

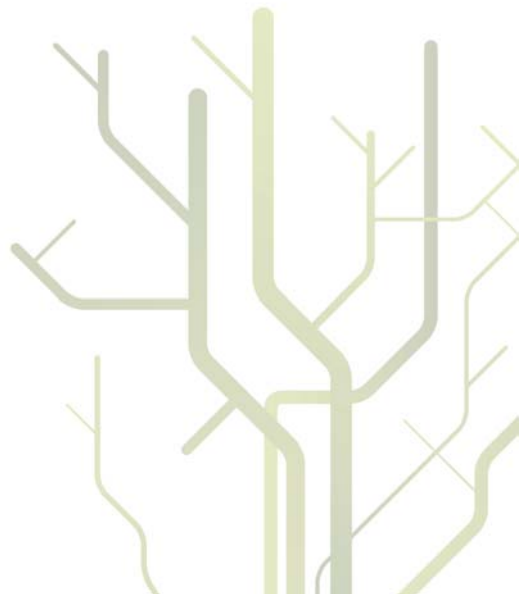
Effects of environmental factors on migratory behaviour of northern Atlantic salmon



Jan Grimsrud Davidsen

A dissertation for the degree of
Philosophiae Doctor

Spring 2010



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Contents

Contents	2
Acknowledgements.....	3
Summary	4
List of papers.....	7
Introduction.....	8
Objectives of the thesis	13
Study sites	15
Methodological approach.....	18
Summary of papers	20
Discussion.....	23
Conclusion	30
Future perspectives	31
Electronic references.....	33
References.....	33
Appendix.....	43
Individual papers	

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Jan Grimsrud Davidsen

Summary

Over the last decades, the abundances of many Atlantic salmon populations have declined drastically both due to anthropogenic and natural factors. The period when salmon enter the sea for the first time, starting as smolts in the river and subsequently as post-smolts in the fjord, is regarded as one of most critical periods in the salmon life history. In addition, salmon can also suffer from high mortality during their return migration through fjords and estuaries both due to predation and coastal fisheries. Despite an increasing number of recent Atlantic salmon migration studies, few have been conducted in northern areas which host some of the largest and most productive salmon populations in the world.

The main aim of this thesis was therefore by use of electronic acoustic tracking and video observation to study how the environment influence on the behaviour patterns of northern Atlantic salmon during their smolt migration in rivers (Tana and Alta), and as post-smolts and homing salmon during their estuary and fjord migration (Alta). Since northern areas have 24 h daylight during summer, special attention was given to the impact of light intensity on salmon migratory behaviour. This also includes a study of direct impact from light intensities on post-smolt swimming behaviour in a south-west Norwegian fjord (Hardanger Fjord) with distinctive day and night periods. Secondly, the observed behaviour of the northern Atlantic salmon was related to other important environmental factors like temperature, river flow, current, tides and wind. Finally, the survival rate of post-smolt during fjord migration, as well as the fjord residency and migratory speeds of both northern post-smolts and homing salmon, were studied for the first time for a northern salmon population. The results were compared with earlier reported findings from southern populations.

The results showed that the northern smolts, post-smolts and homing salmon migrated during both day and night in both the river and fjord. In contrast, the post-smolts in the south-western Hardanger Fjord showed distinctive changes in day and night behaviour by swimming deeper in the water column during the day than during the night. However, the northern smolt behaviour was affected by river flow and water temperature, and the post-smolts in the estuary and fjord seemed to be affected by the tidal cycle and wind-induced currents. The homing salmon were also periodically

affected by wind-induced currents, and similar to the post-smolts, they migrated mainly close to the surface. Further, the homing salmon generally followed the coastline towards the river mouth, and as they approached the estuary, migratory speed was reduced by 75% and the average swimming depth reduced from 2.5 m to 0.5 m. There was no evidence that river entry of these fish was affected by tidal cycles or river flow. The post-smolts used on average only 0.8 days to migrate the first 17 km outward through the fjord (20.5 km day^{-1}). In contrast, the homing adult salmon used 20% more time over the same distance (16.5 km day^{-1}). Finally, the post-smolt survival rate was estimated to be 75% from the estuary and through the first 17 km of the fjord.

The findings of seemingly no difference between day and night migratory behaviour for the northern smolts and post-smolts in the present thesis may be due to the fact that nocturnal migration, as often observed for southern populations, does not provide the northern fish any benefit in regard to sight feeding predators due to the 24 h of daylight. The observed change in day and night swimming depth in the Hardanger Fjord indicated that light intensity may also affect the swimming depth of post-smolts. The relationships between migratory behaviour of northern smolts and post-smolt and water temperature, river flow and tidal cycles found in this thesis, could, as well as the adaptation to the light intensities, be antipredatory strategies.

In total, it seemed like the first-time migrants were more influenced by light, river flow, tidal cycle and fjord currents than the homing salmon. This may be due to their smaller size and higher vulnerability to predation, supported by the fact that 25% of the tagged post-smolts did probably not survive the first 17 km of the fjord migration. The high mortality rate was similar to earlier findings in southern populations during the first few days after sea entry. However, the finding that the homing salmon migrated close to the surface and shoreline, combined with their longer residency in the inner fjord, may greatly have increased their risk of being caught by net fishing targeting salmon along the shoreline in this area.

In conclusion, this thesis indicates that the migration behaviour of northern and southern salmon differ somewhat, and that this is related to local adjustments to the existing abiotic environmental factors typically for the different latitudes, in particular

the light regimes. These local adaptations may be due to phenotypic plasticity and/or different genotypes. The study also highlight the post-smolts and homing salmon phases in fjords and estuaries as important bottlenecks of survival in the Atlantic salmon life cycle, and that variation in both natural and anthropogenic factors during these phases may have large impacts on their migration behaviour, performance and subsequently the total return rate of salmon to their home rivers. An evaluation of the impact from subsequent effects of interventions along the coastline in areas with migratory Atlantic salmon is highly recommended in order to avoid any negative effects on the seaward and homing migration.

List of papers

The present thesis is based on the following papers, which in the following will be referred to by their roman numbers:

- I. Davidsen, J., Svenning, M. A., Orell, P., Yoccoz, N., Dempson, J. B., Niemelä, E., Klemetsen, A., Lamberg, A. & Erkinaro, J. (2005). Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana. *Fisheries Research* 74, 210-222.
- II. Davidsen, J. G., Plantalech Manel-la, N., Økland, F., Diserud, O. H., Thorstad, E. B., Finstad, B., Sivertsgård, R., McKinley, R. S. & Rikardsen, A. H. (2008). Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *Journal of Fish Biology* 73, 1065-1074.
- III. Davidsen, J. G., Rikardsen, A. H., Halttunen, E., Thorstad, E. B., Økland, F., Letcher, B. H., Skarðhamar, J. & Næsje, T. F. (2009). Migratory behaviour and survival rates of wild northern Atlantic salmon (*Salmo salar*) post-smolts: effects of environmental factors. *Journal of Fish Biology* 75, 1700-1718.
- IV. Davidsen, J. G., Rikardsen, A. H., Halttunen, E., Mitamura, H., Thorstad, E. B., Præbel, K., Skarðhamar, J. & Næsje, T. F. (Submitted). Homing behaviour of Atlantic salmon during final marine phase and river entry. *Fisheries Management and Ecology*.

