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Ocean migration of Atlantic salmon

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Front cover photo

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Table of contents

Summary

Atlantic salmon (*Salmo salar*) is experiencing population declines throughout most parts of its distribution range, with changes in the marine environment considered important contributors to the overall decline. Most of the current knowledge about Atlantic salmon's ocean distribution originates from mark-recapture and genetic studies associated with high-sea fisheries and sampling surveys, and therefore, little is known about individuals' movements while at sea. For a greater understanding of the ecological conditions encountered in the marine environment, detailed information of the ocean migration and behaviour is needed. The aims of this thesis were to record the ocean migration and behavioural ecology for post-spawned Atlantic salmon from the Alta River, Norway, and the Miramichi River, Canada, and to quantify the marine mortality of post-spawned adults from large parts of the species' distribution range, using archival telemetry.

Results in this thesis documented that Atlantic salmon from the Alta River displayed an overall fidelity towards Arctic areas, with individual migration routes extending from the eastern Barents Sea to the Jan Mayen Island. These results support recent studies, suggesting that the utilization of these waters has previously been underestimated, particularly for the northernmost populations. In comparison, Atlantic salmon from the Miramichi River displayed an exclusive utilization of the Gulf of St. Lawrence and the Labrador Sea during their ocean migration. Individual migration routes diversified shortly after ocean entry, and after existing the Gulf of St. Lawrence, the overall distribution spanned large parts of the Labrador Sea. The overall variation in ocean migration documented in this thesis indicates that individuals from the same population may experience different ecological conditions during the marine phase, potentially contributing to within-population variation in growth and survival.

During the ocean migration, Atlantic salmon displayed an overall pelagic behaviour. Individuals spent most of their time in the upper 10 m of the water column, diving frequently during daylight hours. For Atlantic salmon from the Alta River, there was a clear seasonal trend in diving intensity, with less diving during the winter, independent of individuals' spatial distribution. In contrast, for Atlantic salmon from the Miramichi River, the overall trend in diving behaviour depended strongly on which habitat they occupied. As diving behaviour is likely a suitable proxy for foraging in Atlantic salmon and other pelagic fishes, these results indicate that individuals from both populations displayed flexible foraging strategies during their ocean migration, influenced by seasonal variation and habitat-specific characteristics.

Furthermore, this thesis documented that a variety of large marine animals, including large fish and toothed whales, preyed on Atlantic salmon during their time at sea. Predation by endothermic fish was most common, occurring primarily in the Gulf of St. Lawrence and in waters spanning from west of the Irish Shelf to the Bay of Biscay. Fewer predation events and mortalities were recorded for Atlantic salmon from northern Europe, which contrasted the higher predation rates and total mortality observed for populations from Canada, Spain, and Ireland.

In conclusion, this thesis revealed several novel aspects of the ocean migration of individual Atlantic salmon and large geographical variation in the ocean mortality. This information is important towards a greater understanding of the ecological process controlling Atlantic salmon's growth and survival in the ocean, which should be further investigated in future research.

List of papers

Paper I:

Strøm, J.F., Thorstad, E.B., Hedger, R.D., and Rikardsen, A.H. 2018. Revealing the full ocean migration of individual Atlantic salmon. Anim. Biotelem. **6**: 2. doi:10.1186/s40317-018-0146-2.

Paper II:

Strøm, J.F., Thorstad, E.B., Chafe, G., Sørbye, S.H., Righton, D., Rikardsen, A.H., and Carr, J. 2017. Ocean migration of pop-up satellite archival tagged Atlantic salmon from the Miramichi River in Canada. ICES J. Mar. Sci. **74**: 1356 – 1370. doi:10.1093/icesjms/fsw220.

Paper III:

Strøm, J.F., Rikardsen, A.H., Righton, D., Campana, S.E., Thorstad, E.B., Stokesbury, M.J.W., Carr, J., Gargan, P., Javierre, P.C., and Aarestrup, K. Ocean predation and mortality of adult Atlantic salmon. Manuscript

Contributions

	Paper I	**Paper II**	**Paper III**
Concept and idea	AHR, EBT	GC, JC	JFS
Study design and methods	AHR, EBT	AHR, GC, JC	AHR, JC, KA, PCJ, PG
Data analyses and interpretation	JFS, RDH	JFS, DR, SHS	JFS, AHR, DR, MJWS, SEC
Manuscript preparation	JFS, AHR, EBT, RDH	JFS, AHR, EBT, DR, GC, JC, SHS	JFS, AHR, DR, EBT, JC, KA, MJWS, PG, SEC

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1 Introduction

Atlantic salmon (*Salmo salar*) is an anadromous fish species distributed across the North Atlantic Ocean, with the majority of individuals performing long-distant ocean feeding migrations. Throughout its distribution range, Atlantic salmon is experiencing prolonged declines, and numerous populations, particularly in the southern part of the distribution range, are currently on the brink of extinction (Chaput 2012, ICES 2017). On a local scale, reductions in population sizes are influenced by various factors including parasite induced mortality from salmon lice infestation, genetic introgression from farmed Atlantic salmon, introduced pathogens, degeneration of freshwater habitats, and overharvesting (Parrish et al. 1998, Forseth et al. 2017). However, due to widespread occurrence of the ongoing population declines, large-scale changes in marine ecosystems are considered important overall contributors, with ocean survival correlating with temperature variations in the North Atlantic Ocean (Friedland et al. 2009, Mills et al. 2013).

