



# Salmonid behaviour under winter conditions

Johan Watz

Faculty of Health, Science and Technology

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Biology

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## **Abstract**

Winter conditions are believed to play an important role in the population dynamics of northern temperate stream fish, challenging the ability of fish to physiologically and behaviourally adapt. Climate change is predicted to increase both mean temperature and temperature fluctuations, especially during winter, leading to dynamic environmental conditions in terms of river ice production and flow. Therefore, knowledge about the winter ecology of stream fish is important for predicting and mitigating anthropogenic impacts on fish production in boreal streams. Stream salmonids are relatively active throughout winter, and behavioural responses to different winter conditions may be critical for survival. Yet, relatively little is known about overwintering behaviour of salmonids, particularly in streams with ice. In this doctoral thesis, I report the results from experimental field and laboratory studies on the behavioural ecology of juvenile salmonids under winter conditions. My results from the field show that salmonids grow more and use a broader range of habitats in the presence of surface ice than in its absence. Results from the laboratory experiments show that the presence of surface ice increases food intake rates, reduces stress and affects social interactions. These laboratory results may explain the positive effects of ice cover on growth that was found in the field experiment. Moreover, I show that drift-feeding ability is reduced at low temperatures, and that nocturnal drift foraging under winter conditions has a low efficiency.

## **Svensk populärvetenskaplig sammanfattning**

Vinterförhållanden kan spela en avgörande roll för förekomsten av fisk i våra vattendrag. Laxfiskar, som till exempel lax, öring och harr, är vinteraktiva och måste därför anpassa sin fysiologi och sitt beteende till en miljö som karaktäriseras av låga och föränderliga vattenflöden, liten tillgång på föda, kallt vatten, is och mörker. Trots att dessa anpassningar är avgörande för chansen att överleva vintern, vet man relativt lite om laxfiskars vinterbeteende, speciellt i vattendrag som täcks av is. I denna avhandling presenterar jag resultat från fält- och laboratoriestudier av laxfiskars beteende under vinterförhållanden. Resultaten visar att närvaron av yttäckande is ökar tillväxt och födointag, minskar stress samt påverkar var fiskar uppehåller sig och hur fiskarna interagerar med varandra. Jag har också undersökt hur laxfiskars beteende i rinnande vatten påverkas av ljusintensitet och vattentemperatur i samband med födointag. Den minskade dagaktiviteten som laxfiskar uppvisar på vintern medför en kostnad i form av försämrad förmåga att fånga byten.

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## List of papers

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

- I. Watz, J., Bergman, E., Piccolo, J.J. and Greenberg, L. (2015) Ice cover affects the growth of a stream-dwelling fish. *Manuscript*.
- II. Watz, J., Bergman, E., Piccolo, J.J. and Greenberg, L. (2013) Effects of ice cover on the diel behaviour and ventilation rate of juvenile brown trout. *Freshwater Biology* **58**, 2325-2332.
- III. Watz, J., Piccolo, J.J., Bergman, E. and Greenberg, L. (2014) Day and night drift-feeding by juvenile salmonids at low water temperatures. *Environmental Biology of Fishes* **97**, 505-513.
- IV. Watz, J., Bergman, E., Piccolo, J.J. and Greenberg, L. (2014) Prey capture rates of two species of salmonids (*Salmo trutta* and *Thymallus thymallus*) in an artificial stream: effects of temperature on their functional response. *Marine and Freshwater Behaviour and Physiology* **47**, 93-99.
- V. Watz, J., Bergman, E., Calles, O., Enefalk, Å., Gustafsson, S., Hagelin A., Nilsson, P.A., Norrgård, J.R., Nyqvist, D., Österling, E.M., Piccolo, J.J., Schneider, L.D., Greenberg, L. and Jonsson, B. (2015) Ice cover alters the behavior and stress level of brown trout *Salmo trutta*. *Behavioral ecology* **26**, 820-827.

Papers II, III, IV and V are reprinted with the permission of John Wiley & Sons, Springer, Taylor & Francis and Oxford University Press, respectively.

## ***Contributions***

### *Paper I*

JW developed the basic idea and concepts, had a leading role in the study design, led and performed the field work, collected the data, ran the statistical tests and wrote the paper. LG, EB and JP contributed to the basic idea and to the study design, and made valuable comments for improving the paper.

### *Papers II – IV*

JW 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 the papers. LG, EB, and JP contributed to the basic idea and to the study design, provided statistical advice, and made valuable comments for improving the papers.

### *Paper V*

This study was performed as a project in which all members of the research group, River Ecology and Management, could participate. JW conceived the idea and concept, had a leading role in the study design, performed laboratory work, ran the statistical tests and wrote the major part of the paper. BJ developed the concept, had a leading role in the study design and in the laboratory work and wrote parts of the paper. EB and LG had leading roles in the study design. AN provided statistical advice. All co-authors performed laboratory work, collected data and made valuable comments to improve the paper.

Johan Watz (JW), Larry Greenberg (LG), Eva Bergman (EB) John Piccolo (JP), Bror Jonsson (BJ), Anders Nilsson (AN).

## Introduction

In northern temperate and boreal streams, environmental conditions may vary greatly both among and within seasons. During winter, stream-dwelling animals face a highly variable environment (Prowse, 2001b), normally associated with dynamic ice phenomena and low, fluctuating temperatures and discharges (Prowse, 2001a; Huusko *et al.*, 2007; Hicks, 2009). These changes in the physical stream environment challenge the capacity of riverine animals to adapt their physiology, activity, behaviour and habitat use to survive both on short and long temporal scales. Overwintering strategies in streams differ, with some animals becoming dormant and others remaining active throughout winter (Marchand, 2014).

Adverse winter conditions constrain winter-active, stream-dwelling animals' physiology and access to resources, and often lead to a negative energy budget that taxes energy reserves (Biro *et al.*, 2004; Giacomini & Shuter, 2013). These adverse and variable conditions may prevail in some streams or segments of streams for long periods of winter, whereas other streams may be stable. For stream fish, the relationship between energetic status, both current and anticipated, and the physical conditions plays a major role in influencing habitat choice, diel activity patterns and risk-taking behaviour (Metcalf & Thorpe, 1992; Bull, Metcalfe & Mangel, 1996; Metcalfe, Fraser & Burns, 1998; Finstad *et al.*, 2010).

A broad understanding of the effects of winter conditions on fish behaviour is needed to predict how populations of stream-dwelling fish respond to environmental change. This understanding is essential to develop tools to conserve threatened populations and increase fish production in rivers and streams. Knowledge about how to accurately predict the effects of altered river ice processes and increasing stream water temperature on fish will be especially crucial to mitigate negative effects of global warming on fluvial ecosystems. This is because the effects of global warming on temperate and boreal freshwaters will be greatest during winter (Jonsson & Jonsson, 2009; IPCC, 2013), and because many stream fish species function as top-predators in running waters and thereby influence the composition and dynamics of the ecosystem.

Winter has been regarded as a critical period for survival of freshwater fish, thus affecting the population dynamics (Cunjak, Prowse & Parrish, 1998; Hurst, 2007). Although behavioural adjustments to the environment are crucial for survival in harsh environments, relatively little is known about the behaviour of overwintering stream fish (Huusko *et al.*, 2007; Brown, Hubert & Daly, 2011). However, recent technological advances in e.g. biotelemetry have increased the possibilities to conduct research on stream fish winter ecology (Roussel, Haro & Cunjak, 2000; Linnansaari *et al.*, 2007; Cooke *et al.*, 2013; Ellis, Linnansaari & Cunjak, 2013). As a result, the number of studies on stream fish carried out under winter conditions has increased recently. Yet, little experimental work has been done to test the effects of environmental factors under winter conditions (Brown *et al.*, 2011; Huusko, Vehanen & Stickler, 2013). In this doctoral thesis, I study the winter behaviour of stream fish by reporting results from a series of field and laboratory experiments, in which I have manipulated factors such as ice cover, temperature, light intensity and food availability, and tested their effects on salmonid behaviour.

### ***The physical instream environment during winter***

At the onset of winter, low solar energy input and declining air temperatures cool the stream water. In slow-flowing stream segments and near the stream edges, low water currents may permit stratification of water layers. In these places, the coldest water will be positioned near the surface, and surface ice may form. In most streams, however, fluid turbulence prevents stratification by mixing of layers, thereby maintaining a uniform temperature throughout the water column. Stream water temperature is therefore typically near 0 °C during winter. For short periods of time, temperature can even fall below 0 °C, and the water becomes supercooled. In supercooled water, ice crystals grow due to secondary nucleation on seed crystals introduced from the air (e.g. snow) or on fragments of ice in the stream (Hicks, 2009). When water turns from liquid to solid phase, heat is released, which limits further supercooling and warms the water back to 0 °C. This type of ice, frazil ice, is either transported in

the water column or adheres to instream structures, where it may continue to grow. When this phenomenon takes place on the stream bottom, it is referred to as anchor ice (Fig. 1, left photograph). Frazil and anchor ice formation generally follow a diurnal cycle, where growth occurs at night and solar energy input prevents growth during the day (Stickler & Alfredsen, 2009). Large quantities of anchor ice may smooth out crevices and irregularities on the stream bottom. Grown thick, anchor ice may create ice dams, whereas accumulation of frazil ice under ice cover may form hanging dams (Hicks, 2009). Both these events may substantially alter stream hydraulics (Brown et al., 2011).

The formation of ice cover starts when the motion of accumulated floating flocks of frazil ice is arrested by obstacles or low water current. The formation of ice cover will then advance upstream as more floating ice flocks arrive. Heat transfer to the air enables freezing of the interstitial water between ice flocks, strengthening the stability of the ice cover. In small streams, bridging of border ice and snow may also form a stationary ice cover. After a stable ice cover has been established (Fig. 1, right photograph), further heat loss to the air is reduced, hindering growth of frazil and anchor ice and reducing the instream light (Hicks, 2009).



**Figure 1.** Ice processes shape the physical environment in the stream and play an important role in the behaviour of stream fish during winter. Anchor ice (milky beige areas near the stream edges in the left photograph) may exclude fish from their winter refuges, whereas surface ice (right photograph) may provide fish with overhead cover (Photo J. Watz).

In large rivers and slow-flowing streams, surface ice may cover almost the entire water course during the whole winter. In steep-gradient streams, on the other hand, ice cover may repeatedly form and break up throughout winter, and the duration of periods with stable ice cover will depend on air temperature. Precipitation in the form of snow will not add to stream discharge and will insulate the stream, whereas rain will weaken the ice cover and increase stream flow, which may eventually mechanically break up the ice cover. Dynamic ice formation is also common downstream of hydroelectric power stations, due to large fluctuations in discharge of released warm water from the hypolimnion of the upstream water reservoir (Simpkins, Hubert & Wesche, 2000). During spring, ice cover will either break up thermally by solar energy input or mechanically by the spring flood, transforming the stream back into an open system. Slow thermal spring meltouts are common in large rivers, whereas fast and dramatic mechanical ice breakups often occur in small steep streams (Huusko *et al.*, 2007).

### ***Temperature, feeding, growth and mortality***

The body temperature of most aquatic poikilothermic animals matches that of the ambient water, making their rates of physiological processes water temperature dependent. Metabolic rates and physical performance are therefore low in cold water, which constrains the scope for growth and activity. Hence, water temperature is the main factor that shapes winter behaviour of stream fish (Huusko *et al.*, 2007; Brown *et al.*, 2011). Low temperatures lead, for example, to reductions in movement, aggression and feeding activity (Jonsson & Jonsson, 2011). In adverse winter conditions, stream fish prioritize minimizing energy expenditure and finding shelter from severe physical conditions and predators (Heggenes *et al.*, 1993; Cunjak, 1996). This priority results in reduced feeding opportunities, and many stream fishes need to survive for long periods without food by catabolizing stored energy reserves (i.e. fat) (Cunjak, 1988b; Berg & Bremset, 1998; Simpkins *et al.*, 2003; Biro *et al.*, 2004). Although little energy is required to fuel the slow standard metabolic rate in cold water, energy deficit is still a major cause of winter mortality (Finstad *et al.*, 2004b; Hurst, 2007), and the anticipated energy

status at the end of winter may determine the minimum amount of food intake that is required to survive (Bull *et al.*, 1996).

