



Winter behaviour of stream salmonids: effects of temperature, light, and ice cover

Johan Watz

Faculty of Health, Science and Technology

Biology

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Faculty of Health, Science and Technology

Department of Environmental and Life Sciences

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+46 54 700 10 00

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Abstract

In boreal streams, stream salmonids typically face low water temperatures and variable ice conditions during winter. To cope with these environmental conditions, stream salmonids adopt different behavioural strategies. The studies presented in this thesis explore how temperature, light intensity, and surface ice affect salmonid behaviour, with focus on drift-feeding and ventilation rates. The first paper reports results from a laboratory study, designed to measure prey capture probabilities and reaction distances of drift-feeding Atlantic salmon, brown trout, and European grayling at light intensities simulating daylight and moonlight. Trials were conducted at seven temperatures, ranging from 2 to 11°C. There was a positive relationship between water temperature and prey capture probability for all three species at both light levels, but the temperature dependence did not scale according to the Metabolic Theory of Ecology. Reaction distance was also positively related to temperature for the three species, which may explain the temperature effects on prey capture probability. In the second paper, the effects of ice cover on the diel behaviour and ventilation rates of brown trout were studied in a laboratory stream. Ice cover is believed to afford protection against endothermic predators, and thus the need for vigilance should be reduced under ice cover. This hypothesis was tested by observing ventilation rates at night, dawn, and during the day in the presence and absence of real, light-permeable surface ice. Further, trout were offered drifting prey during the day to test if ice cover increased daytime foraging activity. Ice cover reduced ventilation rates at dawn and during the day, but not at night. Moreover, trout made more daytime foraging attempts in the presence of ice cover than in its absence. These results suggest that ice cover affects the behaviour of brown trout and presumably has a positive effect on winter survival. Global warming, which reduces the time period when rivers are covered by surface ice, may therefore have negative consequences for many lotic fish populations in boreal streams.

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List of papers

This thesis is based on the following two papers, which are referred to by their Roman numerals.

- I. Watz, J., Piccolo, J., Bergman, E., and Greenberg L. (2013) Day and night drift-feeding by juvenile salmonids at low water temperatures. *Manuscript.*
 - II. Watz, J., Bergman, E., Piccolo, J., and Greenberg L. (2013) Ice cover effects on the diel behaviour and ventilation rate of juvenile brown trout. *Manuscript.*
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Contributions

Johan Watz developed the basic idea and concepts, had a leading role in the study design, performed the laboratory work, collected the data, ran the statistical tests, and wrote both of the papers. Larry Greenberg, Eva Bergman, and John Piccolo contributed to the basic idea and to the study design, provided statistical advice, and made valuable comments for improving both of the papers.

Introduction

Winter conditions may be important for the population dynamics of many stream salmonid populations at high latitudes or altitudes. Juvenile salmonids must rely on both food intake and catabolism of stored fat to survive winter (Metcalf & Thorpe, 1992, Bull, Metcalfe & Mangel, 1996, Carlson, Olsen & Vollestad, 2008). Predation and energy deficits are two of the most important causes of mortality during winter (Hurst, 2007). Therefore, the trade-off between the use of energy reserves and exposure to predators while foraging is one of the key factors that affect winter behaviour (Finstad *et al.*, 2010). Several aspects of the environment, such as temperature, light, and ice processes, as well as predation and competition, may influence this trade-off. There is variation in the reported overwinter mortality rates of stream salmonids (Huusko *et al.*, 2007 and references therein), but the mechanisms responsible for this variation are largely unknown. The study of behavioural responses to different winter conditions in a controlled environment may be a useful tool to explore these mechanisms. This thesis deals with the effect of three environmental factors: temperature, light intensity, and ice cover on the winter behaviour of stream salmonids, with focus on foraging and anti-predator behaviour.

Temperature

In boreal streams, falling temperatures and a decline in solar energy influx start to cool the water when winter approaches. The rate of the in-stream temperature decline depends on air temperature, solar radiation, and the depth and volume of the water (Brown, Hubert & Daly, 2011). Fluid turbulence in running water prevents stratification by mixing of layers, and water temperature is therefore normally completely homogeneous throughout the water body, except for low velocity waters in shallow areas near the stream banks (Hicks, 2009).