Introduction

The enigmatic migration of diadromous fish species, those that migrate between the ocean and freshwater, has been examined for decades (McDowall, 2002). However, many components of their intricate life cycles are still unknown. In theory, diadromous life histories will evolve through natural selection only when migration across the ocean-freshwater boundary provides a gain to individual fitness (lifetime reproductive success) that exceeds the costs of this behaviour (Gross, 1987). The direct benefit is usually better feeding conditions resulting in better growth and a larger size, while the costs may include physiology adjustments to allocation of energy for swimming, and increased probability of mortality, e.g. owing to predation and diseases, during migration (Gross *et al.*, 1988; Jonsson and Jonsson, 1993).

Among the diadromous fishes, much emphasis has been on anadromous species, and one of the most studied of these is the Atlantic salmon (*Salmo salar* L.) (McDowall, 2002). The Atlantic salmon is native to both the southern temperate and northern sub-Arctic regions (see definitions on p. 15) and displays considerable phenotypic plasticity and variability in life history characters (reviewed by Klemetsen *et al.*, 2003). It disperses through large areas and experiences significantly changing environments throughout its life cycle. The environmental influence on the migration through the different habitats may therefore vary both on spatial and temporal scales. Since the abundances of many Atlantic salmon populations have declined drastically over the last decades (Hansen *et al.*, 2008; ICES, 2008), more knowledge about how these different environmental (and anthropogenic) factors influence their migration pattern and abundances is needed. This knowledge is crucial in order to improve the management of the salmon populations and to turn the negative trend observed in the recruitment.

Most forms of the Atlantic salmon are anadromous with a juvenile phase in freshwater, followed by a well-defined physiological change known as smoltification, during which the juvenile becomes able to osmoregulate in sea water and also changes its river colours to a silvery sheen more suitable for the marine environment (McDowall, 1988). During the downstream river migration the juvenile salmon is termed “smolt”, while from sea entry and until the onset of wide annulus formation on

the scales at the end of the first winter in the sea, it is termed “post-smolt” (Allan and Ritter, 1977). Usually after 1–4 years in the sea, the adult salmon returns to its natal river in order to spawn. This precise process of navigation from the feeding sites in the ocean and back to the natal river is called homing.

While movement and migration occur at a number of Atlantic salmon life stages (McCormick *et al.*, 1998; Klemetsen *et al.*, 2003), the focus of the present thesis is on the migratory behaviour of smolts and post-smolts during their initial seaward feeding migration and during the last part of their homing migration as adults through the fjord and during river entry. The period when the salmon enter the sea for the first time, starting as smolts in the river and followed as post-smolts in the fjord, is regarded as one of most critical periods in the salmon life history. In addition, the salmon can also suffer from high mortality during their return migration through fjords and estuaries due to both predation and coastal fishery (Hansen, 1988; Anonymous, 1999). Both of these periods may therefore be potential bottlenecks of survival in the Atlantic salmon life cycle.

The migration between totally different salinity borders may be costly and stressful for the individuals. Both the energy requirements (Jonsson and Jonsson, 1993) and the potential risks of mortality are high (Reitan *et al.*, 1987; Wood, 1987; Hvidsten and Lund, 1988; Feltham, 1995; Spicer *et al.*, 1995; Mather, 1998; Jepsen *et al.*, 2006). Since natural selection would favour the ability to select the most efficient movement pathways possible in order to reduce any potential risk of mortality and waste of time and energy (Brown *et al.*, 2006a), the behaviour of the migrating Atlantic salmon may be expected to be under a strong selection pressure. It is therefore reasonable to believe, that Atlantic salmon are highly adapted to the local environmental factors in order to gain and maintain the best fitness during the migrations.

While biotic factors like food availability and quality, predation and parasites often may have a direct effect on the growth or mortality of individuals (Rikardsen and Dempson, 2010), abiotic factors may act indirectly through the biotic factors (e.g. on food abundance or parasite infection), or directly on the physiological performance of the individual (Hoar and Randall, 1969). In addition, abiotic environmental factors can also be used as guidance during migration, e.g. when finding the most profitable

movement direction or for reducing risk of predation or parasite infection (e.g. salmon lice) (Hasler, 1966; McKeown, 1984). Thus, the abiotic factors can act on different levels and may potentially have a great influence on both the individual migration ability and performance, as well as on the individual mortality risk and growth ability.

Figure 1 shows a qualitative overview of Atlantic salmon studies concerning the effects of abiotic factors like light, temperature, river flow and tidal cycles on the migratory behaviour (Fig. 1, appendix). The overview reveals that there exists a fairly sustainable literature on most of the life phases of southern salmon populations. However, in comparison, similar knowledge related to our northernmost Atlantic salmon populations is limited, despite the fact that northern areas host some of the largest and most productive salmon populations in the world. In southern areas, many salmon studies have been focusing on migratory behaviour during the freshwater stage and some studies have been focusing on the fjord and ocean part of its life cycle. In particular, the impact of river temperature, river flow and light on the smolt migration, and the timing of river entry of homing salmon in relation to tidal cycles and river flow have been given ample attention. However, only few studies have been performed on northern populations and virtually no published information exists on the post-smolt and adult stages in this region.

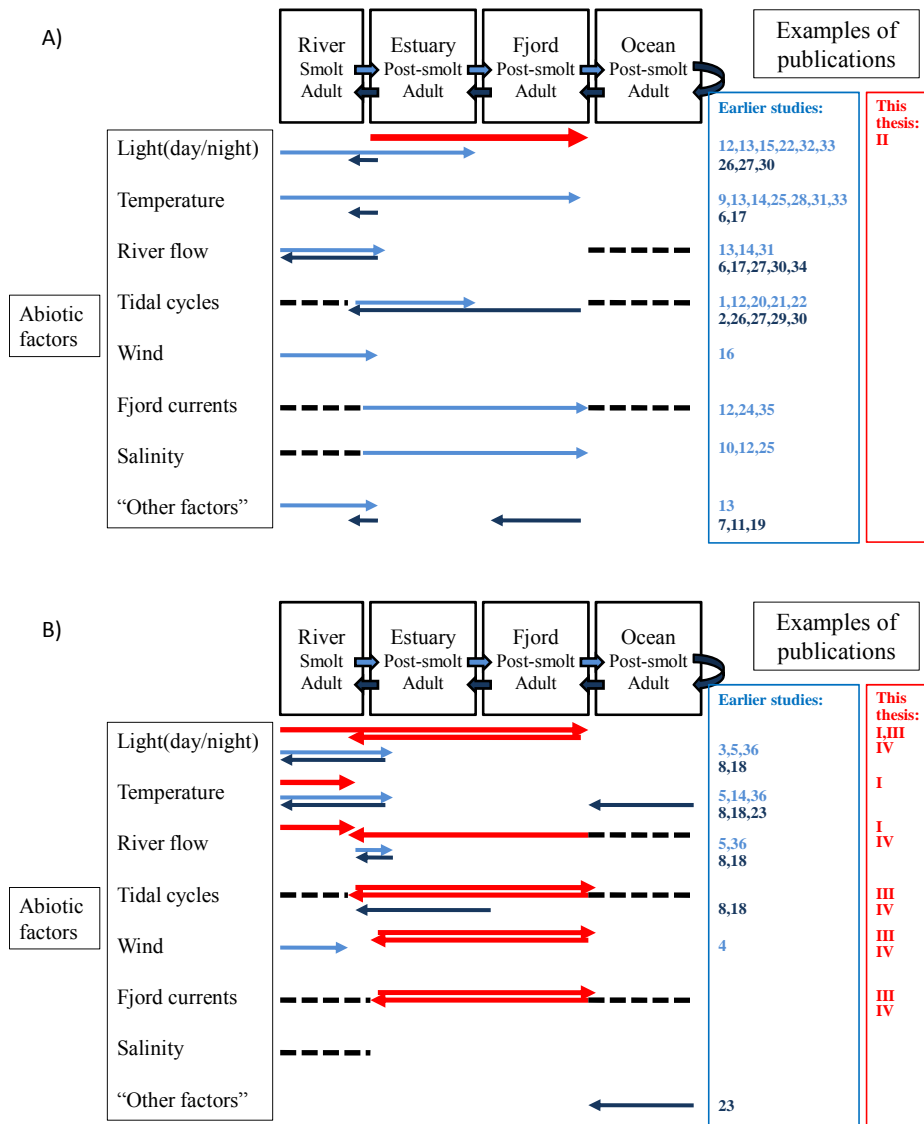


Fig 1. A qualitative overview of studied relationships between environmental factors and migratory behaviour of Atlantic salmon populations from areas south (A) and north (B) of the Arctic Circle during different parts of their migration. Blue arrows show areas covered by earlier studies. Red arrows represent areas covered in this thesis. The direction of an arrow indicates seaward or homing migration. Black dotted lines show habitats where the actual environmental factor is not expected to be important for the salmon migratory behaviour. The blue reference numbers on the right side refer to examples of earlier published studies given in appendix. The red numbers refer to the papers included in this thesis.

