

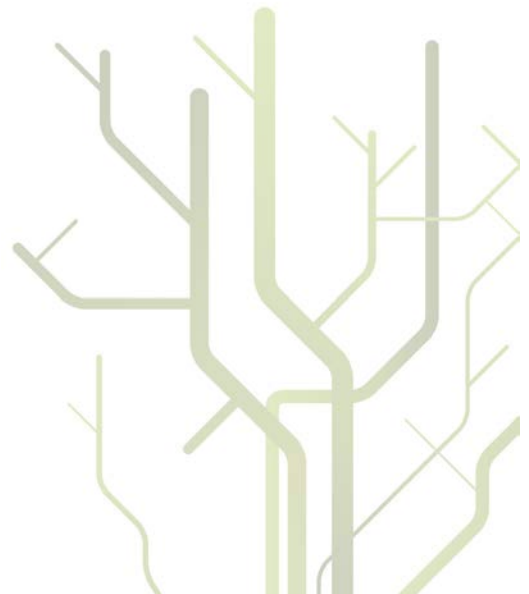
The seasonal migratory behavior of sympatric anadromous Arctic charr and brown trout



Jenny L.A. Jensen

A dissertation for the degree of
Philosophiae Doctor

Spring 2013



“The cure for anything is salt water - sweat, tears, or the sea”

Isak Dinesen

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Autumn 2013

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Summary

Anadromous Arctic charr and brown trout occurs in sympatry in Europe north of 65 °N, and are interesting for comparative studies due to their ecological similarities. Despite this, the catches of Arctic charr have declined in northern Norway while the catches of brown trout in the same geographical area have remained stable or increased. The marine part of these species' life histories is poorly documented and mainly based on Arctic charr and brown trout populations that have access to lakes during their freshwater stay. These populations are documented to overwinter in fresh water and perform feeding migrations to the sea during summer.

This thesis used acoustic and archival telemetry to study fish migrations within and between freshwater and marine habitats. In total, 172 Arctic charr and 169 brown trout were tagged. The main novel finding from this thesis work is that both Arctic charr and brown trout originating from rivers without access to lakes can be found in marine waters also during winter. This contradicts the earlier findings of Arctic charr and brown trout solely overwintering in fresh water, and also their assumed low salinity tolerance at low temperatures. Two Arctic charr populations originating from rivers without access to lakes were studied, the Signaldalen and Skibotn Rivers. The first population had access to suitable overwintering pools in the river, while the second population had less access to suitable overwintering areas due to hydropower production causing loss of ice-cover, formation of frazile ice and reduced discharge. The Signaldalen population remained in fresh water during winter, while large parts (41 – 100%) of the Skibotn population migrated to the sea. Large proportions (28 – 91%) of the brown trout from the Skibotn River also performed marine winter migrations, and during one study year 44% of the tagged individuals migrated from the Skibotn to the Signaldalen Rivers for overwintering. The physical properties of the freshwater habitat may thus be the main factor controlling in which habitat fish reside during the winter. The fish that left the river during winter were recorded in the sea up to 20 km away from the river outlet, and were documented to reside in pure marine waters for periods lasting from a few hours to several months. However, fish of both species mainly resided in the estuary during winter, where they remained in the tidal zone and therefore experienced large salinity shifts according to the high and low tides.

The migratory behaviour of Arctic charr and brown trout during summer was investigated in the previously mentioned Skibotn and Signaldalen populations in the Lyngen fjord, and also in the Hals watercourse (with lakes) populations in the Alta fjord. In the Lyngen fjord, brown trout resided mainly in the outer fjord areas during summer. Around half of the Arctic charr could be found in the outer fjord and the rest mainly in the estuaries during summer. In the Alta fjord, there were no extended estuarine residencies in either species. Instead, there was a strong correlation between water temperature and use of inner *versus* outer fjord areas. When there were temperature differences between the inner and outer fjord areas, the likelihood of finding Arctic charr in the colder area was higher than that of brown trout. The horizontal temperature profile in the Lyngen fjord was different from the Alta fjord, and there may be differences in migratory behaviour between fjords as a response to differences in temperatures and/or other environmental cues.

The results from this thesis may be highly relevant for explaining the spreading of the Atlantic salmon freshwater parasite *Gyrodactylus salaris* from the Skibotn to the Signaldalen River. The parasite can survive and maintain an infection on Arctic charr, and it can also survive on brown trout. The source of infection is known in the Skibotn River, but not in the Signaldalen River. Both Arctic charr and brown trout migrated between the two rivers in times that make it theoretically possible that the parasite could have survived the salinities and temperatures recorded in the fjord. Thus, the possibility that migrating fish can act as vectors for the parasite should be taken into account when deciding on management plans for this and other infected areas. Other management issues that may be addressed based on the present findings is the relatively high harvest rates documented in Arctic charr compared to brown trout in the Lyngen fjord (26 and 7%, respectively). Some populations may also need extra protection from harvest in the estuaries, as fishing is normally not regulated outside the immediate river outlet in northern Norway. Defining means to protect the anadromous Arctic charr populations may be especially important in a future global climate warming scenario. Recent modelling attempts studying the freshwater phase have predicted a decline in degree of anadromy in Arctic charr, and the findings in this thesis work indicates that increasing marine summer temperatures may negatively affect this species.

List of original papers

This thesis is based on the following original papers, which are referred to in the text by their Roman numerals:

- I. Jensen, J. L. A. & Rikardsen, A. H. (2008). Do northern riverine anadromous Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* overwinter in estuarine and marine waters? *Journal of Fish Biology* **73**, 1810-1818.
- II. Jensen, J. L. A. & Rikardsen, A. H. (2012). Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter. *Journal of Fish Biology* **81**, 735-749.
- III. Jensen, J. L. A., Rikardsen, A. H. & Davidsen, J. G. Seasonal migrations and marine area use of sympatric Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* from rivers without access to lakes. (manuscript).
- IV. Jensen, J. L. A., Rikardsen, A. H., Thorstad, E. B., Suhr, A. H., Davidsen, J. G. & Primicerio, R. (submitted). Fjord temperatures shape the marine area use of Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*. *Journal of Fish Biology*.

1. Introduction

What is this study about?

This thesis work was conducted on two of the European salmonids, the Arctic charr *Salvelinus alpinus* L. (1758) and brown trout *Salmo trutta* L. 1758. More specifically, the anadromous forms of these species were studied, which occurs in sympatry in Europe north of 65 °N (Klemetsen *et al.*, 2003). Anadromous Arctic charr and brown trout have many ecological similarities (Klemetsen *et al.*, 2003). Despite these similarities, the catches of Arctic charr have declined in northern Norway, while the catches of brown trout have remained stable or increased in the same geographical area (Anon., 2011). The marine migratory behaviour of these species is poorly documented, and the knowledge base for management is built on populations which have access to lakes during their freshwater stay. Despite the descriptive nature of this thesis, the combination of results from the two study species and the different study areas increases not only the management related understanding, but also the general biological knowledge. As the studies in this project are comparative between Arctic charr and brown trout, the main focus in this synthesis is on the northern areas where these species occurs in sympatry in their anadromous form.