Temperature is the most important abiotic factor that affects metabolic processes in poikilothermic organisms, such as stream salmonids, and salmonids adapt both physiologically and behaviourally as water temperature declines. While many other stream-dwelling animals hibernate during winter, salmonids remain active (Cunjak, 1996, Brown *et al.*, 2011). Low water temperatures slow metabolic rates and reduce energetic requirements, and accordingly the scope for activity is constrained. As a consequence, movement, aggression, and feeding activity are normally relatively low during winter (Huusko *et al.*, 2007, Jonsson & Jonsson, 2011).

According to the Metabolic Theory of Ecology (MTE), the Arrhenius equation describes how metabolic processes scale with temperature (Gillooly *et al.*, 2001, Brown *et al.*, 2004). In the equation, the rate R , scales with temperature according to $e^{-E/kT}$, where E is the activation energy in eV, k is the Boltzmann's constant ($8.617 \cdot 10^{-5}$ eV·K⁻¹), and T is the absolute temperature in K. MTE predicts that E , *i.e.* the slope of the temperature dependence, should range between 0.6 and 0.7 eV (Gillooly *et al.*, 2006, Allen & Gillooly, 2007), as these values reflect the activation energies of the respiratory complex in all ectothermic animals. It has been questioned as to whether or not MTE is universally applicable for all biological rates that are coupled to metabolism (Englund *et al.*, 2011, Rall *et al.*, 2012). While much empirical evidence supports that MTE is valid for many physiological rates, it is not certain that rates influenced by animal behaviour, *e.g.* salmonid drift-foraging, may be accurately predicted by such a coarse universal temperature-dependent function.

Via temperature effects on foraging ability (Watz & Piccolo, 2011), salmonid foraging success is reduced in cold water, and so is the physical ability to escape predators (Webb, 1978, Rimmer, Saunders & Paim, 1985, Graham, Thorpe & Metcalfe, 1996, Huusko *et al.*, 2007). Prey detection and reaction distance also affect foraging success, but their temperature dependence has not been well investigated. Moreover, thermal effects on different aspects of foraging performance may vary among fish species (Bergman, 1987, Taniguchi *et al.*, 1998), and especially if the species use different foraging tactics (Watz *et al.*, 2012).

Light and diel activity

At high latitudes, days are short with low solar radiation input during winter, and the presence of snow-covered ice reduces the already low in-stream light intensity even further. Light conditions in the stream influence its inhabitants in various ways, and stream salmonids adjust their activity patterns to the light regime (Huusko *et al.*, 2007 and references therein). Stream salmonids are mainly visual hunters (Rader *et al.*, 2007, Elliott, 2011), and so are their most important predators during winter (*i.e.* mammals and birds). As a result, the light regime influences salmonid behaviour both through its effects on foraging efficiency and the need for predator vigilance. For instance, juvenile salmonids in darkness have low metabolic costs associated with vigilance, presumably because perceived predation risk is low (Finstad *et al.*, 2004, Helland *et al.*, 2011).

During winter, juvenile salmonids reduce their daytime activity (Heggenes *et al.*, 1993, Fraser *et al.*, 1995, Metcalfe, Fraser & Burns, 1999). The underpinning mechanism that controls the diel activity pattern is most likely a trade-off between the need for energy intake and predator avoidance. Foraging success at night is generally low, but it minimizes exposure to predators (Fraser & Metcalfe, 1997, Metcalfe, Valdimarsson & Fraser, 1997, Valdimarsson *et al.*, 1997). Although nocturnal foraging is low in efficiency, it is often sufficient to cover the basic energetic needs of juvenile salmonids during winter, and daytime activity is thus usually avoided (Orpwood *et al.*, 2006).

Ice cover

In super-cooled stream water, ice grows on surfaces, on suspended particles, and on introduced fragments of other ice crystals (*e.g.* snow), which results in the formation of a slush of tiny ice particles in the water column, frazil ice, or ice on the stream bottom, anchor ice (Fig. 1). Surface ice cover is normally developed through bridging of border ice or by accumulation and freezing of thick flocks of frazil ice (Hicks, 2009). Once a stable surface ice cover has been established further in-stream ice development is hindered and the temperature and light regimes are modified.



