Morten Stickler

Anchor ice formation and habitat choice of Atlantic salmon (*Salmo salar L.*) parr in steep streams

Thesis for the degree of philosophiae doctor

Trondheim, November 2008

Norwegian University of
Science and Technology
Faculty of Civil Engineering
Department of Hydraulic and Environmental Engineering

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ANCHOR ICE FORMATION
AND HABITAT CHOICE OF
ATLANTIC SALMON (*SALMO SALAR* L.) PARR
IN STEEP STREAMS

A dissertation

submitted to the Faculty of Engineering Science and Technology at the

Norwegian University of Science and Technology in fulfillment of the

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By

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"You cannot step twice into the same stream…"

(Heraclitus, quoted by Platon in Cratylus)

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Morten Stickler

Trondheim, June 2008

ABSTRACT

Recent studies report an overall decline in northern populations of Atlantic salmon. As the winter in northern streams can be a critical period for juvenile salmonids, the cold season needs further attention to preserve sustainable populations of the species. Until today, most field and experimental studies have focused on open water conditions (e.g. spring, summer, fall), and less on winter conditions with presence of ice. As river ice has profound impacts on the lotic environment, interdisciplinary studies in natural environments focusing on the linkage between different types of ice and behavioral responses by salmon parr are thus needed. In this PhD study, a multidisciplinary approach have been used focusing on (1) formation of anchor ice and its influence on the physical habitat in steep streams, and (2) habitat use by Atlantic salmon parr in anchor ice affected streams. Results demonstrate that anchor ice formation significantly alter the in-stream heterogeneity by changing riffles into pools on a short temporal scale, leading to a dynamic environment despite stable discharge. Findings suggest that anchor ice may be distinguished between two types according to its formation process: Type I: less dense and forming on top of the substrata. Type II: Dense and forming between the substrata, filling interstitial spaces. Observations of habitat use by Atlantic salmon parr in anchor ice affected streams imply that despite hydraulic (depth, velocity) changes caused by ice formation, parr seem unaffected, and hence question the importance of hydraulic features as single habitat factors. However, findings also imply that parr inhabit two different strategies related to anchor ice formation: First, parr affected by anchor ice Type I demonstrate no or small changes in habitat use, and second, parr affected by Type II experience habitat exclusion and/or entrapment and are forced to relocate into other suitable areas, preferable surface ice covered stream margins. Moreover, observations indicate that pool habitats can be less important winter refuges, whereas riffle habitats are largely utilized, dependent on the type of anchor ice. In view of these findings, the degree of substrata shelter may be the predominant factor in habitat selection of parr during winter. Finally, results indicate that winter may not necessarily result in negative growth, whereas in contrast, the spring ice break-up may lead to a decrease in body mass and hence imply a critical period for parr. The results may be of importance to cold environment freshwater fisheries management in which habitat evaluation and preservation are core objectives. Results may further be of importance in future development of cold water stream habitat modelling tools and in evaluation of thermal changes of natural and anthropogenic environments.

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Chapter one

INTRODUCTION

Research reports an overall decline in Northern populations of Atlantic salmon (*Salmo salar* L.) (ICES, 2007). As streams play a vital role of the salmon life cycle providing spawning and rearing habitats (Schaffer, 2004), the importance of increasing our knowledge of these environments is evident. Today, winter conditions in streams with ice formation are known to have both physical and biological implications (Prowse, 2001) but limited knowledge exist on the matter, in particular knowledge about habitat use and performance of juvenile salmonids ice covered streams (Huusko *et al.*, 2007). With future challenges as increased pressure from anthropogenic disturbances (hydro-regulation, land-use activities) and predicted climate change scenarios (Corell, 2006), northern streams and ecosystems will be put under pressure. During the winter period, fluctuating discharge and variable water temperature may increase the freezing-thawing shifts (Frauenfeld *et al.*, 2007) and amplify the dynamics of in-stream conditions. These changes may have an adverse effect on populations of juvenile salmonids. Thus, to understand the effect of winter on northern stream populations of Atlantic salmon, the lotic winter environment needs further study.

In the following, a multidisciplinary study focusing on habitat choice of Atlantic salmon parr in steep, ice covered streams is presented. A particular focus on dynamic ice formation (anchor ice) is given. The study has two main parts: (1) investigation of anchor ice formation and its influence on the physical habitat, and (2) the influence of anchor ice on habitat choice by Atlantic salmon parr. In this study, data collection in natural conditions has been emphasized. Studies conducted in natural environments are especially lacking within the literature, most probably due to difficulties of collecting data during winter, but such studies are nevertheless essential if we are to understand the dynamics of natural systems. The findings of this study should be of value both for those that work with cold climate freshwater fisheries, and for the development of existing and future hydraulic/habitat modelling tools.

STEEP STREAMS DURING WINTER

In northern temperate (23·5° N to 66·6° N) streams, ice is commonly observed during the winter. Depending on local climate and physical conditions (flow, stream-gradient, morphology), various types of river ice may form and hence change the in-stream environment (Devik, 1944; Prowse, 2001). As ice influences the stream heterogeneity independent of discharge, characterization and quantification of these changes on the physical habitat is important, both in relation to freshwater management and to understand the dynamics of cold climate streams (Alfredsen & Tesaker, 2002; Shen, 2003; Morse & Hicks, 2005; Huusko *et al.*, 2007).

Figure 1. River Sokna, Mid-Norway (62º98' N, 10º23' E, m.a.s.l.: 160 m) covered in anchor ice during a freeze-up winter 2005.