General background for the study

One of the most captivating features of salmonids is their plasticity, *i.e.* their ability to adapt to the surrounding environment (Klemetsen *et al.*, 2003). The migrations performed by many salmonids between fresh and salt water is an excellent example of this ability to adapt, as it includes physiological, morphological and behavioral changes needed in order to cope with the alternating environments (Hoar, 1988). Migrations between fresh and salt water are called diadromy (Lucas & Barras, 2001), and occurs in only 1% of all known fish species (Helfman *et al.*, 2009). Diadromy can be divided into anadromy, catadromy and amphidromy, depending on the direction and purpose of the migration. In anadromy, the fish reproduce in fresh water and

migrate to the sea, whereas spawning migrations from fresh water to the sea are referred to as catadromy. Amphidromy means migrations between fresh and salt water (both directions) without the purpose of breeding (McDowall, 1987, 1997). Seasonal migrations may occur when the use of multiple habitats results in increased lifetime fitness (Gross *et al.*, 1988). At northern latitudes, the sea is generally more productive than fresh water (Gross, 1987) and the growth potential of individuals migrating to this habitat is thus greater than that of conspecifics remaining stationary. In salmonids, body size is strongly related to reproductive success, and hence lifetime fitness (Fleming, 1996). However, the sea is also considered to be a more high risk environment due to the higher numbers of predators in this habitat (Ward & Hvidsten, 2010), and the migrations may come at a high price. Both Arctic charr and brown trout often occur as partial migratory populations, where only a proportion of the population participate in the migration while they reproduce together with their stationary conspecifics (Jonsson & Jonsson, 1993).

Arctic charr and brown trout have many ecological similarities, and are often found in sympatry (Klemetsen *et al.*, 2003). However, there are differences in their distribution ranges (including both freshwater resident and anadromous populations). Arctic charr is the world's northernmost freshwater fish and has a circumpolar distribution, while brown trout is indigenous to Europe, North Africa and western Asia (Klemetsen *et al.*, 2003). Brown trout is a popular angling target and have been introduced to at least 24 countries outside Europe and today has a worldwide distribution (Elliott, 1994). Both species naturally typically inhabit cold, oligotrophic lakes and rivers, but are highly polymorphic and can adjust to a range of limnic habitats (Klemetsen *et al.*, 2003). The thermal limits for survival are about 3°C higher for brown trout than Arctic charr in fresh water (Elliot & Klemetsen, 2002), which may explain the difference in distribution ranges.

As anadromous Arctic charr and brown are popular angling targets under strict management regimes, the body of literature on their migratory behavior is surprisingly small. At northern latitudes, the marine feeding phase during summer have been studied to some extent (*e.g.* Berg & Berg, 1987, 1989; Rikardsen & Amundsen, 2005; Rikardsen *et al.*, 2007a), but very few studies has focused on the winter ecology of sea trout (Rikardsen *et al.*, 2006) and none on

the winter ecology of adult anadromous Arctic charr. Vardnes River (approximately 69 °N) is the northern system where the migratory behavior of sympatric anadromous Arctic charr and brown trout has been most extensively studied during many years of trapping and Carlin-tagging all ascending and descending fish in the river (*e.g.* Berg & Berg, 1987, 1988, 1989, 1993). The findings showed that the mean duration of stay in the sea was 68 days for brown trout and 48 days for Arctic charr. Other studies in northern Norway (Finstad & Heggberget, 1993; Kristoffersen *et al.*, 1994; Rikardsen *et al.*, 1997, 2000) and other parts of the northern hemisphere (Svalbard, Arctic Canada and Labrador, reviewed by Klemetsen *et al.*, 2003) have also showed that Arctic charr normally migrate to sea for one to two months during summer. Other findings from the Vardnes River included that most recaptures of fish occurred within 25 km from the river mouth in littoral fjord areas (Berg & Berg, 1987; Berg & Jonsson, 1989). Based on these trapping studies, factors such as migration timing, growth and freshwater return rates are well documented due to the high numbers of individuals included in a study of all migrating fish.

As the previous paragraph described, the fish from populations originating from rivers with access to lakes migrate to the sea during the summer months. As salmonids are ectotherms they grow faster with increasing temperatures up to a growth optimum (Jobling 1994, 2010). Therefore, they grow especially well in the summer when the marine temperature as well as the marine production is high (Ingvaldsen & Loeng, 2009; Rikardsen & Dempson, 2010). As marine migration also comes with a cost in the form of increased risk of being preyed upon (Ward & Hvidsten, 2010), maximizing the gain by migrating during the summer may be a good evolutionary strategy. Also, it has been believed that the northern populations of anadromous brown trout and especially Arctic charr are restricted to freshwater residency during winter due to indications of low salinity tolerance at low water temperatures (Hoar, 1976; Finstad *et al.*, 1988, 1989, 1998). However, during fishing with nets in two northern fjords during winter, Rikardsen (2004) caught brown trout with salmon lice *Lepeophtheirus salmonis* Krøyer 1837 infections indicating that they must have been at sea for several months. Further, Rikardsen *et al.*, (2006) showed that the same fish had fed during winter while at sea. As the fish were caught in fjords where rivers without access to lakes are common, the authors suggested that the fish had originated from these rivers without lakes. This behavior has previously been described to occur

in brown trout at more southern latitudes, where poor or non-existing overwintering conditions in small streams force the fish into marine waters (Jonsson *et al.*, 2001; Jonsson & Jonsson, 2002; Knutsen *et al.*, 2004; Olsen *et al.*, 2006). In this thesis it was tested if the winter migrating fish came from populations originating from rivers without access to lakes, and if so, if unfavorable winter conditions could be related to the response. It was also tested if Arctic charr displayed the same behavior.

The two rivers representing freshwater habitats without access to lakes in this thesis, the Skibotn and Signaldalen Rivers, are infected with the parasite *Gyrodactylus salaris* Malmberg 1957 (Platyhelminthes: Monogenea). This parasite was introduced to Norway from Sweden with transportations of hatchery reared Atlantic salmon *Salmo salar* L. 1758 smolts in the late 1970-ies. The parasite has strongly reduced or driven to extinction many Norwegian Atlantic salmon populations, as they are not resistant to the parasite (Bakke *et al.*, 2007). The parasite is one of the main threats to Norwegian populations of Atlantic salmon (Anon., 2011). Whereas the parasite is lethal only for Atlantic salmon, both Arctic charr and brown trout can carry the parasite, and it can reproduce and remain an infection on Arctic charr in fresh water (Jansen & Bakke, 1995; Winger *et al.*, 2009). After the documentation of *G. salaris* in the Skibotn River in 1979, it was also found in the neighboring Signaldalen River in 2000 (Knudsen *et al.*, 2004). There is no documentation of how the infection in the Signaldalen River manifested. Among other theories, it has been speculated that salmonids migrating between rivers may have transported the parasite (Knudsen *et al.*, 2004). *Gyrodactylus salaris* is a freshwater parasite, but it can survive for shorter temperature and salinity dependent periods in the sea (Soleng & Bakke, 1997). Information on the marine migratory behavior of Arctic charr and brown trout could therefore be important in evaluating if these species could potentially spread the parasite between rivers.