The impact of the environmental factors on southern and northern populations of Atlantic salmon may vary considerably throughout the year, with 24 h daylight during the summer and the 24 h darkness during winter as one of the main differences between the northern areas and areas below the Arctic Circle. The cycle of day and night is one of the most dramatic features in the nature and almost all species exhibit daily changes in their behaviour and/or physiology (Vitaterna *et al.*, 2001). Therefore, due to the significant variation in diel light intensity between temperate and sub-Arctic areas, southern and northern populations of Atlantic salmon may be affected differently. For example, findings in temperate areas have shown that nocturnal (night) smolt migration is associated with dark nights (Thorpe and Morgan, 1978; Solomon, 1982; Youngson *et al.*, 1983; Hansen and Jonsson, 1985; Hvidsten *et al.*, 1995; Aarestrup *et al.*, 2002; Martin *et al.*, 2009). In contrast, a few studies in sub-Arctic rivers have indicated that smolts may migrate both day and night (Veselov *et al.*, 1998; Carlsen *et al.*, 2004).

The sea temperature may be another major abiotic environmental factor that differs between the temperate and sub-Arctic region, and thus can be expected to affect salmon migratory behaviour. In general, Norwegian Atlantic salmon smolts have been found to enter the sea when the sea temperature is about 8° C (Hvidsten *et al.*, 1998). This regardless of whether the river is situated in the temperate or sub-Arctic region, resulting in that the smolt run in northern Norway is about 5–8 weeks later than in southern Norway (Hvidsten *et al.*, 1998; Rikardsen *et al.*, 2004). The synchrony of smolt migration from the rivers with the ocean temperatures and feeding opportunities is crucial for smolt feeding and survival (Power, 1969; Hvidsten *et al.*, 1995; Hansen, 2000; Hvidsten *et al.*, 2009), as the smolts attempt to match their sea migration with the most profitable ocean conditions (Hvidsten *et al.*, 2009; Rikardsen and Dempson, 2010). The smolts therefore seem to be locally adapted to a “physiological” and “environmental” smolt window, as described by McCormick *et al.* (1998). The “physiological smolt window” is controlled by the photoperiod, temperature and water flow and determines the physiological and behavioural readiness of the smolt for migration and seawater entry. The “environmental smolt window”, however, is the period in which seasonal changes in environmental conditions in rivers, estuaries and the coastal environment are appropriate for high smolt survival. Due to the regional

differences in sea temperature during the spring, the local adaptations to the “smolt windows” may consequently differ between sub-Arctic and temperate rivers.

Differences in fjord morphology are also among the factors that can affect the migration behaviour and survival of salmon. Many southern Norwegian fjords are characterized as long and narrow sill fjords with several rivers draining into them, resulting in a brackish surface water layer. Northern Norwegian fjords are often shorter and wider with only one main river in the fjord bottom. They are usually more productive, more strongly influenced by the coastal and tidal currents, and with less clearly defined sills (Rikardsen *et al.*, 2004). As potential predators are most abundant within fjords (Hvidsten and Lund, 1988; Svenning *et al.*, 2005), a long fjord may increase the predation risk. Northern post-smolts have been hypothesised to have a longer fjord residency compared to southern populations due to assumed higher food abundance in the northern fjords (Rikardsen *et al.*, 2004; Knudsen *et al.*, 2005). This may then increase the predation risk despite the shorter and more open northern fjords. However, the exact fjord residency of northern post-smolts has not been studied directly before.

Objectives of the thesis

As discussed above, only few salmon studies on sub-Arctic populations of Atlantic salmon that relate migration and environmental factors are published. This is despite the fact that environmental conditions may differ substantially between northern and southern areas. In particular, studies on the smolt, post-smolt and homing salmon are missing. The period when the salmon enter the sea for the first time, starting as smolts in the river and followed as post-smolts in the fjord, is regarded as one of most critical periods in the salmon life history. Furthermore, homing adults may suffer from high mortality during their return migration through fjords and estuaries due to both predation and coastal fishery. The main aim of this thesis was therefore to study the behavioural patterns of the northern populations of Atlantic salmon during their smolt migration in rivers (Tana and Alta), and as post-smolts and homing salmon during their estuary and fjord migration (Alta). Special attention was paid to the impact of light intensity on the migratory behaviour. A study of direct impact from light intensities on post-smolt swimming behaviour in a south-west Norwegian fjord (Hardanger Fjord), with distinctive night and day, was therefore included in the thesis.

The observed behaviour in the northern populations was related to earlier findings in southern populations in order to reveal differences and similarities in the migratory behaviour. The specific objectives were to:

- Study how light intensity affects the swimming behaviour of downstream river migrating smolts, fjord-migrating post-smolts and homing adult salmon (papers I, II, III and IV).
- Examine possible correlations between the migratory behaviour of descending smolts, fjord-migrating post-smolts and homing adult salmon and abiotic environmental variables like river flow, water temperature, tidal cycle, fjord currents and wind (papers I, III and IV).
- Study fjord residency and migratory speeds of fjord-migrating post-smolts and homing adult salmon (papers III and IV)
- Estimate post-smolt survival rate during sea entry and fjord migration (paper III).

Study sites

Three of the studies (papers I, III and IV) presented in this thesis were conducted in what in the following is defined as the sub-Arctic region, while one study (paper II) took place in a temperate fjord system. Born and Böcher (2001) used two definitions of the Arctic region (which includes sub-Arctic):

- *The area north of the Arctic Circle (66° 5'N)*
- *The region where the average temperature for the warmest month (July) is below 10° C*

Since the Arctic Circle is the approximate limit of the polar night and midnight sun, and light is the main environmental factor focused on in the four studies presented, the first definition is used as the border between Arctic and temperate areas in this thesis. The terms “sub-Arctic” and “northern” are used for the studies in River Alta, Alta Fjord and River Tana (papers I, III and IV), which all are situated in northern Norway and well above the Arctic Circle (Fig. 2). Sub-Arctic climates are characterised by extreme seasonal variations in the magnitude of solar radiation, with complete or near-complete darkness during winter and near-continuous daylight in summer. “Temperate” and “southern” are used for Atlantic salmon populations from the temperate region, which often is defined as the geographical zone between the Tropic of Cancer (23° 5'N) and the Arctic Circle (Born and Böcher, 2001). One of the studies in this thesis (paper II) took place in the Eidfjord, which is a side-arm of the Hardanger Fjord located in south-western Norway (Fig. 2). The temperate zone is characterised by dark nights both summer and winter.

