Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

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Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2017-0077.R1
Manuscript Type:	Article
Date Submitted by the Author:	21-Jun-2017
Complete List of Authors:	Jensen, Arne; Norwegian Institute for Nature Research, Finstad, Bengt; Norwegian Institute for Nature Research Fiske, Peder; Norwegian Institute for Nature Research (NINA), Aquatic Department
Is the invited manuscript for consideration in a Special Issue? :	N/A
Keyword:	GROWTH < General, SURVIVAL < General, SIZE DISTRIBUTION < General, MARK-RECAPTURE < General, Salmonid

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Evidence for the linkage of survival of anadromous Arctic char and brown trout during winter to marine growth during the previous summer

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Running head: Link between summer growth and winter survival

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Abstract

Data from a 25-year study of anadromous Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in the River Halselva provided evidence that survival during winter was linked to marine growth during the previous summer. The study supported the “critical size and critical period” hypothesis, which postulates that regulation of the abundance of adult salmonids occurs in two major phases. The first phase is marine mortality that occurs shortly after smolts enter salt water, and the second is during the following winter, when individuals that have not attained a critical size are unable to meet minimum metabolic requirements and die. In the present study, growth during summer appeared to be more important to winter survival than body size. Size-selective mortality occurred both at sea during summer and in fresh water during winter, and was more evident for first-time migrants than repeat migrants.

Key words

Growth, survival, size distribution, mark-recapture, salmonid

Introduction

It is generally accepted that animals need to gain weight and store enough energy during periods of the year with rich food supplies to survive periods of the year with lower food availability (Rogers and Smith 1993; Hutchings et al. 1999; Farley et al. 2007; Hurst 2007). For teleost fishes in temperate and alpine areas, winter is considered a survival bottleneck (Johnson and Evans 1991; Cunjak et al. 1998; Cunjak and Therrien 1998), with energy deficiency being the primary cause of mortality (Finstad et al. 2004; Hurst 2007). Predation, thermal stress, parasites, and pathogens might also influence winter mortality (Sogard 1997; Hurst 2007).

Reviewing size-selective mortality in the juvenile stage of teleost fishes, Sogard (1997) found overwhelming evidence from field and laboratory studies that size-selective mortality occurs during winter, and larger members of a cohort are better than smaller

members and conspecifics at tolerating physical extremes and enduring longer periods without food. Further, size-selective mortality may depend on the predator field, but compared to large fish, smaller fish are typically susceptible to a broader spectrum of predators and experience higher mortality rates (Sogard 1997).

Effects of body size and growth rates on mortality of fish larvae and juveniles have been summarized in the “growth-mortality” hypothesis, which suggests that larger and/or faster growing compared to slower growing individuals in a cohort have a higher probability of survival (Ware 1975; Anderson 1988). This hypothesis combines feeding success and predation into an integrated framework: as feeding success increases, growth increases, and the probability of mortality because of starvation and predation decreases (Hare and Cowen 1997). The functional mechanisms behind the “growth-mortality” hypothesis show three concepts: “bigger is better”, “stage duration”, and “growth-selective predation”, which are based on size, time, and actual growth rate, respectively (Takasuka et al. 2004; Islam et al. 2010; Takasuka et al. 2017). The first concept assumes mortality to be negatively size-dependent, leading to a survival advantage for the largest individuals of a cohort (Miller et al. 1988). The “stage duration” hypothesis focuses on the relationship between growth rate and stage duration. Individuals with higher growth rate shortens the vulnerable stage duration, and hence selectively survive, since the probabilities of mortality events will be decreased (Chambers and Leggett 1987; Houde 1987). The third concept, “growth-selective predation”, which was proposed by Takasuka et al. (2003), links growth rates per se to survival directly. A few attempts have been made to distinguish selection by body size from selection by growth rate, and all have been growth analyses based on otolith studies on fish larvae (Hare and Cowen 1997; Takasuka et al. 2003; Takasuka et al. 2004; Islam et al. 2010). These studies concluded that growth rate per se may be as important as body size, and Takasuka et al.