The ice regime in northern steep streams is usually dominated by dynamic ice formation. Dynamic ice formation occurs during cold periods when the water becomes supercooled ($T_{Water} < 0ºC$) (Barnes, 1906), and is described by the formation of tiny ice particles, termed frazil, and ice growth on the stream bottom, termed anchor ice (Altberg, 1936; Devik, 1944). The formation process may take place on a short temporal scale by growth at night and disappearance during day. As turbulence has been suggested to be a key-factor, the appearance of dynamic ice formation is conventionally related to riffles. Based on previous field investigations (see reviews by Shen, 1996; Tatinclaux, 1998; Beltaos, 2000; Prowse, 2001; Shen, 2003; Morse & Hicks, 2005), two mechanisms of anchor ice formation has been proposed: (1) Turbulent heat conduction (Altberg, 1936), and (2) direct nucleation (Michel, 1967). The first formation process, turbulent heat conduction, is defined as transport of frazil (tiny ice particles) from the water surface down to the stream bed, causing underwater ice formation by adhesion (Figure 2). The theory of turbulent heat conduction, (later extended to frazil adhesion, Tsang, 1982), has been supported both through a number of observations in natural environments (Devik, 1944; Schaefer, 1950; Michel, 1971; Arden & Wigle, 1972; Osterkamp *et al.*, 1975; Osterkamp & Gosink, 1983; Marcotte, 1984; Hiryama *et al.*, 2002; Kerr *et al.*, 2002) and by laboratory experiments (see e.g. Carstens, 1966; Daly & Colbeck, 1986; Ye & Doering, 2004; Qu & Doering, 2007). The second formation process, direct nucleation, or accretion, is based upon supercooled water crystallizing at the leading edge of underwater obstacles. Supercooled water is transported from the water surface by turbulence, and in contact with underwater objects, growth of ice crystals starts. However, direct nucleation has rarely been observed in natural environments (but see Arden & Wigle, 1972), but rather theoretically discussed (see Tsang, 1982; Qu & Doering, 2007).

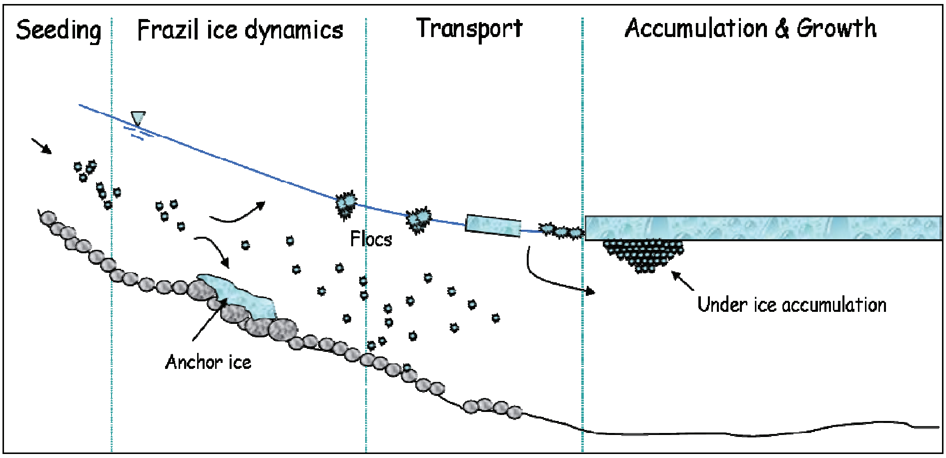

Figure 2. Formation of anchor ice by frazil adhesion (see text for details).

In stream sections with severe anchor ice formation, anchor ice dams may form (Figure 3). These ice dams typically form in sections with large boulders and/or where the stream increases its steepness. Anchor ice dams act as in-stream barriers, affecting the hydraulic heterogeneity by increasing the water level leading to potential physical and ecological implications. The ice dams may temporally store water causing losses in hydro power production (Eythorsson & Sigtryggsson, 1971; Osterkamp *et al.*, 1975), lead to local flooding and freezing of the riparian zone (Prowse & Gridley, 1993) and may have potential negative effects on distribution, migration and survival of stream fish of different cohorts. Nevertheless, few quantitative field studies have focused on the effect of anchor ice dams on the in-stream environment making general statements difficult.

Figure 3. An anchor ice dam in Sokna river, Mid-Norway, during a freeze-up winter 2005. A large pool was established after the formation of an anchor ice dam.

WINTER HABITAT FOR JUVENILE ATLANTIC SALMON

The need for studying winter conditions in streams and their effects on stream fish was first pointed out in 1935 by Hubbs and Trautman. Since then, a number of studies have been carried out, both in natural environments and by using experimental set-ups in artificial flumes (for latest review, see Huusko *et al.*, 2007). The discrepant findings suggest large differences in behaviour among both populations and between individuals, but also reflect the practical challenges that follow when studying behaviour in harsh conditions such as ice covered streams. Nevertheless, recent advances within radio telemetry have increased the efficiency and accuracy of monitoring stream fish, and thus enabled us to more efficiently conduct studies in cold climate stream environments.

