Evolutionary Ecology Research, 2006, **8**: 1249–1262

Adaptation to ice-cover conditions in Atlantic salmon, *Salmo salar* L.

Anders Gravbrøt Finstad* and Torbjørn Forseth

Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway

ABSTRACT

Hypothesis: Salmonid fishes adapt to ice-cover conditions in their home river.

Organism: Atlantic salmon (*Salmo salar*) originating from six Norwegian populations along a climatic gradient (59–70°N) ranging from insignificant natural ice cover (southern populations) to several months of extensive ice cover (northern populations).

Site of experiments: NINA Research Station, Ims, south-western Norway (59°N, 6°E).

Methods: Common environment experiments in tanks (manipulating light) comparing growth, food consumption, and growth efficiency under simulated ice cover (darkness) and no ice (6 h daylight), and comparison of energy-loss rates in semi-natural stream channels with or without simulated ice cover.

Results: Mass standardized growth (Ω) of the three southern populations from ice-free rivers was significantly higher in tanks with light (mean = 0.13) than in darkness (mean = −0.21), whereas the northern populations originating from rivers with ice cover showed smaller or insignificant differences in growth between light (mean = −0.01) and darkness (mean = 0.08). A similar pattern was found for food consumption. In stream channels, the differences in energy loss with and without simulated ice cover increased significantly with increasing latitude of population origin. Fish from the northern populations naturally experiencing extensive ice cover lost more energy without ice than fish from the southern populations, and are thus more susceptible to ice-cover removal.

Keywords: climate changes, countergradient variation, growth, thermal adaptation, thermal performance.

INTRODUCTION

Relationships between animal performance and environmental factors are often described by performance curves, which are continuous reaction-norms that model how a trait value scales with an environmental variable. Such performance functions are important tools for predicting responses to climatic changes (Hodkinson, 1999; Helmuth *et al.*, 2005) and other anthropogenic changes (Jensen, 2003). However, due to adaptations to local environmental

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* Author to whom all correspondence should be addressed. e-mail: anders.finstad@nina.no

conditions, performance curves may vary between populations (Angilletta *et al.*, 2002; Kingsolver and Gomulkiewicz, 2003), and for widely distributed species it is important to identify how environmental and genetic factors interact to shape physiological performance. Adaptations may appear as shifts in the maximum of the performance function (e.g. growth, metabolic rate, developmental rate) that match the prevailing environment [adaptation to local optima (Levinton, 1983)], or as a general elevation of performance in populations from hostile environments [countergradient variation (defined by Levins, 1969; reviewed by Conover and Schultz, 1995)].

Somatic growth rates can have important fitness consequences, are often heritable, and therefore subject to selection (e.g. Roff, 1992; Stearns, 1992). Despite obvious fitness advantages associated with rapid growth rates, organisms usually grow well below their physiological maximum, indicating selective trade-offs (Arendt, 1997; Blanckenhorn, 2000; Carlson *et al.*, 2004). Common environment and transplant experiments have revealed contrasting findings with regard to growth rate variation across environmental clines both within and between species and genera. Although various physiological functions display thermal adaptations (Angilletta *et al.*, 2000), there is little evidence for co-variation in growth among vertebrates. On the other hand, countergradient variation in growth has been reported for invertebrates as well as vertebrates (Berven *et al.*, 1979; Conover and Present, 1990; Nicieza *et al.*, 1994; Conover *et al.*, 1997).

Despite substantial efforts, strong correlations have not been found between thermal conditions in the watershed of origin and limits for growth, thermal growth optima, or maximum growth in salmonid fishes (Elliott, 1994; Jensen *et al.*, 2000; Jonsson *et al.*, 2001; Larson *et al.*, 2005). This apparent lack of thermal adaptations for growth in salmonids [but see Nicieza *et al.* (1994) for a two-population comparison] is surprising given the large natural geographical distribution of these fishes, and the considerable variation in growth potential between populations (Jonsson *et al.*, 2001; Larson *et al.*, 2005). Proposed explanations are phylogenetic constraints or trade-offs between growth and other fitness-related traits (Jonsson *et al.*, 1991; Gotthard *et al.*, 1994; Ricklefs *et al.*, 1994; Fleming and Einum, 1997; Metcalfe and Monaghan, 2001).