(2004) observed that faster growing individuals survived even if they were smaller than their slower-growing conspecifics.

Most studies on the “growth-mortality” hypothesis have been performed on larvae and small juveniles of marine fishes, whereas few such studies on the marine life of anadromous salmonids are available (Beamish and Mahnken 2001). The first 1–4 years of most anadromous salmonids are spent in fresh water, until they smoltify and migrate to the sea, usually when they are 10–25 cm in size (Quinn 2005; Thorstad et al. 2011). The transition from fresh to salt water is a bottleneck in the life cycle of anadromous salmonids, with high mortality, mainly caused by predation by marine fish species, birds, and mammals (Hvidsten and Lund 1988; Hedger et al. 2011; Ward and Hvidsten 2011), and this mortality is partly related to size (the “bigger is better” concept). Beamish and Mahnken (2001) studied Pacific salmon (*Oncorhynchus* spp.) in general and coho salmon (*Oncorhynchus kisutch*) in particular, and proposed that high mortality also occurs in autumn and winter during the first year at sea. Their hypothesis stated that numbers of returning Pacific salmon are linked to fluctuations in climate and oceanic environments during their growth. They introduced the “critical size and critical period hypothesis” that regulation of the final abundance (total returns) occurs in two major stages. The first stage in marine mortality is mostly predation-based and occurs immediately after the smolts enter the sea. The second stage of major mortality occurs in autumn and winter of the first year at sea, when juvenile salmon that have not attained a critical size die, because they are unable to meet the minimum metabolic requirements. According to this hypothesis, growth-based mortalities may occur throughout the summer, but mortalities predominantly occur after summer of their first year at sea, i.e., survival during the winter is linked to growth during the previous summer.

Most anadromous salmonid species, including coho salmon, remain at sea for one or more years before they return to their natal river to spawn, and hence, mortality rates during

the first summer at sea can hardly be separated from mortality rates during the following winter. Only those individuals that survive both periods and return to the river are available for further analysis. However, some salmonids such as anadromous Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in part of their distribution area, including northern Norway, usually return to fresh water the summer following their migration to the sea as smolts, and continue to migrate between fresh water and the sea twice each year for the rest of their lives (Jørgensen and Johnsen 2014; Jensen et al. 2015; Thorstad et al. 2016). Hence, by trapping and individually tagging the fish when they first leave fresh water and recording their body size each time they pass the trap, growth and survival rates can be estimated each time they leave or ascend fresh water. In this way, it is possible to distinguish quantitatively the mortality rates during the two periods included in the “critical size and critical period hypothesis” (i.e., the first summer and first winter after sea migration, respectively).

Such a study has been performed during a 25-year period for anadromous Arctic char and brown trout in the River Halselva in the Arctic region of Norway. First time migrants (smolts) of both species were captured in a permanent fish trap located 200 m above the outlet to the sea, individually tagged, and thereafter recorded each time they passed the fish trap, usually twice each summer, for the rest of their lives (up to the end of 2012, when the trap was removed from the river). By examining these data, the “growth-mortality hypothesis” and the “critical size and critical period hypothesis” were tested.

Material and methods

Study area

The Hals watercourse (70°2'N, 22°57'E) in the Arctic region of Norway has a catchment area of 143 km² and drains into the Alta Fjord (Fig. 1). Approximately 20 km of the watercourse is accessible to anadromous salmonids (Arctic char, brown trout, and Atlantic salmon [*Salmo salar*]), including a 1.2-km² lake located 2.1 km inland and 30 m above sea level (Lake

Storvatn, Fig. 1). Both bodies of water are ice-covered from December to March or April, a period characterized by low flow. A pronounced increase then occurs during the snow-melting period (May–June), followed by a decrease during July–August, yielding a mean annual flow of $4.3 \text{ m}^3 \cdot \text{s}^{-1}$. The outlet is the River Halselva, which 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). Minimum temperature in the outlet—River Halselva—is approximately 0°C during the ice-covered period, then rises steadily until reaching a maximum temperature of approximately 13°C in early August. Respectively, minimum and maximum sea temperatures are approximately 2.5°C in late March and 11°C during late July–early August.

