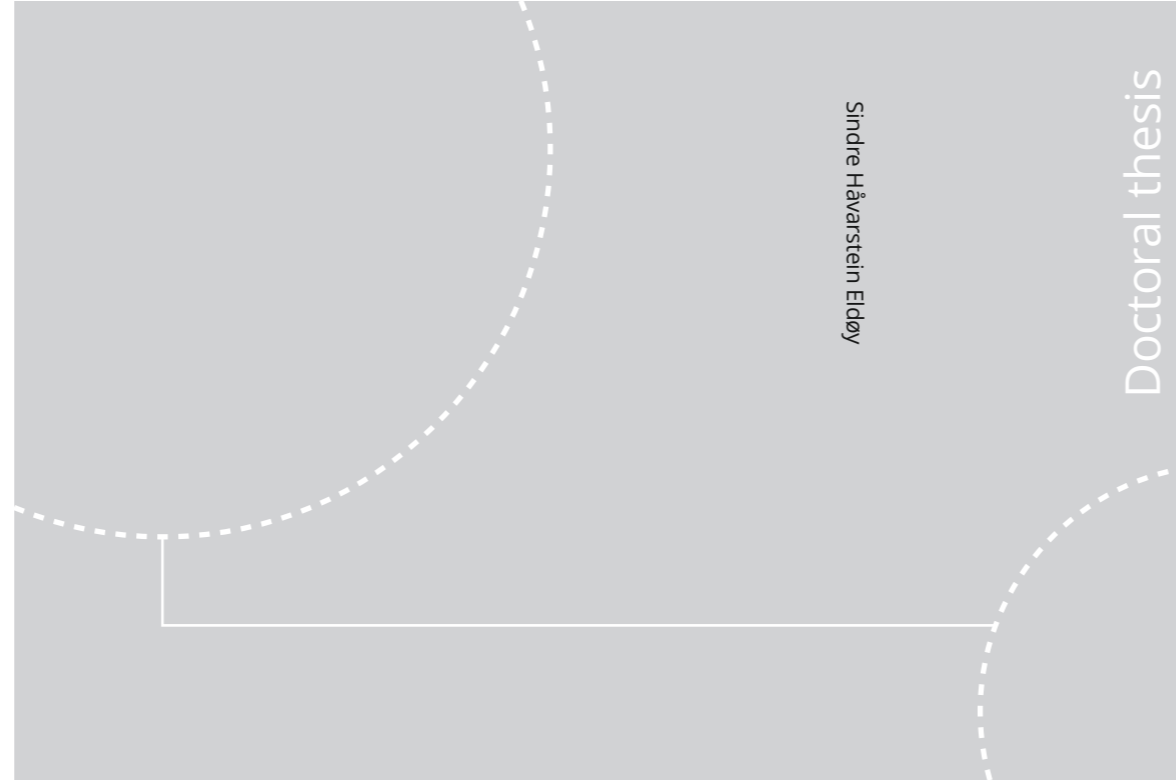


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Norwegian University of Science and Technology
Thesis for the Degree of
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Trondheim, June 2020

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Summary

The marine migration of sea trout (anadromous brown trout, *Salmo trutta*) is an evolutionary adaptation to exploit richer feeding opportunities at sea compared to the freshwater habitat. Over the last decades, there has been a significant decrease in many sea trout populations along the coast of Norway. While at sea, the sea trout commonly reside in coastal areas heavily affected by human activities such as aquaculture, marine traffic, fishing, and establishment of marine infrastructure. The marine migrations are important for the growth of sea trout, and consequently for the recruitment and population dynamics in coastal watersheds. While at sea, the sea trout can display large variation in migratory behaviour. The underlying mechanisms driving this variation are poorly understood. In order to predict the consequences of human activities in marine coastal areas on sea trout and implement effective conservation measures, a better mechanistic understanding of the marine migration patterns of the sea trout is needed.

The first aim of this thesis was to study how physiology, previous life history and experienced environmental conditions affect the marine behaviour of sea trout. The second aim was to examine how salmon farming can affect nearby sea trout populations in terms of marine growth and utilization of marine versus fresh- and brackish water habitats. This was addressed by using two different methodological approaches; *i.* by tracking individual sea trout in the marine environment in three fjord systems in central and northern parts of Norway using acoustic telemetry, and *ii.* by examining growth patterns and chemical composition in sea trout scales. In the studies using the first methodological approach, marine migratory patterns were linked to morphological and physiological state of the individuals (body length, body condition factor and blood plasma triglycerides, protein and calcium) and environmental variables (time of day and season, and seawater temperature) to examine how physiology and environment influenced the migratory pattern of sea trout. Further, the repeatability in migratory behaviour between years was examined by tracking individual sea trout in consecutive marine feeding seasons.

In the study using the second methodological approach, the influence of anthropogenic environmental factors in terms of open cage farming of Atlantic salmon *Salmo salar*, was evaluated. Historically and more recently sampled sea trout scales were analysed, covering time spans of 25-65 years including periods with and without nearby active salmon farms (< 14 km). Scales were sampled from three populations in Norway and two in Ireland. Growth

patterns and scale Ba:Ca levels indicative of the degree of marine residency after first sea entry were obtained by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS).

The results from the tracking studies using acoustic telemetry showed that the marine habitat use of sea trout varied greatly, both temporary and spatially, and within and among populations. Fish in poorer nutritional state, larger fish and females tended to use the marine habitat more extensively than fish in better nutritional state, smaller individuals and males. The swimming depth was generally surface oriented with an overall average swimming depth of 1.7 m in May – September. However, the swimming depth varied with marine habitat type, was deeper during day than night, increased towards late summer, and was positively correlated with body size and seawater temperature. Sea trout displayed significant inter-annual consistency in how they utilized different parts of the fjords and the time of season when they returned to spawning rivers. No differences in the time of season of marine entry or the time spent in the marine environment each year were observed.

The chemistry analyses of sea trout scales showed reduced growth of individual fish after first sea entry in periods coinciding with nearby salmon farming activity. Moreover, increased Ba:Ca levels were also recorded during periods with nearby salmon farming, indicating reduced residency in marine habitats. Back-calculated body length at first sea entry increased in periods with nearby salmon farming activity, suggesting a size-selective marine mortality related to fish farming with the smallest individuals experiencing a larger mortality.

The findings in this thesis show how important aspects of physiology, life history, environmental conditions and anthropogenic activities in the coastal zone strongly influenced the marine migratory behaviour of sea trout. The observed effects of nutritional state on sea trout migratory behaviour suggests that individuals in a poor nutritional state displayed a more risk-taking migration behaviour than fish in better nutritional state. Moreover, the fact that females and larger fish tended to utilize the marine habitat to a greater extent than males and smaller individuals suggest that females and large individuals are more dependent on the marine habitat for feeding and recondition after spawning. The sea trout displayed behavioural responses to both the physiological state and environmental conditions, but also consistency in migratory behaviour among years. The results in the scale chemistry study suggest that both the migratory behaviour and success of the feeding migration were severely

altered by salmon lice infestation, and thereby showed how human activities can significantly affect marine behaviour of sea trout.

In conclusion, the large variation in marine migratory behaviour of sea trout implies that the susceptibility to human activity will not only vary among populations, but also among individuals within populations. This is crucial knowledge for evaluating the effects of anthropogenic factors that can vary both spatially and temporally. The uneven effect of human activities on the individuals within populations can alter population structures by posing increased risk of mortality and/or reduced marine growth on subgroups within the populations with certain behavioural traits. Moreover, if human activities in coastal areas cause decreased growth and increased mortality in individual sea trout, this can lead to altered population dynamics and selection against anadromy, or against certain migratory tactics within the marine migratory continuum of coastal trout populations.

List of papers

The doctoral thesis is based on the following papers, which are hereafter referred to with their Roman numerals:

- I. Eldøy, S.H., Bordeleau, X., Lawrence, M.J., Thorstad, E.B., Finstad, A.G., Whoriskey, F.G., Crossin, G.T., Cooke, S.J., Aarestrup, K., Rønning, L., Sjørnsen, A.G., Davidsen, J.G. (submitted). The effects of nutritional state, sex and body size on the marine migration behaviour of sea trout. Submitted *Marine Progress Series* 22.04.2020.
- II. Eldøy, S.H., Davidsen, J.G., Thorstad, E.B., Whoriskey, F.G., Aarestrup, K., Næsje, T., Rønning, L., Sjørnsen, A.D., Rikardsen, A.H., Arnekleiv, J.A. (2017). Marine depth use of sea trout *Salmo trutta* in fjord areas of central Norway. *Journal of Fish Biology*. **91**:1268-1283
- III. Eldøy, S.H., Bordeleau, X., Crossin, G.T., Davidsen, J.G. (2019). Individual repeatability in marine migratory behaviour: A multi-population assessment of anadromous brown trout tracked through consecutive feeding migrations. *Frontiers in Ecology and Evolution*. **7**:1-12
- IV. Eldøy, S.H., Ryan, D., Roche, W.K., Thorstad, E.B., Næsje, T.F., Sjørnsen, A.D., Gargan, P.D., Davidsen, J.G. (in review). Changes in growth and migration patterns of sea trout before and after the introduction of Atlantic salmon farming. Submitted *ICES Journal of Marine Science* 26.02.2020

Author contributions

Paper I

SHE was the lead author responsible data analysis and manuscript preparation with contributions from all co-authors. SHE, XB, MJL, JGD, LR, and ADS contributed in data generation. XB and MJL conducted the lab analyses of blood plasma metabolites. JGD, EBT, FGW, GTC, SJC and KA contributed to funding.

Paper II

SHE was the lead author responsible for the main part of data analysis and manuscript preparation with contributions from all co-authors. SHE, JGD, LR, and ADS contributed in data generation. JGD, EBT, FGW, KA, TFN, AHR and JVA contributed to funding.

Paper III

SHE was the lead author responsible data analysis and manuscript preparation with contributions from all co-authors. SHE, XB, and JGD contributed in data generation. JGD and GTC contributed to funding.

Paper IV

SHE was the lead author responsible for manuscript preparation with contributions from all co-authors. DR conducted the LA-ICP-MS analyses. SHE, DR, WKR, TFN, ADS, PDG and JGD contributed in data generation. DR, WKR, EBT, TFN and JGD contributed to funding.

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Introduction

Migration is a behavioural phenomenon occurring in a wide range of animal taxa (Dingle, 2014). Although the proximate reasons for migrations are diverse, the common ultimate reason for the migrations is to maximize the fitness of the individuals (Dingle & Drake, 2007; Lennox et al., 2016). During their lifetime, individuals must make life-history trade-offs and allocate energy for sustaining metabolic demands, somatic growth and maturation and reproduction (Zera & Harshman, 2001). Individuals of many fish species alternate between freshwater and the sea to maximize feeding opportunities during their life, which is a migratory strategy termed diadromy (McDowall, 1988). Catadromy, characterized by spawning in saltwater and performing feeding migrations to freshwater habitats, is common in tropical areas, while the opposite strategy, termed anadromy, is common in temperate and high latitude regions (Gross *et al.*, 1988). These strategies are thought to have evolved in response to productivity differences between freshwater and marine habitats (Gross *et al.*, 1988). Many species within the Salmonidae family have populations with anadromous individuals. The propensity to migrate varies among the salmonid species; some species are almost exclusively anadromous, and others nearly exclusively freshwater resident (Jonsson & Berg, 2003).

The brown trout, *Salmo trutta*, is a highly flexible salmonid, and both freshwater resident and anadromous populations are common (Klemetsen *et al.*, 2003). The phenotypic and behavioural flexibility of brown trout has, in combination with human translocation due to its popularity for recreational angling and food, resulted in self-reproducing brown trout populations occurring in all continents except Antarctica (MacCrimmon *et al.*, 1970). For brown trout populations with free access to the sea, the brown trout populations are often partially anadromous, where part of the population perform marine feeding migrations, while other conspecifics remain in the freshwater habitat and mature as freshwater residents (Jonsson & Jonsson, 1993). Anadromy is considered a quantitative threshold trait with genetically determined environmental thresholds for triggering behavioural responses (Ferguson, 2006; Ferguson et al., 2019).

Previous studies on the migratory behaviour of sea trout have shown a variety of patterns in how they use of the marine habitat (Thorstad *et al.*, 2016). While some studies shown that sea trout used relatively confined areas within or close to the estuaries of their watercourse (Honkanen *et al.*, 2020), other studies have shown that sea trout can perform migrations

covering great distances at sea (Birnie-Gauvin *et al.*, 2019b; Kristensen *et al.*, 2019). Similarly, studies have shown temporal use of the marine habitat ranging from few weeks or months during summer, to almost permanent residency in marine habitats after the first sea entry, spending only short time in freshwater during the spawning season (Jensen, 1968; Berg & Berg, 1989; Bendall *et al.*, 2005; Jensen & Rikardsen, 2008). Previous studies suggest that the anadromy of sea trout is a continuum of alternative migratory tactics (Cucherousset *et al.*, 2005; Boel *et al.*, 2014; Bordeleau *et al.*, 2018).

The utilization of the marine habitat of sea trout is influenced by the environment. The environmental conditions have been found to influence the smolt age and smolt size (L'Abée-Lund *et al.*, 1989), and time the season of the sea trout's first migration to the sea (L'Abée-Lund *et al.*, 1989; Jensen *et al.*, 2012). Moreover, conditions in the freshwater habitat seem to largely determine how long periods sea trout remain in freshwater after their first migration to sea. In watersheds with limited water discharge and absence of pools and lakes suitable for residency, sea trout tend to remain in freshwater only for short periods during spawning after their first migration to the sea (Thorstad *et al.*, 2016). Less is known about how the marine environment impact the behaviour of sea trout while at sea. In northern Norway, Jensen *et al.* (2014) found that sea trout tended to seek areas with the highest water temperatures in the fjord. The prey availability likely also influence the marine behaviour (Rikardsen & Amundsen, 2005).

Throughout the lifetime of sea trout, the requirements for prey change as the individual grows larger (Klemetsen *et al.*, 2003). Larger fish need larger prey to meet its metabolic demands, and sea trout have been found to shift towards a more piscivorous diet as they grow (Knutsen *et al.*, 2001; Davidsen *et al.*, 2017). The balance between increased feeding opportunities and risk of mortality is thought to be a strong driver for the adaption of marine behaviour in brown trout, as fecundity is largely correlated with body size (Elliott, 1995), while the migration to the marine habitat imposes increased mortality risk (Jensen *et al.*, 2019). After smoltification and entering the sea, one of the major energy costs of sea trout is spawning (Lien, 1978; Jonsson & Jonsson, 2011). The sea trout is iteroparous, meaning that it can spawn multiple times throughout its lifetime (Went, 1962; Euzenat *et al.*, 1999).

Previous studies have shown that life history stage can affect the migratory behaviour of sea trout. For example, larger, veteran migrants (sea trout that have performed at least one previous migration), have been reported to migrate to sea earlier in spring compared to first-

time migrants (smolts) (Pemberton, 1976; Bohlin *et al.*, 1996; Jonsson & Jonsson, 2009). Some studies have shown that larger trout migrate further away from the river where they were born and spawn, compared to smaller individuals (Jensen *et al.*, 2014; Jonsson & Jonsson, 2014). However, some studies have not found such trends (Berg & Berg, 1987; Berg & Jonsson, 1989), and studies have also indicated that sea trout might reduce or cease the sea migration as they get older (Svårdson & Fagerström, 1982; Bond *et al.*, 2015), perhaps because the costs in terms of mortality risk outweighs the benefit of increased feeding opportunities for the spawning success in the late ontogeny of the individuals.

The nutritional state of individuals at any given time, is determined by net differences over periods of weeks or months between energy intake and energy expenditure (Congleton & Wagner, 2006). Few studies have evaluated the influence of nutritional and physiological state on the marine migratory behaviour of sea trout. As an indirect measure of nutritional state, some studies have documented body condition factor to influence aspects of the marine migrations of sea trout (Davidsen *et al.*, 2014; Eldøy *et al.*, 2015; Bordeleau *et al.*, 2018; Haraldstad *et al.*, 2018). Bordeleau *et al.* (2018) also observed that the pre-migratory levels of blood plasma triglycerides were negatively correlated with the duration of the marine residency. Evaluating the stress levels of pre-migratory veteran sea trout, Birnie-Gauvin *et al.* (2019a) observed that individuals with high baseline cortisol levels migrated towards the sea earlier and were less likely to make it to the sea than individuals with low cortisol levels. In a recent review article assessing the need for knowledge to bring the field of fish migration science forward, Lennox *et al.* (2019) advocated the need for further studies coupling individual physiological state and migratory behaviour was shed light on the mechanistic link between internal state and migrations of fish.

While at sea, sea trout utilize marine water bodies with high degree of human activity, such as aquaculture, marine traffic, fishing, and establishment of marine infrastructure (Nevoux *et al.*, 2019). A recent report from the Scientific Committee for Atlantic Salmon, evaluating the status of 430 Norwegian sea trout populations, concluded that only 20% of the populations were in good or very good state (Anon., 2019). Salmon lice infestation due to Atlantic salmon farming was identified as the anthropogenic factor that by far had the strongest negative effect both in terms of number of affected populations and effect on population sizes. The interaction between aquaculture and the marine migrations of sea trout therefore requires special attention in coastal planning processes and for conservation of the species. The

negative impact factors, such as salmon lice infestation, can vary both temporary and spatially, including vertically in the water column.

In order to understand the consequences of anthropogenic stressors for sea trout populations and develop conservation measures, a better understanding of the marine behaviour of this species is needed, including knowledge about the underlying mechanistic drivers for the migratory continuum the sea trout display at sea. For example, although it is well documented that salmon lice can substantially alter the marine behaviour, growth and survival of sea trout in areas with intensive salmon farming (Taranger *et al.*, 2014; Thorstad *et al.*, 2015; Serra-Llinares *et al.*, 2020), it has proven difficult to quantify the effects of salmon lice infestations on wild sea trout populations due to their variable marine behaviour and complex life histories.

Reduced benefits of the sea trout marine migration due to reduced feeding opportunities or increased stressors, is likely to reduce survival and growth of sea trout at sea, reducing the reproductive capacity and lead to lower ultimate fitness of migratory individuals. It has been suggested that long-term shifts in benefits and risks associated with the marine migration may drive shifts in the marine habitat utilization of populations, and ultimately alter the population structure of sea trout populations by selecting for or against anadromy (Gargan *et al.*, 2006; Thorstad *et al.*, 2015; Archer *et al.*, 2019). However, with the large variation observed among studies, the migratory patterns are still not fully understood, and with the current pressure on sea trout stocks by human activities, there is a crucial need for further knowledge about the marine life of sea trout.

Objective of thesis

The first aim of this thesis was to study how physiology, previous life history and experienced environmental conditions affect the marine behaviour of sea trout. The second aim was to examine how salmon farming can affect nearby sea trout populations in terms of marine growth and utilization of marine versus fresh- and brackish water habitats. This was addressed by using two different methodological approaches; *i.* by tracking individual sea trout in the marine environment in three fjord systems in central and northern parts of Norway using acoustic telemetry, and *ii.* by examining growth patterns and chemical composition of sea trout scales.

In the studies using the first methodological approach, we used acoustic telemetry to map the marine habitat use of sea trout individuals (**paper I, II and III**), examine the influence of physiological drivers for the marine migration behaviour (**paper I**), examine the swimming depth in response to environmental variables (**paper II**), and evaluate the individual consistency in marine migratory patterns between consecutive annual migrations (**paper III**). More specifically, in **paper I** we examined whether nutritional state, sex, and body length influenced an individual's marine migration in terms of tendency to migrate to the sea or remain resident in freshwater and/or estuarine habitats, timing of sea entry, duration of the marine residency and migration distance at sea from the river where the fish were tagged. In **Paper II** we examined the sea trout's swimming depth in response to habitat type (estuary, pelagic, shore with and without steep cliffs), time of day (day vs night) and inter-season comparisons (month during summer, summer vs winter), as well as the seawater temperature and individual's body length at tagging. In **paper III** we examined the degree of annual intra-individual behavioural repeatability in terms of spatial dispersal, migratory timing and duration of marine residency.

In the study using the second methodological approach to address the second aim of this thesis, the growth patterns and chemical composition in sea trout scales from three Norwegian and two Irish sea trout populations were assessed using scale chemistry analyses (**paper IV**). Specifically, we examined whether sea trout had *i.* reduced growth after first sea entry, *ii.* increased Ba:Ca levels in the section of the scale after first sea entry (indicating less use of marine habitats), and *iii.* increased length at first sea entry in periods with nearby salmon farming (<14 km) compared to periods when there was no nearby salmon farming (**paper IV**).

Study sites

The field experiments using acoustic telemetry to track free-ranging, wild sea trout were conducted in three fjord systems in central and northern parts of Norway. Data collected at the Skjerstadvfjorden study site, located at 67°N in northern Norway, were included in **paper I** (Figure 1 and 3). This fjord system has about 225 km² surface area and is separated by the coast by the small strait Saltstraumen. The tagged fish included in **paper I** from the Skjerstadvfjorden study site were tagged in the five watercourses Saltdalselva, Botnvassdraget, Lakselva (Misvær), Laksåga, and Kosmovatnet (Figure 1).

Data collected at the Tosenfjorden study site, located at 65°N in northern Norway, were included in **paper I and III** (Figure 1 and 3). This fjord system consists of two interconnected fjords with a surface area about 150 km², connected to the open sea by a 15 km long strait. For **paper I and III**, the fish were tagged in the two watercourses River Åbjøra and River Urvold (Figure 1 and 3).

The tracking study in Hemnfjorden, located at 63°N in Central Norway, provided data included in **paper II and III** (Figure 2 and 3). The Hemnfjorden study site covers about 60 km² of sea surface and is connected to the open sea through a 36 km long strait. **Paper II** was based on data from fish tagged in River Søa and River Snilldalselva (Figure 2). **Paper III** included data from fish tagged in River Søa (Figure 3).

The fish scale study presented in **paper IV**, included samples from the three watercourses River Levangerelva, River Nidelva and River Straumsvassdraget at 63°N in Central Norway, and River Erriff and River Cashla at 53°N in western Ireland (Figure 4).

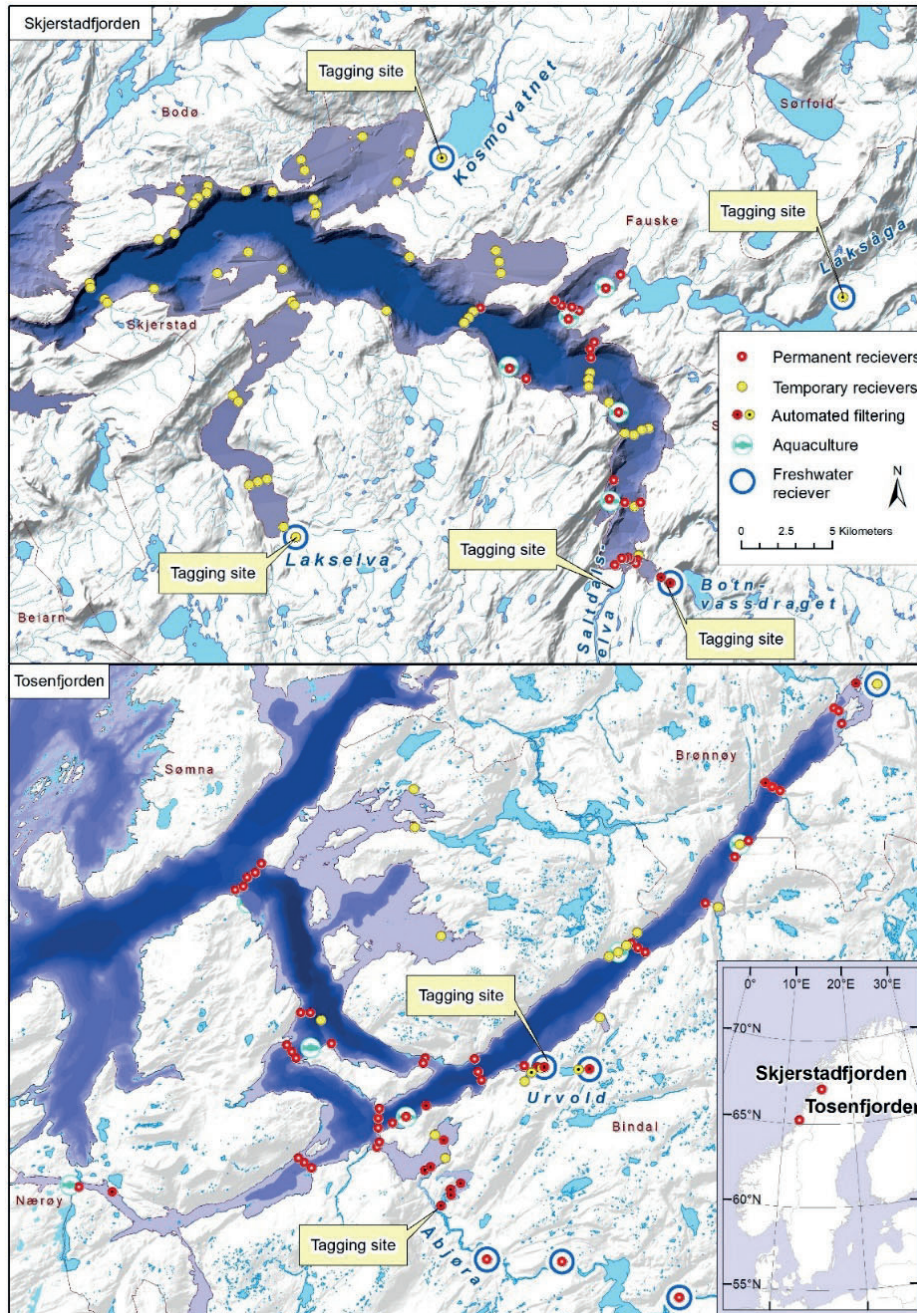


Figure 1: Map of the study areas included in **paper I** indication location of fish tagging sites and acoustic receivers. “Automated filtering” indicates receivers where automatic data filtering was applied to remove false detections (see **paper I** for details).

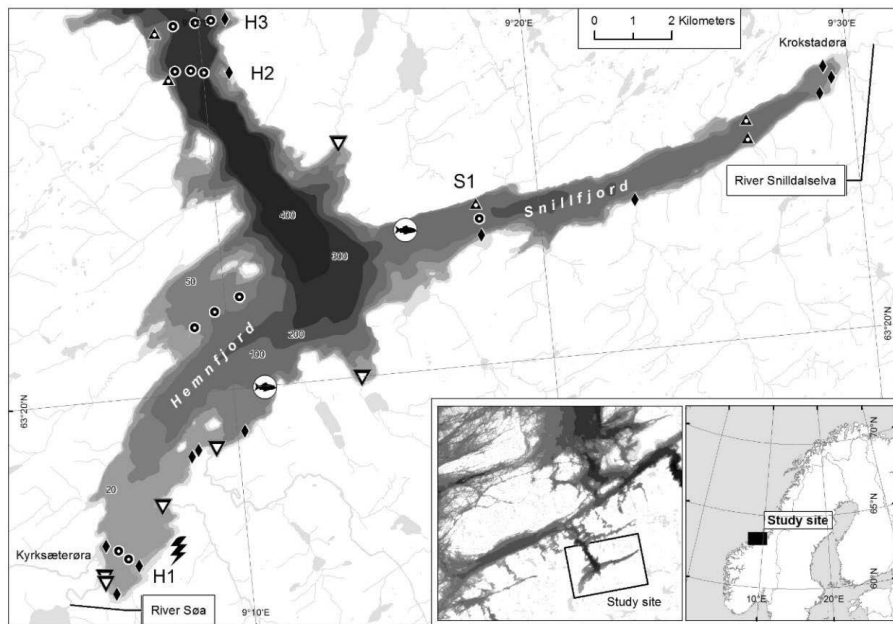


Figure 2: Map over the study area included in **paper II**, indicating locations of tagging sites in River Sjøa and River Snilldalselva, receivers in different habitats (▽ estuary; ◆ near shore area without steep cliffs; ▲ near shore area with steep cliffs; ● pelagic area), and temperature and salinity data loggers (T/S).

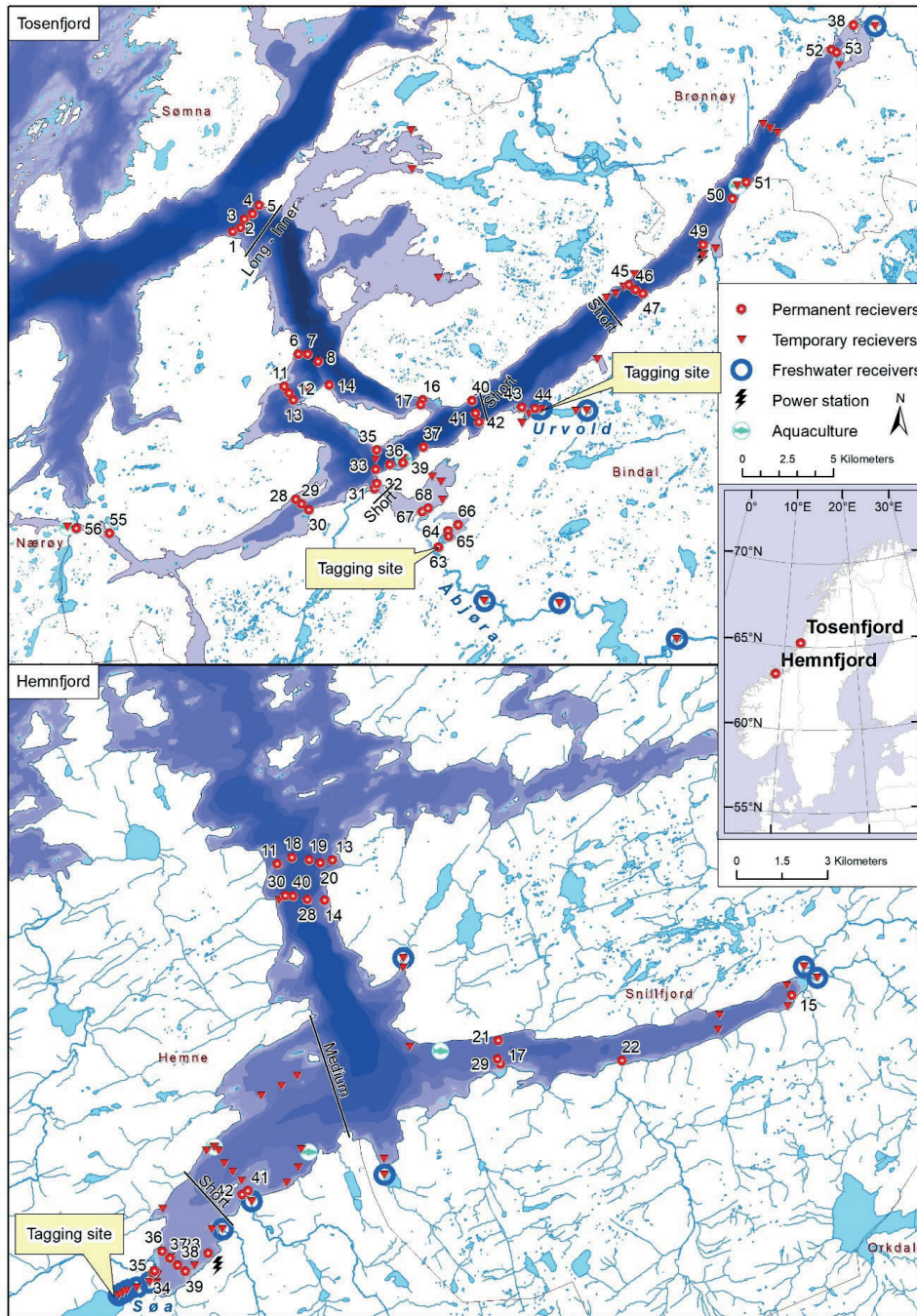


Figure 3: Map of the study areas included in **paper III**, indicating locations of fish tagging sites and acoustic receivers.