While increased marine temperatures have a positive effect on growth and survival during parts of the Atlantics salmon's life-cycle (Friedland et al. 2000, Hvidsten et al. 2009), the overall impact of the ongoing ocean warming on population recruitment is negative (Friedland et al. 2009, Mills et al. 2013). Despite the consensus that altered conditions in the ocean affect the overall survival at sea, the underlying mechanisms are thought to differ between geographical areas (Friedland et al. 2014). For European Atlantic salmon, the large-scale declines have been attributed to temperature-induced shifts in the marine food web that reduce the growth of post-smolt during the first summer at sea (McCarthy et al. 2008, Friedland et al. 2009). In comparison, for North American populations, the overall declines are linked to both changes in predator fields during the post-smolt stage (Friedland et al. 2012, 2014) and deteriorated trophic conditions experienced by older sea-age classes (Mills et al. 2013, Renkawitz et al. 2015).

During the oceanic phase, Atlantic salmon populations experience high density-independent mortalities, which are estimated to vary from 70 to 99% both temporally on an annual basis and spatially between rivers and regions (Anon 2017, ICES 2017). Due to the generally low survival at sea, small changes in the absolute mortality will have a significant impact on Atlantic salmon populations. A reduction in mortality from 95% to 90% will for instance double the number of individuals returning to spawn. For Atlantic salmon, quantifying ocean mortality is notoriously difficult because little is known about individuals' ocean migration, and even the largest populations constitute only a minute fraction of the total prey biomass in marine environments (Cairns 2006). Knowledge of the ocean migration and behaviour ecology of individuals is therefore pivotal because it can help to identify which areas individuals utilize while at sea and provide information about the ecological conditions different populations encounter in the ocean. This will promote an understanding of the variation in marine growth and mortality and of how and why populations fluctuate in size and structure. Such information can subsequently enable more accurate predictions of the number of individuals returning to spawn. While at sea, management of Atlantic salmon is limited to regulation of high-sea fisheries, whereas in coastal waters, and during the freshwater stage, several mitigation measures can be applied because many of the ongoing threats at local scales are partially under anthropogenic influence (Parrish et al. 1998, Forseth et al. 2017). Predictive information about return rates will therefore facilitate a more adaptive management, which could ensure long-term viability of both local populations and the species as a whole.

Most of the information on the ocean migration of Atlantic salmon originates from conventional tagging programs and genetic assignments associated with either marine fisheries or sampling surveys (Reddin et al. 2012, Jacobsen et al. 2012, Jensen et al. 2014, Bradbury et al. 2016, Gilbey et al. 2017). While these studies have provided invaluable information about the ocean distribution of Atlantic salmon (Dadswell et al. 2010, Reddin et al. 2012, Gilbey et al. 2017), they also highlight the principal problem associated with most of the existing knowledge about the species' ocean migration, which is the lack of spatially independent observations of horizontal movements and behaviour, due to the systematic biases to areas where samplings have taken place. Recent developments of microchemical analyses using stable isotopes for describing the ocean distribution of pelagic fishes have partially addressed this need for spatially unbiased information (Schloesser et al. 2010, MacKenzie et al. 2011). Such methods can generate retrospective estimates of individuals' spatial distribution, by comparing the isotope composition in the animal tissue with that of the environment (Trueman et al. 2012). However, these methods are limited to estimating coarse ocean distributions and can only provide information from the surviving individuals. Data obtained from mark-recapture experiments, genetic assignments, and microchemical analysis must therefore be accompanied by more detailed information of individuals' ocean migration, in order to promote a more comprehensive understanding of how individuals interact with the environment and how these interactions shape populations.

In aquatic habitats, spatially unbiased observations of the fine-scale movement and habitat use of long-distant migrants require remote monitoring of individuals, which is now possible through advances within the field of archival telemetry (Hussey et al. 2015). During deployment, archival tags log and store data about the habitat the animal occupies. This ensures unbiased information about the spatial distribution and behaviour of individuals in natural environments. The use of archival tags has revealed novel information about movement regimes for numerous fish species and disentangled important concepts within behavioural ecology (Block et al. 2005, Humphries et al. 2010, Righton et al. 2016, Queiroz et al. 2017).

For pelagic fishes that perform long-distant ocean migrations, the simultaneous acquisition of data on the horizontal migration and vertical movements is of particular importance, because how individuals move within the water column is often considered a suitable proxy for the underlying behavioural state. Overall, depth use in pelagic fish is likely governed by multiple behavioural and ecological functions (Thums et al. 2012, Braun et al. 2015, Righton et al. 2016), although, certain vertical movement patterns are strongly associated with foraging (Wilson and Block 2009, Howey et al. 2016). Simultaneous sampling of data on the depth use and the horizontal distribution could therefore facilitate inference of the operating behaviour modes and identification of geographical areas important for foraging (Walli et al. 2009, Queiroz et al. 2017). Furthermore, as certain types of archival tags also enable quantification of mortality while at liberty, novel information about mortality regimes in the ocean can be provided (Lacroix 2014, Wahlberg et al. 2014). In fisheries research, such information is of substantial importance particularly for vulnerable stocks and populations (Hammill et al. 2014, Chasco et al. 2017). For Atlantic salmon, quantitative estimates of ocean mortality in different geographical areas could further enhance our understanding of trends in population abundance when accompanied with information of ocean migration and behaviour.