Salmonids (family *Salmonidae*), and in particular the Atlantic salmon, are broadly studied within aquatic stream ecology, both in the perspective of their economic importance, e.g. commercial and recreational fisheries and aquaculture, and by the overall concern for the future perspectives of the northern populations of Atlantic salmon (Mills, 2003; ICES, 2007). To further increase our understanding and to improve the management of the salmonids, it is important to include seasonal differences when investigating their behavioural responses to various factors. Today, most studies on juvenile salmonids have focused on open water conditions (e.g. spring, summer, fall), and less on winter conditions including river ice. As the winter have been suggested to be a limiting factor for stream fish populations (Hubbs & Trautman, 1935; Maciolek & Needham, 1952; Hunter, 1992; Bradford, 1997; Cunjak *et al.*, 1998; Annear *et al.*, 2002; Finstad *et al.*, 2004), winter and ice conditions have received increased attention. Previous studies suggest that juvenile salmonids are mostly nocturnal in winter (active at night, sheltering during day). This strategy has been suggested to be a trade-off between predation avoidance and feeding activity (Metcalfe & Thorpe, 1992; Heggenes *et al.*, 1993; Valdimarsson & Metcalfe, 1998). However, it can be discussed as nocturnal activity are not only limited to winter time but may occur throughout the year (Hutchings, 1993). Also, some predators, as e.g. minks (family *Mustelidae*), are predominantly nocturnal in winter (Zielinski, 1986) and less active in cold waters (Egglishaw & Shackley, 1977). Furthermore, the majority of previous research suggests that juvenile salmonids prefer sheltered, low velocity habitats (e.g. pools and stream margins), and are less attracted to riffle habitats. This may be explained by the energetic costs related to high water velocities that are found in riffle areas. A few studies, however, report juvenile salmonids inhabiting riffles during winter (brown trout, brook trout (*Salvenilus fontinalis* M.), rainbow trout (*Onchorynchus mykiss* W.): Needham & Jones, 1959; Atlantic salmon: Smirnov *et al.*, 1976; Roussel *et al.*, 2004), indicating that suitable conditions may exist in these areas.

The impact of various types of ice (surface-, frazil- and anchor ice) on juvenile salmonids can be difficult to generalize as previous studies are few and report disparate findings. Static ice formation demonstrates positive effects, whereas dynamic ice formation may have negative effects on habitat use, performance and survival. Surface ice has been demonstrated to reduce the metabolic rates in salmon parr (Reimers 1963; Finstad et al. 2004b), and to be an important source of cover

(Young, 1995; Gregory & Griffith, 1996; Meyer & Griffith, 1997). Surface ice is also observed to increase the habitat use by juvenile Atlantic salmon parr in areas providing low substrata shelter (Linnansaari *et al.*, In press). Dynamic ice formation, however, has demonstrated to decrease survival (Tack, 1938; Needham & Slater, 1945; Maciolek & Needham, 1952), lead to habitat exclusion (Heggenes *et al.*, 1993; Brown *et al.*, 2000; Prowse, 2001; Barrineau *et al.*, 2005) and freezing of both eggs and juveniles (Prowse & Gridley, 1993). Moreover, long-distance migration has been reported in relation to accumulation of frazil and anchor ice in preferred habitats (Brown *et al.*, 2000; Simpkins *et al.*, 2000; Lindström & Hubert, 2004), indicating unsuitable conditions.

In short, literature at-hand suggests that juvenile salmonids are mainly active at night and prefer sheltered low velocity habitats. River ice may have both positive and negative effects, depending on its type and formation process. Nevertheless, the knowledge on behaviour of different cohorts, density dependent factors (competition, food) and the use of cover in ice-covered streams are still rather limited. Thus, making general statements on the effect of winter conditions on juvenile salmonids are difficult, and hence much remains to be learned.

Figure 4. Is winter a “bottleneck”? An Atlantic salmon parr frozen to the ice, found in River Sokna, Norway, winter 2005.

Chapter two

MATERIALS AND METHODS

Study area

This PhD study has been conducted in three different streams located on the northern hemisphere (between 48º - 63º N, Figure 5). The streams are characterized as steep (> 0.4%, (Tesaker, 1994; , 1996) with different physical characteristics (Table I), but with similar coastal climate conditions. The winter, here defined as a period from first appearance of ice to complete removal of ice in the spring (Wedel, 1990; Cunjak *et al.* 1998), usually lasts for 6 months from the freeze-up in late October to the thermal ice break-up in April. In the following, the study sites are described.

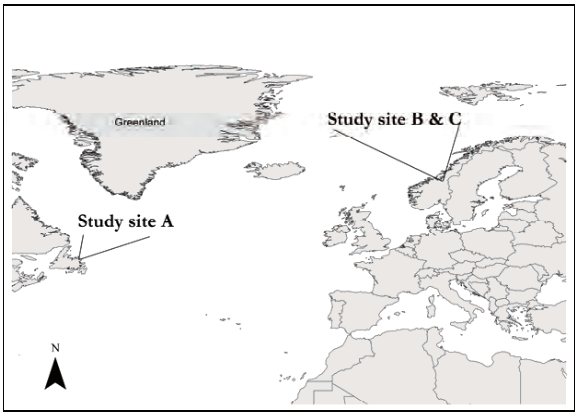

Figure 5. Location of the three study sites A, B and C (see Table I for physical features). Study site A: Southwest Brook, Newfoundland Canada; B: Sokna River, Norway, and C: Orkla River, Norway.