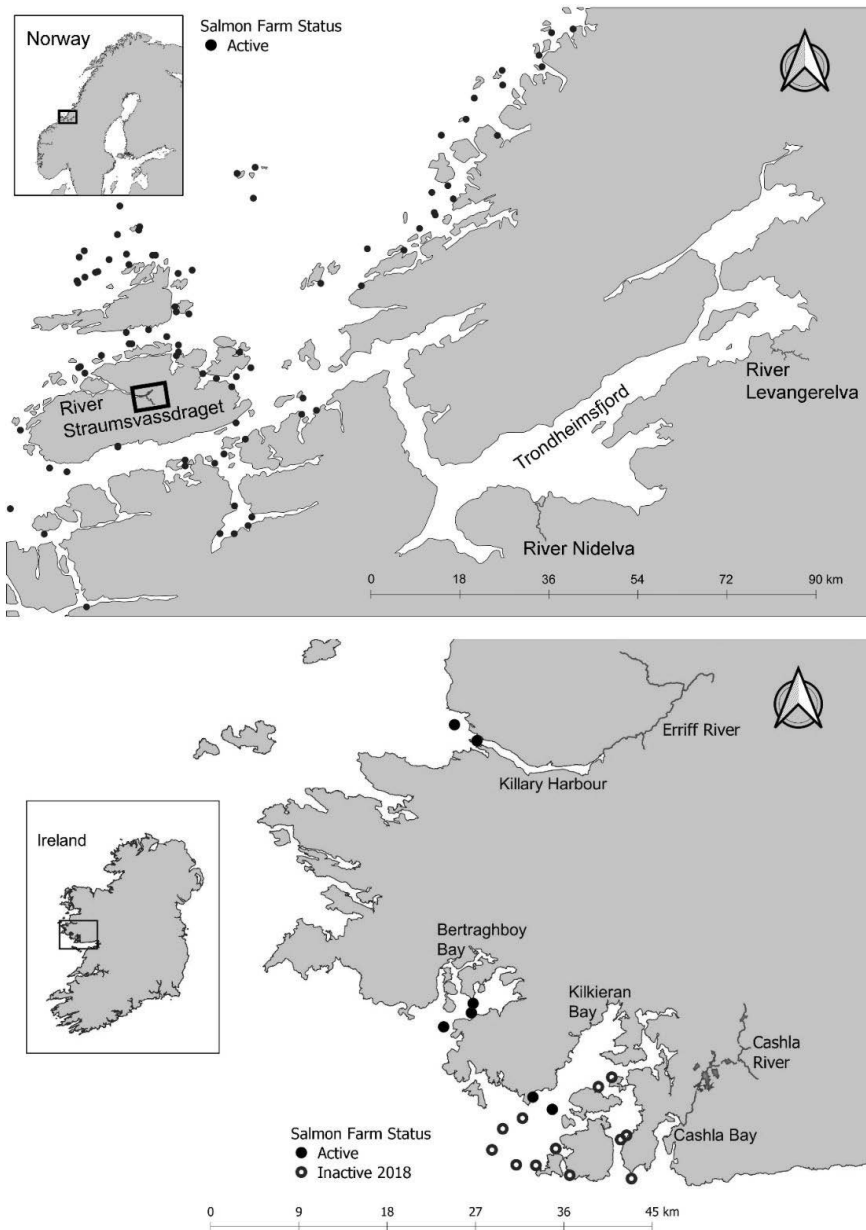


Figure 4: Maps of the study sites Norway (upper) and Ireland (lower) included in **paper IV**. Sea trout scales were sampled from the populations River Straumsvassdraget, River Nidelva and River Lenvangerelva in Norway and River Erriff and River Cashla in Ireland. Black dots indicate active salmon farms during the recent sampling periods, while black circles indicate active salmon farms during the historic sampling periods in Ireland.

Methods

The behavioural patterns of the sea trout studied in **paper I, II and III** were recorded using acoustic telemetry. The electronic tags were surgically implanted in the body cavity (Eldøy *et al.*, 2015), or externally attached beneath the dorsal fin with metal wire through the dorsum of the fish 1-2 cm below the dorsal fin. The tags used were acoustic transmitters that emitted individually coded high frequency sound signals (69 kHz). The migratory patterns of tagged fish were monitored by deploying a network of automated receivers in the various habitats. The range of tag detection is usually expected to be a few hundred meters under normal conditions at sea, but varies with a range of factors including hydrology of the location, background noise levels and the size (output sound effect) of the transmitters (Eldøy *et al.*, 2015; Brownscombe *et al.*, 2020). The acoustic transmitters used in **paper II** had inbuilt depth (pressure) sensors.

The environmental parameters included in the studies were water temperature and salinity recordings from automatic loggers, water column profiles using a manual conductivity-temperature-depth recorder, and information on timing of sunrise and sunset in **paper II**. Water temperature and salmon lice counts reported by the salmon farms to the national authorities were used to describe environmental fluctuations in **paper III**.

A better mechanistic understanding of fish migrations can be obtained by combining the behavioural studies with other disciplines within biology, such as genetics or physiology (Cooke *et al.*, 2008). In **paper I**, genetic analyses were applied to determine the sex of the individuals, and blood plasma assays (blood plasma triglycerides, protein and calcium) were used to evaluate the nutritional state of the individuals beyond only using condition factor as an indirect measure. Nutritional state, sex and body length were linked to data on the timing, duration and distance of the marine migration of tagged individuals.

The life history and migratory patterns of fish can, besides conducting tracking studies, be evaluated by analysing the growth patterns and chemical deposition in calcified body structures such as scales and otoliths (Tzadik *et al.*, 2017). In **paper IV**, scale samples from historic scale collections and more recently sampled scales from three Norwegian and three Irish sea trout populations (covering time spans from 25 to 65 years) were analysed using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). By using the Ba:Ca ratio profile throughout the scale obtained by this method, the body length at first sea

entry could be determined (Ryan *et al.*, 2019). Furthermore, using this method provided indications of the relative marine habitat utilization among the sampled fish compared to the use of freshwater and brackish water habitats (Figure 5).

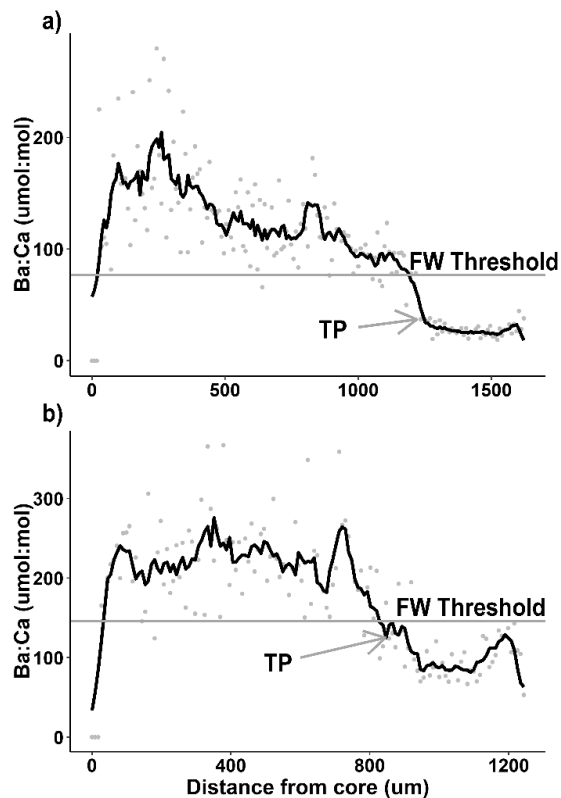


Figure 5: Examples of Ba:Ca profiles of the scales from a) fish id 83_111 (sampled in 1983, body length 303 mm, smolt length 232 mm, one marine migration), and b) fish id 15_14 (sampled in 2015, body length 280 mm, smolt length 193 mm, one marine migration) from River Erriff, Ireland. Grey points denote the data points along the scale transect. The black lines denote the three-point running average of the data points. Freshwater threshold value denotes the 5th percentile of Ba:Ca values from a slightly trimmed freshwater growth region of the scale, and “TP” denotes point of first sea entry (**paper IV**).

Summary of papers

Paper I:

The effects of nutritional state, sex and body size on the marine migration behaviour of sea trout

We studied the migration behaviour of 286 sea trout (27-89 cm) tagged with acoustic transmitters in the spring, in seven populations located in two marine fjord systems in Norway. We examined whether individual nutritional state, sex, and body size influenced marine migration behaviour in terms of *i.* the decision to migrate to the sea or remain resident in freshwater and/or estuarine habitats, *ii.* seasonal timing of sea entry, *iii.* duration of the marine residency, and *iv.* migration distance at sea from the home river. The sea trout were generally in a poor nutritional state in the spring prior to migration. Sea trout in poor body condition and low plasma triglyceride levels were more likely to migrate to sea, and low triglyceride levels were also associated with earlier sea-entry. Additionally, poor body condition increased the probability of individuals remaining longer at sea and migrate further out in the sea compared to better conditioned fish. Females were more likely to migrate to the sea than males. Larger fish were also more likely to migrate to sea instead of remaining in freshwater and estuaries and to disperse over greater distances at sea than smaller fish. In conclusion, this study documented general trends across multiple populations and showed that nutritional state, sex and body size influenced important aspects of the marine migration behaviour of sea trout.

Paper II:

Marine depth use of sea trout *Salmo trutta* in fjord areas of central Norway

The vertical behaviour of 44 veteran sea trout (275–580 mm) in different marine fjord habitats (estuary, pelagic, near shore with and without steep cliffs) was documented during May–February by acoustic telemetry. The swimming depth of sea trout was influenced by habitat, time of day (day v. night), season, seawater temperature and the body length at the time of tagging. Mean swimming depth during May–September was 1.7 m (individual means ranged from 0.4 to 6.4 m). Hence, sea trout were generally surface oriented, but performed dives down to 24 m. Mean swimming depth in May–September was deeper in the near-shore habitats with or without steep cliffs (2.0 m and 2.5 m, respectively) than in the pelagic areas

(1.2 m). May–September mean swimming depth in all habitats was slightly deeper during day (1.9 m) than at night (1.2 m), confirming that sea trout conducted small-scale diel vertical movements. During summer, sea trout residing in near-shore habitat progressively moved deeper over the period May (mean 1.1 m) to August (mean 4.0 m) and then reoccupied shallower areas (mean 2.3 m) during September. In winter (November and February), individuals residing in the innermost part of the fjords were found at similar average depths as they occupied during the summer (mean 1.3 m).

Paper III:

Individual repeatability in marine migratory behaviour: A multi-population assessment of anadromous brown trout tracked through consecutive feeding migrations

Despite that the study of individual repeatability is a common topic in behavioural ecology, virtually nothing is known about inter-annual variability in the marine migratory behaviour of iteroparous salmonids that can complete multiple feeding migrations in their lifespan. Behavioural data from 38 anadromous sea trout during 2–3 consecutive marine feeding migrations in two Norwegian fjord systems, were analysed for intra-individual repeatability in key aspects of their marine migration. Individual brown trout displayed significant inter-annual consistency in marine area use and in the timing of marine exit (*i.e.*, when they returned to spawning rivers), but not in the timing of marine entry or the time spent in the marine environment each year. This study raises new questions about how sea trout respond to changing conditions and anthropogenic factors in the marine environment. Intra-individual repeatability of brown trout linked to changing environmental conditions should therefore be a focus for future studies.

Paper IV

Changes in growth and migration patterns of sea trout before and after the introduction of Atlantic salmon farming

Marine growth has strong implications for reproductive potential and ultimate fitness of sea trout. Hence, the effects of anthropogenic factors on marine growth are important when evaluating population responses and implementing management measures. Temporal changes in growth patterns of sea trout from three Norwegian and two Irish watercourses were

examined, covering time spans of 25 to 65 years. Elemental chemistry Ba:Ca profiles and visual reading of fish scales were used to estimate smolt length and life-time growth after first sea entry. Reduced growth after the first sea entry coincided with periods of nearby (<14 km) salmon farming activity in impacted watersheds in both countries. Increased Ba:Ca levels were also recorded during these periods, likely indicating reduced residency in marine habitats caused by premature return to freshwater and estuaries. An increase in estimated body length at first sea entry coinciding with salmon farming activity, for groups of fish sampled after sea migration, suggests a size-selective marine mortality related to fish farming, with the smallest individuals experiencing a larger mortality.

Discussion

The findings in this thesis show how the marine behaviour of sea trout was influenced by important aspects of physiology (**paper I**), environmental conditions (**paper II**), life history (**paper III**) and anthropogenic activities in terms of open cage salmon farming in the coastal marine habitat (**paper IV**). The highly variable use of the marine habitat among individuals observed in **paper I and III**, suggest that human activities will not affect the individuals in a population to the same extent. For example, individuals that spend prolonged time in marine habitats and migrate further out in the fjord systems may to be more susceptible to salmon lice infestation than individuals spending shorter time and/or performing and remaining closer to the river. This can be expected because salmon lice larva and copepodites do not survive for long in low salinity water (Johnson & Albright, 1991). **Paper II** documented that the sea trout generally stayed in the upper water layer with an average swimming depth of 1.7 meters during May – September, overlapping with the previously observed surface-oriented distribution of salmon lice larva (Heuch *et al.*, 1995; á Norði *et al.*, 2016). In marine areas with freshwater input such as inner fjord areas or areas close to rivers, the surface layer has often lower salinity (example shown in **paper II**), and consequently low abundances of salmon lice larva (IMR, 2020). In Norway, and some other countries, open cage marine farming of Atlantic salmon is a major threat to sea trout populations. Other anthropogenic factors impacting sea trout, such as marine traffic, building of marine infrastructure (docks, and harbours, power production installations etc.) and fishing, can also vary spatially and temporarily in the marine environment.

Given that some individuals are more likely to be impacted by human activities than others, what characterizes the fishes that are more likely to be impacted by human activity at sea?

Paper I examined physiological drivers for migratory patterns across 286 individuals from seven populations in two fjord systems in northern Norway, showing how nutritional state, sex and body size affected the migratory behaviour of sea trout. Sea trout with low nutritional levels were more prone to leave the river and estuaries and migrate to the sea, and individuals with low triglyceride levels migrated to the sea earlier. Fish with a poor body condition prior to the migration remained at sea for a longer time-period than fish with a better condition. This suggests that individuals in a poor pre-migratory nutritional state displayed a more risk-taking migration behaviour than fish in better nutritional state, and that these individuals may be particularly vulnerable to anthropogenic factors at sea. The nutritional state is determined by net differences over periods of weeks or months between energy intake and energy expenditure (Congleton & Wagner, 2006). Poor pre-migratory nutritional state could likely be explained by limited feeding while overwintering and energy expenditure during spawning the previous autumn for post-spawned individuals (Bordeleau *et al.*, 2018; Bordeleau, 2019).

Paper I also documented that females were more likely to migrate to the sea than males, instead of remaining in the freshwater and estuarine areas of the river where they were tagged. In brown trout, the fitness benefits of increasing feeding and somatic growth during marine migrations are thought to be greater for females than males due to the strong correlation between female body size and the number of eggs the female can produce (Elliott, 1995). Larger fish of both sexes were more likely to migrate to the sea, enter the sea earlier, and migrate a longer distance in the sea than smaller fish. These tendencies are likely driven by the need of larger individuals to find more prey of larger size than the smaller fish (Knutsen *et al.*, 2001; Klemetsen *et al.*, 2003; Davidsen *et al.*, 2017). The results presented in **paper I** therefore indicate that individuals that are heavily dependent on the marine habitat for feeding and recondition, also are individuals of high importance for the recruitment in the populations. Human activities in coastal areas that negatively affect these individuals, can therefore be expected to have negative effect on the population sizes and alter population dynamics. Previous studies have suggested that the migratory behaviour of brown trout is a continuum of behavioural responses to the environmental cues experienced by the individuals in coastal trout populations (Cucherousset *et al.*, 2005; Boel *et al.*, 2014; Villar-Guerra *et al.*, 2014; Bordeleau *et al.*, 2018).

Paper II provided new knowledge about the swimming depth of sea trout across seasons and various habitats. The swimming depths of the sea trout coincided with the previously known surface orientation of salmon lice. Combined with previous studies on horizontal use of sea trout, this study illustrated how sea trout utilize marine water bodies commonly influenced by anthropogenic factors such as aquaculture, harbours and marine constructions, marine renewable energy production or other human activity. This suggests that the marine behaviour of sea trout and its susceptibility to coastal anthropogenic factors should be considered in marine planning processes. Slight differences in depth use were observed among individuals and habitats, between night and day as well as throughout the summer season.

Although the nutritional state, body size and environmental conditions influence the marine behaviour of sea trout, results in **Paper III** showed that some key aspects of the annual marine feeding migration of sea trout tend to be repeated between years. Repeatable behaviour is a common phenomenon in nature, but this was the first study to illustrate repeatable behaviour by sea trout, and among few to evaluate behavioural repeatability in salmonid fishes more generally (Taylor & Cooke, 2014). Here, we observed consistent intra-individual marine behaviour over consecutive feeding migrations in terms of marine area use and timing of return to the spawning rivers, but not in the timing of marine entry or the seasonal time spent in the marine environment. The observed consistency in marine migratory behaviour in **paper III**, may suggest that behavioural syndromes exist for the marine migratory patterns of sea trout. Alternatively, there may be causal factors acting over longer time frames that causes individuals to have consistent pre-migratory nutritional state during spring (Bordeleau, 2019). The findings in **paper III** suggest that human activities might not only act differently on individuals in sea trout populations a given year, but that these differences in negative impact on individuals can also remain across feeding migrations. The behavioural consistency observed in **paper III** raises questions on how capable sea trout individuals are in changing their migratory patterns in response to environmental changes.

Paper IV examined whether sea trout in populations near salmon farms had reduced growth after first sea entry, increased Ba:Ca levels in the section of the scale after first sea entry (suggesting reduced use of marine habitats), and increased length at first sea entry during periods with salmon farming activity compared to periods without activity at the farming sites. The chemistry analyses of sea trout scales showed reduced growth of individual fish

after first sea entry in periods coinciding with nearby salmon farming activity. Moreover, increased Ba:Ca levels were also recorded during periods with nearby salmon farming, indicating reduced residency in marine habitats. There was also an increase in estimated length at first sea entry coinciding with salmon farming activity, suggesting a size selective mortality related to fish farming, with the smallest individuals experiencing a larger mortality. The observed reduction in marine growth for surviving individuals have strong implications for the reproductive potential of the individuals as fecundity is strongly correlated to body size (Elliott, 1995), and this may have large implications for the recruitment of populations. It is therefore important that both marine survival and the growth of surviving sea trout are evaluated when assessing the impact of human marine activity on coastal trout populations. The newly developed method applied in **paper IV**, using Ba:Ca profiles obtained by LA-ICP-MS analyses of sampled sea trout scales, provided accurate information about the point of first marine entry (Ryan *et al.*, 2019), but furthermore also indicated a relative change in the use of the marine habitat *versus* freshwater and brackish water habitats. Although further development of the method is needed to better understand how the Ba:Ca profiles are affected by different marine migration patterns, the method applied in **paper IV** provides a promising tool for examining how surviving individuals in sea trout populations are affected by altered environmental conditions at sea.

Although the methodological approaches used in this thesis were found to be highly suitable to address the thesis aims, they also have some limitations. Acoustic telemetry applied in **Paper I-III** uses electronic transmitters and receivers that are relatively expensive, often determining the numbers of study animals and the coverage of receivers that can be included in the studies. The quality of the tracking data is dependent on the receiver coverage in the areas the animals use. Receiver detection range can vary greatly both among sites, but also temporally at each site, in response to hydrologic variables and ambient noise levels (Brownscombe *et al.*, 2020). Capture, handling and tagging the animals have the potential of influencing their subsequent behaviour. Using refined handling and tagging methods, and appropriately sized tags are therefore important to minimise the tag burden on the animals. Another important aspect to consider for both the tracking studies in **paper I-III** and the scale chemistry study in **paper IV**, is how representable the tagged or sampled animals are for the studied populations. Timing and method of capture might target certain subgroups of the population and should together with the limitations mentioned above be considered when analysing and interpreting data from animal behavioural studies. For the scale chemistry

analyses presented in **paper IV**, larger and older sea trout have a more complex life history that make the scale growth patterns and estimation of age more difficult to interpret (Elliott & Chambers, 1996). There is also uncertainty on how spawning events affect the scale chemistry due to chemical deposition (Tzadik *et al.*, 2017), and the older fish sampled for **paper IV** were therefore removed from the analyses.

Conclusion

This thesis has brought new insights into the marine behavior of sea trout, and how nutritional state, sex and body size affect the migratory behavior of sea trout. It has shown that the swimming depth of sea trout is surface-oriented and overlap with previously reported distribution depths of salmon lice. The thesis included the first study on individual repeatability in marine behavior of sea trout across feeding seasons, providing indications that the individual plasticity in migratory behavior might be lower than previously expected. Using a recently developed scale chemistry methodology, temporal changes in marine growth patterns with and without present salmon farming in nearby areas was documented, and furthermore provided data suggesting that the use of fully marine habitats were reduced for the sea trout in periods with nearby salmon farms.

The observed large variation of marine migratory behaviour of sea trout implies that the susceptibility to human activity will not only vary between populations, but also among individuals within populations. This is crucial knowledge for evaluating the effect of anthropogenic factors that can vary both spatially and temporally. For example, the results in this thesis suggest that larger females in poor nutritional state prior to migration are more likely to be exposed to open caged salmon farm related stressors at sea, because these individuals within the population tend to have more pronounced utilization of the marine habitat. The uneven effect of human activities on the individuals within populations can alter population structures by posing increased risk of mortality and/or reduced marine growth on subgroups within the populations with certain behavioural traits. Moreover, if human activities in coastal areas cause decreased growth and increased mortality in individual sea trout, this can lead to altered population dynamics and selection against anadromy, or against certain migratory tactics within the marine migratory continuum of coastal trout populations.

Future perspectives

The first objective of this thesis was to study how physiology, previous life history and experienced environmental conditions affect the marine behaviour of sea trout. Although **paper I, II and III** have provided new insights to this objective, there is still large variation that we could not account for in these studies, and further studies including other physiological, life history and/or genetic explanatory variables are therefore advocated.

Paper I, II and III have illustrated the large variation in marine behaviour between individuals within sea trout populations. The potential of uneven pressure on individuals within populations from human activities have been discussed in this thesis. A further step in understanding the balance between benefits and costs related to marine migration in the migratory continuum of sea trout, is to invest effort into recapture of tracked individuals after their sea journey, in order to assess their migratory success in terms of growth, as well as their costs such as parasite and pathogen loads which might influence their long-term survival and fitness.

Paper I in this thesis and a previous study by Bordeleau *et al.* (2018) showed how the pre-migratory nutritional state of post-spawned sea trout veteran migrants affected their subsequent migratory patterns. However, the relative importance of nutritional state prior to spawning, spawning investment and the energy expenditure overwintering on the pre-migratory nutritional state of individuals in spring is poorly understood. More research on the link between spawning investment and migratory behaviour is advocated to shed light on how behavioural differences within the migratory continuum affect the reproductive potential of individuals and vice versa. Moreover, as global warming is expected to give warmer temperatures and milder winters in the Atlantic region it is expected that the energy expenditure of trout in freshwater habitats will increase (Nevoux *et al.*, 2019). Given the observations in **paper I**, studies examining whether changes in the energy budget while in freshwater can alter the marine migration patterns of fish should be conducted.

Paper III documented that sea trout tend to show consistency in marine migratory patterns among consecutive feeding seasons. The findings in this study can potentially have large implications for management purposes, as it suggests that the behavioural flexibility of individuals may be somewhat restricted. Further studies on the role of intra-individual

repeatability and the inter-annual behavioural response of sea trout to changing environmental conditions are therefore advocated.

Paper IV demonstrated that a newly developed method using Ba:Ca profiles from could be used to assess growth and relative use of marine waterbodies among groups of sea trout from the same watercourse. This method has potential for further development, possibly leading to the possibility of more detailed measures on marine habitat use derived from scale samples. Furthermore, combining the method applied in **paper IV** with other analyses on the scales, such as stable isotope analyses, might shed light on the historical developments in marine habitat use and marine feeding ecology using historical sea trout scale collections.

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Paper I

The effects of nutritional state, sex and body size on the marine migration behaviour of sea trout

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Running headline: Physiological drivers for marine behaviour in sea trout *Salmo trutta*.

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ABSTRACT

The sea trout (anadromous brown trout, *Salmo trutta*) displays extensive among-individual variation in marine migration behaviour. We studied the migration behaviour of 286 sea trout (27-89 cm) tagged with acoustic transmitters in the spring, in seven populations located in two marine fjord systems in Norway. We examined whether individual nutritional state, sex, and body size influenced marine migration behaviour in terms of *i.* the decision to migrate to the sea or remain resident in freshwater and/or estuarine habitats, *ii.* seasonal timing of sea entry, *iii.* duration of the marine residency, and *iv.* migration distance at sea from the home river. The sea trout were generally in a poor nutritional state in the spring prior to migration. Sea trout in poor body condition and low plasma triglyceride levels were more likely to migrate to sea, and low triglyceride levels were also associated with earlier sea-entry. Additionally, poor body condition increased the probability of individuals remaining at sea longer and migrate further out in the sea compared to better conditioned fish. Females were more likely to migrate to the sea than males. Larger fish were also more likely to migrate to sea instead of remaining in freshwater and estuaries and to disperse over greater distances at sea than smaller fish. In conclusion, this study documented general trends across multiple populations and showing that nutritional state, sex and body size influenced important aspects of the marine migration behaviour of sea trout.

This Paper is awaiting publication and is not included in NTNU Open

Paper II

Marine depth use of sea trout *Salmo trutta* in fjord areas of central Norway

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The vertical behaviour of 44 veteran sea trout *Salmo trutta* (275–580 mm) in different marine fjord habitats (estuary, pelagic, near shore with and without steep cliffs) was documented during May–February by acoustic telemetry. The swimming depth of *S. trutta* was influenced by habitat, time of day (day v. night), season, seawater temperature and the body length at the time of tagging. Mean swimming depth during May–September was 1.7 m (individual means ranged from 0.4 to 6.4 m). Hence, *S. trutta* were generally surface oriented, but performed dives down to 24 m. Mean swimming depth in May–September was deeper in the near-shore habitats with or without steep cliffs (2.0 m and 2.5 m, respectively) than in the pelagic areas (1.2 m). May–September mean swimming depth in all habitats was slightly deeper during day (1.9 m) than at night (1.2 m), confirming that *S. trutta* conducted small-scale diel vertical movements. During summer, *S. trutta* residing in near-shore habitat progressively moved deeper over the period May (mean 1.1 m) to August (mean 4.0 m) and then reoccupied shallower areas (mean 2.3 m) during September. In winter (November and February), individuals residing in the innermost part of the fjords were found at similar average depths as they occupied during the summer (mean 1.3 m). The swimming depths of *S. trutta* coincide with the previously known surface orientation of salmon lice *Lepeophtheirus salmonis*. Combined with previous studies on horizontal use of *S. trutta*, this study illustrates how *S. trutta* utilize marine water bodies commonly influenced by anthropogenic factors such as aquaculture, harbours and marine constructions, marine renewable energy production or other human activity. This suggests that the marine behaviour of *S. trutta* and its susceptibility to coastal anthropogenic factors should be considered in marine planning processes.

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Key words: acoustic telemetry; brown trout; marine migration; migratory behaviour; swimming depth.

INTRODUCTION

In rivers with a two-way connectivity for fish to the sea, brown trout *Salmo trutta* L. 1758 populations often consist of both river-resident and anadromous individuals (Klemetsen *et al.*, 2003). Anadromous *S. trutta* perform marine migrations in order to

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maximize their feeding opportunities and ultimately enhance their fitness (Jonsson & Jonsson, 1993). Although the better at-sea feeding opportunities can improve individual fitness, there are also stressors and risks associated with migration, including higher energy expenditures for locomotion and osmoregulation, increased predation risk and exposure to novel pathogens (Thorstad *et al.*, 2016).

Marine survival and behaviour of salmonids are highly variable spatially and temporally, with some of the most influential factors being temperature, physiological state and fish size (Drenner *et al.*, 2012). *Salmo trutta* is among the lesser studied salmonids in the marine environment (Drenner *et al.*, 2012) and present knowledge of the marine distribution and behaviour of the species is incomplete, limiting ability to assess potential threats and implement appropriate conservation measures for this valued species.

In Norway, potential marine stressors and threats for *S. trutta*, such as salmon lice *Lepeophtheirus salmonis* infections associated with Atlantic salmon *Salmo salar* L. 1758 farming activity (Thorstad *et al.*, 2015), may not only vary in time and among sites, but also with depth (Heuch *et al.*, 1995). Knowledge of the use of the water column by *S. trutta* in the marine environment, however, is limited (Rikardsen *et al.*, 2007; Gjelland *et al.*, 2014; Aarestrup *et al.*, 2015). Further knowledge of marine migration, habitats occupied and depth use of *S. trutta* will help in implementing appropriate conservation measures.

The aim of this study was to use acoustic telemetry to examine spatial and temporal variation in marine depths occupied by free-ranging wild *S. trutta* in the Hemnfjord–Snillfjord system in Norway. At this site the horizontal movements and selected marine behaviour of *S. trutta* individuals included in this study were previously analysed (Eldøy *et al.*, 2015). Marine residence time and area use varied among *S. trutta* individuals and marine behaviour was influenced by individual morphology and life-history characteristics (Eldøy *et al.*, 2015). The previous analysis, however, did not consider use of the water column by *S. trutta*. Lack of previous knowledge about *S. trutta* habitat occupancy at sea made accurate predictions difficult and simple null-hypotheses (no effect) were used as background for the different habitat occupancy comparisons (estuary, pelagic, near shore with and without steep cliffs), time of day comparisons (day *v.* night) and inter-season comparison (month during summer, summer *v.* winter) in the present study. Furthermore, the null-hypothesis that the variance in individual daily swimming depth did not vary among habitats during day or night was tested.

MATERIALS AND METHODS

STUDY AREA

The study was performed in a fjord system in Sør-Trøndelag County, central Norway. The fjord's inner part is divided in two interconnected fjord arms, the Hemnfjord and Snillfjord. Together, the two inner fjords cover >60 km² of sea surface and have 65 km of shoreline (Fig. 1). The fjord system is connected to the open sea through a 36 km long strait. Water column depths in the study area ranged from *c.* 0–100 m in the near shore areas, to a maximum of *c.* 400 m in the deepest parts. The study was conducted from 22 April to 4 December 2013 and from 4 February to 1 March 2014. Summer was defined as the period from May to the end of September and winter as November to the end of February (but see below for small site-specific variations in these definitions). The other months of the study were considered transitional periods between seasons.