Objectives of the thesis

Based on the earlier studies referred to in the previous section, there may be profound differences in especially the winter migratory behavior between populations of anadromous Arctic charr and brown trout from different freshwater habitats at northern latitudes. Fish without access to lakes during winter may to a larger extent migrate to the sea. Also, the evidence on where these species reside in the marine habitat during summer is circumstantial. If sound management decisions are to be made regarding the anadromous populations of these two fish species, basic knowledge on when and where the fish are in the sea and the factors controlling these behavioral aspects are essential. As salmonids are highly plastic species that adapt readily to their environment, fish from multiple populations experiencing different environmental cues had to be studied to address these topics. Management implications specific to the study area include whether anadromous fish can spread the parasite *G. salaris* between different freshwater habitats. The individual migratory behavior of two brown trout populations and three Arctic charr populations were studied by use of telemetry in the Lyngen and Alta fjords. Due to opposing trends in catches of anadromous Arctic charr and brown trout at northern latitudes, the two species behavior was compared for detection of interspecific differences throughout the studies. The project aimed to answer the following main questions:

- 1) Do Arctic charr and brown trout use estuarine and marine waters during winter? (**Papers I, II & III**)
- 2) If Arctic charr and brown trout are at sea during winter, are there differences in behavior between populations from rivers with and without access to lakes (**Papers I - IV**)
- 3) Which fjord areas are used by Arctic charr and brown trout during their summer feeding migrations, and which factors control the behavior? (**Paper III & IV**)

In addition, the migratory behavior documented in this thesis is discussed in relation to if anadromous Arctic charr and brown trout could have caused the spreading of *G. salaris* between the two neighboring study rivers in the Lyngen fjord, and also in relation to how the migratory behavior may be influenced by increasing global temperatures.

2. Material and methods

2.1. Study areas

2.1.1. The study fjords

The two fjords where the studies in this thesis were performed, the Lyngen and the Alta fjords, are both located in the sub-Arctic region (as defined by Born & Böcher, 2001). The Lyngen Fjord is a long and narrow fjord stretching *c.* 85 km inland. The study area covered approximately the innermost 35 km, and in this area the fjord is only 4.5 kilometers at its widest. The Alta fjord stretches *c.* 30 km inland and is 15 km at its widest. The bathymetry of both fjords is mostly steep, but the innermost parts have shallower areas and areas that fall dry during low tides. Both fjords have full strength salt water, but has high fresh water input in the inner areas. This strongly influences the currents, temperatures and salinities in the upper water layers of the study areas. For a more detailed description of the study fjords, see **Papers III** (Lyngen fjord) and **IV** (Alta fjord).

2.1.2. The study watercourses

The Arctic charr and brown trout included in this study originated from three different freshwater habitats, the Hals, Signaldalen and Skibotn watercourses. The Hals watercourse has 20 km of river accessible to anadromous salmonids, including the Lake Storvatnet (1.2 km²) located 2 km from the sea. The river and lake are covered with ice from December through March/April. The mean annual flow is 4.3 m³·s⁻¹, characterised by very low discharge during the ice-covered period.

The Signaldalen and Skibotn Rivers does not include lakes in the stretches accessible for fish migrating to the sea. The main channels of the rivers are of similar sizes (average flow approximately 20 m³·s⁻¹; 30 and 20 kilometres of river accessible for anadromous fish,

respectively). Both rivers have substratum consisting of bigger rocks and gravel. However, there are also some profound differences between the rivers. The Signaldalen River has deeper and larger pools than the Skibotn River and is usually ice-covered from November/December through March/April. The Skibotn River is regulated for hydropower purposes, and the power station outlet is located about 10 km upstream from the estuary. The area upstream of the power station outlet has a strongly reduced discharge, and the increased water temperature below the power plant makes the river remain partly ice-free during the winter. Due to the *G. salaris* infection, Atlantic salmon is strongly reduced in numbers and today only occurs sporadically in both rivers (Winger *et al.*, 2008).

For a more detailed description of the study watercourses, see **Papers II** (Skibotn River), **III** (Signaldalen River) and **IV** (Hals watercourse).

2.2. Methodological approach

The studies included in this thesis are all observational and conducted in the field, and used telemetry (Cooke *et al.*, 2004) to study fish migrations. The main benefit of telemetry is that it enables observations of behavior *in situ*, without repeated disturbance of the individual. Telemetry also eliminates the issues associated with holding fish in captivity (crowding, water quality, lack of predators, stress and limited movements, review by Donaldson *et al.*, 2008), which can confound behavioral and mortality studies. Two types of telemetry were used in this study, acoustic (**Papers I, III & IV**) and archival telemetry (**Paper II**). The two methods are described in more detail below.

2.2.1. Archival telemetry

Archival telemetry consists of recording one or multiple parameters that are stored within an electronic device as a function of time (Cooke *et al.*, 2004). These electronic devices are called archival tags or more commonly data storage tags. The tags are attached to the fish, and if the fish is recaptured at the end of the study period, data can be downloaded for further analysis.

Archival tags can record a number of parameters, *e.g.* temperature, tilt, conductivity, depth and day length. The price of tags varies, and generally increases with the number and complexity of the parameters measured. This study mainly used archival temperature tags, but also a smaller number of tags that in addition recorded salinity and depth in order to verify the conclusions drawn from the temperature recordings. The temperature recording tags are relatively inexpensive, meaning that a larger number of fish can be tagged compared with many other alternative telemetry methods. However, due to the need of recapturing tagged fish to download the data, the method is only cost efficient if a high proportion of the fish can be recaptured. The need for recaptures is the greatest disadvantage of archival tags, while the perhaps greatest advantage is that they give continuous data. Continuous data is difficult to attain with other telemetry methods, which if it is to be achieved is logistically much more demanding and significantly more expensive (Hanson *et al.*, 2008). Data from archival tags gives no direct information on the horizontal position of an individual, but needs to be related to recorded environmental parameters (*e.g.* sea surface temperatures and/or day length, Chittenden *et al.*, 2013) if positioning is to be achieved.

2.2.1.2. Acoustic telemetry

Acoustic telemetry, as most other telemetry methods, is rapidly developing, and today gives scientists the opportunity not only to document the position of an individual, but also to record a wide range of parameters such as acceleration, depth and heart rates (Cooke *et al.*, 2004). Acoustic telemetry relies on the propagation of sound waves through water, and can thus be used in both fresh and salt water. However, the distance the sound waves can travel before they lose their energy (range) is not very long (up to a few hundred meters in the sea). The range also varies with waves and currents, debris in the water and other obstacles for the movement of the pressure waves that sound consists of (Thorstad *et al.*, 2000). The sound waves are created by electronic devices called acoustic tags, and the code that is transmitted from each tag is unique enabling recognition of individual fish. When a tag is within the detection range of a hydrophone receiver, the transmitted code can be registered. The receivers can be manually or automatically operated, where the automatic receiver generally store detections within the internal memory as a

function of time. The studies included in this thesis are based on recording the position of the fish using acoustic telemetry. Acoustic telemetry does not rely on recaptures of the animals after tagging to retrieve data, which is an advantage over archival telemetry. However, acoustic telemetry gives no information when the tagged fish reside outside the detection range of the receivers, and acoustic telemetry is also logistically more demanding due to the need of receivers and/or manual tracking.