Study site A, Southwest Brook, is an unregulated stream located in the Terra Nova National Park (48º36' N, 53º58' W) on the northeast coast of Newfoundland, Canada. The Southwest Brook is a small stream with an average winter discharge of 0·4 m^3s^{-1}. The selected study section was approximately 300 m long, with a steep stream gradient favouring dynamic ice formation. In ice-free conditions, the reach is riffle dominated with sections of walks and pools (see Table II for definitions). Study site B, Sokna River, is an unregulated stream located in Mid-Norway (62º98’ N, 10º23’E). It is a small (average winter discharge of 2 m^3s^{-1}), steep stream favoring anchor ice formation. The field study was carried out in a 350 m long stream reach, consisting predominant of riffle with a smaller section of walk area. Study site C, Orkla River, Mid-Norway (63°17’ N, 9°50’E), is a regulated stream with a mean winter flow of 50 m^3s^{-1}. Due to the local climate, regulation regime and its steep stream gradient, the river system has a high production of frazil and anchor ice. The selected study site was located in the middle portion of the river system, approximately 10 km downstream of the nearest power plant outlet. The study site is 250 m long, representing riffle, glide, and walk sections, and is largely influenced by severe anchor ice formation in winter.

Table I: Summary of physical characteristics in the study sites given by their average winter discharge (Q), stream gradient (I), maximum water depth (Y_{Max}), average wetted width (WW), and dominant substrata (D_{50}).

Study site	**Q (m^3s^{-1})**	**I (%)**	**WW (m)**	**Y_{Max} (m)**	**D_{50} (mm)**
Southwest Brook	0·4	1·3	11·5	2·0	97
Sokna	2·0	1·8	23·5	1·0	165
Orkla	50·0	0·5	45·0	2·0	72

Collection of physical data

To describe the effect of dynamic ice formation on the physical habitat in steep streams, data of a number of physical characteristics have been collected. The data collection can be distinguished in two groups: (1) monitoring changes in the hydraulic heterogeneity caused by river ice, and (2) monitoring anchor ice and its formation process. In (1) changes in the hydraulic heterogeneity were observed as changes in discharge (pressure sensor and manual measure), water depth and water velocity (Sontek Flow meter, 10-MHz ADV, Acoustic Doppler Velocity profiler) and by using a hydro-morphological unit (HMU) classification system (Borsányi *et al.*, 2004). In the latter, four classes were employed: 1) shallow riffle; 2) shallow glide; 3) walk and 4) pool (see Table II for definitions). Substrata were measured by the b-axis (shortest axis) and classified using the Wenthworth scale. The substrata embeddedness was measured according to the method by Schälchli (2002) by visual determination using five classes: 0-20%, 20-40%, 40-60%, 60-80% and 80-100%, in which low values reflect low degree of embeddedness (i.e. high degree of interstitial spaces). In (2) anchor ice formation was monitored measuring spatial (total station: Sokkia SET 600, Leica TS 306, or DGPS (Differential GPS) and temporal distribution, thickness, density and its formation process, both on a micro (< 10 m) scale and on a meso (10 – 100 m) scale. Photo, video and underwater video recording was also conducted. In addition, high resolution temperature sensors (SeaBirds Electronics, SBE39, ± 0·002°C) were used to quantify the amount of supercooling related to the formation of anchor ice, and underwater light meters (Onset Computer Corp., HOBO RH) to investigate underwater light changes due to ice formation (both surface- and anchor ice). Finally, measurements (Sontek ADV, 10 MHz, velocity range 250 ms^{-1}) of turbulence, here defined as velocity fluctuations around its mean during two minutes, were made to investigate its effect on anchor ice formation and density.

Table II: Physical features of hydro-morphological units (HMU's), mesohabitat classes, used in the study. The method is based on the system by Borsányi *et al.* (2004)

Habitat class	**Name of class**	**Surface**	**Depth**	**Velocity**
G2	Shallow riffle	Broken surface	< 0·7 m	> 0·5 ms^{-1}
B2	Shallow glide	Smooth/rippled	< 0·7 m	> 0·5 ms^{-1}
B1	Deep glide	Smooth/rippled	> 0·7 m	> 0·5 ms^{-1}
C	Pool	Smooth/rippled	> 0·7 m	< 0·5 ms^{-1}
D	Walk	Smooth/rippled	< 0·7 m	< 0·5 ms^{-1}

Monitoring of Atlantic salmon parr

Atlantic salmon parr monitored in the present study ranged from 75 – 170 mm (fork length, L_F). Two different techniques were used to monitor parr: (1) Radio telemetry (paper IV) and (2) Passive Integrated Transponder (PIT) technology (paper V and VI). In the respective studies, a number of salmon parr (see paper IV, V, VI for details) were caught by electro fishing within the study sites using a 24 V backpack electro fisher (Smith Root Inc., model 12-B). Salmon parr were kept in captivity for observation of any potential effects from electro-fishing before tagging. Tagging was conducted using radio transmitters (Model Lotek MBFT 7M; 7.3 ·18 m, 1.4 g in air, and 9M; 8.2 ·19 mm, 1.8 g in air, Lotec Wireless) and Passive Integrated Transponders (Texas Instruments, RI-TRP-WRHP; length: 23·1 mm; diameter: 3·9 mm; weight: 0·6 g in air). As the size of tags have been discussed to have potential effects on fish behaviour (Jepsen *et al.*, 2004), procedures suggested by Robertson *et al.* (2003) (radio) and Roussel *et al.* (2000) (PIT) has been followed to ensure minimal impacts of tagging. All parr were kept for 24 hours before releasing them into their respective habitats where they had been captured. No post-mortality was observed in any of the conducted studies.