Adaptations to thermal conditions, however, might not be explained by temperature responses alone. Indirect effects of temperature such as changes in ice conditions, which are particularly sensitive to small thermal changes, could have a severe effect on the physiological performance and ecology of animals during critical periods of the year (Adrian *et al.*, 1999; Solberg *et al.*, 2001; Aars and Ims, 2002; Forchhammer *et al.*, 2002; Finstad *et al.*, 2004a). Ice-cover conditions on northern hemisphere watersheds are being reduced in line with the increase in global temperatures (Magnuson *et al.*, 2000). For juvenile Atlantic salmon (*Salmo salar* L.), ice cover is an important characteristic of the habitat during winter, and there is evidence to suggest local intraspecific adaptations to ice-cover conditions (Finstad *et al.*, 2004a).

In the present study, we report covariation between ice-cover conditions and growth and energy turnover in juvenile Atlantic salmon. The results originate from two series of common environment experiments using Atlantic salmon from populations with contrasting ice-cover conditions. We first test for effects of ice-cover-induced alterations in light conditions on growth, food consumption, and growth efficiency in a benign laboratory environment. Then, we test for the effects of manipulated ice-cover conditions in a more hostile semi-natural environment (artificial stream channels).

MATERIALS AND METHODS

Experimental site and fish

Atlantic salmon juveniles commonly spend 1–5 years in fresh water before migrating to the sea. The native distribution spans a broad environmental gradient from the Mediterranean climate regions of southern Spain to sub-arctic areas in northern Norway. We used one-summer-old (0+) first-generation hatchery-reared offspring of parents originating from six rivers (five for the stream channel experiments) along a latitudinal gradient ranging from 59° to 70°N (Table 1). Juvenile Atlantic salmon inhabit coastal rivers for which latitude is a convenient proxy for ice-cover conditions. The rivers used in the present study group into two categories: rivers with long periods of ice cover each winter (the three northernmost rivers) and rivers lacking ice cover completely or with only insignificant periods of ice cover during winter (the three southernmost rivers) (Table 1).

All experiments, as well as rearing of eggs and hatching, were conducted at the NINA Research Station, Ims, southwestern Norway (59°N, 6°E) from January to March in 2003, 2004, and 2005. For each laboratory cohort, eggs were collected from a minimum of five females, and fertilized with one male per female. After fertilization, the fish from each population were reared in common tanks. Before winter acclimatization, the fish were maintained at the same ambient temperatures and light regime. Two months before the start of the experiment, the fish were held at gradually declining temperatures and day lengths (1°C and 1 h per week) to simulate natural autumn conditions, until the final temperature (≈ 1°C) and photoperiod (6 h light/18 h dark) were reached.

Tank experiments

To simulate light conditions experienced by fish with ice cover and without ice cover during winter, two similar tank compartments were created and light isolated as in a photo laboratory darkroom. The no-ice treatment received 6 h light (≈ 70 lux) and 18 h darkness, whereas the ice-cover conditions were simulated by rearing the fish in darkness. Light levels in the dark treatment were similar to those measured *in situ* under surface ice with snow cover. In late winter (22 April 2001), light levels (LI-250 Light Meter with LI-190SA Quantum Sensor or LI-192SA Underwater Quantum Sensor, LI-COR Inc.) under ice cover

Table 1. Latitude of native river for the study populations, ice-cover indices (– = non-significant ice-cover, + = long periods with ice cover), mean initial wet mass (standard deviation in parentheses) of the fish, the types of experiments performed (T = tank, SC = stream channel), and year of the experiments

Population	Latitude (°N)	Ice cover	Wet mass (g)	Type of experiment	Year
Imsa	59.0	–	23.5 (3.4)	T, SC	2003 and 2004
Suldal	59.3	–	19.0 (4.5)	T	2003
Lone	60.0	–	6.7 (2.5)	T, SC	2005
Gaula	62.3	+	7.6 (2.7)	T, SC	2005
Namsen	64.5	+	13.2 (5.8)	T, SC	2005
Alta	70.0	+	17.2 (4.8)	T, SC	2003