Fish sampling

During 1987–2012, fish were sampled via permanent fish traps placed 200 m upstream from the sea: Wolf traps (Wolf 1951) (apertures 10 mm, inclination 1:10) for descending fish and fixed box traps for ascending fish. All passing fish larger than 10 cm were trapped, and Arctic char (sea char) and the brown trout (sea trout) were predominant in the watercourse, but Atlantic salmon and European eels (*Anguilla anguilla*) were also present. The traps were operated during the ice-free period (April through October) and were emptied twice per day (at 8:00 and 20:00 h) to record morphological data before release. Natural tip 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.

Smolts (i.e. first time migrants, see definition by Allan and Ritter 1977) of brown trout and Arctic char were tagged with individually numbered Carlin tags (Carlin 1955). The size range of these smolts were between 18–28 cm and all smolts that migrated to sea before 1 August 1988 to 2012 were included in the present study (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 among descending fish

during autumn. First time migrants smaller than 18 cm were also omitted. They were not individually tagged, but fin clipped in a systematic manner to enable future identification of year of descent (Jensen et al. 2012).

In general, smolts of Arctic char in the Hals watershed migrate before brown trout, with pronounced peaks and 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). The annual descent of naturally produced Arctic char and brown trout smolts were, respectively, 500–3600 (mean = 1350) and 300–1400 (mean = 950 individuals) (Jensen et al. 2012).

The standardized mass-specific growth rate (Ω , % d⁻¹) was used to eliminate the effect of growth rate differences in initial body sizes, and was estimated as (Ostrovsky 1995):

$$\Omega = 100 \times \frac{M_1^b - M_0^b}{(t_1 - t_0) \times b}$$

where M_0 is the body mass of the fish at descent from the river and M_1 the body mass of the same fish when returning to the river later the same year, t_0 is the date when the fish descended, t_1 the date when the fish ascended again, $t_1 - t_0$ is the duration of the stay at sea, and b is the allometric mass exponent for the relationship between specific growth rate and body mass (0.31 for brown trout, Elliott et al. 1995). The same value of b was used for Arctic char (Larsson et al. 2005). Ω effectively eliminated the effect of growth rate differences in initial body sizes (Sigourney et al. 2008; Finstad et al. 2011a; Forseth et al. 2011).

Return rate to the fish trap was used as a proxy for survival rate in this study. Except for the first summer at sea, the estimated return rates appeared to closely reflect survival rates because only a few individuals of both species were absent from the river for one or more years before they returned, and only a few others stayed more than one year in fresh water before they returned to sea (Jensen et al. 2015). Further, as few as 3.9% and 2.4% of Arctic

char and brown trout, respectively, which were captured by anglers in the watercourse had remained more than one year after their latest occurrence in the fish trap, and these may have changed from a migratory to a stationary life. Return rates the first summer at sea, however, underestimated sea survival, especially for brown trout (Jensen et al. 2015). Most of the recovered Arctic char returned to the River Halselva to overwinter already the same summer as they migrated to sea as smolts (97.8%), whereas more brown trout (39.6%) overwintered one to four times in other watersheds before most of them eventually returned to the River Halselva upon maturation (Jensen et al. 2015). The proportion of post-smolts re-occurring in the fish trap the first summer, however, proved to be a significant early sign of overall survival of each smolt cohort (Jensen et al. 2015).

Statistical analyses

SPSS (version 23) was used for statistical analyses. Comparisons of means were conducted using a one-way analysis of variance (ANOVA), and duration of sea sojourns and winter freshwater stays were tested using paired sample *t*-tests. Binary logistic regression was used to distinguish the relative importance of increases in mass of Arctic char and brown trout during sea sojourns on survival compared with their length at ascent after the sojourns on survival during the subsequent winter in fresh water.

