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Salmonid fishes in a changing climate: The winter challenge

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Preface

This thesis is submitted to the Faculty of Sciences and Technology, the Norwegian University of Science and Technology (NTNU) for the degree of Philosophiae Doctor (PhD). The thesis consists of five papers and a general introduction that gives the theoretical background and summarises the work. The research founding the basis of the thesis has been carried out at the Norwegian Institute for Nature Research (NINA) and the PhD study was affiliated to the Department of Biology, NTNU. The study was funded through the project Environmental Friendly Water Resources Management in a Changing Climate and a New Energy Market (NFR grant no 145208/210) financed by the Norwegian Research Council, Statkraft Energy, Norwegian Electricity Industry Association and the Norwegian Directorate for Nature Management.

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List of Papers

The thesis is based on the following papers, which in the following will be referred to by their roman numbers:


IV. Finstad A.G. & Forseth, T. The effect of ice-cover on energy turnover and winter survival in Arctic char, brown trout and Atlantic salmon. Manuscript.

V. Finstad, A.G. & Forseth, T. Adaptation to ice-cover in Atlantic salmon Salmo salar. Manuscript
Introduction

Climate changes and biological impacts

The performance of individual animals is governed both by the surrounding physical environment and interactions with other individuals. As a result, both the abundance and distribution of a species will depend upon the physical features of the habitat (MacArtur & Willson 1967, Kerr & Currie 1999, Brown et al. 2001, Loreau et al. 2001) as well as on biotic interactions (Gaston 2000, Loreau et al. 2001).

Climatic indices have shown global trends towards higher temperatures during the 20th century. During this period surface temperature has increased by an average of 0.7 °C and model-based scenarios predict a further global increase in temperatures (Houghton et al. 2001). This may change the composition of biological communities directly through extinction and immigration of species caused by species differences in physiological thresholds, and indirectly, through alternation of biotic interactions (Davis et al. 1998, Walter et al. 2002). During the past two decades, there has been a rapidly growing focus on causes and consequences of climate changes for individuals, populations, communities and ecosystems.

Climatic fluctuations influence population dynamics, and a significant proportion of annual variation in the size of natural populations may be explained by variation in large-scale climate phenomena such as the North Atlantic Oscillation (NAO) or the El Niño Southern Oscillation (ENSO) (e.g. Ottersen et al. 2001, Stenseth et al. 2002, Walter et al. 2002). Recently, there has also been an increasing amount of correlative evidence for relationships between large-scale climatic indicators and the composition of biological communities (Brown et al. 2001, Loreau et al. 2001, Lekve et al. 2003). Correlative studies linking
population fluctuations or species distribution patterns with climate indicators are important in order to identify the sensitivity of populations, communities and ecosystems to climate changes. A growing body of evidence indicates that recent changes in global climate have affected biological systems (reviewed by Stenseth et al. 2002, Walther et al. 2002). However, such approaches do not unravel the mechanisms causing the observed patterns and may, therefore, have insufficient predictive ability in terms of forecasting future changes (Helmuth et al. 2005).

Biological responses to climate changes are diverse, and vary widely among populations and species. Effects on populations are the sum of the responses on individual organisms. A mechanistic approach to understand the interactions between populations and the environment may, therefore, start by predicting environmental effects on individual performance. Individual performance under different environmental conditions may be illustrated as performance curves or reaction norms (Huey & Kingsolver 1989, Kingsolver et al. 2004). An important class of continuous reaction norms are thermal performance curves, which describes how the trait value (performance; e.g. growth, food consumption or growth efficiency) scale with temperature. However, such curves may be altered through short time, seasonal or life-time acclimatisation or through natural selection (Wilmer et al. 2000, Angilletta et al. 2002, Kingsolver & Gomulkiewicz 2003). Response to environmental changes may therefore be complex due to adaptations, acclimations or geographical variation in environmental adversities. Furthermore, the potential for adaptations and the speed of the evolutionary processes relative to the time-scale of environmental changes will ultimately determine the biological impacts of climate changes.
Acclimatization and seasonal variation in performance

In seasonal environments, organisms are exposed to changes in resource abundance and face variable mortality risks during the different stages of the annual cycle. Most populations, therefore, respond to regular or systematic environmental fluctuations (Fretwell 1972). On the individual level, this may result in seasonal modifications of the performance function through acclimation to annual cyclic changes in the environment. For example, physiological acclimation involves expression of allozymes, modifications of cell membranes, or alterations of the intracellular environment (Somero et al. 1996). Climate change does not produce a simple change in global average temperature; rather it involves a characteristic set of changes in diurnal, seasonal, and geographic patterns of temperature, precipitation, and other atmospheric conditions. The extent and impact of critical seasons may, therefore, be affected by climatic fluctuations (Houghton et al. 2001, Parkinson & Cavalier 2002).

Adaptations and intra-specific variation in performance

Beyond the within generation capacity for animals to adapt to environmental changes by acclimatization, evolutionary responses may occur across generations. Among ectotherms, two contrasting hypotheses for thermal adaptation are proposed, which are adaptation to local optima (Levinton 1983) or the countergradient variation hypothesis (reviewed by Conover & Scultz 1995). The first hypothesis implies that natural selection shift the optimal performance temperature (e.g. growth, metabolic rate, developmental rate) to match the temperatures in a new or changed thermal niche, and assumes that performance at one temperature is traded off against performance at another. The alternative countergradient variation hypothesis suggests that populations from hostile environments (low temperature, short season for growth, strong competition) perform better at all temperatures than conspecifics from more favourable environments. In addition to evolutionary changes of the performance function per se, natural
selection may also alter the capacity for thermal performance to be modified by acclimatization (Kingsolver & Huey 1998).

**Winter as a bottleneck for temperate organisms**

The ability of species to occupy a given environment may in many cases be determined by seasonal energetic bottlenecks within the annual cycle (Weiner 1992). Wintertime is such a period for many animals living in temperate and arctic region. Climatic factors influencing winter survival may have a strong impact on population dynamics, biological composition of the ecosystem and the geographical distribution of species (e.g. Post & Stenseth 1998, Baukema et al. 2000, Sæter et al. 2000, Humphries et al. 2002, Quayle et al. 2002). In addition, the impact of future climate changes on the northern hemisphere is predicted to be largest during wintertime (e.g. Benestad 2004). Animals with life cycles of more than one year commonly show adaptations to seasonal occurring adversities. This may involve migration to other climatic zones, or over-wintering in a state of hibernation in a protected place nourishing on stored body energy. For animals over-wintering in an active state, reduced food availability and environmental adversities commonly leads to a negative energy budget. Individuals often depend upon a combination of stored energy reserves and active feeding in order to survive the winter (e.g. Metcalfe & Thorpe 1992, Bull et al. 1996).

**Causes of winter mortality**

Energy deficiency is suggested as a main source of winter mortality for many animals in northern areas (e.g. Johnson & Evans 1991, Miranda & Hubbard 1994, Solberg et al. 2001, Biro et al. 2004, Potatov et al. 2004). Indirect evidence of energy related mortality has also been provided by comparisons of survival of different size groups of freshwater fishes. Due to
a combination of allometric scaling of metabolic rate and the comparable lower ability to store energy for smaller fish, depletion rates of energy stores increase with decreasing size, and for several species, larger individuals are shown to have a higher probability of winter survival than smaller, both in experimental studies under simulated winter conditions (Oliver et al. 1979, Post & Evans 1989, Johnson & Evans 1991) and in field studies of natural populations (Post & Evans 1989, Miranda & Hubbard 1994).

**Effects of ice-cover on aquatic systems**

The predicted changes in winter climate may directly affect the performance of animals, in particular ectothermic animals, in which the rate of physiological processes (metabolism, growth etc.) is strongly influenced by ambient temperature (Wootton 1994). However, changes in climatic conditions are not simply predictable in terms of temperature responses. In addition, indirect effects of temperature increases may severely affect biological processes. Ice conditions are particularly sensitive to small thermal changes. Minor changes in temperature may therefore have a relatively large impact on the biota by inducing freezing or thawing. For example, mild winters leading to ice crust formation are known to restrict access to food resources and lead to increased mortality due to starvation in Arctic ungulates (Solberg et al. 2001, Forchammer et al. 2002) and to decreased winter survival in tundra voles (Aars & Ims 2002). In aquatic ecosystems, variations in ice-cover conditions may have large impact on both individual organisms and ecosystems by dramatically changing important habitat factors such as light and temperature (e.g. Adrian et al. 1999, Quayle et al. 2002).