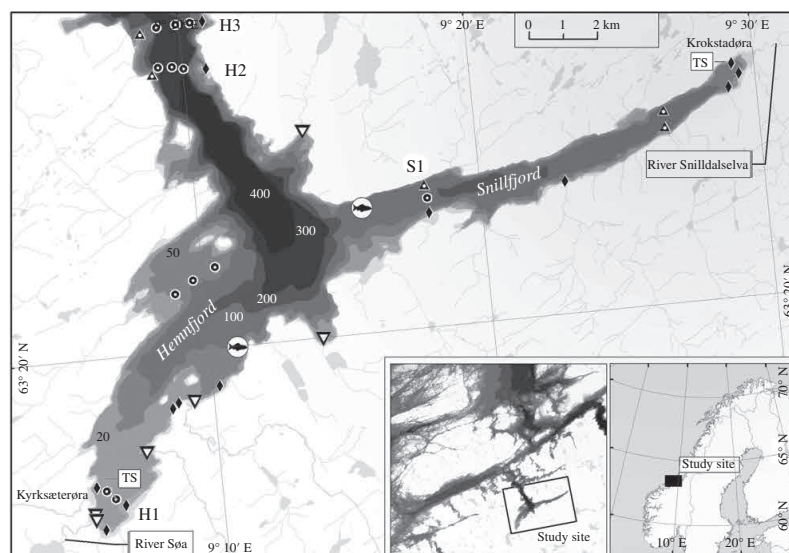


FIG. 1. Locations of automatic acoustic receivers in different habitats (∇ , estuary; \blacklozenge , near shore area without steep cliffs; \blacktriangle , near shore area with steep cliffs; \bullet , pelagic area) and aqua culture locations (\odot) in the study area. Data loggers are indicated by (T) temperature and (S) salinity.

There were two active *S. salar* farms within the fjord system during the study (Fig. 1). Weekly salmon lice counting conducted by the farmers showed average lice values ranging from 0 to 1.25 salmon lice in motile stages and from 0 to 0.3 adult female salmon lice per *S. salar* in the salmon pens within the study period.

ENVIRONMENTAL VARIABLES

Three temperature and salinity recorders (DST milli-CT; www.star-oddi.com), recordings stored every 10th minute, were deployed at 1 m depth in the fjord system. The first was 1 km from the mouth of the River Sjøa in the Hemnfjord (array H1), the second 600 m from the mouth of the River Snilldalselva in the Snillfjord and the third at the middle receiver of the outermost receiver array (array H3; Fig. 1). Profiles of conductivity and temperature were recorded from 0 to 15 m in the central part of Hemnfjord on 1 May and 15 August 2013 using an SD204 conductivity–temperature–depth recorder (SAIV A/S; www.saivas.no).

FISH CAPTURE AND TAGGING

Forty-four *S. trutta* that had previously undertaken marine migrations (*e.g.* were veteran migrants, of which some were previous spawners and some had not spawned before) were tagged with individually coded ADT-9-long acoustic transmitters equipped with depth sensors (9 mm \times 39 mm, mass in air 6.8 g, minimum tag duration 267 days, depth resolution 10 cm, max depth 100 m, power output 146 dB re 1 μ Pa at 1 m, nominal delay 30–90 s; Thelma Biotel AS, www.thelmabiotel.com). The *S. trutta* came from two watercourses draining into the fjord. At the mouth of River Snilldalselva, 15 *S. trutta* (mean total length, $L_T = 381$, s.d. = 53, range 275–460 mm) were captured using constantly monitored gillnets (35–42 mm mesh width)

and tagged during 22–23 April 2013. An additional 29 *S. trutta* (L_T mean = 417, s.d. = 55, range 330–580 mm) were captured using gillnets and tagged at the mouth of River Sjøa during 3–12 May 2013. The tagged *S. trutta* had a mean body condition factor of 0.95 (s.d. = 0.13, range 0.75–1.33). Based on scale growth-ring deposition patterns, the *S. trutta* had a mean L_T at smoltification (back-calculated L_T assuming linear relationship between body length and scale growth, Závorka *et al.*, 2014) of 143 mm (s.d. = 39, range 96–246 mm), a mean smolt age of 2.4 years (s.d. = 0.6, range 2.0–4.0 years), had undertaken a mean of 3.1 previous marine migrations (s.d. = 0.9, range 2.0–6.0) and had a mean age of 5.6 years (s.d. = 1.0, range 4.0–8.0) at the time of tagging. The tags were surgically inserted through a 1.5–2.0 cm incision into the body cavity of *S. trutta* anaesthetized with 2-phenoxyethanol (EC No. 204-589-7; Sigma; www.sigmaaldrich.com; 0.5 ml l⁻¹ water). The recovered *S. trutta* were released close to their capture site (Eldøy *et al.*, 2015).

TRACKING OF TAGGED *S. TRUTTA*

The tagged *S. trutta* were tracked using 39 VR2W acoustic receivers (Vemco, Inc.; www.vemco.com) moored 5 m below the sea surface (Fig. 1). The receivers operated from 22 April to 1 December 2013 and again from 6 February 2014 to 1 March 2014. The distance between receivers in the receiver arrays ranged between 332 and 660 m (Array H1, H2, H3 and S1; Fig. 1). The receivers were not operational during December – January due to logistical constraints. Tag detection range was tested at the central receiver of array H1 (Fig. 1) on 22 August 2013 (calm, clear weather, high tide) by deploying acoustic transmitters similar to those used in the study at 3 and 5 m depth and at increasing distance to the receiver in steps of 50 m. Maximum detection range was 350 m at both depths. The detectability at acoustic monitoring arrays H1 and H2 (Fig. 1) were further investigated by controlling if any *S. trutta* had passed the array without being registered. Here, all the individuals were registered at the investigated arrays prior to first registration outside the arrays, indicating that the arrays successfully detected passing *S. trutta*.

DATA FILTERING

Salmo trutta depths could only be recorded when a tagged individual was within the range of an acoustic receiver. Before use, the depth sensing acoustic tags were tested at water surface and at 5 m depth. The results indicated that there was no need for subsequent calibration of the recorded depth data. The 42 *S. trutta* generated 1 161 998 valid detections during the study. In addition, there were 1137 registrations containing false transmitter identifications (ID), which were discarded. Two *S. trutta* were never recorded. As 136 821 (12%) of the registrations were suspected to be from either dead *S. trutta* or a shed tag (Thorstad *et al.*, 2013), these registrations were excluded from analyses. A data filter was added to the data from the two receivers in the mouth of the River Sjøa and the three innermost receivers in Snillfjord, because these receivers contained higher frequencies of false detections, probably due to code collisions when a large number of tagged *S. trutta* were within the receiver range simultaneously. The data filter required at least two registrations from a tagged individual within a time span of 10 min to accept the registrations, which excluded an additional 16 881 (1.5%) of the registrations from analyses.

DEFINING HABITAT AT RECEIVER LOCATIONS

The habitat at each receiver (*i.e.* the area within its range) was categorized as either estuarine, near shore without steep cliffs, near shore with steep cliffs or pelagic habitat (Fig. 1). Receivers deployed near river mouths in the fjord were highly influenced by the freshwater outflow and categorized as estuarine habitat. Receivers deployed near shore (<200 m), or in areas with shallow water (<15 m depth), were defined as near-shore habitat without steep cliffs. Receivers deployed over deep water with steep cliffs, but no shallow areas, along the shoreline were described as near-shore habitat with steep cliffs. Finally, receivers deployed over deep water, >600 m from the shore and without shallow areas (<15 m depth) within the receiver range were defined as pelagic habitat.

DATA ANALYSES

Analyses of swimming depth during summer for *S. trutta* tagged at the River Snilldalselva covered the period 1 May–1 October 2013 and for *S. trutta* tagged at the River Sjøa from tagging (3–12 May) until 1 October 2013. Analyses of swimming depth during winter covered the periods 1 November–1 December 2013 and 6 February–1 March 2014 (acoustic receivers were not deployed during 4 December 2013–6 February 2014). To distinguish between summer and winter residence at sea, data from October were not included because some individuals were showing transitional behaviour and only spent a few days at sea, probably due to spawning. Swimming depths were compared among habitats and between day and night. Day time was defined as the time between sunrise and sunset using the calculator of the Astronomical Applications Department of the US Naval Observatory (aa.usno.navy.mil) for the coordinates 63° 22' 00.0" N; 9° 13' 00.0" E. Night was defined as the time between sunset and sunrise.

All statistical analyses were conducted using R Studio 1.0.44 (RStudio Team, 2015). For analysis of factors influencing the swimming depth of *S. trutta* during summer, a mixed-effect model was constructed using the lme function in the R package lme (Pinheiro *et al.*, 2017), where *S. trutta* ID was assigned as a random factor. The initial global model included log-transformed swimming depth as the response variable, habitat, body length, month during summer, water temperature and time of day (day *v.* night) as fixed effects, as well as fish ID as a random effect. Akaike's information criterion was used to identify the best fitting model using the dredge function in the R package MuMin (Barton, 2013). The function cor.test in R was used to evaluate whether *S. trutta* L_T correlated with the individual difference in swimming depth between day and night. For analysis of difference in means between two groups, paired *t*-tests were conducted assuming unequal variance between groups. For non-normally distributed data, paired Mann–Whitney *U*-tests were applied for comparisons of two groups. To test for differences in swimming depth among habitats, Tukey's HSD (R-package Multcomp; Hothorn *et al.*, 2008) tests were conducted on a mixed-effects model (lme function in the R package lme; Pinheiro *et al.*, 2017) including log-transformed swimming depth as response variable, habitat as fixed effect and fish ID as random effect. Individual mean values were used to calculate the population mean values in order to keep the data points independent.

The proportions of detections at different depths were compared between the littoral and pelagic habitat during summer. Individual daily movement activity within habitats during day and night, hereafter referred to as vertical movement activity (VMA), was investigated by calculating individual standard deviation values from daily mean swimming depth. VMA values generated from <10 registrations were excluded from further analyses. To test for significant differences in VMA among habitats and between day and night, Tukey's HSD (R-package Multcomp; Hothorn *et al.*, 2008) were conducted on a mixed-effect model (lme function in the R package lme; Pinheiro *et al.*, 2017) including daily s.d. of individual swimming depth as the response variable, Julian day, habitat and time of day (day *v.* night) as fixed effects and fish ID as a random effect. In order to account for data heterogeneity, a combination of variance structures was added to the model (varComb function in the R package lme; Pinheiro *et al.*, 2017), combining the varConstPower for Julian day and the varIdent function for habitat. The data and residuals of the models and groups in the statistical tests were visually inspected to check for assumption violations.

RESULTS

Mean daily water temperature during summer at 1 m depth in the outer part of the study area was similar to or slightly lower than that in the inner parts of both Hemnfjord and Snillfjord (Table I). Water temperatures increased towards the end of July and thereafter declined (Fig. 2). Salinities at 1 m depth during summer were brackish in both the outer study area and in the inner parts of Hemnfjord and Snillfjord (Table I). The water column temperature and salinity in the central Hemnfjord were relatively stable from 0 to 15 m depth in both April (5° C; salinity 33) and August (13° C; salinity 34–37, Fig. 3).

TABLE I. Temperature and salinity measured by data loggers at 1 m depth during study of *Salmo trutta* in the inner parts of Hemnfjord, inner parts of Snillfjord and in outer parts of the study area (Fig. 1) during May–September 2013, November 2013 and February 2014

| | Temperature (°C) | | Salinity Mean \pm s.d. |
|----------------------------|------------------|----------|-----------------------------|
| | Mean \pm s.d. | Range | |
| May–September 2013 | | | |
| Inner parts of Hemnfjord | 13.4 \pm 2.9 | 4.8–18.3 | 26 \pm 7 |
| Inner parts of Snillfjord | 12.9 \pm 3.0 | 5.3–17.9 | 24 \pm 5 |
| Outer areas | 12.6 \pm 2.5 | 5.1–16.2 | 21 \pm 2 |
| November 2013 | | | |
| Inner parts of Hemnfjord | 9.3 \pm 0.6 | 6.7–10.8 | 31 \pm 2 |
| Inner parts of Snillfjord | 8.0 \pm 2.3 | 2.0–10.8 | 16 \pm 7 |
| Outer areas | 8.8 \pm 0.8 | 6.1–10.2 | 24 \pm 1 |
| February 2014 ^a | | | |
| Inner parts of Hemnfjord | 6.9 \pm 0.3 | 5.8–7.7 | 35 \pm 0 |

^a4 February to 1 March.

The temperature at 1 m depth during November was similar in the different fjord areas. The water was less saline in the inner parts of Snillfjord, than the other areas during November (Table I). The mean water temperature at 1 m depth in the inner parts of Hemnfjord was 6.9° C and was close to full saline sea water during 4 February–1 March (Table I). Temperature and salinity were not recorded at the outer site and in Snillfjord in February due to logistical constraints.

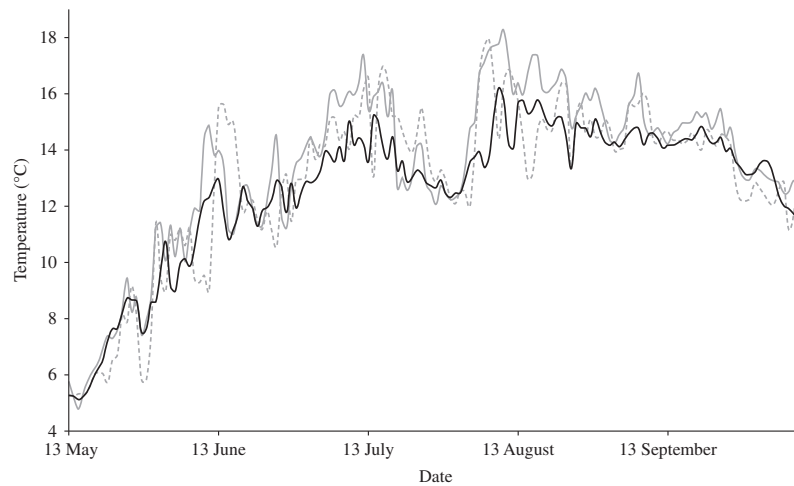


Fig. 2. Mean daily water temperatures at 1 m depth in the inner part of Hemnfjord (—), inner part of Snillfjord (---) and outer part of the study area (.....) in the period 1 May 2013–1 October 2013.

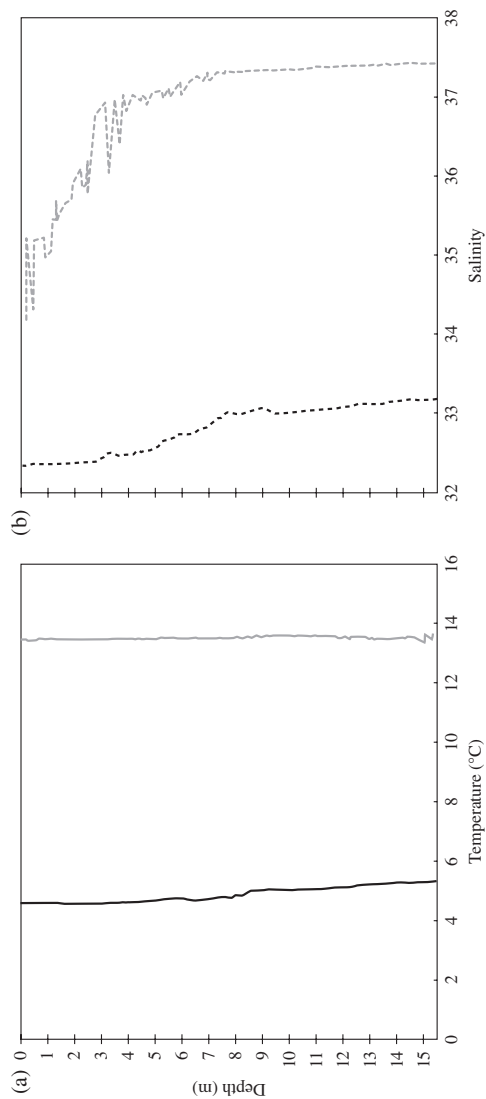


FIG. 3. (a) Temperature and (b) salinity at 0–15 m depth in central areas of Hemnfjord and Smilfjord on 18 April 2013 (—) and 22 August 2013 (---).

TABLE II. Model selection for estimating the determinants of the swimming depth of *Salmo trutta* during summer.^a

| Model | AIC | Δ AIC | AIC weights | d.f. |
|--------------------------|---------|--------------|-------------|------|
| [<i>D, H, M, L, T</i>] | 1643565 | 0 | 0.998 | 11 |
| [<i>D, H, M, T</i>] | 1643577 | 12.31 | 0.002 | 10 |
| [<i>D, H, M, L</i>] | 1651227 | 7662.29 | 0 | 10 |
| [<i>D, H, M</i>] | 1651241 | 7676.01 | 0 | 9 |
| [] | 1981745 | 338 180.32 | 0 | 3 |

^aThe models estimate the relative contributions to the swimming depth from the variables time of day (day v. night, *D*), habitat (*H*), month during summer (*M*), body length (*L*) and water temperature (*T*). AIC is the score based on Akaike's information criterion.

The four best mixed effect models all indicated that the swimming depth of *S. trutta* during summer was influenced by habitat, time of day (day v. night) and month, while the best model (marginal $R^2_{GLMM} = 0.37$, $P < 0.001$) also included water temperature and L_T as explanatory variables (Tables II and III). Mean swimming depth for all *S. trutta* in all habitat types during summer was 1.7 m (s.d. = 1.3, range of individual means = 0.4–6.4). The deepest depths recorded for the different individuals varied between 4.6 m and 24.0 m (mean of deepest recordings from all individuals 14.1 m, s.d. = 4.9). In the near-shore habitat without steep cliffs, *S. trutta* moved progressively deeper from May until August, but thereafter moved closer to the surface again. The number of *S. trutta* recorded in the pelagic and the near-shore habitat with steep cliffs, however, was low from June to September (Fig. 4). The *S. trutta* resided slightly deeper during day than at night within all types of marine habitats ($P < 0.05$; Table IV and Fig. 5). L_T did not correlate with the swimming depth difference between day and night (Pearson's correlation = 0.08, $n = 40$, $P > 0.05$).

The Tukey HSD *post hoc* test on the mixed-effect model of swimming depth revealed that the *S. trutta* had greater swimming depth in both near-shore habitat without (mean = 2.0, s.d. = 1.5, range = 0.4–6.7 m), and with steep cliffs (mean = 2.5, s.d. = 1.6, range = 0.3–7.1 m), compared with the estuarine habitat (mean = 0.9, s.d. = 0.5, range = 0.4–2.6 m, $P < 0.001$). The Tukey HSD *post hoc* test also showed that *S. trutta* were recorded deeper in both the near-shore habitat without steep cliffs and the near-shore habitat with steep cliffs compared with the pelagic habitat (mean = 1.2, s.d. = 1.1, range = 0.1–4.9 m, $P < 0.001$). Finally, the Tukey HSD *post hoc* test revealed that swimming depths of *S. trutta* were greater in the pelagic habitat than in the estuarine habitat ($P < 0.001$) and deeper in the near-shore habitat with steep cliffs compared with near-shore habitat without steep cliffs ($P < 0.001$).

The depth distribution of individual registrations varied between habitats (Table V). Vertical movements were generally larger during day than night ($P < 0.001$; Table VI). The Tukey HSD *post hoc* tests on the mixed effect VMA model (Table III) revealed that the VMA were greater in the near-shore habitats compared with the estuarine and pelagic habitats during day ($P < 0.01$). Similarly, the Tukey HSD *post hoc* tests showed that the VMA were greater in the near-shore habitat without steep cliffs compared with the estuarine and pelagic habitat ($P < 0.001$) and greater in the near-shore habitat with cliffs compared with the pelagic habitat ($P < 0.05$) during night.

TABLE III. Summary of intercept and fixed effects from mixed effect models on swimming depth of *Salmo trutta* during summer (\log_{10} -transformed) and vertical movement activity (VMA)

| Model | Effect | Estimate (95% C.I.) | <i>t</i> | d.f. | <i>P</i> | |
|------------------------------------|------------------------------------|----------------------|----------------------|--------|----------|--------|
| Swimming depth during summer | (Intercept) | 0.53 (0.41, 0.65) | 8.91 | 825266 | <0.001 | |
| | Habitat: Estuary | -0.73 (-0.75, -0.71) | -68.58 | 825266 | <0.001 | |
| | Habitat: Near shore without cliffs | -0.03 (-0.05, -0.01) | -3.22 | 825266 | <0.05 | |
| | Habitat: Pelagic | -0.44 (-0.47, -0.41) | -29.49 | 825266 | <0.001 | |
| | Body length | 0.18 (0.10, 0.27) | 4.37 | 38 | <0.001 | |
| | Month: May | -0.70 (-0.71, -0.70) | -165.66 | 825266 | <0.001 | |
| | Month: June | -0.50 (-0.50, -0.50) | -182.7 | 825266 | <0.001 | |
| | Month: July | -0.11 (-0.11, -0.10) | -41.63 | 825266 | <0.001 | |
| | Month: September | -0.24 (-0.24, -0.23) | -90.97 | 825266 | <0.001 | |
| | Water temperature | 0.14 (0.13, 0.14) | 87.3 | 825266 | <0.001 | |
| | Time of day: Night | -0.36 (-0.37, -0.36) | -220.53 | 825266 | <0.001 | |
| | VMA | (Intercept) | 0.72 (0.52, 0.92) | 7.08 | 5137 | <0.001 |
| | | Julian Day | 0.00 (0.00, 0.00) | 13.15 | 5137 | <0.001 |
| | | Habitat: Estuary | -0.39 (-0.58, -0.20) | -4.09 | 5137 | <0.001 |
| Habitat: Near shore without cliffs | | -0.04 (-0.23, 0.14) | -4.46 | 5137 | >0.05 | |
| Habitat: Pelagic | | -0.13 (-0.41, 0.16) | -0.88 | 5137 | >0.05 | |
| Time of day: Night | | -0.16 (-0.18, -0.14) | -16.69 | 5137 | <0.001 | |

Six individuals were recorded at near-shore or river mouth receivers in the innermost parts of Hemnfjord (two individuals) and Snillfjord (four individuals) during winter. Despite winter temperatures, the fjord was not ice covered. Mean individual swimming depth was 1.3 m (s.d. = 0.5, range 0.5–1.9). The deepest depths recorded during winter for these individuals varied between 9.7 m and 34.2 m (mean of deepest recordings 20.9 m, s.d. = 9.5). The *S. trutta* had greater individual mean swimming depth during day (mean = 2.0 m, s.d. = 0.6 m, range 1.3–2.9 m) than at night (mean = 1.0 m, s.d. = 0.5 m, range 0.3–1.7 m) also during the winter period (Paired *t*-test, $t > 0.05$, d.f. = 5, $P < 0.001$).

DISCUSSION

Swimming depths of *S. trutta* individuals in this study were generally surface oriented, but influenced by habitat (estuary, pelagic, near shore with or without steep cliffs), time of day (day *v.* night), month of summer, water temperature and *S. trutta* size. *Salmo trutta* had deeper swimming depths in near-shore areas compared with pelagic areas. The swimming depth in estuaries was shallower than in other habitats, possibly influenced by the shallow nature of these areas. The *S. trutta* followed in winter showed similar depth-use patterns in the winter as during the summer, but it should be noted that the number of tagged individuals detected at sea during winter was low. The surface-orientation of *S. trutta* in this study is similar to that observed for electronically

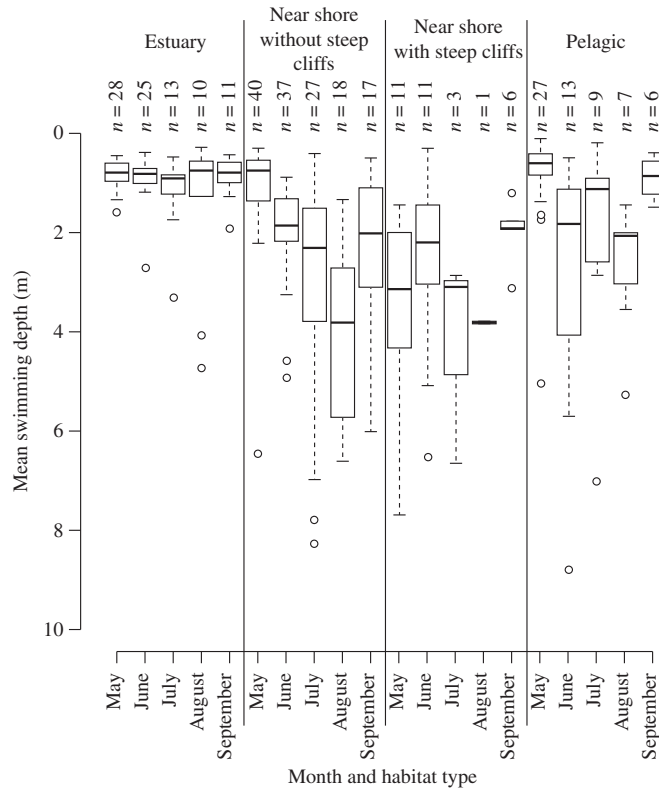


Fig. 4. Monthly average *Salmo trutta* swimming depth in estuarine habitat, near shore habitat without steep cliffs, near shore habitat with steep cliffs and pelagic habitat during summer (1 May–1 October 2013). The box-and-whisker plots show median values (—), the interquartile ranges (box) and the 5th and 95th percentiles (whiskers) and outliers (O).

tagged, free-ranging wild *S. trutta* in previous studies. Rikardsen *et al.* (2007) found that *S. trutta* stayed close to the surface in the Alta fjord in northern Norway, recording a mean swimming depth of 1.8 m (eight *S. trutta* tagged with data storage tags). Gjelland *et al.* (2014) observed that *S. trutta* infested with salmon lice (*L. salmonis*) were mainly recorded between 1 and 3 m depth in the Etnefjord, south-western Norway. The present study confirms that this surface orientation is exhibited by the species across a range of different marine habitat types and remains consistent across seasons.

Salmo trutta are vulnerable to infestation with salmon lice because of their surface-oriented behaviour, which overlaps with the distribution of salmon lice larvae (Heuch *et al.*, 1995; á Norði *et al.*, 2016). On the other hand, in coastal areas with a surface layer of fresh water, owing to high influx of fresh water from rivers, *S. trutta* may be protected against salmon lice due to their surface orientation, because

TABLE IV. Difference in mean swimming depth of *Salmo trutta* between day and night when recorded in various marine habitats (based on individual mean values) in summer (1 May–1 October 2013)^a

| Habitat | Mean swimming depth (m) | | | W | P |
|---------------------------------|-------------------------|-------|------------|-----|--------|
| | Day | Night | Difference | | |
| Estuary | 1.0 | 0.7 | 0.3 | 399 | <0.001 |
| Near shore without steep cliffs | 2.1 | 1.3 | 0.8 | 805 | <0.001 |
| Near shore with steep cliffs | 2.7 | 1.7 | 1.0 | 45 | <0.05 |
| Pelagic | 1.3 | 0.8 | 0.5 | 257 | <0.05 |
| Total marine | 1.9 | 1.2 | 0.7 | 794 | <0.001 |

^aPaired Mann–Whitney *U*-test *P*-values describe level of statistical significance between the swimming depths during day and night.

salmon lice do not cope well with freshwater and brackish water (Wootten *et al.*, 1982; Johnson & Albright, 1991; Bricknell *et al.*, 2006). The local *S. salar* farmers reported varying salmon lice concentrations in the pens during the study period, indicating that the *S. trutta* individuals probably experienced variable lice infection pressure depending on their spatial and temporal use of the marine habitat. Salmon lice infestation was earlier been found to alter the marine behaviour of *S. trutta* regarding timing of return

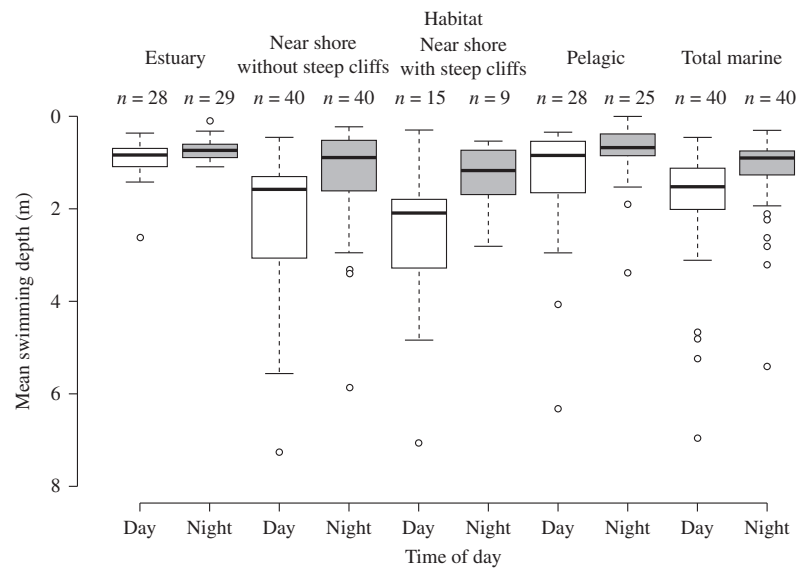


FIG. 5. Individual *Salmo trutta* mean swimming depth in different habitats during day (□) and night (■) during summer (1 May–1 October 2013). The box-and-whisker plots show median values (—), the interquartile ranges (boxes) and the 5th and 95th percentiles (whiskers) and outliers (○).

TABLE V. Frequency distribution (%) of the registrations at different depths (m) from the surface for tagged individual *Salmo trutta* (*n*) when residing in different habitats during summer (1 May–1 October 2013)

| Depth (m) | | Estuarine | Near-shore | Near shore | Pelagic |
|-----------|-------|-----------------------------|--|---|-----------------------------|
| | | habitat (<i>n</i> = 29) | habitat without steep cliffs (<i>n</i> = 40) | habitat with steep cliffs (<i>n</i> = 15) | habitat (<i>n</i> = 28) |
| 0–0.5 | Mean | 8 | 10 | 7 | 19 |
| | Range | 0–47 | 0–46 | 0–71 | 0–78 |
| 0.5–1.5 | Mean | 76 | 42 | 22 | 57 |
| | Range | 41–96 | 1–70 | 0–62 | 13–100 |
| 1.5–3.0 | Mean | 14 | 25 | 42 | 14 |
| | Range | 2–46 | 0–48 | 6–88 | 0–62 |
| 3.0–5.0 | Mean | 1 | 12 | 14 | 4 |
| | Range | 0–13 | 0–52 | 0–50 | 0–28 |
| 5.0–10.0 | Mean | 1 | 9 | 13 | 4 |
| | Range | 0–20 | 0–87 | 0–78 | 0–33 |
| >10 | Mean | 0 | 1 | 1 | 1 |
| | Range | 0–3 | 0–19 | 0–6 | 0–13 |

to estuaries and rivers (Birkeland, 1996; Bjørn *et al.*, 2001; Gjelland *et al.*, 2014). Furthermore, Bui *et al.* (2016) found that farmed *S. salar* in salmon pens altered their swimming depth in response to high infestation rates of salmon lice. It remains unknown, however, whether depth distributions of *S. trutta* individuals observed in the

TABLE VI. Vertical movement activity (VMA) of tagged *Salmo trutta* when recorded in different habitats during day and night.^a

| Habitat | Time of day | | | | Paired Mann–Whitney <i>U</i> -test | | | | |
|---------------------------------------|-------------|--------------|-------------|--------------|---|----------|-----------------------|-----------------------|----------|
| | Day | | Night | | Hypothesis (<i>H</i> ₀) | <i>W</i> | <i>n</i> ₁ | <i>n</i> ₂ | <i>P</i> |
| | Mean (m) | Range (m) | Mean (m) | Range (m) | | | | | |
| Estuary | 0.4 | 0.2–1.3 | 0.2 | 0.0–0.7 | VMA day ≤ VMA night | 369 | 29 | 28 | <0.001 |
| Near shore without steep cliffs | 0.8 | 0.3–1.8 | 0.4 | 0.1–1.0 | VMA day ≤ VMA night | 814 | 40 | 40 | <0.001 |
| Near shore with steep cliffs | 0.9 | 0.4–1.3 | 0.4 | 0.2–0.6 | VMA day ≤ VMA night | 45 | 15 | 9 | <0.001 |
| Pelagic | 0.5 | 0.0–1.6 | 0.2 | 0.0–0.6 | VMA day ≤ VMA night | 186 | 27 | 21 | <0.001 |

^aPaired Mann–Whitney *U*-test statistics describe differences in VMA of *S. trutta* during day and night.

current study were in whole or in part a response to salmon lice infestation, as their actual infection rates could not be documented.