2.2.3. Handling and tagging effects

The fish tagging performed in this thesis included capture, anaesthesia, external attachment or surgical implantation of the tag, and recovery of the fish. The procedure sometimes also included storing of fish. This handling and tagging of fish may cause negative effects on *e.g.* swimming performance (Brown *et al.*, 2006), growth and survival (Rikardsen, 2000). Reducing these possible effects is not only important in order to conform to international and national ethical requirements, but ultimately to avoid drawing false conclusions of a study due to abnormal individual behaviour (Bridger & Booth 2003; Jepsen *et al.*, 2002, 2005).

Adverse effects related to the tagging event can be mitigated by handling the fish as carefully as possible. All fish in the current study were tagged during spring or fall, at temperatures below 9 °C. Stress responses to fish handling are temperature dependent in salmonids, where low temperatures can increase survival, reduce behavioral responses and decrease stress hormones (Strange *et al.*, 1977; Thorstad *et al.*, 2003). Time in captivity was held at a practical minimum and all fish surgery was performed under anaesthesia (by use of 2-phenoxyethanol), in order to reduce stress. Both surgical implantation of tags and external tagging was performed by experienced personnel. The tags used were as small as possible, to reduce possible negative effects on the fish carrying the tag (mean 0.9% of bodyweight for Arctic charr and 0.5% for brown trout). Recovery was performed by letting the fish regain consciousness in calm parts of the rivers and swim away at own will. The practical handling procedures were chosen as the tagging team has good experience with these procedures during tagging of Atlantic salmon (*i.e.* very low mortality). The fish handling has thus been as optimal

as practically possible. After fish tagging in the Skibotn River, snorkeling and visual observations from the river shore was performed to confirm that the fish were recovering. Fish of both species were on multiple occasions observed to participate in spawning around 30 minutes after tagging, wherefore it is believed that the tagging procedures used caused little behavioral response.

2.2.4. Clarifications related to the interpretation of results

In order to draw inferences about a population based on a sample of individuals, a representative group of individuals must be studied. In this study, data was only collected from experienced migrants and mainly mature fish. This is because the fish have to be large enough to carry the weight of the tags, and the tags have to be of a certain size to get the battery capacity needed for the studies. The study may thus not be representative of the entire population.

Other than the bias towards experienced migrants, the sampling method in the populations without access to lakes probably ensured individuals representative of the whole spawning populations to be included in the study, as multiple river pools and spawning grounds spread over large stretches of the rivers were netted. In the Hals watercourse tagging, there was between-year difference in the sizes of the tagged Arctic charr, as smaller individuals were included during the second study year. Smaller individuals of Arctic charr descend the Hals watercourse later than larger individuals, and the Arctic charr were accordingly tagged later in the season during the second study year. The data analyses performed in **Paper IV** used year and fish length as variables, and the inferences drawn are likely representative of the population.

Freshwater return rates of fish with acoustic transmitters are presented in **Papers III** and **IV**. These are considered minimum estimates and are not presented as survival rates due to methodological and behavioral factors. Fish may lose their tags or the tags may malfunction (documented in all studies in this thesis), and the fish can then return to the river without being detected. Both Arctic charr and brown trout can also stray to other rivers (Berg & Jonsson, 1989; Klemetsen *et al.*, 2003) or theoretically reside in the sea during the winter and return the consecutive year.

After tagging, the fish behavior may be affected until the fish have recovered completely (Bridger & Booth, 2003). The time this takes varies among species and individuals (*e.g.* Mellas & Haynes, 1985), and has not been thoroughly studied in Arctic charr or brown trout. In the populations originating from the rivers without access to lakes, the study of the behavior was not initiated until many days, weeks or even months after tagging (*i.e.* the fish were not tracked until then) and short-term handling effect was not considered a problem in the data analyses. In the Hals watercourse, the fish were tracked shortly after the tagging event. To avoid documenting unnatural behavior, the first two days of data was excluded from the analyses.

Seasonality is an important aspect of this thesis. As the fish are not responding to a human calendar, defining different seasons is difficult as they may vary between years, areas and in relation to environmental factors. Seasons are defined in **Papers II** and **III**, but they differ somewhat. In **Paper II**, the seasons were defined according to observations made of the freshwater habitat (mainly to river freeze up and ice-break). The winter season was defined in a more restrictive manner in **Paper III**, to avoid defining fish as residing in the sea during winter in periods that may also have been defined as early spring. Throughout this synthesis, the more restrictive manner (*i.e.* where winter is defined as lasting until the end of March) is used.

2.3. Study material

This thesis used both acoustic and archival tags. In total, 172 Arctic charr and 169 brown trout were tagged, of which 57 Arctic charr and 34 brown trout were tagged in the Hals watercourse which has access to lakes, and the remaining fish in the Skibotn and Signaldalen Rivers which don't have access to lakes. The acoustically tagged fish in **Paper I** and the first study year in **Paper III** are the same individuals, but they were used to answer two different research questions related to the freshwater and marine habitat, respectively. The study included 111 Arctic charr and 73 brown trout tagged with acoustic tags, and 61 Arctic charr and 96 brown trout tagged with archival tags. In the archival tags study, 21 Arctic charr and 32 brown trout were recaptured. However, due to tag malfunctions and shedding of tags, archival data was retrieved from 10 of the Arctic charr tags and 22 of the brown trout tags.

3. Summary of results

Paper I: Do northern riverine anadromous Arctic charr *Salvelinus alpinus* and sea trout *Salmo trutta* overwinter in estuarine and marine waters?

The study was performed on fish from the Skibotn River, *i.e.* populations without access to lakes. Acoustic telemetry was used to study the within-river migratory behavior. The study generated data from nine Arctic charr and 14 brown trout by manual tracking of tagged fish in the river combined with automatic logging in the estuary. The results showed that just after spawning in late September and the three months after, both species left the spawning areas and migrated to pools located further downstream. By mid-December, all Arctic charr had left the river and had been registered in the estuary. One month later, in mid-January, all but three brown trout had been registered in the estuary, and only one brown trout was never registered in the estuary during winter. This first study on winter migrations thus contradicted the general assumption that both species, and in particular Arctic charr, overwinter in fresh water at northern latitudes. However, harsh overwintering conditions due to the hydropower plant in the river were observed, including low water levels upstream of the power plant and extensive formation and damming of frazile ice in the super-cooled water downstream from the power plant outlet. It was speculated that these conditions may have affected the migratory behavior and triggered the winter migrations to the estuary.

Paper II: Archival tags reveal that Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* can use estuarine and marine waters during winter.

