trout. This is in accordance with a higher gonadosomatic index measured in brown trout than in Arctic char (Fleming 1998; Crespi and Teo 2002), suggesting that brown trout invest more energy in reproduction, at the expense of longevity, than Arctic char.

The residence time at sea was longer for brown trout than for Arctic char, in accordance with the results of other studies where these two species are found in sympatry (Klemetsen et al. 2003). The duration of the sea migration is a trade-off between increased mortality risk at sea and gaining body mass for storing enough energy reserves for surviving the winter and as reproductive investment (Gross 1987). Gaining body mass is especially important for females, as reproductive potential is determined by the number and quality of their eggs, and larger females produce more eggs and are more successful on the spawning grounds (Klemetsen et al. 2003; Hendry et al. 2004). In Arctic char, most of the annual growth is gained during the first few weeks at sea (Berg and Berg 1989; Rikardsen et al. 2000), and marine prey has been estimated to account for about 90% of the annual diet of anadromous Arctic char (Swanson et al. 2011). Similar to Arctic char, growth rate of brown trout seems to be highest during the first part of the sea migration and decreases throughout the summer (Berg and Berg 1987; Olsen et al. 2006). Hence, during late summer the reward of staying at sea will be diminished, and at least in northern areas the fish will return to fresh water. Moreover, a late-summer reduction in food rations is considered more energetically taxing during warm rather than cold years. Environmental conditions, combined with higher predation risk at sea, indicate that an early return to fresh water during the late summers of warm years would likely be favourable for survival (Jensen et al. 2018b).

The ESF estimates suggest that a female brown trout smolt of the Halselva population has the potential during her lifetime to produce about four times as many eggs as a female Arctic char smolt, suggesting that the anadromous fraction of brown trout is more robust to environmental changes than Arctic char. To our knowledge, these are the first published estimates of ESF on anadromous Arctic char or brown trout. In a sustainable population, two offspring are expected per family. In the Hals watershed, the smolt fitness of female Arctic char smolts was estimated to be 250 eggs per female, and hence an egg-to-smolt survival of at least 0.8% is necessary to maintain the anadromous part of the population. For brown trout, with an estimated smolt fitness of 973 eggs per female smolt, an egg-to-smolt survival of 0.2% will be enough. Data on egg-to-smolt survival of Arctic char and brown trout are difficult to estimate, because most populations are only partially migratory, and both migratory and resident individuals may produce both migratory and resident offspring (Jonsson and Jonsson 1993). However, Thomson and Lyndon (2018) estimated the egg-to-smolt survival of an anadromous brown trout population in Orkney, UK, as 0.65%. In Atlantic salmon, whose juveniles have a similar way of living to that of brown trout, and which is sympatric with brown trout and Arctic char in the Hals watershed, usually all females and the predominating portion of males smoltify and migrate to sea. In this species, published egg-to-smolt survival rates are from 0.2% to 6.0% and mainly in the lower end of this range (Symons 1979; Chadwick 1982; Hutchings and Jones 1988;

Fig. 7. Length distribution (cm) of mature resident fish caught during gill net surveys in Lake Storvatn in July 1989 and August 1994: (a) brown trout in 1989, (b) brown trout in 1994, (c) Arctic char in 1989, and (d) Arctic char in 1994. [Colour online.]

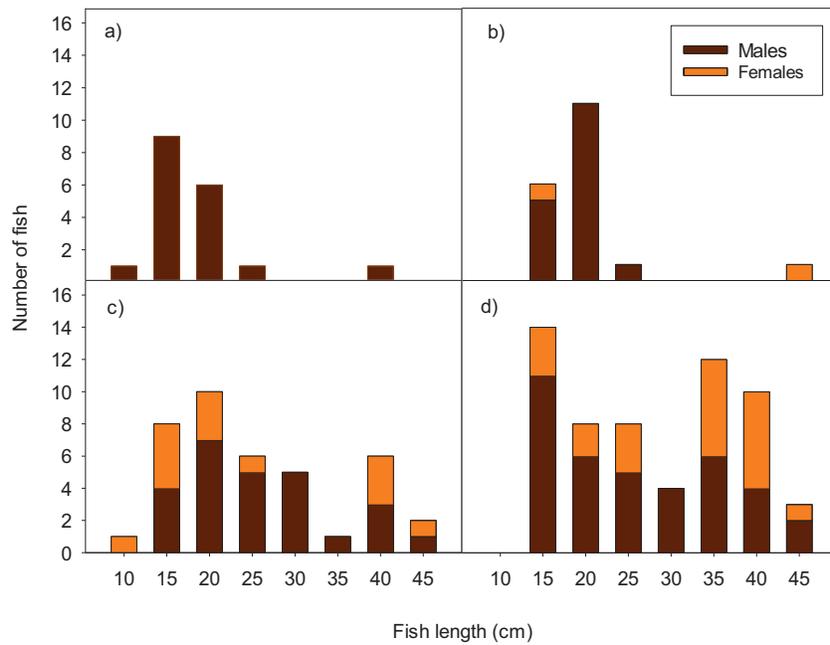
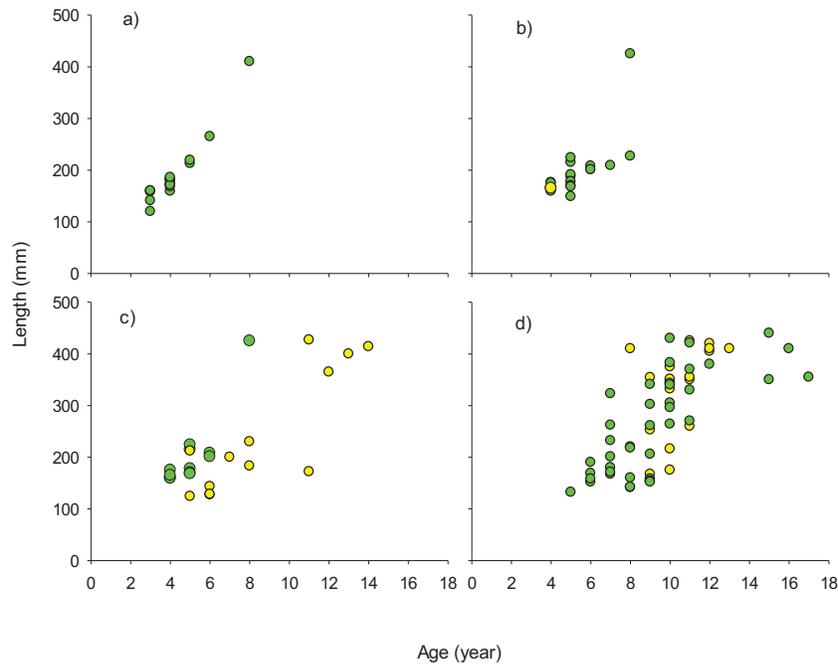