Tracking of salmon parr were conducted using radio telemetry (Lotek Wireless) and PIT technology (Texas Instruments Inc.; TIRIS S-2000 RI-CTL-MB2A), following procedures described by Robertson *et al.* (2003) (radio transmitters), Roussel *et al.* (2000) (PIT) and Linnansaari *et al.* (2007) (PIT). When using PIT technology, manual in-stream tracking was performed concurrently with two sets of hand-held antennae. Maximum reading distance (70 cm) and spatial accuracy (± 15 cm in x-y-direction, Linnansaari *et al.*, 2007 and personal experiences) were tested on each survey using a test tag on the stream bank. Water, ice, substrata and metal seemed to have no impacts on the reading distance whatsoever. All tracking, both radio and PIT, was done in an upstream direction to reduce the possibility of driving individuals from their positions. When an individual was detected, a marker was dropped and its position (x-, y-coordinate) was subsequently geo-referenced (morning positions were geo-referenced in the afternoon, and afternoon/night positions were geo-referenced the following morning) using a theodelite (total station; paper V: Leica 307, paper V/VI: Sokkia SET 600; spatial accuracy = ± 2 cm).

Statistical analysis

In this study a quantitative approach has been implemented. Both parametric and non-parametric analyses have been used, although the latter was most frequent as highly skewed distributions were observed in most cases (violation of normality was determined by the Shapiro-Wilk's test). In cases with non-normal distributions, the median, range, skewness and kurtosis were used to examine trends and clustering. Furthermore, although classical experimental design would have included replication in the presented research (Underwood, 1993), conducting studies under natural conditions with ice formation makes replication by its definition impractical. Despite this shortcoming, studies under natural environments are important to further understand natural processes across temporal and spatial scales. However, the importance of replication has been considered through repeated measures over time and space using fixed experimental set-ups. Statistical analyses were performed using SPSS 15·0 for Windows (SPSS Inc. 2006), and considered significant at the level of P = 0·05. Graphs and illustrations have been made in Sigma Plot 10·0 (Systat. Software, Inc. 2006) and Arc Info 9·2 (ESRI Inc. 2006), respectively.

Chapter three

ORGANIZATION OF THE THESIS

This PhD study is based upon a multidisciplinary approach in two steps: (1) Investigation of anchor ice formation in streams and its influence on the physical stream habitat, and (2) the influence of anchor ice on habitat use by Atlantic salmon parr. A natural part of this progress has been to review the state-of-the-art research within winter behaviour of stream salmonids and hence is included in this thesis as a basis for the given studies (paper I). The first step (1) is reflected by papers II - III. Paper II considers controlling factors of anchor ice formation in natural environments, and paper III demonstrates the effect of anchor ice formation on the physical habitat in a steep stream. The second step (2) is reflected by papers IV - VI. Paper IV considers the effect of dynamic ice formation on movement and habitat use of Atlantic salmon parr in a steep regulated stream. Paper V considers the effect of anchor ice dams on distribution of salmon parr in a natural, steep stream, and paper VI considers stream gradient-related movement and growth of salmon parr during winter in a natural, steep stream. In the following, main findings from each individual paper are given:

SUMMARY OF THE SCIENTIFIC PAPERS

Paper I: Life in the ice lane: The winter ecology of stream salmonids

What is the state of research on winter habitat of juvenile salmonids?

A review of winter behaviour of salmonids states that future winter research should focus on (1) being able to predict the dynamics of freezing and ice processes at different scales, especially at the local scale, (2) studying fish behaviour, habitat use and preference under partial and full ice cover, (3) evaluating the impacts of man-induced environmental modifications (e. g. flow regulation, land-use activities) on the ecology of salmonids in winter, and (4) identifying methods to model and assess winter habitat conditions for salmonids.

Paper II: Anchor ice formation in streams: A field study

What are the main factors controlling anchor ice formation in steep streams? Is anchor ice only restricted to high turbulent reaches, i.e. riffles? Are there differences between anchor ice formation and its density?

This paper presents a field study focusing on anchor ice formation in three different stream environments with different physical characteristics. Distribution and formation of anchor ice was investigated under various hydraulic, morphologic and climatic conditions. Particularly, the formation process and density of anchor ice versus level of turbulence and supercooling has been emphasized. Findings demonstrate that anchor ice formation in natural environments is not restricted to riffles, but may form in low turbulent reaches such as 'walk' and 'glide' areas (see Table II for definitions). Thus, using boundary conditions based on water depth and/or water velocity as criteria for spatial distribution of anchor ice formation should be employed with care. Furthermore, anchor ice may be distinguished by two types: Type I: Less dense, forming on top of substrata, Type II: Dense, forming between substrata filling interstitial spaces. Here, the findings suggest that the spatial distribution of the two types of anchor ice is linked to the level of turbulence, and may be expressed by the Reynolds number.

Paper III: The influence of dynamic ice formation on the hydraulic heterogeneity in a steep stream

How do anchor ice and anchor ice dams affect in-stream heterogeneity?

The formation of anchor ice and anchor ice dams was monitored throughout a freeze-up in a small, steep stream. A differential GPS combined with a HMU system were used to quantify in-stream changes caused by anchor ice formation. During the study, extensive dynamic ice formation occurred leading to the formation of a number of anchor ice dams (max height: 190 cm) within the study site. The anchor ice dams significantly altered the in-stream hydraulic heterogeneity by changing riffle sections into a series of pools. Anchor ice dams increased the water level and the wetted area by 44% and 60%, respectively, despite constant discharge. The increase in water depth reduced the overall water velocity and initiated further static ice formation. Hence, anchor ice formation may play a key role in further development of surface ice on steep streams. The findings suggest that the current paradigm that emphasizes the role of discharge as the main controller of hydraulic heterogeneity may call for a modification in streams that experience seasonal ice formation.