Despite the statistical significance of the diel movements of *S. trutta* observed in this study, the biological significance of these movements is unclear since the difference in swimming depth between day and night was not large (1 m or less). The small difference in depth use between day and night could be explained by the minor differences in light between day and night during mid-summer due to the bright summer nights at the latitude of the study area. The small-scale difference in depth use between day and night, however, was consistent among seasons, suggesting it is a general pattern rather than resulting from summer light conditions in the study area.

Vertical day–night movements are common in many aquatic taxa (Hays, 2003). The phenomenon is thought to be governed by light (Appenzeller & Leggett, 1995) and earlier studies have suggested that such migratory behaviour might be triggered by body temperature regulative behaviour, feeding activity and anti-predator behaviour (Clark & Levy, 1988). Diel vertical movement patterns have previously been recorded by Davidsen *et al.* (2008) for *S. salar* post-smolt and they suggested that the observed vertical movement was a result of a trade-off between avoiding predation by avian and marine predators, feeding or osmoregulatory advantages. This might also be the case for the *S. trutta* in the present study. As the size of the veteran *S. trutta* tagged in the present study was larger than post-smolt of *S. salar*, the tagged individuals in the present study might have shown less anti-predator behaviour than the *S. salar* post-smolt in the study by Davidsen *et al.* (2008). No effect of body size on diurnal changes in swimming depth was found. This may suggest that although large individuals are less prone to predation than smaller ones, predation still has highly undesirable effects on individual fitness and that antipredator behaviour therefore may be a basic instinct that remains active through all *S. trutta* life stages.

Pemberton (1976) investigated the diel feeding of *S. trutta* and found increased intake of mid-water and surface prey and a decrease in benthic prey during the night. They suggested that *S. trutta* were more likely to detect prey that were above the substratum or at the surface at night and that there could be varying conspicuousness of littoral prey between day and night. In the present study, an increased variability in depths used during day compared with at night was observed, possibly reflecting episodic benthic feeding activity, at least in the near-shore and estuary habitats. Hence, the difference between day and night in the present study might partly be explained by a shift in prey type and be linked to changes in the detectability of the different prey.

The increased swimming depth from May towards August coincided with an increase in water temperature. Rikardsen *et al.* (2007) observed similar patterns in the Altafjord in northern Norway, where *S. trutta* progressively resided in deeper water as temperatures increased during the month of June. It might be suggested that *S. trutta* actively regulated their ambient temperature by seeking water layers of preferred temperatures, as earlier suggested by Rikardsen *et al.* (2007) and Jensen *et al.* (2014). Jensen *et al.* (2014) suggested that *S. trutta* actively sought out the warmest areas in the fjord. In contrast, *S. trutta* in the present study tended to reside deeper when the temperature increased, suggesting that they moved into colder water during the warmest periods in summer. The study of Jensen *et al.* (2014) was performed in the northern portion of the species range in an area with lower sea temperatures, which may explain the species differences between the two sites. The warmest temperatures (16 and 18° C) recorded

at 1 m depth in this study were in the outer part of the study area and in the inner parts of both Hemnfjord and Snillfjord, respectively.

Rikardsen *et al.* (2007) reported that individual mean ambient temperatures for *S. trutta* in the Alta Fjord in June and July ranged between 12 and 13°C. Another possible reason for the deeper swimming towards late summer might be a shift in prey type, or that the prey also moved deeper due to changing water temperatures. Stomach analyses of *S. trutta* caught in previous studies showed that polychaetes and marine crustaceans were important early in the season, while fishes were more important during late summer (Knutsen *et al.*, 2001; Rikardsen *et al.*, 2006). This may suggest that prey type varies with seasonal changes in prey availability and potentially explain the difference in swimming depth over the summer.

In conclusion, *S. trutta* were surface-oriented during their marine migration, both during summer and also in winter. Body size influenced the depth use of *S. trutta* during summer. Body size also influenced horizontal movements of the same individuals, showing that individual morphology and life history influenced the marine behaviour of *S. trutta* (Eldøy *et al.*, 2015). Slight differences in depth use among individuals and habitats, between day and night, as well as during the summer season, were observed. These are clearly important to the animals, but the biological significance of these small changes are at present unclear. Water temperature was positively correlated with swimming depth, which might suggest that *S. trutta* actively adjusted their body temperature by seeking preferred ambient temperatures. Collectively, the present study and that of Eldøy *et al.* (2015) illustrate that *S. trutta* utilize coastal water bodies commonly influenced by anthropogenic factors such as aquaculture, harbours and marine constructions, marine renewable energy production or other human activity. This suggests that the effects from anthropogenic factors may vary both among *S. trutta* populations and among individuals within a population according to their temporal and spatial movements in marine coastal areas. Behavioural differences among populations are thus important to account for when assessing the effects of human activities in the coastal zone and when introducing fishing regulations for *S. trutta* and for fisheries where *S. trutta* might be captured as bycatch.

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Paper III



Individual Repeatability in Marine Migratory Behavior: A Multi-Population Assessment of Anadromous Brown Trout Tracked Through Consecutive Feeding Migrations

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Trout Tracked Through Consecutive
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Despite that the study of individual repeatability is a common topic in behavioral ecology, virtually nothing is known about inter-annual variability in the marine migratory behavior of iteroparous salmonids that can complete multiple feeding migrations in their lifespan. Behavioral data from 38 anadromous brown trout (*Salmo trutta*), tracked by acoustic telemetry in 2–3 consecutive marine feeding migrations in two Norwegian fjord systems, were analyzed for intra-individual repeatability in key aspects of their marine migration. Individual brown trout displayed significant inter-annual consistency in marine area use and in the timing of marine exit (i.e. when they returned to spawning rivers), but not in the timing of marine entry or the time spent in the marine environment each year. Our study raises new questions about how anadromous brown trout respond to changing conditions and anthropogenic factors in the marine environment. Intra-individual repeatability of brown trout linked to changing environmental conditions should therefore be a focus for future studies.

Keywords: behavioral repeatability, habitat use, marine migration, migratory timing, *Salmo trutta*, sea trout, migratory continuum

INTRODUCTION

The post-spawning feeding migrations of iteroparous fish species have evolved to allow nutritionally depleted individuals the opportunity to exploit richer feeding habitats in an effort to precondition for future reproductive events. Needless to say, the mechanisms and patterns of migration can vary widely both within and among populations, as may the degree of individual flexibility and/or repeatability of migratory behavior in response to environmental fluctuations. Behavioral repeatability has been documented in various taxa (Bell et al., 2009), including species and populations of birds, mammals, and fish (e.g., Dias et al., 2010; Lea et al., 2015; Müller et al., 2015; Leclerc et al., 2016). For predatory fish feeding in the marine habitat, the availability, and distribution of resources in the marine environment can vary between years (Dragesund et al., 1997; Rikardsen and Amundsen, 2005), which should favor flexibility in traits like migration timing, distance, and duration of residency in various habitats if the organisms have reliable cues from the environment to adjust their behavior in response to the environmental changes (Reed et al., 2010).

The Salmonidae is a family of freshwater spawning fishes, where several of its species initiate feeding migrations to the marine environment (Pavlov and Savvaitova, 2008). Among these, brown trout *Salmo trutta* is a widely distributed, facultatively anadromous species known to display a continuum of migratory strategies ranging from freshwater residency and potamodromy to estuarine, short and long-distance marine migrations, both among and within populations (Cucherousset et al., 2005; Boel et al., 2014; del Villar-Guerra et al., 2014; Eldøy et al., 2015; Flaten et al., 2016; Bordeleau et al., 2018). As an iteroparous species, anadromous brown trout can undertake multiple annual marine feeding migrations during its lifetime (L'Abée-Lund et al., 1989; Thorstad et al., 2016), where the freshwater residency between marine migratory seasons is usually characterized by spawning and overwintering with opportunistic feeding (Davidsen et al., 2017) that have limited importance for somatic growth (Knutsen et al., 2001). While the drivers of the brown trout migratory continuum have remained somewhat mysterious, growing scientific evidence indicates a role of individual physiological and nutritional state, metabolic rate, and food availability (Olsson et al., 2006; Wysujack et al., 2009; Davidsen et al., 2014; Eldøy et al., 2015; Bordeleau et al., 2018). Despite high inter-individual variability in migratory behavior, the degree of intra-individual behavioral flexibility to changing environments and its consequences in terms of growth, survival, and ultimate fitness remain obscure. Beyond the role of environmental variability, the migratory behavior of anadromous brown trout can be influenced by anthropogenic impacts on coastal waterways, such as marine traffic, harbors and other near-shore infrastructure, renewable energy production, fisheries, and aquaculture (Thorstad et al., 2016; Aldvén and Davidsen, 2017). Importantly, recent work using acoustic telemetry has documented inter-annual shifts in the marine habitat use of different groups of anadromous brown trout in response to aquaculture-associated salmon lice abundances (Halttunen et al., 2018). However, due to logistical constraints imposed by battery life of acoustic transmitters, and relatively high mortality between spawning events (Fleming and Reynolds, 2004), no previous studies have yet assessed the inter-annual flexibility in the marine migrations of brown trout tracked through multiple years.

In order to investigate the degree of variation in behavior of brown trout individuals between consecutive marine feeding seasons, we extracted behavioral (movement) data from trout tagged in acoustic telemetry studies in two Norwegian fjord systems between 2012 and 2017 (e.g., Eldøy et al., 2015; Bordeleau et al., 2018). Studies of migratory species in various taxa have shown that individuals can exhibit both consistency and repeatability in behavior (Bell et al., 2009). Given the lack of previous studies on intra-individual repeatability in annual marine migratory behavior for salmonids, we chose not to make *a priori* predictions from specific hypotheses. Instead, we explored this unique dataset to investigate whether key behavioral aspects of the intra-individual marine behavior of anadromous brown trout was repeated among years. Specifically, we analyzed the degree of annual intra-individual behavioral repeatability in terms of (i) spatial dispersal, (ii) migratory timing, and (iii) duration of marine residency.

MATERIALS AND METHODS

Study Area

The study was conducted in two fjord systems in central and northern parts of Norway (Figure 1). The Hemnfjord system consists of two interconnected fjords with more than 60 km² surface area and about 65 km of shoreline and is connected to the open sea by a 36 km long strait (Figure 1, Eldøy et al., 2015). The Tosenfjord system consist of two interconnected fjords with about 150 km² surface area and more than 270 km of shore line, connected to the open sea by a 15 km long strait (Figure 1). Several watercourses with partially anadromous populations of brown trout drain into both fjord systems. The Hemnfjord study area is described in detail by Eldøy et al. (2015, 2017) and Flaten et al. (2016), while the Tosenfjord study area is described by Bordeleau et al. (2018).

Environmental Variables

Both fjord systems had aquaculture facilities with farmed salmon in open net pens during the study periods. Sea temperature and salmon lice count data from the salmon farms was downloaded from the Norwegian Fish Health Database (www.barentswatch.no), and all available recordings from marine aquaculture locations in the two fjord systems were combined. Data on sea temperatures and salmon lice counts (here shown as counts of all life stages combined) in the farms located within each fjord system revealed seasonal and annual variations in both temperature (Figure 2) and salmon lice infestation levels (Figure 3).

Acoustic Tracking

In the Sjøa watercourse in Hemnfjord, a total of 100 brown trout were tagged in freshwater or in the estuary and tracked with acoustic receiver arrays in the fjord system in 2012–2014 (Figure 1). In Tosenfjord, a total of 274 brown trout were tagged in freshwater and estuaries of River Åbjøra and Urvold watercourse and tracked with acoustic receiver arrays in the fjord during 2015–2017 (Figure 1). In general, anadromous brown trout in the two fjord systems migrate to sea each summer for feeding and return again to freshwater for spawning and/or overwintering during late summer (Eldøy et al., 2015; Bordeleau et al., 2018). The fish were either tagged during spring after spawning and prior to their marine migration, or in the autumn prior to potential spawning. For fish tagged during autumn, the tracking started at their outwards migration during the following spring. All fish included in this study were tagged following the same protocol. The fish were captured by rod fishing or gillnets that were continuously monitored and kept in holding nets for up to 4 h prior to tagging. The fish were sedated using 2-phenoxy ethanol for 4 min prior to making a 2 cm incision in the body cavity and inserting the sterilized acoustic tag. The incision was closed by 2–3 sutures, before the fish were placed in a recovery tank for up to 15 min and subsequently released at the site of tagging. The expected battery lifetime of the acoustic tags ranged from 15 to 24 months (Table 1). See Eldøy et al. (2015) and Bordeleau et al. (2018) for further details. Arrays of acoustic receivers (Vemco Inc., Canada models VR2, VR2W, and

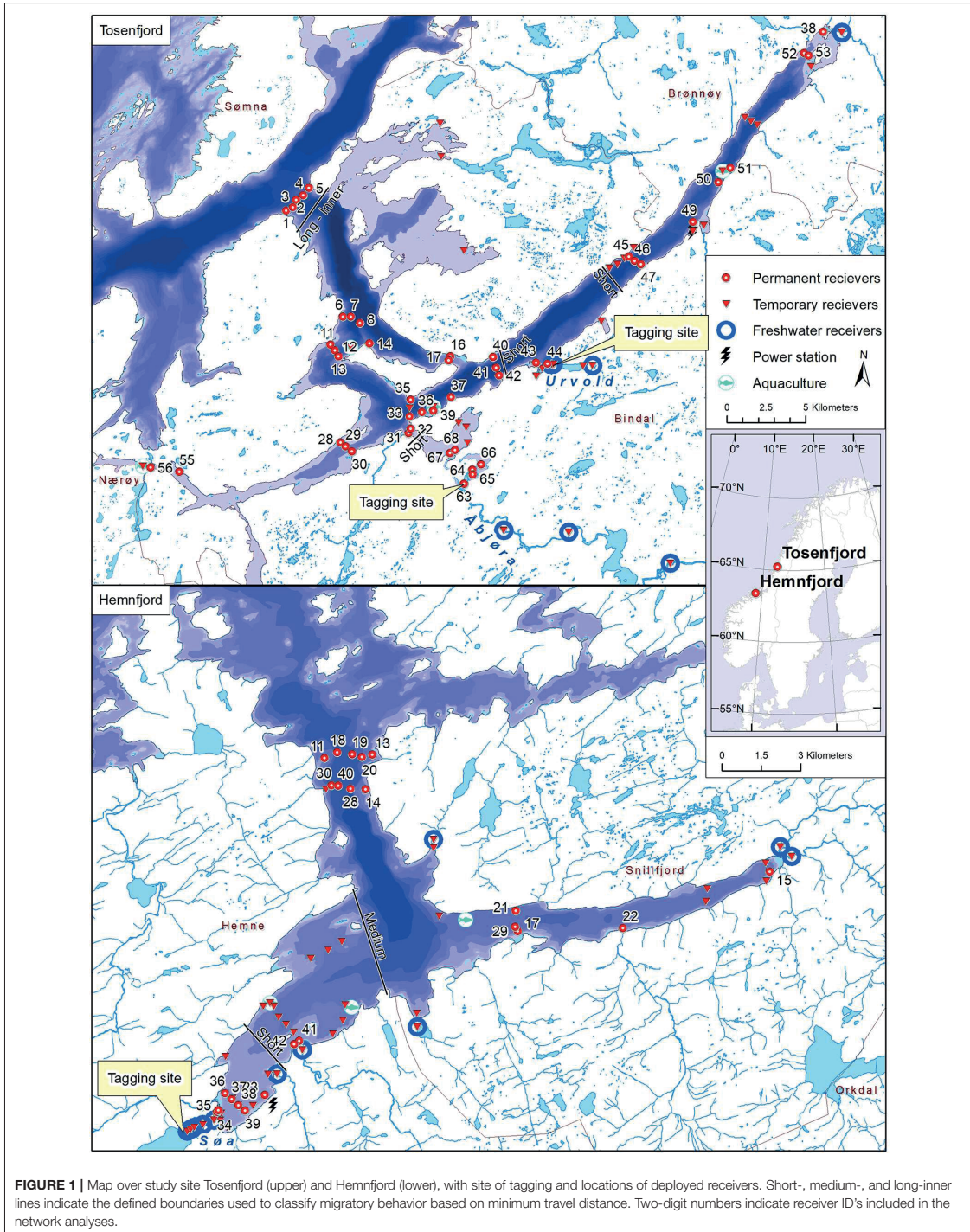


FIGURE 1 | Map over study site Tosenfjord (upper) and Hemnfjord (lower), with site of tagging and locations of deployed receivers. Short-, medium-, and long-inner lines indicate the defined boundaries used to classify migratory behavior based on minimum travel distance. Two-digit numbers indicate receiver ID's included in the network analyses.

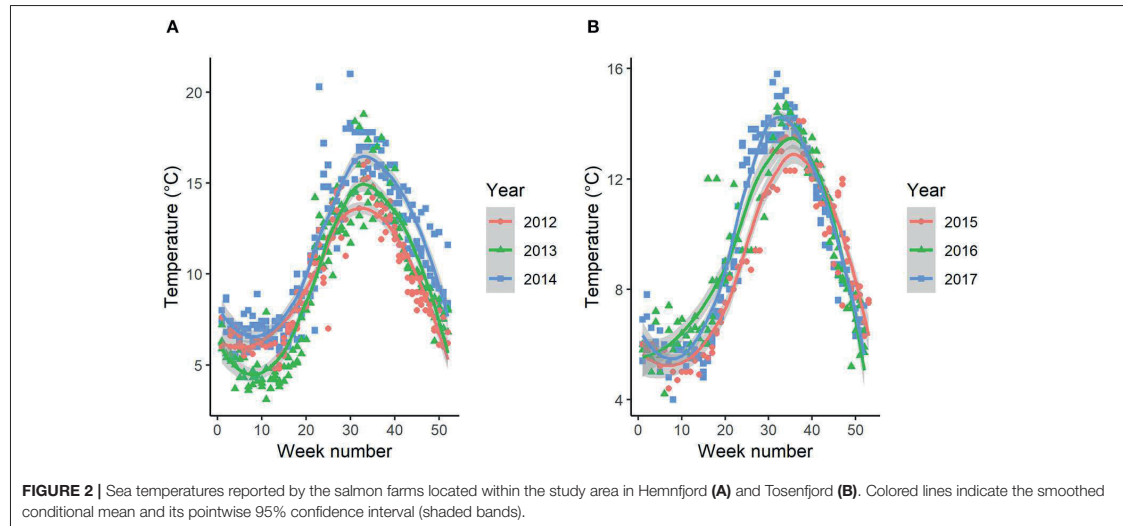


FIGURE 2 | Sea temperatures reported by the salmon farms located within the study area in Hemnfjord (A) and Tosenfjord (B). Colored lines indicate the smoothed conditional mean and its pointwise 95% confidence interval (shaded bands).

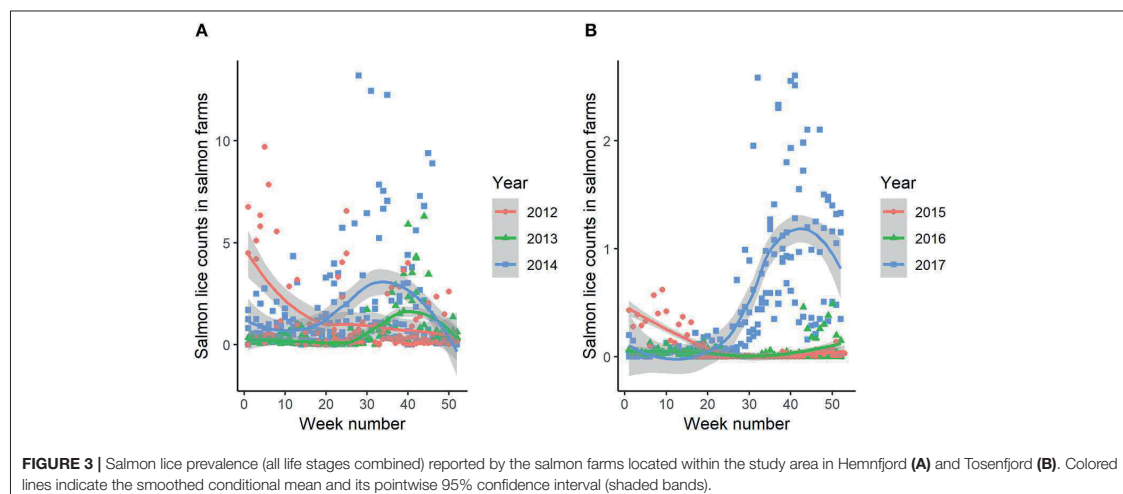


FIGURE 3 | Salmon lice prevalence (all life stages combined) reported by the salmon farms located within the study area in Hemnfjord (A) and Tosenfjord (B). Colored lines indicate the smoothed conditional mean and its pointwise 95% confidence interval (shaded bands).

VR2-AR) were deployed at various locations in both freshwater, estuaries and saltwater in the two fjord systems to map the movements of the tagged brown trout (Figure 1). In Hemnfjord, receiver ID 34 and 35 were deployed in the estuary of River Sjøa and represented the transition zone between freshwater and saltwater. In Tosenfjord, receiver ID 44 was deployed in the estuary of River Urvold and receiver ID 63–68 were deployed in the estuarine parts of River Åbjøra. See Eldøy et al. (2015) and Bordeleau et al. (2018) for further details.

Prior to statistical analyses, the tracking data was filtered for false registrations resulting from noise in the surroundings of the receivers and/or code collision of simultaneously transmission from multiple transmitters (Pincock, 2012). Receivers found to

contain frequently false detections were filtered by adding a filter that required at least two registrations within a 10-min time span to accept the registrations. The data was further visually inspected for false detections, and obviously false detections were removed prior to the statistical analyses. See Eldøy et al. (2015) and Bordeleau et al. (2018) for further details.

Data Analyses

All statistical analyses were conducted using R version 3.5.3 (R Core Team, 2019) and RStudio version 1.2.1335 (RStudio Team, 2019). Spearman's rank correlation was used to test the intra-individual correlation in migratory behavior between first and second year of tracking (Hanson et al., 2010; Taylor and

TABLE 1 | Summary of capture timing and location, body size, and tag information of tracked fish.

| Fish ID | Study site | Watercourse | Tagging date | Natural body size (mm) | Transmitter ID | Transmitter model | Estimated battery life (months) |
|---------|------------|-------------|--------------|------------------------|----------------|-----------------------------|---------------------------------|
| F01 | Hemnfjord | Sea | 2012-04-12 | 350 | A69-1206-813 | Thelmabiotel MP-9-long | 15 |
| F02 | Hemnfjord | Sea | 2012-04-12 | 350 | A69-1206-818 | Thelmabiotel MP-9-long | 15 |
| F03 | Hemnfjord | Sea | 2012-04-12 | 350 | A69-1206-820 | Thelmabiotel MP-9-long | 15 |
| F04 | Hemnfjord | Sea | 2012-04-12 | 350 | A69-1206-821 | Thelmabiotel MP-9-long | 15 |
| F05 | Hemnfjord | Sea | 2012-04-12 | 380 | A69-1206-822 | Thelmabiotel MP-9-long | 15 |
| F06 | Hemnfjord | Sea | 2012-04-13 | 360 | A69-1206-816 | Thelmabiotel MP-9-long | 15 |
| F07 | Hemnfjord | Sea | 2012-04-13 | 440 | A69-1206-825 | Thelmabiotel MP-9-long | 15 |
| F08 | Hemnfjord | Sea | 2012-04-14 | 380 | A69-1206-841 | Thelmabiotel MP-13 | 17 |
| F09 | Hemnfjord | Sea | 2012-09-17 | 430 | A69-1303-20613 | Vemco V13-1x | 20 |
| F10 | Hemnfjord | Sea | 2012-09-18 | 390 | A69-1303-20615 | Vemco V13-1x | 20 |
| F11 | Hemnfjord | Sea | 2012-09-18 | 570 | A69-1303-20618 | Vemco V13-1x | 20 |
| F12 | Hemnfjord | Sea | 2012-09-18 | 370 | A69-1303-20620 | Vemco V13-1x | 20 |
| F13 | Hemnfjord | Sea | 2012-09-18 | 470 | A69-1303-20621 | Vemco V13-1x | 20 |
| F14 | Tosenfjord | Åbjøra | 2015-04-10 | 600 | A69-1303-21 | Thelmabiotel ATID-MP-13 | 24 |
| F15 | Tosenfjord | Urvoll | 2015-04-11 | 440 | A69-1303-24 | Thelmabiotel ATID-MP-13 | 24 |
| F16 | Tosenfjord | Urvoll | 2015-04-11 | 590 | A69-1303-25 | Thelmabiotel ATID-MP-13 | 24 |
| F17 | Tosenfjord | Urvoll | 2015-04-11 | 628 | A69-1303-28 | Thelmabiotel ATID-MP-13 | 24 |
| F18 | Tosenfjord | Urvoll | 2015-05-07 | 500 | A69-1105-53 | Thelmabiotel ATT-MP-13 | 19 |
| F19 | Tosenfjord | Åbjøra | 2015-05-07 | 420 | A69-1303-23 | Thelmabiotel ATID-MP-13 | 24 |
| F20 | Tosenfjord | Urvoll | 2015-05-07 | 330 | A69-1303-6 | Thelmabiotel ATID-MP-9-LONG | 15 |
| F21 | Tosenfjord | Åbjøra | 2015-09-03 | 410 | A69-1303-304 | Thelmabiotel ATID-MP-13 | 24 |
| F22 | Tosenfjord | Urvoll | 2015-09-04 | 475 | A69-1303-301 | Thelmabiotel ATID-MP-13 | 24 |
| F23 | Tosenfjord | Urvoll | 2015-09-29 | 470 | A69-1303-339 | Thelmabiotel ATID-MP-13 | 24 |
| F24 | Tosenfjord | Urvoll | 2016-05-04 | 290 | A69-1303-474 | Thelmabiotel ATID-MP-9-LONG | 15 |
| F25 | Tosenfjord | Urvoll | 2016-05-04 | 440 | A69-1303-529 | Thelmabiotel ATID-MP-13 | 24 |
| F26 | Tosenfjord | Urvoll | 2016-05-04 | 390 | A69-1303-530 | Thelmabiotel ATID-MP-13 | 24 |
| F27 | Tosenfjord | Urvoll | 2016-05-05 | 330 | A69-1303-475 | Thelmabiotel ATID-MP-9-LONG | 15 |
| F28 | Tosenfjord | Åbjøra | 2016-05-23 | 410 | A69-1303-501 | Thelmabiotel ATID-MP-13 | 24 |
| F29 | Tosenfjord | Åbjøra | 2016-05-25 | 390 | A69-1303-524 | Thelmabiotel ATID-MP-13 | 24 |
| F30 | Tosenfjord | Åbjøra | 2016-05-25 | 410 | A69-1303-525 | Thelmabiotel ATID-MP-13 | 24 |
| F31 | Tosenfjord | Åbjøra | 2016-05-26 | 480 | A69-1303-517 | Thelmabiotel ATID-MP-13 | 24 |
| F32 | Tosenfjord | Åbjøra | 2016-05-26 | 450 | A69-1303-518 | Thelmabiotel ATID-MP-13 | 24 |
| F33 | Tosenfjord | Åbjøra | 2016-05-26 | 430 | A69-1303-519 | Thelmabiotel ATID-MP-13 | 24 |
| F34 | Tosenfjord | Urvoll | 2016-05-26 | 510 | A69-1303-522 | Thelmabiotel ATID-MP-13 | 24 |
| F35 | Tosenfjord | Urvoll | 2016-05-27 | 390 | A69-1303-515 | Thelmabiotel ATID-MP-13 | 24 |
| F36 | Tosenfjord | Urvoll | 2016-05-30 | 450 | A69-1303-513 | Thelmabiotel ATID-MP-13 | 24 |

Cooke, 2014; Nelson et al., 2015). Data on sea temperature and salmon lice prevalence were plotted using r-package ggplot2 (Wickham, 2016), using the “geom_smooth” function to produce smoothed trend lines. Marine migratory tactics were classified as short- medium- and long distance migration in Hemnfjord for each tracking season, based on how far out in the fjord system the fish was detected (Figure 1, Eldøy et al., 2015). Similarly, marine migratory tactics were defined as short, long-inner, and long-outer distance migrants based on migratory distance in Tosenfjord (Figure 1, Bordeleau et al., 2018), where fish remaining resident in the estuary of River Åbjøra were considered as short distance migrants. Only fish observed returning to freshwater the second season, being detected after 1 July in the second tracking, season or qualifying for the longest

distance migratory tactic in the second tracking season were included in this analysis. The categorical variables of migration distance were transformed to ordinal structure according to relative migration distance (short = 1, medium/long-inner = 2, and long/long-outer = 3) prior to testing the intra-individual consistency using Spearman’s correlation test.

Network analysis and bipartite graphs were made using the r-package igraph (Csardi and Nepusz, 2006), as previously demonstrated on acoustic telemetry data by Finn et al. (2014). Here, the individual’s total yearly count of detections for each marine receiver that was operative through all the study years (numbered receivers in Figure 1) was used to compare the individual’s marine area use among years. Only fish observed returning to freshwater the second season, being detected after 1

July in the second tracking season, or qualifying for the longest distance migratory tactic in the second tracking season were included in the network analysis. The number of detections was used as weights for the link (edges) between tracked fish and associated receivers. Receivers and tracked fish were grouped using the igraph “cluster_walktrap” function (using 6 steps for Hemnfjord and 11 steps for Tosenfjord), which uses a random-walk algorithm to try to find densely connected subgraphs (communities) within the network (Csardi and Nepusz, 2006; Finn et al., 2014). The results of the grouping within the network of each fjord system were organized as an ordinal variable according to distance in the network plot and geographic location of the receivers (Figure 1) prior to evaluating inter-individual consistency among years using the Spearman’s correlation test. Timing of marine entry was defined as the time of the first detection on a receiver deployed in estuarine or marine waters preceding detection on a receiver deployed in freshwater. Timing of marine exit was defined as the time of the last detection on a receiver deployed in estuarine or marine waters prior to detection on a receiver deployed in freshwater. An exception was made for river Åbjøra, where the two outermost receivers in the river mouth (station 67 and 68, Figure 1) were defined as estuarine and receivers deployed further upstream in the large parts of the watercourse influenced by tidal water (station 63–66, Figure 1) were defined as “freshwater” in the marine timing and duration analyses. Marine duration was calculated as the yearly accumulated time spent in the marine environment, where periods of freshwater residency between the first marine entry and the last marine exit were excluded. Individuals that were only residing in tidally influenced parts of river Åbjøra were excluded from analyses of timing and duration of marine migration.