Fig. 8. Relationship between age (year) and size (mm) of mature resident fish caught during gill net surveys in Lake Storvatn in July 1989 and August 1994: (a) brown trout in 1989, (b) brown trout in 1994, (c) Arctic char in 1989, and (d) Arctic char in 1994. Males are denoted by green dots and females by yellow. [Colour online.]



Kennedy and Crozier 1993; Cunjak and Therrien 1998). Survival of juvenile salmonids is density-dependent (Symons 1979; Elliott 1994), and egg-to-smolt survival depends on several environmental factors, such as temperature, sedimentation, shelter, predation, etc. In the River Halselva, annual mean temperature is low, and the estimated mean smolt age of Arctic char is 5.04 years and of brown trout is 4.88 years (Jensen et al. 2012), which is higher than in the more southern parts of the species' distribution. Symons (1979) suggested mortality rates for Atlantic salmon juveniles living in lotic habitats of 90%–95% in the first year and 40%–

60% per year in the following years in fresh water. Hence, because of the high smolt ages, egg-to-smolt survival of the *Halselva* populations of salmonids is expected to be in the lower part of the survival range.

The ESF estimates suggest that anadromous populations of brown trout are less vulnerable to environmental variation than anadromous Arctic char, and this is reflected in their geographic distribution in Europe. While anadromous brown trout are distributed all along the western coast of Europe from northern Portugal to Russia, including Iceland, the British Islands, and the

Baltic Sea (Elliott 1994), anadromous Arctic char is found in Europe north of 65°N (northern Norway, Russia, and Iceland) and in northern Canada and Greenland (Klemetsen et al. 2003). Costs of sea-run migration in Arctic char apparently outweigh profits of feeding at sea farther south. Thermal performances of the two species are almost identical, with a lower temperature limit for growth at about 5 °C, maximum growth at about 15 °C, and an upper temperature limit for growth at 21–23 °C, with slightly higher growth rate at maximum growth for Arctic char. Growth efficiency (per unit of food) is, however, twice as high in Arctic char than in brown trout (Larsson et al. 2005; Forseth et al. 2009; Finstad et al. 2011). Thus, because of the higher energy turnover efficiency, Arctic char may attain positive growth at much lower levels of energy intake than do brown trout and hence perform better in cold, unproductive lakes than brown trout (Finstad et al. 2011). Finstad and Hein (2012) predicted that in the future, climate-driven increases in terrestrial primary production will increase primary production in lakes and ultimately reduce the prevalence of anadromy in Arctic char populations. This is supported by the findings in the Halselva watershed that Arctic char already currently return earlier to fresh water, and hence have a shorter sea migration, in years with high sea temperatures in August compared with years with lower sea temperatures in the same month (Jensen et al. 2018b).

To the best of our knowledge, this is the first study comparing daily mortality rates of anadromous salmonids in fresh water and at sea and the first ESF estimates of anadromous Arctic char and brown trout. Daily mortality rates were 5–15 times higher at sea than in fresh water, and higher for first-time migrants than for veteran migrants of both Arctic char and brown trout, inferring a clear trade-off between increased body mass gain and mortality risk during the sea migration. Mean values for ESF was lower for Arctic char than for brown trout, suggesting that the anadromous fraction of brown trout is more robust to environmental changes than Arctic char.

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