Fig. 1. Ice processes play a major role in shaping the habitat and behaviour of stream salmonids during winter. Anchor ice can be seen as milky gray areas near the edges in the portion of the stream lacking surface ice. Photo J. Watz.

Ice cover prevents rapid in-stream temperature fluctuations and habitat exclusion caused by dynamic ice processes, *e.g.* development of anchor and frazil ice (Brown *et al.*, 2011, Prowse, 2001a). In addition to stabilizing the environment, surface ice may function as overhead cover (Meyers, Thuemler & Kornely, 1992, Young, 1995, Prowse, 2001b), and under stationary ice cover, salmonids change their behaviour; for example, they increase site fidelity (Linnansaari *et al.*, 2009) and daytime activity (Linnansaari, Cunjak & Newbury,

2008). Moreover, stream salmonids under ice cover have been reported to use otherwise unsuitable substrates, *i.e.* small substrate sizes (Linnansaari *et al.*, 2008, Linnansaari *et al.*, 2009), and even suffer lower mortality during periods with ice cover than during ice-free periods (Linnansaari & Cunjak, 2010). A plausible explanation for the seemingly beneficial effect of ice cover is that it offers protection from endothermic predators and may reduce vigilance costs (Finstad *et al.*, 2004, Linnansaari *et al.*, 2008).

Objectives

The main objective of this thesis was to study the behaviour of stream salmonids in relation to different aspects of winter conditions, specifically the effects of temperature, light intensity, and ice cover. This objective was pursued by conducting experiments in laboratory stream channels. In the first study, my main interest was to describe and compare the effects of low temperatures on drift-feeding efficiencies for different salmonid species, and to explore whether or not prey capture probability scaled with temperature according to MTE. As low temperatures induce a shift in activity towards nocturnality, a key objective was to describe prey capture probability rates in light regimes simulating both day and night conditions. Moreover, a secondary objective was to explore thermal effects on reaction distance, a potential underlying factor that may explain temperature-dependent foraging success. The objective of the second study was to shed light on mechanisms that may explain why stable ice cover seems to increase overwinter survival rates in juvenile stream salmonids. In particular, I was interested in the effects of surface ice on perceived predation risk, as expressed by effects on ventilation rates and daytime foraging activity.

Materials and methods

The studies in this thesis were conducted at the aquarium facility at Karlstad University from 2010 through spring 2012. This facility contains different kinds of artificial stream channels, suitable for a wide range of behavioural studies of stream fishes.

For the foraging trials in Paper I, two aquaculture facilities in central Sweden (Bröderna Olsson, Vallsta and Fortum, Brattfors) provided farmed young-of-the-year Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and European grayling (*Thymallus thymallus*), whose parents were of wild origin. The species were of similar sizes (mean masses and total lengths (\pm SD): salmon 9.19 ± 1.98 g, 83.9 ± 9.19 mm; trout 9.33 ± 2.41 g, 93.5 ± 9.33 mm; grayling 7.34 ± 1.73 g and 103.9 ± 7.19 mm). After acclimation, individual fish were studied at temperatures ranging from 2 to 11 °C at simulated moonlight (0.1 lx) and daylight (300 lx). The experimental arena ($1.10 \times 0.24 \times 0.16$ m; $l \times w \times d$) was created in a 2-m-long stream channel, and mean water velocity was $0.13 \text{ m}\cdot\text{s}^{-1}$. Chironomid larvae were used as prey and were introduced at 12-s intervals. At each combination of light and temperature, six fish of each species were used, in total 198 fishes. All trials were filmed, and from the video footage of the drift-feeding fishes, prey capture probability was measured at both light levels, and reaction distance, *i.e.* the distance between the fish and its