For Atlantic salmon, the first archival tagging programs were initiated in the 1990s (Sturlaugsson 1995, Karlsson et al. 1996, Sturlaugsson and Thorisson 1997, Westerberg et al. 1999). While these pioneer studies presented the first detailed insights into the behaviour of individual Atlantic salmon at sea, limited information of the ocean migration was provided, as they were confined to describing the final stage of the marine phase. Since the early 2000s, the number of published archival tagging studies on Atlantic salmon has increased steadily (Table 1). Although several novelties about the ocean phase have been revealed, the use of archival tags for describing the ocean migration of Atlantic salmon is still in its infancy.

Table 1: Chronological overview of the archival tagging studies on Atlantic salmon, using data storage tags (DSTs) and pop-up satellite archival tags (PSATs), including the papers in this thesis. Sample size reflects the number of tags with a sufficient amount of data, with number in parenthesis indicating the total number of tagged fish.

Tagging location	**Life stage**	**Study aim**	**Tag type**	**Variables**	**Sample size**	
Iceland	Adults	Homing	DST	Temperature and depth	30 (60)	Sturlaugsson 1995
Baltic Sea	Adults	Homing	DST	Temperature and depth	14 (35)	Karlsson et al. 1996
Iceland	Adults	Homing	DST	Temperature and depth	47 (100)	Sturlaugsson et al. 1997
Baltic Sea	Adults	Homing	DST	Temperature and depth	35 (211)	Westerberg et al. 1999
Newfoundland	Post-spawned adults	Thermal habitat	DST	Temperature	11 (139)	Reddin et al. 2004
Newfoundland	Post-smolts	Thermal habitat	DST	Temperature	15 (311)	Reddin et al. 2006
Norwegian Sea	Post-smolts	Depth use	DST	Temperature and depth	5 (413)	Holm et al. 2006
Iceland	Adults	Homing	DST	Temperature, depth, tilt, and magnetism	2 (9)	Sturlaugsson et al. 2009
Newfoundland	Post-spawned adult	Temperature and depth use	DST	Temperature and depth	11 (139)	Reddin et al. 2011
Northern Norway	Post-spawned adults	Ocean migration	PSAT	Temperature, depth, and geolocation	2 (2)	Chittenden et al. 2013a
Northern Norway	Post-spawned adults	Ocean distribution	DST	Temperature and depth	14 (316)	Chittenden et al. 2013b
Bay of Fundy	Post-spawned adults	Ocean migration	PSAT	Temperature, depth, and geolocation	39 (55)	Lacroix 2013
Bay of Fundy	Post-spawned adults	Predation	PSAT	Temperature, depth, and geolocation	39 (55)	Lacroix 2014
Iceland	Post-smolts	Ocean distribution	DST	Temperature and depth	7 (598)	Guðjónsson et al. 2015
Scotland	Adults	Homing	PSAT	Temperature, depth, and geolocation	47 (50)	Godfrey et al. 2015
Norway	Post-spawned adults	Depth use	DST and PSAT	Temperature, depth, and geolocation	104 (707)	Hedger et al. 2017a
Northern Norway	Post-spawned adults	Growth and survival	DST and PSAT	Temperature, depth, and geolocation	56 (551)	Hedger et al. 2017b
Northern Norway	Post-spawned adults	Spatial distribution	DST	Temperature, depth, and geolocation	6 (197)	Paper I
Gulf of St. Lawrence	Post-spawned adults	Ocean migration	PSAT	Temperature, depth, and geolocation	16 (43)	Paper II
Northeast and northwest Atlantic	Post-spawned adults	Predation	PSAT	Temperature, depth, and geolocation	156 (227)	Paper III

The principal aim of this thesis is to provide much needed spatially independent information of the ocean migration and behaviour of European and North American Atlantic salmon using archival tags. As a secondary aim, the predation and mortality of Atlantic salmon from rivers extending most of the species' distribution range were investigated, by inferring mortality from archival tagging data. The explicit aims of the thesis are as follows:

- Provide a simultaneous description of the horizontal migration and vertical movements of post-spawned Atlantic salmon from Northern Norway, using high resolution archival tags deployed throughout the entire ocean residency (paper I).
- Describe the horizontal migration and investigate patterns in depth use of post-spawned Atlantic salmon from the Gulf of St. Lawrence region, Canada, using pop-up satellite archival tags (PSATs) (paper II).
- Quantify the mortality of Atlantic salmon tagged with PSATs throughout large parts of the species' distribution range, investigate the geographical distribution of predation events, and identify the most likely predators (paper III).

Before presenting the results of these studies (chapter 4), the thesis will include: I) a description of the archival tags used for quantifying ocean migration in fishes (chapter 2.1), II) a description of the methods and challenges associated with reconstructing the horizontal migration of pelagic fish in general and of Atlantic salmon in particular (chapter 2.2 – 2.4), and III) a summary of what we have learned about the ocean distribution of Atlantic salmon from conventional sampling and genetic analyses (chapter 3). The thesis will also encompass: IV) a discussion of the findings in relation to previous studies (chapter 5), and V) an elaboration of how further use of archival telemetry can promote a more comprehensive understanding of the ocean distribution of Atlantic salmon and their ecology while at sea (chapter 6).