Snow and ice-cover on watersheds during winter creates a major contrast in habitat characteristics compared to summer conditions, particularly with regard to light. Ice-cover may also provide cover from potential terrestrial predators. Variation in ice-cover conditions
is therefore likely to affect the energy balance of the individuals both directly through light
induced changes in metabolism caused by the effect of melatonin secretion mediated by the
pineal gland when exposed to light (Wendelaar Bonga 1993) and indirectly by affecting the
trade-off between feeding and predation risk (Metcalfe & Thorpe 1992, Bull et al. 1996,
Metcalfe et al. 1999). Surface ice-cover may accordingly be hypothesised to be an important
habitat characteristic in northern aquatic ecosystems, potentially affecting the energy turnover
of aquatic organisms during a season which is expected to be critical for survival, and for
which climate model scenarios predict the largest temperature increases. Historical data
demonstrate a reduction of ice-cover of watersheds on the northern hemisphere during the last
150 years (Magnuson et al. 2000). This decrease corresponds with an increase in air
temperatures. A large body of evidence derived both from historical trends and global climate
model scenarios now points towards a future decline in ice-cover of aquatic habitats in the
northern hemisphere (Magnuson et al. 2000, Blenckner et al. 2002, Yoo & D’Odorico 2002,

Study species

Fishes of the family Salmonidae, Atlantic salmon (Salmo salar), brown trout (Salmo trutta)
and Arctic char (Salvelinus alpinus), were chosen as study species. Teleost fishes commonly
functions as top-predators of freshwater ecosystems of the northern hemisphere, and may be
considered as keystone species (Lampert & Sommer 1997) which may have a large impact on
the composition and functioning of the ecosystem. In addition, salmonid fishes are convenient
research animals because of their value in commercial and recreational fisheries, as well as in
aquaculture. This has led to considerable basic knowledge of their biology. Understanding
how predicted climatic changes will affect different species of salmonid fishes is important
both from a commercial and conservation point of view.
The native distribution range of salmonid fishes span over a broad environmental gradient, from the subtropical regions in Southern Spain to polar areas in Northern Norway and Canada (Klemetsen et al. 2003). Arctic char is the northernmost distributed freshwater fish and extend into the high Arctic whereas Atlantic salmon and brown trout are only distributed as far north as the continent of Europe. In the southern direction, Atlantic salmon and brown trout extend to southern Europe and northern Africa whereas at lower latitudes Arctic char are only found in scattered Alpine locations. Salmonid fishes have a plastic life history and may be anadromous, spending parts of the juvenile phase in freshwater and migrating to sea as adults, or stationary, spending their whole life cycle in freshwater. Whereas Arctic char and brown trout commonly spend their whole life cycle in freshwater and form stationary non-migration populations throughout their distribution range, Atlantic salmon has less flexible life history and almost obligatory migrate to sea after spending one to five years in freshwater.
Aims of the thesis

The aim of the thesis was to investigate how increases in winter temperatures may affect the performance of ectothermic vertebrates in temperate and sub-arctic freshwater ecosystems. Salmonid fishes were used as model organisms and the following questions were asked:

i) Does winter mortality in freshwater fishes depend on the levels of storage energy?

ii) Is there a seasonal variation in the thermal performance of salmonid fishes, and does such variation coincide with local adaptations to annual fluctuations in thermal conditions?

iii) May changes in ice-cover affect the energy turnover of fishes?

iv) Can ice-cover induced changes in the energy budget of individual fish affect their winter survival?

v) Does the effect of ice-cover on the energy turnover and winter survival vary among species and will such interspecific variation concede with adaptations predicted from the distribution range of the species?

vi) Are there intraspecific adaptations to the present latitudinal variation in ice-cover conditions?

Methodological approach

In order to assess the effect of altered environmental variables on individuals and populations, an integrative basis of bioenergetic modelling, laboratory experiments and studies of natural populations were used. Bioenergetic is the study of energy flow in animals and provides a functional framework with a standardized, common energetic currency, suited to link physiological processes with ecological functions. Energy budgets are key elements in
bioenergetics, which describe how energy in food intake is divided among growth processes (somatic growth, storage of energy, growth of reproductive tissue), metabolism, and excretion.

In the present thesis, winter mortality was linked to levels of stored energy by a field study from a northern Atlantic salmon population where population frequency distributions for specific somatic energy were compared among sampling periods. Interspecific differences in seasonal acclimatization were studied by performing common environment experiments on Atlantic salmon and establish models for thermal performance of winter acclimatized fish. These models were then compared to previously published thermal performance models for summer acclimatized salmon. Furthermore, the effect of changes in ice-cover conditions on the energy budget of the individual fish was studied using a series of common environment experiments in both laboratory and semi-natural environment. The latter experiments aimed at testing both interspecific and intraspecific variation in the effect of ice-cover. The results from these experiments were linked to winter mortality using bioenergetic modelling, where the input parameters originated from both field studies and experiments. The purpose of this conceptual modelling was not to provide quantitative predictions, but to demonstrate how environmental induced changes in the energy budget of individual fish may affect populations through the energy dependence of winter survival.
Results in summary

Paper I:

Energy dependence of winter survival (question i) was investigated by sampling juvenile (2 and 3 yr old) Atlantic salmon at monthly intervals throughout three consecutive winters in a Norwegian river located at 70 °N. Energy selective mortality was tested for by comparing the population frequency distributions for specific somatic energy among sampling periods. Changes in the distributions of specific energy, corresponding to a removal of low energy individuals, were observed between several of the sampling periods. By using energetic modelling it was demonstrated that neither metabolic processes nor feeding could be responsible for the observed shifts in the shape of the energy distributions. Negative energy dependent mortality was retained as the most likely explanation for the observations. No changes in mean size of the fish, or in the shape of the size distributions, were apparent among sampling periods, indicating that mortality was linked to levels of storage energy rather than body size per se. Furthermore, the study indicated a critical energy level for survival of juvenile salmon corresponding with the depletion of storage lipids.

Paper II:

The aim was to test for seasonal variation in thermal performance among juvenile Atlantic salmon populations, and if such variation concede with local adaptations to annual fluctuations in thermal conditions (question ii). Thermal performance models for maximum growth and food consumption of winter-acclimatized Atlantic salmon juveniles were established using common environment experiments. The fish were first generation hatchery reared and originated from three Norwegian rivers situated at 59 °N (two rivers) or 70 °N (one river). The established models were then compared to published growth and food consumption models established for summer-acclimatized fish from the same populations.
All populations maintained positive growth and had a substantial energy intake for the whole range of experimental temperatures (1-6 °C). This contrasts growth models based on summer acclimatized Atlantic salmon, where growth and energy intake ceases at approximately 5 °C. The rates of growth and food consumption varied significantly among populations. Winter-acclimatized fish from the northern population had a higher mass-specific growth rate, higher energy intake and higher growth efficiency than the southern populations. The observed differences in winter performance among populations contrasted models developed using summer-acclimatized salmon, where fish from the northern population had the lowest growth efficiency. The experiment provided evidence that thermal performance is seasonal dependent and indicated local adaptation to annual fluctuations in thermal conditions.

**Paper III:**

In order to test if changes in ice-cover may affect the energy turnover of salmonid fishes (question iii), juvenile Atlantic salmon was held under manipulated light conditions in a tank environment and under simulated ice-cover in semi natural stream channels. Light conditions in the laboratory tank environment were adjusted to simulate habitats with ice-cover (24 h darkness) and without ice-cover (6 h natural day length, 18 h darkness). Metabolism, food consumption and energy balance were measured for first generation hatchery reared fish from three populations originating from rivers at 59 °N (two populations) and 70 °N (one population) which varied ice-cover conditions. Thus, we also explored the potential for adaptive variation in responses to altered ice-cover conditions. The fish from the northernmost population was also tested for energetic consequences of ice-cover removal in semi-natural stream channels.
In the laboratory experiments, resting metabolism was on average 30 % lower under simulated ice-cover than under natural day length for all three populations. However, salmon from the northern population grew equally well in dark and light conditions, whereas fish from the southern population grew significantly poorer in the dark and had negative growth efficiency in the dark. Fish from all populations fed more under natural day compared to the dark, and the northern population had higher consumption than the southern population. The relative high growth rate of fish from the northern populations in the dark compared to the southern population was partly due to higher food consumption and partly due to higher growth efficiency.

Under semi-natural conditions, the lack of ice-cover induced strong negative effects on the energy budget. Juveniles held in stream channels with simulated ice-cover lost 23 % less energy than those held in channels with transparent cover. This difference in energy loss was partly (50 %) due to higher food consumption under simulated ice and partly (30 %) due to light induced differences in resting metabolic rate.

Based on the findings of paper I that energetic deficiencies is an important cause of winter mortality, the results of this paper indicated that changes in ice-cover conditions following climatic change may significantly affect winter survival, particularly in northern populations.

**Paper VI:**

The aim paper IV was to test whether the effect of ice-cover on energy turnover demonstrated in paper III differed among salmonid species, and if such variation coincided with the geographical distribution of the species (question iv). Furthermore, it was tested if the changes in energy turnover following ice-cover removal were of a scale that is likely to affect winter
survival (*question v*). Sympatric Arctic char, Atlantic salmon and brown trout originated from a southern watershed located at 59 °N and Arctic char and Atlantic salmon originating from watersheds located at 70 °N where included in the study. The fish used were first generation hatchery reared, and the experimental setup was identical to the one used in paper III. The main input parameters to the energetic model were energy loss rates observed in the semi-natural stream channels and energy thresholds for survival (paper I).

Simulated ice-cover in stream channels reduced energy loss rates in northern populations of Arctic char and Atlantic salmon as well as in southern char, but not in southern population of salmon and brown trout. All groups maintained under simulated ice-cover (darkness) had lower metabolic rates than those held under natural day length irrespective of species or population. Among southern populations, only Arctic char had positive growth in darkness, and growth was poorer in darkness for all species. In contrast, northern Atlantic salmon grew equally well in both light conditions and northern Arctic char grew best in darkness.

