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**Salmonid fishes in a
changing climate:
The winter challenge**

Doctoral thesis
for the degree of Philosophiae Doctor

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Norwegian University of Science and Technology
Faculty of Natural Sciences and Technology
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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:

- I. Finstad, A.G., Ugedal, O., Forseth, T. & Næsje, T. 2004. Energy related juvenile winter mortality in a northern population of Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*. 61: 2358-2368.
- II. Finstad, A.G., Næsje, T.F. & Forseth, T. 2004. Seasonal acclimatization of thermal performance in juvenile Atlantic salmon (*Salmo salar* L.). *Freshwater Ecology* 49: 1459-1467.
- III. Finstad, A.G., Forseth, T., Næsje, T.F. & Ugedal, O. 2004. The importance of ice-cover for energy turnover in juvenile Atlantic salmon. *Journal of Animal Ecology* 73: 959-966.
- 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 (MacArthur & 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 & Cavalieri 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, Forchhammer 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 (Metcalf & 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, Parkinson & Cavalieri 2002, Assel et al. 2003).

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 function 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 ectothermal 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 coincide 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 were 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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Paper I

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Paper IV

**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 (Forchhammer 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 through 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, \pm 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 (Ω %) (Ostrovsky 1995)

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

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 tank 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 ≈ 6 hours at the start of the experiments to ≈ 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: $\pm 0.01 \text{ g}$) 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 (\pm 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

$$E = J(M_1 - M_0) \quad (2)$$

where $M_1 = (M_0^b + b\Omega/100)^{1/b}$ 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 SD) at $5500 \text{ J g}^{-1} \pm 275$ (e.g. Berg and Bremseth 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 $9.8 \text{ J g}^{-1} \text{ day}^{-1}$) was lower than for fish reared in 6 h daylight (range 6.0 to $23.5 \text{ J g}^{-1} \text{ day}^{-1}$) 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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Figure legends

Fig. 1: Mean (\pm SE) mass standardized growth (upper pannel) 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 (\pm 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).

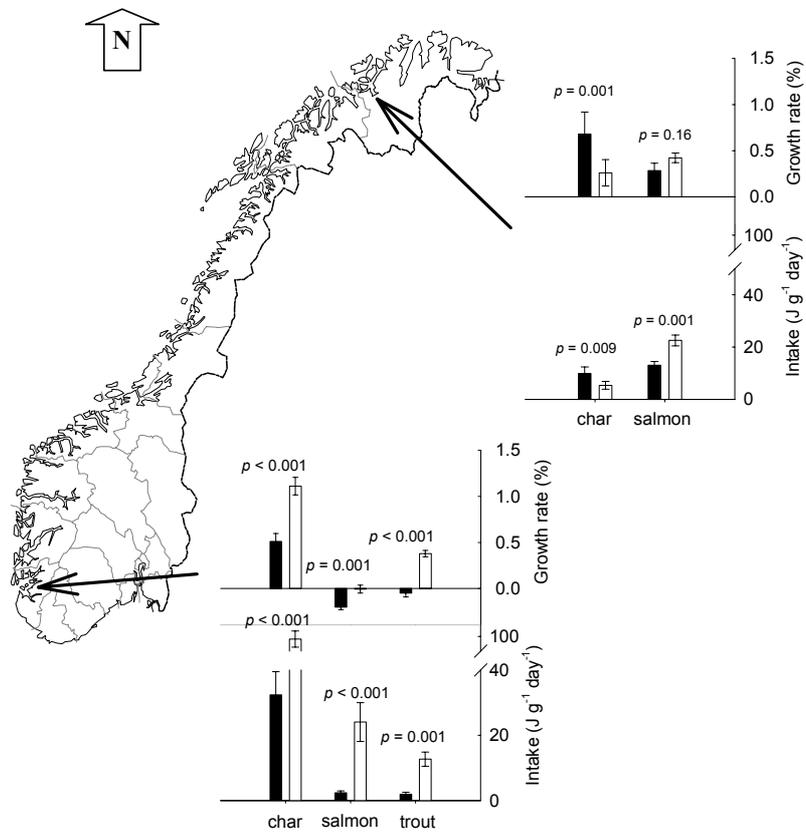


Fig. 1, Finstad and Forseth

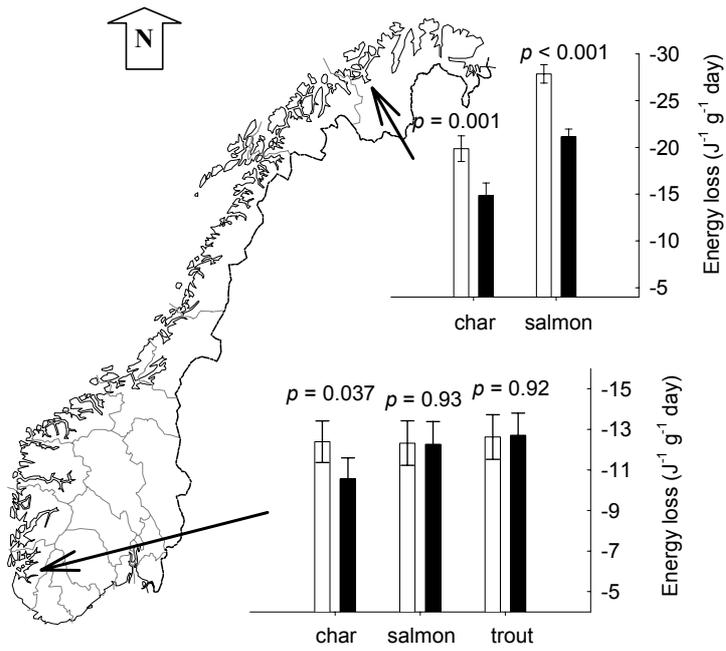


Fig. 2, Finstad and Forseth

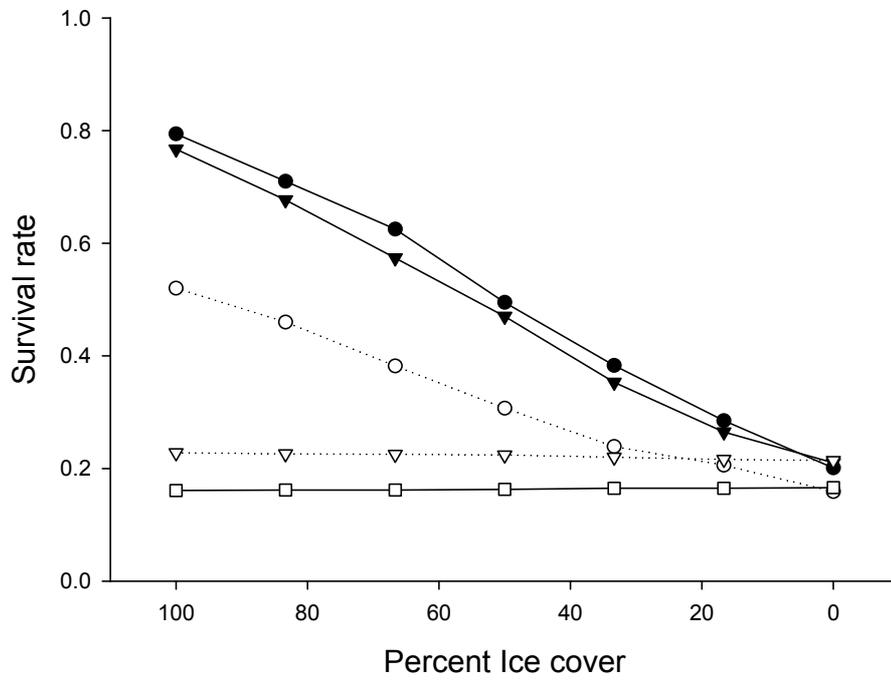


Fig. 3, Finstad and Forseth

Paper V

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 Schultz 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 (co-variation). 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 constraints 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 ($\Omega\%$) (Ostrovsky 1995)

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

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

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

where $M_I = (M_0^b + b\Omega/100)^{1/b}$, Φ is the estimated daily energy intake ($\text{J g}^{-1} \text{day}^{-1}$), 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 ($J = -2847 + 36797D_{prop}$, $p < 0.001$, $R^2 = 0.98$, $N = 60$). 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 ≈ 6 h at the start of the experiment to ≈ 9 h at the end. The outlets of the channels were blocked by a screen to prevent escapes and were cleaned daily. Mean temperature was 2.8 °C during the experimental periods. Water was run in the channels for 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: ± 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 a 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 were 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 (Metcalfé 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.

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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 (\pm SD) of the fish before the start of the experiments.

Population	Latitude	Ice-cover	Wet mass
Imsa	59.0	-	23.5 (3.4)
Suldal	59.3	-	19.0 (4.5)
Lone	60.0	-	6.7 (2.5)
Gaula	62.3	+	7.6 (2.7)
Namsen	64.5	+	13.2 (5.8)
Alta	70.0	+	17.2 (4.8)

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*

Source	df	Growth rate			Consumption			Growth efficiency		
		MS	F	p	MS	F	p	MS	F	p
<i>IC</i>	1	0.31	8.51	0.004	0.25	0.53	0.46	186.5	4.532	0.034
<i>(P(IC))</i>	4	2.24	61.19	<0.001	29.40	61.80	<0.001	788.4	19.163	<0.001
<i>L(P(IC))</i>	1	2.78	75.93	<0.001	55.14	115.92	<0.001	938.4	22.811	<0.001
<i>IC x L</i>	1	0.95	25.84	<0.001	14.23	29.92	<0.001	731.8	17.79	<0.001
Residuals	232	0.04			0.48			41.1		

Figure legends

Fig. 1. Mean (\pm 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 (\pm 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).

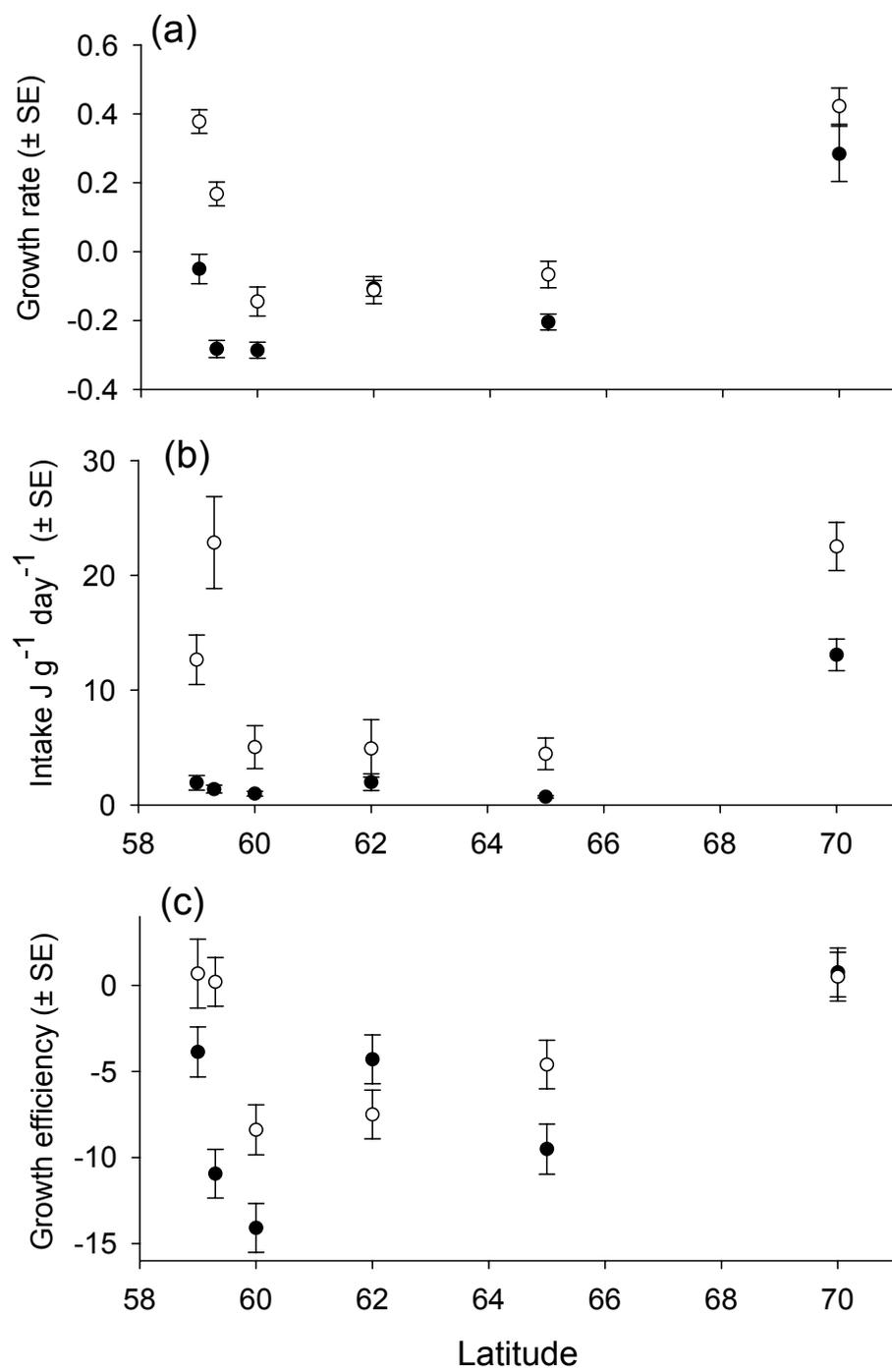


Figure 1

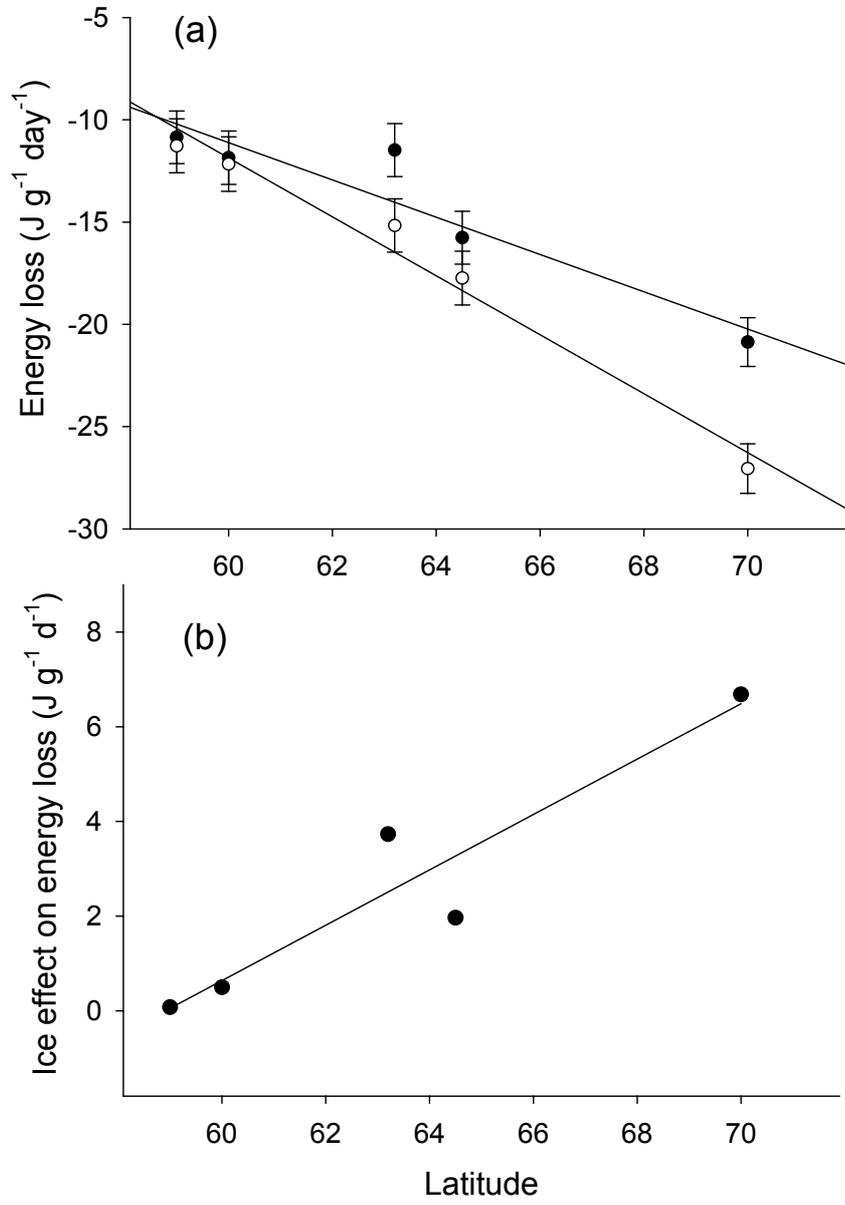


Figure 2

Doctoral theses in Biology
Norwegian University of Science and Technology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos. Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr. philos. Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos. Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient. Botany	Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i>
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympatric species of newts (<i>Triturus</i> , <i>Amphibia</i>) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook <i>Corvus frugilegus</i> .
1984	Anne Margrethe Cameron	Dr. scient. Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient. Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (<i>Trichoptera</i>) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.
1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit <i>Parus montanus</i> .
1987	Jarle Inge Holten	Dr. philos. Bothany	Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient. Botany	Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i>
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.

- 1988 Hans Christian Pedersen Dr. philos. Zoology Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
- 1988 Tor G. Heggberget Dr. philos. Zoology Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
- 1988 Marianne V. Nielsen Dr. scient. Zoology The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
- 1988 Ole Kristian Berg Dr. scient. Zoology L. The formation of landlocked Atlantic salmon (*Salmo salar* L.).
- 1989 John W. Jensen Dr. philos. Zoology Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
- 1989 Helga J. Vivås Dr. scient. Zoology Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
- 1989 Reidar Andersen Dr. scient. Zoology Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
- 1989 Kurt Ingar Draget Dr. scient. Botany Alginate gel media for plant tissue culture,
- 1990 Bengt Finstad Dr. scient. Zoology Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
- 1990 Hege Johannesen Dr. scient. Zoology Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
- 1990 Åse Krøkje Dr. scient. Botany The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
- 1990 Arne Johan Jensen Dr. philos. Zoology Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
- 1990 Tor Jørgen Almaas Dr. scient. Zoology Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
- 1990 Magne Husby Dr. scient. Zoology Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
- 1991 Tor Kvam Dr. scient. Zoology Population biology of the European lynx (*Lynx lynx*) in Norway.
- 1991 Jan Henning L'Abée Lund Dr. philos. Zoology Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.
- 1991 Asbjørn Moen Dr. philos. Botany The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
- 1991 Else Marie Løbersli Dr. scient. Botany Soil acidification and metal uptake in plants
- 1991 Trond Nordtug Dr. scient. Zoology Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods.
- 1991 Thyra Solem Dr. scient. Botany Age, origin and development of blanket mires in Central Norway
- 1991 Odd Terje Sandlund Dr. philos. Zoology The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
- 1991 Nina Jonsson Dr. philos. Aspects of migration and spawning in salmonids.

1991 Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992 Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992 Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (<i>Phleum pratense</i> L.)
1992 Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i>
1992 Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992 Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993 Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O ⁶ -methylguanine-DNA methyltransferase in mammalian cells
1993 Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993 Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects.
1993 Bård Pedersen	Dr. scient Botany	Theoretical studies of life history evolution in modular and clonal organisms
1993 Ole Petter Thangstad	Dr. scient Botany	Molecular studies of myrosinase in Brassicaceae
1993 Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> .
1993 Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993 Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
1994 Peder Fiske	Dr. scient. Zoology	Sexual selection in the lekking great snipe (<i>Gallinago media</i>): Male mating success and female behaviour at the lek.
1994 Torbjørn Forseth	Dr. scient. Zoology	Bioenergetics in ecological and life history studies of fishes.
1994 Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
1994 Nils Røv	Dr. scient. Zoology	Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i> .
1994 Annette-Susanne Hoepfner	Dr. scient Botany	Tissue culture techniques in propagation and breeding of Red Raspberry (<i>Rubus idaeus</i> L.)
1994 Inga Elise Bruteig	Dr. scient Bothany	Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers
1994 Geir Johnsen	Dr. scient Botany	Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses
1994 Morten Bakken	Dr. scient. Zoology	Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i> .
1994 Arne Moksnes	Dr. philos. Zoology	Host adaptations towards brood parasitism by the Cuckoo.

1994 Solveig Bakken	Dr. scient Bothany	Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply
1995 Olav Vadstein	Dr. philos Botany	The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions.
1995 Hanne Christensen	Dr. scient. Zoology	Determinants of Otter <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i> .
1995 Svein Håkon Lorentsen	Dr. scient. Zoology	Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition.
1995 Chris Jørgen Jensen	Dr. scient. Zoology	The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity
1995 Martha Kold Bakkevig	Dr. scient. Zoology	The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport.
1995 Vidar Moen	Dr. scient. Zoology	Distribution patterns and adaptations to light in newly introduced populations of <i>Mysis relicta</i> and constraints on Cladoceran and Char populations.
1995 Hans Haavardsholm Blom	Dr. philos Bothany	A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden.
1996 Jorun Skjærmo	Dr. scient Botany	Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae.
1996 Ola Ugedal	Dr. scient. Zoology	Radiocesium turnover in freshwater fishes
1996 Ingibjörg Einarisdóttir	Dr. scient. Zoology	Production of Atlantic salmon (<i>Salmo salar</i>) and Arctic charr (<i>Salvelinus alpinus</i>): A study of some physiological and immunological responses to rearing routines.
1996 Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996 Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics.
1996 Gunnar Henriksen	Dr. scient. Zoology	Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region.
1997 Gunvor Øie	Dr. scient Bothany	Eevaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae.
1997 Håkon Holien	Dr. scient Botany	Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters.
1997 Ole Reitan	Dr. scient. Zoology	Responses of birds to habitat disturbance due to damming.
1997 Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
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Zoology neurons in the pine weevil (*Hylobius abietis*), analysed by
gas chromatography linked to electrophysiology and to mass
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Solberg Zoology Norwegian moose (*Alces alces*) population: consequences of
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Saastad Botany the Sphagnum recurvum complex (Bryophyta): genetic
variation and phenotypic plasticity.
- 1998 Bjarte Mortensen Dr. scient. Metabolism of volatile organic chemicals (VOCs) in a head
Botany liver S9 vial equilibration system in vitro.
- 1998 Gunnar Austrheim Dr. scient. Plant biodiversity and land use in subalpine grasslands. – A
Botany conservation biological approach.
- 1998 Bente Gunnveig Dr. scient. Encoding of pheromone information in two related moth
Berg Zoology species
- 1999 Kristian Dr. scient. Behavioural and morphological characteristics in Northern
Overskaug Zoology Tawny Owls *Strix aluco*: An intra- and interspecific
comparative approach
- 1999 Hans Kristen Dr. scient. Genetic studies of evolutionary processes in various
Stenøien Bothany populations of nonvascular plants (mosses, liverworts and
hornworts)
- 1999 Trond Arnesen Dr. scient. Vegetation dynamics following trampling and burning in the
Botany outlying haylands at Sølendet, Central Norway.
- 1999 Ingvar Stenberg Dr. scient. Habitat selection, reproduction and survival in the White-
Zoology backed Woodpecker *Dendrocopos leucotos*
- 1999 Stein Olle Dr. scient. A study of driftwood dispersal to the Nordic Seas by
Johansen Botany dendrochronology and wood anatomical analysis.
- 1999 Trina Falck Dr. scient. Muscle development and growth in early life stages of the
Galloway Zoology Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus*
hippoglossus L.)

1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (<i>Micromisistius poutassou</i>), haddock (<i>Melanogrammus aeglefinus</i>) and cod (<i>Gradus morhua</i>) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient. Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lokeus</i> .
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (<i>Salmo salar</i>) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient. Botany	The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (<i>Luscinia s. svecica</i>)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (<i>Salmo salar</i> L.) and Brown trout (<i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions
1999	Frode Ødegaard	Dr. scient. Zoology	Host specificity as parameter in estimates of arthropod species richness
1999	Sonja Andersen	Dr. scient. Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000	Ingrid Salvesen, I	Dr. scient. Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000	Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (<i>Cuculus canorus</i>) and its host: adaptations and counteradaptations in a coevolutionary arms race
2000	Pavlos Makridis	Dr. scient. Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000	Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (<i>Loxodonta africana</i>)
2000	Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (<i>Salvelinus alpinus</i>), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000	Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (<i>Salmo trutta</i>) in two mining-contaminated rivers in Central Norway
2000	Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001	Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species
2001	Olga Hilmo	Dr. scient. Botany	Lichen response to environmental changes in the managed boreal forest systems
2001	Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (<i>Symphodus melops</i> L.)
2001	Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts

2002 Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>)
2002 Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002 Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002 Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (<i>Castor fiber</i>)
2002 Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A ₂ in Monocytes During Atherosclerosis Development
2002 Terje Thun	Dr. philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002 Birgit Hafjeld Borgen	Dr. scient	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002 Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002 Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and
2002 Henrik Jensen	Dr. scient Biology	Causes and consequences of individual variation in fitness-related traits in house sparrows
2003 Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003 Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatus</i> L.
2003 Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003 Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
2003 Cyril Lebogang Taolo	Dr. scient Biology	Population ecology, seasonal movement and habitat use of the African buffalo (<i>Syncerus caffer</i>) in Chobe National Park, Botswana
2003 Marit Stranden	Dr.scient Biology	Olfactory receptor neurones specified for the same odorants in three related Heliothine species (<i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i>)
2003 Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i>
2003 David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments
2003 Åsa A Borg	Dr.scient Biology	Sex roles and reproductive behaviour in gobies and guppies: a female perspective
2003 Eldar Åsgard Bendiksen	Dr.scient Biology	Environmental effects on lipid nutrition of farmed Atlantic salmon (<i>Salmo Salar</i> L.) parr and smolt
2004 Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004 Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004 Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i>
2004 Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities

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 (<i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i>).
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 (<i>Fragaria x ananassa</i>): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i>
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 Røstelién	Dr.scient Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005 Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005 Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (<i>Halichoerus grypus</i>) pups and their impact on plasma thyrid 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 <i>Echinops</i> spp. growing in Ethiopia