2 Methods

2.1 Archival tags

The two most commonly used archival tags for collecting spatially independent information of the ocean migration and behaviour of fish are pop-up satellite archival tags (PSATs) and basic archival tags, often referred to as data storage tags (DSTs). While both these tag types log and archive data, they differ in terms of how data are retrieved (Thorstad et al. 2013). For DSTs, data retrieval depends on recapture, and tags can be attached either externally or internally to the fish, due to their usual small size (Thorstad et al. 2013). This enables DSTs to log data about the habitat use while at liberty, in addition to provide information of the physiological state of the animal if tags are implanted and equipped with appropriate sensors (e.g. Walli et al. 2009, Prystay et al. 2017). In contrast, archived data from PSATs can be accessed without physical recovery, because the tags have a release mechanism that enables the tag to detach, surface, and transmit data to passing satellites (Thorstad et al. 2013). Despite developments aiming to miniaturize PSATs, they are still substantially larger than the smallest DSTs, and can therefore only be used on larger fish. Data transmission occurs either at a pre-programmed date, or if certain anomalies are recorded. This allows retrieval of data from fish that have died and facilitates estimates of mortality regimes in the open ocean, which are otherwise difficult to obtain (Béguer-Pon et al. 2012, Lacroix 2014). Due to the external release mechanism, PSATs are constrained to external attachment, and therefore limited to log external variables that describe the fish's habitat use. Transmitted data from PSATs are often retrieved at a lower temporal resolution compared to data from DSTs, with occasional gaps in the time series, due to variability in satellite coverage and the depletion of the tag's battery. However, if PSATs are physically retrieved, the logged data are fully available.

Overall, PSATs have been the most commonly used tag type for describing the ocean distribution and behaviour of pelagic fishes, as most studies have been conducted with limited prior information of species' ocean migration and expected tag-retrieval rates. However, in recent years, as information of the ocean migration of pelagic fishes has accumulated, the use of DSTs has become more frequent. Currently, both PSATs and DSTs are able to record environmental variables such as light, temperature, and depth, facilitating quantification of individuals' ocean distribution and behaviour while at liberty. This makes the suitability of DST and PSATs in studies of the ocean migration of fishes determined by the likelihood of tag retrieval, the relevance of the temporal resolution of the logged variables, and the importance of data retrieval from individuals that died.

In this thesis, DSTs were used to describe the full ocean migration of post-spawned Atlantic salmon from the Alta River, Northern Norway (paper I). PSATs were used to describe the ocean migration of adults from the Miramichi River, Canada (paper II), and to quantify the mortality of Atlantic salmon from large parts of the species' distribution range (paper III). The DSTs used in paper I were LAT-2810 light-based geolocation tags (Lotek Wireless Inc., Canada), which were programmed to record temperature, depth, and light intensity at 30-s intervals. These time series were available upon tag retrieval, along with daily summaries of the logged data that included daily geolocation estimates based on the light data and estimates of sunrise, sunset, and local noon. The tags weighed 12.8 g in air and comprised of a tag body (13 mm × 44 mm) that was surgically implanted in the body cavity of the fish and a light censoring antenna (175 mm long), which exited through the body wall.

The PSATs used in paper II and III were X-tags (12 × 3.2 cm, 40 g in air), which were manufactured by Microwave Telemetry (Columbia, MD, USA) and transmitted data to the

Argos satellite system (www.argos-system.org). During deployment, the X-tags recorded temperature, depth, and light intensity at 2-min intervals, however, these data were only available if the tags were physically retrieved. Data transmitted to satellites consisted of temperature and depth time series of varying resolutions, a summary file of the recorded variables, daily geolocation estimates, and estimates of sunrise and sunset. The optimal temporal resolution of the transmitted time-series data depended on the deployment period. For tags scheduled to detach within 6 months of tagging, the optimal resolution of time-series data consisted of recordings at 15 min intervals. For tags with deployments exceeding 6 months, the ideal resolution was 30 min. All tags were deployed identically by attaching the tag externally to a silicon cushioned harness that allowed release at the pre-programmed date or if certain anomalies were recorded. In addition, all fish tagged with PSATs in paper II were simultaneously fitted with a VEMCO V9 acoustic transmitter (29 9mm, VEMCO, Halifax, NS, Canada). VEMCO VR2W and VR4 receivers were strategically deployed covering the entry and exit points of the Gulf of St. Lawrence, allowing accurate estimates of individual residency within this region. For further details about the DSTs and PSATs used and the attachment methods, see the methods sections in papers I-III.

2.2 Geolocation by light

Although not obligate, light-based geolocation estimates are often essential for detailed descriptions of the horizontal migration in pelagic fish, because regular communication between tags and satellites is impossible for completely submerged animals. The basic principles of light-based geolocation emphasize on estimating the timing of sunrise and sunset, based on logged light data, from which estimates of latitude and longitude can be calculated. Sunrise and sunset are defined as when the limb of the sun appears or disappears over the horizon. Once these twilight events are derived, standard astronomical equations can be applied to calculate latitude, based on the day length, and longitude, from the time of local noon.