This study was also performed on fish from the Skibotn River. Archival tags that measured ambient water temperature were used to study the migrations of Arctic charr and brown trout between areas with different water temperatures. Tags that in addition measured salinity were used as validation of the method. The ambient temperature method could distinguish between periods of residency in the river, estuary and sea. It was shown that 91% of the brown trout and 80% of the Arctic charr utilized the estuarine and/or marine environment

during the winter. Arctic charr on average entered the estuary on 12 January, the marine environment on 26 February, and had continuous marine residence lasting up to 55 days. The Arctic charr spent on average 40 days in the estuary and 25 days in the sea during the winter. Brown trout on average entered the estuary on 15 December, the marine environment on 4 January, and had continuous marine residence lasting up to 39 days. The brown trout spent on average 34 days in the estuary and 50 days in the sea during the winter. Most individuals of both species frequently shifted between the three habitats, and there was large individual variation in migratory behavior. Some individuals spent the entire winter in the river, while others spent the majority of the winter in the sea. The study demonstrated that the proportion of fish in the estuarine and marine habitat was as high as indicated in **Paper I**, and also that while residing in the estuary the fish experienced large shifts in salinity up to four times a day according to the high and low tides.

Paper III: Seasonal migrations and marine area use of sympatric Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta* from rivers without access to lakes.

The study was performed on fish from the Signaldalen River which holds suitable overwintering conditions, and fish from the Skibotn River which holds less suitable overwintering conditions. The estuary and fjord migratory behavior of Arctic charr and brown trout were investigated by using acoustic telemetry. The study was conducted during two full year cycles, and hence included both winter and summer migratory behavior. Between 55% and 100% of the fish tagged in the Skibotn River left the river during winter, while all fish from the Signaldalen River overwintered in fresh water. During the second study year, 44% of the brown trout that left the Skibotn River during fall and winter migrated to the Signaldalen River. During the marine winter migrations, fish of both species were recorded in both the inner and outer fjord areas at distances up to 20 km from the river outlet. Individual fish remained at sea for periods lasting from a few hours to many months, but the majority of individuals resided in the estuary. In addition to the between-river winter differences, there were interspecific and seasonal differences in migratory behavior and area use. Around 50% of the tagged Arctic charr could be found in the estuary throughout the year, while the remaining individuals were found mainly in

the river during winter and in the outer fjord areas during summer. Brown trout remained to a greater extent than Arctic charr in fresh water during the winter and in the outer fjord areas during the summer. The harvest rates were relatively high in Arctic charr compared to brown trout (26 and 7%, respectively).

Paper IV: Fjord temperatures shape the marine area use of Arctic charr *Salvelinus alpinus* and brown trout *Salmo trutta*.

The study was performed on fish from the Hals watercourse, *i.e.* on fish with access to lakes in the freshwater habitat. The marine summer migratory behaviour and spatial area use of sympatric Arctic charr and brown trout in the Alta fjord was investigated and compared during two years by use of acoustic telemetry. The main finding from the study was that the marine water temperatures seemed to affect the migratory behaviour of these species during summer. Arctic charr left the inner fjord and moved to the outer fjord when the temperature in the inner areas increased (around 8 °C), whereas brown trout more actively migrated to areas with higher water temperatures (up to 14 °C). The difference in temperature use in the fjord areas corresponded to the preferred temperatures of Arctic charr (9 – 12 °C) and brown trout (12 – 16 °C) documented in other studies. The likelihood of finding fish in the outer fjord areas increased with fish length irrespective of species, but the relationship was much weaker than the relationship between temperature and area use. Individuals of both species mainly used the littoral fjord areas, and to a lesser extent the pelagic areas. The study indicated that high fjord temperatures may lead to increased overlap in spatial area use of Arctic charr and brown trout.

4. Discussion

The work in this thesis was aimed at answering the questions raised at the beginning of this synthesis, and the results are here discussed in relation to these. The first two questions: 1) if Arctic charr and brown trout migrate to the sea during winter and 2) if the physical properties of the freshwater habitat influence the decision to migrate are discussed together. The similarities and differences between the two species are discussed in relation to the research questions when appropriate. This is followed by a discussion on if the parasite *G. salaris* could theoretically have been transported between the Skibotn and Signaldalen Rivers with migratory fish, and also a brief discussion on how these species and their migratory behavior may be affected by increasing global temperatures

Do Arctic charr and brown trout use estuarine and marine waters during winter (Papers I - III), and if they do, are there differences in winter migratory behavior between populations from rivers with and without access to lakes (Papers I – IV).

The biologically most interesting result from this thesis is perhaps that both Arctic charr and brown trout can be found in estuarine and marine waters during winter (**Papers I – III**). This contradicts the general view that both these species solely overwinter in fresh water at northern latitudes (*e.g.* Berg & Berg, 1989, 1993; Klemetsen *et al.*, 2003; Jensen *et al.*, 2012). All the mentioned previous investigations of the marine migration timing of Arctic charr and brown trout have been on populations with access to lakes, by use of traps and individual Carlin tagging. As trapping studies can only be performed during the ice-free season, it is theoretically possible that these studies gave biased information as winter migrations would be difficult to record. The migratory behavior of the fish from the watercourse without access to lakes (Hals watercourse) in this thesis work was in correspondence with the described general view of river outmigration and return times. None of the tagged fish from the Hals watercourse (**Paper IV**) were registered in the sea during early winter the year following tagging, despite automatic receivers being deployed in the fjord in April and the tag batteries lasting until May. Also, data

from a study in the Hals watercourse using temperature and depth archival tags showed that both species overwintered in the lake and had a low activity pattern when the lake was covered with ice (A. Rikardsen *et al.*, unpublished data).

The findings from this thesis work suggest that the winter migrations to the marine habitat may be related to the physical conditions of the freshwater habitat, or more specifically to the availability of suitable overwintering areas. Lack of overwintering areas in watercourses have been shown to result in brown trout leaving the river for the sea at more southern latitudes (Knutsen *et al.*, 2004; Olsen *et al.*, 2006) The three study rivers may be seen as a gradient from bad to good overwintering conditions. The hydropower influenced Skibotn River has poor overwintering conditions due to loss of ice-cover, formation of frazile ice and reduced discharge, whereas the Signaldalen River has better overwintering areas in the form of deeper pools within the river. The Hals watercourse has good stable overwintering conditions in the lake. The fish with access to suitable overwintering areas stayed in the river during winter, while the Skibotn populations migrated to the sea. During one study years almost half of the brown trout that left the Skibotn River during winter migrated to the Signaldalen River, indicating that there may be advantages in overwintering in this more stable freshwater habitat. The relationship between which post-spawning individuals overwinter in a river and which migrates to the sea during fall has been investigated in Atlantic salmon (Halttunen *et al.*, 2013). The study was conducted in the Alta River, which is a large river with good overwintering conditions that drains into the Alta fjord. The study showed that if an individual could energetically afford to do so, it should remain in the river under stable cold conditions until the most energetically profitable time of outmigration, which was the spring. However, if an individual's energy reserves were seriously depleted after spawning, the individual should accept the riskier marine habitat during fall. The reasoning may be transferable to degrees of suitable overwintering freshwater habitats. If the conditions in the river are stable enough to provide an overwintering environment where energy can be preserved, an individual should stay. If the conditions are unstable and causing a risk of losing energy, an individual may migrate to sea.