Both River Tana (70°N, 28°E) (paper I) and River Alta (70°N 23°E) (papers III and IV) are sub-Arctic rivers in northern Europe, which drain through a fjord before entering the open ocean (Fig. 2). They are among the northernmost Atlantic salmon rivers in the world and support some of the most productive Atlantic salmon populations. River Tana has a catchment area of 16.386 km² and about 1000 km of river stretches are accessible to ascending salmon. The study in River Tana (paper I) was conducted close to the mouth of the tributary River Utsjoki, which is situated 106 km from the mouth of River Tana. In River Alta, which has a catchment area of 7 400

km², the lowermost 46 km is available for migrating salmon. Smolt ages in both rivers vary between 2 and 7 years, but most salmon migrate at 3–5 years of age (Erkinaro, 1997; Ugedal *et al.*, 2008). During the main smolt run in late June to middle July (Hvidsten *et al.*, 1998), the temperature in the rivers usually varies from 8–15° C. After 1–4 years in the ocean, the adult salmon returns to the two rivers to spawn during May–August. The river temperatures during this period vary from 3–15° C. Spring ice break-up is normally in the middle of May and the rivers usually freeze in October or November. River Alta drains into the Alta Fjord (papers III and IV). The fjord is 15 km at its widest and 488 m at its deepest (Fig. 2) and opens through three channels to the northern Atlantic Ocean. The tidal range is 1.5–2.5 m. The estuary was in this thesis defined as the first 3 km of the fjord, measured from the river mouth.

The study in the Hardanger Fjord (paper II), south-western Norway (Fig. 2), was conducted in Eidfjord (60°29 N; 7°05 E) which is situated in the innermost part of the 150 km long Hardanger Fjord. A freshwater input exists throughout the year with a maximum in June and July. During the study period in Mai 2006, salinity varied from 18–26 above and 22–28 below the halocline. Surface water temperature varied from 7–12° C. The Atlantic salmon used in this study were hatchery-reared smolts from the Statkraft Energy AS hatchery in Eidfjord with wild parents of the River Lærdal stock. The Lærdal River (61°08 N; 7°23 E) is located 144 km from the ocean and have a catchment area of 1184 km².

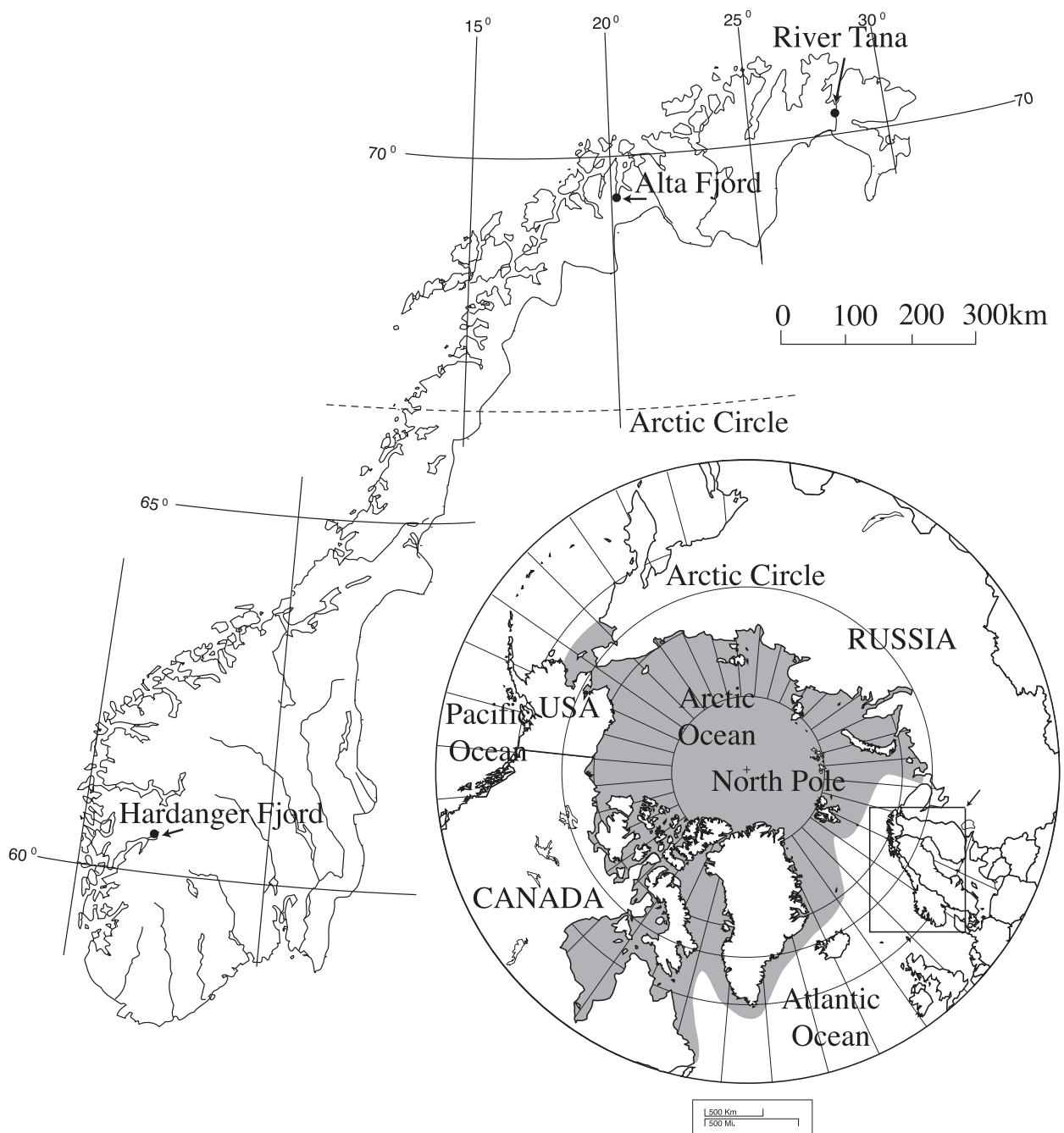


Fig. 2. Map showing the three study sites used in this thesis. The Arctic Circle was used as the border between northern and southern populations of the Atlantic salmon. Grey area indicates the maximum sea ice extent.

Methodological approach

All studies included in the thesis are observational. Two different approaches were used to detect relationships between environmental variables and the Atlantic salmon migration: submerged video cameras (paper I) and acoustic telemetry (papers II, III and IV).

Submerged video cameras

A matrix of submerged video cameras that covered the entire water column across the River Utsjoki was used to provide information on the exact timing, positioning in the water column and the swimming direction of all the individual smolts during river descent (paper I). The use of submerged video cameras when monitoring fish migrations enables the observations on undisturbed individuals. Fyke nets and other kind of fish traps have earlier often been used in studies of smolt migration when assessing timing of river descent. However, results from these studies have indicated that traps may influence the migratory behaviour observed (Pyefinch and Mills, 1963; Veselov *et al.*, 1998). For example, if a smolt tries to avoid a trap by maintaining its position with its head directed upstream against the current, it may later continue its downstream migration at dark when it is less aware of the actual position of the trap, and the recorded time of passage may not reflect natural behaviour (Veselov *et al.*, 1998). The use of traps may therefore have influenced the observed diel migration pattern in earlier studies. By using submerged video cameras no such behaviour is expected. The use of submerged video cameras may therefore be a very useful tool in order to monitor the total fish migration at one locality throughout the whole season. It may, however, have limited functionality during periods of flooding and high turbidity.