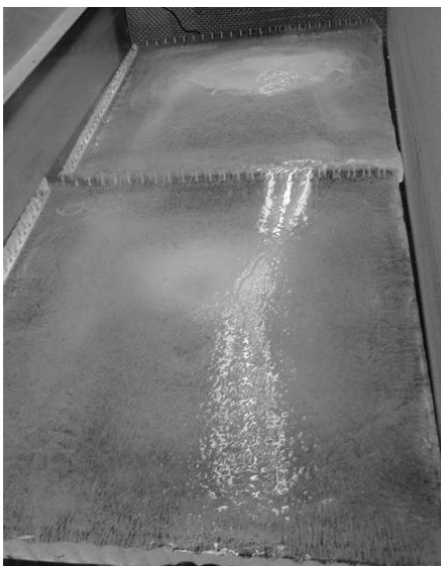


Fig. 2. In Paper II, two ice sheets were placed over the water surface of a laboratory stream channel to create ice cover for the fish. Photo J. Watz.

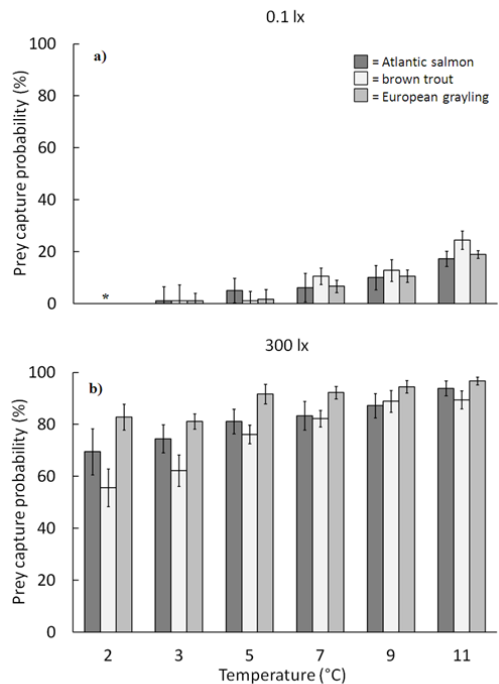
prey, when the fish starts to orient its body towards the predicted point-of-capture (Vogel & Beauchamp, 1999, Mazur & Beauchamp, 2003), was measured at 300 lx. For each species and at both light levels, temperature *vs.* prey capture probability data were fit to the Arrhenius equation (Brown *et al.*, 2004) to test if the temperature dependence of prey capture in drift-feeding salmonids could accurately be predicted by the universal temperature dependence proposed by MTE.

For Paper II, 40 juvenile brown trout (mean mass and total length (\pm 1 SD): 3.0 ± 0.99 g and 74 ± 9.4 mm),

collected via electrofishing in the River Lillån, Västergötland, Sweden, were used. Pairs of fish were observed and filmed in the presence and absence of ice cover in a 1.2×0.54 m section of a 7-m-long stream channel (Fig. 2). The experimental arena had two microhabitats of approximately equal size: a shallow upstream section (depth 0.12 m; water velocity $0.14 \text{ m}\cdot\text{s}^{-1}$) and a deep, somewhat slower flowing, downstream section (depth 0.20 m; water velocity $0.08 \text{ m}\cdot\text{s}^{-1}$). Infrared lamps and an infrared-sensitive video camera were used to film fish three times a day: at night, dawn, and during the day. Average light intensities in the stream channel at the three times of day were < 0.1 , 14, and 581 lx, respectively, and the presence of ice reduced in-stream light intensities by approximately 50 %. Water temperature was held at $4 \text{ }^\circ\text{C}$. A trial for each time of day consisted of (1) observing ventilation rates, (2) identifying whether the fish were swimming or resting on the substrate, and (3) describing the use of the two sections and (4) the level of aggression. After these observations were completed for the day, three chironomid larvae were introduced into the stream channel every min during 10 min, and the number of foraging attempts was counted. Data were analysed for the effects of ice cover and time of day.

Summary of results

For all three species tested in Paper I, prey capture probability was much higher in simulated daylight than in simulated moonlight, and there was a positive relationship between prey capture probability and temperature (Figs 3 a – b). The temperature effect was similar among the species, but grayling had a slightly higher prey capture probability than brown trout in daylight. Also, reaction distance was positively related to temperature for all three species, and brown trout had a shorter reaction distance than the other two species. Activation energies, extracted from data fitted to the Arrhenius equation, indicated that drift-feeding did not scale with temperature according to MTE, as activation energies were lower in moonlight and much higher in daylight than values predicted by MTE.



Figs 3 a – b. Mean prey capture probabilities (± 1 SE) of three species of salmonids drift-feeding at temperatures ranging from 2 to 11 °C at a) 0.1 lx and b) 300 lx, respectively ($n = 6$). At 0.1 lx, no data were collected for fish at the lowest temperature, which is indicated by the asterisk.

In paper II, time of day affected ventilation rates, which tended to be highest during the day and lowest at night. Ice cover significantly reduced ventilation rates at dawn and during the day, but not at night (Fig. 4), and fish made more daytime foraging attempts in the presence of ice cover than in its absence. Daytime ventilations rates under ice were lower than those of fish under ice-free conditions at dawn, when light levels were considerably lower. The presence of ice cover increased the use of the deep section, but section use was not affected by time of day. Conversely, time of day influenced swimming activity, switches between sections, and aggression, with a peak at dawn, but there were no effects of ice cover.

Discussion

Although metabolic rates slow down at low temperatures and thus reduce the need for food intake, energy deficit is one of the major causes for winter mortality in freshwater fishes (Hurst, 2007). Winter growth in stream salmonids is normally negligible (Cunjak, 1996), but even so some fish may require a relatively high energy intake rate, for example, for smolt transformation in anadromous fish (Metcalf & Thorpe, 1992) and for maturation in spring-spawning species. The cause of winter deaths due to energy deficiency may be related to difficulties with food acquisition in cold water. These difficulties may be caused by low prey densities (Martin *et al.*, 2001), poor capture ability (Elliott, 2011, Watz *et al.*, 2012), or a depressed appetite (Metcalf & Thorpe, 1992, Bull *et al.*, 1996). Because low temperatures also reduce the ability to escape predators, juvenile stream salmonids reduce their diurnal activity and are often restricted to nocturnal foraging. In particular, the combination of low temperature and low light intensity makes drift-feeding very low in efficiency (Paper I), and fish need to trade-off starvation against predation risk. Ice cover may, however, reduce predation risk from endothermic predators and increase daytime foraging activity (Paper II), which enhances the overall drift-feeding efficiency (Paper I). Ice cover also reduces metabolic costs (Paper II), presumably because there is little need for predator vigilance.

Habitat preferences of stream salmonids differ between summer and winter, and habitats with low water velocities are normally used during winter (Hartman, 1965, Heggenes *et al.*, 1993, Riley *et al.*, 2006, Huusko *et al.*, 2011). When Cunjak (1996) ranked the most important factors that determine the suitability of winter habitat for stream salmonids, protection from adverse physicochemical conditions was prioritized the highest, followed by protection from predators, and access to food was considered the least important factor. Yet, these three factors are not independent of each other, and it is problematic to view them separately. This is because abiotic factors, predation risk, energetic demands, and foraging activity interact in complex ways to influence winter behaviour and habitat selection. For instance, if food density is high in habitats with ample foraging opportunities (*e.g.* suitable depths and velocities) fish may reduce daytime

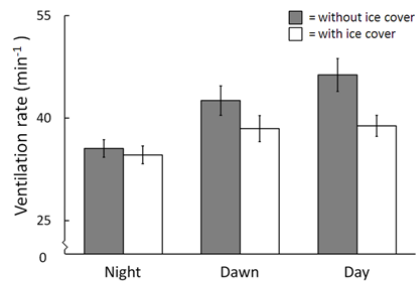


Fig. 4. Mean ventilation rates (beats min⁻¹) for juvenile brown trout at night, dawn, and during the day in the absence and presence of ice cover. Error bars indicate ± 1 SE.

activity to reduce predation risk, because nocturnal food intake rates cover most of the basic energetic requirements (Railsback & Harvey, 2011). Therefore, one possible explanation for the preference for slow water velocities during winter might be that there is only a short time window for prey capture at low light levels and temperatures (as discussed in Paper I). To be able to build accurate habitat selection and bioenergetics models that include the choice between diurnal and nocturnal foraging, day and night foraging efficiency functions for different environmental conditions, such as temperature (Paper I), are needed. Furthermore, ice cover might affect diel activity and thus habitat selection (Linnansaari *et al.*, 2008, Linnansaari *et al.*, 2009), as ice cover may provide sufficient protection against both endothermic predators and dynamic in-stream ice formation (Hicks, 2009, Brown *et al.*, 2011).

In Paper I, temperature functions were obtained for prey capture probability in Atlantic salmon, brown trout, and European grayling for light conditions simulating an overcast day and a moonlit night. The temperature effects on prey capture probability did not agree well with predictions of MTE. At low temperatures, swimming ability is reduced (Webb, 1978, Rimmer *et al.*, 1985, Ojanguren & Braña, 2000), which should reduce foraging efficiency (Watz & Piccolo, 2011), but also temperature effects on reaction distance may play a role (Paper I). Drift-feeding is a foraging mode largely influenced by behavioural decisions (Ringler, 1985) and the data in Paper I suggest that the temperature dependence of drift-feeding may be difficult to model using a coarse universal function, as the one proposed by MTE.

The effect of ice cover on metabolic costs were studied in Paper II, and the results therein extend those from other studies that examine this effect (*e.g.* Finstad *et al.*, 2004, Linnansaari *et al.*, 2008, Helland *et al.*, 2011). For example, I found that daytime foraging activity was increased by the presence of ice cover, and that ice cover reduced ventilation rates, and thus metabolic rate, at dawn and during the day, but not at night. The time-dependent difference in ventilation rates probably reflects temporal differences in perceived predation risk. At night, when light levels were very low, ice cover had little effect on ventilation rates, presumably because the fish's predators are visual hunters. Interestingly, ventilation rates under ice cover during the day, when in-stream light intensity was relatively high, were lower than those in the absence of ice at dawn, when light intensity was low. This difference in ventilation rates indicates that the underlying mechanism was probably not an effect of light *per se*. Surface ice is likely viewed as protective overhead cover by stream salmonids.

Future research

It has been suggested that ice cover reduces overwinter mortality (Linnansaari & Cunjak, 2010, Hedger *et al.*, 2013), but these studies have largely been descriptive. Field experiments, with manipulation of ice cover, would shed light on this hypothesis. In addition to effects on survival, it would be interesting to explore if ice cover reduce weight-loss of stream salmonids during winter. Field experiments could also be used as a tool to investigate the influence of ice cover on both microhabitat and mesohabitat selection. Further, I am interested in individual variation in behavioural strategies related to winter conditions. For example, do different species, year classes, and individuals with different coping styles and standard metabolic rates react differently to ice cover? Differences in adaptation to foraging in darkness under ice cover have been suggested to mediate competition between brown trout and Arctic char (*Salvelinus alpinus* L.) in lakes (Helland *et al.*, 2011). Does river ice affect competition between lotic species? Are there ice cover effects on intraspecific competition? Controlled experiments in the laboratory or in semi-natural outdoor stream channels might provide a useful means for answering some of these questions.

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Winter behaviour of stream salmonids: effects of temperature, light, and ice cover

In boreal streams, salmonids typically face low water temperatures and variable ice conditions from autumn to spring. The studies presented in this thesis explore how temperature, light intensity, and ice cover affect salmonid behaviour, with focus on drift-feeding and ventilation rates. In Paper I, drift-foraging was studied at light intensities simulating daylight and moonlight at seven temperatures ranging from 2 to 11°C. There was a positive relationship between temperature and foraging success at both light levels, but the temperature-dependence did not scale according to the Metabolic Theory of Ecology. Moreover, reaction distance was positively related to temperature. In Paper II, the effects of ice cover on behaviour and ventilation rate of brown trout were studied. Ice cover is believed to afford protection against predators, and thus the need for vigilance should be reduced under ice. This hypothesis was tested by observing ventilation rates at night, dawn, and during the day in the presence and absence of surface ice. Ice cover reduced ventilation rates and increased daytime foraging activity, suggesting that ice cover presumably has a positive effect on winter survival.

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