Paper IV: Mid-winter activity and movement of Atlantic salmon parr during ice formation events in a Norwegian regulated river

How does anchor ice formation affect the distribution and movement of Atlantic salmon parr in a regulated stream?

Distribution and movement of Atlantic salmon parr was monitored mid-winter using radio telemetry in a steep, regulated stream. Within the study site, extensive anchor ice formation occurred by formation at night and disappearance during day. The anchor ice displayed high density forming between the substrata and filling interstitial spaces. Monitored radio tagged parr displayed large movements both night and day, thus no clear nocturnal behaviour was evident. Furthermore, parr were observed to relocate from anchor ice exposed areas (riffles) at night seeking cover along surface ice covered stream banks. Also, a group of parr were observed to be trapped within a small pool along the bank due to a rapid decrease in discharge. Findings from this study indicate a potential negative impact by anchor ice formation on habitat use of parr in terms of forced relocation and large movements. This can be explained by that anchor ice observed in this study formed between the substrata and hence excluding potential substrata cover. Also, the findings imply that hydropeaking during winter may be critical towards parr by potential stranding, particularly in shallow stream bank habitats. Hence, overall findings imply that in steep, regulated streams the physical conditions may be especially harsh during winter. This may further pose a challenge towards performance (growth, survival) of parr during winter in such systems, although not investigated in this study.

Paper V: Habitat use of Atlantic salmon *Salmo salar* L. parr in a dynamic winter environment: the influence of anchor-ice dams

How do changes in stream heterogeneity caused by the formation of anchor ice dams affect distribution of Atlantic salmon parr?

The effect of anchor ice dams on the physical habitat and distribution of Atlantic salmon parr was investigated by Passive Integrated Technology to monitor parr during two freeze-up periods in a small, steep stream. During the study, changes in the hydraulic heterogeneity (i.e. depth, velocity, mesohabitat composition) caused by anchor ice dams demonstrated small/no effects on distribution of Atlantic salmon parr. Results question the importance of depth and velocity as single factors in habitat choice and distribution of salmon parr in steep streams, although the degree of anchor ice formation should be considered. Furthermore, large individual variation in habitat use among parr was observed; however, overall small home ranges in low embedded areas indicated high site fidelity to these habitats. The findings imply that access to suitable substrata shelter (low embeddedness) may override other habitat characteristics such as water depth and velocity.

Paper VI: Stream gradient-related movement and growth of Atlantic salmon parr during winter

Are there within-population differences in habitat use and performance of Atlantic salmon parr during winter in steep streams? Are pool habitats preferred habitats, while in contrast; riffles are less utilized or even avoided?

Habitat use and growth of Atlantic salmon parr were monitored throughout the winter (November – May) in two sub reaches with different stream gradients (low and high gradient), and hence different ice regimes, in a small natural stream. The low gradient stream section was characterized by static ice formation (stable conditions), whereas the high gradient was characterized by dynamic ice formation (unstable conditions). Passive Integrated Technology was implemented by using both fixed antennae and manual tracking devices monitoring between- and within-gradient movement, respectively. Throughout the winter, parr demonstrated nocturnal activity, small movements and high site fidelity in both stream sections confirming the consensus of low winter activity. However, salmon parr inhabiting the less steep stream gradient section demonstrated larger movements than salmon parr in the high gradient stream section. Furthermore, salmon parr were less attracted to pools, whereas in contrast, parr showed high site fidelity to riffle areas. Findings suggest that low embedded substrata can be the key component in habitat selection by salmon parr during the winter. Finally, winter growth by parr was found to be stable/slight positive, whereas the spring (thermal) ice break-up may cause body mass reduction indicating a critical period.

Chapter four

CONCLUSION

The main objective in the present study was to investigate the influence of dynamic ice formation on habitat choice by Atlantic salmon parr in steep streams. In the following, the main conclusions from the present study can be summarized by five main points:

1. The formation of anchor ice has profound impacts on steep stream heterogeneity, and should be considered when evaluating physical conditions in such environments. Discharge, as the controlling factor for changes in the hydraulic heterogeneity, may therefore require modification in streams that experience seasonal ice formation, particularly in areas with dynamic ice formation. This is especially important for cold-climate stream habitat modelling. In figure 6, changes in water level caused by dynamic ice formation, but with stable discharge, are illustrated.

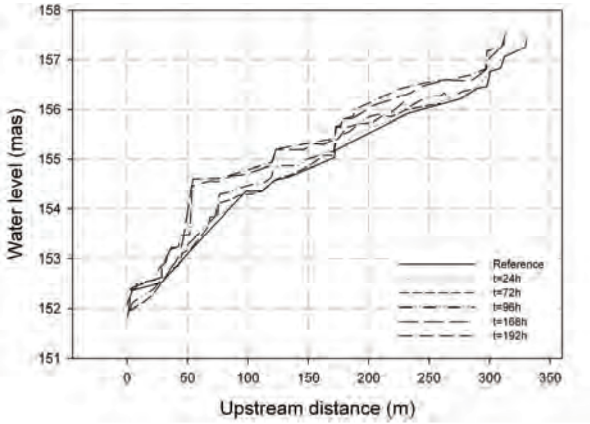

Figure 6. Changes in water level caused by dynamic ice formation in a small, steep stream during a freeze-up (figure from paper III). “Reference” indicates ice-free condition, and “t” accumulated time during the freeze-up.