An alternative explanation to why Arctic charr and brown trout were found in estuarine and marine waters during winter is that these individuals left the river because they were attracted to more profitable conditions at sea. Whereas the extensive estuarine winter residency documented in **Papers I – III** may be related to feeding (Pemberton, 1976), predator avoidance is an alternative and maybe more plausible explanation (Thorpe, 1994). However, especially brown trout but also Arctic charr were documented at distances of at least 20 km away from the Skibotn River outlet during winter. As there are energetic costs to migrations, they should only be performed when they result in a potential gain (Jonsson & Jonsson, 1993). It is known that brown trout at more southern latitudes feed in marine waters during winter (Knutsen *et al.*, 2004; Olsen *et al.*, 2006), and brown trout have also been demonstrated to feed in two fjords close to the Lyngen fjord during winter (Rikardsen *et al.*, 2006). As these species are highly opportunistic feeders (Klemetsen *et al.*, 2003), they may simply be utilising the resources as they are available. It is also possible that the fish are forced to feed at sea during winter after leaving fresh water, as the temperature is higher in the sea than in fresh water during winter, and increased temperature causes increased energy demands in the ectothermic fish (Knutsen *et al.*, 2004). The alternative explanation to why Arctic charr and brown trout left the Skibotn River during winter, that they are drawn to profitable conditions at sea, can thus not be overlooked. As there was large individual variation in the winter migratory behaviour among the Skibotn River fish, it is possible that the reason for the migrations differs between individuals (as suggested for Atlantic salmon, Halttunen *et al.*, 2013) or that the migratory behaviour is the result of a combination of leaving the harsh conditions in the river and being drawn to profitable conditions at sea.

The archival tag study showed that both Arctic charr and brown trout experienced large shifts in salinities according to the high and low tides during winter in the estuary (**Paper II**). These shifts in salinity are believed to be physiologically stressful for salmonids due to energy demands to regulate plasma ions (McCormick, 2001). Arctic charr smolts cannot survive salinity stress at low temperatures during winter (Finstad *et al.*, 1989; Arnesen *et al.*, 1993; Finstad & Heggberget, 1993), but larger individuals of salmonids generally handle salinity stress better than smaller ones (Hoar, 1976; McCormick & Saunders, 1987; Finstad & Ugedal, 1998; Ugedal *et al.*, 1998). Adult Arctic charr from a Canadian population have been documented to survive in full-strength saltwater (salinity 32) at temperatures below 0 °C during late summer (Bystriansky *et*

al., 2007), and larger brown trout have been found in marine waters (salinities up to 29) at low winter temperatures (down to 3 °C) in southern Norway (Knutsen *et al.*, 2004). These previous studies in combination with the findings in this thesis clearly show that adult Arctic charr and brown trout from some populations clearly tolerate high salinities at low water temperatures, contradicting much of the earlier assumptions.

In summary, the findings from this thesis work clearly shows that both Arctic charr and brown trout can be found in estuarine and marine waters during winter. It seems plausible that the behaviour is related to the availability of suitable overwintering areas in the freshwater habitat, but it cannot be excluded that at least some fish are drawn to the sea for increased feeding opportunity.

Which fjord areas are used by Arctic charr and brown trout during their summer feeding migrations, and which factors control the summer migratory behavior? (Paper III & IV).

This thesis work provides novel knowledge of the fjord summer migratory behavior of sympatric Arctic charr and brown trout. The previous studies of the migratory behavior of these species were mainly performed by trapping and individual Carlin tagging, where recaptures were used for estimates of migratory behavior (*e.g.* Berg & Jonsson, 1989). The use of telemetry provides a detail level that could not be achieved with these previous techniques, and makes not only individual descriptions of migratory behavior possible, but also more thorough investigations of the factors controlling it.

The migratory behavior of salmonids is most likely affected by a number of environmental parameters (Thorstad *et al.*, 2011), which may affect species differently (**Paper IV**) and may differ between areas (**Paper III & IV**). Both Arctic charr and brown trout resided mainly within the Lyngen and Alta study fjords. This is in accordance with the previous recapture studies, where both species have been documented to stay within 25 km of their native river (Berg & Berg, 1987; Berg & Jonsson, 1989). The summer migratory behavior documented in this thesis work differed among Arctic charr and brown trout, and also between the Alta and Lyngen fjords. The environmental recordings from the Alta fjord study (**Paper IV**) were more

detailed than those from the Lyngen fjord (**Paper III**), and this study allowed more detailed analyses of the correlation between the migratory behavior and predictor variables. The Alta fjord study showed that both species used both the inner and outer fjord areas, and that temperature was a strong predictor for if a species was be found in the inner or outer fjord. Arctic charr were more likely than brown trout to be found in the area with the lowest temperatures. This is in accordance with a previous archival temperature study from the Alta fjord, which demonstrated that the temperatures experienced during the marine migrations were on average 10.7 °C for Arctic charr and 12.1 °C for brown trout (Rikardsen *et al.*, 2007b). Studies on freshwater resident populations have shown that both Arctic charr and brown trout grow optimally at around 16 °C, while Arctic charr prefers water between 9 and 12 °C and brown trout between 12 and 16 °C (see Larsson, 2005). The findings in this thesis indicate that there may be differences in preferred temperatures among these species also at sea. The outer fjord areas are generally colder than the inner areas in the geographical region where these species occur in sympatry (Eilertsen & Skarðhamar, 2006), and Arctic charr may thus generally be utilising the outer fjord areas to a greater extent than brown trout. Detailed knowledge on the marine migratory behavior of these species is sparse, but a recent acoustic telemetry study from Arctic Canada showed that Arctic charr resided in outer coastal areas also in this part of the world (Morris & Greene, 2012).

As mentioned in the previous paragraph, the outer coastal areas are often colder than the inner areas in the geographical regions where Arctic charr and brown trout occur in sympatry (Eilertsen & Skarðhamar, 2006). The migratory behavior of Arctic charr and brown trout documented in the Lyngen fjord (**Paper III**) differed in some aspects from that documented in the Alta fjord (**Paper IV**), as neither Arctic charr nor brown trout used the inner areas of the Lyngen fjord to any great extent. In the Alta fjord, both Arctic charr and brown trout were found to utilize the inner fjord, but Arctic charr left the inner area for the outer as temperatures in the inner fjord increased to above 8 °C. However, in the Lyngen fjord the temperature was below 8 °C and similar in the inner and outer areas during the majority of the migratory period for Arctic charr. Temperature may thus not play an important role for where in the sea Arctic charr and brown trout are found in all geographical areas, as the fjords may be thermally homogenous during the migratory period. After Arctic charr returned to freshwater in mid-July, the fjord

temperature fluctuated between 11 and 17 °C. The highest temperatures were measured as peaks in the inner fjord areas. Except for these peaks in temperature, the outer fjord was generally warmer than the inner (between 11 and 14 °C). These temperatures are within the experimentally documented preferred temperatures of brown trout, (Larsson, 2005) and also correspond to the temperatures preferred by the species in the Alta fjord study.