RESULTS

Of the 374 tagged individuals from the two fjord systems, we could extract data from 36 individuals (Table 1) to explore the intra-individual repeatability in area use, timing of marine entry, timing of marine exit, and/or marine residence time among consecutive marine feeding seasons. Of these, 10 individuals from Hemnfjord and eight individuals from Tosenfjord were tracked throughout two full marine seasons (i.e., they migrated back to freshwater after the second feeding migration). For two individuals from Tosenfjorden, tracking data could be extracted from three consecutive marine feeding migrations. Generally, the tagged individuals displayed a relative consistent marine behavior on the evaluated aspects of their marine behavior between the two or three consecutive marine feeding seasons of tracking (Table 2). However, the degree of consistency varied among individuals, with some individuals displaying large variations in some of the measured behavioral aspects among years (Table 2).

Marine Area Use of Tagged Anadromous Brown Trout

A wide range maximum migratory distances were observed, ranging from remaining resident in the estuarine areas of the watercourse where the fish were tagged—to utilizing large parts of

the fjord system and spending a significant amount of their total marine residence time in areas outside the outermost receiver arrays. There was a strong and significant intra-individual correlation between the observed migratory tactic during the first and second year of tracking in both Hemnfjord (Spearman’s rank-correlation; $r_s = 0.84$, $n = 12$, $P < 0.001$) and Tosenfjord ($r_s = 0.96$, $n = 18$, $P < 0.001$) when marine migratory behavior was classified as defined by Eldøy et al. (2015) and Bordeleau et al. (2018) for Tosenfjord (Figure 1). For Hemnfjord, 9 of 12 tracked fish were assigned to the same migratory tactic in both marine seasons. For Tosenfjord, 16 of 18 individuals were assigned to the same migratory tactic in both years. The annual consistency in marine area use of tagged individuals during the 2 consecutive years of tracking was further investigated by network analyses (Figures 4, 5; Table 2). There was a strong and significant intra-individual correlation between the assigned network group during the first and second year of tracking in both Hemnfjord (Spearman’s rank-correlation; $r_s = 0.77$, $n = 12$, $P = 0.003$) and Tosenfjord ($r_s = 0.89$, $n = 18$, $P < 0.001$). The grouping analysis of network structure using a cluster walk trap algorithm on the network in Hemnfjorden resulted in two different groups; one containing receiver locations in the inner and central part of Hemnfjorden and one containing receiver locations in outer and eastern parts of the fjord system (Figure 4). In this fjord system, 11 of 12 of the tagged fish were assigned to the same community unit both years (Table 2). For Tosenfjord, the grouping analysis of network structure using a cluster walk trap algorithm resulted in seven different community with associated tagged fish and receiver locations (Figure 5). Here, 12 of 18 tagged fish that were followed for 2 years were assigned to the same community both years (Table 2). One of the two fish that was tracked and analyzed for three consecutive seasons was assigned to the same community all years. However, two of the fish tracked during two seasons, and the one fish tracked for three seasons that changed community, transitioned between communities that all had associated receivers in the estuarine areas of the Åbjøra watercourse.

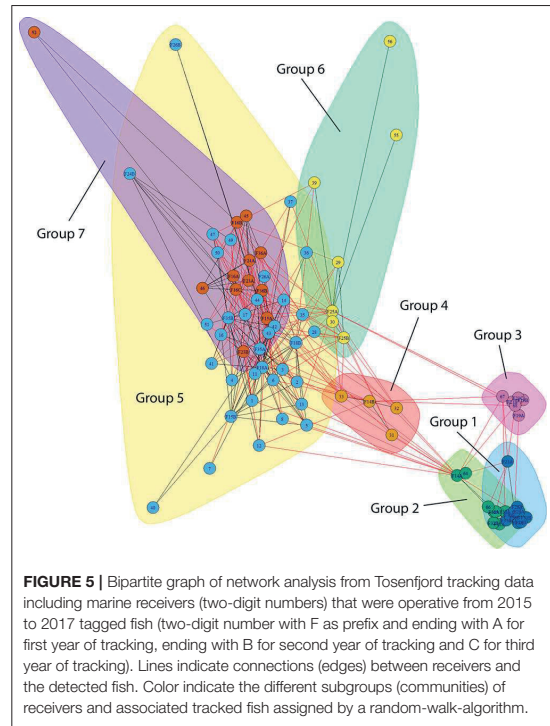
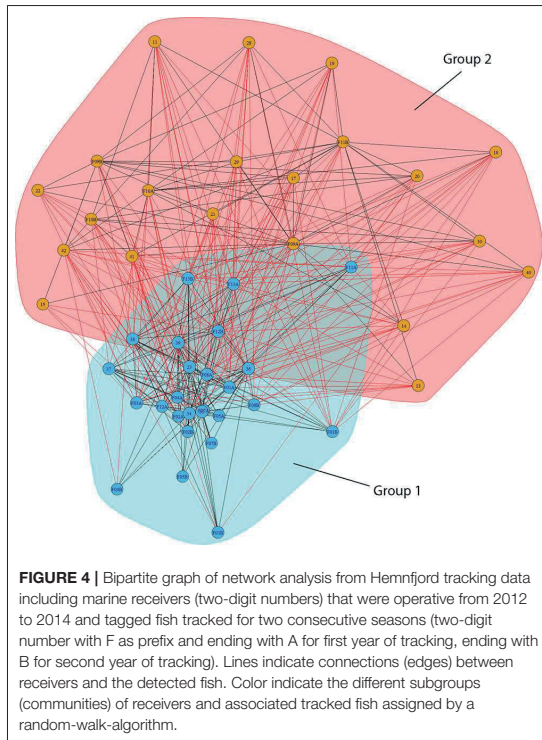
Timing of Start and End of Marine Feeding Migration

Average day of year for marine entry was 123.8 ($n = 27$, $SD = 15.8$, range 103.0–151.0) for the first year of tracking and 120.2 ($n = 27$, $SD = 24.0$, range 64.4–155.7) for the second year of tracking. There was a weak and non-significant intra-individual correlation of the timing of marine entry between the first and second year of tracking (Figure 6, Spearman rank-correlation; $r_s = 0.32$, $n = 27$, $P = 0.10$). Average individual difference in the timing of sea entry between the consecutive years was 18.0 days ($n = 27$, $SD = 15.0$ days, range 0.2–50.6 days).

Average day of year for marine exit was 207.1 ($n = 17$, $SD = 57.5$, range 151.8–332.8) for the first year of tracking and 190.5 ($n = 17$, $SD = 43.9$, range 140.0–296.4) for the second year of tracking. There was a strong and significant intra-individual correlation of marine exit timing between the first and second year of tracking (Figure 6, Spearman rank-correlation; $r_s = 0.81$, $n = 17$, $P < 0.001$). Average difference in the timing of exit

TABLE 2 | Summary of individual's behavioral characteristics among years of tracking.

| Fish ID | Study site | Strategy—migratory distance | | | Area use—network analyses grouping | | | Marine entry (day of year) | | | Marine exit (day of year) | | | Marine duration (days) | | |
|---------|------------|-----------------------------|----------|----------|------------------------------------|--------|--------|----------------------------|--------|--------|---------------------------|--------|--------|------------------------|--------|--------|
| | | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 | Year 1 | Year 2 | Year 3 |
| F01 | Henniford | Long | Long | na | 1 | 1 | na | 103 | 131 | na | 167 | 175 | na | 63.7 | 43.9 | na |
| F02 | Henniford | Medium | Long | na | 1 | 1 | na | na | na | na | na | na | na | 263.8 | 263.4 | na |
| F03 | Henniford | Long | Long | na | 1 | 1 | na | 107 | 125 | na | 152 | 166 | na | 44.6 | 41.2 | na |
| F04 | Henniford | Medium | Long | na | 1 | 1 | na | 103 | 139 | na | 320 | 296 | na | 149.2 | 13.1 | na |
| F05 | Henniford | Short | Short | na | 1 | 1 | na | 107 | 137 | na | 285 | 265 | na | 164.7 | 128.8 | na |
| F06 | Henniford | na | na | na | na | na | na | 111 | 64 | na | na | na | na | na | na | na |
| F07 | Henniford | Short | Medium | na | 1 | 1 | na | 103 | 128 | na | 274 | 264 | na | 170.8 | 136.8 | na |
| F08 | Henniford | Long | Long | na | 1 | 1 | na | 134 | 116 | na | na | na | na | na | na | na |
| F09 | Henniford | Long | Long | na | 2 | 2 | na | 138 | 97 | na | 168 | 140 | na | 30.3 | 43.0 | na |
| F10 | Henniford | Long | Long | na | 2 | 2 | na | 110 | 82 | na | 175 | 156 | na | 65.6 | 73.9 | na |
| F11 | Henniford | Long | Long | na | 1 | 2 | na | 119 | 98 | na | na | na | na | na | na | na |
| F12 | Henniford | Long | Long | na | 1 | 1 | na | 107 | 71 | na | 171 | 154 | na | 64.4 | 82.4 | na |
| F13 | Henniford | Long | Long | na | 1 | 1 | na | 110 | 86 | na | 175 | 153 | na | 64.9 | 67.1 | na |
| F14 | Toseniford | Long_out | Long_out | na | 2 | 4 | na | 105 | 107 | na | 163 | 160 | na | 57.8 | 52.8 | na |
| F15 | Toseniford | Long_out | Long_out | na | 7 | 5 | na | 128 | 139 | na | na | na | na | na | na | na |
| F16 | Toseniford | Long_in | Long_in | Long_out | 7 | 7 | 7 | 124 | 120 | 134 | 193 | 190 | 195 | 68.5 | 69.9 | 60.4 |
| F17 | Toseniford | na | na | na | na | na | na | 115 | 120 | na | na | na | na | na | na | na |
| F18 | Toseniford | Long_out | Long_out | na | 5 | 5 | na | 136 | 146 | na | 191 | 182 | na | 54.8 | 35.9 | na |
| F19 | Toseniford | Short | Short | na | 3 | 3 | na | na | na | na | na | na | na | na | na | na |
| F20 | Toseniford | na | na | na | na | na | na | 131 | 133 | na | na | na | na | na | na | na |
| F21 | Toseniford | Short | Short | Short | 1 | 3 | 3 | na | na | na | na | na | na | na | na | na |
| F22 | Toseniford | na | na | na | na | na | na | 135 | 134 | na | na | na | na | na | na | na |
| F23 | Toseniford | Long_in | Long_in | na | 7 | 7 | na | 120 | 127 | na | 178 | 184 | na | 57.9 | 56.6 | na |
| F24 | Toseniford | Long_in | Long_out | na | 7 | 5 | na | 138 | 137 | na | na | na | na | na | na | na |
| F25 | Toseniford | Long_in | Long_in | na | 6 | 6 | na | 143 | 136 | na | 210 | 181 | na | 66.6 | 44.7 | na |
| F26 | Toseniford | Short | Short | na | 5 | 5 | na | 139 | 156 | na | 333 | 197 | na | 193.8 | 41.2 | na |
| F27 | Toseniford | na | na | na | na | na | na | 132 | 132 | na | na | na | na | na | na | na |
| F28 | Toseniford | Short | Short | na | 1 | 1 | na | na | na | na | na | na | na | na | na | na |
| F29 | Toseniford | Short | Short | na | 1 | 1 | na | na | na | na | na | na | na | na | na | na |
| F30 | Toseniford | Short | Short | na | 2 | 1 | na | na | na | na | na | na | na | na | na | na |
| F31 | Toseniford | Short | Short | na | 2 | 1 | na | na | na | na | na | na | na | na | na | na |
| F32 | Toseniford | Short | Short | na | 2 | 2 | na | na | na | na | na | na | na | na | na | na |
| F33 | Toseniford | Short | Short | na | 1 | 1 | na | na | na | na | na | na | na | na | na | na |
| F34 | Toseniford | na | na | na | na | na | na | 146 | 149 | na | na | na | na | na | na | na |
| F35 | Toseniford | Long_out | Long_out | na | 5 | 5 | na | 147 | 134 | na | 185 | 183 | na | 37.7 | 49.3 | na |
| F36 | Toseniford | Long_in | Long_out | na | 7 | 7 | na | 151 | 100 | na | 181 | 192 | na | 30.4 | 91.4 | na |



between the consecutive years was 21.1 days ($n = 17$, $SD = 30.8$ days, range 2.1–135.8 days).

Migratory Duration

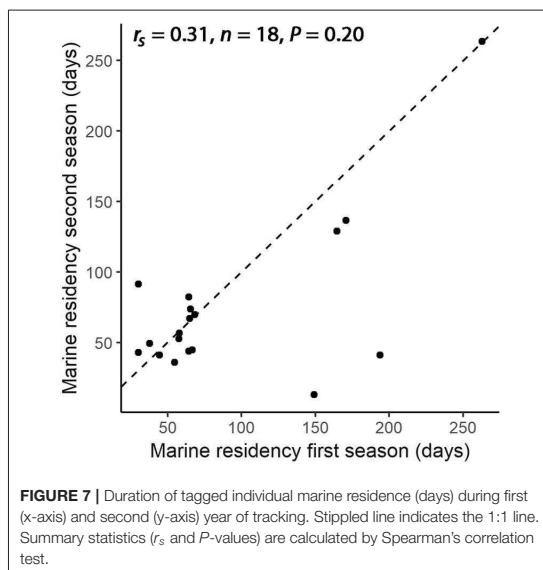
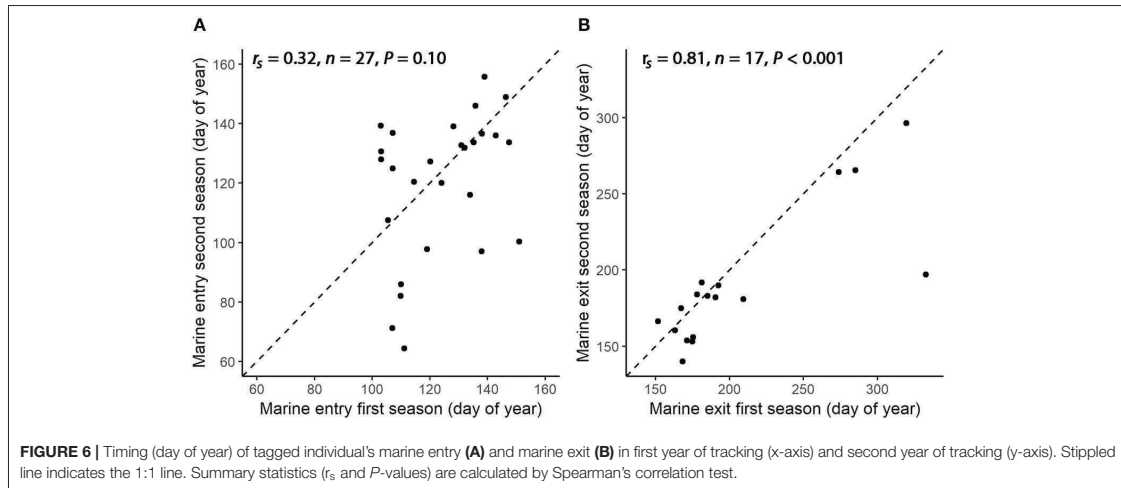
Average marine residency was 91.6 days ($n = 18$, $SD = 66.4$, range 30.3–262.8) for the first year of tracking and 74.2 ($n = 18$, $SD = 56.7$, range 13.1–263.4) for the second year of tracking. There was no significant correlation of marine residence time between the first and second year of tracking (Figure 7, Spearman's rank-correlation; $r_s = 0.31$, $n = 18$, $P = 0.20$). The difference in the duration of the marine migration between the two seasons varied greatly among the individuals, ranging from 0.7 days to 152.6 days ($n = 18$, mean = 30.3 days, $SD = 44.4$ days).

DISCUSSION

This study revealed that some key aspects of the annual marine feeding migration of anadromous brown trout tend to be repeatable between years. Repeatable behavior is a common phenomenon in nature, but this is to our knowledge the first study to illustrate repeatable behavior by anadromous brown trout, and is among the few to evaluate behavioral repeatability in salmonid fishes more generally (Taylor and Cooke, 2014). Although large phenotypic and behavioral variability has been observed among brown trout in previous studies (Klemetsen

et al., 2003; Thorstad et al., 2016; Halttunen et al., 2018), and previous studies suggest pre-migratory nutritional state as a driver for the migratory continuum of brown trout (Bordeleau et al., 2018), this study suggests that the intra-individual behavioral flexibility during the marine migration is low. However, despite the general repeatability of marine migration behavior, the degree of repeatability varied greatly among individuals, with some individuals displaying large intra-individual variance among the 2 years of tracking.

Variation in behavioral traits among years can be divided into an individual effect and a residual effect, where the individual effect is thought to be determined by genetics and previous experiences (Bell et al., 2009; Biro and Stamps, 2010; Conrad et al., 2011). This study was not designed in a way that allowed us to evaluate the importance of environmental experience to the observed trends of behavioral repeatability. Due to low number of tracking years (only 2 years for most individuals, Table 2), low number of different environments, and the relatively low sample size, it was not possible to evaluate how yearly variation in environmental factors affected the behavior of anadromous brown trout. Sea temperature and salmon lice abundances reported by salmon farms in the two fjord systems suggest some degree of environmental fluctuation throughout the season and among years, and previous studies have in fact reported that the abundance of certain prey in Norwegian fjords can vary greatly among years (Dragesund



et al., 1997; Rikardsen and Amundsen, 2005). It is therefore likely that the anadromous brown trout in our study experienced somewhat varying conditions interannually during their marine migrations, despite the observed individual consistency in their marine behavior. Alternatively, the observed differences in environmental conditions experienced by the tagged fish might not have been drastic enough to trigger intra-individual changes in marine habitat use patterns.

Inter-annual variation in individual marine area use was evaluated with two different approaches; subjectively defined lines by the distance from watercourse of tagging, and by

performing network analyses to investigate the relationship between every tagged fish and receivers deployed in the fjord and grouping them by using a random-walk-algorithm. Using both methods, the fish from both fjord systems showed a strong and significant individual consistency in marine area use between the two tracking seasons. Previous studies have revealed that the area use of individuals in anadromous brown trout populations can vary greatly (Thorstad et al., 2016). Migratory tactics within brown trout populations have previously been linked with nutritional status in spring prior to seasonal marine feeding migrations, where fish in low body condition Eldøy et al. (2015) and low nutritional physiological state Bordeleau et al. (2018) were more likely to migrate further out in the fjord system. Bordeleau et al. (2018) suggested that individuals with poor body condition in spring may be more prone toward feeding in the distant, outer areas, where potentially better feeding conditions occur, in order to regain their energy reserves. The observed consistency in marine area use raises questions about whether there could be causal factors that act over longer time-frames, which might cause individual pre-migratory nutritional status during spring to be maintained across years. For example, it could be speculated that marine habitat or prey preferences have the potential to affect energy storage, energy investment into reproduction, and post-spawning nutritional state prior to the next feeding season (Bordeleau, 2019). However, the links between marine migratory behavior and prey choice, growth, reconditioning of body condition and subsequent spawning investment is poorly understood.

The individual migratory behavior of the tagged individuals was relative consistent among years despite some observed yearly variation in sea water temperature and salmon lice prevalence in salmon farms. Previous studies have linked both horizontal and vertical marine responses of anadromous brown trout to variation in seawater temperature (Rikardsen et al., 2007; Jensen et al., 2014; Eldøy et al., 2017; Kristensen et al., 2018). It has been

thoroughly documented that open cage salmon farming can lead to the unnaturally high infestation of wild salmonids and alter their marine behavior (Thorstad et al., 2015; Finstad et al., 2017). Halttunen et al. (2018) documented shifts in the marine area use of different groups of anadromous brown trout in response to salmon lice abundance in Hardangerfjord, Southern Norway, and observed that brown trout utilized outer areas less in years when the risk of salmon lice infestation was high, compared with years with lower infestation risk. However, the variation in salmon lice infestation levels in the study by Halttunen et al. (2018) was probably greater than in our study, as they investigated the behavior of brown trout in years when salmon production cycles were active vs. the behavior of brown trout in years when all salmon farms in the inner fjord were fallow. There was a marginally non-significant, intra-individual correlation in timing of marine entry between the 2 years of tracking. Previous studies have documented that previous life history, morphology and physiology affect the timing of seaward migrations in salmonid populations (Halttunen et al., 2013; Thorstad et al., 2016), and so intra-individual consistency in timing of marine entry is thus expected. However, environmental conditions such as the timing of ice melting and increased water temperature and discharge has also been found to influence the timing of migration (Thorstad et al., 2016). Inter-annual variation in environmental conditions in the freshwater habitat is therefore likely to have influenced the annual timing of marine entry in the present study.

In contrast to timing of marine entry, a strong and significant intra-individual correlation was found for the timing of marine exit between the 2 years of tracking. This suggests that life history, physiological state and/or individual effects have some influence on the timing of when individuals end their marine feeding season. Marine exit was in the present study defined as the last detection at a marine or estuarine receiver prior to detection at a receiver in freshwater. Because marine exit timing varied so little between years, brown trout were probably able to migrate into freshwater under most water discharge conditions, and so inter-annual environmental conditions in the rivers probably had little influence on the timing of their movement into freshwater. More likely, the timing of marine exit and freshwater entry was probably more influenced by life history, stage of maturity, and sex, as previously shown (Thorstad et al., 2016). Regarding the inter-annual marine residence time of brown trout, we found no significant intra-individual relationship. If the timing of marine entry is mainly influenced by the environmental conditions in the freshwater habitat, and there is strong consistency in marine exit timing, the varying environmental conditions in freshwater prior to marine entry are likely the main determinants of the marine residence time of brown trout. Alternatively, marine residence time in brown trout has been inversely correlated with individuals nutritional state (i.e., plasma triglycerides) prior to migration, such that depleted fish spend more time at sea reconditioning (Bordeleau et al., 2018).

In summary, this study revealed a strong tendency for individual, inter-annual repeatability in anadromous brown trout with respect to migratory decisions and marine habitat use patterns. While the causes remain obscure, this is the first study assessing the intra-individual behavioral repeatability

of a salmonid fish species in relation to aspects of their spatiotemporal marine habitat use during consecutive annual feeding migrations. The findings of this study may have strong potential implications for management purposes. The role of intra-individual repeatability and the inter-annual behavioral response of anadromous brown trout to changing environmental conditions should therefore be a focus for future studies.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The experimental procedures followed national ethical requirements and were approved by the Norwegian National Animal Research Authority (permit No. 2012/22965 & 2015/8518).

AUTHOR CONTRIBUTIONS

SE was as the lead author responsible for the main part of the data analyses and on writing the paper. SE has further contributed considerable in field work and obtaining the dataset. XB was central in the initial idea of the paper and contributed significantly in terms of study design and contributed on feedback and input in the process of writing the paper. XB has further contributed in field work in the Tosenfjord study site and have during his work in this fjord system also contributed in the analyses these data. GC has contributed significantly in planning, study design, and the writing of the paper. JD was the PI of the two tracking studies that this paper is based on and has through this role significantly contributed to study design, field work, and project management. Further, he has contributed to this specific study with planning, study design, and writing of the paper.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The handling editor and reviewer, NS, declared their involvement as co-editors in the Research Topic, and confirm the absence of any other collaboration.

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Paper IV

Changes in growth and migration patterns of sea trout before and after the introduction of Atlantic salmon farming

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Running headline: Growth of anadromous brown trout *Salmo trutta*

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ABSTRACT:

Marine growth has strong implications for reproductive potential and ultimate fitness of sea trout. Hence, the effects of anthropogenic factors on marine growth are important when evaluating population responses and implementing management measures. Temporal changes in growth patterns of sea trout from three Norwegian and two Irish watercourses were examined, covering time spans of 25 to 65 years. Elemental chemistry Ba:Ca profiles and visual reading of fish scales were used to estimate smolt length and life-time growth after first sea entry. Reduced growth after the first sea entry coincided with periods of nearby (<14 km) salmon farming activity in impacted watersheds in both countries. Increased Ba:Ca levels were also recorded during these periods, likely indicating reduced residency in marine habitats caused by premature return to freshwater and estuaries. An increase in estimated length at first sea entry coinciding with salmon farming activity, for groups of fish sampled after sea migration, suggests a size-selective marine mortality related to fish farming, with the smallest individuals experiencing a larger mortality.

INTRODUCTION

Migration is an evolutionary adaptation common in a wide range of animal taxa, enabling individuals to increase survival and fitness by escaping unfavourable conditions, exploiting increased feeding opportunities with temporal or spatial peaks in ecosystem production and/or using different habitats throughout their ontogeny (Dingle & Drake, 2007; Lennox *et al.*, 2016). Anadromy is a migratory strategy common among many salmonid fish species, which is characterised by spawning in freshwater and marine feeding migrations. Brown trout *Salmo trutta* (L.) is a highly adaptable salmonid species. Populations in watercourses with access to the sea consist of both freshwater-resident individuals and individuals migrating to the sea (hereafter termed sea trout) (Jonsson & Jonsson, 1993; Klemetsen *et al.*, 2003). Migratory individuals exploit the richer feeding opportunities at sea to gain a larger body size, higher female fecundity, competitive advantages on the spawning ground and ultimately a potentially greater fitness than their freshwater-resident conspecifics (Thorstad *et al.*, 2016). However, marine migrations may also expose the individuals to higher risks of predation and being infected by pathogens or parasites (Jensen *et al.*, 2019). As anadromy is considered a quantitative threshold trait, the proportion of anadromous individuals in a population is thought to be partly governed by the relative fitness of resident versus migratory individuals of previous generations (Ferguson, 2006; Ferguson *et al.*, 2019). Reduced marine growth and

increased marine mortality reduce the ultimate fitness benefits of marine migrations, and may thus result in selection against anadromy if the cost exceeds the benefits of migration (Thorstad *et al.*, 2015). In a common garden experiment, Archer *et al.* (2019) observed low tendency of smoltification for fish from a population within the Burrishole system, which had been exposed to high rates of sea lice transmission from local salmon farms (Poole *et al.*, 1996; Poole *et al.*, 2007), and suggested that salmon farming possibly had imposed strong selection against anadromy in this population.

While at sea, sea trout commonly reside in coastal areas within 100 km from their natal river, which may be areas heavily influenced by human activities such as Atlantic salmon farming and other aquaculture activities, marine traffic, habitat alterations by industrial infrastructure, power production, and commercial fishing (Aldvén & Davidsen, 2017; Nevoux *et al.*, 2019). The negative impacts on sea trout by Atlantic salmon farming have attracted particular attention over the last decades (Thorstad *et al.*, 2015; Gargan *et al.*, 2016; Moore *et al.*, 2018). Open net pen farming, normally with up to 200,000 individuals per pen in Norway, and 20,000-50,000 individuals per pen in Ireland, involves a major increase in host density and elevated levels of the naturally occurring parasite salmon louse *Lepeoptherius salmonis* K., which negatively affect wild salmonids in areas with intensive salmon farming (Costello, 2009; Jansen *et al.*, 2012; Thorstad *et al.*, 2015). For sea trout, salmon lice infestations can cause increased mortality, with smaller individuals being more vulnerable than larger individuals (Skaala *et al.*, 2014; Taranger *et al.*, 2014; Serra-Llinares *et al.*, 2020). Hence, it can be expected that larger post-smolts will have better survival than smaller post-smolts in periods with a high salmon lice infestation pressure. Salmon lice infestation can also negatively affect the growth of surviving individuals by causing osmoregulatory problems, negative stress responses, reduced feeding activity and interrupted feeding migrations (e.g. Birkeland & Jakobsen, 1997; Bjørn & Finstad, 1997; Wells *et al.*, 2007). Indeed, some studies have documented reduced body mass and condition factor of infested individuals compared to control fish (Bjørn & Finstad, 1997; Dawson *et al.*, 1998; Shephard *et al.*, 2016).

Scale reading is a commonly applied method for examining the life history and growth of fish (e.g. Dahl, 1911; Haraldstad *et al.*, 2016). Due to the variable and complex life history and habitat use of sea trout (Thorstad *et al.*, 2016; Birnie-Gauvin *et al.*, 2019), interpretation of growth patterns based on scale reading can be difficult and often subjective (Elliott & Chambers, 1996; Campbell *et al.*, 2015; Ryan *et al.*, 2019). The interpretation of growth patterns of fish in freshwater *versus* seawater habitats can be considerably improved by

validating scale reading with chemical analyses of the scales, because the elemental composition of scales is affected by the chemical properties of the water where the fish reside and grow (Wells *et al.*, 2000; Hutchinson & Trueman, 2006). Strontium (Sr) and barium (Ba) levels in calcified structures are commonly used to determine whether individuals of anadromous fish have migrated between freshwater and the sea, because there are low strontium levels and high barium levels in freshwater compared to the sea (Tzadik *et al.*, 2017). Chemical stability may be lower for fish scales than for otoliths, but advantages of using scales include non-lethal sampling methods, labour-effective preparation of samples and accessibility to historic samples through existing fish scale collections (Courtemanche *et al.*, 2006; Campbell *et al.*, 2015; Tzadik *et al.*, 2017). For sea trout, it has been shown that chemical analyses of Ba:Ca profiles in scales are more accurate and reproducible than visual scale readings for evaluating length at sea entry and marine growth (Ryan *et al.*, 2019).

Sea trout commonly utilize fully marine habitats with high salinity during their marine feeding migrations (Thorstad *et al.*, 2016). However, heavily salmon lice infested sea trout have been observed to increasingly reside in estuaries and freshwater during times when they would be expected to be in marine habitats (Tully *et al.*, 1993; Birkeland, 1996). Estuarine waters and freshwater habitats have significantly higher levels of available barium for incorporation into calcified structures compared to marine waterbodies (Walther & Limburg, 2012). Therefore, it is likely that sea trout that reside in estuarine habitats as opposed to marine habitats, or spend prolonged periods in freshwater because of premature return to freshwater, will exhibit elevated Ba:Ca values in the part of the scales that reflects the lifetime growth after the first sea entry.

In this study, we had access to historic and recent scale samples from sea trout in three rivers in Norway and two rivers in Ireland, covering periods of 25 to 65 years. The main aims were to examine if sea trout in populations with nearby salmon farms would have *i.* reduced growth after first sea entry, *ii.* increased Ba:Ca levels in the section of the scale after first sea entry, and *iii.* increased length at first sea entry in periods with salmon farming activity compared to periods without activity at the farming sites, which would indicate a size selective mortality until they were sampled in freshwater later in life. The methods developed by Ryan *et al.* (2019) were used, by analysing scale Ba:Ca profiles obtained by laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) to identify the first freshwater-marine transition. This was combined with traditional scale reading to determine length at first marine entry (hereafter referred to as smolt length), life time growth after the first sea entry,

and number of marine migrations, and to measure average Ba:Ca levels during their life time after the first sea entry.