2. Anchor ice can be distinguished by two types: i) Type I: Less dense, forming on top of substrata, ii) Type II: Dense, forming between substrata and filling interstitial spaces. The two anchor ice types can further be indirectly expressed by the Reynolds number. In figure 7, the two anchor ice types are given according to their densities. As the two types modify the substrata embeddedness different, the characteristics of anchor ice formation are important to consider when conducting in-stream assessments in steep streams.

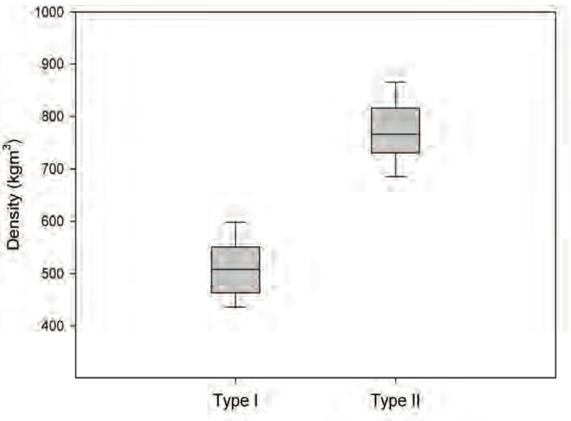

Figure 7. Two types of anchor ice are distinguished according their densities. Boxes imply the inter-quartile range, whiskers the 90th percentile and the solid line median value.

3. The effect of dynamic ice formation on habitat use of Atlantic salmon parr depend on the type of anchor ice. Type I has small/no impact in which habitat choice by parr are almost unaffected. In contrast, Type II demonstrates negative effects in terms of habitat exclusion with increased movement activity and enlarged home ranges. Therefore, the type of anchor ice may have different effects on parr winter performance. Figure 8 reports home range sizes of parr in stream environments affected by

anchor ice Type I and Type II. Home range sizes related to Type II can be found in Alfredsen *et al.* (2004)

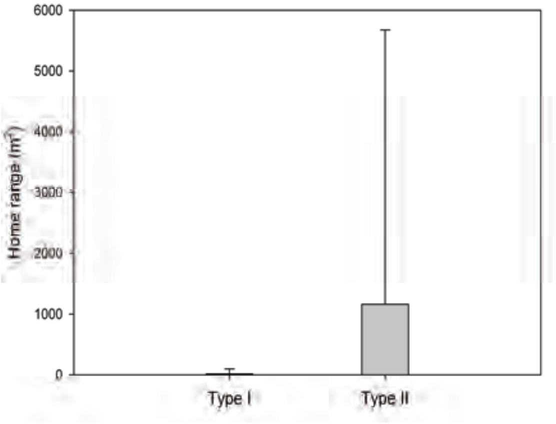

Figure 8. Size of home ranges by Atlantic salmon parr in areas affected by anchor ice type I (median = 16 m^2) and Type II (median = 1163 m^2). Bars represent median value and whiskers the 90th percentile.

4. Riffle habitats are suitable for Atlantic salmon parr during winter, whereas pools are less utilized. However, the degree of dynamic ice formation and size of winter floods should be considered. A potential explanation for parr using riffles is the shelter availability in these areas. Coarse, low embedded substrata provide refuge against energy demanding water velocities and potential diurnal predators. Thus, low embedded substrata may be the controlling factor in habitat choice by parr during winter in steep streams, and thus offset the need to change habitat, even in dynamic environments caused by dynamic ice formation.

5. The winter in steep streams is not necessarily a limiting factor in parr performance (i.e. growth). The access to cover and food can be adequate thereby reducing the potential of less success. In contrast, the physical conditions during the spring ice break-up may be especially severe. Ice-runs and increased discharge may exceed the holding-velocities for parr leading to unsuitable conditions due to increased energetic costs. Thus, the spring

ice break-up may lead to a decrease in body mass, and hence imply a critical period (Figure 9.

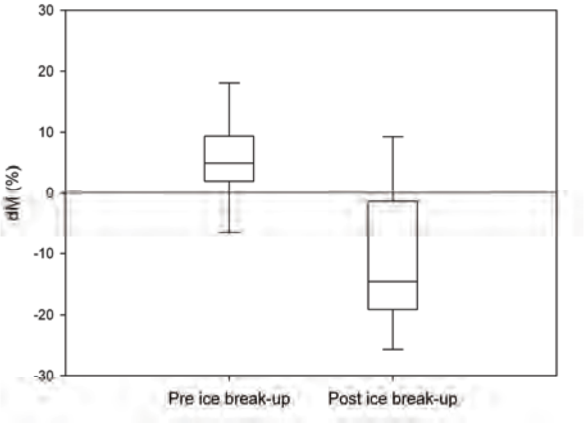

Figure 9. Change in body mass of Atlantic salmon parr before (pre, median = 4·8%) and after (post: median = -14·5%) the thermal ice break-up (April/May). Boxes imply inter-quartile range, whiskers the 90th percentile and the solid line the median value.

FUTURE RECOMMENDATIONS

The interaction between the physical habitat and the behaviour of juvenile salmonids is complex. In winter time, a stream environment may change radically by the formation of different types of ice, even on a short temporal scale, leading to a dynamic environment. Furthermore, juvenile salmonids, as reflected by the disparate findings from previous work, may demonstrate large individual behavioural differences both in time and space. Thus, to study, observe and interpret winter behaviour of juvenile salmonids is indeed a challenge. To further understand winter behaviour of stream fish and the dynamics of the environment they are utilizing, future research should focus on the following main issues:

- *Anchor ice formation and its effect on the physical habitat:* Although the effect of anchor ice on the physical habitat of stream salmonids has been investigated in this and some previous studies, more studies are needed. In particular, relations between anchor ice formation, density and turbulence should be investigated. How does the turbulence affect the anchor ice density in natural streams? Can density differences of anchor ice be linked to hydro-morphological units (HMU's)? Are dimensionless numbers less accurate to forecast anchor ice formation?