While straightforward in principle, estimating sunrise and sunset from measured light levels is a complex process, because the relationship between the light intensity and the solar elevation angle is not universal (Ekstrom 2004). The earliest light-based geolocation methods estimated sunrise and sunset as the time when the rate of change in light intensity exceeded a certain threshold (Hill and Braun 2001). These threshold methods provide robust estimates of longitudes because an erroneous threshold will not affect the midpoint between twilight events as long as the error is symmetrical (Hill and Braun 2001, Ekstrom 2004). However, as twilight thresholds are notoriously difficult to determine, threshold methods possess a fundamental problem for estimating latitudes because the inaccuracy will be fully included in the estimated day length from which the latitude is directly derived from (Ekstrom 2004). Although threshold methods are still useful for estimating longitudes (Queiroz et al., 2017, paper I) and several approaches have been suggested to minimize the latitude error (Hill and Braun 2001, Ekstrom 2004), most light-based geolocations are currently done by models that incorporate all recorded light data over the twilight periods (Basson et al. 2016). These models are often termed template models and infer sunrise and sunset by comparing the recorded light data with predicted light curves at various sun angles, increasing the accuracy of latitude estimates while correcting for variability in cloud cover between twilight events (Ekstrom 2004). However, rapid changes in light intensity during sunrise and sunset remain problematic (Ekstrom 2004). This, in combination with the inevitable problem of estimating latitudes around the equinoxes, when day lengths are equal across all latitudes, suggest that even the most sophisticated light-based geolocations should be treated with uncertainty (Basson et al. 2016). For species inhabiting polar regions, obtaining positional estimates based on light data is further complicated by the constant daylight during the polar summer and the absence of a sunrise during the polar night.

2.3 State-space models

For animal telemetry data, each observational method is subject to its own type of errors and even the most accurate tracking tools, such as GPS and Argos estimates, harbour a degree of uncertainty (Patterson et al. 2008). Consequently, as passive tracking of animals has become more common, the need for a framework that incorporates the errors in the estimates instead of discarding them, has increased.

State-space models are statistical models that handle time-series data and estimate the state of an unobservable variable based on observable data (Patterson et al. 2008, Jonsen et al. 2013). In state-space models designed to handle animal telemetry data, the most common state variables are the animal's position (e.g. Thygesen et al. 2009), its behavioural mode (e.g. Patterson et al. 2009), or a combination of both (e.g. Pedersen et al. 2011). State-space models consist of a process model (i.e. time update), which is a formalization of how the state variable changes over time, and an observational model (i.e. data update) that weights these predictions depending on the observed data (Figure 1). This link between the underlying process and the observations enables assessing the likelihood of the biological data while quantifying the uncertainty of the estimated states (Patterson et al. 2008). In a geolocation context, the process model is often defined as a random walk between defined time steps, which can be formalized by one of various diffusion processes (Jonsen et al. 2013).

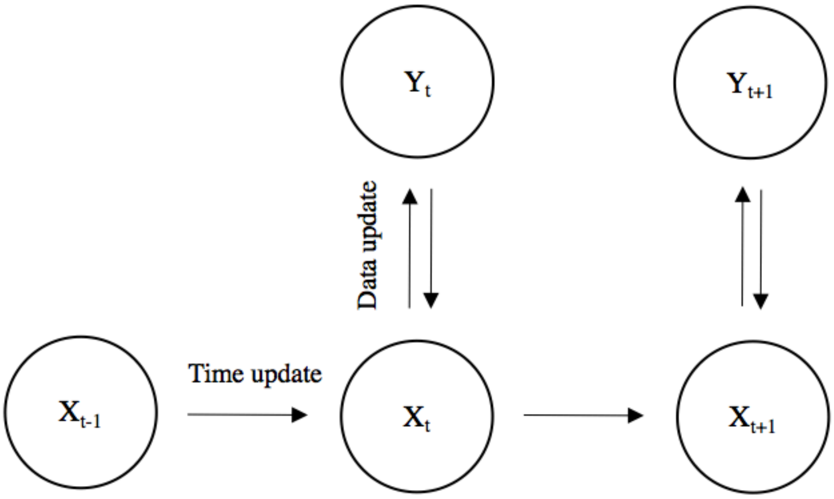

Figure 1: Schematic representation of a general state-space model, where $\mathbf{X}_{t-1} \ldots \mathbf{X}_{t+1}$ are unobservable states and $\mathbf{Y}_t \ldots \mathbf{Y}_{t+1}$ are observed data.

State-space models have secured a particularly firm foothold within the field of fish migration, where errors associated with estimates are rarely negligible and often consist of complex spatial and temporal structures (Pedersen 2010). Several classes of state-space models exist, with Kalman filter (KF) and hidden Markov models (HMM) most commonly applied in fish species that perform long-distant ocean migrations (Sibert et al. 2003, Pedersen 2010). KFs are parametric methods that assume a Gaussian distribution for the error structure and require a stable input of light-based geolocations. These techniques work well for geolocating pelagic fishes in temperate oceans (e.g. Lam et al. 2008, Galuardi and Lutcavage 2012) and offer computational advantages because it is sufficient to estimate the mean and variance in order to obtain the positional probability distribution. However, when either light-based geolocations are difficult to obtain, or the assumption of Gaussian errors is unreasonable, other geolocation methods are required. HMMs are non-parametric state-space models that enable geolocation of animals in complex geographical environments and in situations when light-based geolocations are difficult to obtain (Pedersen 2010). Consequently, HMMs offer greater realism when fish encounter complex barriers between land and sea, because they can easily prevent movement onshore, and they are applicable when either the behaviour or origin of the fish prevent reliable light-based geolocation estimates (Pedersen et al. 2008, Braun et al. 2018)

2.4 The hidden Markov model

In paper I and paper II, the ocean migration of Atlantic salmon was described using a hidden Markov model (HMM), because the tagged individuals either inhabited regions where light-based geolocation was impossible for large parts of their time at liberty (paper I), or encountered complex boundaries between land and ocean during parts of their migration (paper II). The HMM discretized time and space, using a time-step length of one day and a 10 km equidistant grid. This spatial domain was used to accommodate the decrease in distance between longitudes towards the poles. The posterior distribution at each time step was estimated by a two-step forward running Bayesian filter and a backward smoothing step that ensured that these distributions were conditioned on the entire time series (Pedersen 2010).