MATERIAL AND METHODS

STUDY AREA

Sea trout (body length 25-51 cm) were collected for scale sampling in three rivers in Norway and two rivers in Ireland. In Norway, sea trout were collected in River Straumsvassdraget at Hitra Island outside the Trondheimsfjord, and in the River Nidelva and River Levangerelva within the Trondheimsfjord (Figure 1). The salmon farming industry in Norway started in the early 1970's on the coast outside the Trondheimsfjord and has since then become a major industry. There were no active salmon farming sites within the Trondheimsfjord, during the historic sampling years in River Nidelelva and River Levangerelva. Hence, the historic samples from River Straumsvassdraget (1953) were sampled before any salmon farming was established, while the distance to the nearest aquaculture site for River Nidelva and River Levangerelva were >50 and >100 km, respectively, during the period of historic scale sampling. In recent years, there have been numerous salmon farming sites along the coast outside the fjord. The Trondheimsfjord has recently not been used for open cage salmon farming, because the fjord was protected as a "Norwegian salmon fjord" in 2002, leading to liquidation of existing salmon farms (established after the historic sampling years in River Nidelva and River Levangerelva) and banning of future salmon farming within the fjord. Hence, the distance from the nearest salmon farming sites in recent sampling periods for the Norwegian rivers was 12 km, >50 km and >100 km for River Straumsvassdraget, River Nidelva and River Levangerelva, respectively. The salmon farms within 30 km from the river mouth of River Straumsvassdraget slaughtered their fish during early spring 2017, and were largely fallow during the summer, while there was more activity at these sites in 2018 (Barentswatch, 2020). However, the model of salmon lice larva densities developed by the Institute of Marine Research, Norway, indicated elevated infestation pressure in the areas around River Straumsvassdraget both in 2017 and 2018. The same models also indicate periodically increased salmon lice infestation levels within the Trondheimsfjord in recent years due to salmon farming, including areas close to both River Nidelva and River Levangerelva, although with lower intensities than the areas outside the fjord (IMR, 2020). Actual salmon lice counts on sea trout from the study sites were not available for the rivers in Norway.

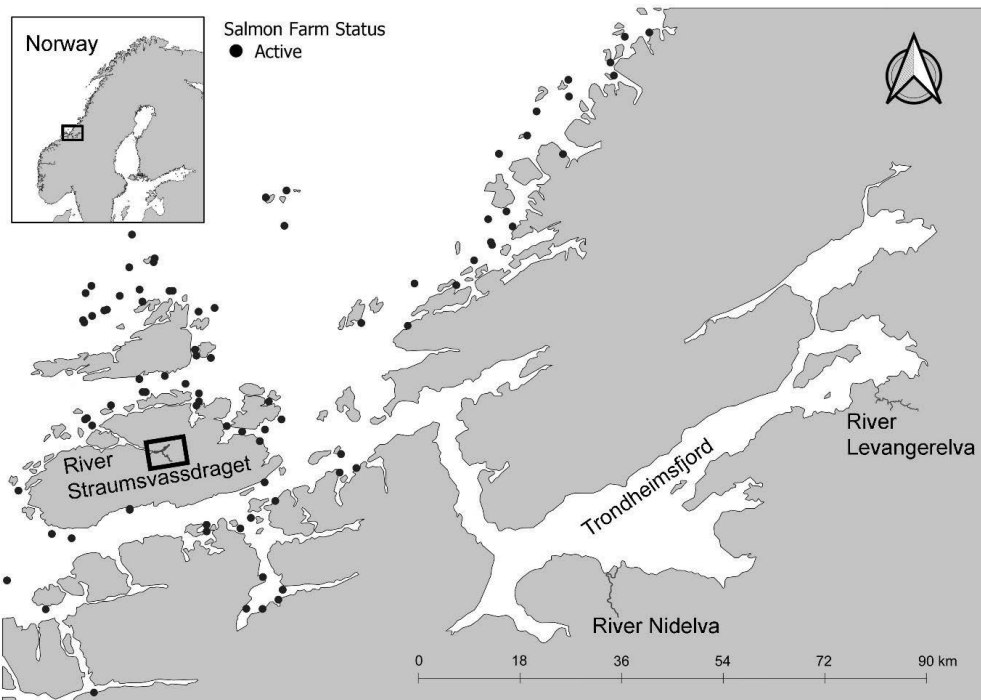


Figure 1: Study area with the River Straumsvassdraget, River Nidelva and River Levangerelva in Central Norway. Black dots denote active open cage salmon farming sites that reported salmon lice counts to the authorities in 2017 and/or 2018.

In Ireland, samples were collected from the River Erriff in County Mayo and the River Cashla in County Galway (Figure 2). The River Erriff drains into the 15 km long fjord of Killary Harbour, where open cage salmon farming sites at Rosroe and Inishdeighil are located just inside the mouth of the fjord and outside the fjord, respectively. Farming of Atlantic salmon in Killary Harbour in proximity to the River Erriff started in 1986, hence after the historic scale samples were collected. During the smolt run period in April and May 2015, the inner site at Rosroe held large one sea winter farmed salmon with an average salmon lice load of 8.1 mobile lice per fish. In the same period in 2016, the outer Inishdeighil site was the only active site and held farmed salmon smolts with an average salmon lice load of 0.3 mobile lice per farmed fish, indicating that the farmed salmon lice infestation pressure in Killary was significantly greater during the 2015 sea trout smolt run. It should be noted that another farmed salmon site, Clare Island smolt site, was active during the April and May period in 2016, located 24 km to the north of Killary Harbour. Data on salmon lice levels on sea trout captured migrating upstream in the Aasleagh trap on the River Erriff were available in 2015

and 2016. Average salmon lice load (all life stages) on sea trout in 2015 was high at 27.5 per fish ($n = 11$) in May, 11.8 ($n = 20$) in June and 25.0 ($n = 34$) in July. Salmon lice levels on sea trout were significantly lower in 2016, at 5.8 ($n = 241$) in June, 4.4 ($n = 268$) in July and 1.0 ($n = 51$) in August.

The River Cashla drains into Cashla Bay (Figure 2). In the late 1980s when the historic scale samples were collected, salmon farming was active in the neighbouring Greatman's Bay 13 km away, and at numerous sites in Kilkieran Bay, 16-20 km from the River Cashla. In recent years, the nearest active salmon farm was located 26 km from the River Cashla in Kilkieran Bay (Figure 2).

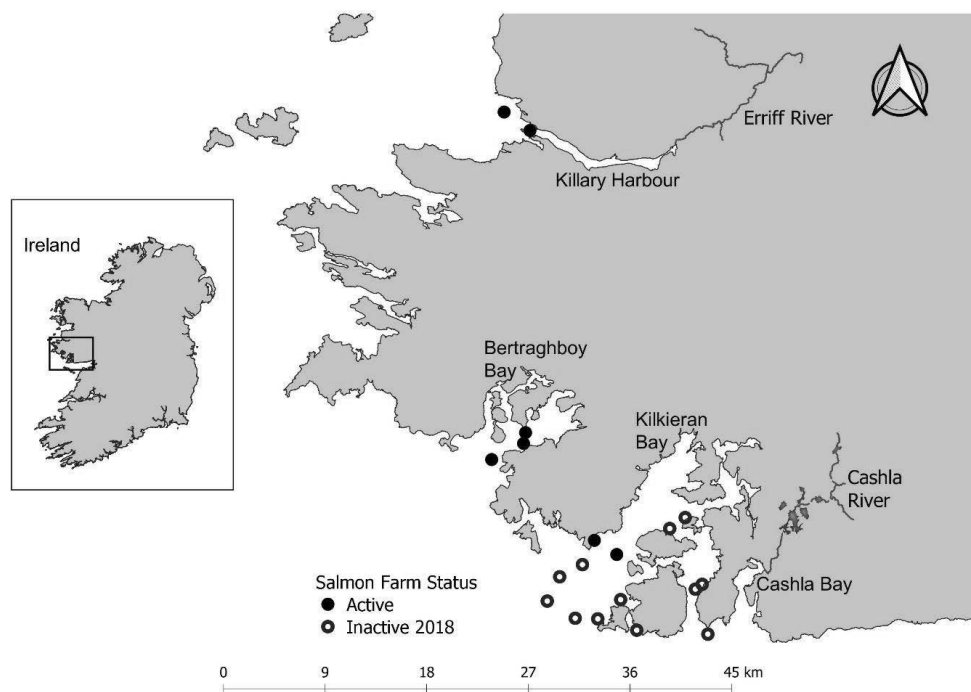


Figure 2: Study area with the River Erriff, and River Cashla in Western Ireland. Black dots denote open cage Atlantic salmon farming sites that were active during recent years when sea trout were sampled. Black circles denote Atlantic salmon farming sites that were active during historic sampling of sea trout, but inactive in 2018.

SCALE SAMPLING

Scales were obtained from the collections at the Norwegian University of Science and Technology University Museum, the Norwegian Institute for Nature Research, and the Inland Fisheries Ireland (Table 1). Additional fish were collected and sampled from River Straumsvassdraget at Hitra Island and River Levangerelva during 2017 and 2018 (Table 1). The samples from River Straumsvassdraget were caught by gill net fishing in Lake Hustadvatnet. In River Nidelva, the historic samples were collected by recreational anglers, while the samples from 2011-2013 were collected by scientific personnel using rods and gillnets in the river. The samples from the 1980's from River Levangerelva originated from recreational rod fisheries in the river, while the samples from 2017-2018 were collected by the authors using rods and light fishing with landing nets in the river and estuary, and a bag net in the estuary. In River Erriff, the samples from 1983 were collected in the recreational rod angling fisheries, while the samples from 2015 and 2016 were collected from fish in the Aasleagh Falls fish trap, where all up-migrating fish are captured immediately upstream of the tidal interface. For the River Erriff, the data included in this study was a randomized sub-sample from a larger collection of scales, while from all other rivers all available and relevant samples were analysed. The samples from River Cashla originated from the recreational rod fisheries. Scales from trout scales that did not exhibit Ba:Ca profiles indicating that the fish had been at sea were excluded from further analyses.

SCALE PREPERATION AND LA-ICP-MS ANALYSIS

One non-regenerated scale from each of the sampled trout were selected and manually cleaned using an acid washed nylon brush prior to ultrasonically cleaning for four minutes in element grade 3% hydrogen peroxide followed by triple rinsing in 18.2M Ω deionised water. The cleaned scales were mounted on petrographic slides with the basal plate facing down. Linear transects were analysed from the nucleus of the scale towards the edge of the scale along the midline of the anterior axis using a NWR213 New Wave Research laser ablation system, coupled to a Perkin Elmer DRC-e inductively coupled plasma mass spectrometer (LA-ICP-MS). The concentrations of ^{43}Ca , ^{23}Na , ^{24}Mg , ^{55}Mn , ^{66}Zn , ^{88}Sr and ^{138}Ba were analysed for every 9.01 μm along the scale transect. Raw LA-ICP-MS data were processed using the Iolite data reduction software with reduction scheme "Trace Elements" (Paton et al., 2011) using a ^{43}Ca concentration of 374000ppm as an internal standard. The concentration of ^{138}Ba was selected as the element to describe the transaction from fresh- to saltwater because Ryan *et al.* (2019) found this to be the element measured that was the least affected by post-

depositional change. The ^{138}Ba elemental concentration values were converted to molar concentrations and standardised to calcium (Ba:Ca) prior to further analyses. Further details of the LA-ICP-MS method are described by Ryan *et al.* (2019).

DETERMINING SMOLT LENGTH

The Ba:Ca profiles were characterized by three distinct regions: A region representing the juvenile phase until first sea entry with high Ba:Ca values, a transition region with decreasing Ba:Ca values and a zone representing lifetime growth (both marine and potential freshwater growth) after the first sea entry (Ryan *et al.*, 2019).

A freshwater threshold value was defined as the 5th percentile of Ba:Ca values from a slightly trimmed freshwater growth region for each scale starting 50 μm after the start point in the scale nucleus until 50-100 μm before the start of the transition region (Figure 3). The first of greater than two consecutive Ba:Ca values in the scale transects below this threshold value was defined as the point of first sea entry (Figure 3). Smolt length was calculated as the number of Ba:Ca measurements before the transition point divided by the total number of measurements and multiplied by the body length (mm) of the fish at the time of scale sampling, assuming a linear relationship between body length and scale length. Further details of the method used to estimate growth are described by Ryan *et al.* (2019).

Table 1: Overview of sea trout sampling groups, time of sampling, sample sizes (n), sampling method, owner of scale collection; Norwegian Institute for Nature Research (NINA), Norwegian University of Science and Technology University Museum (NTNU) and Inland Fisheries Ireland (IFI), and distance to nearest active salmon farm in years of sampling. Freshwater resident trout and fish with more than three seasonal marine migrations are excluded.

| Study site | Sampling period | Sampling years | Sampling dates (dd.mm.) | n | Scale collection | Sampling method | Distance to salmon farm |
|--------------------------|-----------------|----------------|-------------------------|-----|------------------|--|-------------------------|
| River Straums-vassdraget | Historic | 1953 | 16.09.-28.10. | 27 | NINA | Gillnets in Lake Husvatnet | No farming |
| River Straums-vassdraget | Recent | 2017-2018 | 25.09.-10.10. | 50 | NTNU | Gillnets in Lake Husvatnet | 12 km |
| River Nidelva | Historic | 1983-1986 | 05.06.-25.08. | 23 | NTNU | Recreational rod fisheries | >50 km |
| River Nidelva | Recent | 2011-2013 | 16.04.-14.09. | 29 | NTNU | Rod fishing / Gillnets in river | > 50 km |
| River Levangereelva | Historic | 1987-1991 | 03.07.-31.08. | 25 | NTNU | Recreational rod fisheries | >100 km |
| River Levangereelva | Recent | 2017-2018 | 29.08.-02.11. | 20 | NTNU | Rod fishing / Bag net in River and Estuary | >100 km |
| River Erriff | Historic | 1983 | 08.08.-11.10. | 39 | IFI | Recreational rod fisheries | No farming |
| River Erriff | Recent | 2015 | 09.07.-20.09. | 31 | IFI | Aasleagh Falls Trap | 14 km |
| River Erriff | Recent | 2016 | 01.07.-18.08. | 29 | IFI | Aasleagh Falls Trap | 17 km |
| River Cashla | Historic | 1988 | 07.07.-07.09. | 47 | IFI | Recreational rod fisheries | 13 km |
| River Cashla | Recent | 2018 | 10.07.-27.09. | 39 | IFI | Recreational rod fisheries | 26 km |

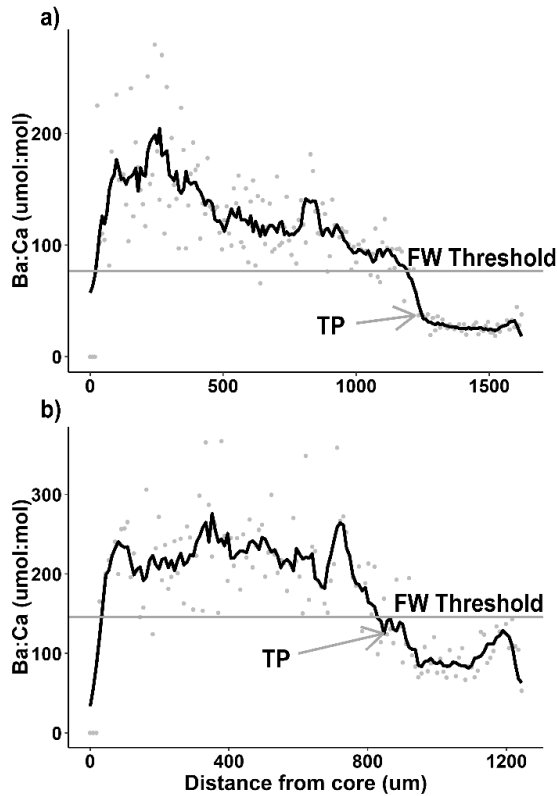


Figure 3: Examples of Ba:Ca profiles of a) fish id 83_111 (sampled in 1983, body length 303 mm, smolt length 232 mm, one marine migration) and b) fish id 15_14 (sampled in 2015, body length 280 mm, smolt length 193 mm, one marine migration) from River Erriff, Ireland. Grey points denote the data points along the scale transect. The black lines denote the three point running average of the data points. Freshwater threshold value denotes the 5th percentile of Ba:Ca values from a slightly trimmed freshwater growth region, “TP” denotes point of first sea entry.

DETEMINING LIFE TIME GROWTH AND Ba:Ca LEVELS AFTER FIRST SEA ENTRY

Estimated growth after first sea entry was calculated as the body length at time of scale sampling minus the estimated smolt length. An average Ba:Ca value for the growth after first sea entry was calculated for each fish. The mean value was calculated for all the measurements in sections of the scale starting 50-100 μm after end of the Ba region of transition from freshwater to saltwater to 50 μm before the transect end point (Ryan *et al.*, 2019).

DETERMINING THE NUMBER OF MARINE MIGRATIONS

Sea trout with various numbers of marine migrations were included, but the scale chemistry analysis was not sufficiently refined to determine short-time periods of freshwater re-entry and multiple transitions between fresh- and saltwater habitats. Therefore, it was necessary to combine the chemistry analyses with ordinary scale reading in order to classify the number of annual marine migrations the sea trout had conducted. Combining scale chemistry analyses, which provided an estimate of smolt length, with ordinary scale reading of the number of growth seasons after smoltification provided more objective results compared to traditional scale reading alone. Scales from the Norwegian fish were pressed against Lexan plates, and their imprint was photographed using a Leica M165C and Leica MC170HD. Scales from the Irish fish were photographed using an Olympus BX51 and Q-imaging Micro-publisher 5.0. Using the information about the smolt length derived from the Ba:Ca profiles as a reference point, the number of marine migrations was determined by experienced scale reading personnel by visual interpretation. Sea trout for which the number of marine migrations could not be confidently determined were excluded from further analysis.

STATISTICAL ANALYSES

Statistical analyses were conducted by using RStudio version 1.2.1355 (RStudio Team, 2019) and R version 3.5.3 (R Core Team, 2019). Figures were made by using the R package ggplot 2 (Wickham, 2016). For statistical comparisons between two groups, we used two-sided *t*-tests, or two-sided Wilcoxon tests for non-normally distributed data checked by using a Shapiro-Wilk test. ANOVA or TUKEY ANOVA was used for statistical comparisons of three groups. For comparisons among three groups with non-normally distributed data and/or heterogenous variance, Kruskal-Wallis rank sum tests and Wilcoxon's tests were applied (Fox *et al.*, 2012). Sea trout caught in River Nidelva in 1983-1986 with one marine migration were excluded from statistical analyses because of possible bias in the recreational fisheries towards fast growing individuals in this sea age class. Statistical comparisons of Ba:Ca levels in the growth after the first sea entry zone were not conducted for River Levangerelva because of differences in timing and method of sampling between the historically and recently collected fish. Fish that had four or more marine migrations prior to sampling, were excluded from further analysis because of low number of observations in this age group and uncertainty regarding their spawning history.

RESULTS

In River Straumsvassdraget in Norway, sea trout with ≤ 3 marine migrations sampled in 2017-2018 did not differ in body length (Wilcox-test; $n = 53$, $P = 0.14$), but had performed a higher number of marine migrations (Wilcox-test test; $n = 53$, $P = 0.002$) compared to the fish sampled in 1953 (Figure 4). In River Nidelva, the fish sampled in 2011-2013 had a shorter body length (t -test; $n = 33$, $P < 0.001$), but did not differ in number of marine migrations (Wilcox-test; $n = 33$, $P = 0.48$) compared to fish sampled in 1983-1986 (Figure 4). In River Levangerelva, the fish sampled in 2017-2018 had a shorter body length (t -test; $n = 31$, $P = 0.007$), and fewer marine migrations (Wilcox-test; $n = 31$, $P < 0.001$) than fish sampled in 1987-1991 (Figure 4).

In River Erriff in Ireland, sea trout with ≤ 3 marine seasons sampled in 2015-2016 did not differ in body length (Wilcox-test; $n = 95$, $P = 0.066$), or number of marine migrations ($n = 95$, $P = 0.44$) compared to fish sampled in 1983 (Figure 4). In River Cashla, fish sampled in 2018 did not differ in body length (t -test; $n = 77$, $P = 0.15$), but had fewer marine migrations (Wilcox-test; $n = 77$, $P = 0.014$) compared to fish sampled in 1988 (Figure 4).

In River Straumsvassdraget, Norway, sea trout that had performed one marine migration were shorter, had poorer growth after first sea entry, and had higher Ba:Ca levels in the scale section after first sea entry in 2017-2018 (a period with nearby salmon farming) than in 1953 (pre-salmon farming, Table 2). Moreover, fish that had performed two marine migrations had a larger smolt length in 2017-2018 than in 1953 (Table 2). In River Nidelva, sea trout that had performed two marine migrations had larger Ba:Ca levels in the scale section after first sea entry in 2011-2013 than in 1983-1986 (Table 2). In River Levangerelva, there were no differences in growth patterns between fish sampled in 2017-2018 and 1987-1991 (Table 2).

In River Erriff, Ireland, sea trout that had performed one marine migration were shorter, had poorer growth after first sea entry, and had higher Ba:Ca levels in the scale section after first sea entry in 2015-2016 (a period with nearby salmon farming) than in 1983 (pre-salmon farming, Table 2). In River Cashla, sea trout that had performed one marine migration had higher growth after first sea entry, lower Ba:Ca levels in the scale section after first sea entry and shorter smolt length in 2018 (when nearby salmon farming had ceased) than in 1988 (a period with nearby salmon farming). No other differences between groups when comparing

historic and recent samples were found for these variables in any of the rivers in Norway and Ireland (Table 2).

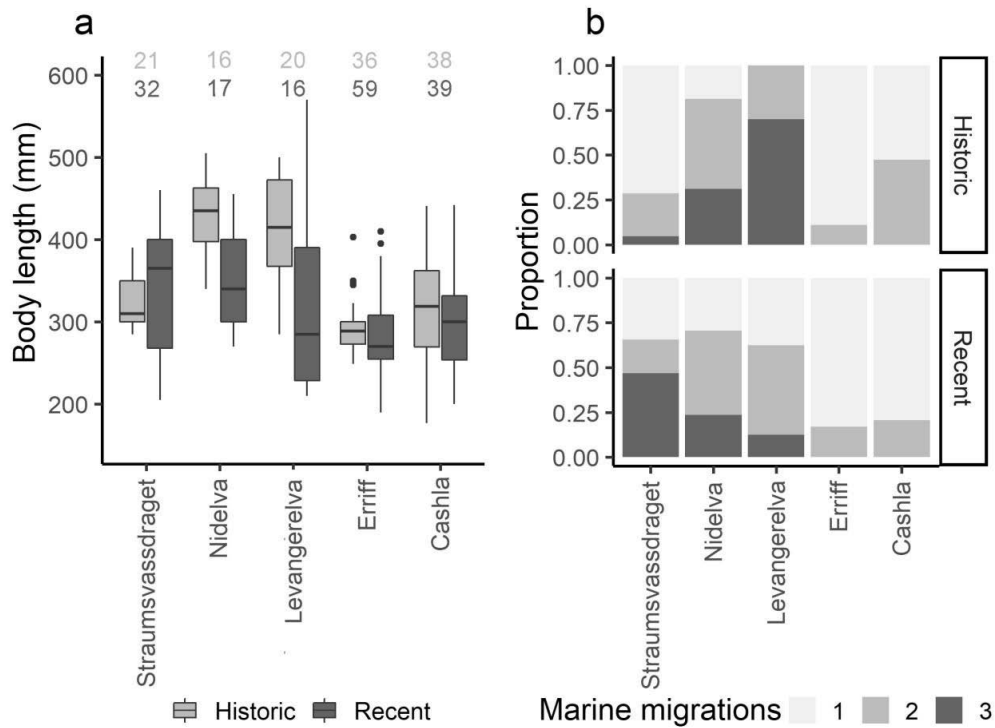


Figure 4: Body length (a) and distribution (proportions) of number of marine migrations (b) for sea trout with ≤ 3 marine seasons captured and analysed using LA-ICP-MS. The box plots (a) show the interquartile range (boxes), median (horizontal line in boxes), the 5th and 95th percentiles (whiskers) and outliers (dots). The stacked bar-plot (b) shows the relative numbers of marine age classes among sampled groups for the historic samples (upper panel) and recently sampled fish (lower panel). Number of observations in each group is denoted above the boxes.

Table 2: Summary statistics and statistical comparisons between sea trout sampled during historic and recent periods from the study rivers in Norway and Ireland. Values in bold indicate statistically significant results. Number of marine migrations indicate the number of feeding growth seasons (summers) the sea trout had spent in saline waters.

| Historic samples | Watercourse / Year | | | River Straumsvassdraget 1953 | | | River Nidelva 1983-1986 | | | River Levangelve 1987-1991 | | | River Erriff 1983 | | | River Cashla 1988 | | |
|--|-------------------------|----------------------|------------------|------------------------------|----------|------------------|-------------------------|----------|------------------|----------------------------|----------------------|------------------|----------------------|----------------------|----|-------------------|---|--|
| | Number of samples | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 1 | 2 | |
| Body length (mm) | n | 316 | 342 | 360 | 397 | 425 | 459 | na | 391 | 419 | 284 | 361 | 272 | 368 | | | | |
| | mean | 21 | 35 | na | 38 | 50 | 36 | na | 80 | 59 | 18 | 28 | 38 | 25 | | | | |
| | sd | 285-350 | 305-390 | na | 370-440 | 340-500 | 410-505 | na | 285-480 | 310-500 | 249-323 | 345-403 | 177-320 | 333-441 | | | | |
| | range | 107 | 182 | 220 | 187 | 247 | 270 | na | 240 | 272 | 98 | 172 | 74 | 152 | | | | |
| Growth after first marine entry (mm) | n | 17 | 42 | na | 29 | 63 | 22 | na | 79 | 61 | 18 | 47 | 37 | 39 | | | | |
| | mean | 70-149 | 128-230 | na | 170-221 | 180-333 | 239-299 | na | 123-336 | 143-344 | 68-150 | 102-201 | 20-191 | 67-209 | | | | |
| | sd | 6.9 | 7.3 | 4.7 | 12.3 | 9.6 | 12.2 | na | 2.7 | 3.1 | 37.1 | 65.0 | 55.7 | 67.2 | | | | |
| | range | 2.5 | 3.2 | na | 4.2 | 4.8 | 8.0 | na | 0.9 | 1.0 | 19.1 | 9.4 | 20.6 | 19.2 | | | | |
| Ba:Ca after first marine entry | n | 209 | 160 | 140 | 210 | 178 | 189 | na | 151 | 146 | 186 | 189 | 199 | 216 | | | | |
| | mean | 15 | 24 | na | 61 | 38 | 29 | na | 22 | 25 | 25 | 75 | 41 | 31 | | | | |
| | sd | 188-239 | 135-186 | na | 149-270 | 125-239 | 144-224 | na | 131-190 | 92-193 | 145-232 | 144-301 | 104-273 | 169-296 | | | | |
| | range | | | | | | | | | | | | | | | | | |
| Recent Samples | Watercourse / Year | | | River Straumsvassdraget 1953 | | | River Nidelva 1983-1986 | | | River Levangelve 1987-1991 | | | River Erriff 1983 | | | River Cashla 1988 | | |
| | Number of samples | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 1 | 2 | |
| Body length (mm) | n | 11 | 6 | 15 | 5 | 8 | 4 | 6 | 8 | 2 | 49 | 10 | 31 | 8 | | | | |
| | mean | 263 | 348 | 403 | 316 | 376 | 355 | 248 | 317 | 530 | 269 | 343 | 281 | 373 | | | | |
| | sd | 39 | 54 | 34 | 46 | 80 | 44 | 48 | 81 | 57 | 33 | 50 | 39 | 41 | | | | |
| | range | 205-360 | 240-380 | 340-460 | 275-380 | 270-455 | 300-400 | 210-340 | 210-420 | 490-570 | 190-350 | 235-410 | 200-334 | 331-442 | | | | |
| Growth after first marine entry (mm) | n | 60 | 131 | 161 | 110 | 193 | 190 | 114 | 202 | 343 | 70 | 131 | 106 | 168 | | | | |
| | mean | 21-100 | 96-172 | 87-252 | 53-167 | 102-281 | 128-229 | 104-143 | 123-272 | 314-372 | 6-158 | 39-215 | 78-155 | 131-207 | | | | |
| | sd | 19.5 | 15.3 | 14.1 | 15.6 | 15.7 | 16.3 | 9.2 | 12.5 | 8.5 | 52.1 | 46.9 | 29.0 | 33.3 | | | | |
| | range | 8.9 | 8.5 | 6.1 | 8.1 | 4.6 | 8.3 | 5.2 | 7.6 | 2.8 | 42.4 | 24.5 | 13.5 | 13.8 | | | | |
| Ba:Ca after first marine entry | n | 4.5-33.5 | 7.7-31.3 | 6.3-29.7 | 6.8-25.8 | 6.8-21.7 | 4.2-22.8 | 3.7-15.9 | 3.3-28.9 | 6.6-10.5 | 5.0-206.2 | 13.0-82.9 | 12.0-65.3 | 14.4-54.0 | | | | |
| | mean | 202 | 217 | 243 | 206 | 184 | 165 | 134 | 115 | 187 | 199 | 212 | 175 | 205 | | | | |
| | sd | 29 | 45 | 58 | 72 | 45 | 17 | 33 | 46 | 15 | 29 | 28 | 30 | 26 | | | | |
| | range | 166-260 | 144-281 | 108-341 | 133-327 | 112-267 | 139-176 | 103-197 | 54-187 | 176-198 | 103-297 | 180-276 | 121-229 | 158-235 | | | | |
| Change from Historic to Recent samples | Number of samples | | | n | | | n | | | n | | | n | | | n | | |
| | Body length (mm) | 26 | 11 | na | 8 | 16 | na | na | na | 14 | 16 | 81 | 14 | 51 | 26 | | | |
| Growth after first marine entry (mm) | estimate | -54 | 6 | na | na | -49 | na | na | -74 | 111 | -15 | -18 | 9 | 5 | | | | |
| | t-test / wilcoxon-test* | P < 0.001* | P = 0.65* | na | na | P = 0.17 | na | na | P = 0.12 | P = 0.18 | P = 0.010 | P = 0.54* | P = 0.58* | P = 0.78 | | | | |
| | estimate | -47 | -51 | na | na | -55 | na | na | -38 | 70 | -28 | -41 | 32 | 16 | | | | |
| | t-test / wilcoxon-test* | P < 0.001* | P = 0.49 | na | na | P = 0.11 | na | na | P = 0.33 | P = 0.10 | P < 0.001* | P = 0.070 | P < 0.001* | P = 0.20 | | | | |
| Ba:Ca after first marine entry | estimate | 12.62 | 8.01 | na | na | 6.11 | na | na | na | na | 15.07 | -18.04 | -26.69 | -33.35 | | | | |
| | t-test / wilcoxon-test* | P < 0.001* | P = 0.074 | na | na | P = 0.020 | na | na | na | na | P = 0.19* | P = 0.070 | P < 0.001* | P < 0.001* | | | | |
| | estimate | 13 | 8 | na | na | 6 | na | na | 10 | 5 | 15 | -18 | -27 | -34 | | | | |
| | t-test / wilcoxon-test* | P = 0.51* | P = 0.030 | na | na | P = 0.79 | na | na | P = 0.082 | P = 0.09 | P = 0.023* | P = 0.19* | P = 0.032 | P = 0.37 | | | | |

For fish sampled in the River Erriff, the body length (ANOVA, $n = 81$, $P < 0.001$), growth after first sea entry (Kruskal-Wallis test; $n = 81$, $P < 0.001$), Ba:Ca levels in the scale section after first sea entry (Kruskal-Wallis test; $n = 81$, $P < 0.001$) and smolt length (Kruskal-Wallis test; $n = 81$, $P = 0.018$) differed among years for the sea trout that had performed one marine feeding migration (Figure 5). Here, the fish sampled in 2015 were shorter (Tukey HSD, $P < 0.001$), had poorer growth after first sea entry (Wilcox test; 1983-2015; $P < 0.001$, 2015-2016; $P = 0.048$), and higher Ba:Ca levels in the scale section after first sea entry (Wilcox test; $P < 0.001$) than the fish sampled in 1983 and 2016 (Figure 5). Furthermore, the growth after first sea entry was poorer (Wilcox test; $P < 0.001$), and smolt length larger ($P < 0.05$) when comparing fish sampled in 2016 to fish sampled in 1983 (Figure 5). No other differences in these variables were found among years for the sea trout from River Erriff that had performed one marine migration prior to sampling (Figure 3, Tukey HSD/Wilcox tests; $P > 0.072$).