(at 50 cm water depth) in the River Alta varied from 6.3 $\mu\mathrm{mol}\cdot\mathrm{s}^{-1}\cdot\mathrm{m}^{-2}$ at midday to < 0.01 $\mu\mathrm{mol}\cdot\mathrm{s}^{-1}\cdot\mathrm{m}^{-2}$ at night. Throughout most of the winter, light levels under the ice are similar to night-time values due to the polar night. Light intensity in the laboratory dark treatment was < 0.01 $\mu\mathrm{mol}\cdot\mathrm{s}^{-1}\cdot\mathrm{m}^{-2}$.

Husbandry was conducted using red photo laboratory darkroom light, which is expected to be physiologically undetectable for salmonids (Ali, 1961; Dodt, 1963). Both light regimes received the same inflow water, and the temperatures were therefore the same in the two treatments (≈ 1°C). The experimental set-up was identical to the one described in Finstad *et al.* (2004a). Due to logistic constraints, the experiments were run in three different years (Table 1). However, salmon from the Imsa watercourse were used in experiments both in 2003 and 2004, in order to test for consistency in treatment effects between years. The effects of year of experiment, light treatment, and the interaction between the two were tested by analysis of variance (ANOVA) with growth rate as the dependent variable. The effect of replicates (tanks) was non-significant ($P = 0.74$) and therefore removed from the model (Underwood, 1997). We were unable to detect any between-year variation in growth and although the effect of light differed slightly between years, its effect was minimal (mean growth (Ω) in light and dark in 2003 = 0.19 and 0.02, respectively; mean growth (Ω) in light and dark in 2004 = 0.38 and −0.05, respectively) (year of experiment, $F_{1,76} = 0.24$, $P = 0.24$; light treatment, $F_{1,76} = 29.30$, $P < 0.001$; light × year, $F_{1,76} = 6.30$, $P = 0.014$). The fish used in the experiments in 2003 and 2004 came from different parents, and thus the lack of between-year effects supports the conclusion that we subsequently test for population differences and not for between-family variations.

In each light treatment, we used 12 tanks with two replicates for each of the six populations. The tanks were 45 × 45 cm and 60 cm deep, had a water flow of 2 litres per minute, and a water depth of 30 cm. Experimental units were randomly distributed within each section to avoid systematic tank effects. Ten individually marked (Alcian blue in fins and adipose fin clipping) fish were used in each tank. Each fish was weighed after approximately 48 h of starvation at the beginning and end of experiments. Oxygen saturation was always close to 100% during the experiment. All experiments lasted for 48 days and no fish died during the study.

The fish were fed until satiated with caesium chloride-enriched granulated fish food (Felleskjøpet, Sandnes, Norway; caesium concentration 14.1 ppm fresh mass, energy value 21.6 $\mathrm{kJ}\cdot\mathrm{g}^{-1}$ fresh mass) administered from automatic feeders. The caeseum in the food was used to estimate energy intake (Φ) as described in Forseth *et al.* (2001) and Jonsson *et al.* (2001), who also provide a further description and validation of the method. The estimate of food consumption is based on estimating the intake of caesium from an observed change in caesium body burden with time. Based on known rates of assimilation and elimination, food consumption is obtained by dividing the caesium intake by the concentration in food.

Growth was measured as the standardized (to a 1-g fish) mass-specific growth rate (Ω%) (Ostrovsky, 1995)

$$\Omega = \frac{M_t^b - M_0^b}{b \cdot t} \cdot 100 \qquad (1)$$

where M_0 and M_t are the respective body masses (g) at the beginning and end of each experiment, t is the experimental period (days), and b is the allometric mass exponent (0.31) for the relation between specific growth rate and body mass (Elliott and Hurley, 1997). Average daily growth efficiency (K_G) for each individual, standardized to an initial mass (M_0) at 1 g, was calculated as:

$$K_G = J(M_1 - M_0)/\Phi M_0^{0.766} \tag{2}$$

where $M_1 = (M_0^b + b\Omega/100)^{1/b}$, Φ is the estimated daily energy intake ($\mathrm{J \cdot g^{-1} \cdot day^{-1}}$), and the mass scaling of food consumption (0.766) was assumed to be similar to the scaling for brown trout (*Salmo trutta* L) (Elliott and Hurley, 1998). J is the mass-specific energy ($\mathrm{J \cdot g^{-1}}$). Mass-specific energy (J) was estimated using the dry mass to wet mass relationship. Because of differences in water-binding capacity of fat and proteins, the proportion of dry mass (D_{prop}) is closely linked to specific energy (Hartman and Brandt, 1995). The relationship between the proportion of dry mass and specific energy was established from a sub-sample of the fish ($J = -2847 + 36797D_{\text{prop}}$, $P < 0.001$, $R^2 = 0.98$, $n = 60$). Specific energy content for the fish in this sub-sample was measured by proximate composition of lipid and proteins determined gravimetrically after extraction and controlled combustion as described in Berg and Bremset (1998).

The experimental set-up was planned as an ANOVA with tank (replicates) nested within population and population nested within ice-cover conditions of home river (with or without ice), yielding three replicated populations for each ice-cover condition. In accordance with Underwood (1997), we removed the tank effect from the model using $\alpha > 0.25$ as a criterion for *post-hoc* pooling of replicates. We also analysed the data as means (population within light treatment) regressed against latitude of the population origin using analysis of covariance (ANCOVA).

Stream channel experiments

For five of the populations (Table 1), we also studied the effects of ice cover on energy use and feeding in outdoor semi-natural stream channels, under conditions more similar to the natural environment experienced by wild salmonids during winter. The experimental set-up consisted of nine rectangular stream channels (485×50 cm), with a water depth of approximately 30 cm and gravel substrate. Water flow through each channel was 50 litres per minute. Each stream channel was divided in two equal sized compartments in the longitudinal direction using wood planks. Working with natural ice cover is very difficult in an experimental setting, and ice cover was therefore simulated by covering one compartment of the stream channel with black light-impermeable plastic. The other was covered with clear plastic to prevent drift of exogenous material into the system while allowing natural daylight. The ice-cover treatments were randomized with respect to the left and right part of the stream channels. Although the longitudinal separation of the different stream channels prevented influx of light into the ice-cover treatment, we were unable to prevent potential small fluxes of water between the different compartments. The different populations were therefore not mixed within stream channels, to prevent between-population interaction effects caused by olfactory cues. We used three replicates of each ice-cover treatment and population, except for the 2003 experiments with the River Alta salmon, which was run as a pilot study with five replicates (Finstad *et al.*, 2004a). Day lengths increased from ≈6 h at the start of the experiment to ≈9 h at the end. The outlets of the channels were blocked by a screen to prevent escapes and were cleaned daily. Mean temperature was 2.8°C during the experimental periods. Water was run in the channels for 10 weeks before the experiments to permit colonization of an invertebrate fauna. In addition, drifting invertebrates were naturally present in the supply water, which is drained from a nearby lake.

At the beginning of the experiments, ten individually marked (Alcian blue in fins and adipose fin clipping) and weighed (precision of ±0.01 g) fish were released into each replicate. At the end of the study periods, the channels were drained and the fish were collected, killed, weighed, and had their stomach contents removed. The fish were stored at −24°C before specific energy was determined as described above. Standardized mass-specific growth rates were determined according to equation (1). Daily average food consumption (C) in each channel was estimated from the mean mass of stomach contents ($S_{\mathbf{mean}}$) and estimated gastric evacuation rate (R) (Eggers, 1979):

$$C = 24RS_{\mathbf{mean}} \tag{3}$$

where $R = ae^{bT}$ (T is the temperature and a and b are estimated constants). Parameter estimates for a and b were taken from brown trout (Elliott, 1972). At the low ambient temperatures in the present experiments, one single sample (stomach contents in individual fish at termination of the experiment) is sufficient to obtain estimates of food consumption for that day (Finstad, 2005). The experiments lasted for 31, 54, and 61 days in 2003, 2004, and 2005 respectively. In total, 18 of 340 fish died during the study.