While low water temperatures and light intensities reduce feeding success (Fraser & Metcalfe, 1997; Watz & Piccolo, 2011; Watz *et al.*, 2012), stable, benign conditions may permit stream fish to actively feed throughout winter (Heggenes & Borgstrøm, 1988; French *et al.*, 2014). Even with poor assimilation efficiencies and slow gastric evacuation rates in cold water (Elliott, 1972; Cunjak & Power, 1987), some individuals may exhibit positive growth rates during winter (Wysujack *et al.*, 2009; Puffer *et al.*, 2014). Therefore, energy deficits and mortality rates during the winter season, previously considered as an energetic bottleneck for stream fish, may not necessarily exceed those during other seasons (Carlson, Olsen & Vollestad, 2008), but may vary greatly among years, streams, species, cohorts and individuals, depending on context (Huusko *et al.*, 2007).

Poor swimming capacity of stream fish in cold water reduces the ability to escape predators (Webb, 1978), and particularly predation from endothermic predators may be a major cause of winter mortality (Heggenes & Borgstrøm, 1988; Harvey & Nakamoto, 2013; Day, Westover & McMillan, 2015). The trade-off between obtaining foraging opportunities and predator avoidance, a trade-off that shapes diel activity patterns during winter, is thus influenced by temperature (Fraser *et al.*, 1995) through its effects on energetic requirements and physical performance (Orpwood, Griffiths & Armstrong, 2006).

### ***Predation and its effect on diel activity***

Predation has both direct and indirect effects on prey populations. Predators consume prey, but they also affect the behaviour and habitat choice of the prey (Preisser, Bolnick & Benard, 2005; Orrock *et al.*, 2013). Various taxa prey upon stream fish during winter, including other fish, such as burbot (*Lota lota*), northern pike (*Esox lucius*) and various salmonid species, as well as birds and mammals (Alexander, 1979; Heggenes & Borgstrøm, 1988; Harvey & Nakamoto, 2013). Because of the low activity of poikilothermic animals in cold water, it is possible that predation by piscivorous fish does not contribute substantially to the winter mortality of stream fish. Conversely,

the activity of endothermic animals is not reduced by low temperatures to the same extent as that of poikilothermic animals, and slow-moving stream fishes in cold water are therefore preferred prey during winter by many birds and semi-aquatic mammals, for example mergansers, kingfishers, herons and mustelids (Gerell, 1967; Alexander, 1979; Harvey & Nakamoto, 2013).

To reduce predation risk, fish seek instream shelter in crevices in coarse bottom substrates, stream wood, vegetation, pools and undercut banks (Hartman, 1963; Bustard & Narver, 1975; McMahon & Hartman, 1989; Huusko *et al.*, 2007; Jonsson & Jonsson, 2011). Many stream fishes also suppress daytime activity during winter, presumably to reduce predation risk, and only emerge from their shelters at night (Cunjak, 1988a; Griffith & Smith, 1993; Contor & Griffith, 1995; Fraser & Metcalfe, 1997; Metcalfe & Steele, 2001; David & Closs, 2003). This diel activity pattern may also be an adaptation that allows fish to move away from dynamic instream ice formations that normally take place at night (Heggenes *et al.*, 1993), but this seems unlikely as daytime activity is normally reduced at winter temperatures in the absence of river ice (Fraser, Metcalfe & Thorpe, 1993).

### ***Activity in relation to river ice***

In the Northern Hemisphere about 60 % of the large river basins develop river ice (Allard, Buffin-Bélangier & Bergeron, 2011), and when present it contributes to the instream habitat for stream fish (Prowse, 2001b). At high latitudes and altitudes, winter conditions may even prevail for a more than half of the year, making winter the normal state. River ice influences fish behaviour and may play an important role in growth and survival (Brown *et al.*, 2011).

High densities of frazil ice create adverse conditions for stream fish, which are forced to move away (Jakober *et al.*, 1998; Simpkins *et al.*, 2000) or suffer increased mortality (Maciolek & Needham, 1952). Anchor ice that fills the interstitial spaces in the stream bottom and blankets the stream floor excludes fish from their winter refuges (Jakober *et al.*, 1998; Brown, 1999). Conversely, patchy, unconsolidated anchor ice does not seem to have negative consequences for

overwintering stream fish (Roussel *et al.*, 2004; Linnansaari *et al.*, 2009), and may even be used as cover (Stickler *et al.*, 2008).

Stable winter conditions in streams are associated with low overwinter mortality (Linnansaari & Cunjak, 2010; Hedger *et al.*, 2013), whereas unstable winter conditions, as well as other dramatic changes in the environment, may be stressful (Flores *et al.*, 2012). Once stationary ice cover has been established, it stabilizes the in-stream thermal environment and reduces light intensity, especially when the ice is covered by snow. Stream fish benefit from this stable physical environment. Surface ice has also been suggested to function as overhead cover (Meyers, Thuemler & Kornely, 1992; Young, 1995; Prowse, 2001b), offering protection from terrestrial piscivores (Finstad *et al.*, 2004a).

Stream fish change their habitat use and movement patterns under ice cover (Meyer & Griffith, 1997; Lindstrom & Hubert, 2004; Linnansaari & Cunjak, 2013). Also, it is possible that the presence of surface ice induces daytime activity. Linnansaari, Cunjak & Newbury (2008) showed that daytime activity was positively related to surface ice thickness in two semi-natural experimental streams, but in a recent field study, daytime activity did not increase during periods with ice cover (Linnansaari & Cunjak, 2013). In these studies, passive integrated transponder telemetry was used to assess activity by tracking fish movement through the surface ice, using the “blind spot” technique (Linnansaari *et al.*, 2007). This technique may not have the resolution needed to record activity on a small spatial scale. In cold water, stream fish may be reluctant to spend energy on long foraging bouts, but still actively drift feed or hold position by hovering within a small area, and such behaviours might only be discriminated from sheltering by other techniques (e.g. direct observations).

## Objective

The objective of this doctoral thesis is to investigate the behaviour and growth of stream-dwelling fish exposed to different winter conditions. Specifically, stream salmonids (Fig. 2) were selected as study animals and three research questions were explored: (1) does ice cover affect growth and habitat use?, (2) if so, what might be the underlying mechanisms of such an effect? and (3) how is drift-foraging behaviour affected by winter-like conditions? The work described in this thesis consists of laboratory and field experiments, and I address the proposed research questions in five papers. Paper I reports the results from a field experiment, in which ice cover was simulated by suspending plastic sheeting over sections of a boreal forest stream and comparing these with sections lacking artificial ice cover. In this paper, the growth and spatial positions of brown trout (*Salmo trutta*) were evaluated in relation to ice cover. The study described in Paper II explores some of the mechanisms that explain why ice cover might increase growth. In this study, I used direct observations of the diel behaviour of brown trout in a laboratory stream with and without natural ice cover. In Papers III and IV, I describe and compare the drift-feeding behaviour and efficiency of brown trout, Atlantic salmon (*S. salar*) and European grayling (*Thymallus thymallus*) subjected to different temperatures, light intensities and prey densities. Finally, the study reported in Paper V, which was a joint-effort project for the whole River Ecology and Management research group at Karlstad University, explores how social interactions between brown trout individuals are affected by group composition and the presence of ice cover.



**Figure 2.** Stream salmonids were chosen as study species. The photograph shows a juvenile brown trout from Djupadalsbäcken Creek (Photo F. Laaksonen).

## Methods

The studies in this thesis were conducted both in the field and in the laboratory from 2010 through spring 2015. The field experiment was carried out in a forest stream in central Sweden, and the laboratory studies were conducted in the stream aquarium facility at Karlstad University. This research facility offers the possibility to conduct a wide range of behavioural studies on lotic organisms in replicated artificial streams.

### *Field experiment*

#### *Study site*

The study site for the work described in Paper I was a third order boreal forest stream, Djupadalsbäcken, situated in Örebro County (WGS 84 N59° 29.825', E14° 32.232'). At stable mid-winter conditions, this stream has a typical winter discharge of 0.2 m<sup>3</sup> s<sup>-1</sup>. The catchment area is regularly limed, and pH and conductivity stay relatively stable around 6 and 30 µS cm<sup>-1</sup>, respectively. The stream runs through coniferous forest with Norwegian spruce (*Pice abies*), silver birch (*Betula pendula*) and European alder (*Alnus glutinosa*). The stream is inhabited by brown trout, European brook lamprey (*Lampetra planeri*), northern pike (*Esox lucius*) and Eurasian minnow (*Phoxinus phoxinus*), and American mink (*Neovison vison*) is common in the area.

#### *Artificial ice cover, fish tagging and tracking*

Ten 30-m-long experimental stream sections, separated by buffer zones, were selected, five of which were covered with artificial surface ice, and the other five sections functioned as controls. Artificial ice cover was suspended c. 10 cm over the water surface, and it consisted of semi-transparent polyethylene plastic sheeting attached to wooden poles, and was fastened to poles driven into the stream banks (Fig. 3).



**Figure 3.** Artificial ice cover was suspended over five 30-m-long stream sections and consisted of semi-transparent polyethylene plastic sheeting attached to wooden poles (Photo J. Watz).

In late November, 265 brown trout were collected by electrofishing, length measured, weighed, tagged and released back into the stream. Trout were tagged by inserting passive integrated transponders into their body cavities (Fig. 4). From January through April, tagged trout were tracked on 17 occasions (13 during the day and four at night), using a portable antenna and a backpack reader. The positions of trout across the stream width were recorded in the presence and absence of natural and artificial ice cover. In May, at the end of the experiment, I electrofished the stream, and 437 trout were collected, length measured, weighed and scanned for tags. The length frequency distribution of the electrofished trout allowed me to identify one-summer-old trout (means  $\pm$  SD; November:  $n = 116$ ,  $2.20 \pm 0.68$  g and  $59.5 \pm 5.5$  mm, May:  $n = 268$ ,  $2.72 \pm 0.78$  g and  $66.9 \pm 6.3$  mm), but not fish from older cohorts.



**Figure 4.** Brown trout were tagged with 12 mm passive integrated transponders. The scar from the incision on a recaptured trout can be seen in the photograph as a fine, 2-mm-long dark line anterior of the pelvic fins (Photo F. Laaksonen).

## ***Laboratory experiments***

### *Experimental fish*

Wild and hatchery-reared fish were used in the laboratory studies described in Papers II–V (Table 1). One-summer-old trout, electro-fished in the River Lillån (WGS 84 N57° 50.383', E14° 6,567') were used in the study in Paper II. For the studies in Papers III–V, Fortum Generation AB (Gammelkroppa and Brattfors) provided hatchery-reared, one-summer-old brown trout (origin: River Klarälven in Papers III and IV) and Atlantic salmon (origin: River Klarälven), and Bröderna Olsson (Vallsta) provided hatchery-reared one-summer-old European grayling (origin: River Ljusnan). The parents of all fishes were of wild origin except for the brown trout used in the study in Paper V, which were fourth-generation fish that originated from Lake Konnevesi, Finland.