The study demonstrated that Arctic char, in accordance with its extreme northern distribution, appeared most sensitive to changes in ice-cover (both populations were affected). However, the intraspecific variation was larger than the interspecific, and northern populations of Atlantic salmon appeared more severely affected than southern populations of Arctic char. Thus, the northern salmonid populations, probably adapted to long winters with ice-cover, may be particularly vulnerable to changes in ice cover conditions.

**Paper V:**

Paper III and IV provided provisional evidence for intraspecific adaptations to the contrasting ice-cover conditions experienced by populations at different latitudes. The aim of the
experiments presented in paper V was to firmly test for adaptive variation of energetic response to reduced ice-cover (question vi). The experimental setup was identical to the experiments presented in Paper III and IV, and the fish used was first generation hatchery reared Atlantic salmon with parents originating from six populations with home rivers located along a climatic gradient (from 59 to 70 °N) ranging from insignificant natural ice-cover (southern populations) to several months of extensive ice-cover (northern populations).

First, we compared growth, food consumption and energy turnover efficiency in a laboratory tank environment manipulating light. No geographical pattern in overall growth rates was apparent. However, whereas all populations reduced growth rates in darkness, the reduction in the three southernmost populations (59 to 60 °N), not experiencing ice-cover in their natural habitat was almost four times as large as the reduction in northern populations (62 to 70 °N) naturally experiencing extensive periods of ice-cover each winter. The differences in light effects on growth of fish from the northern populations in the dark compared to the southern populations were partly due both to a comparable higher consumption and to a comparably higher growth efficiency in the dark.

In correspondence with the results from the laboratory experiments, there was also a genotype to environment interaction for fish held in semi natural stream channels. Atlantic salmon from northern populations held in channels with simulated ice-cover lost less energy than those held in channels with transparent cover, whereas energy loss did not differ between ice-cover treatments in fish from southern populations.

The lack of geographical trends in growth performance per se underlines the contrasting findings of countergradient growth adaptations in previous studies of thermal performance of
ectothermal vertebrates. However, the present study demonstrates that adaptation to secondary environmental effects of temperature changes may be as important as thermal performance when predicting the effect of changing environmental conditions on organisms.

**Discussion**

Based on the questions asked in the introduction, the following main conclusions are drawn:

i) Winter mortality of juvenile Atlantic salmon depended on levels of storage energy, and appeared to follow the depletion of lipid reserves.

ii) Thermal performance differed between winter and summer acclimatized Atlantic salmon and this difference coincided with annual temperature fluctuations in the native river of the fish.

iii) Changes in ice-cover conditions changed the energy turnover of salmon, and thereby affected the energy budget and the speed at which energy levels were reduced during wintertime.

iv) The effect of altered ice-cover conditions on energy turnover differed among species and populations of salmonids.

v) Intraspecific variation in the response to ice-cover changes is likely to originate from local adaptations to different ice-cover conditions experienced by the fish throughout the species’ distribution range.

vi) Changes in ice-cover conditions are likely to affect winter survival of species and populations of the same species differently. Northern populations and species with a northern distribution range, probably adapted to long winters with extensive ice-cover, appear to be particularly vulnerable to changes in winter climate.
The present thesis demonstrated that changes in physiological performance caused by environmental changes may affect winter survival of salmonids. This was achieved by linking mechanisms for winter survival (paper I) with environmental effects on energetic performance (paper IV). Furthermore, both intraspecific variation in seasonal acclimation as well as interspecific and interspecific variations in ice-cover response were addressed (paper II, IV and V). Together, the papers presented in this thesis provide a functional framework for understanding how alternations in winter temperatures and ice-cover conditions may influence the performance and winter survival of salmonid fishes.

A mechanistic understanding for how climate changes affects energy turnover and survival of salmonid fishes during wintertime yields the possibilities for qualitative predictions. Probably resulting from adaptations to local climate adversities, there were large differences in the predicted response between species and populations of the same species. The results presented in paper IV indicate that a removal of ice cover is likely to affect winter survival of Arctic char, Atlantic salmon and brown trout differently. This means that future changes in ice-cover conditions directly may influence species composition. However, a range of biotic interactions are also affected by climate (Kingsolver 1989). If each species respond differently to climate changes, it must be expected that both the species composition, relative abundance and species composition will change. Inevitably, also the number and identity of competitors will change. Such changes in the relative abundance may have cascading effects on other levels of the food chain, which again may feed back on competitive interactions. For example, altered ice-cover conditions may change the outcome of competition among salmonids, and thus indirectly alter the dominance ratios between species. Since these fishes are top-predators in their respective ecosystems, changing the relative dominance of different species may affect rest of the ecosystems through top-down effects (Lampert & Sommer 1997).
The results from the experiments presented in Paper III - IV indicated that Arctic char and Atlantic salmon populations from the north performed relatively better under simulated ice-cover than southern populations, and thus provided suggestive evidence of adaptive variation in ice-cover response among salmonids. This was firmly tested in paper V using six populations of Atlantic salmon from a broad environmental gradient. These experiments demonstrated that northern populations indeed perform relatively better under simulated ice-cover than southern populations, both in laboratory environment and in semi-natural stream channels. This means that removal of ice-cover, due to climate changes or other anthropogenic changes in thermal conditions, is likely to affect winter survival of juvenile Atlantic salmon in northern populations severely, whereas southern populations may remain indifferent. Interesting is also the lack of geographical trends in growth performance per se (Paper V). These results are in agreement with previous studies, which not have found any indication on thermal adaptations or countergradient variation in growth of salmonid fishes (Jonsson et al. 2001, Larson et al. 2005). Paper V thus underlines the contrasting findings of thermal adaptations or countergradient growth in ectothermal vertebrates (c.f. Larson et al. 2005). The present study does, however, demonstrate adaptations to environmental factors closely correlated with thermal conditions, even if thermal adaptations are lacking. Furthermore, in addition to evolutionary changes of the performance function, natural selection may also alter the capacity for thermal performance to be modified by acclimatization (Kingsolver & Huey 1998). Variation in thermal acclimatization between populations of Atlantic salmon was demonstrated in paper II. This variation coincided with the range of thermal fluctuation in the native rivers of the fish, as the largest difference between summer and winter performance models was found in the Northern River Alta, where the span between summer and winter temperatures is the largest.
Adaptive variation in traits determining performance under different climatic conditions means that climatic changes will affect populations differently. However, adaptations also indicates that traits determining performance are evolutionary labile and therefore may be altered by natural selection. This means that predictions from physiological models may not be stable on a temporal scale. In this context, it is a great challenge to predict which traits that are evolutionary labile and which that not are likely to be altered by natural selection. Rapid evolution of adaptive traits may occur in populations exposed to divergent environments (review in Hendry & Kinnison 1999). However, the long term effects of climatic changes will ultimately be determined by the speed at which natural selection are able to change the mean performance of individuals relative to the speed of changes in environmental conditions.

Insight in the ecological and evolutionary mechanisms driving interactions between the environment and organisms is important in order to avoid inaccurate or erroneous predictions of the effect of climatic changes. Performance models provide necessary steps in understanding how large-scale climatic fluctuations affect organism and populations. However, in order to make realistic predictions, a closer integration of physiological performance models with field data on individual physiology and population parameters are probably needed. Also, information on how natural selection can modify the relationship between environment and individual performance are essential. Particularly, it is important to determine which species and populations that can respond rapid enough evolutionary to avoid extinction, and who that can not.
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Inter-and intraspecific variation in sensitivity to changes in ice-cover among salmonid fishes

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Abstract Ice-cover of northern aquatic habitats is declining due to global warming, potentially affecting aquatic organisms and communities. Here, we tested the sensitivity of populations and species to changes in ice-cover, using northern salmonid fishes (Arctic char, Atlantic salmon and brown trout) as model organisms, by a combination of laboratory (manipulating light) and semi-natural experiments (manipulating cover), and a conceptual winter mortality model. In the laboratory environment, southern populations of all species grew poorer in darkness (simulating ice-cover) than under 6 h daylight (simulating no ice-cover). Among southern populations, Arctic char differed from the other species by obtaining positive growth rates in darkness. In contrast, northern Atlantic salmon grew equally well in both light regimes and northern Arctic char grew better in darkness than in light. Correspondingly, simulated ice-cover in semi-natural stream channels reduced energy loss in northern Arctic char and Atlantic salmon as well as in southern Arctic char, but not in southern Atlantic salmon and brown trout. The observed difference in ice-cover effect on energy loss affected modelled mortality. While Arctic char in accordance with its extreme northern distribution appear most sensitive of the three species to changes in ice-cover, the intraspecific variation was larger than the interspecific. Thus, northern salmonid populations experiencing long winters are particularly vulnerable to increased winter mortality when ice-cover is reduced. Our study demonstrated that different species and populations of the same species respond differently to removal of ice cover and that complex community changes may occur as ice conditions changes in a new climate.

Keywords climate change, energy turnover, ice-cover, growth
Introduction

It is now ample evidence that recent climate changes affect biological systems (e.g. Stenseth et al. 2002; Walther et al. 2002). Although the predicted increase in temperatures of the northern hemisphere directly will affect physiological processes, particularly among ectothermic animals, changes in environmental conditions are not predictable simply in terms of temperature responses. Other indirect effects of temperature such as changes in ice conditions, that are particularly sensitive to small thermal changes, may also severely affect ecosystems. Winter is a bottleneck period for many organisms and climatic factors affecting winter survival may have a strong impact on both population dynamics, species composition of the ecosystem and the geographical distribution of individual species (e.g. Post and Stenseth 1998; Beukema et al. 2000; Sæther et al. 2000; Quayle et al. 2002). For example, in terrestrial ecosystems, mild winters leading to ice crust formation may increase mortality in Arctic ungulates (Forchammer et al. 2002; Solberg et al. 2001) and tundra voles (Aars and Ims 2002). In aquatic ecosystems, variation in ice-cover conditions may impact survival of organisms and ecosystem functioning (e.g. Adrian et al. 1999; Quayle et al. 2002; Finstad et al. 2004a).