Results

During the 25-year study period, the mean duration of the first sea sojourn of anadromous Arctic char and brown trout was 34.0 ± 1.2 ($\pm$ SE) and 55.2 ± 0.9 days, respectively. Moreover, their total growth during their first sojourn was 66.7 ± 5.2 and 148.0 ± 6.0 g, and the mean standardized mass-specific growth rate (Ω) was $7.24 \pm 0.40\%$ day⁻¹ and $8.33 \pm 0.25\%$ day⁻¹, respectively. All these values were significantly higher for brown trout than for Arctic char (pairwise *t*-tests, $P < 0.001$).

The return rate of Arctic char the same summer as they left the river as smolts was $32.7 \pm 2.5\%$ ($\pm$ SE), and among the ascending individuals, $44.1 \pm 3.0\%$ returned to the sea the subsequent spring. Correspondingly, $20.8 \pm 1.9\%$ of the brown trout that left the river as smolts returned to the river later the same summer, and among the ascending individuals, $62.3 \pm 2.9\%$ descended the subsequent spring.

For both species, size selective mortalities were detected during both the first and second sea sojourn, as well as for the third sea sojourn for Arctic char. Small individuals were overrepresented among those that did not return (Fig. 2), and the mean length was significantly smaller for those that died (Table 1).

For both species, significant relationships were established between survival during the winter subsequent the first sea sojourn and standardized specific growth rate at sea during the first sea sojourn (Fig. 3a, b). Furthermore, significant relationships between winter survival and total marine growth increments in mass during the first sea sojourn (Fig. 3c, d), as well as between winter survival and body length at ascent after the first sea sojourn were detected (Fig. 3e, f). Growth increments in mass during the first sea sojourn proved to be more important for subsequent winter survival than body length at ascent (Table 2). Similar results were found after the second and third sea sojourn as well (Table 2).

For the first, second, and third sea sojourn for both species, the mean mass increment during the sea sojourn was higher for individuals that returned from fresh water to the sea than those that did not return, although this was not significant for Arctic char for their third sea sojourn (Table 3). Frequency distributions of mass increments during the first three sea sojourns for individuals that survived until the next winter, and those that did not return (Fig. 4), corroborate these results.

Discussion

The present study provides evidence that survival of anadromous Arctic char and brown trout during winter is linked to growth during the previous summer at sea. High growth rates at sea during summer resulted in increased survival in fresh water during the following winter. Moreover, size-selective mortality occurred both at sea during summer and in fresh water during winter, in accordance with the “growth-mortality” hypothesis. A clear relationship between growth and survival during the first marine sojourn was previously established for the same populations (Jensen et al. 2017), because fewer individuals return to the river after the first sea sojourn in years with low growth rates compared with those with higher growth rates at sea. Hence, individuals growing slowly while at sea face higher mortality risks than faster growing individuals both when at sea in summer and during the subsequent winter in fresh water. This is partly in line with the “critical size and critical period” hypothesis by Beamish and Mahnken (2001). The main deviation from this hypothesis is that marine growth per se during summer in the present study was more important for winter survival than body size.

The findings that growth per se was more important for survival than body size is in accordance with the “growth-selective predation” concept of the “growth-mortality” hypothesis. This concept works when slower-growing individuals are more vulnerable to predation mortality than faster-growing conspecifics of the same somatic size (Takasuka et al. 2017). Slower-growing individuals would be physiologically in a poor condition and thus have a lower potential to initiate antipredator behaviours (Fuiman and Magurran 1994; Skajaa et al. 2003; Takasuka et al. 2017).

The first period of high mortality after smoltification in anadromous salmonids occurs shortly after the smolts enter sea water and is predation-based and size-dependent (Parker 1971; Klemetsen et al. 2003; Ward and Hvidsten 2011; Thorstad et al. 2016). The results of the present study corroborate this, although survival rates were probably overestimated

because only first time migrants larger than 18 cm were included in the analyses. However, mortality due to tagging effects might underestimate marine survival (Strand et al. 2002). In addition, the present study demonstrated that in Arctic char, size-dependent mortality also took place during the second and third sea sojourn, as well as during the second sea sojourn for brown trout, corresponding to individual body lengths of up to approximately 350 mm (400–450 g) for both species. Because Arctic char stay for a shorter period at sea than brown trout (Jensen et al. 2017), they use longer time to reach this size.