As described above, the relationship between marine area use and water temperature corresponded to the previously documented preferred temperatures of Arctic charr and brown trout. However, the water temperature *per se* may not be affecting the area use. The marine migrations are performed for increased feeding opportunities (Gross, 1987), and the prey availability may be the most important controlling factor for where in the sea these species are found. Temperature may be correlated with the prey availability (Huntley & Lopez, 1992), and the differing area use of Arctic charr and brown trout may thus be a response to prey availability and not temperature. Both these species are highly opportunistic feeders (Klemetsen *et al.*, 2003), wherefore relating prey choice to migratory behavior is difficult. Large dietary overlap has been documented between these species in years with high abundances of herring (Rikardsen *et al.*, 2007a; Rikardsen & Amundsen, 2005). However, between years and geographical areas the two species have been documented to differ in prey choice, with two differences being that *S. trutta* is more piscivorous than *S. alpinus*, and that the latter species includes more surface insects in their diet (Klemetsen *et al.*, 2003; Rikardsen *et al.* 2007a). These differences in prey choice may explain the difference in migratory behavior in the Lyngen fjord, as the abundance of surface insects may be higher in the estuary due to drift from the river, whereas the abundance of fish prey may be higher in the outer fjord areas (Dragesund, 1995). A recent study of the temperature and depth use of Arctic charr in Arctic Canada showed that acoustically tagged fish may feed in nutrient rich waters of very low temperatures and move into warmer waters to enhance digestion (Spares *et al.*, 2012). As there were temperature differences between the river and sea in the period when Arctic charr were at sea (see **Paper II**), it cannot be excluded that the Lyngen fjord Arctic charr residing in the estuary may have been controlling digestion by moving between water layers of different temperatures.

In summary, the summer migratory studies of Arctic charr and brown trout showed that the marine area use differed between species, and that anadromous Arctic charr may reside in colder waters than brown trout during the marine summer feeding migration. The difference in area use in relation to water temperatures corresponded to the previously documented different preference temperatures of the two species. However, the differences may also be related to differences in prey choice and availability, which may be affected by water temperatures.

Can anadromous fish spread *G. salaris* between rivers?

The acoustic study in the Lyngen fjord (**Paper III**) generated data on the migratory durations of fish alternating between the Skibotn and Signaldalen Rivers. These data were not presented in any of the manuscripts in this thesis. For evaluation of the potential risk of spreading of *G. salaris* by fish migrating between the rivers, the migration duration times were calculated from the last registration in the estuary of one river until the first registration in the estuary of the other. The salinity and temperature was measured at two meters depth in the fjord midway between the rivers (area c, Fig. 1, **Paper III**), and the monthly minimum recordings were used. The durations of the between-river migrations were evaluated in combination with the environmental recordings from the fjord and the previously documented survival estimates at different temperatures and salinities of the parasite (Soleng & Bakke, 1997, see Table 1 below) to evaluate if fish migrations could theoretically have spread the parasite between the two rivers.

Table 1. Survival of the Atlantic salmon parasite *Gyrodactylus salaris* at different temperatures and salinities (data adapted from Soleng & Bakke, 1997).

Temperature (°C)	Salinity	Survival (hours)
1,4	10	240
6	10	132
12	10	72
1,4	15	78
6	15	54
12	15	24
1,4	20	42
6	20	21
12	20	12

The results showed that fish migrations between the two study rivers occurred within durations (migratory durations as short as 7 hours) that rendered spreading of the parasite possible in October after spawning and during the spring and summer (May – July) (Table 2). In total, six Arctic charr and 14 brown trout were documented to migrate between the two study rivers. This resulted in 33 migrations events, whereof 22 could theoretically have led to spreading of the parasite (Table 2).

Four migrations to the Manndalen River located approximately 25 km away from the Skibotn River were also documented. All migrations occurred at the end of May, with durations of 13, 36, 36 and 42 hours.

Table 2. The minimum monthly temperatures and salinities recorded in the Lyngen fjord 2006 – 2007, and the numbers and duration of migrations between the Skibotn and Signaldal Rivers performed by anadromous Arctic charr and brown trout. The proportions of migrations occurring within a time frame and at temperatures and salinities that could potentially lead to spreading of *G. salaris* were theoretically estimated based on survival data on *G. salaris* at different temperatures and salinities recorded by Soleng & Bakke (1997).

Month	Minimum temp. recorded (°C)	Min. salinity	Number of migrations between rivers	Duration (h) of migration between rivers (min – max)	Number and proportion of migrations with potential for <i>G. salaris</i> spreading
Oct	5	22	6	15 (9-32)	5 (83%)
Nov	3	31	2	9 (8 & 9)	
Dec	2	31	4	31 (10-66)	
Apr	1	29	1	7	
May	4	10	11	46 (14-159)	10 (91%)
June	4	10	5	25 (9-37)	5 (100%)
July	9	14	4	80 (11-100)	2 (50%)

In the evaluation of the potential spreading risk, the minimum monthly between-river migratory durations were used. This may be maximizing the evaluation of the potential risk of spreading. However, there are previously documented aspects of the fish migratory behavior that

may suggest the opposite. While residing at sea during summer, Arctic charr normally stayed at average depths of 1.2 meters and brown trout on 1.8 meters (Rikardsen *et al.*, 2007b). The temperature and salinity measurements were made at two meters depth in the Lyngen fjord. This means that the waters used by the fish may have been less saline than the recordings in the fjord, due to the stratification of less saline water at the top of the water column (Simpson *et al.*, 1990).

The between-river migrations occurred mainly during fall and in spring. In these periods, the river temperatures were low (see Fig. 2 in **Paper II**) and hence caused a cold brackish water layer in the fjord. Low temperatures increase the survival time of *G. salaris* in brackish water (Soleng & Bakke, 1997). The infection of *G. salaris* on Arctic charr has been shown to be low in the Skibotn River in spring and early summer, but at its highest in the fall after spawning (Winger *et al.*, 2008). Even though only a low proportion of the between-river migrations occurred during the fall, this period may thus have the highest risk of parasite spreading with migrating fish. Also, whereas this thesis work has established that both Arctic charr and brown trout can tolerate full strength sea water at low temperatures, they may still migrate in the brackish water layers during winter. Between-river migratory durations of as little as seven hours were documented during the winter months, and if the fish migrate in the uppermost water layers the parasite spreading risk cannot be isolated to the fall and spring. Due to the reproductive strategy of the parasite, it is highly infectious and only a few individuals may be needed for the parasite to establish in a new watercourse where available hosts are abundant (Bakke *et al.*, 2007).

In summary, it is theoretically possible that the Atlantic salmon parasite *G. salaris* was spread between the Skibotn and Signaldalen Rivers by marine migrating Arctic charr and/or brown trout. These findings may need to be considered by management institutions in treatment plans of infected areas, as leaving rivers untreated for long periods of time may increase the risk of spreading to neighboring rivers. Specifically for the Lyngen area, the potential for spreading to the Manndalen River should be evaluated further, as migrations between the Skibotn and Manndalen Rivers with durations that could allow the parasite to survive in brackish water were documented.