A future decline in ice-cover of aquatic ecosystems is predicted in the northern hemisphere (e.g. Magnuson et al. 2000; Assel et al. 2003), significantly affecting habitat characteristics by increasing the inflow of light (Finstad et al. 2004a) and by removing shelter providing protection from terrestrial predators. Ice-cover conditions has been shown to influence the energy turnover in Atlantic salmon (Salmo salar), both trough physiological responses to altered light conditions and through altered behaviour (Finstad et al. 2004a). Energy deficiency is likely to be a main source of winter mortality for freshwater fishes in northern areas (e.g. Post et al. 1998; Finstad et al. 2004b; Biro et al. 2005), and the duration of the ice-
covered period is therefore expected to directly influence survival. Although there is an increasing body of correlative evidence for relationships between climatic indicators (such as the North Atlantic Oscillation Index) and species assemblages (e.g. Brown et al. 2001; Loreau et al. 2001; Lekve et al. 2003), they only provide the first steps for predicting effects of climate changes. For realistic predictions a mechanistic understanding is important (Hallet et al. 2004).

Here, we test for inter- and intraspecific variation in the effect of reduced ice-cover on energy turnover and winter survival among salmonid fishes by combining laboratory and semi-natural experiments with a simple winter mortality model. The effect of simulated ice-cover was tested for three different species and five populations of salmonid fishes in common environment experiments using hatchery reared juvenile Atlantic salmon, Arctic char (Salvelinus alpinus) and brown trout (Salmo trutta). These species are distributed throughout a wide geographic area, from southern Europe to the Sub-Arctic. To test for intraspecific variation in the response to ice-cover conditions, we used Arctic char and Atlantic salmon originating from northern Norway (70 °N, 6 months of ice-cover) and Arctic char, Atlantic salmon and brown trout from southern Norway (59 °N, a few days of ice-cover).

**Material and methods**

Experimental site and origin of experimental fish

All experiments were conducted at the NINA Research Station in South-western Norway (59°N) from January to March 2003 (Atlantic salmon from the River Alta, 70°N), January to March 2004 (Atlantic salmon, Arctic char and brown trout from the River Imsa, 59°N) and
January to March 2005 (Arctic char from the River Hals, 70°N). All experiments were conducted using one summer old (0+) first generation hatchery reared juvenile fish. For each laboratory cohort, eggs were collected from a minimum of five females, and fertilized with one male per female. Rearing of eggs and hatching were conducted at the NINA Research Station. Prior to winter acclimatisation the fish were maintained at the same ambient temperatures and light regime. Two months before experimental start-up, the fish were held at gradually declining temperatures and day lengths (≈ 1 °C and one h per week) to simulate the natural autumn conditions, until the final temperature (0.9 °C) and photoperiod (6 h light and 18 h dark) were reached.

Result from the 2003 experiments on the River Alta salmon are previously presented in Finstad et al. (2004a), where also further details on the methodology for the present study are given. Mean weight of fish included in the analyses (g, ± SD) was 15.5 (6.14) for the River Alta Atlantic salmon, 42.0 (7.56) for the River Hals Arctic char and 20.2 (5.01), 18.2 (2.32) and 29.1 (6.14) for the River Imsa Atlantic salmon, Brown trout and Arctic char, respectively. Mass differences were accounted for by mass standardising growth and food consumption rates according to published allometries (e.g. Elliott and Hurley 1997; Elliott and Hurley 1998) or by using mass as covariate (Finstad et al. 2004a) in the statistical analyses.

Metabolism, growth and food consumption in laboratory environment

Metabolism, growth and food consumption were measured in two tank compartments with light conditions simulating ice-cover (darkness) or no ice (6 h light). Temperature was maintained at ≈ 1°C (mean 1.3 ± 0.5 SD) during the metabolic measurements and the growth and food consumption experiments. In natural habitats, ice cover in combination with snow
considerably reduces perceived light levels during wintertime. In order to simulate light conditions experienced by fish under ice cover and without ice during winter, two similar tank compartments were created and light isolated as in a photo lab darkroom. The no-ice treatment received 6 h light (≈ 70 lux) and 18 h dark, while the ice cover condition was simulated by rearing the fish in darkness. Light levels in the laboratory dark treatment resembled light intensity measured under ice-cover with snow on top (Finstad et al. 2004a). Husbandry as well as operation of the respirometer in the ice treatment was conducted using red photo-lab 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 temperature was therefore identical in the two treatments.

Resting metabolic rates (Jobling 1994) were estimated from oxygen consumption of individual fish in respirometry tubes (180 x 50 mm). After one night acclimation in the tubes, three measurements of oxygen consumption were taken for each fish and average metabolic rate calculated (Jobling 1994). The oxycalorific coefficient was set to 13.59 kJ g⁻¹ (Jobling 1994). For each species and population, 15 individuals and one empty chamber (control) were measured in both treatments. To ensure that only inactive fish were included, the 10 fish with the lowest oxygen consumption was used. We used a recycling system as described by Finstad et al. (2004a) in 2003 and a flow through system following the description by Cutts et al. (1998) in 2004 and 2005. Metabolic rates of Atlantic salmon from the southern population were measured in both systems, and while estimated oxygen consumption differed somewhat between methods the effect of light treatment did not (ANCOVA with mass as covariate; method x light, $F_{1,35} = 0.45, p = 0.50$).
For comparison of growth rate and food consumption we used 12 tanks where two replicates of each of the two light regimes were run for each of the six populations. The tanks were 45 × 45 cm and 60 cm deep, had a water flow of 2 l per min and water level 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 the end of the experiment. Oxygen saturation was always close to 100 % during the experiment. All experiments lasted for 48 days and no fish died during the study.

Growth was measured as the standardized mass-specific growth rate (\( \Omega \) %) (Ostrovsky 1995)

\[
\Omega = \frac{M_t^b - M_0^b}{b \cdot t} \cdot 100
\]  

(1)

where \( M_0 \) and \( M_t \) are the respective body mass (g) at the beginning and end of each experiment, \( t \) is the experimental period (days) and \( b \) is the allometric mass exponent for the relation between specific growth rate and body mass fixed at 0.3 (Elliott and Hurley 1997; Larson et al. 2005). The fish were fed to satiation with CsCl enriched granulated fish food (Felleskjøpet, Sandnes, Norway; Cs concentration 14.1 ppm fresh mass, energy value 21.6 kJ g\(^{-1}\) fresh mass) administered from automatic feeders. The Cs in the food was used to estimate energy intake as described in Forseth et al. (2001) and Jonsson et al. (2001), who also give a further description and validation of the method.

Tank effects were tested for and removed according to Underwood (1997) before further analyses. Salmon from the Imsa watercourse was used in experiments both in 2003 and 2004 and we found no between year variation in the effect of light on growth rates (ANOVA; light
x year, $F_{1,116} = 1.73, p = 0.19)$. Due to a distinct bimodal distribution of growth rates within the northern Arctic char (half of the fish in each thank had neutral growth and half of the fish had very high growth rates) only the upper two growth quartiles were used in the statistical comparison between light treatments for this population.

Effects of ice-cover in semi-natural habitat

To study the effect of ice-cover on the energy use and feeding under conditions more similar to the natural environment experienced by wild salmonids during winter, we used outdoor semi-natural stream channels. The experimental set-up consisted of 9 stream channels (485 x 50 cm), with water depth of approximately 30 cm and gravel substrate. Water flow through each channel was 50 l min$^{-1}$. Each stream channel was divided in two equal sized compartments in the longitudinal direction using wood planks. Working with natural-ice-cover was not possible as water at freezing temperatures is logistically difficult to handle in controlled experimental settings. Ice-cover was therefore simulated by covering one compartment of the stream-channel with black light-impermeable material. The remaining was covered with clear plastic to prevent drift of exogenous material into the system while allowing natural daylight. This design also ensured that water temperatures were identical in the two treatments. Day length increased from $\approx 6$ hours at the start of the experiments to $\approx 9$ hours at the end. We used three replicates of each treatment and population with ice-cover effects nested within stream channels and population, except for the 2003 experiments with the River Alta Atlantic salmon, which was run as a pilot study with five replicates (Finstad et al. 2004a). At the beginning of the experiment, ten individually marked (Alcian blue in fins and adipose fin clipping) and weighed (precision: $\pm 0.01$ g) fish were released into each replicate. At the end of the study period, the channels were drained and the fish collected,
killed, weighted and stomach content was removed. The fish were stored at -24 °C before specific energy was determined as described by Finstad et al. (2004c). Mass specific growth rate was determined according to equation (1). Food consumption was estimated by the method of Eggers (1979) as described by Finstad (2005). The study lasted for 31, 54 and 61 days in 2003, 2004 and 2005 respectively. In total, 18 out of 340 fish died during the study.