The second period of high mortality, as proposed by Beamish and Mahnken (2001), occurs during the autumn and winter following the first summer at sea. Although this second period of high mortality may be difficult to prove for salmonid species that spend one year or more at sea before they return to fresh water, it has been made probable for several species. These include coho salmon (Beamish et al. 2004), pink salmon (*Oncorhynchus gorbuscha*) (Moss et al. 2005; Cross et al. 2008), sockeye salmon (*Oncorhynchus nerka*) (Farley et al. 2007; Farley et al. 2011), chinook salmon (*Oncorhynchus tshawytscha*) (Tovey 1999; Duffy and Beauchamp 2011) and Atlantic salmon (McCarthy et al. 2008). The results of the present study demonstrated this second period of high mortality.

Are mortality rates during autumn and winter linked to the size of the fish at the end of the previous summer or growth rates during that summer? The present study provided evidence that high growth rates were more important than size for winter survival in both Arctic char and brown trout. In most other salmonid studies, however, the methods used could not distinguish between these two alternatives. Using data from coded wire tag release groups of hatchery chinook salmon, Duffy and Beauchamp (2011) concluded that mortality after July was strongly size dependent. Based on studies of spacing between circuli in scales of coho salmon, Beamish et al. (2004) concluded that individuals that survived the winter had significantly larger spacing between circuli on their scales, indicating that brood year strength

was related to growth during the first marine year. Similarly, Moss et al. (2005) found that surviving pink salmon exhibited significantly wider circuli spacing on the region of the scale formed during early marine residence than did juveniles collected at sea during their first summer in the sea. At the same circuli, a significantly larger average scale radius for returning adults than for juveniles suggested that faster-growing juveniles had higher survival rates and that significant size-selective mortality occurred after the juveniles were sampled. Based on a long-term study of circuli spacing in scales of a Norwegian Atlantic salmon population, McCarthy et al. (2008) found a significant positive correlation between post-smolt growth and pre-fishery abundance of Norwegian Atlantic salmon during the third, fourth, and fifth months (July, August, and September) at sea. They suggested that a decrease in post-smolt growth during that time might be driving the overall decrease in pre-fishery abundance in Norway. Utilizing data from large-scale fisheries for Bristol Bay sockeye salmon, Farley et al. (2011) provided evidence that marine mortality of juvenile fish after their first summer at sea could be large and that the first winter at sea might be the critical period for survival. Furthermore, they found differences in the seasonal energetic signatures for lipids and proteins, and suggested that during winter, the fish did not starve, but instead the larger fish apparently used energy stores to minimize predation.

All the above-mentioned studies were performed on species that remained more than one year to sea before returning to their natal rivers, and were mainly based on analyses of growth from scales. Here, we were able to address uncertainties that affected earlier work, because Arctic char and brown trout return to fresh water the same summer as they migrate to sea as smolts, and continue to move between the sea and fresh water twice each year for the rest of their lives (Jensen et al. 2015). Hence, we were able to estimate growth directly via measuring individual lengths and mass during both ascent and descent journeys, and had precise data on migration and return dates. The main deviation from the previous studies was

that Arctic char and brown trout stayed in fresh water during winter, whereas the other species remained in salt water.

Some human activities may affect marine growth of the two species, and hence affect survival rates both at sea and in fresh water. One example is the future climate change, which is expected to affect the timing of seaward migration and return migration, as well as marine growth (Reist et al. 2006; Jonsson and Jonsson 2009; Jørgensen and Johnsen 2014). In the Hals watercourse, the timing of the seaward migration was negatively correlated with mean river temperature at descent (Jensen et al. 2012). Furthermore, a negative relationship was detected between the mean duration of first sea sojourn and average sea temperatures during late summer (Jensen et al. 2017). However, neither species exhibited a significant relationship in their standardized mass-specific growth rate or total marine growth and sea temperatures, possibly because of low inter-annual variation in sea temperatures during the study period (Jensen et al. 2017).