Acoustic telemetry

Acoustic telemetry was used to automatically track a subset of the seaward migrating Atlantic salmon smolts/post-smolts and the homing Atlantic salmon in River Alta and the Alta Fjord (papers III and IV). In addition, it was used to manually track the hatchery reared Atlantic salmon post-smolts the first hours after release into the Hardanger Fjord (paper II). While submerged video cameras can provide information of all migrating individuals at one spot in the river, use of acoustic telemetry may give

detailed information about e.g. migratory speed, swimming depth and horizontal distribution over an extended period and a larger geographical area (Thorstad *et al.*, 2007; Lacroix, 2008; Serrano *et al.*, 2009).

A challenge associated with detecting relationships between environmental variables and the migration of fish is the lack of information on how many fish that are present up- or downstream of the counting site (Trépanier *et al.*, 1996). An increase in counts at one spot in the river may not necessarily mean that conditions for migration are improved, but could reflect increased fish abundance for other reasons (Thorstad *et al.*, 2008). As an example, many studies analysing timing of river entry are based on data from counting fences or automatic radio logger stations situated at one fixed position in the river or river mouth (e.g. Økland *et al.*, 2001; Dahl *et al.*, 2004; Jonsson *et al.*, 2007). The use of acoustic tagging and several arrays of listening stations in the fjord and estuary, will instead give additional information about the salmon already before it enters the river. However, a limiting factor in these kinds of studies is the cost of acoustic tags, which then often results in a reduced number of individuals to track.

Another challenge when conducting acoustic telemetry studies is that handling and tagging of the fish may influence its behaviour and swimming performance (Brown *et al.*, 2006b) as well as its risk of being captured in fisheries (Rikardsen and Thorstad, 2006). For Atlantic salmon post-smolts, Moore *et al.* (2000) has recommended tags to be <5% of the fish mass to minimize effects on behaviour and survival. However, Jepsen *et al.* (2005) argued that there is no applicable “rule” for a tag/fish size relationship, but that the appropriate maximum relationship is driven by the specific study objectives, the tagging method and the species/life stage involved. A consequence of the tag/fish size relationship used in the present thesis was that the post-smolts vertical behaviour only could be examined for hatchery reared post-smolts, since wild post-smolts were too small for the current generation of acoustic depth sensing transmitters.

Summary of papers

Paper I:

Spatial and temporal migration of wild Atlantic salmon smolts determined from a video camera array in the sub-Arctic River Tana.

Spatial and temporal migratory behaviour of wild Atlantic salmon smolts was investigated in the River Utsjoki, a tributary of the sub-Arctic River Tana, using submerged video cameras that covered the entire water column across the river. The matrix of cameras provided information on the exact time, position in water column and swimming direction of individual smolts. The smolt migration started in the beginning of June and ended in the middle of July, i.e. during the period of midnight sun. Smolts migrated all day, with an overall peak from 0700 to 1000 hours. In the beginning of the smolt run, the migration was mainly during daytime hours. However, in the end of the run they migrated more equally both day and night. This change in migratory behaviour may have been a trade-off between utilizing the warmer water in the day early in the season and the more darker hours in the night later in the season. Hours of sunshine and change in water level explained 55% of the day-to-day variation in numbers of migrating smolts. Most smolts migrated actively (head first) in the lower part of the water column with only 4% observed in the upper 30 cm surface water layer.

Paper II:

Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity.

In order to study possible correlation between light intensity and swimming depth of Atlantic salmon post-smolts, eight hatchery-reared individuals were implanted with acoustic depth sensing transmitters. After release to the outlet of River Eio, the post-smolts were manually tracked for 5–12 h in the temperate Hardanger Fjord, south-western Norway. The post-smolts spent most of their time (49–99%) at 1–3 m depth during the day, whereas four of seven fish were found close (<0.5 m) to the surface at night, with a strong negative cross-correlation between general swimming depth and surface light intensity. Hence, the actual swimming depth of post-smolts during their early marine migration may depend on the light conditions, although the individual variation in vertical movement pattern was large. No cross-correlations between light

intensity and swimming depth during daytime periods with rapid changes in light intensity were found, indicating that other factors than light intensity were important in initiating the irregular dives that were recorded down to 6.5 m depth.

Paper III:

Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors.

To study smolt behaviour and survival of a northern Atlantic salmon population during river descent, sea entry and fjord migration, 120 wild smolts were tagged with acoustic tags and registered at four automatic listening station arrays in the mouth of the north Norwegian River Alta and throughout the Alta Fjord. An estimated 75% of the post-smolts survived from the river mouth, through the estuary and the first 17 km of the fjord. Survival rates in the fjord varied with fork length (L_F), and ranged from 97.0 to 99.5% km^{-1} . On average, the post-smolts spent 1.5 days (36 h, range 11–365 h, 20.5 km day^{-1}) travelling from the river mouth to the last fjord array, 31 km from the river mouth. The migratory speed was slower ($1.8 L_F \text{ s}^{-1}$) in the first 4 km after sea entry compared with the next 27 km ($3.0 L_F \text{ s}^{-1}$). Post-smolts entered the fjord more often during the high or ebbing tide (70%). There was no clear diel migration pattern within the river and fjord, but most of the post-smolts entered the fjord at night (66%, 2000–0800 hours), despite the 24 h daylight at this latitude. The tidal cycle, wind-induced currents and the smolts' own movements seemed to influence migratory speeds and routes in different parts of the fjord. A large variation in migration patterns, both in the river and fjord, might indicate that individuals in stochastic estuarine and marine environments are exposed to highly variable selection regimes, resulting in different responses to environmental factors on both temporal and spatial scales. Post-smolts in the northern Alta Fjord had similar early marine survival rates to those observed previously in southern fjords; however, fjord residency in the north was shorter.

Paper IV:

Homing behaviour of Atlantic salmon during final marine phase and river entry.

The behaviour of wild adult Atlantic salmon during their homing migration was studied by tagging 74 individuals with acoustic tags in the Alta Fjord in northern Norway. They were tagged and released 19–34 km from the mouth of the River Alta, and registered by five arrays of acoustic listening stations deployed across the fjord and in the river mouth. A comparison at 17 microsatellite loci confirmed the River Alta origin of the fish. Mean migratory speed the last 17 km before river entry was 16.5 km day^{-1} . Median migratory speed was reduced from 34 to $7 L_F \text{ min}^{-1}$ and mean swimming depth from 2.5 to 0.5 m as the salmon approached the estuary. The salmon generally followed the coastline towards the river mouth; however, wind-induced currents periodically seemed to move the salmon out to the central part of the fjord. River flow, diel periodicity and tidal cycles alone or together did not affect the timing of river entry. The finding that the homing salmon migrated close to the surface and shoreline, combined with their longer residency in the inner fjord, increase their risk of being caught by net fishing targeting salmon along the shoreline in this area.

Discussion

Effects of light intensity on the migratory behaviour

The present thesis provides new knowledge about the daily light-dark cycle governing rhythmic changes in the behaviour of northern populations of Atlantic salmon. Until now, our knowledge on the circadian migration behaviour of Atlantic salmon has mainly been limited to southern populations where the migration patterns observed have been nocturnal (e.g. Moore *et al.*, 1995; Smith and Smith, 1997; Ibbotson *et al.*, 2006), whereas more or less no information has existed on the migratory patterns in northern latitudes with little or no diurnal light cycle. Papers I, III and IV in this thesis indicate that northern Atlantic salmon smolts, post-smolts and homing adults have similarly movement behaviour during day and night. Further, the study of post-smolts in the Hardanger Fjord, which has distinctive day and night periods (paper II), indicate that light intensity also affects the swimming depth of the fish; the post-smolts swam deeper in the water column during the day than during the night.