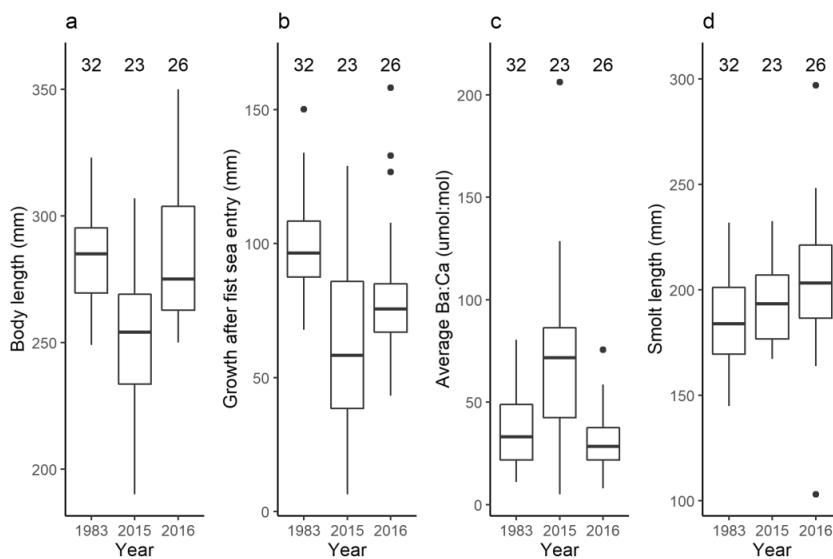


Figure 5: Comparison of body length (a), growth after first sea entry (b) Ba:Ca levels in the scale section after first sea entry (c) and smolt length (d) among sampling years for fish with one marine migration in the River Erriff. The x-axis indicates the year of sampling for the fish. No aquaculture was established in 1983. Nearby salmon farms were active in 2015, and merely fallow in 2016. Box plots show the interquartile ranges (boxes), medians (horizontal line in boxes), the 5th and 95th percentiles (whiskers) and outliers (dots). Number of observations in each group is denoted above the boxes.

DISCUSSION

Significant differences in growth and chemical composition of the scales were observed when comparing the historic and recently sampled fish both from populations in Norway and Ireland. In the populations with nearby aquaculture locations (< 14 km, River Straumsvassdraget, River Erriff and River Cashla), reduced lifetime growth and increased Ba:Ca levels after first sea entry coincided with periods of salmon farming activity. This suggests that the sea trout had reduced marine growth and spent increased time in estuarine and freshwater habitats when influenced by nearby salmon farming. The observed reduction in growth is consistent with previous studies comparing growth of sea trout before and after introduction of intensive salmon farming activity in nearby areas (Poole *et al.*, 1996; Butler & Walker, 2006; Fjortoft *et al.*, 2014). Using scales, Fjortoft *et al.* (2014) compared the growth of sea trout in River Etneelva over a 25-year period and found that the marine growth was significantly reduced after the introduction of salmon farming in the fjord, and estimated a 20-40% reduction in body mass after the first summer at sea. Butler & Walker (2006) documented a gradual decrease in marine growth rates of sea trout in River Ewe in Scotland after introduction of nearby marine salmon farming in 1987. In Ireland, Poole *et al.* (1996) observed a reduction in marine growth for sea trout in the River Burrishole after 1990, and concluded that it was likely linked to premature return of salmon lice-infested fish. Previous studies have found that increased salmon lice larva densities in the water and increased infestation rates on sea trout are typically found <30 km from salmon farms (reviewed by Thorstad *et al.*, 2015). In River Erriff, lower lifetime growth and higher Ba:Ca levels in the scales after first sea entry were observed in 2015 compared to 2016, coinciding with larger salmon lice production at the nearby farm and higher salmon lice levels on sea trout collected in the nearby River Aasleagh trap in 2015 than in 2016. While salmon lice infestation pressure from salmon farms was lower in 2016 than 2015 for the River Erriff, other salmon farms were present to the north of Killary, which may have contributed to a larger salmon lice infestation pressure than in 1983 for the River Erriff sea trout. This may have contributed to the lower body length and poorer growth after first sea entry seen in 2016 than in 1983. The presence of farmed salmon in close proximity to the sampled rivers and the associated salmon lice infestation pressure on sea trout in these areas most likely contributed to the observed reduction in lifetime growth after first sea entry.

Isolating the effect of salmon farming and associated increase in infestation pressure by salmon lice on the growth and survival of wild salmonids can be difficult due to multiple

factors that can influence the sea trout growth over the study periods (Thorstad *et al.*, 2015; Shephard & Gargan, 2017), which is also the case in this study. Variation in marine growth of sea trout among years have previously been observed in areas without salmon farming, and has been suggested to be influenced by climatic conditions and variation in marine prey availability (Berg & Jonsson, 1990; Kallio-Nyberg *et al.*, 2015). Important pelagic prey species, such as sprat *Sprattus sprattus*, herring *Clupea harengus* and small sandeel *Ammodytes tobianus* (Knutsen *et al.*, 2001; Rikardsen & Amundsen, 2005; Davidsen *et al.*, 2017) can vary greatly among years (ICES, 2020).

No differences in lifetime growth after first sea entry were found between old and new samples from the River Nidelva and River Levangerelva, which are situated in the Trondheimsfjord system where no open cage salmon farming sites were active during the periods of sampling in these rivers. However, the number of samples for each sea age group from these rivers is small leading to low statistical power to detect differences. Although the distance from the river mouth to the nearest active farms was large for the River Nidelva (>50 km) and River Levangerelva (>100 km), the salmon lice models run by the Institute of Marine Research suggest that salmon farming can periodically lead to increased salmon lice infestation rates within the Trondheimsfjord and in the areas close to both River Nidelva and River Levangerelva in some years (IMR, 2020). Also, although most sea trout seem to remain within 100 km of their watercourse of origin (Thorstad *et al.*, 2016), some can migrate substantially longer distances (Birnie-Gauvin *et al.*, 2019). It is therefore not unlikely that sea trout from River Nidelva and River Levangerelva may migrate to the outer areas of Trondheimsfjord, where the modelled salmon lice infestation pressure is periodically high (IMR, 2020). It should also be noted that the time period between historic and recent samples varies among the watercourses, with the samples from River Straumsvassdraget watercourse representing the longest time interval. Moreover, it cannot be excluded that climate change has impacted the populations in different ways, because their freshwater, estuarine and marine habitats near the Rivers have different characteristics.

The elevated Ba:Ca levels in the scale section after first sea entry that coincided with periods of salmon farming activity in River Straumsvassdraget, River Erriff and River Cashla suggest that the sea trout sampled during high salmon farming activity to a greater extent resided in estuarine- and freshwater habitats after their first migration to the marine environment compared to fish sampled in periods when the nearby farming sites were inactive. Elevated Ba:Ca levels were also observed for sea trout that had performed two marine migrations in

River Nidelva when comparing fish sampled in 2011-2013 to fish sampled in 1983-1986. Freshwater and estuarine waterbodies have higher concentrations of available Barium for absorption in the fish scales (Walther & Limburg, 2012; Tzadik *et al.*, 2017). Previous studies have documented that sea trout heavily infested with salmon lice tend to seek estuaries and freshwater (Tully *et al.*, 1993; Birkeland, 1996; Birkeland & Jakobsen, 1997), likely to regain osmotic balance, but which also results in reduce lice loads because salmon lice do not survive in freshwater and has a poor survival in brackish water (Johnson & Albright, 1991). A recent telemetry study showed that sea trout spent more time close to the river mouth in years with active salmon farms in the area compared to years when the farm was fallow (Halttunen *et al.*, 2018). Combining telemetry and artificial infestation, Serra-Llinares *et al.* (2020) documented that sea trout infested with salmon lice had higher mortality, remained closer to the estuary and returned to freshwater earlier than the non-infested control group.

Studies linking scale Ba:Ca levels to the behaviour of sea trout need to be performed to verify causes for the observed differences in Ba:Ca concentrations and to quantify the effect of estuarine and freshwater residency on the overall Ba:Ca levels. Ba:Ca levels in the juvenile zone of the scales (before the smolt migration to the sea) were generally decreasing with increasing seasons at sea, suggesting a gradual degradation of the freshwater Ba:Ca signal over time when residing in the marine habitat. Similarly, the overall Ba:Ca levels after the point of first freshwater entry are likely elevated by post-depositional change when the fish reside in estuarine or freshwater habitats even though it may have initially migrated to fully marine habitats. Chemical post-depositional change in scales has been documented in previous studies (Tzadik *et al.*, 2017). However, there may be several causes for this, including diffusion of the deposited barium to saltwater, active reabsorption of the fish in response to a requirement for barium in biological processes, and secondary growth of the scale leaving a thin layer of saltwater-deposited material over the part of the scale grown in freshwater (Metz *et al.*, 2014; Seeley *et al.*, 2015).

The observed increase in estimated length at first sea entry coinciding with salmon farming activity for groups of fish sampled after sea migration, suggests an increased size-selective marine mortality related to fish farming, with the smallest individuals experiencing a larger mortality. Previous studies have documented that smaller individuals are more vulnerable to both salmon lice infestation and predation (Taranger *et al.*, 2014; Thorstad *et al.*, 2015; Serra-Llinares *et al.*, 2020). However, smolt length may also be influenced by changes in climate,

river productivity and/or density dependent competition in the freshwater habitat (Klemetsen *et al.*, 2003).

As body size is strongly correlated with fecundity (Elliott, 1995), reduced marine growth due to anthropogenic factors is likely to have negative impact on the reproductive capacity of the spawning populations of sea trout and reduce the population productivity. In one of the rivers included in this study, River Erriff, Gargan *et al.* (2016) documented significant decreases in the number and length of post-spawned sea trout, the estimated number of eggs deposited, sea trout rod catches, the proportions of older sea trout and the frequency of repeat spawners in the period following establishment of the nearby salmon farm in 1986. Reduced marine growth and increased risk of mortality at sea can ultimately lead to selection against anadromy and lower proportions of marine migrants in partially migratory populations (Gargan *et al.*, 2006; Thorstad *et al.*, 2015; Archer *et al.*, 2019). Methods for monitoring growth of sea trout and incorporating sustained marine growth as a conservation aim in the management for sea trout populations is therefore crucial in order to maintain anadromy as a common migratory strategy within coastal brown trout populations.

We used laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) to complement traditional scale readings of historic and recently collected scale samples and improve the interpretation of the brown trout's life history in this study. Traditional scale reading is based on visual interpretation and/or morphometrical measurements, identifying the points of significant changes in distance between deposited annuli or circuli (Dahl, 1911; Elliott & Chambers, 1996; McCarthy *et al.*, 2008). Poor growth in the marine habitat or growth stagnation in periods during summer can lead to scale growth that is difficult to interpret using traditional scale reading (Beamish & McFarlane, 1983). Failing to interpret scales with ab-normal growth patterns might potentially lead to bias in analyses by excluding fish with certain behavioural or growth patterns. Estimating smolt-length and life time growth after first sea entry by LA-ICP-MS scale chemistry, is a ruled-based method that can be an alternative to traditional reading or be used in combination with traditional reading for increased scale interpretation confidence (Ryan *et al.*, 2019). Moreover, the results in this study suggest that the Ba:Ca levels in the scale after first sea entry can be used to detect changes in the use of marine versus freshwater and/or estuarine habitats. More research on this method is advocated to further develop scale chemistry profiling as a method to monitor time trends for sea trout growth and quantifying the utilization of various habitats.

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|------|------------------------|-----------------------|--|
| 1974 | Tor-Henning Iversen | Dr. philos Botany | The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism |
| 1978 | Tore Slagsvold | Dr. philos Zoology | Breeding events of birds in relation to spring temperature and environmental phenology |
| 1978 | Egil Sakshaug | Dr. philos Botany | The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton |
| 1980 | Arnfinn Langeland | Dr. philos Zoology | Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake |
| 1980 | Helge Reinertsen | Dr. philos Botany | The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton |
| 1982 | Gunn Mari Olsen | Dr. scient Botany | Gravitropism in roots of <i>Pisum sativum</i> and <i>Arabidopsis thaliana</i> |
| 1982 | Dag Dolmen | Dr. philos Zoology | Life aspects of two sympatric species of newts (<i>Triturus</i> , <i>Amphibia</i>) in Norway, with special emphasis on their ecological niche segregation |
| 1984 | Eivin Røskaft | Dr. philos Zoology | Sociobiological studies of the rook <i>Corvus frugilegus</i> |
| 1984 | Anne Margrethe Cameron | Dr. scient Botany | Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinizing hormone in male mature rats |
| 1984 | Asbjørn Magne Nilsen | Dr. scient Botany | Alveolar macrophages from expectorates – Biological monitoring of workers exposed to occupational air pollution. An evaluation of the AM-test |
| 1985 | Jarle Mork | Dr. philos Zoology | Biochemical genetic studies in fish |
| 1985 | John Solem | Dr. philos Zoology | Taxonomy, distribution and ecology of caddisflies (<i>Trichoptera</i>) in the Dovrefjell mountains |
| 1985 | Randi E. Reinertsen | Dr. philos Zoology | Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds |
| 1986 | Bernt-Erik Sæther | Dr. philos Zoology | Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach |
| 1986 | Torleif Holthe | Dr. philos Zoology | Evolution, systematics, nomenclature, and zoogeography in the polychaete orders <i>Oweniimorpha</i> and <i>Terebellomorpha</i> , with special reference to the Arctic and Scandinavian fauna |
| 1987 | Helene Lampe | Dr. scient Zoology | The function of bird song in mate attraction and territorial defence, and the importance of song repertoires |
| 1987 | Olav Hogstad | Dr. philos Zoology | Winter survival strategies of the Willow tit <i>Parus montanus</i> |
| 1987 | Jarle Inge Holten | Dr. philos Botany | Autecological investigations along a coast-inland transect at Nord-Møre, Central Norway |

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| 1987 | Rita Kumar | Dr. scient Botany | Somaclonal variation in plants regenerated from cell cultures of <i>Nicotiana sanderae</i> and <i>Chrysanthemum morifolium</i> |
| 1987 | Bjørn Åge Tømmerås | Dr. scient Zoology | Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction |
| 1988 | Hans Christian Pedersen | Dr. philos Zoology | Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care |
| 1988 | Tor G. Heggberget | Dr. philos Zoology | Reproduction in Atlantic Salmon (<i>Salmo salar</i>): Aspects of spawning, incubation, early life history and population structure |
| 1988 | Marianne V. Nielsen | Dr. scient Zoology | The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (<i>Mytilus edulis</i>) |
| 1988 | Ole Kristian Berg | Dr. scient Zoology | The formation of landlocked Atlantic salmon (<i>Salmo salar</i> L.) |
| 1989 | John W. Jensen | Dr. philos Zoology | Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth |
| 1989 | Helga J. Vivås | Dr. scient Zoology | Theoretical models of activity pattern and optimal foraging: Predictions for the Moose <i>Alces alces</i> |
| 1989 | Reidar Andersen | Dr. scient Zoology | Interactions between a generalist herbivore, the moose <i>Alces alces</i> , and its winter food resources: a study of behavioural variation |
| 1989 | Kurt Ingar Draget | Dr. scient Botany | Alginate gel media for plant tissue culture |
| 1990 | Bengt Finstad | Dr. scient Zoology | Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season |
| 1990 | Hege Johannesen | Dr. scient Zoology | Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung |
| 1990 | Åse Krøkje | Dr. scient Botany | The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test |
| 1990 | Arne Johan Jensen | Dr. philos Zoology | Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmon (<i>Salmo salar</i>) and brown trout (<i>Salmo trutta</i>): A summary of studies in Norwegian streams |
| 1990 | Tor Jørgen Almaas | Dr. scient Zoology | Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues |
| 1990 | Magne Husby | Dr. scient Zoology | Breeding strategies in birds: Experiments with the Magpie <i>Pica pica</i> |
| 1991 | Tor Kvam | Dr. scient Zoology | Population biology of the European lynx (<i>Lynx lynx</i>) in Norway |
| 1991 | Jan Henning L'Abêe Lund | Dr. philos Zoology | Reproductive biology in freshwater fish, brown trout <i>Salmo trutta</i> and roach <i>Rutilus rutilus</i> in particular |
| 1991 | Asbjørn Moen | Dr. philos Botany | The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands |
| 1991 | Else Marie Løbersli | Dr. scient Botany | Soil acidification and metal uptake in plants |
| 1991 | Trond Nordtug | Dr. scient Zoology | Reflectometric studies of photomechanical adaptation in superposition eyes of arthropods |
| 1991 | Thyra Solem | Dr. scient Botany | Age, origin and development of blanket mires in Central Norway |

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| 1991 | Odd Terje Sandlund | Dr. philos Zoology | The dynamics of habitat use in the salmonid genera <i>Coregonus</i> and <i>Salvelinus</i> : Ontogenic niche shifts and polymorphism |
| 1991 | Nina Jonsson | Dr. philos Zoology | Aspects of migration and spawning in salmonids |
| 1991 | Atle Bones | Dr. scient Botany | Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase) |
| 1992 | Torggrim Breiehagen | Dr. scient Zoology | Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher |
| 1992 | Anne Kjersti Bakken | Dr. scient Botany | The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (<i>Phleum pratense</i> L.) |
| 1992 | Tycho Anker-Nilssen | Dr. scient Zoology | Food supply as a determinant of reproduction and population development in Norwegian Puffins <i>Fratercula arctica</i> |
| 1992 | Bjørn Munro Jenssen | Dr. philos Zoology | Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks |
| 1992 | Arne Vollan Aarset | Dr. philos Zoology | The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans. |
| 1993 | Geir Slupphaug | Dr. scient Botany | Regulation and expression of uracil-DNA glycosylase and O ⁶ -methylguanine-DNA methyltransferase in mammalian cells |
| 1993 | Tor Fredrik Næsje | Dr. scient Zoology | Habitat shifts in coregonids. |
| 1993 | Yngvar Asbjørn Olsen | Dr. scient Zoology | Cortisol dynamics in Atlantic salmon, <i>Salmo salar</i> L.: Basal and stressor-induced variations in plasma levels and some secondary effects. |
| 1993 | Bård Pedersen | Dr. scient Botany | Theoretical studies of life history evolution in modular and clonal organisms |
| 1993 | Ole Petter Thangstad | Dr. scient Botany | Molecular studies of myrosinase in Brassicaceae |
| 1993 | Thrine L. M. Heggberget | Dr. scient Zoology | Reproductive strategy and feeding ecology of the Eurasian otter <i>Lutra lutra</i> . |
| 1993 | Kjetil Bevanger | Dr. scient Zoology | Avian interactions with utility structures, a biological approach. |
| 1993 | Kåre Haugan | Dr. scient Botany | Mutations in the replication control gene trfA of the broad host-range plasmid RK2 |
| 1994 | Peder Fiske | Dr. scient Zoology | Sexual selection in the lekking great snipe (<i>Gallinago media</i>): Male mating success and female behaviour at the lek |
| 1994 | Kjell Inge Reitan | Dr. scient Botany | Nutritional effects of algae in first-feeding of marine fish larvae |
| 1994 | Nils Røv | Dr. scient Zoology | Breeding distribution, population status and regulation of breeding numbers in the northeast-Atlantic Great Cormorant <i>Phalacrocorax carbo carbo</i> |
| 1994 | Annette-Susanne Hoepfner | Dr. scient Botany | Tissue culture techniques in propagation and breeding of Red Raspberry (<i>Rubus idaeus</i> L.) |
| 1994 | Inga Elise Bruteig | Dr. scient Botany | Distribution, ecology and biomonitoring studies of epiphytic lichens on conifers |
| 1994 | Geir Johnsen | Dr. scient Botany | Light harvesting and utilization in marine phytoplankton: Species-specific and photoadaptive responses |

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| 1994 | Morten Bakken | Dr. scient Zoology | Infanticidal behaviour and reproductive performance in relation to competition capacity among farmed silver fox vixens, <i>Vulpes vulpes</i> |
| 1994 | Arne Moksnes | Dr. philos Zoology | Host adaptations towards brood parasitism by the Cuckoo |
| 1994 | Solveig Bakken | Dr. scient Botany | Growth and nitrogen status in the moss <i>Dicranum majus</i> Sm. as influenced by nitrogen supply |
| 1994 | Torbjørn Forseth | Dr. scient Zoology | Bioenergetics in ecological and life history studies of fishes. |
| 1995 | Olav Vadstein | Dr. philos Botany | The role of heterotrophic planktonic bacteria in the cycling of phosphorus in lakes: Phosphorus requirement, competitive ability and food web interactions |
| 1995 | Hanne Christensen | Dr. scient Zoology | Determinants of Otter <i>Lutra lutra</i> distribution in Norway: Effects of harvest, polychlorinated biphenyls (PCBs), human population density and competition with mink <i>Mustela vison</i> |
| 1995 | Svein Håkon Lorentsen | Dr. scient Zoology | Reproductive effort in the Antarctic Petrel <i>Thalassoica antarctica</i> ; the effect of parental body size and condition |
| 1995 | Chris Jørgen Jensen | Dr. scient Zoology | The surface electromyographic (EMG) amplitude as an estimate of upper trapezius muscle activity |
| 1995 | Martha Kold Bakkevig | Dr. scient Zoology | The impact of clothing textiles and construction in a clothing system on thermoregulatory responses, sweat accumulation and heat transport |
| 1995 | Vidar Moen | Dr. scient Zoology | Distribution patterns and adaptations to light in newly introduced populations of <i>Mysis relicta</i> and constraints on Cladoceran and Char populations |
| 1995 | Hans Haavardsholm Blom | Dr. philos Botany | A revision of the <i>Schistidium apocarpum</i> complex in Norway and Sweden |
| 1996 | Jorun Skjærmo | Dr. scient Botany | Microbial ecology of early stages of cultivated marine fish; impact fish-bacterial interactions on growth and survival of larvae |
| 1996 | Ola Ugedal | Dr. scient Zoology | Radiocesium turnover in freshwater fishes |
| 1996 | Ingibjörg Einarsdottir | Dr. scient Zoology | Production of Atlantic salmon (<i>Salmo salar</i>) and Arctic charr (<i>Salvelinus alpinus</i>): A study of some physiological and immunological responses to rearing routines |
| 1996 | Christina M. S. Pereira | Dr. scient Zoology | Glucose metabolism in salmonids: Dietary effects and hormonal regulation |
| 1996 | Jan Fredrik Børseth | Dr. scient Zoology | The sodium energy gradients in muscle cells of <i>Mytilus edulis</i> and the effects of organic xenobiotics |
| 1996 | Gunnar Henriksen | Dr. scient Zoology | Status of Grey seal <i>Halichoerus grypus</i> and Harbour seal <i>Phoca vitulina</i> in the Barents sea region |
| 1997 | Gunvor Øie | Dr. scient Botany | Evaluation of rotifer <i>Brachionus plicatilis</i> quality in early first feeding of turbot <i>Scophthalmus maximus</i> L. larvae |
| 1997 | Håkon Holien | Dr. scient Botany | Studies of lichens in spruce forest of Central Norway. Diversity, old growth species and the relationship to site and stand parameters |
| 1997 | Ole Reitan | Dr. scient Zoology | Responses of birds to habitat disturbance due to damming |
| 1997 | Jon Arne Grøttum | Dr. scient Zoology | Physiological effects of reduced water quality on fish in aquaculture |

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| 1997 | Per Gustav Thingstad | Dr. scient Zoology | Birds as indicators for studying natural and human-induced variations in the environment, with special emphasis on the suitability of the Pied Flycatcher |
| 1997 | Torgeir Nygård | Dr. scient Zoology | Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as |
| 1997 | Signe Nybø | Dr. scient Zoology | Impacts of long-range transported air pollution on birds with particular reference to the dipper <i>Cinclus cinclus</i> in southern Norway |
| 1997 | Atle Wibe | Dr. scient Zoology | Identification of conifer volatiles detected by receptor neurons in the pine weevil (<i>Hylobius abietis</i>), analysed by gas chromatography linked to electrophysiology and to mass spectrometry |
| 1997 | Rolv Lundheim | Dr. scient Zoology | Adaptive and incidental biological ice nucleators |
| 1997 | Arild Magne Landa | Dr. scient Zoology | Wolverines in Scandinavia: ecology, sheep depredation and conservation |
| 1997 | Kåre Magne Nielsen | Dr. scient Botany | An evolution of possible horizontal gene transfer from plants to soil bacteria by studies of natural transformation in <i>Acinetobacter calcoaceticus</i> |
| 1997 | Jarle Tufto | Dr. scient Zoology | Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models |
| 1997 | Trygve Hesthagen | Dr. philos Zoology | Population responses of Arctic charr (<i>Salvelinus alpinus</i> (L.)) and brown trout (<i>Salmo trutta</i> L.) to acidification in Norwegian inland waters |
| 1997 | Trygve Sigholt | Dr. philos Zoology | Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (<i>Salmo salar</i>) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet |
| 1997 | Jan Østnes | Dr. scient Zoology | Cold sensation in adult and neonate birds |
| 1998 | Seethaledsumy Visvalingam | Dr. scient Botany | Influence of environmental factors on myrosinases and myrosinase-binding proteins |
| 1998 | Thor Harald Ringsby | Dr. scient Zoology | Variation in space and time: The biology of a House sparrow metapopulation |
| 1998 | Erling Johan Solberg | Dr. scient Zoology | Variation in population dynamics and life history in a Norwegian moose (<i>Alces alces</i>) population: consequences of harvesting in a variable environment |
| 1998 | Sigurd Mjøen Saastad | Dr. scient Botany | Species delimitation and phylogenetic relationships between the <i>Sphagnum recurvum</i> complex (Bryophyta): genetic variation and phenotypic plasticity |
| 1998 | Bjarte Mortensen | Dr. scient Botany | Metabolism of volatile organic chemicals (VOCs) in a head liver S9 vial equilibration system in vitro |
| 1998 | Gunnar Austrheim | Dr. scient Botany | Plant biodiversity and land use in subalpine grasslands. – A conservation biological approach |
| 1998 | Bente Gunnveig Berg | Dr. scient Zoology | Encoding of pheromone information in two related moth species |
| 1999 | Kristian Overskaug | Dr. scient Zoology | Behavioural and morphological characteristics in Northern Tawny Owls <i>Strix aluco</i> : An intra- and interspecific comparative approach |
| 1999 | Hans Kristen Stenøien | Dr. scient Botany | Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts) |
| 1999 | Trond Arnesen | Dr. scient Botany | Vegetation dynamics following trampling and burning in the outlying haylands at Sølendet, Central Norway |

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| 1999 | Ingvar Stenberg | Dr. scient Zoology | Habitat selection, reproduction and survival in the White-backed Woodpecker <i>Dendrocopos leucotos</i> |
| 1999 | Stein Olle Johansen | Dr. scient Botany | A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis |
| 1999 | Trina Falck Galloway | Dr. scient Zoology | Muscle development and growth in early life stages of the Atlantic cod (<i>Gadus morhua</i> L.) and Halibut (<i>Hippoglossus hippoglossus</i> L.) |
| 1999 | Marianne Giæver | Dr. scient Zoology | Population genetic studies in three gadoid species: blue whiting (<i>Micromisistius poutassou</i>), haddock (<i>Melanogrammus aeglefinus</i>) and cod (<i>Gadus morhua</i>) in the North-East Atlantic |
| 1999 | Hans Martin Hanslin | Dr. scient Botany | The impact of environmental conditions of density dependent performance in the boreal forest bryophytes <i>Dicranum majus</i> , <i>Hylocomium splendens</i> , <i>Plagiochila asplenigides</i> , <i>Ptilium crista-castrensis</i> and <i>Rhytidiadelphus lokeus</i> |
| 1999 | Ingrid Bysveen Mjølnørød | Dr. scient Zoology | Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (<i>Salmo salar</i>) revealed by molecular genetic techniques |
| 1999 | Else Berit Skagen | Dr. scient Botany | The early regeneration process in protoplasts from <i>Brassica napus</i> hypocotyls cultivated under various g-forces |
| 1999 | Stein-Are Sæther | Dr. philos Zoology | Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe |
| 1999 | Katrine Wangen Rustad | Dr. scient Zoology | Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease |
| 1999 | Per Terje Smiseth | Dr. scient Zoology | Social evolution in monogamous families: |
| 1999 | Gunnbjørn Bremset | Dr. scient Zoology | Young Atlantic salmon (<i>Salmo salar</i> L.) and Brown trout (<i>Salmo trutta</i> L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions |
| 1999 | Frode Ødegaard | Dr. scient Zoology | Host specificity as a parameter in estimates of arthropod species richness |
| 1999 | Sonja Andersen | Dr. scient Zoology | Expressional and functional analyses of human, secretory phospholipase A2 |
| 2000 | Ingrid Salvesen | Dr. scient Botany | Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture |
| 2000 | Ingar Jostein Øien | Dr. scient Zoology | The Cuckoo (<i>Cuculus canorus</i>) and its host: adaptations and counteradaptations in a coevolutionary arms race |
| 2000 | Pavlos Makridis | Dr. scient Botany | Methods for the microbial control of live food used for the rearing of marine fish larvae |
| 2000 | Sigbjørn Stokke | Dr. scient Zoology | Sexual segregation in the African elephant (<i>Loxodonta africana</i>) |
| 2000 | Odd A. Gulseth | Dr. philos Zoology | Seawater tolerance, migratory behaviour and growth of Charr, (<i>Salvelinus alpinus</i>), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard |
| 2000 | Pål A. Olsvik | Dr. scient Zoology | Biochemical impacts of Cd, Cu and Zn on brown trout (<i>Salmo trutta</i>) in two mining-contaminated rivers in Central Norway |
| 2000 | Sigurd Einum | Dr. scient Zoology | Maternal effects in fish: Implications for the evolution of breeding time and egg size |
| 2001 | Jan Ove Evjemo | Dr. scient Zoology | Production and nutritional adaptation of the brine shrimp <i>Artemia</i> sp. as live food organism for larvae of marine cold water fish species |