Different species were not mixed within channels in order to avoid possible confounding effects of olfactory cues, yielding a design with light effect nested within stream channel and species. We were therefore not able to test for ice x species interactions. Mean temperature (±SD) was 2.2 °C (0.8) in 2003, 2.5 °C (0.3) in 2004, and 3.9 °C (0.7) in 2005. These minor differences in temperatures between experiments are not likely to influence the effect of ice cover on the energy balance of the fish. Water was run in the channels for ten weeks prior to the experiments to establish an invertebrate fauna, and prey also drifted with the supply water throughout the experiment. Duration of the experiment was 31 days in 2003, 54 days in 2004 and 33 days in 2005. Individual energy loss rates \( E \) were calculated as

\[
E = J(M_1 - M_0) \tag{2}
\]

where \( M_1 = (M_0 + bQ/100)^{1/b} \) and \( J \) is the mass specific energy \((J \, g^{-1})\).

Modelling winter survival

The effect of changes in ice-cover on winter survival was explored by energetic modelling. Salmonids deplete their energy resources during winter and mortality is linked to a lower threshold of body energy (Biro et al. 2004; Finstad et al. 2004b). Thus, the probability of
survival depends on the amount of storage energy in the autumn, the rate of depletion and the lower energy threshold for survival. We constructed a virtual population \((N = 1000)\) where body energy in autumn was normally distributed with a mean \((\pm \text{SD})\) at 5500 J g\(^{-1}\) \(\pm 275\) (e.g. Berg and Bremsseth 1998, Finstad et al. 2003). Daily change in body energy of individual fish was simulated during a 150 day long winter, using population, species and ice-cover treatment specific depletion rates from the stream channel experiments. Energy depletion rates for salmon and char from the northern populations were scaled to match depletion rates in the southern populations because temperature varied somewhat between years. This will not change the relative difference between ice-cover treatments. The proportion of fish maintaining body energy above 4000 J g\(^{-1}\) (Crossin et al. 2004; Finstad et al. 2004b) was interpreted as the survival rate. The simulation was repeated with the duration of surface ice-cover varying from 0 to 100% of the winter period.

In nature, storage energy in autumn and energy thresholds for survival may vary and model results should therefore only be interpreted qualitatively. However, variation in parameter values for storage energy threshold levels will not change the relative effects of ice-cover on survival except for at very high mortality or very high survival. Our modelling approach is therefore efficient in demonstrating relative differences between populations and species in their sensitivity to altered ice cover conditions.

**Results**

**Metabolism, growth and food consumption in tank environment**

Resting metabolic rate of fish reared in darkness (range 3.7 to 9.8 J g\(^{-1}\) day\(^{-1}\)) was lower than for fish reared in 6 h daylight (range 6.0 to 23.5 J g\(^{-1}\) day\(^{-1}\)) for all species and populations
(ANCOVA with ln mass as covariate, all $F_{1,17} > 6.01$, all $p < 0.025$). However, the effect of light treatment on metabolic rate did not differ between populations (ANCOVA: ln mass, $F_{1,89} = 13.02$, $p < 0.001$; Population, $F_{4,89} = 11.42$, $p < 0.001$; Light, $F_{1,89} = 46.98$, $p < 0.001$; Light x Population, $F_{4,89} = 0.46$, $p = 0.76$).

The effect of light treatment on mass standardised growth rates did however differ between species (Fig. 1) in southern populations (ANOVA: light, $F_{2,114} = 67.54$, $p < 0.001$; species, $F_{2,114} = 119.69$, $p < 0.001$; light x species, $F_{2,114} = 5.59$, $p = 0.005$). Whereas all species retained positive or neutral growth rates in the 6 h light treatment, only Arctic char was able to sustain positive growth in the dark (Fig. 1). In contrast, the difference between species was smaller and marginally insignificant in northern populations (ANOVA: light, $F_{1,76} = 0.92$, $p = 0.34$; species, $F_{1,76} = 0.62$, $p = 0.43$; light x species, $F_{1,76} = 3.61$, $p = 0.061$). The growth response to light treatment differed significantly between southern and northern populations of both Arctic char and Atlantic salmon (ANOVA: population, both $F_{2,76} > 4.93$, $p < 0.029$; light, both $F_{1,76} > 0.34$, $p < 0.56$; population x light, both $F_{1,76} > 6.87$, $p < 0.01$). Whereas southern Atlantic salmon had negative growth rates in the dark treatment, the northern Atlantic salmon population grew equally well in darkness and in light. Furthermore, whereas southern Arctic char grew better in light than in dark, northern Arctic char grew better in darkness than in light.

The effect of light treatment on food consumption differed between species (Fig. 1) both in northern (ANOVA: light, $F_{1,76} = 1.62$, $p = 0.206$; species, $F_{1,76} = 27.99$, $p < 0.001$; light x species, $F_{1,76} = 13.18$, $p = 0.001$) and in southern populations (ANOVA: light, $F_{2,114} = 32.16$, $p < 0.001$; species, $F_{2,114} = 40.96$, $p < 0.001$; light x species, $F_{2,114} = 8.10$, $p = 0.001$). The effect of light treatment on food consumption differed between southern and northern populations of
char (ANOVA: population, $F_{1,76} = 50.37, p < 0.001$; light, $F_{1,76} = 13.67, p < 0.001$; light x population, $F_{1,76} = 18.22, p < 0.001$), but not between salmon populations (ANOVA: population, $F_{1,76} = 38.94, p < 0.001$; light, $F_{1,76} = 35.87, p < 0.001$; population x light, $F_{1,76} = 0.14, p = 0.70$).

Energy loss in semi-natural environment

All fish reared in semi-natural stream channels had negative growth rates and mean energy loss rates ranged from 27 to 10 J g$^{-1}$ day$^{-1}$ (Fig. 2). There were no effects of ice-cover treatment on the energy loss for southern populations of Atlantic salmon and brown trout. In contrast, Arctic char from the southern population had 14% lower energy loss under simulated ice as compared to without ice (10.5 and 12.4 J g$^{-1}$ day$^{-1}$ respectively). Both Atlantic salmon and Arctic char from the northern populations had lower energy loss rates in the ice-cover treatment than without ice-cover and northern Arctic char reduced energy loss with 25% under ice cover compared to without ice (12.8 and 14.8 J g$^{-1}$ day$^{-1}$ respectively) whereas northern Atlantic salmon reduced energy loss rates with 24% under ice cover compared to without ice (21.1 and 27.5 J g$^{-1}$ day$^{-1}$ respectively).

Modelled winter survival

The effect of ice-cover on modelled winter survival differed considerably between both species and between populations of the same species (Fig. 3). The modelled winter survival of northern populations of Arctic char and of Atlantic salmon was significantly reduced by a removal of ice-cover. This illustrates that the observed differences in energy depletion rates between ice-cover treatments in the stream channels was large enough to effect survival for
northern populations. For both northern Arctic char and Atlantic salmon, a decrease in the ice-cover period with 20 % resulted in ca. 10 % lower survival (Fig. 3). Also, the survival rate of the southern Arctic char population decreased rapidly with decreasing duration of the ice-cover period. However, this response was considerably weaker than for northern Arctic char. In contrast, survival rates of southern Atlantic salmon and brown trout was not influenced by changes in ice-cover conditions.

Discussion

Here, we demonstrate that declining ice-cover significantly affect energy turnover in salmonid fishes on a scale that may reduce winter survival considerably. However, there was large intra- and interspecific variation in the response to ice-cover and the intraspecific variation was larger than the interspecific. Whereas northern populations of char and salmon, and the southern population of char were affected negatively by ice-cover removal, southern populations of both salmon and trout did not show any significant response. All fish maintained in constant darkness had lower metabolic rates than fish held on natural day-length but the effect of light did not differ between populations and species. Thus, the difference in energetic response to declining ice-cover between species and populations must be caused by differences in activity metabolism and food acquisition efficiency.

The differences in response to simulated ice are likely to reflect adaptations to longer and darker winter periods in Arctic char as well as in northern populations of Atlantic salmon. Atlantic salmon from the southern population was used both in this and in a previous experiment (Finstad et al. 2004a) and showed similar response to altered light regime in both studies. Replicated experiments with fish from the same population, but using offspring from different parents, therefore supports the assumption that between population differences are
due to adaptive differences and not experimental artefacts, such as between family variation. Although char in accordance with its extreme northern distribution (Klemetsen et al. 2003) appear most sensitive to changes in ice-cover conditions of the three species, care should always be taken when interpreting phenotype-environment correlations as adaptations. Indeed, the better performance of char in the dark may be due to the general superior performance (compared to other salmonids) at low light intensities. Arctic char is known to inhabit deep parts of lakes and find their prey at low ambient light levels (Langeland et al. 1991). However, the parallel intraspecific variation in growth response to light regimes for salmon and char (Fig. 1) points towards adaptations to long winters with ice-cover in northern populations.