In the process model, individuals were assumed to move according to a random walk and movements were formalized by the diffusion equation (Codling et al. 2008):

$$\partial\phi(\mathbf{x},t)/\, \partial \mathrm{t} = \mathrm{D}\nabla^2\phi(\mathbf{x},t) \qquad (1)$$

where $\phi(\mathbf{x},t)$ is the probability that a fish is present at location $\mathbf{x}$ at time t, ∇ is the spatial gradient operator and D represents the diffusivity parameter. Here, movement probabilities were constructed by solving equation (1) using the finite difference method (see Thygesen et al., 2009) multiple times for each time step, in order to implement a realistic movement scheme. Movement onto land was prevented by setting transition probabilities onshore to zero and the retained probability was then normalized to prevent loss of probability mass. The diffusivity parameter, D, was fixed to the highest possible value that prevented numerical oscillations and ensured that the stability criterion of finite difference method was met (i.e. positive probabilities).

In the observational model, daily likelihoods at the grid positions, $L(\mathbf{x},t)$, were constructed using filtered latitudes (LAT) and longitudes (LON), daily mean temperatures at the surface (SST), and the daily maximum depths (MD) (see paper I and II for further details):

$$L(\mathbf{x},t) = L_{\mathrm{LAT}}(\mathbf{x},t) \times L_{\mathrm{LON}}(\mathbf{x},t) \times L_{\mathrm{SST}}(\mathbf{x},t) \times L_{\mathrm{MD}}(\mathbf{x},t) \tag{2}$$

The posterior distributions of the time and data update, $\phi(\mathbf{x},t)$, were then calculated:

$$\phi(\mathbf{x},t) = \frac{\phi(\mathbf{x},t\text{-}1) * \mathrm{TP} * L(\mathbf{x},t)}{\lambda(\mathrm{t})} \tag{3}$$

where $\lambda(t)$ denotes the normalization constant, $\phi(\mathbf{x},t\text{-}1)$ is the posterior distribution the previous day, and TP is the transition probabilities obtain from equation (1). To filter the posterior distributions conditioned on all data in the time series, the backward smoothing algorithm given by Thygesen at al. (2009) and Pedersen (2010) was applied. In paper I, individual migration routes were reconstructed using the mean of 1000 random sampled tracks generated by a backward sweep of the daily posterior distributions (Thygesen et al. 2009). In paper II, the most likely migration routes were estimated using the Viterbi algorithm (Viterbi 2006)

The reliability of the HMM was tested in both paper I and II by manipulating the input data. In paper I, the model's sensitivity was investigated by reconstructing tracks excluding the end locations, and by altering the start and end coordinates. Furthermore, in order to assess the potential impact of tag inaccuracy, all tracks were reconstructed with input temperatures increased and decreased by 0.3 °C (paper I). These tests indicated a limited overall impact of changing the start and end locations, and a negligible difference when altering the input temperatures (paper I). For tracks with omitted end points, deviations from the true tracks were only present during the final stage of the migration for tags deployed in 2013 and 2014 (paper I). As geolocations during this period were largely driven by temperature, the temporal overlap and similar annual magnitude of the divergence may suggest a mismatch between satellite and tag data during the final stage of the migration.

In paper II, the simultaneous deployment of PSATs and acoustic tags increased the number of known positions as detections at the acoustic arrays were treated as fixed locations in the HMM. Here, the model's performance was assessed by running alternative reconstructions omitting the acoustic fixes for the fish detected by the receiver arrays when passing the Strait of Belle Isle, 767 km from the river mouth (paper II). For the fish detected by the acoustic arrays at the Strait of Belle Isle, the omission of acoustic detections had no impact on the reconstructed tracks, with fish exiting the Gulf of St. Lawrence on the same date.

2.5 Study area

While the predation and mortality estimates encompassed Atlantic salmon from Canada, Denmark, Ireland, Norway, and Spain (paper III), descriptions of the ocean migration (paper I and II) only included individuals from the Alta River, Northern Norway and the Miramichi River, Canada (Figure 2). Due to their geographical location, these populations were considered representative for Atlantic salmon from Northern Norway and the Gulf of St. Lawrence region, which are areas with several important Atlantic salmon populations.

The Alta River is located north of the Arctic Circle (Figure 2, 70°N 23.4°E), has a drainage area of 7 400 km^2, and a 46 km stretch accessible for Atlantic salmon. The river is renowned for its large-sized Atlantic salmon and is therefore a priced destination for recreational anglers. In 1987, a hydropower dam was built upstream of the accessible Atlantic salmon habitat. While this has had a negative impact on the recruitment of Atlantic salmon in the uppermost stretches, the overall effect on the total production has been limited (Ugedal et al. 2017). In comparison to Atlantic salmon from other regions, the declines in population sizes for North Norwegian Atlantic salmon are limited (Anon 2017). In the Alta River, the spawning population is of sufficient size to maintain recruitment, with annual catches primarily ranging between 10 and 20 t since the mid-1970s (Ugedal et al. 2017).