The nocturnal migration observed for smolts in areas with dark nights is thought to be an adaptive behaviour to minimize the predation risk from sight-feeding predators (Solomon, 1982). In contrast, in sub-Arctic rivers with bright nights and hence a less chance of hiding, a 24 h migration pattern (papers I, III) can instead *reduce* the predation risk, as the smolts will reach the river mouth faster than they would if they moved only during night-time. Further, the change from daytime migration to a more 24 h migration, as observed in the smolt-run in River Tana (paper I), may also be an antipredatory strategy. Salmon are relatively more vulnerable to endothermic predators such as birds when temperatures are low due to their slower escape response (Webb, 1978; Veselov and Shustov, 1991). Thus, it is suggested, that the change in diel migratory behaviour throughout the season may have been a trade-off between utilizing the warmer water during daytime early in the season and the darker hours in the night later in the season. The post-smolt behaviour of swimming deeper during daytime (paper II) is also suggested being an antipredatory strategy. A similar diel migratory pattern has earlier been observed in post-smolts indirectly by use of temperature sensing data storage tags (Reddin *et al.*, 2004), but the present study was the first paper that directly correlated post-smolt migratory behaviour with light intensity.

Despite the general pattern of a 24 h migratory movement pattern in the studied northern populations, 2/3 of the post-smolts seemed to enter the Alta Fjord at night (paper III). This difference from the general pattern may be an adaptation to the increased predation risk immediately after sea entry (Hvidsten and Lund, 1988; Dieperink *et al.*, 2002; Jepsen *et al.*, 2006). It may be speculated, that the smolts aggregate close to the river mouth and then pass the river mouth in larger groups by night in order to decrease the predation pressure. In earlier studies of southern Atlantic salmon populations, post-smolts have been found to mainly continue the nocturnal migratory behaviour from the river when migrating through the estuaries (Moore *et al.*, 1995; Lacroix *et al.*, 2004; Martin *et al.*, 2009). In contrast, there was no diel pattern in the adult salmon timing of river entry during their homing migration (paper IV). The two different strategies in timing of passing the river mouth can be explained by the adult salmon not experiencing the same predation level as the considerably smaller post-smolts. However, the adult salmon behaviour during river entry differed from what have been observed for southern populations where most of the homing adults seem to enter the river during night (e.g. Potter, 1988; Smith and Smith, 1997).

In summary, the northern smolts, post-smolts and homing adult salmon studied in the present thesis migrated both day and night through the river and fjord. These findings differ from the general observations of nocturnal migration patterns among southern populations of Atlantic salmon. The observed 24 h migration pattern of northern salmon is probably due to the fact that salmon has less chance to “hide in the dark” at northern latitudes compared to their companions in the south. Thus, in order to reduce the time they are exposed to sight feeding predators, smolts and post-smolts should rather migrate both day and night in order to reach the open ocean where they are assumed to be less vulnerable to predators. Homing salmon in northern areas may also use the same strategy to reduce their chance to be eaten by marine predators (e.g. seals in the fjord and estuary) in order to reach their spawning areas.

Effects of other abiotic environmental factors

Patterns of migratory movement by fishes are strongly influenced by environmental conditions (Lucas and Baras, 2001). Especially river flow, water temperature and tidal cycles have often been related to Atlantic salmon migrations (Fig 1), however fjord currents and wind may also be important factors. None of these environmental factors studied in this thesis (papers I, III and IV) did, as opposite to the light intensity, seem to influence the migratory behaviour of the studied salmon differently from what has been observed in earlier studies on southern populations of Atlantic salmon (see Fig. 1 and appendix for references). For example, river flow was found to affect the smolt migration (paper I), but not the river entry of homing adult salmon (paper IV) and such relationships are commonly reported from southern populations (Hesthagen and Garnås, 1986; Hvidsten *et al.*, 1998; Dahl *et al.*, 2004).

For example, the daily numbers of descending smolts in the River Utsjoki were positively related to both low and increasing water levels (paper I). Decreasing (Hvidsten *et al.*, 1998; Veselov *et al.*, 1998) and increasing water levels (Solomon, 1978; Hesthagen and Garnås, 1986; Greenstreet, 1992) have both been found to be important factors influencing the smolt run. High water flow may be favourable for the migrating smolts for several reasons. For example, the smolts are transported downstream without expending much energy in active swimming. Also, the rivers may be turbid during high discharges and the water surface often forms ripples, which might give cover from sight feeding predators. When the smolt leaves the river, swimming in outgoing tide currents as observed in 70% of the post-smolts in the Alta Fjord (paper III), may further decrease the risk of predation. Predation on salmonid post-smolts in the river mouth and estuary can be a major mortality factor (Hvidsten and Lund, 1988; Dieperink *et al.*, 2002; Jepsen *et al.*, 2006) and a fast migration through these areas may reduce this. The adult salmon has also been found to utilize the river flow and tides during the homing migration. Earlier studies have shown that increased water discharge may be an important proximate factor stimulating adult Atlantic salmon to enter small rivers from sea (Jonsson *et al.*, 2007), but may also act in combination with other environmental factors such as water temperature, light, tides and water chemistry (Jonsson, 1991; Potter *et al.*, 1992; Smith and Smith, 1997). Changes in river flow were, however, not found to influence the timing of river entry for the homing adult salmon (paper IV). The fact that no correlation between river

flow, tidal cycle and river entry of the adult salmon was found in this study may be explained by the generally large discharge of the River Alta ($75\text{--}130\text{ m}^3\text{ sec}^{-1}$) during the study period. Due to this, the salmon were probably able to safely enter the river and migrate upstream without support from flooding tides or increased river discharge.

The river temperature was, as discussed earlier, likely to be important in setting the observed change in the diel smolt migration pattern throughout the season (paper I). Temperature has been suggested as an important factor regulating the physiology and subsequently the behaviour of fish (Høgåsen, 1998; Claireaux *et al.*, 2006; Oppedal *et al.*, 2007). Similar to the impact of water temperature on the smolts diel migratory behaviour (paper I), water temperature is also likely to directly affect the post-smolts migration pattern the first hours and days after sea entry due to osmoregulatory challenges. Due to large spatial and temporal variation in seawater temperature and salinity gradients in estuaries and fjords, migration in the habitats must be stressful for the post-smolts. However, it is challenging to compare swimming behaviour and the accurate temperature or salinity experienced by the individual post-smolt (see e.g. Plantalech Manel-la *et al.*, 2009). The development of new electronic tags may, however, make this possible in the near future.

Fjord residency and migratory speeds

In general, the post-smolts (paper III) migrated 25% faster (20.5 km day^{-1}) through the innermost 17 km of the fjord than the homing salmon (16.5 km day^{-1}) (paper IV). The post-smolts did further increase their swimming speed out of the fjord, whereas the homing adult salmon decreased their swimming speed as they approached the estuary and river mouth.

The migratory speed of the post-smolts (paper III) throughout the Alta Fjord was slightly faster (in km day^{-1}) than observed in earlier studies from southern areas (Lacroix and McCurdy, 1996; Lacroix *et al.*, 2004; Thorstad *et al.*, 2007). Northern post-smolts may therefore use less time to enter the open ocean than their southern companions. Furthermore, the results are in contrast to earlier post-smolt studies on diet and parasites from the same fjord (Rikardsen *et al.*, 2004; Knudsen *et al.*, 2005), where a prolonged feeding migration was expected. The expectation was based on a

hypothesis of potential prolonged fjord residency of northern post-smolts due to generally better feeding conditions in the north.