Possible effects of increasing global temperatures

As anadromous fish migrate between fresh and salt water, altered climate conditions may act on both the freshwater and marine parts of their lives. Modeling attempts have predicted a declining trend in degree of anadromy in Arctic charr related to increasing freshwater primary production as a result of increasing global temperatures (Finstad & Hein, 2012). The benefits of migrations to the marine habitat would be reduced if the freshwater habitat became more productive, resulting in a larger proportion of fish remaining in fresh water. Why the increased production would not act in the same manner for brown trout has not been studied, but may be related to that Arctic charr and brown trout can occupy different habitats in lakes (Langeland *et al.*, 1991). Increased primary production would act primarily on the pelagic areas (Primicerio *et al.*, 2007), which are normally inhabited by Arctic charr when these species occur in sympatry (Langeland *et al.*, 1991). The alteration in contrast between fresh water and the sea may not be as strong in the littoral areas occupied by brown trout, and this species may thus not be as strongly affected by the increased freshwater production related to increasing global temperatures.

This thesis showed that marine water temperature correlated to the marine area use of Arctic charr and brown trout in the Alta fjord. The marine migratory behaviour may thus be affected by increasing global sea temperatures. As the outer coastal areas are often colder than the inner areas at northern latitudes (Eilertsen & Skarðhamar, 2006), the outer coastal areas may be acting as a thermal refuge for Arctic charr under current environmental conditions. This refuge may be removed in a warming climate scenario, which may affect Arctic charr negatively. The current study also showed that increasing sea temperatures may lead to increasing area use overlap between Arctic charr and brown trout. An alteration of migratory behaviour may also lead to changes in interactions with other species (Van der Putten *et al.*, 2010). As Arctic charr is only a strong competitor at low temperatures (Langeland *et al.*, 1991; Helland *et al.*, 2011), increased species interaction at sea due to climate warming may not benefit Arctic charr. Conclusive climate studies most likely need to be performed over longer time intervals or larger geographical areas than the studies included in this thesis. However, this thesis has provided some insight into how the migratory behaviour of anadromous Arctic charr and brown trout may be affected in a potential warming climate scenario. As northern Norway is suggested as an area

that will act as a thermal refuge for Arctic charr in a future warmer climate (Lassalle & Rochard, 2009), understanding the environmental factors affecting this species behaviour is valuable.

5. Concluding remarks and implications

This thesis work has provided new insight into the marine migratory behavior of sympatric anadromous Arctic charr and brown trout. In summary, it has been demonstrated that both species can be found in the marine habitat during winter, that the environmental conditions in the freshwater habitat may influence the overwintering behavior, and that there are interspecific differences in summer migratory behavior which may be related to differences in temperature preference between species. The summer area use also differed between fjords, indicating that there may be differences in where the fish reside in response to differing environmental conditions. Between-river migrations by Arctic charr and brown trout making spreading of the parasite *G. salaris* plausible were also documented. The findings in this thesis indicate that the summer marine migratory behavior is temperature dependent, and that a temperature increases may affect Arctic charr but not brown trout negatively. As it has been suggested that the current declining trend in catches of Arctic charr is related to increasing global temperatures (Anon., 2011), the species may need extra management attention in the years to come. Documenting and understanding how increasing temperatures affects both anadromous Arctic charr and brown trout is then essential, as well as identifying the management tools available to protect the anadromous Arctic charr populations from further human impact.

Management implications and future research needs

As discussed above, there may be negative effects of increasing global temperatures on Arctic charr. These global effects cannot be managed, but identifying means to reduce the human impact in the form of harvest may be a tool considered by management institutions. This thesis work has identified at least three areas where management can be improved if necessary:

- Incorporating the migratory behavior of marine winter migrating populations into the management plans, by *e.g.* restricting harvest in the estuaries and sea during winter.

- Protecting fish against harvest in the estuaries during summer, which may decrease the capture rates for especially Arctic charr.
- Generally decreasing the harvest rates of Arctic charr. The harvest rates for Arctic charr may be higher than the harvest rates of brown trout, as documented in the Lyngen area.

The second and third point would specifically protect the Arctic charr. As anadromous brown trout is seemingly stable or increasing in numbers in the areas where the two species occur in sympatry (Anon., 2011), identifying points where only Arctic charr can be protected would be beneficial as the recreational value of brown trout fishing would then be intact. However, the large individual behavioral differences in combination with the differences in area use between fjords may indicate that the migratory behavior need to be studied in more populations if a solid knowledge base for management decisions is to be achieved. Also, further documenting the effect of marine temperatures on the migratory behavior may be of particular interest. An understanding of which factors control the migratory behavior would most likely be very valuable knowledge in the face of a potentially rapidly changing environment.

Acknowledgements

The road to a degree of Philosophiae Doctor has for me been a fun, challenging and sometimes frustrating experience, with many unpredictable turns followed by great and sometimes not so great discoveries. Hopefully, this description will fit my continued scientific career, because it has really been some amazing years. As with most great experiences, it has involved many wonderful people along the way.

First, I'd like to thank my main supervisor Audun Rikardsen. It has been some crazy and exiting years full of challenges, and for that I am truly grateful. I would also like to thank my co-supervisor, Eva Thorstad, whose relaxed attitude and focused thinking have provided balance in a sometimes hectic workday. From the two of you I have learned that nothing is impossible, and that the impossible is best done while sipping a glass of red wine. You have really made a great supervisory team.

A good work environment is very important, perhaps especially during the challenging time of graduate studies. The Freshwater Group has provided a both scientifically and socially good work place, with great opportunities for learning. Science is indeed a social endeavor, and I feel privileged to have been allowed to share these years with you. Per-Arne Amundsen and Rune Knudsen deserve special thanks from me and most other students, for always making time for a coffee, and for keeping our ambitions high.

Science can build great friendships. I thank Cedar Chittenden, Cesilie Lien and Elina Halttunen for chats, discussions, waffles, wine, concerts, movies, coffee-breaks and otherwise keeping me sane. You guys rock!

I also want to thank Frøydis Strand for excellent graphical work, often performed on very short deadlines. Finn Økland deserves thanks for great guidance through all the electronically related challenges that comes with telemetry work and Tor Næsje for giving me the opportunity to fish and tag in beautiful rivers. Jan Davidsen also deserves special thanks, for initiating and organizing some of the projects included in my thesis, and for providing good field company

during my early years as a student. The members of Skibotn JFF have also provided excellent field company, as well as many good laughs. I also want to thank the crew on FF Johan Ruud for deployment of receivers in the fjords, Benjamin and Gunn Hykkerud for housing us in Alta, and last but not least all the friendly fishermen in the Alta fjord.

My wonderful friends and fellow students all deserve thanks for making my time in Tromsø a great experience. Keeping a balance between work and fun is crucial, and without you there would have been way too many hours at the office.

Last I would like to thank my family. I come from a long line of outdoors and angling enthusiasts, and I guess my family's interest has rubbed off on me. I am eternally grateful to my wonderful parents, for teaching me to love nature, for keeping my feet planted on the ground, and for always supporting me. You may be far away, but your support mean more to me than I have words for.

Jenny Jensen,

Tromsø,

Summer 2013

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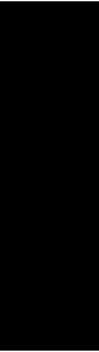
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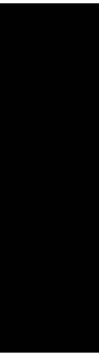
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Paper I

Paper II



Paper III



Paper IV