- *The effect of restoration on winter regimes in streams.* Restoration and remedial actions are today a common procedure of freshwater fisheries management to increase the habitat quality of degraded streams. However, the influence of restoration of streams on the ice regime has gained limited attention despite its importance. Studies focusing on changes in the ice regime and ice formation due to restoration should be emphasized

- *Incorporation of anchor ice formation in habitat modelling tools.* The effect of ice formation, and in particular dynamic ice formation, needs to be addressed in future use of stream habitat modelling tools. Ice formation has profound impacts on the in-stream heterogeneity, and is thus critical to be considered.

- *Performance by salmon parr in regulated stream systems during winter:* In many northern countries hydro-power is the dominant energy source. The river systems controlled by hydro-power largely affect the physical in-stream conditions and their ecosystems. In future, the energy demand is expected to increase which will further increase the pressure on these environments. Although a few winter studies have been conducted in regulated streams, including the present study, the temporal scale and number of individuals being investigated are generally low and more knowledge is needed. In particular, to investigate growth and survival rates of juvenile salmonids in regulated streams that experience extensive dynamic ice formation during winter are recommended.

- *The effect of mid-winter dynamics and spring ice-break-up on salmon parr behavior and performance:* With future climate predictions, northern stream systems and their ecosystems will be put under a particular pressure. Also, future energy demand and potential increase in energy production and hydropeaking will increase the dynamics of northern streams and alter the natural ice regime. Although multiple mid-winter ice break-ups and changed timing and severity of the spring ice-break-up can be expected in these systems, both their physical and biological implications in winter conditions are largely unknown. Studies focusing on these periods are recommended, in particular the effect of the spring ice break-up on growth and survival of parr.

- *Habitat use and performance during winter of adult Atlantic salmon.* Today, studies on adult salmon and their life phase in stream environment during winter are largely lacking. Studies considering their habitat use and performance related to various stream environments and ice formation, in particular extensive dynamic ice formation, are recommended.

In view of previous winter work, including the present study, knowledge on dynamic ice formation under natural conditions and its impact on the lotic environment is still limited. If we are to understand the dynamics of northern streams affected by ice formation and its environmental impacts, future multidiscipline studies are needed. More importantly, to avoid scale inconsistency (Folt *et al.*, 1998) future field studies should include multiple year-sampling in streams that are subjected to both static and dynamic ice formation. Different sampling techniques should be avoided if possible.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on a number of original papers, paper I – VI. In all but paper I, the undersigned have been responsible for the planning, conducting analyses and writing the papers. In paper I[1], the undersigned was responsible for the second chapter, *"The ice lane: Winter conditions in streams"*, but actively contributed in the remaining chapters by suggesting ideas/changes, and editing. Furthermore, the undersigned has also taken part in all the fieldwork described in the included papers. Given co-authors have contributed significantly to choice of study design, tagging of fish, data collection and analysis, and by commenting manuscripts.

Paper I: Life in the ice lane: The winter ecology of stream salmonids.

A. Huusko, L. Greenberg, M. Stickler, T. Linnansaari, M. Nykänen, T. Vehanen, Koljonen, S., P. Louhi, K. Alfredsen. 2007.

River Research and Applications **23**, 469-491.

Paper II: Anchor ice formation in streams: A field study.

M. Stickler and K. Alfredsen.

In review: Hydrological Processes.

Paper III: The influence of dynamic ice formation on the hydraulic heterogeneity in a steep stream.

M. Stickler, K. Alfredsen, H. P. Fjeldstad.

In review: Hydrology Research.

Paper IV: Mid-winter activity and movement of Atlantic salmon parr during ice formation events in a Norwegian regulated river.

M. Stickler, K. Alfredsen, D. Scruton, C. Pennell, F. Økland. 2007.

Hydrobiologia **582**, 81-89.

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[1] The first author and the co-authors have approved inclusion of this paper in the thesis.

Paper V: Habitat use of Atlantic salmon *Salmo salar* L. parr in a dynamic winter environment: the influence of anchor-ice dams.

M. Stickler. E. Enders, C. Pennell, D. Cote, K. Alfredsen, D. Scruton.

In press: Journal of Fish Biology **73**, 926-944.

Paper VI: Stream gradient-related movement and growth of Atlantic salmon (*Salmo salar* L.) parr during winter.

M. Stickler, E. Enders, C. Pennell, D. Cote, K. Alfredsen, D. Scruton. 2008.

Transactions of the American Fisheries Society **137**, 371-385.

Appendix A

Original publications

Paper I

Life in the ice lane: The winter ecology of stream salmonids

Paper II

Anchor ice formation in streams: A field study

Paper III

The influence of dynamic ice formation on the hydraulic heterogeneity in a steep stream

Is not included due to copyright

Paper IV

Mid-winter activity and movement of Atlantic salmon parr during ice formation events in a Norwegian regulated river

Is not included due to copyright

Paper V

Habitat use of Atlantic salmon Salmo salar L. parr in a dynamic stream environment: the influence of anchor-ice dams

Paper VI

Stream gradient-related movement and growth of Atlantic salmon (Salmo salar L.*) parr during winter*