### *Stream aquaria*

Two types of artificial streams were used in the experiments: (1) 1.2 × 1.0 m riffle sections of 7-m-long artificial streams (Papers II and V) and (2) 2.0 × 0.24 m stream tanks (Papers III and IV). In the 7-m-long streams, built-in chilling systems and pumps cooled and recirculated water at a discharge of 8 L s<sup>-1</sup>. The 2-m-long streams tanks had 600 L water reservoirs placed underneath, and externally chilled water was pumped from the reservoirs to the stream tanks (5 L s<sup>-1</sup>). All streams were illuminated with fluorescent tubes with adjustable light intensities (simulating twilight and daylight), and to simulate moonlight, a LED penlight was used (Paper II). Infrared lamps and video cameras with an infrared sensitive mode enabled night observations (Papers II and III). In foraging trials, thawed bloodworms (Chironomidae) were used as drifting prey. Ice cover was created by freezing distilled water in large plastic trays, and ice blocks were suspended immediately over the water surface (Papers II and V; Fig. 5).

**Table 1.** Summary of the experimental design and fish used in the laboratory studies described in Papers II-VI.

Paper	Treatments	Response variables	Experimental fish	Wild / hatchery-reared	n	Total length (mm; mean $\pm$ SD)	Mass (g; mean $\pm$ SD)
II	Ice cover (2 levels: presence and absence) Time of day (3 levels: night, dawn and day)	Aggression Feeding rate Habitat use Swimming activity Ventilation rate	Pairs of <i>Salmo trutta</i>	w	40	74 $\pm$ 9.4	3.0 $\pm$ 0.99
III	Light intensity (2 levels: 0.1 and 300 lx) Temperature (6 levels: 2, 3, 5, 7, 9 and 11 °C)	Feeding rate Reaction distance	Individual <i>S. trutta</i> , <i>S. salar</i> and <i>Thymallus thymallus</i>	h h h	66 66 66	94 $\pm$ 9.3 84 $\pm$ 9.2 104 $\pm$ 7.2	9.3 $\pm$ 2.4 9.2 $\pm$ 2.0 7.3 $\pm$ 1.7
IV	Prey density (5 levels: 5, 10, 30, 60 and 90 prey min <sup>-1</sup> ) Temperature (2 levels: 5 and 11 °C)	Feeding rate	Individual <i>S. trutta</i> and <i>T. thymallus</i>	h h	10 10	95 $\pm$ 6.3 108 $\pm$ 6.3	8.1 $\pm$ 1.6 7.7 $\pm$ 1.3
V	Group composition (3 levels: groups of fish with high, low and mixed resting metabolic rates) Ice cover (2 levels: presence and absence)	Aggression Eye and body colour Feeding rate Swimming activity Ventilation rate	<i>S. trutta</i> in groups of four	h	48	98 $\pm$ 5.7	8.7 $\pm$ 1.6



**Figure 5.** Ice sheets were placed over the stream channel. Brown trout under ice cover were observed at night ( $< 0.1$  lx), dawn (8 lx) and day (300 lx). At night, fish behaviour was filmed, using infrared lamps and video cameras with an infrared sensitive mode (Photo J. Watz).

### *Experimental design and data collection*

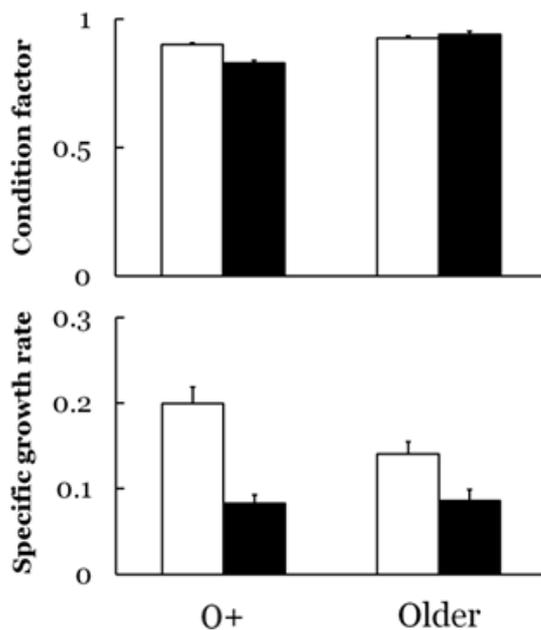
The laboratory experiments were designed to test the influence of temperature, light, prey density, ice cover and social context on fish behaviour, foraging and signs of stress. More specifically, effects on ventilation rate (a proxy for oxygen consumption and metabolic rate), habitat use, swimming activity, drift-feeding rate, reaction distance, aggression and colouration were assessed by direct observations and by viewing video footages (Table 1).

## Summary of results

Fish subjected to different winter conditions in various treatments responded both physiologically and behaviourally by altering, for instance, activity, feeding and sheltering patterns (Table 2). Surface ice cover had substantial effects on growth and antipredator responses, and also influenced social interactions. Fish were able to drift forage at low temperatures during the day, albeit with reduced efficiency. In darkness at low temperatures, there were few successful prey captures.

### *Paper I*

Trout in this field study generally moved relatively little over the course of winter, and more than 60 % of the trout moved less than 30 m in the upstream-downstream direction. The specific growth rate of recaptured one-summer-old trout that had spent winter under artificial ice cover was about twice as high as that of trout in controls. Artificial ice cover also affected the specific growth rate of older trout positively, but the effect was weaker than for the one-summer-old trout (Fig 6). Furthermore, Fulton's condition factor, calculated for all trout electrofished at the end of the experiment (tagged and untagged), was affected positively by the presence of artificial ice cover for one-summer-old but not for older trout.

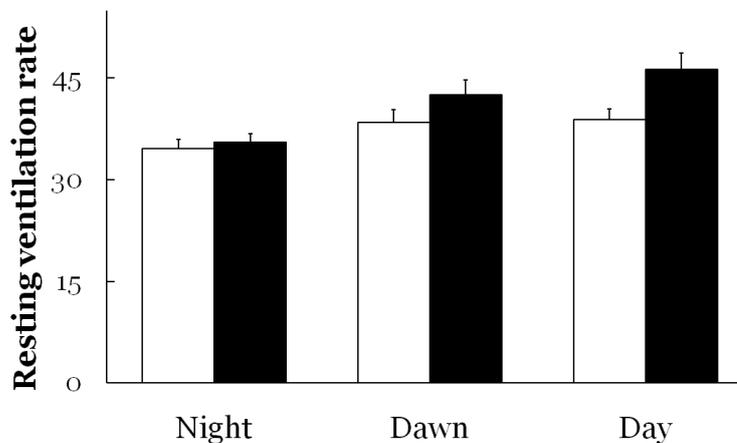


**Figure 6.** Mean condition factor and specific growth rate (% day<sup>-1</sup>) for one-summer-old (O+) and older brown trout in sections with (open bars) and without (filled bars) artificial ice cover. Condition factor was calculated for all trout captured in May, and trout were assigned to treatment and controls based on point of capture. Specific growth rates were calculated for recaptured tagged trout, which were assigned to treatment or control based on the sections where they had been detected  $\geq 80$  % of the time during tracking surveys. Error bars indicate 1 SE. Modified from paper I.

The condition factor of one-summer-old trout electrofished in sections with artificial ice cover was 9 % higher than that of trout in controls. In addition, the spatial distribution of trout extended across the entire stream width in the presence of ice cover. Trout without overhead ice cover were generally found near stream edges or under undercut banks during the day, but were more evenly distributed at night.

### *Paper II*

Resting ventilation rates were lowest at night, intermediate at dawn and highest during the day (Fig. 7). Trout had lower resting ventilation rates in the presence of ice cover than in its absence, especially during the day. Moreover, trout used the deep section of the stream tank to a larger extent with than without ice cover. Time of day influenced the level of swimming activity and aggression, behaviours which were not affected by ice cover. During the day, a larger number of foraging attempts were made by trout in the presence of ice cover than in its absence.

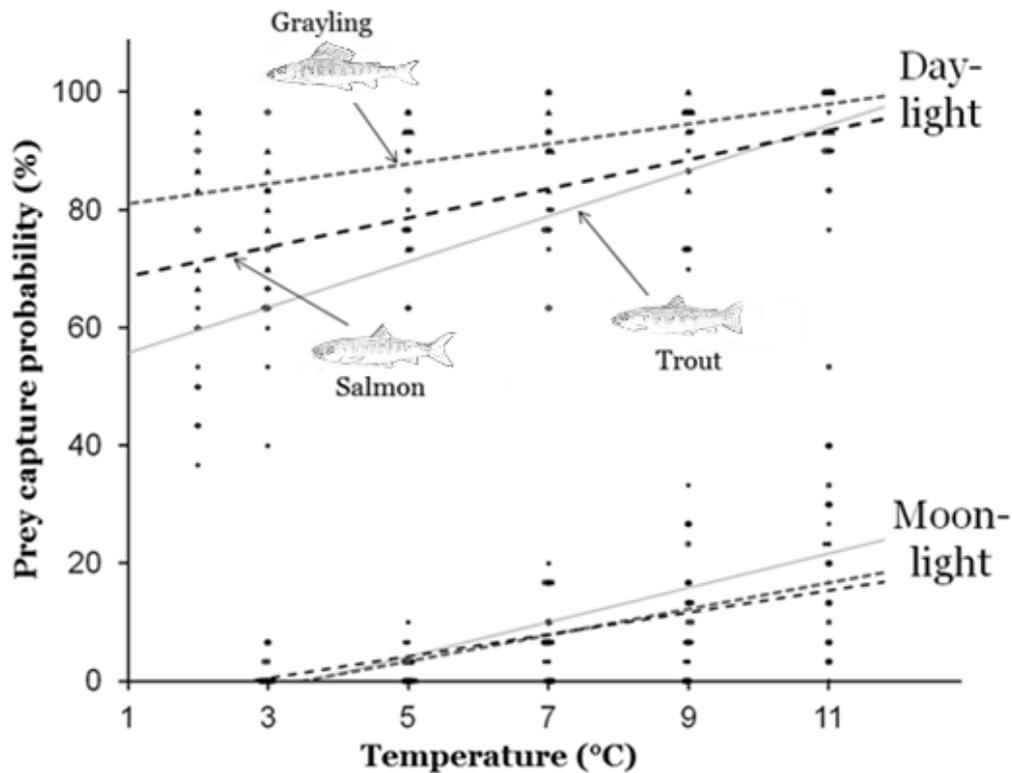


**Figure 7.** Mean ventilation rates (beats min<sup>-1</sup>) for brown trout juveniles in a laboratory stream at night, dawn, and during the day in the absence (open bars) and presence (filled bars) of ice cover. Error bars indicate 1 SE. Modified from Paper II.

### *Paper III*

Drift feeding success was positively related to water temperature, and was substantially higher in daylight than in moonlight (Fig. 8). A typical fish captured about 1 % of the presented prey at 3 °C in moonlight, whereas at 11 °C in daylight fish normally captured most prey. There was also a positive relationship between reaction distance (only measured in daylight) and temperature. All three species used in

this study were affected similarly by temperature and light, but there were subtle differences between species. Brown trout had lower prey capture probabilities than European grayling in daylight and had shorter reaction distances than both Atlantic salmon and European grayling.



**Figure 8.** Prey capture probabilities of three species of salmonids, drift feeding at temperatures ranging from 2 to 11 °C at 0.1 lx (moonlight) and 300 lx (daylight), respectively. Regression lines are fitted to the data (solid lines: brown trout; dashed lines: Atlantic salmon; dotted lines: European grayling). At 0.1 lx, no data were collected for fish at the lowest temperature. Modified from Paper III.

#### *Paper IV*

Prey density positively affected prey capture rates of both brown trout and European grayling, and the shape of this relationship followed a sigmoidal type 3 functional response curve. At high prey densities, prey capture rates were higher at 11 °C than at 5 °C, which is probably because of the inverse relationship between temperature and handling time. There was also a difference between the two species, with

brown trout tending to have lower capture rates than European grayling when prey were delivered at 2-s-long intervals or less.