Our results indicate that future changes in ice-cover conditions due to global warming are likely to affect the over-winter survival of salmonids. Furthermore, the large differences in sensitivity to ice-cover shown between species illustrate the potential for ice-cover to influencing future species composition. However, other factors associated with climatic changes, such as length of growing season and temperature is likely to affect winter survival through the size dependence of over-winter mortality (e.g. Post et al. 1998; Post and Evans 1989). Such effects are also likely to affect species differently. Also, population and ecosystems responses to altered abiotic factors may depend on the interactions within the biotic components (e.g. Forchhammer and Post 2004). However, the present study demonstrates that altered ice-cover conditions will affect performance and survival of salmonid species differently during a period of the year consider to be a key bottleneck period, and thus, probably directly alter the dominance ratios between species. Teleost fishes are top-predators in northern aquatic ecosystems, and changing the relative dominance of
different species may affect rest of the ecosystems through top-down effects (Lampert and Sommer 1997).

Ice-cover conditions may influence both production and taxonomic composition of aquatic plants and invertebrates (Douglas and Smol 1999). Furthermore, snow and ice conditions appear to have an increasingly dominant role in structuring aquatic ecosystems with increasing latitude (Sorvari et al. 2002, Rühland et al. 2003). Settling and thawing of ice are threshold processes, that when exceeded may initiate abrupt regime shifts in aquatic community composition, as revealed by a recent paleoecological study on algae and invertebrate communities in Arctic lakes (Smol et al. 2005). Using northern salmonid fish species as a model, we have shown that different species and populations of the same species respond differently to changes in ice conditions. Similar variability in response is also expected to occur in other taxonomic groups and complex ecosystem changes may occur as ice-cover conditions changes in a new climate.

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References


Figure legends

**Fig. 1:** Mean (± SE) mass standardized growth (upper panel) and food consumption (lower panel) for Arctic char, Atlantic salmon and brown trout from the southern populations and Arctic char and Atlantic salmon from the northern populations, reared in darkness (black bars) or in 6 h daylight (open bars). *p* values (*t*-test, two sided, d.f. = 18 for northern Arctic char and 38 for all other populations) are given for comparison between light regimes within populations.

**Fig 2:** Mean (± SE) mass standardised (to a 20 g fish) loss of energy in channels with clear plastic (open bars) and with opaque cover (black bars) for Arctic char, Atlantic salmon and brown trout from the southern populations and for Arctic char and Atlantic salmon from the northern populations. *p* values (ANCOVA with mass as covariate) is given for comparisons between ice-cover treatments within species.

**Fig. 3:** Modelled over-winter mortality as a function of duration of the ice-covered period (percent of winter period) based on observed energy depletion rates in different ice-cover treatments in the stream channels for Arctic char from the southern (open circles) and northern population (closed circles), brown trout and Atlantic salmon from the southern populations (open rectangles and open triangles, respectively) and Atlantic salmon from the northern population (closed triangles).
Fig. 1, Finstad and Forseth
Fig. 2, Finstad and Forseth
Fig. 3, Finstad and Forseth
ADAPTATION TO ICE-COVER IN ATLANTIC SALMON SALMO SALAR L.

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Abstract. - We compared the energetic response of juvenile Atlantic salmon *Salmo salar* to simulated ice-cover conditions in tank environment (manipulating light) and in stream channels (manipulating cover). The fish originated from six populations along a climatic gradient (59 – 70 °N) ranging from insignificant natural ice-cover (southern populations) to several months of extensive ice-cover conditions (northern populations). First, we compared growth, food consumption and energy turnover efficiency under simulated ice-cover (darkness) and no ice (natural short, 6 h light, day length) in favourable laboratory tank environments. No geographical pattern in overall growth rates was apparent. However, whereas all populations reduced growth rates in darkness, the reduction in southern populations was almost four times the reduction in northern populations. This population effect was due to higher food consumption and higher growth efficiency in the dark for fish from the northern populations. There was also a corresponding genotype by environment interaction for fish held in semi natural stream channels. Atlantic salmon from northern populations held in channels with simulated ice-cover lost less energy than those held in channels with transparent cover. On the other hand, energy loss did not differ between ice-cover treatments in fish from southern populations. The lack of geographical trends in growth performance in the present study underlines contrasting findings of countergradient growth adaptations in ectothermal vertebrates. However, the present study demonstrate adaptations to environmental factors closely correlated with the organisms thermal niche, even if thermal adaptations *per se* are lacking.

Key words. – Thermal adaptation, countergradient variation, climate changes, thermal performance, growth.
INTRODUCTION

The relationship between animal performance and the environment is often described with performance curves, which are continuous reactions-norms that describe how a trait value may scale 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 conditions, performance curves may vary between populations (Angilletta et al. 2002; Kingsolver and Gomulkiewicz 2003). Thus, for species with wide geographical distributions it is important to identify how environmental and genetic factors interact to shape physiological performance. Two contrasting hypotheses for such adaptations are proposed; co-variation or adaptation to local optima (Levinton 1983) and the countergradient variation hypothesis (defined by Levins 1969; reviewed by Conover and Scultz 1995). The first hypothesis implies that natural selection shift the optimum of the performance function (e.g. growth, metabolic rate, developmental rate) to match the prevailing environment, and assumes that performance in one environment is traded-off against performance in another. The alternative counter-gradient variation hypothesis suggests that populations from hostile environments (low temperature, short season for growth, strong competition) perform better at all environmental conditions than conspecifics from more favourable environments. For example, selection may favour fast-growing genotypes in northern or high altitude populations due to e.g. size-related mortality factors increasing with increasing adversity (Conover and Schultz 1995). A shorter growth season may then be counteracted by a higher growth rate leading to a reduction in observed phenotypic variance across environments.

Somatic growth-rates can have important fitness consequences, are often heritable, and therefore subject to selection (e.g. Roff 1992; Stearns 1992). 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. There is little evidence among vertebrates that the optimal temperature for growth match prevailing environmental temperature, indicating a lack of adaptation to local thermal conditions (covariation). However, counter-gradient variation in growth is being supported by studies on invertebrates and a few species of vertebrates such as Green frog (Berven et al. 1979), Atlantic silverside (Conover and Present 1990), Striped bass (Conover et al. 1997) and growth and digestive performance of Atlantic salmon from Spain and Scotland (Nicieza et al. 1994a; Nicieza et al. 1994b). In contrast, for salmonid fishes, no correlation have been found between thermal conditions in the river of origin and limits for growth, thermal growth optima or maximum growth (Elliott 1994; Jensen et al. 2001; Jonsson et al. 2001; Larson et al. 2005).

This apparent lack of thermal adaptations for growth in salmonides 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 (Ricklefs et al. 1994; Gotthard et al. 1994; Jonsson et al. 1991; Fleming and Einum 1997; Metcalfe and Monaghan 2001). Adaptations to thermal conditions, however, may 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, may severely affect the physiological performance and ecology of animals during critical periods of the year (Forchhammer et al. 2002; Solberg et al. 2001; Aars and Ims 2002; Adrian et al. 1999; Finstad et al. 2004). For salmonids there is suggestive evidence for local intraspecific adaptations to ice-cover conditions (Finstad et al. 2004).
In the present study we report co-variation in juvenile Atlantic salmon between growth and energy turnover and ice-cover condition. The results originate from two series of common environment experiments where we first test for direct effects of ice-cover induced alternations in light conditions on growth, food consumption and energy turnover in favourable laboratory environment. Thereafter, we test for geographical variation in responses by manipulating ice-cover conditions in more adverse semi-natural environment (artificial stream channels).

**MATERIAL AND METHODS**

*Experimental site and fish*

Atlantic salmon (*Salmo salar* L.) commonly spends from one to five years in freshwater prior to migrating to the sea. The native distribution spans a broad environmental gradient from the Mediterranean regions of Southern Spain to sub-arctic areas in Northern Norway. For the present study we used one summer old (0+) first generation hatchery reared juveniles. The parents originating from six rivers along a latitudinal gradient spanning from 59 to 70 °N (Table 1). Juvenile Atlantic salmon inhabits 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 naturally experiencing long periods of ice-cover each winter (three northernmost rivers) and rivers lacking ice-cover completely or only having insignificant periods of ice-cover during wintertime (three southernmost rivers) (Table 1).

All experiments, as well as rearing of eggs and hatching were conducted at the NINA Research Station, Ims, in 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. Prior to winter acclimatisation the fish were
maintained at the same ambient temperatures and light regime. Two months before experimental start-up, the fish were held at gradually declining temperatures and day lengths (1 °C and one h per week) to simulate natural autumn conditions, until the final temperature (≈1 °C) and photoperiod (6 h light and 18 h dark) were reached.

**Growth and food consumption in tank environment**

In order to simulate light-conditions experienced by fish under ice-cover and without ice-cover during winter, two similar tank compartments were created and light isolated as in a photo-lab darkroom. The no-ice treatment received 6 h light (≈ 70 lux) and 18 h dark, while the ice-cover condition was simulated by rearing the fish in darkness. Light levels in the dark treatment were similar to light-levels measured under surface ice with snow cover (see Finstad et al. 2004a). Husbandry was conducted using red photo-lab 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 temperature was therefore the same in the two treatments (≈1 °C). The experimental setup was identical to the one described in Finstad et al. (2004a). Due to logistic constrains the experiments were run in three different years. However, salmon from the Imsa watercourse was used in experiments both in 2003 and 2004 in order to test for consistency in growth rates between years. We were unable to detect any between year variation in the effect of light on mass-specific growth rates (Year, F_{1,116} = 0.38, p = 0.53; Light, F_{1,116} = 19.94, p < 0.001; Light x Year, F_{1,116} = 1.73, p = 0.19).