The Miramichi River is located in the western Gulf of St. Lawrence (Figure 2, 47.2°N, 65.0°W). The river consists of two main branches, the Southwest Miramichi and Northwest Miramichi. Both branches consist of several tributaries accessible for Atlantic salmon, draining a combined area of ~12 000 km^2. The river hosts the largest Atlantic salmon population in North America, which has declined substantially during the past decades from an estimated size of over 80 000 returning individuals in the 1990s to less than 20 000 fish in recent years (DFO 2015, 2018). This decline is considered largely attributed to ongoing changes in the ocean, due to the absence of aquaculture in the Gulf of St. Lawrence and the fact that the decline has persisted despite the implementation of numerous mitigation measures (Parker 2013, Wallace and Curry 2017, DFO 2018).

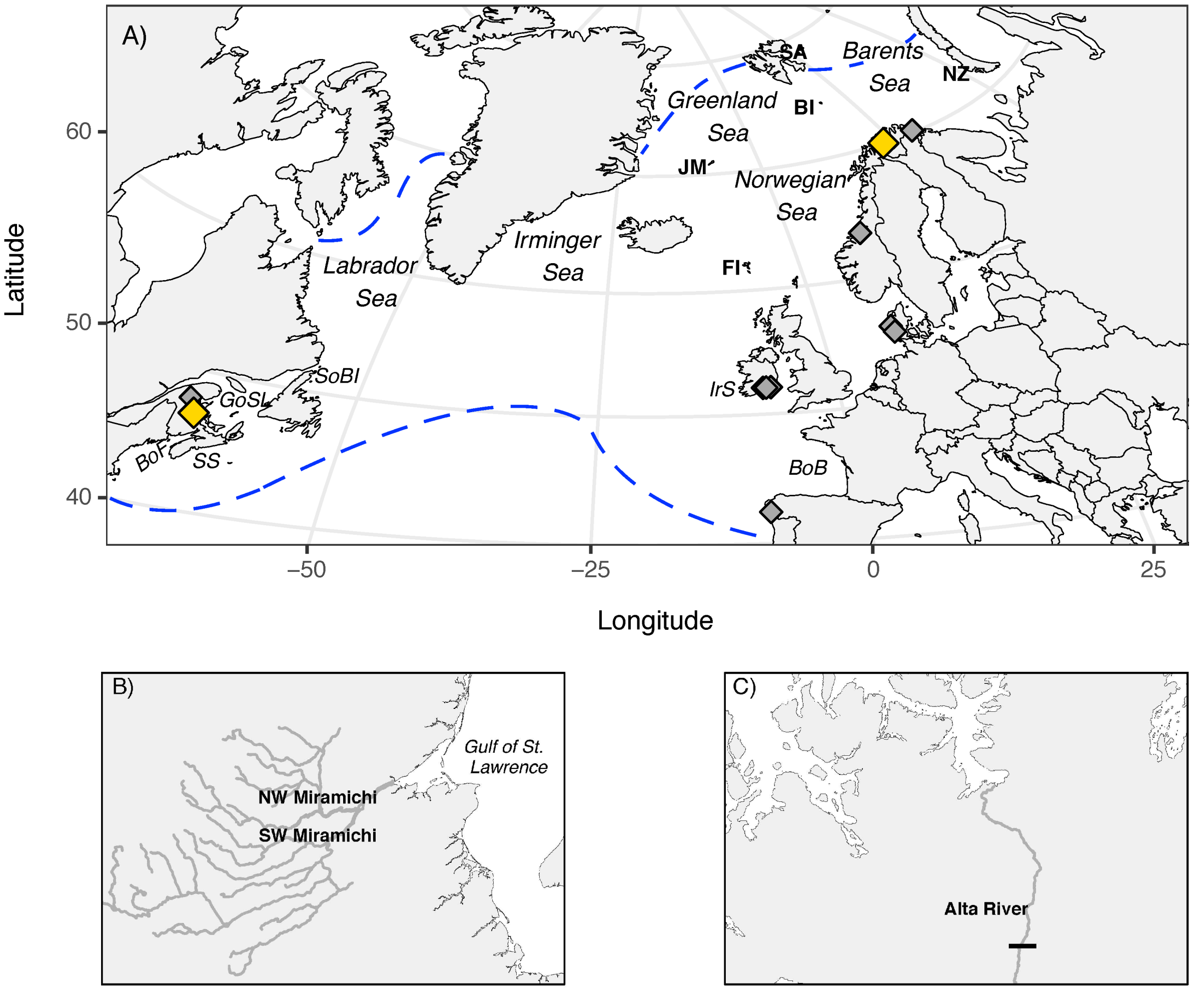

Figure 2: A) Map of the North Atlantic Ocean, with blue lines indicating the northern and southern limit of the ocean distribution of Atlantic salmon. Yellow diamonds indicate the location of the Miramichi and Alta River and grey diamonds indicate the origin of the other Atlantic salmon populations included in this thesis. Abbreviations: *BI* = Bear Island, *BoB* = Bay of Biscay, *BoF* = Bay of Fundy, *FI* = Faroe Islands, *GoSL* = Gulf of St. Lawrence, *IrS* = Irish Shelf, *JM* = Jan Mayen Island, *NZ* = Novaya Zemlya, *SA* = Svalbard, *SoBI* = Strait of Belle Isle, and *SS* = Scotian Shelf. B) Map of the Miramichi River with its the two main branches. C) Map of the Alta River, with black horizontal line indicating the location of the hydropower dam.