#### *Paper V*

Trout were more aggressive in the presence of ice cover than in its absence. Trout in groups composed of individuals with high resting metabolic rate increased their swimming activity under ice cover by 400 %, trout in mixed resting metabolic rate groups by 56 %, whereas the swimming activity of trout in low resting metabolic rate groups was not affected by ice cover. Due to overall high and variable activity, variation in ventilation rates was high, and ventilation rates could not be measured on resting trout. Also, during the foraging trials, all prey were usually captured. Hence, there was no effect of ice cover or group composition on ventilation rates or the number of captured prey. However, group composition affected the degree to which a single individual could monopolize the food resource, with the degree of monopolization being highest in the mixed metabolic rate group (67 %), followed by high (52 %) and low (38 %) resting metabolic rate groups. Food monopolization was not affected by ice cover. Both ice cover and group composition influenced the body colour. Trout were pale in low, had intermediate colouration in high and were darkly coloured in mixed resting metabolic rate groups, and trout were paler with than without ice cover. Both dark body and eye colour are indicators of stress, but eye colour varied during a trial, whereas body colour was consistent within a trial.

**Table 2.** Summary of results from the studies described in Papers I–VI, detailing dependent and significant explanatory variables ( $\alpha = 0.05$ ).

Paper	Treatments	Dependent (significant explanatory variables)	Comment
I	Ice cover, time of day	Growth (ice cover) Use of stream width (ice cover, time of day)	Increased growth under ice (time of day not applicable) Expanded use of stream width under ice and at night
II	Ice cover, time of day	Aggression (time of day) Feeding rate (ice cover) Habitat use (ice cover) Swimming activity (time of day) Ventilation rate (time of day, ice cover × time of day)	Most aggression at dawn Increased feeding under ice (only measured during the day) Increased use of deep section under ice Most activity at dawn Low at night, high during the day; reduced under ice during the day
III	Light intensity, temperature, species	Feeding rate (light intensity, temperature, species, light intensity × species) Reaction distance (temperature, species)	Positively related to light and temperature; lower for trout than grayling in daylight Positively related to temperature; lowest for trout (only measured in daylight)
IV	Prey density, species, temperature	Feeding rate (prey density, temperature, prey density × species, prey density × temperature)	Positively related to prey density; at high prey densities: positively related to temperature and lower for trout than for grayling
V	Group composition, ice cover	Aggression (ice cover) Eye colour (none) Body colour (group composition, ice cover) Feeding rate (none) Swimming activity (ice cover, group type × ice cover) Ventilation rate (none)	More aggression under ice Light in low resting metabolic rate groups and dark in mixed resting metabolic rate groups; light under ice cover High under ice cover, mainly for high resting metabolic rate groups

## Discussion and concluding remarks

Harsh winter conditions may challenge lotic fish to physiologically and behaviourally respond to survive. Predation, energy deficits, adverse physical conditions, or a combination of these are major causes of winter mortality (Huusko *et al.*, 2007). In addition, stressors experienced before the onset of winter may have carryover effects on winter survival (Midwood *et al.*, 2015). Stable winter conditions, as well as diverse habitats, seem crucial for overwintering stream-dwelling fish (Brown *et al.* 2011; Huusko *et al.* 2013), and ice cover may provide such stable winter conditions (Finstad *et al.*, 2004a; Linnansaari *et al.*, 2008; Linnansaari & Cunjak, 2010; Hedger *et al.*, 2013).

This thesis extends previous work on lotic fish during winter with focus on the role of ice (Finstad, 2005; Huusko *et al.*, 2007; Linnansaari, 2009; Brown *et al.*, 2011; Huusko *et al.*, 2013). Based on a series of field and laboratory experiments, this thesis contributes to our understanding of the role of surface ice for overwintering stream fish (Papers I, II and V), as well as describes diel drift-feeding behaviour in cold water (Papers III and IV).

In relation to the stated objective of my thesis, I make the following conclusions:

- 1) Overwintering in streams underneath surface ice increases growth rates, and the effects of ice cover may be largest for one-summer-old fish.
- 2) In the presence of ice cover, trout expand their use of habitat, presumably a result of a reduced need for instream shelter.
- 3) In addition to its stabilizing effects on the physical environment, ice cover may reduce predation risk, as surface ice likely functions as overhead cover against terrestrial predators. As a consequence, antipredator behaviours such as vigilance and sheltering may be less important under ice cover. Thus, foraging activity can be increased.

- 4) Ice cover alters social interactions between fish. This effect may be caused by a reduced need for antipredator behaviours, leading to an increased propensity to actively swim, drift feed and be involved in more social encounters.
- 5) Drift-feeding efficiency is substantially higher during the day than at night. At low temperatures, nocturnal prey capture probabilities are especially low. Therefore, increased daytime foraging under ice cover may have large effects on energy intake, at least when the ice permits light penetration.

Trout that spent winter under simulated ice cover in Djupadalsbäcken Creek (Paper I; Fig. 9) grew better than those in control sections. These experimental results are consistent with the observations from a field study carried out in a large Norwegian river, where Atlantic salmon grew more in an ice-covered than in an ice-free area of the river (Hedger *et al.*, 2013). This consistency may indicate that the effect of ice on growth may apply to stream salmonids in general and possibly to other lotic fish species. Increased growth under surface ice has several possible explanations. Ice cover and snow insulate the stream and reduce temperature fluctuations and adverse dynamic instream ice formation (Hicks, 2009; Brown *et al.*, 2011). Furthermore, surface ice likely functions as overhead cover, reducing the need for vigilance and possibly also stress (Papers II and V). Hence, the reduced need for vigilance may permit trout to spend considerable amounts of time on socially, conspicuous behaviours and foraging during the day (Linnansaari *et al.*, 2008; Papers II and V).

In ice-free streams, juvenile salmonids have been widely observed to emerge only at night from their refuges at low temperatures (Fraser *et al.* 1993; Heggenes *et al.*, 1993; Greenberg *et al.* 1996). Ice cover and snow reduce instream light intensity, making the light regime more night-like. Reduced light intensity may partly explain the observed increased daytime activity (Linnansaari *et al.*, 2008). Yet, the results from Papers II and V suggest that additional explanations may be involved since trout in these studies were affected by ice cover despite high instream light intensities (c. 300 lx). Possibly, stream fish are adapted to respond to the presence of surface ice and not solely to low light intensity. If this is true, fish may benefit energetically by foraging during daytime, because drift-feeding efficiency at low temperatures

is poor in darkness, but relatively high when the ice permits some light penetration (Papers II-V).

During winter, juvenile salmonids use habitats where they can shelter, for instance in coarse bottom substrates, stream wood, aquatic vegetation or undercut banks (Huusko *et al.* 2007). However, under surface ice Atlantic salmon parr have been observed to use stream habitats that otherwise provide only a limited amount of instream cover (Linnansaari *et al.*, 2009). These observations are corroborated by the field experiment described in Paper I, where ice cover resulted in an expansion of the distribution of brown trout across the stream's width; i.e. trout moved out from the undercut banks in the presence of ice cover, also during the day. In contrast, other studies have shown that Atlantic salmon do not emerge from their daytime winter shelters regardless of ice conditions (Linnansaari & Cunjak, 2013). The effect of ice cover on the diel activity patterns probably varies depending on species, stream conditions (e.g. light regime, hydrology and prey availability) and the energetic requirements and status of the fish. In the laboratory, I observed that only trout in groups consisting of individuals with high resting metabolic rates substantially increased their swimming activity as a response to surface ice (Paper V). These trout may need to adjust their behaviour to permit relatively high energy intake rates, which are required to meet their metabolic demands. One such adjustment may be to respond to a reduced perceived predation risk by increasing daytime activity under ice cover. Nocturnal foraging should always be preferred if it is sufficient to meet the fish's energetic requirements (Orpwood *et al.*, 2006), which might partly explain the contrast between the results in this thesis and those of Linnansaari & Cunjak (2013).

From an applied point of view, the results in this thesis highlight the need to consider effects of stream management on overwintering fish, particularly when management affects ice processes. Such considerations might, for instance, include placing bounders that break the surface and thereby facilitate surface ice formation, as well as mapping groundwater inputs and releases by warm hypolimnic water from dams and reservoirs. However, stream ice processes are normally not considered when modelling hydraulics to assess winter habitat availability for stream salmonids, e.g. in minimum environmental flow assessments in regulated rivers (Huusko *et al.* 2013). To

be able to accurately predict overwintering success, it is necessary both to develop hydraulic modelling tools that take ice processes into account and to increase our understanding of the performance and habitat selection of fish under winter conditions with and without different types of stream ice.

The dramatic physical changes in the stream environment during winter, caused by for example river ice and low temperatures, affect not only stream fish, but the entire riverine ecosystem (Prowse, 2001b; Weber *et al.*, 2013; Lind, 2015). For many lotic organisms, winter may be a critical period, and therefore knowledge about the winter ecology of different riverine taxa and a holistic ecosystem approach may be crucial for developing tools to restore degraded rivers in boreal areas.



**Figure 9.** Djupadalsbäcken Creek (Photo J. Watz).

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# Paper I



# ICE COVER AFFECTS THE GROWTH OF A STREAM-DWELLING FISH

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## ABSTRACT

Protection provided by shelter is important for survival and affects time and energy budgets of animals. In freshwaters at high latitudes and altitudes, surface ice during winter has been suggested to function as overhead cover for fish, reducing predation risk from terrestrial piscivores. We simulated ice cover by suspending plastic sheeting over five 30-m-long stream sections in a boreal forest stream and examined its effects on growth and habitat use of brown trout (*Salmo trutta*) during winter. Trout that spent winter under artificial ice cover grew more than those in control sections. Moreover, tracking of trout tagged with passive integrated transponders showed that in the absence of ice cover habitat use during the day was restricted to the stream edges, often under undercut banks, whereas under ice cover, trout used the entire stream's width. These results indicate that the presence of surface ice cover may improve the energetic status and broaden habitat use of stream fish during winter. Reductions in the duration and extent of ice cover due to climate change, therefore, will likely alter time and energy budgets, with potentially negative effects on fish production.

## INTRODUCTION

In highly seasonal environments, winter may be a stressful period for animals that do not migrate or hibernate (Marchand 2014). Physiological constraints and reduced resource availability during winter can lead to negative energy budgets (Hurst 2007; McNamara and Houston 2008), which may require catabolism of stored fat for survival (Young 1976; Houston and McNamara 1993; Giacomini and Shuter 2013). The severity of winter conditions and, as a consequence, winter mortality rates can be highly variable and therefore drive population dynamics (Abbott et al. 1985; Coulson et al. 1997; Garvey et al. 2004).

Behavioural strategies to cope with harsh environmental conditions may be influenced by the availability of shelter (Staines 1976; Bonnet et al. 2013). Because of the need to trade off foraging opportunity against predator avoidance, shelter availability affects time and energy budgets (Briones-Fourzán et al. 2007; Finstad et al. 2007; Kollberg et al. 2014; Larranaga and Steingrímsson 2015). Time spent on anti-predator activities, such as predator vigilance, may result in reduced growth as a consequence of fewer foraging opportunities and an elevated metabolic rate due to stress (Millidine et al. 2006). Shelters are usually heterogeneously distributed in space, and in some systems shelter availability may also vary temporally. For instance, seasonal changes in foliage density affect risk of bird nest predation (Borgmann et al. 2013), and snow is a major factor that influences lemmings' and voles' habitat choice and behaviour because of the negative relationship between predation risk and snow cover depth (Reid et al. 2012). Another example is ice cover in shallow freshwaters at high latitudes and altitudes. In these waters, there are often important energy linkages between the aquatic environment and the riparian zone (Schindler and Scheuerell 2002; Baxter et al. 2005); allochthonous material that falls into the water may fuel production, and aquatic invertebrates and fish may become food for terrestrial animals. Surface ice cover disrupts this linkage during winter and may therefore have large effects on the ecosystem. Functioning as overhead cover, surface ice may influence the time and energy budgets of fish as ice cover may severely reduce or completely eliminate feeding opportunities for terrestrial piscivores.