Using 12 tanks, two replicates of each of the two light regimes were run for each of the six populations. The tanks were 45 × 45 cm and 60 cm deep, had a water flow of 2 l per min and water level 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 the end of the experiment. 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 to satiation with CsCl enriched granulated fish food (Felleskjøpet, Sandnes, Norway; Cs concentration 14.1 ppm fresh mass, energy value 21.6 kJ g⁻¹ fresh mass) administered from automatic feeders. The Cs in the food was used to estimate energy intake (Φ) as described in Forseth et al. (2001) and Jonsson et al. (2001), who also give a further description and validation of the method.

Growth was measured as the standardized mass-specific growth rate (Ω%) (Ostrovsky 1995)

\[
Ω = \frac{M_t^b - M_0^b}{b \cdot t} \cdot 100
\]

(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:

\[
K_G = \frac{J(M_1 - M_0)}{ΦM_0^{0.766}}
\]

(2)
where $M_1 = (M_0^b + b \Omega/100)^{1/b}$, $\Phi$ is the estimated daily energy intake (J g$^{-1}$ day$^{-1}$), and the mass scaling of food consumption was assumed to be similar to the scaling for brown trout (0.766; Elliott and Hurley 1998). $J$ is the mass specific energy (J g$^{-1}$) estimated from the relationship between dry mass proportion ($D_{prop}$) and specific energy (Hartman and Brandt, 1995) established from a sub-sample of the fish ($J = -2847 + 36797 D_{prop}$, p < 0.001, $R^2 = 0.98$, $N = 60$). Specific energy content for the fish in this sub-sample was determined by proximate composition of lipid and proteins as described in Berg and Bremset (1998).

The experimental setup 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 conditions. 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 ANCOVA.

*Ice-cover in semi-natural habitat*

To study the effect of ice-cover on energy use and feeding under conditions more similar to the natural environment experienced by wild salmonids during winter, we used outdoor semi-natural stream channels. The experimental set-up consisted of 9 stream channels (485 x 50 cm), with a water depth of approximately 30 cm and gravel substrate. Water flow through each channel was 50 l min$^{-1}$. Each stream channel was divided in two equal sized compartments in the longitudinal direction using wood planks. Working with natural-ice-cover was not practically possible within our experimental settings. Ice-cover was therefore simulated by covering one compartment of the stream-channel with black light-impermeable plastic. The remaining was covered with clear plastic to prevent drift of exogenous material.
into the system while allowing natural daylight. Although the longitudinal separation of the different stream channels efficiently prevented influx of light into the ice-cover treatment, we were not able to prevent some flux of water between the different compartments. The different populations were therefore not mixed within stream channels in order to prevent between-population interaction effects caused by olifactoral cues. We used three replicates of each treatment and population with ice-cover effects nested within stream-channels and population, except for the 2003 experiments with the Alta River salmon, which was run as a pilot study with five replicates (Finstad et al. 2004a). Daylengths increased from $\approx 6$ h at the start of the experiment to $\approx 9$ h at the end. The outlets of the channels were blocked by a screen to prevent escapes and were cleaned daily. Mean temperature was $2.8 \, ^\circ\text{C}$ during the experimental periods. Water was run in the channels for ten weeks prior to the experiments to permit colonisation of an invertebrate fauna. In addition, drifting invertebrates were naturally introduced with the supply water from a nearby lake throughout the experiments.

At the beginning of the experiment, ten individually marked (Alcian blue in fins and adipose fin clipping) and weighed (precision: $\pm 0.01$ g) fish were released into each replicate. At the end of the study period, the channels were drained and the fish were collected, killed, weighted and had their stomach content removed. The fish were stored at $-24$ °C before specific energy was determined as described above. Mass specific growth-rate was determined according to equation (1). Food consumption was estimated by the method of Eggers (1979) as described by Finstad (2005). The study lasted for 31, 54 and 61 days in 2003, 2004 and 2005 respectively. In total, 18 out of 340 fish died during the study.

The experimental setup was planned with a hierarchical design with ice-cover treatment nested within individual channels (Replicates). Post-hoc pooling of replicates was conducted
in accordance with 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 variable, and ice-cover as factor. Latitude was used as a proxy for ice-cover condition in the native river and introduced into the model as covariate.
RESULTS

Growth and food consumption in tank environment

Mass standardised growth rate varied considerably between populations (Fig. 1 a). We were not able to detect any significant 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. Furthermore, due to this lack of an overall latitudinal effect on growth it was not possible to detect any significant latitude x 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 x light, $F_{1,8} = 0.44, p = 0.53$). However, the mean difference between growth in light and growth in darkness decreased with increasing latitude (Spearman rank correlation, $r = -0.80, p = 0.052$). The overall reduction of growth rates in the dark treatment was almost four times as large in the three southern populations not experiencing ice-cover in their natural habitat compared to the northern populations naturally experiencing extensive periods of ice-cover. 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 river and thereby test for the light x ice-cover interaction using individual fish as dependent variable after removing the effect of between population variations in growth. The nested ANOVA model revealed a highly significant effect of the light x ice-cover condition interaction on mass specific growth rates (Table 2).

Mass standardised food consumption varied considerably between populations and as for growth rates, there was no clear geographical pattern in the mean food consumption of the different populations (Fig. 1 b) (ANCOVA; latitude, $F_{1,8} = 1.79, p = 0.22$; light, $F_{1,8} = 0.31, p = 0.60$; latitude x light, $F_{1,8} = 0.18, p = 0.66$). Fish from all populations had higher consumption in light than in darkness, but there was a clear latitudinal trend in the difference
between consumption in the light and in the dark treatment. Whereas mean food consumption for the southern populations was reduced with almost 50% in the dark treatment, the overall reduction in food consumption for the northern populations held in darkness was only about 10%. Both light and ice-cover gradients, as well as the light x ice-cover interaction significantly affected consumption rates when tested for using consumption from individual fish as dependent variable (Table 2).

Growth efficiency mirrored the ice-cover gradient variation in growth and food consumption. There was no clear geographical pattern in growth efficiency measured as means of populations and ice-cover treatments (Fig. 1 b) (ANCOVA; latitude, $F_{1,8} = 2.94, p = 0.18$; light, $F_{1,8} = 1.49, p = 0.25$; latitude x light, $F_{1,8} = 1.26, p = 0.29$). However, both light and ice-cover gradients, as well as the light x ice-cover interaction significantly affected growth efficiency when tested for using consumption from individual fish as dependent variable in an nested ANOVA model (Table 2).

**Ice-cover in semi-natural habitat**

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 g$^{-1}$ day$^{-1}$ in the two southern populations and from 11.5 to 27.1 g$^{-1}$ day$^{-1}$ in the three northern population (Fig. 2 a). Energy loss rates did not differ between ice-cover treatments in the southern populations. In contrast, northern populations tended to performed better under simulated ice-cover than without. The experiments revealed a genotype-by-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 dependent variable (ANCOVA; latitude, $F_{1,6} = 107.5, p$
< 0.001; ice-cover, $F_{1,6} = 4.66, p < 0.074$; latitude x ice-cover, $F_{1,6} = 5.47, p < 0.058$) (Fig. 2 a). The interaction between population origin and the effect of ice-cover on performance resulted from an increase in the difference between energy loss-rates under ice-cover and without ice-cover with increasing latitude (Fig. 2 b) (Pearson $r = 0.94, p = 0.016$).

Food consumption varied between populations, and ranged from 0.45 to 5.7 J g$^{-1}$ day$^{-1}$. However, we where unable to detect any ice-cover effect or geographical trend in food consumption when measured as 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 x ice-cover, $F_{1,6} = 1.20, p < 0.32$). However, the overall frequency of feeding (fish with food in stomach content at the end of the experiment) increased with increasing latitude (ANCOVA; latitude, $F_{1,6} = 12.31, p = 0.013$; ice-cover, $F_{1,6} = 1.72, p = 0.23$; latitude x ice-cover, $F_{1,6} = 1.71, p < 0.24$), although we did not discover any significant overall effect of ice-cover or any latitude x ice effect on the frequency of fish feeding.
DISCUSSION

Our common environment experiments revealed that the effect of simulated ice-cover differed among Atlantic salmon populations originating from rivers naturally experiencing ice-cover during wintertime and those that do not. Fish from northern populations performed better under simulated ice-cover conditions both in laboratory environment and in semi-natural stream-channels. This suggests that traits determining ice-cover response have a genetic component (Reznick and Travis 1996). In accordance with previous studies of growth-rate adaptations in salmonids (Elliott 1994; Jensen et al. 2000; Jonsson et al. 2001; Larson et al. 2005), we did not find any indications of elevated growth or food consumption rates in northern populations. This further support the lack of co-variation or countergradient variation in growth in this species, particularly since the experimental populations originated from a wide environmental gradient (59 °N to 70 °N) with extensive variation both in the length of the growth season and in environmental adversities.