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| 2001 | Olga Hilmo | Dr. scient Botany | Lichen response to environmental changes in the managed boreal forest systems |
| 2001 | Ingebrigt Uglem | Dr. scient Zoology | Male dimorphism and reproductive biology in corkwing wrasse (<i>Symphodus melops</i> L.) |
| 2001 | Bård Gunnar Stokke | Dr. scient Zoology | Coevolutionary adaptations in avian brood parasites and their hosts |
| 2002 | Ronny Aanes | Dr. scient Zoology | Spatio-temporal dynamics in Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>) |
| 2002 | Mariann Sandsund | Dr. scient Zoology | Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses |
| 2002 | Dag-Inge Øien | Dr. scient Botany | Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway |
| 2002 | Frank Rosell | Dr. scient Zoology | The function of scent marking in beaver (<i>Castor fiber</i>) |
| 2002 | Janne Østvang | Dr. scient Botany | The Role and Regulation of Phospholipase A ₂ in Monocytes During Atherosclerosis Development |
| 2002 | Terje Thun | Dr. philos Biology | Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material |
| 2002 | Birgit Hafjeld Borgen | Dr. scient Biology | Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth |
| 2002 | Bård Øyvind Solberg | Dr. scient Biology | Effects of climatic change on the growth of dominating tree species along major environmental gradients |
| 2002 | Per Winge | Dr. scient Biology | The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in <i>Arabidopsis thaliana</i> and the Ral GTPase from <i>Drosophila melanogaster</i> |
| 2002 | Henrik Jensen | Dr. scient Biology | Causes and consequences of individual variation in fitness-related traits in house sparrows |
| 2003 | Jens Rohloff | Dr. philos Biology | Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control |
| 2003 | Åsa Maria O. Espmark Wibe | Dr. scient Biology | Behavioural effects of environmental pollution in threespine stickleback <i>Gasterosteus aculeatur</i> L. |
| 2003 | Dagmar Hagen | Dr. scient Biology | Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach |
| 2003 | Bjørn Dahle | Dr. scient Biology | Reproductive strategies in Scandinavian brown bears |
| 2003 | Cyril Lebogang Taolo | Dr. scient Biology | Population ecology, seasonal movement and habitat use of the African buffalo (<i>Syncerus caffer</i>) in Chobe National Park, Botswana |
| 2003 | Marit Stranden | Dr. scient Biology | Olfactory receptor neurones specified for the same odorants in three related Heliothine species (<i>Helicoverpa armigera</i> , <i>Helicoverpa assulta</i> and <i>Heliothis virescens</i>) |
| 2003 | Kristian Hassel | Dr. scient Biology | Life history characteristics and genetic variation in an expanding species, <i>Pogonatum dentatum</i> |
| 2003 | David Alexander Rae | Dr. scient Biology | Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Arctic environments |
| 2003 | Åsa A Borg | Dr. scient Biology | Sex roles and reproductive behaviour in gobies and guppies: a female perspective |
| 2003 | Eldar Åsgard Bendiksen | Dr. scient Biology | Environmental effects on lipid nutrition of farmed Atlantic salmon (<i>Salmo salar</i> L.) parr and smolt |
| 2004 | Torkild Bakken | Dr. scient Biology | A revision of Nereidinae (Polychaeta, Nereididae) |

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|------|----------------------------|-----------------------|--|
| 2004 | Ingar Pareliusson | Dr. scient Biology | Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar |
| 2004 | Tore Brembu | Dr. scient Biology | Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in <i>Arabidopsis thaliana</i> |
| 2004 | Liv S. Nilsen | Dr. scient Biology | Coastal heath vegetation on central Norway; recent past, present state and future possibilities |
| 2004 | Hanne T. Skiri | Dr. scient Biology | Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (<i>Heliothis virescens</i> , <i>Helicoverpa armigera</i> and <i>Helicoverpa assulta</i>) |
| 2004 | Lene Østby | Dr. scient Biology | Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment |
| 2004 | Emmanuel J. Gerreta | Dr. philos Biology | The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania |
| 2004 | Linda Dalen | Dr. scient Biology | Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming |
| 2004 | Lisbeth Mehli | Dr. scient Biology | Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (<i>Fragaria x ananassa</i>): characterisation and induction of the gene following fruit infection by <i>Botrytis cinerea</i> |
| 2004 | Børge Moe | Dr. scient Biology | Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage |
| 2005 | Matilde Skogen Chauton | Dr. scient Biology | Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples |
| 2005 | Sten Karlsson | Dr. scient Biology | Dynamics of Genetic Polymorphisms |
| 2005 | Terje Bongard | Dr. scient Biology | Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period |
| 2005 | Tonette Røstelién | PhD Biology | Functional characterisation of olfactory receptor neurone types in heliothine moths |
| 2005 | Erlend Kristiansen | Dr. scient Biology | Studies on antifreeze proteins |
| 2005 | Eugen G. Sørmo | Dr. scient Biology | Organochlorine pollutants in grey seal (<i>Halichoerus grypus</i>) pups and their impact on plasma thyroid hormone and vitamin A concentrations |
| 2005 | Christian Westad | Dr. scient Biology | Motor control of the upper trapezius |
| 2005 | Lasse Mork Olsen | PhD Biology | Interactions between marine osmo- and phagotrophs in different physicochemical environments |
| 2005 | Åslaug Viken | PhD Biology | Implications of mate choice for the management of small populations |
| 2005 | Ariaya Hymete Sahle Dingle | PhD Biology | Investigation of the biological activities and chemical constituents of selected <i>Echinops</i> spp. growing in Ethiopia |
| 2005 | Anders Gravbrot Finstad | PhD Biology | Salmonid fishes in a changing climate: The winter challenge |
| 2005 | Shimane Washington Makabu | PhD Biology | Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana |
| 2005 | Kjartan Østbye | Dr. scient Biology | The European whitefish <i>Coregonus lavaretus</i> (L.) species complex: historical contingency and adaptive radiation |

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|------|---------------------------|-----------------------|--|
| 2006 | Kari Mette Murvoll | PhD Biology | Levels and effects of persistent organic pollutants (POPs) in seabirds, Retinoids and α -tocopherol – potential biomarkers of POPs in birds? |
| 2006 | Ivar Herfindal | Dr. scient Biology | Life history consequences of environmental variation along ecological gradients in northern ungulates |
| 2006 | Nils Egil Tokle | PhD Biology | Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on <i>Calanus finmarchicus</i> |
| 2006 | Jan Ove Gjershaug | Dr. philos Biology | Taxonomy and conservation status of some booted eagles in south-east Asia |
| 2006 | Jon Kristian Skei | Dr. scient Biology | Conservation biology and acidification problems in the breeding habitat of amphibians in Norway |
| 2006 | Johanna Järnegren | PhD Biology | <i>Acesta oophaga</i> and <i>Acesta excavata</i> – a study of hidden biodiversity |
| 2006 | Bjørn Henrik Hansen | PhD Biology | Metal-mediated oxidative stress responses in brown trout (<i>Salmo trutta</i>) from mining contaminated rivers in Central Norway |
| 2006 | Vidar Grøtan | PhD Biology | Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates |
| 2006 | Jafari R Kideghesho | PhD Biology | Wildlife conservation and local land use conflicts in Western Serengeti Corridor, Tanzania |
| 2006 | Anna Maria Billing | PhD Biology | Reproductive decisions in the sex role reversed pipefish <i>Syngnathus typhle</i> : when and how to invest in reproduction |
| 2006 | Henrik Pärn | PhD Biology | Female ornaments and reproductive biology in the bluethroat |
| 2006 | Anders J. Fjellheim | PhD Biology | Selection and administration of probiotic bacteria to marine fish larvae |
| 2006 | P. Andreas Svensson | PhD Biology | Female coloration, egg carotenoids and reproductive success: gobies as a model system |
| 2007 | Sindre A. Pedersen | PhD Biology | Metal binding proteins and antifreeze proteins in the beetle <i>Tenebrio molitor</i> - a study on possible competition for the semi-essential amino acid cysteine |
| 2007 | Kasper Hancke | PhD Biology | Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae |
| 2007 | Tomas Holmern | PhD Biology | Bushmeat hunting in the western Serengeti: Implications for community-based conservation |
| 2007 | Kari Jørgensen | PhD Biology | Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth <i>Heliothis virescens</i> |
| 2007 | Stig Ulland | PhD Biology | Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (<i>Mamestra brassicae</i> L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry |
| 2007 | Snorre Henriksen | PhD Biology | Spatial and temporal variation in herbivore resources at northern latitudes |
| 2007 | Roelof Frans May | PhD Biology | Spatial Ecology of Wolverines in Scandinavia |
| 2007 | Vedasto Gabriel Ndibalema | PhD Biology | Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania |
| 2007 | Julius William Nyahongo | PhD Biology | Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania |

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| 2007 | Shombe Ntaraluka Hassan | PhD Biology | Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania |
| 2007 | Per-Arvid Wold | PhD Biology | Functional development and response to dietary treatment in larval Atlantic cod (<i>Gadus morhua</i> L.) Focus on formulated diets and early weaning |
| 2007 | Anne Skjetne Mortensen | PhD Biology | Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios |
| 2008 | Brage Bremset Hansen | PhD Biology | The Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>) and its food base: plant-herbivore interactions in a high-arctic ecosystem |
| 2008 | Jiska van Dijk | PhD Biology | Wolverine foraging strategies in a multiple-use landscape |
| 2008 | Flora John Magige | PhD Biology | The ecology and behaviour of the Masai Ostrich (<i>Struthio camelus massaicus</i>) in the Serengeti Ecosystem, Tanzania |
| 2008 | Bernt Rønning | PhD Biology | Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, <i>Taeniopygia guttata</i> |
| 2008 | Sølvi Wehn | PhD Biology | Biodiversity dynamics in semi-natural mountain landscapes - A study of consequences of changed agricultural practices in Eastern Jotunheimen |
| 2008 | Trond Moxness Kortner | PhD Biology | The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (<i>Gadus morhua</i>): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations |
| 2008 | Katarina Mariann Jørgensen | Dr. scient Biology | The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation |
| 2008 | Tommy Jørstad | PhD Biology | Statistical Modelling of Gene Expression Data |
| 2008 | Anna Kusnierczyk | PhD Biology | <i>Arabidopsis thaliana</i> Responses to Aphid Infestation |
| 2008 | Jussi Evertsen | PhD Biology | Herbivore sacoglossans with photosynthetic chloroplasts |
| 2008 | John Eilif Hermansen | PhD Biology | Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania |
| 2008 | Ragnhild Lyngved | PhD Biology | Somatic embryogenesis in <i>Cyclamen persicum</i> . Biological investigations and educational aspects of cloning |
| 2008 | Line Elisabeth Sundt-Hansen | PhD Biology | Cost of rapid growth in salmonid fishes |
| 2008 | Line Johansen | PhD Biology | Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution |
| 2009 | Astrid Jullumstrø Feuerherm | PhD Biology | Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease |
| 2009 | Pål Kvello | PhD Biology | Neurons forming the network involved in gustatory coding and learning in the moth <i>Heliothis virescens</i> : Physiological and morphological characterisation, and integration into a standard brain atlas |
| 2009 | Trygve Devold Kjellsen | PhD Biology | Extreme Frost Tolerance in Boreal Conifers |
| 2009 | Johan Reinert Vikan | PhD Biology | Coevolutionary interactions between common cuckoos <i>Cuculus canorus</i> and <i>Fringilla</i> finches |

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| 2009 | Zsolt Volent | PhD Biology | Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter |
| 2009 | Lester Rocha | PhD Biology | Functional responses of perennial grasses to simulated grazing and resource availability |
| 2009 | Dennis Ikanda | PhD Biology | Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (<i>Panthera leo</i>) in Tanzania |
| 2010 | Huy Quang Nguyen | PhD Biology | Egg characteristics and development of larval digestive function of cobia (<i>Rachycentron canadum</i>) in response to dietary treatments - Focus on formulated diets |
| 2010 | Eli Kvingedal | PhD Biology | Intraspecific competition in stream salmonids: the impact of environment and phenotype |
| 2010 | Sverre Lundemo | PhD Biology | Molecular studies of genetic structuring and demography in <i>Arabidopsis</i> from Northern Europe |
| 2010 | Iddi Mihijai Mfunda | PhD Biology | Wildlife Conservation and People's livelihoods: Lessons Learnt and Considerations for Improvements. The Case of Serengeti Ecosystem, Tanzania |
| 2010 | Anton Tinchov Antonov | PhD Biology | Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis |
| 2010 | Anders Lyngstad | PhD Biology | Population Ecology of <i>Eriophorum latifolium</i> , a Clonal Species in Rich Fen Vegetation |
| 2010 | Hilde Færevik | PhD Biology | Impact of protective clothing on thermal and cognitive responses |
| 2010 | Ingerid Brænne Arbo | PhD Medical technology | Nutritional lifestyle changes – effects of dietary carbohydrate restriction in healthy obese and overweight humans |
| 2010 | Yngvild Vindenes | PhD Biology | Stochastic modeling of finite populations with individual heterogeneity in vital parameters |
| 2010 | Hans-Richard Brattbakk | PhD Medical technology | The effect of macronutrient composition, insulin stimulation, and genetic variation on leukocyte gene expression and possible health benefits |
| 2011 | Geir Hysing Bolstad | PhD Biology | Evolution of Signals: Genetic Architecture, Natural Selection and Adaptive Accuracy |
| 2011 | Karen de Jong | PhD Biology | Operational sex ratio and reproductive behaviour in the two-spotted goby (<i>Gobiusculus flavescens</i>) |
| 2011 | Ann-Iren Kittang | PhD Biology | <i>Arabidopsis thaliana</i> L. adaptation mechanisms to microgravity through the EMCS MULTIGEN-2 experiment on the ISS: The science of space experiment integration and adaptation to simulated microgravity |
| 2011 | Aline Magdalena Lee | PhD Biology | Stochastic modeling of mating systems and their effect on population dynamics and genetics |
| 2011 | Christopher Gravningen Sørmo | PhD Biology | Rho GTPases in Plants: Structural analysis of ROP GTPases; genetic and functional studies of MIRO GTPases in <i>Arabidopsis thaliana</i> |
| 2011 | Grethe Robertsen | PhD Biology | Relative performance of salmonid phenotypes across environments and competitive intensities |
| 2011 | Line-Kristin Larsen | PhD Biology | Life-history trait dynamics in experimental populations of guppy (<i>Poecilia reticulata</i>): the role of breeding regime and captive environment |
| 2011 | Maxim A. K. Teichert | PhD Biology | Regulation in Atlantic salmon (<i>Salmo salar</i>): The interaction between habitat and density |

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| 2011 | Torunn Beate Hancke | PhD Biology | Use of Pulse Amplitude Modulated (PAM) Fluorescence and Bio-optics for Assessing Microalgal Photosynthesis and Physiology |
| 2011 | Sajeda Begum | PhD Biology | Brood Parasitism in Asian Cuckoos: Different Aspects of Interactions between Cuckoos and their Hosts in Bangladesh |
| 2011 | Kari J. K. Attramadal | PhD Biology | Water treatment as an approach to increase microbial control in the culture of cold water marine larvae |
| 2011 | Camilla Kalvatn Egset | PhD Biology | The Evolvability of Static Allometry: A Case Study |
| 2011 | AHM Raihan Sarker | PhD Biology | Conflict over the conservation of the Asian elephant (<i>Elephas maximus</i>) in Bangladesh |
| 2011 | Gro Dehli Villanger | PhD Biology | Effects of complex organohalogen contaminant mixtures on thyroid hormone homeostasis in selected arctic marine mammals |
| 2011 | Kari Bjørneraas | PhD Biology | Spatiotemporal variation in resource utilisation by a large herbivore, the moose |
| 2011 | John Odden | PhD Biology | The ecology of a conflict: Eurasian lynx depredation on domestic sheep |
| 2011 | Simen Pedersen | PhD Biology | Effects of native and introduced cervids on small mammals and birds |
| 2011 | Mohsen Falahati-Anbaran | PhD Biology | Evolutionary consequences of seed banks and seed dispersal in <i>Arabidopsis</i> |
| 2012 | Jakob Hønborg Hansen | PhD Biology | Shift work in the offshore vessel fleet: circadian rhythms and cognitive performance |
| 2012 | Elin Noreen | PhD Biology | Consequences of diet quality and age on life-history traits in a small passerine bird |
| 2012 | Irja Ida Ratikainen | PhD Biology | Foraging in a variable world: adaptations to stochasticity |
| 2012 | Aleksander Handå | PhD Biology | Cultivation of mussels (<i>Mytilus edulis</i>): Feed requirements, storage and integration with salmon (<i>Salmo salar</i>) farming |
| 2012 | Morten Kraabøl | PhD Biology | Reproductive and migratory challenges inflicted on migrant brown trout (<i>Salmo trutta</i> L.) in a heavily modified river |
| 2012 | Jisca Huisman | PhD Biology | Gene flow and natural selection in Atlantic salmon |
| 2012 | Maria Bergvik | PhD Biology | Lipid and astaxanthin contents and biochemical post-harvest stability in <i>Calanus finmarchicus</i> |
| 2012 | Bjarte Bye Løfaldli | PhD Biology | Functional and morphological characterization of central olfactory neurons in the model insect <i>Heliothis virescens</i> . |
| 2012 | Karen Marie Hammer | PhD Biology | Acid-base regulation and metabolite responses in shallow- and deep-living marine invertebrates during environmental hypercapnia |
| 2012 | Øystein Nordrum Wiggen | PhD Biology | Optimal performance in the cold |
| 2012 | Robert Dominikus Fyumagwa | Dr. Philos Biology | Anthropogenic and natural influence on disease prevalence at the human –livestock-wildlife interface in the Serengeti ecosystem, Tanzania |
| 2012 | Jenny Bytingsvik | PhD Biology | Organohalogenated contaminants (OHCs) in polar bear mother-cub pairs from Svalbard, Norway. Maternal transfer, exposure assessment and thyroid hormone disruptive effects in polar bear cubs |
| 2012 | Christer Moe Rolandsen | PhD Biology | The ecological significance of space use and movement patterns of moose in a variable environment |

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| 2012 | Erlend Kjeldsberg Hovland | PhD Biology | Bio-optics and Ecology in <i>Emiliania huxleyi</i> Blooms: Field and Remote Sensing Studies in Norwegian Waters |
| 2012 | Lise Cats Myhre | PhD Biology | Effects of the social and physical environment on mating behaviour in a marine fish |
| 2012 | Tonje Aronsen | PhD Biology | Demographic, environmental and evolutionary aspects of sexual selection |
| 2012 | Bin Liu | PhD Biology | Molecular genetic investigation of cell separation and cell death regulation in <i>Arabidopsis thaliana</i> |
| 2013 | Jørgen Rosvold | PhD Biology | Ungulates in a dynamic and increasingly human dominated landscape – A millennia-scale perspective |
| 2013 | Pankaj Barah | PhD Biology | Integrated Systems Approaches to Study Plant Stress Responses |
| 2013 | Marit Linnerud | PhD Biology | Patterns in spatial and temporal variation in population abundances of vertebrates |
| 2013 | Xinxin Wang | PhD Biology | Integrated multi-trophic aquaculture driven by nutrient wastes released from Atlantic salmon (<i>Salmo salar</i>) farming |
| 2013 | Ingrid Ertshus Mathisen | PhD Biology | Structure, dynamics, and regeneration capacity at the sub-arctic forest-tundra ecotone of northern Norway and Kola Peninsula, NW Russia |
| 2013 | Anders Foldvik | PhD Biology | Spatial distributions and productivity in salmonid populations |
| 2013 | Anna Marie Holand | PhD Biology | Statistical methods for estimating intra- and inter-population variation in genetic diversity |
| 2013 | Anna Solvang Båtnes | PhD Biology | Light in the dark – the role of irradiance in the high Arctic marine ecosystem during polar night |
| 2013 | Sebastian Wacker | PhD Biology | The dynamics of sexual selection: effects of OSR, density and resource competition in a fish |
| 2013 | Cecilie Miljeteig | PhD Biology | Phototaxis in <i>Calanus finmarchicus</i> – light sensitivity and the influence of energy reserves and oil exposure |
| 2013 | Ane Kjersti Vie | PhD Biology | Molecular and functional characterisation of the IDA family of signalling peptides in <i>Arabidopsis thaliana</i> |
| 2013 | Marianne Nymark | PhD Biology | Light responses in the marine diatom <i>Phaeodactylum tricorutum</i> |
| 2014 | Jannik Schultner | PhD Biology | Resource Allocation under Stress - Mechanisms and Strategies in a Long-Lived Bird |
| 2014 | Craig Ryan Jackson | PhD Biology | Factors influencing African wild dog (<i>Lycaon pictus</i>) habitat selection and ranging behaviour: conservation and management implications |
| 2014 | Aravind Venkatesan | PhD Biology | Application of Semantic Web Technology to establish knowledge management and discovery in the Life Sciences |
| 2014 | Kristin Collier Valle | PhD Biology | Photoacclimation mechanisms and light responses in marine micro- and macroalgae |
| 2014 | Michael Puffer | PhD Biology | Effects of rapidly fluctuating water levels on juvenile Atlantic salmon (<i>Salmo salar</i> L.) |
| 2014 | Gundula S. Bartzke | PhD Biology | Effects of power lines on moose (<i>Alces alces</i>) habitat selection, movements and feeding activity |
| 2014 | Eirin Marie Bjørkvoll | PhD Biology | Life-history variation and stochastic population dynamics in vertebrates |
| 2014 | Håkon Holand | PhD Biology | The parasite <i>Syngamus trachea</i> in a metapopulation of house sparrows |
| 2014 | Randi Magnus Sommerfelt | PhD Biology | Molecular mechanisms of inflammation – a central role for cytosolic phospholipase A2 |

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| 2014 | Espen Lie Dahl | PhD Biology | Population demographics in white-tailed eagle at an on-shore wind farm area in coastal Norway |
| 2014 | Anders Øverby | PhD Biology | Functional analysis of the action of plant isothiocyanates: cellular mechanisms and in vivo role in plants, and anticancer activity |
| 2014 | Kamal Prasad Acharya | PhD Biology | Invasive species: Genetics, characteristics and trait variation along a latitudinal gradient. |
| 2014 | Ida Beathe Øverjordet | PhD Biology | Element accumulation and oxidative stress variables in Arctic pelagic food chains: <i>Calanus</i> , little auks (<i>Alle alle</i>) and black-legged kittiwakes (<i>Rissa tridactyla</i>) |
| 2014 | Kristin Møller Gabrielsen | PhD Biology | Target tissue toxicity of the thyroid hormone system in two species of arctic mammals carrying high loads of organohalogen contaminants |
| 2015 | Gine Roll Skjervø | Dr. philos Biology | Testing behavioral ecology models with historical individual-based human demographic data from Norway |
| 2015 | Nils Erik Gustaf Forsberg | PhD Biology | Spatial and Temporal Genetic Structure in Landrace Cereals |
| 2015 | Leila Alipanah | PhD Biology | Integrated analyses of nitrogen and phosphorus deprivation in the diatoms <i>Phaeodactylum tricorutum</i> and <i>Seminavis robusta</i> |
| 2015 | Javad Najafi | PhD Biology | Molecular investigation of signaling components in sugar sensing and defense in <i>Arabidopsis thaliana</i> |
| 2015 | Bjørnar Sporsheim | PhD Biology | Quantitative confocal laser scanning microscopy: optimization of in vivo and in vitro analysis of intracellular transport |
| 2015 | Magni Olsen Kyrkjeide | PhD Biology | Genetic variation and structure in peatmosses (<i>Sphagnum</i>) |
| 2015 | Keshuai Li | PhD Biology | Phospholipids in Atlantic cod (<i>Gadus morhua</i> L.) larvae rearing: Incorporation of DHA in live feed and larval phospholipids and the metabolic capabilities of larvae for the de novo synthesis |
| 2015 | Ingvild Fladvad Størdal | PhD Biology | The role of the copepod <i>Calanus finmarchicus</i> in affecting the fate of marine oil spills |
| 2016 | Thomas Kvalnes | PhD Biology | Evolution by natural selection in age-structured populations in fluctuating environments |
| 2016 | Øystein Leiknes | PhD Biology | The effect of nutrition on important life-history traits in the marine copepod <i>Calanus finmarchicus</i> |
| 2016 | Johan Henrik Hårdensson Berntsen | PhD Biology | Individual variation in survival: The effect of incubation temperature on the rate of physiological ageing in a small passerine bird |
| 2016 | Marianne Opsahl Olufsen | PhD Biology | Multiple environmental stressors: Biological interactions between parameters of climate change and perfluorinated alkyl substances in fish |
| 2016 | Rebekka Varne | PhD Biology | Tracing the fate of escaped cod (<i>Gadus morhua</i> L.) in a Norwegian fjord system |
| 2016 | Anette Antonsen Fenstad | PhD Biology | Pollutant Levels, Antioxidants and Potential Genotoxic Effects in Incubating Female Common Eiders (<i>Somateria mollissima</i>) |
| 2016 | Wilfred Njama Marealle | PhD Biology | Ecology, Behaviour and Conservation Status of Masai Giraffe (<i>Giraffa camelopardalis tippelskirchi</i>) in Tanzania |
| 2016 | Ingunn Nilssen | PhD Biology | Integrated Environmental Mapping and Monitoring: A Methodological approach for end users. |
| 2017 | Konika Chawla | PhD Biology | Discovering, analysing and taking care of knowledge. |

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| 2017 | Øystein Hjorthol Opedal | PhD Biology | The Evolution of Herkogamy: Pollinator Reliability, Natural Selection, and Trait Evolvability. |
| 2017 | Ane Marlene Myhre | PhD Biology | Effective size of density dependent populations in fluctuating environments |
| 2017 | Emmanuel Hosiana Masenga | PhD Biology | Behavioural Ecology of Free-ranging and Reintroduced African Wild Dog (<i>Lycaon pictus</i>) Packs in the Serengeti Ecosystem, Tanzania |
| 2017 | Xiaolong Lin | PhD Biology | Systematics and evolutionary history of <i>Tanytarsus</i> van der Wulp, 1874 (Diptera: Chironomidae) |
| 2017 | Emmanuel Clamsen Mmassy | PhD Biology | Ecology and Conservation Challenges of the Kori bustard in the Serengeti National Park |
| 2017 | Richard Daniel Lyamuya | PhD Biology | Depredation of Livestock by Wild Carnivores in the Eastern Serengeti Ecosystem, Tanzania |
| 2017 | Katrin Hoydal | PhD Biology | Levels and endocrine disruptive effects of legacy POPs and their metabolites in long-finned pilot whales of the Faroe Islands |
| 2017 | Berit Glomstad | PhD Biology | Adsorption of phenanthrene to carbon nanotubes and its influence on phenanthrene bioavailability/toxicity in aquatic organism |
| 2017 | Øystein Nordeide Kielland | PhD Biology | Sources of variation in metabolism of an aquatic ectotherm |
| 2017 | Narjes Yousefi | PhD Biology | Genetic divergence and speciation in northern peatmosses (<i>Sphagnum</i>) |
| 2018 | Signe Christensen- Dalgaard | PhD Biology | Drivers of seabird spatial ecology - implications for development of offshore wind-power in Norway |
| 2018 | Janos Urbancsok | PhD Biology | Endogenous biological effects induced by externally supplemented glucosinolate hydrolysis products (GHPs) on <i>Arabidopsis thaliana</i> |
| 2018 | Alice Mühlroth | PhD Biology | The influence of phosphate depletion on lipid metabolism of microalgae |
| 2018 | Franco Peniel Mbise | PhD Biology | Human-Carnivore Coexistence and Conflict in the Eastern Serengeti, Tanzania |
| 2018 | Stine Svalheim Markussen | PhD Biology | Causes and consequences of intersexual life history variation in a harvested herbivore population |
| 2018 | Mia Vedel Sørensen | PhD Biology | Carbon budget consequences of deciduous shrub expansion in alpine tundra ecosystems |
| 2018 | Hanna Maria Kauko | PhD Biology | Light response and acclimation of microalgae in a changing Arctic |
| 2018 | Erlend I. F. Fossen | PhD Biology | Trait evolvability: effects of thermal plasticity and genetic correlations among traits |
| 2019 | Peter Sjolte Ranke | PhD Biology | Demographic and genetic and consequences of dispersal in house sparrows |
| 2019 | Mathilde Le Moullec | PhD Biology | Spatiotemporal variation in abundance of key tundra species: from local heterogeneity to large-scale synchrony |
| 2019 | Endre Grüner Ofstad | PhD Biology | Causes and consequences of variation in resource use and social structure in ungulates |
| 2019 | Yang Jin | PhD Biology | Development of lipid metabolism in early life stage of Atlantic salmon (<i>Salmo salar</i>) |
| 2019 | Elena Albertsen | PhD Biology | Evolution of floral traits: from ecological context to functional integration |
| 2019 | Mominul Islam Nahid | PhD Biology | Interaction between two Asian cuckoos and their hosts in Bangladesh |

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| 2019 | Knut Jørgen Egelie | Phd Biology | Management of intellectual property in university-industry collaborations – public access to and control of knowledge |
| 2019 | Thomas Ray Haaland | Phd Biology | Adaptive responses to environmental stochasticity on different evolutionary time-scales |
| 2019 | Kwaslema Malle Hariohay | Phd Biology | Human wildlife interactions in the Ruaha-Rungwa Ecosystem, Central Tanzania |
| 2019 | Mari Engvig Løseth | Phd Biology | Exposure and effects of emerging and legacy organic pollutants in white-tailed eagle (<i>Haliaeetus albicilla</i>) nestlings |
| 2019 | Joseph Mbyati Mukeka | Phd Biology | Human-Wildlife Conflicts and Compensation for Losses in Kenya: Dynamics, Characteristics and Correlates |
| 2019 | Helene Løvstrand Svarva | Phd Biology | Dendroclimatology in southern Norway: tree rings, demography and climate |
| 2019 | Nathalie Briels | Phd Biology | Exposure and effects of legacy and emerging organic pollutants in developing birds – Laboratory and field studies |
| 2019 | Anders L.Kolstad | Phd Biology | Moose browsing effects on boreal production forests – implications for ecosystems and human society |
| 2019 | Bart Peeters | Phd Biology | Population dynamics under climate change and harvesting: Results from the high Arctic Svalbard reindeer |
| 2019 | Alex Kojo Datsomor | Phd Biology | The molecular basis of long chain polyunsaturated fatty acid (LC-PUFA) biosynthesis in Atlantic salmon (<i>Salmo salar L</i>): In vivo functions, functional redundancy and transcriptional regulation of LC-PUFA biosynthetic enzymes |
| 2020 | Ingun Næve | Phd Biology | Development of non-invasive methods using ultrasound technology in monitoring of Atlantic salmon (<i>Salmo Salar</i>) production and reproduction |
| 2020 | Rachael Morgan | Phd Biology | Physiological plasticity and evolution of thermal performance in zebrafish |
| 2020 | Mahsa Jalili | Phd Biology | Effects of different dietary ingredients on the immune responses and antioxidant status in Atlantic salmon (<i>Salmo salar L.</i>): possible nutrionomics approaches |
| 2020 | Haiqing Wang | Phd Biology | Utilization of the polychaete <i>Hediste diversicolor</i> (O.F. Millier, 1776) in recycling waste nutrients from land-based fish farms for valueadding applications' |
| 2020 | Louis Hunninck | Phd Biology | Physiological and behavioral adaptations of impala to anthropogenic disturbances in the Serengeti ecosystems |
| 2020 | Kate Layton-Matthews | Phd Biology | Demographic consequences of rapid climate change and density dependence in migratory Arctic geese |
| 2020 | Amit Kumar Sharma | Phd Biology | Genome editing of marine algae: Technology development and use of the CRISPR/Cas9 system for studies of light harvesting complexes and regulation of phosphate homeostasis |
| 2020 | Lars Rød-Eriksen | Phd Biology | Drivers of change in meso-carnivore distributions in a northern ecosystem |