In running waters, the effects of low temperature on fishes' metabolic rates and physical performances result in reduced abilities to drift-feed (Watz and Piccolo 2011; Watz et al. 2012; 2014a) and escape predators (Webb 1978). In northern latitudes and high elevations this may play an especially important role in population dynamics because low water temperatures are prevalent for a large part of the year. The winter behaviour of lotic fishes may therefore be particularly affected by the trade-off between foraging opportunities and predator avoidance (Huusko et al. 2007). If predation risk

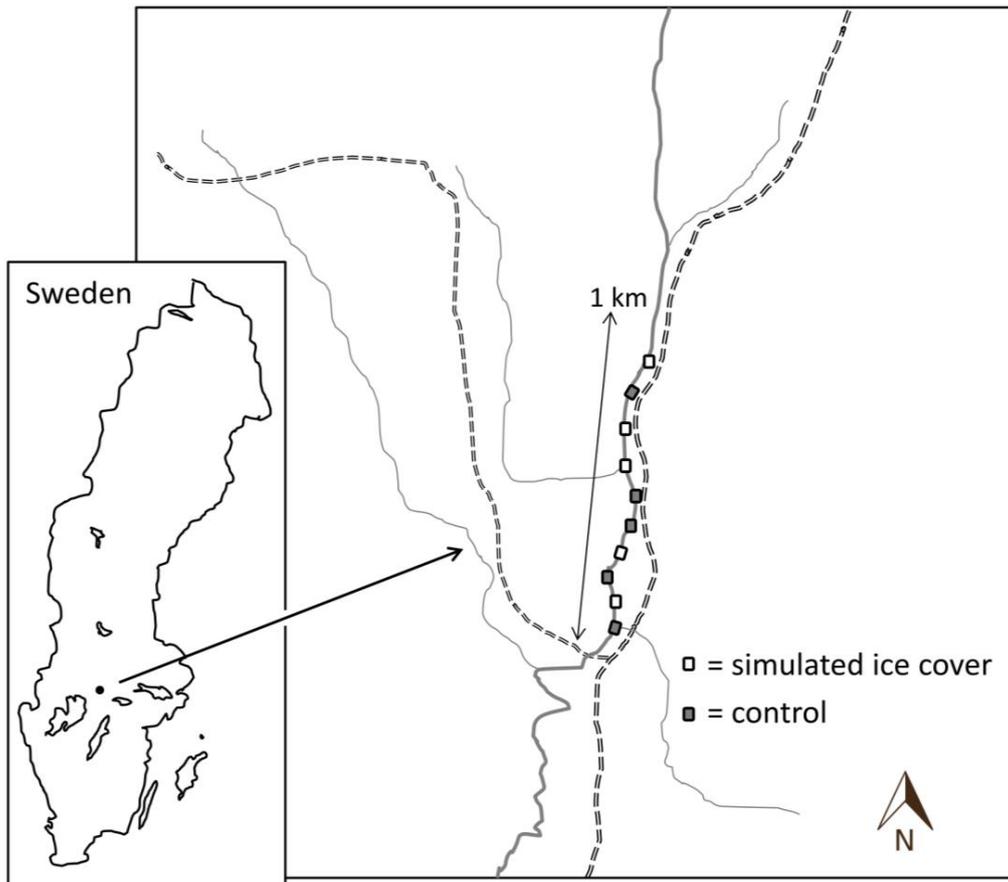
is mainly posed by terrestrial predators, periods with ice cover should relax predation pressure and alter the time budgets of fish so that more time may be spent on foraging (Watz et al. 2013), movement (Linnansaari et al. 2008) and interactions with conspecifics (Watz et al. 2015). These effects should be largest on fish from the youngest size classes, as small fish are more likely to be preyed upon than large fish (see references in Gustafsson et al. 2010). A stable ice cover throughout winter has indeed been observed to increase survival rates of juvenile stream fish (Linnansaari and Cunjak 2010; Hedger et al. 2013). Hence, the predicted and reported effects of climate change on stream ice dynamics, resulting in shorter periods with stable ice cover (Magnuson et al. 2000; Benson et al. 2012) could have important implications for population dynamics of stream fish, because survival of the youngest size classes may influence population size (Cattanéo et al. 2002; Biro et al. 2004; Borgström and Museth 2005).

The behaviour and growth of fish under surface ice has been studied in the field (Brown 1999; Brown et al. 2000; Linnansaari et al. 2009; Hedger et al. 2013; Linnansaari and Cunjak 2013) For example, Linnansaari et al. (2009) reported that juvenile Atlantic salmon (*Salmo salar*) under surface ice used habitats that generally are avoided in the absence of ice cover, and Hedger et al. (2013) showed that juvenile Atlantic salmon in an ice-covered river section depleted their energy reserves at a slower rate than in an ice-free section. However, none of these studies have involved manipulative field experiments. In this field study, we manipulated ice cover to test its effects on behaviour and growth of fish in a boreal forest stream. Using brown trout (*S. trutta*) as the study organism, we investigated whether or not growth and habitat use were influenced by ice cover. We predicted that ice cover would (1) increase overwinter growth and condition factor and (2) lead to a broader spatial distribution of the fish.

## MATERIALS AND METHODS

### *Study site*

The study was carried out from November 2012 through May 2013 in an approximately 1-km-long reach of Djupadalsbäcken Creek (Fig. 1), a third order boreal forest stream located in central Sweden (WGS 84 N59° 29.825', E14° 32.232'). Throughout the study, conductivity and pH were relatively stable (24–30  $\mu\text{S cm}^{-1}$  and 6.2–6.5, respectively). In the study reach, brown trout and European brook lamprey (*Lampetra planeri*) were abundant. Northern pike (*Esox lucius*) also occurred, albeit in very low numbers. Eurasian minnow (*Phoxinus phoxinus*) and possibly European bullhead (*Cottus gobio*) inhabit the system, but were not observed during the study.



**Fig. 1.** Map showing the location of the study stream. Artificial ice cover was suspended over five 30-m-long sections (white boxes) and five sections were used as controls (grey boxes). The study reach (~ 1 km) was demarcated in the upstream, northern end by a small waterfall and in the downstream, southern end by a culvert.

The mean width of the reach was on average 2.7 m, and the bottom substrate consisted of silt, sand, gravel, stones and boulders. In the upstream part of the reach, large stones and boulders were more frequent and the stream was narrower and had fewer pools than in the downstream end, where the stream meandered. The downstream sections were dominated by fine substrates. Instream wood was heterogeneously distributed with the highest densities found in the middle of the reach. Undercut banks provided instream cover for the fish where other types of shelters were lacking. Norwegian spruce (*Pice abies*), silver birch (*Betula pendula*) and European alder (*Alnus glutinosa*) were the most common trees in the riparian zone. Endothermic piscivores that hunt in boreal forest streams during winter include American mink (*Neovison vison*), European otter (*Lutra lutra*) (Wise et al. 1981; Heggenes and Borgstrøm 1988) and several bird species, for example owls (Strigiformes) (Harvey and Nakamoto 2013). At the study site, we observed mink tracks in the snow relatively often, whereas otter only occurs sporadically in the area.

### *Fish capture and tagging*

We electrofished the stream reach in November 2012. After capture, trout were anaesthetised with tricaine methanesulfonate (MS-222) and total length (mm) and wet mass (accuracy 0.1 g) were measured. Using the length distributions from the electrofished trout, we were able to determine the size range of one-summer-old trout, but it was not possible to determine to which year-class older trout belonged. Therefore, we used two size classes in the statistical analyses: one-summer-old and older trout.

We tagged 99 one-summer-old and 166 older trout ( $n = 265$ ) individually by inserting half duplex  $12 \times 2.15$  mm passive integrated transponders (PIT; Oregon RFID, Portland, USA) into the abdominal cavity (Prentice et al. 1990), a technique that has a negligible effect on the behaviour and growth of juvenile brown trout (Acolas et al. 2007). Trout were carefully released back to the stream at exactly the same location from which they had been collected to reduce the risk of trout moving into new areas. At the end of the experiment in May 2013, we electrofished the reach again and collected 437 trout. We measured lengths and wet masses, and we scanned the trout for tags.

### *Ice cover*

For the experiment, we selected ten 30-m-long sections along the study reach. Each section was separated by a 30–60-m-long buffer zone from adjoining sections (Fig. 1). The criteria for the selection of experimental sections were: access for installing artificial ice cover, relatively similar habitat and the occurrence of one-summer-old trout. The length of the experimental sections (30 m) was selected based on the reported limited winter movement of brown trout, which is often less than 10 m (Palm, Brännäs & Nilsson 2009). Along the edges of each of the ten experimental sections, we drove wooden poles into the banks. Five of the sections were randomly selected as controls. Over the remaining five, we suspended artificial ice cover. Ice cover was created by attaching 0.2-mm-thick semi-transparent polyethylene plastic (Byggmax AB, Solna, Sweden) to wooden poles (Fig. 2), and the artificial ice cover was attached to the poles along the banks. The plastic sheet absorbed approximately 25 % of the light (corresponding to an approximately 4 cm thick natural ice sheet), and was positioned approximately 10 cm over the water surface. We placed temperature and light intensity data loggers (HOBO Pendant, Onset Computer Corp., Bourne, USA) on the bottom of the stream in treatment and control sections. The experiment started after completion of the artificial ice cover on 17-Dec-2012, and the experiment was terminated on 15-May-2013 when the artificial ice was removed. During the course of winter and early spring, the artificial ice cover was damaged twice due to spates (Fig. 3) and had to be repaired (7–8-Jan and 23-Apr, respectively).



**Fig. 2.** Two photographs of the same downstream end of a section with artificial, plastic ice cover. During the course of winter, there were periods when light could penetrate through the artificial ice cover (left photograph) and periods when snow limited light penetration (right photograph).

### *Fish tracking*

We tracked tagged trout throughout winter using a backpack PIT-detector and a handheld pole antenna (Oregon RFID, Portland, USA). Tracking surveys always started at the downstream end of the reach, and the person carrying the PIT-detector moved upstream, wading in the stream or walking on the bank along the stream or on the ice. The entire wetted width of the stream was searched with the pole antenna. The maximum detection distance was approximately 60 cm, and in shallow areas, we could locate the positions of detected trout with an accuracy of approximately 10 cm using the “blind-spot” method (Linnansaari et al. 2007). This method uses the inability of the round inductor loop antenna to detect tags in its centre. When a tag is located in the central “blind-spot”, no detection is registered, but moving the antenna in any direction will cause detection, indicating the position of the trout. We could not use the blind-spot method in deep areas, e.g. pools, reducing the accuracy to approximately 30 cm. We did not observe trout fleeing from the person holding the antenna, and flight responses to this type of tracking have been shown to be non-existent in cold water (Ellis et al. 2013). During this study, we carried out 17 tracking surveys (13 during the day and 4 at night) in conditions both with (11 surveys) and without (6 surveys) natural surface ice, and the number of detections in a single survey ranged from 34 to 102.

### *Data analysis*

In the analyses, we assessed growth and how it was related to habitat use, specifically whether or not trout spent the winter under the artificial ice cover. We calculated the specific growth rate, SGR (% growth day<sup>-1</sup>), and Fulton's condition factor, K, of recaptured tagged trout. For the calculation of  $SGR = 100 \times (\ln M_{\text{after}} - \ln M_{\text{before}}) T^{-1}$ , we used wet masses before,  $M_{\text{before}}$  (g), and after,  $M_{\text{after}}$  (g), the experiment and the duration of the experiment,  $T$  (days). We calculated K from wet masses,  $M_{\text{after}}$  (g), and total lengths,  $L_{\text{after}}$  (mm), where  $K = 100\,000 \times M_{\text{after}} \times L_{\text{after}}^{-3}$ . As we did not know the locations of the trout between the tracking surveys, we categorised trout as either belonging to sections with artificial ice cover or controls using three different approaches. Categorisation approaches included: using the sections in which trout (1) were captured, tagged and released in November, (2) were recaptured in May and (3) had the most detections during the tracking surveys. For approach (3), we included only trout that did not move between sections to a large extent. To identify what level of site fidelity to use, we initially compared three different inclusion criteria: trout that were found more than 80, 85 and 90 % in the same section, respectively. The choice of inclusion criterion did not have any substantial effect on the results and did not affect the interpretation, and hence we chose the 80 % limit to maximize sample size.