Another example is the aquaculture industry for farmed salmonids, which might experience stronger negative effects in the wild populations of these two species than earlier expected. In areas with intensive farming, the abundance of salmon lice (*Lepeophtheirus salmonis*) in the sea has increased, and negatively affects wild salmonid populations (Finstad et al. 2011b; Vollset et al. 2014; Thorstad et al. 2015; Vollset et al. 2016). For anadromous brown trout, premature return migration to fresh water because of high salmon lice infestations has caused reduced sea growth and increased marine mortality (Birkeland 1996; Wells et al. 2007; Fjærtøft et al. 2014; Gjelland et al. 2014; Skaala et al. 2014). Salmon lice may induce osmoregulatory dysfunction, physiological stress, anemia, reduced feeding and growth (Shephard et al. 2016), increased susceptibility to secondary infections, reduced disease resistance, and ultimately mortality of individual fish (Thorstad et al. 2015). In addition to these earlier known disadvantages, increased winter mortality might also occur

because of the premature return migration to fresh water and hence decreased marine growth during the previous summer as stated above.

In conclusion, Arctic char and brown trout survival in freshwater during winter was linked to marine growth during the previous summer. High growth rate at sea during summer resulted in increased survival the following winter. Moreover, size-selective mortality occurred both at sea during summer and in fresh water during winter, in accordance with the “growth-mortality” hypothesis. Individuals growing slowly while at sea face higher mortality risks than faster growing individuals both when at sea in summer and during the subsequent winter in fresh water. This is partly in line with the “critical size and critical period” hypothesis. The main deviation from this hypothesis is that marine growth per se during summer in the present study was more important for winter survival than body size.

Acknowledgments

This study was financed by the Norwegian Environment Agency, Statkraft Energi AS, and the Norwegian Institute for Nature Research (NINA). This work could not have been carried out without invaluable assistance with the traps in the River Halselva from the staff at the Talvik Research Station.

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Table 1. Mean length (mm, $\pm$ 95% CI) of Arctic char and brown trout at migration to the sea in the first, second, and third summer after smoltification, separated between individuals that returned to the River Halselva (Returned) and those that did not return (Disappeared). Results of ANOVA tests to distinguish between the two groups. Pooled data for the period 1988–2012.

	Returned		Disappeared		ANOVA	
	Length	n [*]	Length	n	F [†]	P [‡]
Arctic char						
1. summer	218.14 $\pm$ 0.76	3892	210.52 $\pm$ 0.52	8008	266.5	< 0.001
2. summer	281.47 $\pm$ 1.94	905	270.04 $\pm$ 2.80	509	45.3	< 0.001
3. summer	338.24 $\pm$ 2.73	547	326.17 $\pm$ 6.38	157	15.01	< 0.001
Brown trout						
1. summer	213.08 $\pm$ 0.69	4227	207.72 $\pm$ 0.40	10972	182.2	< 0.001
2. summer	304.56 $\pm$ 1.93	1003	301.58 $\pm$ 2.14	943	4.14	0.042
3. summer	394.31 $\pm$ 2.71	606	391.61 $\pm$ 3.75	333	1.33	0.249

^{*}n = number of individuals, [†]F = F-value of the ANOVA test, [‡]P = significance level.

Table 2. Results of tests (binary logistic regression) to distinguish the relative importance of increase in mass (g) of Arctic char and brown trout during the first, second, and third sea sojourn from length at ascent (mm) after the same sojourns on survival during the subsequent winter in fresh water. Pooled data for the period 1988–2012.