The homing salmon (paper IV) reduced migratory speed and swimming depth as it approached the estuary. The longer transit time compared with the post-smolt and the reduction in travel rates and swimming depth may all have been indications of the need to adapt to the fresh water and/or for localising the brackish water and the odour from the home river (Quinn, 1990; Hansen and Quinn, 1998). A consequence of the longer transit time in the estuary than in other parts of the fjord, is an increased risk of being eaten by predators (Pierce *et al.*, 1990) or caught by net fishing in this area. This risk is further enhanced by the general pattern of swimming along the shore line. Therefore, it is suggested that the last part of the homing salmon fjord migration may also be an important bottleneck of survival, especially in areas with extensive coastal net fisheries. Further, the observed behaviour suggests that location of fish farms, the building of boat harbours, industrial development, gravel extraction and other physical developments along the coastline may influence the Atlantic salmon during the homing migration. There might therefore be a need for evaluating the subsequent effects of such interventions along the coastline on the homing migration of salmon.

Survival rates of northern post-smolts

In order to explain the general decline in the abundances of many Atlantic salmon populations in Europe and North America (Hansen *et al.*, 2008; ICES, 2008), increased attention has been given to survival in the sea (Hvidsten *et al.*, 2009). Especially, the period of sea entrance and the first few months of marine life have been considered as a period of major marine mortality (Hvidsten and Lund, 1988; Jacobsen and Hansen, 2000; Hvidsten *et al.*, 2009). Osmotic stress while entering saltwater is suggested to induce a less-effective antipredatory behaviour (Handeland *et al.*, 1996) and the exposure to predators immediately after sea entry may be very high (Hvidsten and Lund, 1988; Dieperink *et al.*, 2002; Jepsen *et al.*, 2006). Knowledge of the level of the initial marine survival is therefore important in order to localize the overall bottlenecks during the total marine phase of the Atlantic salmon migration.

The estimated post-smolt survival rate (paper III) of 75% over the first 17 km through the estuary and fjord indicated that post-smolts also in the northern Alta Fjord had a high mortality during the first few days after sea entry. This is particularly clear when taking into consideration that the study covers only a small fraction of their 1–4 year marine period through the northern Atlantic Ocean and Barents Sea (Holst *et al.*, 2000; Rikardsen *et al.*, 2008; Thorstad *et al.*, 2010). However, the survival rate was higher than those observed in Romsdalsfjorden, southern Norway (Thorstad *et al.*, 2007), but lower than in Passamaquoddy Bay in Canada (Lacroix *et al.*, 2004).

As with the southern populations of Atlantic salmon, the present study shows that the onset of the marine migration of northern post-smolts may be a bottleneck where they experience high mortality over a short time period compared with the rest of their marine phase. Therefore, this thesis provides further support for the general belief that the period of first migration to sea is critical in the overall survival of Atlantic salmon. However, the post-smolt survival may vary considerably between years (Hvidsten *et al.*, 2009), and further studies should focus on estimating the extent of annual variation during the early marine phase of post-smolt and how this relates for environmental factors

Phenotypic plasticity or different genotypes?

In order to fully understand how environmental factors influence individual behaviour, it is essential to reveal the importance of geno- and phenotypes in and between populations. While genotype in this context is the genetic constitution of an individual, phenotypic plasticity is the ability of a single genotype to produce more than one alternative form of morphology, physiological state, and/or behaviour in response to environmental conditions. One of the most important phenotypical traits in evolutionary ecology is variation in behaviour (West-Eberhard, 1989).

The considerable phenotypic plasticity and the variability in life history characters displayed by the Atlantic salmon (Klemetsen *et al.*, 2003) are of great importance for the persistence of populations, especially when confronted with habitat change and environmental perturbations (Beechie *et al.*, 2006). There is, however, ample evidence that natural selection can play a major diversifying role in salmonid populations. Studies of Atlantic salmon and other salmonids indicate that i.a.

predation risk appears to be a particularly influential and widespread agent of selection (Garcia de Leaniz *et al.*, 2007). Atlantic salmon return to their natal river and this precise homing may generate and maintain local adaptations through natural selection (Thorstad *et al.*, 2010). It has been documented that salmon populations in different rivers (Taylor, 1991; Verspoor *et al.*, 2005; Garcia de Leaniz *et al.*, 2007) and subpopulations within rivers (Heggberget *et al.*, 1986; 1988; Summers, 1996; Verspoor *et al.*, 2005) may differ both ecologically and genetically. Following this, the variation in circadian behaviour between northern and southern populations of the Atlantic salmon, as described in this thesis, may be due to differences in both genotypes and/or in phenotypic plasticity.

Comparison of the present studies on northern Atlantic salmon populations (papers I, III and IV) with earlier studies on southern populations may help to establish a relationship between the phenotype (trait) and specific features of the environment (ecological correlates). Such comparative studies may provide clues to the potential adaptive significance of the trait(s) and, in the case of clines, perhaps also on the specific agents of selection (Garcia de Leaniz *et al.*, 2007). Thus, the apparently different diel migratory behaviour between northern and southern populations of Atlantic salmon may be a good background for future projects to study if behavioural differences between Atlantic salmon populations are caused by variation in genotypes and/or by phenotypic plasticity. Garcia de Leaniz *et al.* (2007) suggested that use of multiple perspectives like comparative and breeding studies, reciprocal transplant experiments, mark-recapture studies, experimental manipulation and use of quantitative methods in genetics and genomics would provide the most compelling cases for such adaptation. One example of this kind of approach was given by Finstad *et al.* (2010), who studied adaptive winter survival strategies. By use of comparative and common environment studies they demonstrated that Atlantic salmon populations along a latitudinal gradient have differences in feeding motivation, indicating population differences in the genetic basis for the behavioural trade-off between feeding and sheltering.

Conclusion

This thesis shows that northern smolt, post-smolt and homing adult salmon may have different circadian behaviour from that of southern populations and these studies have thus filled some of the knowledge gaps in this regard (Fig. 1). The results indicate that northern smolts, post-smolts and homing adult salmon migrated both day and night through the river and fjord. These findings were generally opposite to earlier findings for southern populations of Atlantic salmon, where the salmon have been observed to migrate most often during the night. This is presumed to be in order to avoid sight feeding predators. In northern areas nocturnal migration will be a less effective antipredator strategy due to the 24 h daylight conditions experienced at these latitudes. Instead, a 24 h migration pattern may reduce the time the individuals use to reach their designated areas and hence lower the predation risk.

River flow, water temperature, tidal cycle, fjord currents and wind did not, unlike light intensity, seem to result in differences in migratory behaviour between northern and southern populations of Atlantic salmon. On the other hand, it seemed like both northern and southern first-time migrants were seemingly and more influenced by these environmental variables than the homing adult salmon. However, the post-smolts migrated 25% faster through the innermost 17 km of the fjord than the homing adults. The post-smolts increased their swimming speed as they moved outward the fjord, whereas the homing salmon decreased their swimming speed as they approached the estuary and river mouth. That the post-smolts migratory behaviour was more influenced by the environmental factors measured in the included studies may be due to their smaller size and higher vulnerability to predation. This is supported by the fact that 25% of the tagged post-smolts probably did not survive the first 17 km of the fjord migration. However, the finding that the homing salmon migrated close to the surface and shoreline, combined with their longer residency in the inner fjord, may have greatly increased their risk of being caught by net fishing targeting salmon in this area.

In sum, this thesis indicates that the migration behaviour of northern and southern salmon differ somewhat, and that this is related to local adjustments to the existing abiotic environmental factors typically for the different latitudes, in particular the light

regimes. These local adaptations may be due to phenotypic plasticity and/or different genotypes. The study also highlights the post-smolts and homing salmon phases in fjords and estuaries as important bottlenecks of survival in the Atlantic salmon life cycle, and that variation in both natural and anthropogenic factors during these phases may have large impacts on their migration behaviour, performance and subsequently the total return rate of salmon to their home rivers. An evaluation of the impact from subsequent effects of interventions along the coastline in areas with migratory Atlantic salmon is highly recommended in order to avoid any negative effects on their seaward and homing migration.