The three approaches used for analyses of SGR and K showed similar results, with all showing effects of ice cover (see Results). Hence, we elected to perform an additional analysis of K using approach (2) on all trout captured in May (i.e. tagged and untagged trout pooled), as K, in contrast to SGR, does not require recapturing fish.

Approaches (1), (2), and (3) resulted in 57, 53 and 35 recaptured tagged trout being used in the analyses, respectively. The additional analysis of K performed on tagged and untagged trout used 187 trout. We used all three approaches of assigning recaptured tagged trout to either the ice cover treatment or the control to assess the effects of ice cover and size class on SGR and K, and the additional analysis of K used only approach (2), resulting in seven two-way ANOVAs with the term section nested within ice cover treatment included.

The positions of trout across the stream width were calculated as a proportion, ranging from zero to one. This proportion was calculated as the distance between the trout and the nearest stream edge divided by half of the stream width. A trout positioned right at the stream edge was therefore assigned the value zero, and a trout positioned in the middle of the stream was assigned the value one. From the day and night tracking surveys, we compared positions of trout across the width of the stream channel in the

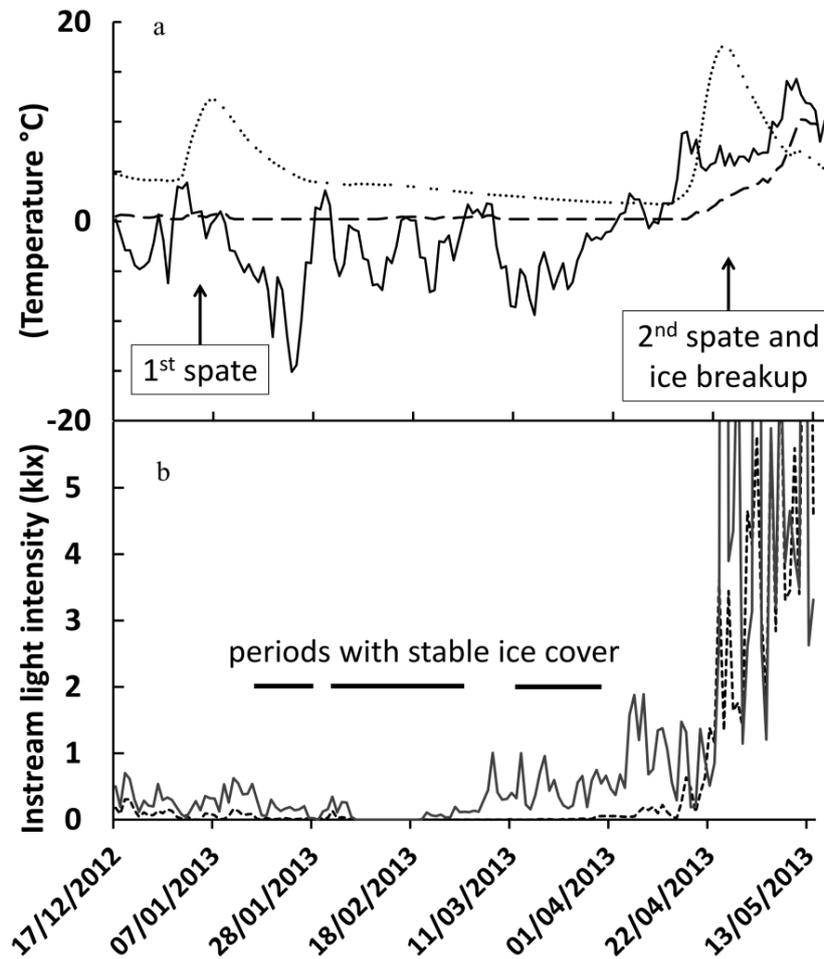
sections with artificial ice cover with positions of trout in ice-free areas in control sections. As an additional check to verify that the artificial ice cover had a similar effect as natural ice cover on stream width use, we also compared the positions of trout in the presence and absence of natural ice cover in the buffer zones. We used the data from the buffer zones for this comparison to have a large sample size and also because this allowed us to use two different data sets to conduct two independent analyses: (1) treatments vs. ice-free controls and (2) the presence vs. absence of natural ice cover in buffer zones.

In the analyses of stream width use, we only used the positions of recaptured trout (i.e. apparent survival). We tested the effects of day/night, ice cover and size class on arcsine square root transformed proportions with mixed models, using trout ID as subjects and dates as a repeated variable. The term section nested within ice cover was included as a main effect for analysis (1), and for the additional analysis (2), section was included as a main effect. Non-significant terms ( $P > 0.05$ ) were removed stepwise, the least significant term first. The terms section and section nested within ice cover treatment, were not removed from the final models. All statistical analyses were performed using SPSS 20 (IBM, Armonk, NY, USA).

## RESULTS

### *Abiota*

Monthly mean water temperature ranged from 0.3–0.4 °C from December through March and increased in April (1.1 °C) and May (7.2 °C) (Fig. 3). There was no temperature difference between treatment and control sections during the course of the experiment (repeated measures ANOVA,  $F = 0.52$ ,  $df = 1,5$ ,  $P = 0.50$ ). There were major cold-spells on several occasions during the course of winter (Fig. 3). Natural surface ice occurred during about 60 % of the study period both in control and buffer sections from December until the end of April, but it never covered the entire reach, with the exception of a few days in January and in April. In the control sections, ice cover normally ranged from non-existing to almost complete coverage with patches of open water. Although winter flow remained fairly stable with a typical discharge of approximately  $0.2 \text{ m}^3 \text{ s}^{-1}$ , snowmelt during a mild period in January resulted in a spate (Fig. 3). A second spate occurred with ice break-up in the last days of April. Reliable and comparable instream light data, measured at approximately 20 cm depth, could only be obtained from two loggers under artificial ice cover and two loggers from control sections. The light intensity under the artificial ice cover was generally lower than in the control sections, apart from periods with snow on stable natural surface ice and after the second spate (Fig. 3).

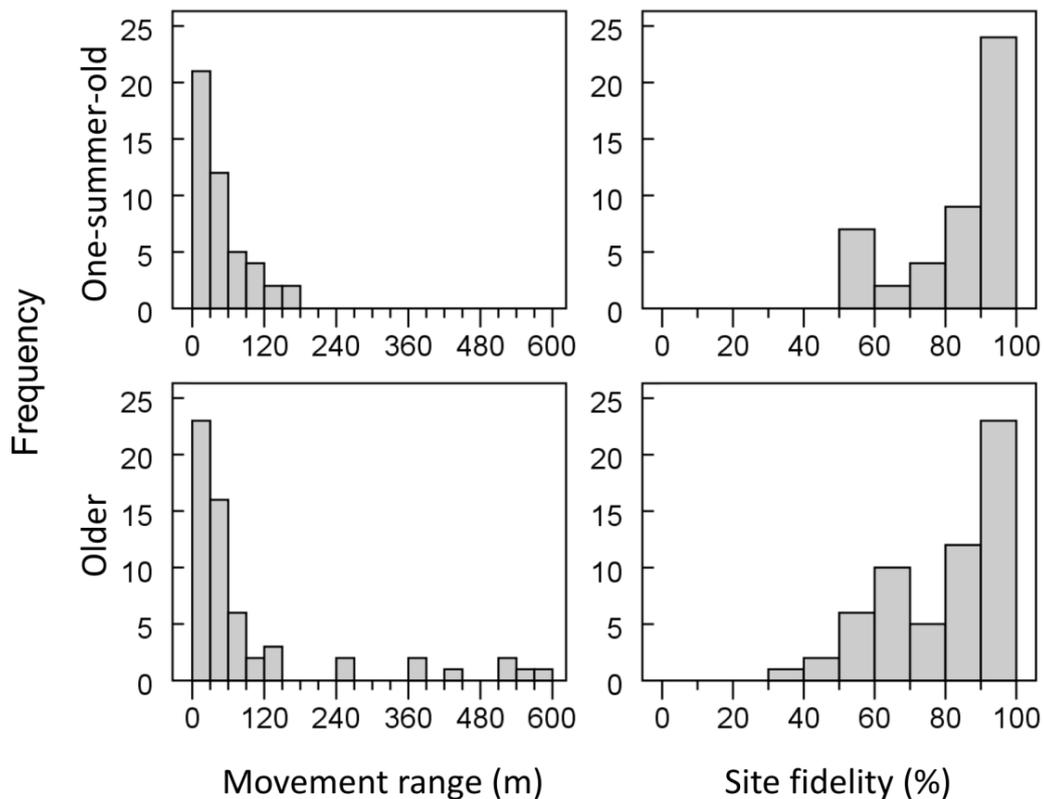


**Fig. 3.** The experiment started in December 2012 and finished in May 2013. (a) Air temperature (solid line) and water temperature (dashed line) of the study stream from experiment start to finish. Discharge data could not be obtained for the study stream, but discharge from a nearby stream from the same catchment is shown instead (dotted line). The timing of two high flow events (spates) in the study stream is also shown. (b) Mean instream light intensity at 12:00 AM from two light loggers in control sections (solid line) and from two light loggers under artificial ice cover (dashed line). Loggers were placed at a depth of approximately 20 cm.

### *Movement*

One-summer-old trout moved little in the upstream-downstream direction over the course of winter (Fig. 4). More than 60 % of trout from this size class moved less than 30 m and 44 % of them moved less than 15 m, which also was the median distance moved. Eleven percent of the one-summer-old trout moved more than 100 m. Although most of the trout from the large size class (61 %) also moved less than 30 m, this size class included more trout

that moved long distances; for example, 22 % moved more than 100 m and 7 % more than 500 m (Fig. 4). Mean site fidelity (proportion of detections of an individual in the same place) was almost the same for one-summer-old and older trout (84 and 80 %, respectively; Mann-Whitney,  $U = 1186$ ,  $n = 104$ ,  $P = 0.34$ ). For one-summer-old trout, SGR did not correlate with movement or site fidelity (Pearson,  $n = 45$ ,  $r = -0.093$  and  $0.214$ ,  $P = 0.54$  and  $0.16$ ). For older trout, SGR did not correlate with movement range (Pearson,  $n = 59$ ,  $r = -0.198$ ,  $P = 0.132$ ), but there was a weak positive relationship between SGR and site fidelity (Pearson,  $n = 59$ ,  $r = 0.266$ ,  $P = 0.042$ ).

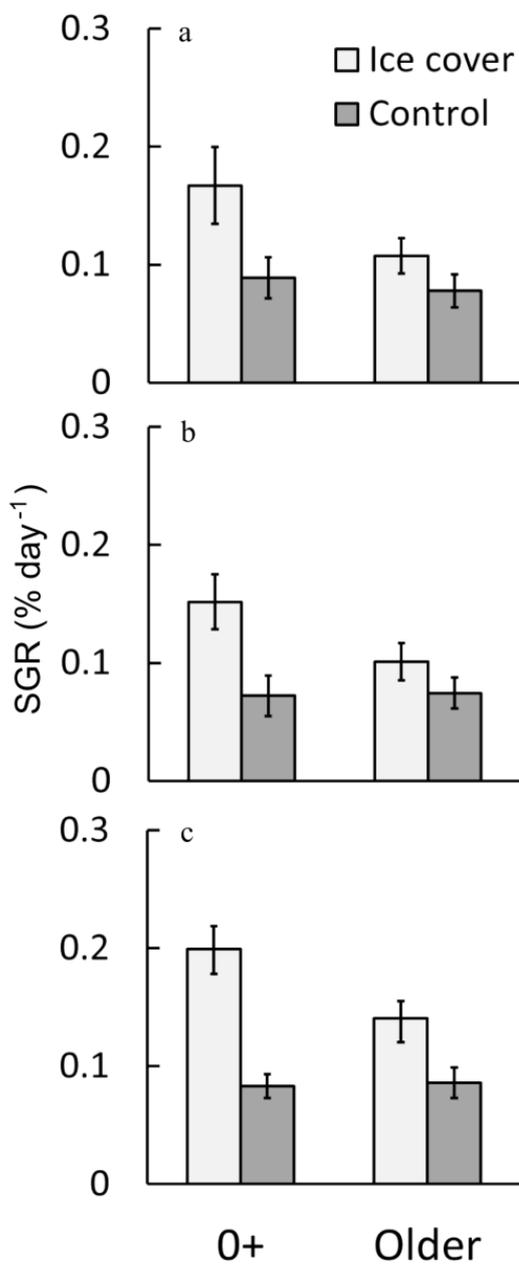


**Fig. 4.** Maximum range of movement in the upstream-downstream direction (left panels) and site fidelity (right panels) of one-summer-old (upper panels) and older (lower panels) brown trout (*Salmo trutta*) based on tracking surveys ( $n = 17$ ) over the winter. Site fidelity was defined as the percentage of detections trout had in the same place.

#### *Growth and recaptures*

Using data from all electrofished trout, one-summer-old trout were on average  $59.5 \pm 5.5$  mm and  $2.20 \pm 0.68$  g in November and had grown to  $66.9 \pm 6.3$  mm and  $2.72 \pm 0.78$  g in May (means  $\pm$  SD). Corresponding values for older trout were  $122.8 \pm 31.1$  mm;  $23.0 \pm 17.6$  g in November and

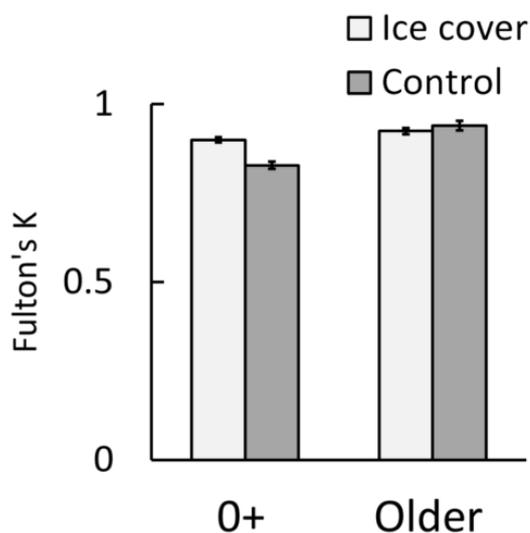
134.1 ± 31.6 mm; 26.1 ± 18.6 g in May. Of the 265 tagged trout, 48 one-summer-old and 60 older trout were recaptured, which correspond to 48 and 36 % apparent survival for the two size classes, respectively. We found 14 tags from one-summer-old and 30 tags from older trout on the stream bottom, indicating that they either died or lost their tags (13 and 17 % of the tagged trout from the two size classes, respectively). There was no difference in recapture rate between one-summer-old and older trout ( $\chi^2 = 3.06$ ,  $df = 1$ ,  $n = 265$ ,  $P = 0.08$ ). Recaptured, tagged one-summer-old trout had grown between 5.5 and 19 % in length and between -5.2 and 71 % in mass. For older trout, the corresponding ranges were -1.4–17 % and 0.2–52 %, respectively.



**Fig. 5.** Mean specific growth rate, SGR, ( $\pm$ SE) for one-summer-old (0+) and older brown trout (*Salmo trutta*) in sections with and without artificial ice cover. SGR was calculated for tagged, recaptured trout assigned to sections with artificial ice cover or control sections using three different approaches: (a) point of release at the start of the experiment ( $n = 57$ ), (b) point of recapture after the experiment had been terminated ( $n = 53$ ) and (c) the sections where the trout had been detected  $\geq 80\%$  of the time during the tracking surveys ( $n = 35$ ).

The effects of artificial ice cover on the SGR and K of tagged trout were assessed by separate two-way ANOVAs based on (1) point of release in November, (2) point of recapture in May and (3) tracking data. Regardless of approach, there were significant positive effects of ice cover on SGR (Fig. 5; Table 1), as well as on K (Table 1). When using the point of recapture approach, there was also a significant interaction effect between size class and ice cover treatment on both SGR and K, so that ice cover had larger effects for one-summer-old than for older trout. This interaction effect was not found for SGR when using the other two approaches, but for K, this interaction effect was also significant using approach (3). Furthermore, stream section nested within ice cover treatment had a significant effect on SGR when using the point of release approach, but it did not have a significant effect in any of the other ANOVAs (Table 1).

Condition factor, K, for all one-summer-old and older trout (tagged and untagged) captured in May was  $0.87 \pm 0.08$  and  $0.92 \pm 0.06$ , respectively (means  $\pm$  SD). Pooling tagged and untagged trout resulted in a large sample size ( $n = 187$ ), and the additional analysis of K on tagged and untagged trout pooled thus had large statistical power. Ice cover had a significant positive effect on K, and one-summer-old trout had significantly lower K than older trout. There was also a significant ice cover  $\times$  size class interaction term, indicating that the effect of ice cover was larger for one-summer-old than for older trout. One-summer-old trout captured in sections with artificial ice cover had on average 8.7 % higher K than those captured in control sections, whereas K of older trout differed little between treatment and control (Fig. 6). Moreover, there was a significant effect of stream section nested within ice cover (Table 1).



**Fig. 6.** Mean Fulton's conditions factor, K, ( $\pm$ SE) for one-summer-old (0+) and older brown trout (*Salmo trutta*) captured in sections with artificial ice cover or control sections after the experiment had been terminated (both tagged and untagged trout;  $n = 187$ ).

**Table 1.** Results from two-way ANOVAs, showing the effects of artificial ice cover and size class on specific growth rate (% day<sup>-1</sup>), SGR, and Fulton's condition factor, K, of recaptured tagged brown trout (*Salmo trutta*). In the analyses, three approaches were used to assign recaptured tagged trout to treatments or controls: first, the point of release in November, second, the point of recapture in May and, third, where trout had been detected most of the time during the tracking surveys throughout winter. The table also shows results from an additional two-way ANOVA, analysing the effects on K of tagged and untagged trout using the point of capture in May.

Variable	Source of variation	<i>F</i>	df	<i>P</i>	$\eta_p^2$
Specific growth rate ( <i>point of release</i> )	Ice cover	6.86	1, 45	<b>0.012</b>	0.43
	Size class	3.25	1, 45	0.078	0.28
	Ice cover × size class	0.69	1, 45	0.412	0.09
	Section(ice cover)	2.56	8, 45	<b>0.022</b>	0.64
Specific growth rate ( <i>point of recapture</i> )	Ice cover	10.08	1, 41	<b>0.003</b>	0.59
	Size class	2.02	1, 41	0.163	0.25
	Ice cover × size class	4.13	1, 41	<b>0.049</b>	0.41
	Section(ice cover)	1.81	8, 41	0.102	0.65
Specific growth rate ( <i>tracking surveys</i> )	Ice cover	16.95	1, 23	<b>&lt; 0.001</b>	0.81
	Size class	3.15	1, 23	0.089	0.54
	Ice cover × size class	2.16	1, 23	0.155	0.47
	Section(ice cover)	1.24	8, 23	0.319	0.75
Fulton's condition factor ( <i>point of release</i> )	Ice cover	8.34	1, 45	<b>0.006</b>	0.16
	Size class	0.72	1, 45	0.400	0.02
	Ice cover × size class	1.56	1, 45	0.218	0.03
	Section(ice cover)	1.64	8, 45	0.139	0.23
Fulton's condition factor ( <i>point of recapture</i> )	Ice cover	16.73	1, 41	<b>&lt; 0.001</b>	0.29
	Size class	0.965	1, 41	0.332	0.02
	Ice cover × size class	13.34	1, 41	<b>0.001</b>	0.25
	Section(ice cover)	2.11	8, 41	0.057	0.29
Fulton's condition factor ( <i>tracking surveys</i> )	Ice cover	17.90	1, 23	<b>&lt; 0.001</b>	0.44
	Size class	0.66	1, 23	0.427	0.03
	Ice cover × size class	7.47	1, 23	<b>0.012</b>	0.25
	Section(ice cover)	1.97	8, 23	0.097	0.41
Fulton's condition factor ( <i>tagged and untagged trout;</i> <i>point of recapture</i> )	Ice cover	6.14	1, 175	<b>0.014</b>	0.04
	Size class	44.16	1, 175	<b>&lt; 0.001</b>	0.20
	Ice cover × size class	14.23	1, 175	<b>&lt; 0.001</b>	0.08
	Section(ice cover)	2.13	8, 175	<b>0.036</b>	0.10

Within control sections, the amounts of instream shelter may have differed, possibly affecting growth. Among the controls, mean SGR (averaged from approach (1) – (3) and size classes pooled) ranged from 0.02 to 0.10 % day<sup>-1</sup>, and mean K of tagged and untagged trout (size classes pooled) ranged from 0.81 and 0.88. Both the lowest mean SGR and K were found in the most downstream control section, a section in which sand and silt were the most common types of bottom substrate. The second most upstream control section (located in the middle of the reach) had high densities of stream wood, and among the controls this section had the highest mean SGR. Apart from the control with the lowest mean K, mean K did not differ substantially (range: 0.86 – 0.88).

#### *Trout location across the stream*

Trout detected under artificial ice cover used more of the stream channel width than those detected in control sections in the absence of natural surface ice. Trout also used more of the stream width at night than during the day (Fig. 7). There was no difference between one-summer-old and older trout in this regard. The artificial ice cover and natural surface ice had similar effects on stream width use (Table 2), and without ice cover during the day, the majority of trout were found at the stream edges, often under the undercut banks.

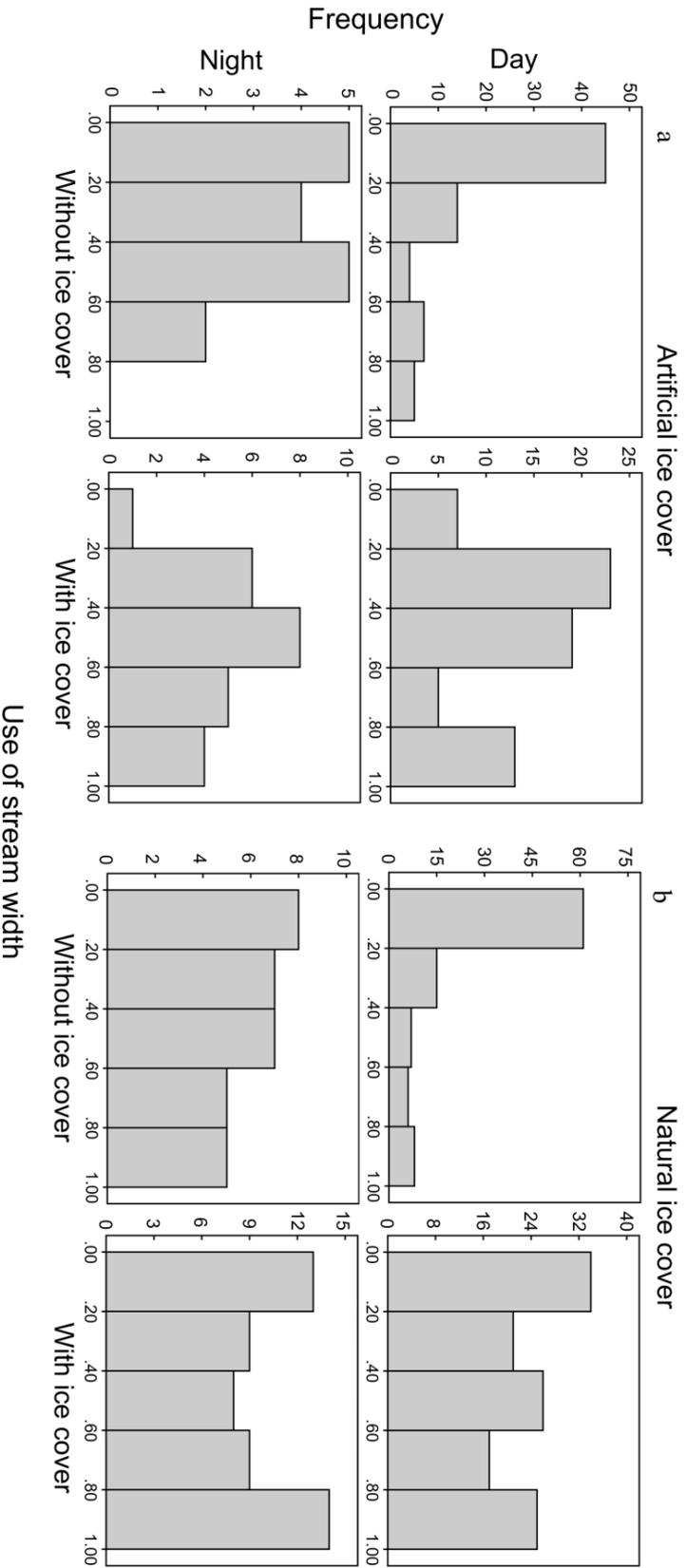
**Table 2.** Results from linear mixed effects models for brown trout, detailing significant explanatory variables ( $\alpha = 0.05$ ) that affected use of stream width for each model. In the upper model, arcsine square root transformed data were used from trout detected in sections with artificial ice cover and from trout without ice cover in control sections. In the lower model, arcsine square root transformed data from trout detected in the buffer zones with and without natural ice cover were used in the analysis.

Dependent variable	Significant explanatory variables	<i>F</i>	df	Estimate ( $\pm$ SE)	<i>P</i>
Use of stream width ( <i>artificial ice cover vs. open controls sections</i> )	Ice cover	9.31	1, 159.97	0.122 ( $\pm$ 0.061)	<b>0.003</b>
	Time of day	4.02	1, 136.59	0.689 ( $\pm$ 0.204)	<b>0.047</b>
Use of stream width ( <i>with vs. without natural ice cover in buffer zones</i> )	Ice cover	30.02	1, 287.53	0.258 ( $\pm$ 0.046)	< <b>0.001</b>
	Time of day	11.40	1, 259.80	0.159 ( $\pm$ 0.047)	< <b>0.001</b>

When control sections and buffer zones were partially covered by ice, surface ice generally occurred as border ice near the stream edges, making it impossible to detect trout without ice cover near the stream edges or to detect trout with ice cover in the middle of the stream. Therefore, there is a bias in the assessment of trout location. Our results, however, show a pattern opposite to this bias (trout used more of the stream width in the presence of ice cover than in its absence), which makes our results conservative, and the effect of ice cover on trout location across the stream might be even larger than we report.

## DISCUSSION

This study showed that in the presence of ice cover trout had higher growth rates and used more of the available stream habitat than in the absence of ice cover. This suggests that ice cover may play an important role in overwintering in streams at high altitudes and latitudes. Several factors may contribute to a beneficial effect of a stable ice cover on stream fish growth and survival (Finstad et al. 2004; Linnansaari and Cunjak 2010; Hedger et al. 2013). First, as ice and snow prevent thermal heat loss to the air, water temperature is relatively stable under full ice cover (Hicks 2009), and stream fish under the ice therefore suffer less from problems with frazil ice and acclimatization (Huusko et al. 2007). Second, surface ice reduces in-stream light intensities, in particular when the ice is covered with snow. Reduced light levels influence both activity patterns (Valdimarsson et al. 1997; Valdimarsson and Metcalfe 2001) and reduce metabolic rate (Finstad et al. 2004). Third, ice cover reduces predation risk from piscivorous mammals and birds. Consequently, the trade-off between exposure while foraging and starvation faced by stream fish during winter might be affected by overhead ice cover, with, for example, the presence of ice resulting in more time spent foraging (Watz et al. 2013). It is likely that daytime activity under ice cover (Linnansaari et al. 2008; Watz et al. 2013) carries relatively low risk of predation. Conversely, without ice cover juvenile salmonids are restricted to nocturnal foraging (Heggenes et al. 1993). Because foraging efficiency in cold water is low in darkness (Watz et al. 2014b), relatively more time and effort are required to meet the energetic needs than would be the case if the fish could forage during the day. Moreover, trout under ice cover exhibit less signs of stress (Watz et al. 2015), and overhead cover reduces maintenance metabolism (Millidine et al. 2006), affecting a fish's energy balance. In our study, all three of the above mentioned effects of ice cover may have contributed to the effect of the artificial ice cover on growth. However, the stabilising effect on water temperature probably played a minor role, as we could not find any difference in water temperature between sections with artificial ice cover and controls.



**Fig.7.** Positions of brown trout (*Salmo trutta*) across the stream width during the day (upper panels) and at night (lower panels). (a) Left panels show positions of trout in the absence and right panels presence of artificial ice cover. (b) Left panels show positions of trout in the absence and right panels presence of natural ice cover. A value of zero represents a detection at the stream edge and a value of one a detection in the middle of the stream. Trout not recaptured at the end of the experiment are not included. Data are pooled from 17 tracking surveys and 109 trout.

During winter, different lotic fish species have been observed to be associated with specific microhabitats (e.g. Heggenes et al. 1993; Cunjak 1996; Mäki-Petäys et al. 2004; Riley et al. 2006; Johnson and Douglass 2009), often low velocity habitats with coarse bottom substrate. Yet, few studies have recorded microhabitat selection in the presence of ice cover (Huusko et al. 2007; Brown et al. 2011), and it is possible that the need for instream shelter (i.e. large stones, woody debris and undercut banks) is reduced under surface ice (Gregory and Griffith 1996; Linnansaari et al. 2009). In our study, trout were mostly restricted to the undercut banks when ice cover was lacking, particularly during the day. In contrast, when ice cover was present, either in the form of artificial plastic or natural surface ice, trout used the entire stream width, both at night and during the day. The use of an increased proportion of available stream habitat would likely allow trout to access more favourable feeding conditions, one possible explanation for increased growth under ice cover.

We expected that growth and habitat use would vary among the control sections. The controls had likely different amounts of instream shelter and stream morphology, and therefore we included section in the analyses. Contrary to our expectations, section did not affect stream width use, and it only affected SGR when using the point of release approach. Section did however affect K when analysing tagged and untagged trout pooled. The most downstream control section had little stream wood, and the bottom substrate consisted of sand and silt. Not surprisingly, this was also the control section in which trout had the lowest SGR and K. As we did not monitor the daily development of natural surface ice in controls and buffer zones, we do not know the extent to which differences in natural ice conditions among sections contributed to growth differences among controls. As variation in SGR was about the same for controls and treatments, it seems likely that differences in ice development among control sections probably had little effect on growth.

Winter in streams with highly-variable environmental conditions (e.g. stream flows, temperatures and instream ice formations) may be harsh for brown trout juveniles, and can result in a substantial decrease in energy reserves over the course of winter (Berg and Bremset 1998). In extremely adverse winter conditions, brown trout has even been reported to shrink in length (Huusko et al. 2011). Conversely, in relatively constant, benign winter conditions, stream-dwelling brown trout may have positive growth rates (French et al. 2014), possibly an effect of active feeding throughout winter (Cunjak and Power 1987; Heggenes et al. 1993). In the related Atlantic salmon (*S. salar*), Hedger et al. (2013) found that juveniles in an ice-free site of a large Arctic river depleted their energy fat storage faster than juveniles in an ice-covered site, with effects on their condition factor. We manipulated ice cover in a small boreal forest stream and found a similar effect of ice

cover on condition factor for brown trout, indicating that the effects of ice cover may be general for salmonid populations, possibly even for other lotic species as well.

The linkage between terrestrial piscivores and stream fish should be altered if surface ice acts as a barrier between predator and prey. While stream fish benefit directly from reduced predation risk and indirectly by altered energy and time budgets, terrestrial piscivores may be negatively affected by the presence of ice cover (Skierczyński et al. 2008). For instance, river otter (*Lontra canadensis*) selects where to hunt on the basis of its access to water, and hence the extent of ice cover affects the otter's diet (Reid et al. 1994; Day et al. 2015). Moreover, fish are the preferred prey of American mink during winter (Gerell 1967), and mink can be the major cause of mortality for fish in small streams (Heggenes and Borgstrøm 1988). During periods with ice cover, mink switch to feeding on other types of prey, e.g. small birds and mammals (Skierczyński et al. 2008). It is possible that many generalist predators may increase stream fish prey and reduce terrestrial prey in their diets during winter if they have increased access to open water. Hence, changes in river ice dynamics may have effects on the ecosystem well outside the boundaries of the stream.

Natural surface ice may have properties that are difficult to simulate, such as changing thickness, light attenuation and refraction and perhaps effects on sound transmission. We cannot be certain how well our artificial ice cover simulated a natural one. Yet, the artificial and natural ice cover had similar effects on where trout were found across the stream width. While our study design did not allow us to assess the effects of natural surface ice on growth, the effects of the artificial ice cover are consistent with previous correlational data from field studies (Hedger et al. 2013). Because surface ice sometimes occurred in the control sections, it is possible that the effect sizes reported in this study are conservatively assessed. Although trout in our study remained relatively stationary, there were some movements between sections. These movements were likely a source of noise in the data, in particular if these movements took place between tracking surveys and thus were undetected.

Global warming has changed ice conditions in many streams in the Northern Hemisphere (Magnuson et al. 2000), and the duration of periods with ice cover has decreased noticeably in both streams and lakes. For example, ice-outs in 16 rivers in New England, USA, occur more than 11 days earlier today than in the 1930s (Hodgkins et al. 2005), and during the past 25 years all Swedish large lakes have experienced a shift towards earlier ice breakups and more years without any ice cover (Weyhenmeyer et al. 2008). Moreover, ice thickness has been reported to be considerably reduced in many rivers today compared to times before the modern era (Hodgkins et al. 2005). Using brown trout as a test species, we have shown

that the presence of ice cover substantially increases overwinter growth and affects habitat use. Studies of future climate conditions predict that the current trend of less ice cover in fluvial systems will likely continue, with possible negative effects on the energy balance and overwinter survival of fish (Jonsson and Jonsson 2009), with presumed effects on population dynamics.

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# Salmonid behaviour under winter conditions

Winter conditions are believed to play an important role in the population dynamics of northern temperate stream fish, challenging the ability of fish to physiologically and behaviourally adapt. Climate change is predicted to increase both mean temperature and temperature fluctuations, especially during winter, leading to dynamic environmental conditions in terms of river ice production and flow. Therefore, knowledge about the winter ecology of stream fish is important for predicting and mitigating anthropogenic impacts on fish production in boreal streams.

Stream salmonids are active throughout winter, and behavioural responses to different winter conditions may be critical for survival. Yet, relatively little is known about overwintering behaviour of salmonids, particularly in streams with ice. This doctoral thesis focuses on the behavioural ecology of salmonids under winter conditions, and results from field and laboratory experiments show that the presence of surface ice increases food intake rates, reduces stress and affects social interactions, with effects on growth and habitat use. Moreover, drift-feeding ability is reduced at low temperatures, and nocturnal drift foraging under winter conditions has a low efficiency.

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