The experimental set-up was planned with a hierarchical design with ice-cover treatment nested within individual channels (replicates). There was no effect of replicates on rate of energy loss ($P = 0.74$), and the stream channels were therefore pooled before final analyses (Underwood, 1997). We tested for geographical variation in response to ice-cover treatment using ANCOVA, with mean mass-specific energy loss for each ice-cover treatment and population as response variables, and ice-cover as a factor. Latitude was used as a proxy for ice-cover condition in the native river and introduced into the model as a covariate.

RESULTS

Growth and food consumption in the tank environment

Mass standardized growth rate varied considerably among populations (Fig. 1a). We were not able to detect any significant linear effects on growth of latitudinal location of the home river or of light treatment when growth was measured as means for each population within light treatment. Neither did we observe any significant latitude × light treatment interaction in these analyses (ANCOVA: latitude, $F_{1,8} = 2.86$, $P = 0.13$; light, $F_{1,8} = 0.59$, $P = 0.46$; latitude × light, $F_{1,8} = 0.44$, $P = 0.53$). Although visual inspection suggested a non-linear latitudinal trend in growth rates (Fig. 1a), no significant non-linear (quadratic) latitudinal growth patterns were observed in either treatment. In contrast to the lack of relationships between latitude and growth rate *per se*, there was a near significant decrease in the difference between growth in light and growth in darkness with increasing latitude (Spearman rank correlation, $r = -0.80$, $P = 0.052$). The overall increase of growth rates in the light treatment was almost four times as large in the three southern populations not experiencing ice cover in their natural habitat as in the northern populations naturally experiencing extensive periods of ice cover. Furthermore, only the northernmost population was able to sustain a positive growth rate in darkness. We also analysed the data using ice cover as a categorical variable (no ice cover; three southern rivers: ice cover; three northern rivers). This approach enabled us to nest population within ice-cover condition in native

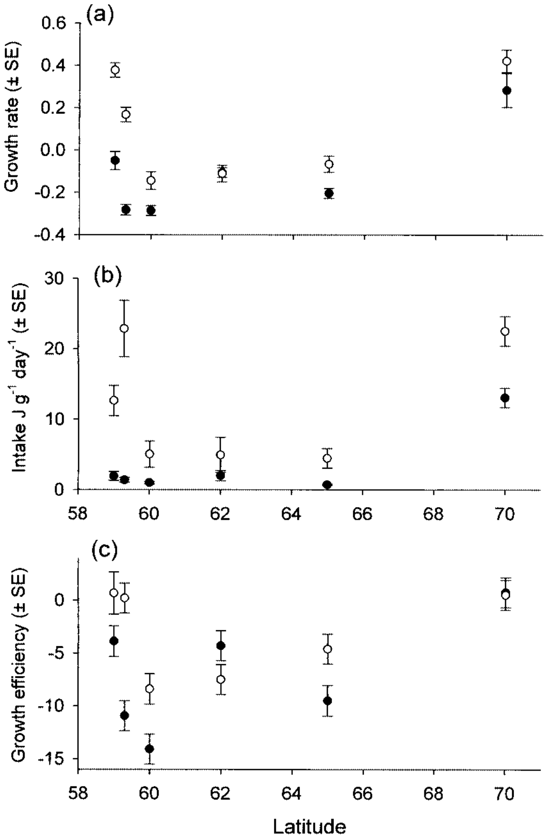

Fig. 1. Mean (± standard error) mass-specific growth (a), food consumption (b), and growth efficiency (c) for six populations of juvenile Atlantic salmon reared in darkness (solid dots) or in 6 h daylight (open dots) plotted against latitude of population origin (proxy for ice-cover conditions of home river). The three southernmost populations have non-significant ice cover in their natal river, whereas the ice-cover period increases with increasing latitude for the remaining populations.

rivers and thereby test for the light × ice-cover condition interaction after removing the effect of between-population variations in growth. The nested ANOVA model revealed a highly significant effect of the light × ice-cover condition interaction on mass-specific growth rates (Table 2).

Mass standardized food consumption varied considerably between populations, but no linear latitudinal effects on mean food consumption of the different populations were observed (Fig. 1b) (ANCOVA: latitude, $F_{1,8} = 1.79$, $P = 0.22$; light, $F_{1,8} = 0.31$, $P = 0.60$; latitude × light, $F_{1,8} = 0.18$, $P = 0.66$). Fish from all populations consumed more in light than in darkness, as for growth rate there was no overall clear geographical food consumption to latitude relationship. Although there was no significant linear or non-linear (quadratic) relationship between food consumption and latitude in the light treatment, food consumption increased non-linearly with latitude in the dark (latitude, $F_{1,3} = 18.63$, $P = 0.023$; latidude^2, $F_{1,3} = 20.06$, $P = 0.021$) and only the northernmost population consumed substantial food in darkness. This resulted in a non-significant latitudinal trend

Table 2. Results of ANOVA for the effects of geographical position (northern or southern) used as a proxy for ice-cover conditions of native river (*IC*), population (*P*), and light treatment (*L*) on growth rate, food consumption, and growth efficiency

		Growth rate			Consumption			Growth efficiency		
Source	d.f.	MS	*F*	*P*	MS	*F*	*P*	MS	*F*	*P*
IC	1	0.31	8.51	0.004	0.25	0.53	0.46	186.5	4.532	0.034
(*P*(*IC*))	4	2.24	61.19	<0.001	29.40	61.80	<0.001	788.4	19.163	<0.001
L(*P*(*IC*))	1	2.78	75.93	<0.001	55.14	115.92	<0.001	938.4	22.811	<0.001
$IC \times L$	1	0.95	25.84	<0.001	14.23	29.92	<0.001	731.8	17.79	<0.001
Residuals	232	0.04			0.48			41.1		

Note: The main effect of population (*P*) was nested within geographical location (*IC*) and the main effect of light (*L*) was nested within population and native river.

in the difference between consumption in the light and in the dark treatment. However, whereas mean food consumption for the southern populations was reduced by almost 50% in the dark treatment, the overall reduction in food consumption for the northern populations held in darkness was only about 10%. Both the light and ice-cover gradients, as well as the light × ice-cover interaction, had a significant effect on consumption rates based on consumption by individual fish (Table 2).

Growth efficiency mirrored the ice-cover gradient variation in growth and food consumption, and there was no clear geographical pattern in growth efficiency measured as means of populations and ice-cover treatments (Fig. 1c) (ANCOVA: latitude, $F_{1,8} = 2.94$, $P = 0.18$; light, $F_{1,8} = 1.49$, $P = 0.25$; latitude × light, $F_{1,8} = 1.26$, $P = 0.29$). Nor was there any significant non-linear (quadratic) relationship between latitude and growth efficiency in the dark or light treatment. There was, however, a difference between northern and southern populations in the light response of growth efficiency. Southern populations increased growth efficency in light more than northern populations (Fig. 1c). Both the light and ice-cover gradients, as well as the light × ice-cover interaction, had a significant effect on growth efficiency when using consumption as the dependent variable in a nested ANOVA model (Table 2).

Energy loss in semi-natural environment

All juvenile Atlantic salmon held in the semi-natural stream channels experienced a net energy loss during the experimental period. Mass-specific energy loss among populations and ice-cover treatments ranged from 10.8 to 12.1 $J \cdot g^{-1} \cdot day^{-1}$ in the two southern populations and from 11.5 to 27.1 $J \cdot g^{-1} \cdot day^{-1}$ in the three northern populations (Fig. 2a). Energy loss rates did not differ between ice-cover treatments in the southern populations. In contrast, although northern populations performed worse than southern populations under both conditions, their relative performance was better with simulated ice cover than without. The experiments revealed a genotype × environment interaction between latitude of population origin and ice-cover treatment in the stream channels when using mean energy loss for each population and ice-cover treatment as the dependent variable (ANCOVA: latitude, $F_{1,6} = 107.5$, $P < 0.001$; ice cover, $F_{1,6} = 4.66$, $P < 0.074$;

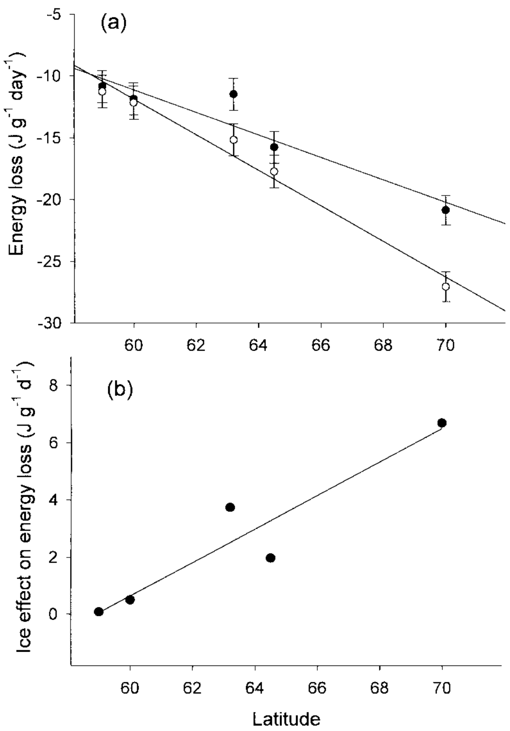

Fig. 2. Mean (± standard error) mass standardized (to a 20-g fish) loss of energy in stream channels with clear plastic (open dots) and with opaque cover (solid dots) (a), and mean difference in energy loss between the ice-cover and no ice-cover treatments (b) for juvenile Atlantic salmon from five populations, plotted against latitude of population origin (proxy for ice-cover conditions of home river).

latitude × ice-cover, $F_{1,6} = 5.47$, $P = 0.058$). The interaction was due to an increase in the difference between energy loss rates under ice cover and without ice cover with increasing latitude (Fig. 2b) (Pearson $r = 0.94$, $P = 0.016$).

Food consumption varied between populations (range 0.45 to 5.7 $\mathrm{J \cdot g^{-1} \cdot day^{-1}}$), but no significant ice-cover effect or geographical trend in food consumption was observed when comparing means for each population and ice-cover treatment (ANCOVA: latitude, $F_{1,6} = 0.73$, $P = 0.42$; ice cover, $F_{1,6} = 1.30$, $P = 0.29$; latitude × ice cover, $F_{1,6} = 1.20$, $P = 0.32$). However, the overall frequency of feeding (fish with food in their stomachs at the end of the experiment) increased significantly with increasing latitude, whereas treatment effects remained non-significant (ANCOVA: latitude, $F_{1,6} = 12.31$, $P = 0.013$; ice cover, $F_{1,6} = 1.72$, $P = 0.23$; latitude × ice cover, $F_{1,6} = 1.71$, $P = 0.24$).

DISCUSSION

The effects of simulated ice cover differed between Atlantic salmon populations originating from ice-covered rivers during winter and ice-free rivers. Fish from southern populations performed relatively better than fish from northern populations under simulated ice-free conditions both in the laboratory and semi-natural environment, indicating adaptation to local ice-cover conditions.

In accordance with previous studies of thermal growth adaptations in salmonids (Elliott, 1994; Jensen *et al.*, 2000; Jonsson *et al.*, 2001; Larson *et al.*, 2005), we did not observe any pattern consistent with the hypothesis of thermal adaptation, although the experimental populations originated from a wide environmental gradient (59–70°N) with extensive variation both in the length of the growth season and environmental adversity. Growth rates varied largely among populations, but were highest in the southernmost and northernmost populations. The present results thus confirm that countergradient variation in growth is rare or non-existent among the salmonids studied, and that the large variation in growth rates between populations is due to other factors (Jonsson *et al.*, 2001; Larson *et al.*, 2005).

In contrast to the lack of correlations between thermal conditions or adversity of the environment and growth rates *per se*, the differences in response to simulated ice conditions among populations were large and likely due to adaptations to local environmental conditions. In the tank experiments, the southernmost and northernmost populations grew better than the intermediate populations in the light treatment, whereas growth in darkness was elevated in the northernmost population. The difference in the light effect on growth rate between the southern and northern populations was due to an increase in growth in light for the southern populations and an elevated growth in darkness for the northernmost population. It could be that the elevated growth rates in the northernmost population represent adaptations to the low ambient light levels experienced during extensive periods with ice cover in combination with a long winter with polar nights.

Replicated experiments with Atlantic salmon from the southern populations (Finstad *et al.*, 2004a; present study), using offspring from different parents, showed a similar response to alteration in light regime. This supports the assumption that among-population differences are due to adaptive differences and not experimental artefacts, such as between-family variation. Although care should always be taken when interpreting genotype × environment correlations as adaptations, environmental factors that alter energy turnover during winter are likely to be a potent selective force. The winter period is regarded as a survival bottleneck in temperate freshwater fishes (Cunjak and Therrien, 1998; Cunjak *et al.*, 1998). Winter survival in salmonids depends strongly on the ability to retain critical amounts of body energy (Finstad *et al.*, 2004b; Biro *et al.*, 2004), and ice cover has been shown to have profound effects on the energy turnover of juvenile Atlantic salmon (Finstad *et al.*, 2004a).

We did not observe any significant ice-cover or latitudinal effects on food consumption for fish held in stream channels. This is probably due to the coarse method of estimation (estimate for one day based on one sample of stomach contents), and there was a clear latitudinal effect on the frequency of the feeding in the stream channels. The frequency of feeding may also be used as a proxy for the level of activity of the fish, indicating higher activity in fish from northern populations. Populations experiencing long winter periods depend more strongly on consumed relative to stored energy (Metcalfe and Thorpe, 1992; Bull *et al.*, 1996), and our results therefore suggest an adaptive elevation of feeding motivation to meet the increased demand for energy intake by the northern populations. The observed food consumption was lower than previously estimated for wild juvenile Atlantic salmon during wintertime (Berg and Bremset, 1998; Finstad *et al.*, 2004b). The higher energy losses in northern populations of salmon in both treatments (ice and no ice) may therefore be due to the fish increasing their feeding activity without being able to obtain sufficient food because of the low prey densities in the stream channels.

The proximate causes for the observed variation in response to ice-cover conditions in Atlantic salmon are likely to involve a combination of both behavioural and physiological factors. Reduced energy loss rate under simulated cover in stream channels in the northernmost population (the River Alta) has been explained by lowered metabolic costs in darkness combined with increased food consumption (Finstad *et al.*, 2004a). However, the effect of light on resting metabolic rate did not differ between the southernmost and northernmost populations (Finstad *et al.*, 2004a). Variation in energetic response to simulated ice cover in stream channels between populations is therefore likely to be linked to differences in behaviour, food acquisition, and energy turnover efficiency.

The lack of correlations between growth rates and temperature or environmental adversity in the present study, and in previous studies on thermal adaptations in salmonids (Elliott, 1994; Jensen *et al.*, 2000; Jonsson *et al.*, 2001; Larson *et al.*, 2005), contrast the findings of counter-gradient and local optima thermal adaptation in other ectothermal animals. However, the results of the present study demonstrate adaptation to an environmental factor closely correlated with the organism's thermal niche, indicating that interactions with other temperature-correlated factors may impose selection, possibly overriding or masking simple direct thermal relationships. Such correlated environmental factors should be considered in studies of thermal adaptation in ectothermal animals.

Ice cover in the northern hemisphere is declining (Magnuson *et al.*, 2000), and different populations of Atlantic salmon will, according to our results, respond differently to ice-cover reductions in the short term. Although growth in light was just as high for the northernmost population as for the southernmost one, the relatively poorer performance in stream channels without cover indicate that northern populations may be less adapted to ice-free environments than southern populations, and will therefore be most affected. However, the long-term responses to environmental changes also depend on the species' ability to adapt to new environmental conditions. As is clear from the intraspecific variation in ice-cover response among Atlantic salmon juveniles, such adaptations are likely to occur, although the speed remains unknown. Quantitative information on evolutionary rates is essential when predicting biological responses to environmental changes (Hendry and Kinnison, 1999), and it is therefore a challenge to integrate evolutionary and ecological theory to construct predictive scenarios for how populations will respond to global warming.

ACKNOWLEDGEMENTS

We thank Andrew Hendry, Ole Kristian Berg, and Frode Vinje for comments on the manuscript and the staff at the NINA Research Station and Anne Lohrmann for technical assistance. The study was supported by the Norwegian Research Council (NFR 145208/210), Statkraft Energy, and the Norwegian Directorate for Nature Management.

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