	Increase in mass		Length at ascent		Alive	Dead	†Nagelkerke R ²
	Wald	P*	Wald	P	n ₁ ‡	n ₂ §	
Arctic char							
1. sojourn	143.6	<0.001	13.0	<0.001	1373	2244	0.187
2. sojourn	15.8	<0.001	1.72	0.19	598	303	0.032
3. sojourn	4.64	0.031	4.49	0.034	347	194	0.014
Brown trout							
1. sojourn	51.9	<0.001	0.18	0.668	1852	979	0.126
2. sojourn	13.7	<0.001	3.19	0.074	694	286	0.026
3. sojourn	5.9	0.015	0.03	0.854	393	193	0.035

*P = significance level estimated by Wald statistics; [†]Nagelkerke R² = Nagelkerke squared

multiple correlation coefficient; [‡]n₁ = number of individuals that descended to the trap after the

winter; [§]n₂ = number of individuals that did not descend to the trap after the winter

Table 3. Mean mass (g, $\pm$ 95% CI) of Arctic char and brown trout when they ascended the fish trap in the River Halselva after one, two, and three summers at sea, sorted by individuals that returned to the fish trap after the following winter (Returned) and individuals that did not descend (Disappeared). Pooled data for the period 1988–2012.

	Returned		Disappeared		ANOVA	
	Mass	n [*]	Mass	n	F [†]	P [‡]
Arctic char						
1. summer	84.0 $\pm$ 2.16	1373	49.8 $\pm$ 1.73	2244	579.5	< 0.001
2. summer	159.1 $\pm$ 4.64	598	138.5 $\pm$ 7.28	301	23.7	< 0.001
3. summer	216.6 $\pm$ 11.4	347	209.1 $\pm$ 11.2	194	1.08	> 0.05
Brown trout						
1. summer	170.3 $\pm$ 2.69	1853	128.5 $\pm$ 4.43	980	280.0	< 0.001
2. summer	322.8 $\pm$ 6.88	694	298.7 $\pm$ 10.0	286	14.3	< 0.001
3. summer	470.7 $\pm$ 14.4	393	422.9 $\pm$ 18.9	193	14.9	< 0.001

^{*}n = number of individuals, [†]F = F-value of the ANOVA test, [‡]P = significance level.

Figure captions

Fig. 1. Map of the study area, with the location of the fish traps in the River Halselva for trapping of all ascending and descending fish.

Fig. 2. Length distribution of Arctic char and brown trout at their entrance to the sea, separated between those that died during the subsequent sea sojourn (●), and those that were still alive (i.e. had subsequently returned to the fish trap) after the sea sojourn (○). Arctic char at their a) first, b) second, and c) third summer at sea, and brown trout at their d) first, e) second, and f) third summer at sea. Pooled data for the period 1988–2012.

Fig. 3. Relationship between mean standardized specific growth rate (Ω , % d⁻¹) during the first sea sojourn and fresh water survival (%) during the following winter for a) Arctic char ($y = 5.00x + 7.44$, $r^2 = 0.469$, $F_{1,22} = 19.47$, $P < 0.001$) and b) brown trout ($y = 6.67x + 6.47$, $r^2 = 0.360$, $F_{1,22} = 12.37$, $P = 0.002$); relationship between mean total growth increment (g) during the first sea sojourn and fresh water survival (%) during the following winter for c) Arctic char ($y = 0.49x + 11.0$, $r^2 = 0.784$, $F_{1,22} = 79.69$, $P < 0.001$) and d) brown trout ($y = 0.32x + 14.2$, $r^2 = 0.482$, $F_{1,22} = 20.48$, $P < 0.001$); and relationship between mean length (mm) at ascent to the river after the first sea sojourn and fresh water survival (%) during the following winter for e) Arctic char ($y = 1.03x - 214$, $r^2 = 0.763$, $F_{1,22} = 70.70$, $P < 0.001$) and f) brown trout ($y = 0.987x - 213$, $r^2 = 0.445$, $F_{1,22} = 17.66$, $P < 0.001$).

Fig. 4. Frequency distribution of mass increment (g) during the summer sea sojourn of individuals that survived the following winter (○) and those that died during the winter (●) for Arctic char during their a) first, b) second, and c) third sea sojourn, and brown trout during their d) first, e) second, and f) third sea sojourn. Pooled data for the period 1988–2012.

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