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 between populations were strong, and are likely to reflect adaptations to local environmental conditions. Replicated experiments with Atlantic salmon from the southern populations (Finstad et al. 2004a and the present study), using offspring from different parents, showed similar response to altered light-regime. This supports the assumption that between-population differences are due to adaptive differences and not experimental artefacts, such as between family variation. Furthermore, this genotype-to-environment interaction was underlined by the latitude of the home river to ice-cover treatment interaction effect on the energetic response of fish held in stream channels. Nevertheless, care should always be taken when interpreting genotype-to-environment correlations as adaptations. The superior
performance of northern salmon in the dark may be caused by correlated environmental factors. However, ice-cover has a profound effect on the energy turnover of juvenile Atlantic salmon (Finstad et al. 2004a) and winter survival in salmonids depends directly on the individual ability to retain critical levels of body energy (Finstad et al. 2004b, Biro et al. 2005). Furthermore, the winter period is regarded a survival bottleneck in temperate freshwater fishes (Cunjak and Therrien 1998; Cunjak et al. 1998) and environmental factors that alter energy turnover during wintertime are therefore likely to be a potent selective force.

Proximate causes for the observed variation in response to alternation of ice-cover conditions in Atlantic salmon are likely to involve a combination of both behavioural and physiological factors. Reduced energy loss rates under cover in stream channels in the northernmost population (River Alta) were explained by lowered metabolic costs in darkness combined with an increased in 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 reduced cover in stream channels between populations are therefore probably linked to differences in behavioural, food acquisition as well as energy turnover efficiency. We did not find any ice-cover or latitudinal effects on food consumption, probably due to the limitations of the method of estimation.

There was clear latitudinal effect on the frequency of the feeding in the stream channels. The frequency of feeding may be used as a proxy on the activity level of the fish, indicating a higher activity in northern populations. An increase in the duration of the winter period will increase the dependence on consumed energy relative to stored (Metcalf and Thorpe 1992; Bull et al. 1996) and our results therefore suggest an adaptive elevation of feeding motivation in order to meet increased energy intake demands for the northern populations. The observed
food consumption was inferior to what previously has been estimated for wild juvenile Atlantic salmon during wintertime (Finstad et al. 2004b; Berg and Bremseth 1998). A relatively higher energy loss in northern populations of salmon may therefore be due to increased activity and low prey densities in the stream channels.

The lack of correlations between growth rates and temperature of environmental adversities in the present study, or in previous studies on thermal adaptations in salmonids (Elliott 1994; Jensen et al. 2000; Jonsson et al. 2001; Larson et al. 2005), contrast findings of countergradient and thermal adaptation in other ectothermal animals. Small differences in realised thermal niche between populations or lack of genetic variation due to phylogenetic constraints have been suggested as an explanation for the similar performance of salmonids at different latitudes (Larsson et al. 2005). The present study demonstrates an adaptation to environmental factors closely correlated with the organisms thermal niche, even if thermal adaptations per se are lacking. The environment-to-genotype correlation with regard to ice-cover conditions indicate that complex interactions with other temperature correlated factors may impose a selective regime on the populations and possible override and disguise simple direct thermal relationships.

ACKNOWLEDGMENT

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Table 1. Latitude of native river, ice-cover indices (- insignificant ice-cover, + long periods with ice-cover) and mean wet mass (± SD) of the fish before the start of the experiments.

<table>
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<th>Ice-cover</th>
<th>Wet mass</th>
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<tr>
<td>Imsa</td>
<td>59.0</td>
<td>-</td>
<td>23.5 (3.4)</td>
</tr>
<tr>
<td>Suldal</td>
<td>59.3</td>
<td>-</td>
<td>19.0 (4.5)</td>
</tr>
<tr>
<td>Lone</td>
<td>60.0</td>
<td>-</td>
<td>6.7 (2.5)</td>
</tr>
<tr>
<td>Gaula</td>
<td>62.3</td>
<td>+</td>
<td>7.6 (2.7)</td>
</tr>
<tr>
<td>Namsen</td>
<td>64.5</td>
<td>+</td>
<td>13.2 (5.8)</td>
</tr>
<tr>
<td>Alta</td>
<td>70.0</td>
<td>+</td>
<td>17.2 (4.8)</td>
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Table 2. Analysis of variance table for geographical position (northern or southern) used as proxy for ice-cover conditions of native river ($IC$), population ($P$) and light treatment ($L$). The main effects of population ($P$) was nested within geographical location ($IC$) and main effects of light ($L$) nested within $P$ and $IC$.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Growth rate</th>
<th></th>
<th>Consumption</th>
<th></th>
<th>Growth efficiency</th>
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<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>p</td>
<td>MS</td>
<td>F</td>
<td>p</td>
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<tr>
<td>$IC$</td>
<td>1</td>
<td>0.31</td>
<td>8.51</td>
<td>0.004</td>
<td>0.25</td>
<td>0.53</td>
<td>0.46</td>
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<tr>
<td>($P(IC)$)</td>
<td>4</td>
<td>2.24</td>
<td>61.19</td>
<td>&lt; 0.001</td>
<td>29.40</td>
<td>61.80</td>
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<td>$L(P(IC))$</td>
<td>1</td>
<td>2.78</td>
<td>75.93</td>
<td>&lt; 0.001</td>
<td>55.14</td>
<td>115.92</td>
<td>&lt; 0.001</td>
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<tr>
<td>$IC \times L$</td>
<td>1</td>
<td>0.95</td>
<td>25.84</td>
<td>&lt; 0.001</td>
<td>14.23</td>
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<td>Residuals</td>
<td>232</td>
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Figure legends

Fig. 1. Mean (± SE) mass-specific growth (a), food consumption (b) and growth efficiency (c) for juvenile Atlantic salmon reared in darkness (black dots) or in 6 h daylight (open dots) plotted against latitude of population origin (proxy for ice cove conditions of home river).

Fig 2. Mean (± SE) mass standardised (to a 20 g fish) loss of energy in stream-channels with clear plastic (open dots) and with opaque cover (black dots) (a), and mean difference in energy loss between the ice-cover and no ice-cover treatments (b) for juvenile Atlantic salmon, plotted against latitude of population origin (proxy for ice-cover conditions of home river).
Figure 1
Figure 2

(a) Energy loss (J g^{-1} day^{-1}) against Latitude.

(b) Ice effect on energy loss (J g^{-1} d^{-1}) against Latitude.
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<td>Annette-Susanne Hoepfner</td>
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<td>Tissue culture techniques in propagation and breeding of Red Raspberry (<em>Rubus idaeus</em> L.)</td>
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<td>Inga Elise Bruteig</td>
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<td>Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers</td>
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<td>Geir Johnsen</td>
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<td>Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses</td>
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<td>Morten Bakken</td>
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<td>Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <em>Vulpes vulpes</em>.</td>
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<td>Arne Moksnes</td>
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<td>Growth and nitrogen status in the moss <em>Dicranum majus</em> Sm. as influenced by nitrogen supply</td>
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<td>Olav Vadstein</td>
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<td>Jan Fredrik Børseth</td>
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<td>Gunnar Henriksen</td>
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<td>Evaluation of rotifer <em>Brachionus plicatilis</em> quality in early first feeding of turbot <em>Scophthalmus maximus</em> L. larvae.</td>
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<td>Per Gustav Thingstad</td>
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<td>Trina Falck Galloway</td>
<td>Muscle development and growth in early life stages of the Atlantic cod (<em>Gadus morhua</em> L.) and Halibut (<em>Hippoglossus hippoglossus</em> L.)</td>
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<td>Hans Martin Hanslin</td>
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<td>Environmental effects on lipid nutrition of farmed Atlantic salmon (Salmo Salar L.) parr and smolt</td>
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<td>2004</td>
<td>Torkild Bakken</td>
<td>Dr. scient</td>
<td>Biology</td>
<td>A revision of Nereidinae (Polychaeta, Nereididae)</td>
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<td>2004</td>
<td>Ingvar Pareliussen</td>
<td>Dr. scient</td>
<td>Biology</td>
<td>Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitanterely Forest Reserve, Madagascar</td>
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<td>2004</td>
<td>Tore Brembu</td>
<td>Dr. scient</td>
<td>Biology</td>
<td>Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in Arabidopsis thaliana</td>
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<td>2004</td>
<td>Liv S. Nilsen</td>
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<td>Biology</td>
<td>Coastal heath vegetation on central Norway; recent past, present state and future possibilities</td>
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2004 Hanne T. Skiri Dr.scient Biology Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens*, *Helicoverpa armigera* and *Helicoverpa assulta*).

2004 Lene Østby Dr.scient Biology Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment.

2004 Emmanuel J. Gerreta Dr. philos Biology The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania.

2004 Linda Dalen Dr.scient Biology Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming.

2004 Lisbeth Mehli Dr.scient Biology Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria x ananassa*); characterisation and induction of the gene following fruit infection by *Botrytis cinerea*.

2004 Børge Moe Dr.scient Biology Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage.

2005 Matilde Skogen Chauton Dr.scient Biology Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples.

2005 Sten Karlsson Dr.scient Biology Dynamics of Genetic Polymorphisms.

2005 Terje Bongard Dr.scient Biology Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period.

2005 Tonette Rastelien Dr.scient Biology Functional characterisation of olfactory receptor neurone types in heliothine moths.

2005 Erland Kristiansen Dr.scient Biology Studies on antifreeze proteins.

2005 Eugen G. Sørmo Dr.scient Biology Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyroid hormone and vitamin A concentrations.

2005 Christian Westad Dr.scient Biology Motor control of the upper trapezius.

2005 Lasse Mork Olsen Dr.scient Biology Interactions between marine osmo- and phagotrophs in different physicochemical environments.

2005 Åslaug Viken Dr.scient Biology Implications of mate choice for the management of small populations.

2005 Ariaya Hymete Sahle Dingle Dr. scient Biology Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia.