



Adaptations to ice-cover conditions in salmonid fishes

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Here, I review a series of experiments from laboratory environment and in seminatural stream-channels where the effects of ice-cover conditions on salmonid winter performance are tested. The experiments were run using common environment on six different populations (hatchery reared fish) of Atlantic salmon from 59 °N to 70 °N, two populations of Arctic char (59 °N and 70 °N), and one population of brown trout (59 °N). Intraspecific variation in ice-cover response of Atlantic salmon indicated adaptations to ice-cover conditions in home rivers. Growth of the three southern populations from ice free rivers was significantly higher in tanks with light than in darkness, whereas the northern populations originating from rivers with ice-cover showed smaller or insignificant differences in growth between light and darkness. A similar pattern was found for food consumption. In stream channels, northern populations performed better under simulated ice-cover than without, whereas southern populations remained indifferent to ice-cover treatment. The differences in energy loss with and without simulated ice-cover increased significantly with increasing latitude of population origin. Intraspecific variation in ice-cover response was larger than the interspecific. Both northern and southern Arctic char reduced energy-loss rates under simulated ice-cover compared to no ice-cover in stream channels, whereas southern populations of Atlantic salmon and brown trout remained indifferent to ice-cover treatment. Because energetic deficiencies are assumed to be an important cause of winter mortality, our study indicates that lack of ice cover significantly may affect winter survival, particularly in northern populations. However, changes in ice-cover conditions are likely to affect different populations and species of salmonid fishes differently and the scope for evolutionary response to changes in ice-cover conditions may vary between species.

1. Introduction

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). The ability of species to occupy a given environment may in many cases be determined by seasonal energetic bottlenecks (Weiner 1992). Wintertime is a bottleneck for many animals living in temperate and arctic region. Some animals migrate to other climatic zones or overwinter in a state of hibernation. For animals overwintering in 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). It follows that energy deficiency is suggested as a main source of winter mortality for many northern distributed fish species (e.g. Johnson & Evans 1991, Biro et al. 2004, Finstad et al. 2004a). Indirect evidence of energy related mortality has also been provided by comparisons of survival of different size groups. Due to a combination of allometric scaling of metabolic rate and the comparable lower ability to store energy for smaller fish, energy depletion rates decrease with increasing size. For several species, larger individuals have higher probability of winter survival than smaller (Post & Evans 1989, Miranda & Hubbard 1994).

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 will therefore affect the energy balance of the individual 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; Finstad et al. 2004b) and indirectly by affecting the trade-off between feeding and predation risk (Metcalfe & Thorpe 1992, Bull et al. 1996, Metcalfe et al. 1999; Finstad et al. 2004b). Surface ice-cover is accordingly 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). Global warming issues, and also on a more local scale, hydropower regulations, makes the studies of biological effects of changed river ice-processes both timely and important.

In this paper, I review a series of experiments that test for effects of ice-cover on the energy balance of salmonid fishes (Finstad et al. 2004, Finstad 2005, Finstad & Forseth 2006). The following questions form the basis for the experiments: i) Will changes in ice-cover affect the energy turnover of fishes? ii) Does the effect of ice-cover on the energy turnover and winter survival vary among species and will such interspecific variation concede with adaptations

predicted from the distribution range of the species? iii) Are there intraspecific adaptations to the present latitudinal variation in ice-cover conditions?

2. Methodological approach

In order to assess the effect of altered environmental variables on individuals and populations, bioenergetic modeling and laboratory experiments 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.

The effect of changes in ice-cover conditions on the energy budget of the individual fish was studied using common environment experiments in both laboratory and semi-natural environment. Both interspecific and intraspecific variation in the effect of ice-cover was tested using fish reared in common environment (i.e. sorting out the genetic basis for the response). 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 modeling 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.

3. Results and discussion

3.1. Effects of ice-cover on Atlantic salmon

In order to test if changes in ice-cover may affect the energy turnover of salmonid fishes, juvenile Atlantic salmon was held under manipulated light conditions in a tank environment and under simulated ice-cover in semi natural stream channels (Finstad et al. 2004b). 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. 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 (Fig. 1). 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 (Fig. 2).

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 (Fig 3).

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

3.2 Intraspecific variation in ice-cover response

In order to test if the demonstrated effect of ice-cover on energy turnover differed among salmonid species, and if such variation coincides with the species geographical distribution, experiments were run with Atlantic salmon, Arctic char and brown trout (Finstad 2005). 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. Sympatric Arctic char, Atlantic salmon and brown trout originated from a southern watershed located at 59 °N and Arctic char and Atlantic salmon originating from watersheds located at 70 °N where included in the study. The fish used were first generation hatchery reared, and the experimental setup was identical to the one used in Finstad et al. (2004) review in the previous paragraph.

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. The effect of changes in ice-cover on winter survival was explored by energetic modeling. 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.* 2004a). 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 s.d.) at $5500 \text{ J g}^{-1} \pm 275$ (e.g. Berg & 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. The observed differences in energy depletion rates between ice-cover treatments in the stream channels had large effect on the modeled winter survival for the northern populations of char and salmon, and a 20 % increase in the ice-cover period resulted in ca. 10 % higher survival (Fig. 4). Likewise, the survival rate of the southern char population increased rapidly with increasing duration of the ice-cover, but the response was weaker than for northern char. In contrast, survival rates of southern salmon and trout was not influenced by changes in ice-cover conditions

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.

3.3. Adaptive variation in ice-cover response

The previous two studies provided provisional evidence for intraspecific adaptations to the contrasting ice-cover conditions experienced by populations at different latitudes. The aim of the the last series of experiments (Finstad & Forseth 2006) was to firmly test for adaptive variation of energetic response to reduced ice-cover. The experimental setup was identical to the previously presented experiments. 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 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 (Fig. 5). 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.

3.4. Conclusion

A mechanistic understanding for how changes in ice-cover affects energy turnover and survival of salmonid fishes during wintertime yields the possibilities for qualitative predictions. Probably resulting from adaptations to local ice conditions, there were large differences in the predicted response between species and populations of the same species. Removal of ice cover is also 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, biotic interactions are may also be affected. If each species respond differently, 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).

Northern populations of Arctic char and Atlantic salmon performed relatively worse without simulated ice-cover than southern populations. This means that removal of ice-cover, due to climate changes or other anthropogenic changes in thermal conditions (e.g. hydropower regulation), is likely to affect winter survival of northern salmonid populations severely, whereas southern populations may remain indifferent.

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.

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Figure legends:

Fig. 1: Mean (\pm SE) resting metabolism ($\text{J g}^{-1} \text{d}^{-1}$) for the River Alta (70 °N), Suldal and Imsa (59 °N) populations reared in darkness (black bars) or 6 h light (open bars) at 1.3 °C. (Figure redrawn from Finstad et al. 2004b)

Fig. 2: Mean (\pm SE) mass-specific growth (A), food consumption (B) and growth efficiency (C) for the River Alta (70 °N), Suldal and Imsa (59 °N) populations reared in darkness (black bars) or in 6 h daylight (open bars). *p* values (*t*-test, two sided) are given for comparison between light regimes within populations ($N = 40$). (Figure redrawn from Finstad et al. 2004b)

Fig. 3: Mean mass specific energy loss and mean mass specific energy intake (\pm SE) for the River Alta (70 °N) juvenile salmon reared in semi-natural stream channels with opaque cover simulating ice (black bars) and in channels with clear cover simulating no ice (open bars).

Fig. 4: Modeled 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 char from the southern- (open circles) and northern population (closed circles), trout and salmon from the southern populations (open rectangles and open triangles, respectively) and salmon from the northern population (closed triangles).

Fig 5: Mean (\pm SE) mass standardised (to a 20 g fish) loss of energy in stream-channels with simulated ice-cover (open dots) and without (black dots) (a), and mean difference in energy loss between the ice-cover and no ice-cover treatments (b) for juvenile Atlantic salmon from five populations, plotted against latitude of population origin (proxy for ice-cover conditions of home river). (Figure redrawn from Finstad & Forseth 2006).

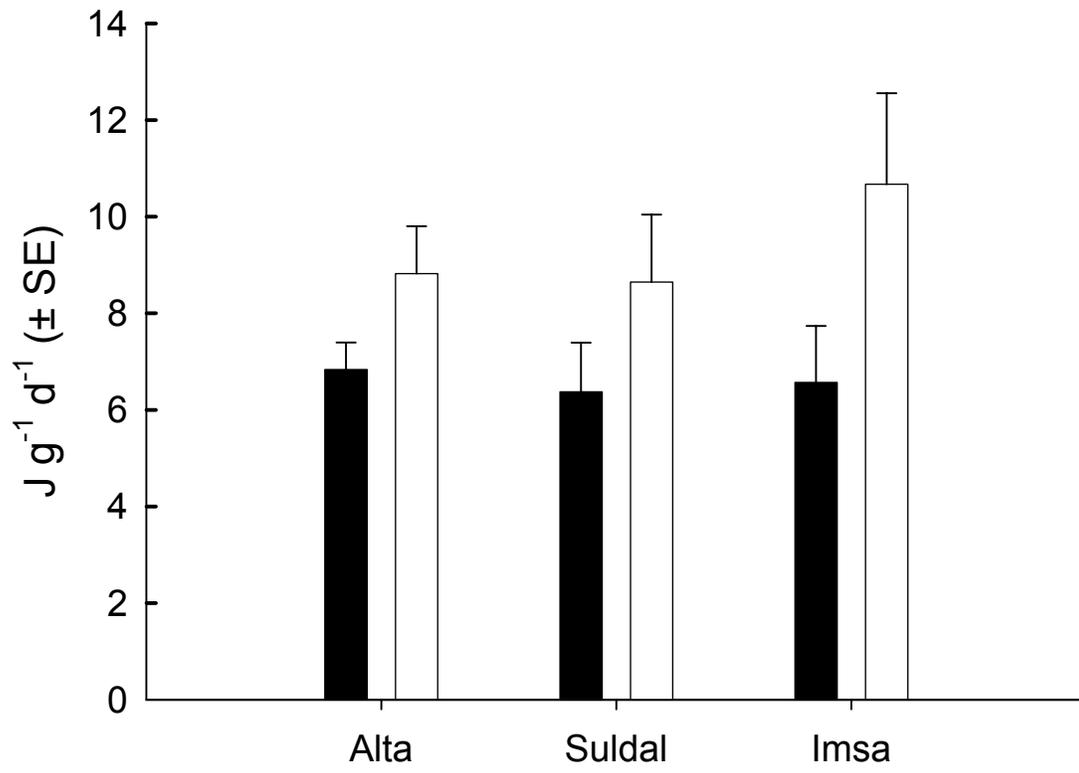


Fig. 1.

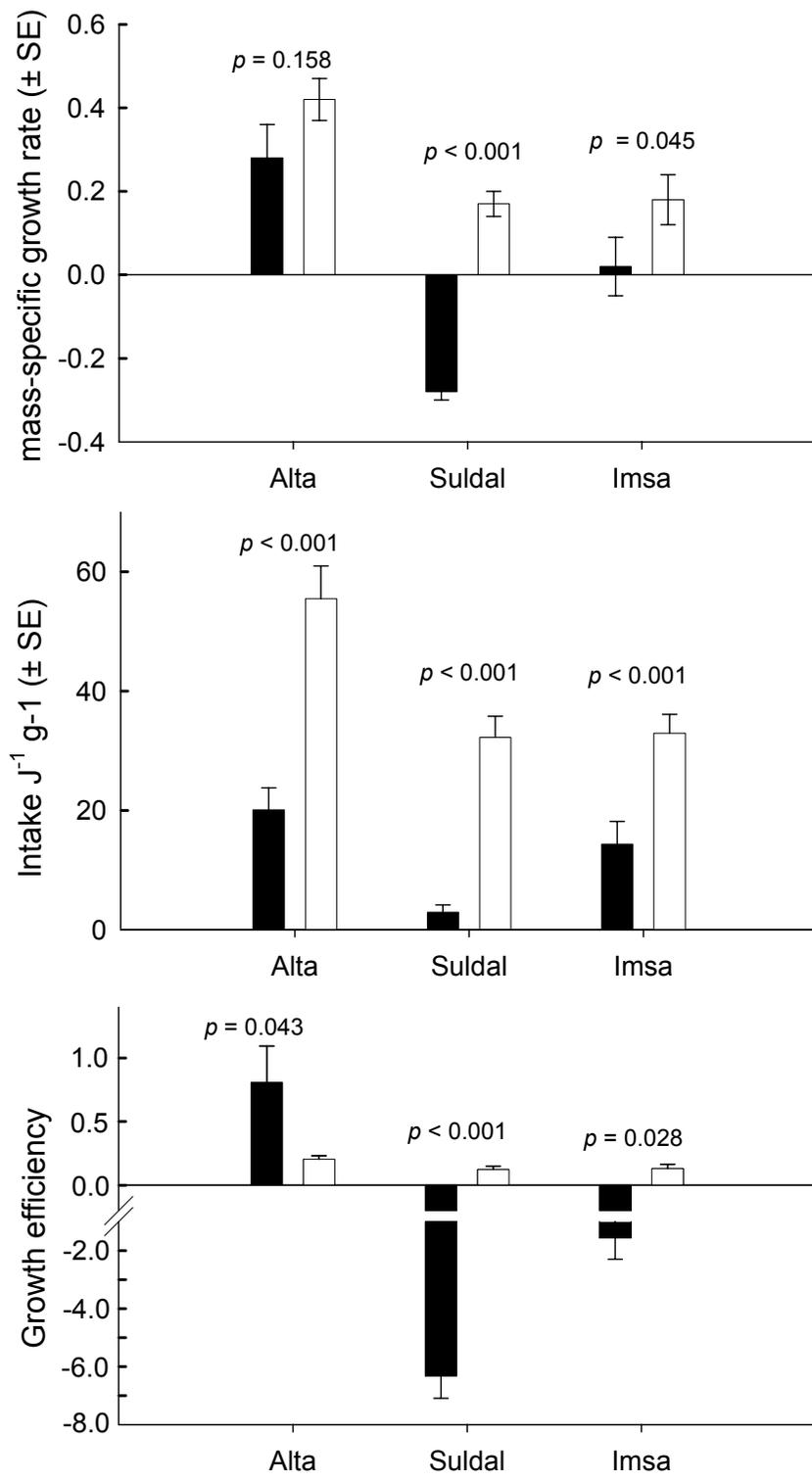


Fig. 2.

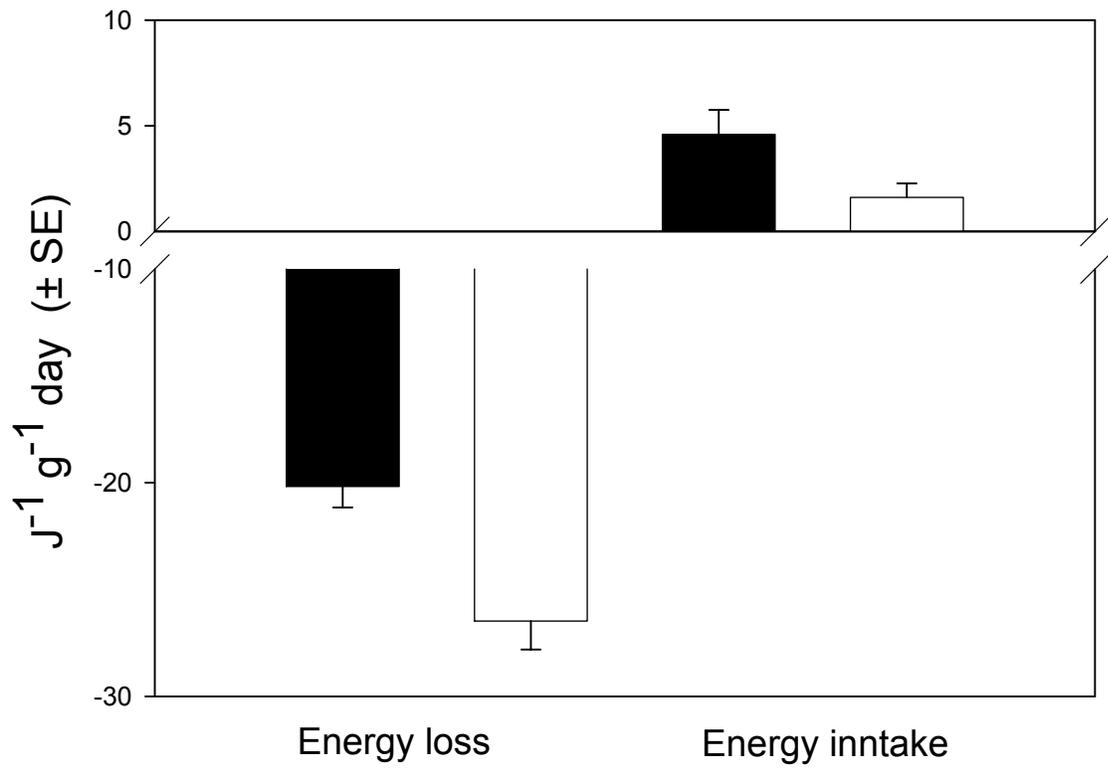


Fig. 3

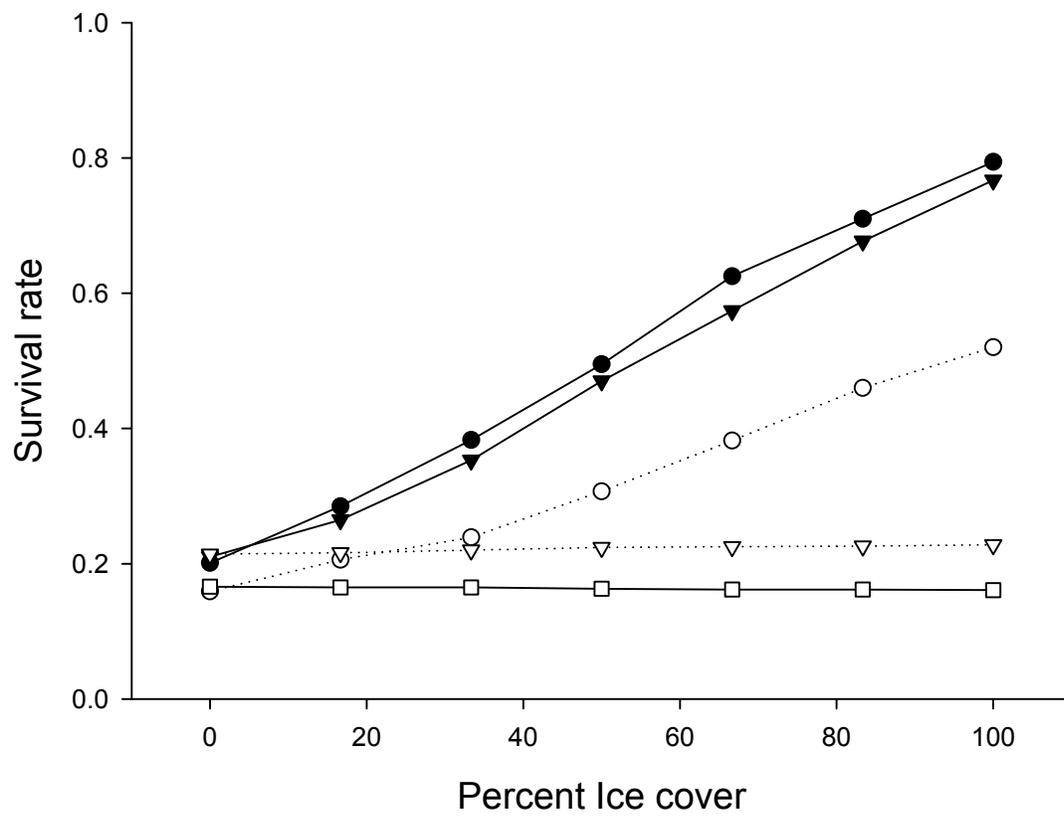


Fig. 4.

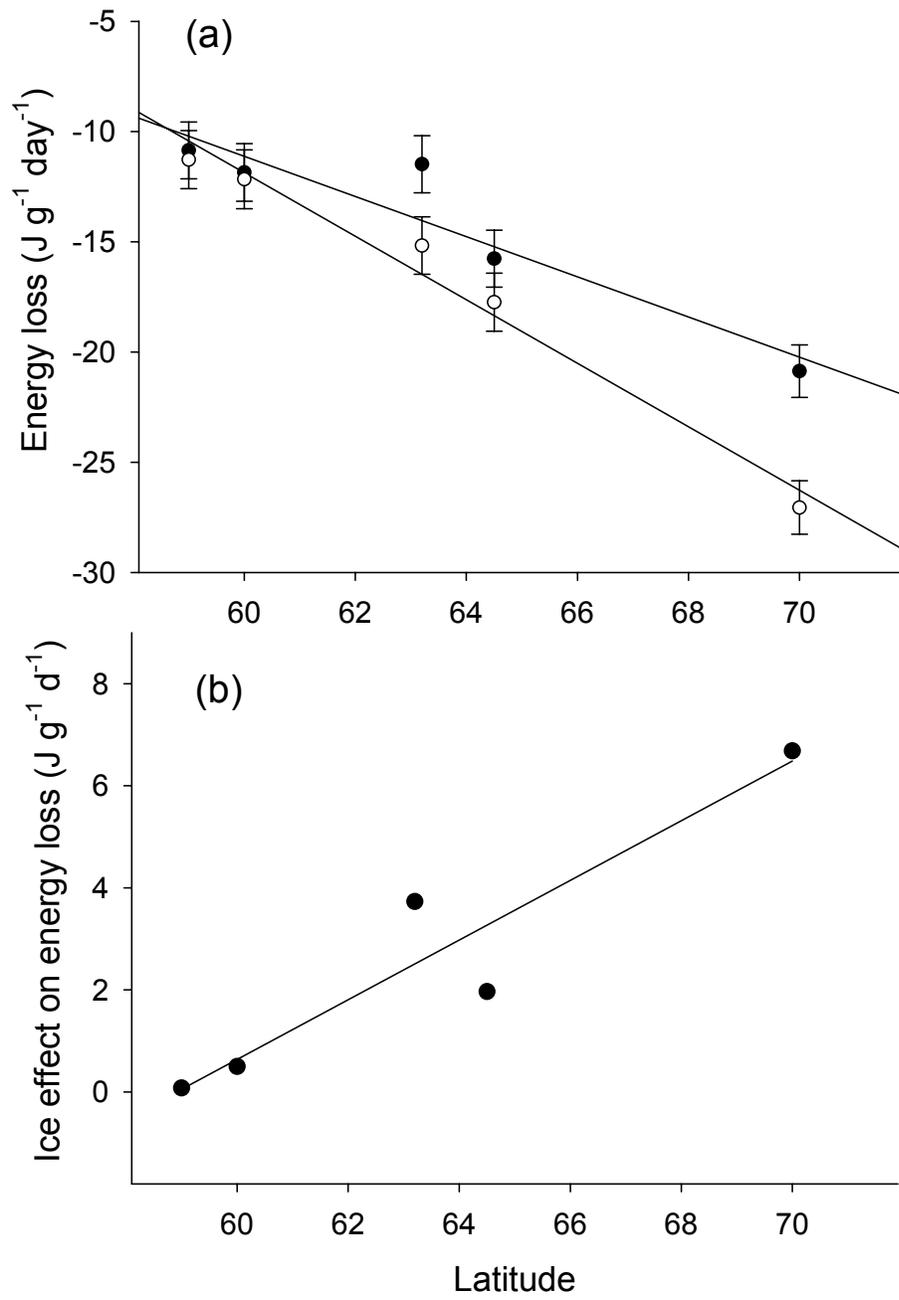


Fig. 5.