Future perspectives

Despite the increasing number of Atlantic salmon movement studies, there are still large gaps in our knowledge of its life cycle. As shown in figure 1, only sparse information related to open ocean migrations exists and this is especially true for northern populations. The reason for this lack of knowledge is mainly due to the challenge of following individual salmon in the ocean. However, new technology like the “Pop-off satellite tag”, which combines data storage tags and satellite data transmission, makes it now possible to track adult salmon from the rivers to their feeding areas in the ocean (Thorstad *et al.*, 2010). Further, the new and upcoming generation of acoustic transmitters with statistical processing capacity sensing i.a. depth, salinity and temperature, as well as smaller data storage tags that can be used in tagging post-smolts, may also make it possible to get very detailed datasets concerning the fjord migration. Together, such technology may greatly improve our knowledge on the Atlantic salmon migrations, as well as for other fishes, and advance our ability to pinpoint the most important bottlenecks of survival in their life cycle.

A better understanding of the coastal and oceanic components of the Atlantic salmon life cycle is important. A significant number of populations may be impacted by anthropogenic changes in their coastal habitats (Anonymous, 1999), and in addition climate change may modify the ocean environment (Anonymous, 1999; Greene and Pershing, 2007) and hence alter migration routes and survival. Other threats in the coastal zone are the salmon lice (*Lepeophtheirus salmonis* Krøyer) and escapements of farmed salmon, both of which are considered to have a major negative impact on

wild salmon stocks. As a consequence of the serious decline in the Atlantic salmon populations, Norway has established 29 national salmon fjords as one of several measures to save the wild salmon (Anonymous, 2009). In these fjords, the protection is directed at salmon farming operations and intervention in the estuaries of the watercourses. A continued expansion in this system of national salmon fjords may help to protect and strengthen the largest and healthiest salmon stocks and thus possible reduce anthropogenic impacts on some of the most important phases in the salmon life.

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Appendix

List of papers describing examples of studies on the effect from abiotic factors on migratory behaviour of Atlantic salmon. The reference numbers refer to the numbers given in Fig. 1.

Reference number	Author(s)	Year	Title
1	Aprahamian & Jones	(1997)	The seaward movement of Atlantic salmon smolts in the Usk estuary, Wales, as inferred from power station catches
2	Aprahamian <i>et al.</i>	(1998)	Movement of adult Atlantic salmon in the Usk estuary, Wales
3	Bakshantansky & Nesterov	(1974)	The downstream migration of the young salmon in the Arctic
4	Bakshantansky <i>et al.</i>	(1976)	Predators effect on the behaviour of Atlantic salmon smolts in the period of downstream migration
5	Carlsen <i>et al.</i>	(2004)	Diel periodicity and environmental influence on the smolt migration of Arctic charr, <i>Salvelinus alpinus</i> , Atlantic salmon, <i>Salmo salar</i> , and brown trout, <i>Salmo trutta</i> , in northern Norway
6	Dahl <i>et al.</i>	(2004)	The timing of spawning migration: implications of environmental variation, life history and sex
7	Døving <i>et al.</i>	(1985)	Role of olfaction in the behavioural and neuronal responses of Atlantic salmon, <i>Salmo salar</i> , to hydrographic stratification
8	Erkinaro <i>et al.</i>	(1999)	Return migration of Atlantic salmon in the River Tana: the role of environmental factors
9	Fraser <i>et al.</i>	(1993)	Temperature dependent switch between diurnal and nocturnal foraging in salmon
10	Handeland <i>et al.</i>	(1996)	Osmotic stress, antipredator behaviour, and mortality of Atlantic salmon (<i>Salmo salar</i>) smolts
11	Hasler	(1966)	Underwater guideposts - Homing of salmon
12	Hedger <i>et al.</i>	(2008)	Active migration of wild Atlantic salmon <i>Salmo salar</i> smolt through a coastal embayment
13	Hvidsten <i>et al.</i>	(1995)	Downstream migration of Atlantic salmon smolts in relation to water flow, water temperature, moon phase and social interaction
14	Hvidsten <i>et al.</i>	(1998)	Sea water temperature at Atlantic salmon smolt entrance
15	Ibbotson <i>et al.</i>	(2006)	Diel migration pattern of Atlantic salmon smolts with particular reference to the absence of crepuscular migration
16	Jacobsen & Järvi	(1977)	Antipredator beteende hos tvåårig lax <i>Salmo salar</i> L

17	Jonsson <i>et al.</i>	(2007)	Factors affecting river entry of adult Atlantic salmon in a small river
18	Karppinen <i>et al.</i>	(2004)	Return migration of one-sea-winter Atlantic salmon in the River Tana
19	Kuparinen <i>et al.</i>	(2009)	Lunar periodicity and the timing of river entry in Atlantic salmon <i>Salmo salar</i>
20	Lacroix <i>et al.</i>	(2004)	Migration of Atlantic salmon post-smolts in relation to habitat use in a coastal system
21	McCleave	(1978)	Rhythmic aspects of estuarine migration of hatchery-reared Atlantic salmon (<i>Salmo salar</i>) smolts
22	Moore <i>et al.</i>	(1995)	The migratory behaviour of wild Atlantic salmon (<i>Salmo salar</i>) smolts in the estuary of the River Conway, North Wales
23	Niemelä <i>et al.</i>	(2004)	Temporal synchrony and variation in abundance of Atlantic salmon (<i>Salmo salar</i>) in two subarctic Barents Sea rivers: influence of oceanic conditions
24	Økland <i>et al.</i>	(2006)	Swimming speeds and orientation of wild Atlantic salmon post-smolts during the first stage of the marine migration
25	Plantalech Manel-la <i>et al.</i>	(2009)	Vertical movements of Atlantic salmon post-smolts relative to measures of salinity and water temperature during the first phase of the marine migration
26	Potter	(1988)	Movements of Atlantic salmon, <i>Salmo salar</i> L., in an estuary in south-west England
27	Potter <i>et al.</i>	(1992)	Estuarine movements of adult Atlantic salmon (<i>Salmo salar</i> L.) in Christchurch Harbour, southern England
28	Reddin <i>et al.</i>	(2004)	Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (<i>Salmo salar</i> L.) during their early marine life
29	Smith <i>et al.</i>	(1981)	Orientation and energetic efficiency in the offshore movements of returning Atlantic salmon <i>Salmo salar</i> L
30	Smith & Smith	(1997)	Tidal and diel timing of river entry by adult Atlantic salmon returning to the Aberdeenshire Dee, Scotland
31	Solomon	(1978)	Some observations on Salmon smolt migration in a chalkstream
32	Solomon	(1982)	Smolt migration in Atlantic salmon (<i>Salmo salar</i> L.) and sea trout (<i>Salmo trutta</i> L.)
33	Thorpe <i>et al.</i>	(1994)	Temperature dependence of switch between nocturnal and diurnal smolt migration in Atlantic salmon
34	Thorstad <i>et al.</i>	(1998)	Migratory behaviour of adult wild and escaped farmed Atlantic salmon, <i>Salmo salar</i> L. before, during and after spawning in a Norwegian river
35	Thorstad <i>et al.</i>	(2004)	Migration speeds and orientation of Atlantic salmon and sea trout post-smolts in a Norwegian fjord system
36	Veselov <i>et al.</i>	(1998)	The pattern of Atlantic salmon smolt migration in the Varzuga river (White Sea basin)