3 What we know about the ocean migration of Atlantic salmon from conventional tagging experiments and genetic analyses

During the ocean migration, time spent at sea vary with sex, geography, and life stage. In some rivers, most first-time migrants mature after one year at sea (1SW), while for other populations multi-sea winter (MSW) maiden fish are common (Klemetsen et al. 2003). For repeat spawners, the ocean migration rarely exceed one year, with individuals returning to spawn in consecutive or alternate years (Klemetsen et al. 2003). Consecutive spawners are generally less common in more northern areas (Erkinaro et al. 2018), and individuals that display this life-history strategy are known to contribute substantially to the spawning stock in several North American rivers (Downton et al. 2001, Chaput and Jones 2006).

The ocean distribution of Atlantic salmon spans the North Atlantic Ocean. Fish originating from rivers draining into the Baltic Sea will not be emphasized in this thesis as their marine migration is mainly confined to this largely enclosed sea. After entering the marine environment, both post-smolts and post-spawned adults move rapidly through fjords and coastal waters (Halttunen et al. 2009, Thorstad et al. 2012), spending the initial phase migrating to various ocean feeding grounds in the North Atlantic Ocean. Individual migration routes likely depend on environmental factors, such as food availability, temperature, salinity, and water currents, in addition to geographical origin and sea-age (Dadswell et al. 2010, Jonsson and Jonsson 2011). Overall, conventional mark-recapture programs and ocean sampling surveys have revealed utilization of waters ranging from the eastern Barents Sea to the Labrador Coast with the northernmost oriented fish inhabiting waters off Svalbard (SALSEA-Merge 2007, Miller et al. 2012, Jensen et al. 2014). While studies describing the ocean migration of Atlantic salmon by conventional tagging, sampling surveys, and genetic analyses fail to provide detailed information about the migration routes and behaviour, they have identified important ocean areas and postulated general migration patterns (Dadswell et al. 2010, Miller et al. 2012, Gilbey et al. 2017). In particular, data from the mixed-stock fisheries off the Faroe Islands and West Greenland have, in combination with systematic sampling surveys of Atlantic salmon in the open ocean, increased our general understanding of the ocean distribution by identifying specific regions in the Norwegian and Labrador Sea as important areas for various populations and life stages (Holm et al. 2003, Reddin et al. 2012, Sheehan et al. 2012, Jacobsen et al. 2012, Bradbury et al. 2016, Gilbey et al. 2017).

European Atlantic salmon are mainly distributed in the northeast Atlantic Ocean, with regions within the Norwegian Sea considered to be the principal oceanic feeding grounds (Holm et al. 2003, Hansen and Jacobsen 2003). However, Atlantic salmon from UK, Ireland, and Norway constitute a substantial proportion of the catches in the West Greenland fishery, indicating that transatlantic migration is common for some European populations (Reddin et al. 2012, Bradbury et al. 2016). In the northeast Atlantic Ocean, post-smolts appear to follow surface currents northwards into the Norwegian Sea, where they spread in a fan-like distribution across various latitudes (Holm et al. 2000). While resident in the Norwegian Sea, Atlantic salmon from northern Europe occur in greater numbers at higher latitudes during winter months compared to their southern European counterparts, which display a more southern distribution closer to the Faroe Islands, with a higher abundance in the autumn (Jacobsen et al. 2001, 2012). For Atlantic salmon from Northern Norway and Russia, little information exists of the ocean migration and individuals from these areas are assumed to utilize more north-eastern waters than Atlantic salmon from other European regions (Jonsson and Jonsson 2011). Overall, this separation in spatial distribution between populations of different geographical origin is supported by the predominance of North Norwegian Atlantic salmon caught in coastal waters off Svalbard (Jensen et al. 2014) and the spatial separation between fish returning to distinct regions of the UK (MacKenzie et al. 2011).

In contrast to European Atlantic salmon, transatlantic migration has been considered less common for North American individuals (Reddin et al. 2012). However, a recent genetic analysis revealed that a substantial proportion of the fish caught in the high-sea fishery off the Faroe Islands was of North American origin (Gilbey et al. 2017). For North American Atlantic salmon, the Labrador Sea is considered the principal ocean feeding ground for most populations, with individuals from different life stages and geographical origins displaying a year-round presence in these waters (Reddin and Short 1991, Reddin and Friedland 1993). Overall, North American Atlantic salmon are known to enter the Labrador Sea in summer and overwinter in the southern Labrador Sea (Reddin 2006). In the following spring, individuals are thought to either return to the river as 1SW fish or migrate towards summer feeding grounds off Newfoundland, Labrador, and Greenland (Reddin 2006, Miller et al. 2012). Revisions of historical tag recoveries have indicated a greater occurrence of US Atlantic salmon off East Greenland compared to fish from Canada (Reddin et al. 2012), which may suggest some geographical separation in ocean migration based on origin. Genetic analyses of Atlantic salmon caught in the West Greenland fishery may further support this spatial differentiation, as most of the sample originated from either the Gulf of St. Lawrence or Central Labrador, although the low contribution of the more southern stocks could be strongly influenced by their current status (Bradbury et al. 2016).

Despite the indications that ocean distributions vary among populations both in the northeast and northwest Atlantic Ocean, the magnitude of the diversification is not well known based on conventional data. By comparing trends in return rates of Atlantic salmon from Europe, a temporal synchrony in abundance was documented for populations from rivers draining the Barents Sea (Niemelä et al. 2004), while a divergent pattern was evident between Norwegian and Scottish populations (Vøllestad et al. 2009). This suggests that that a persistent spatial separation in the ocean distribution may be present among geographically separated populations (Vøllestad et al. 2009). While data from high-sea fisheries and scientific sampling surveys have facilitated mapping of spatial distributions based on limited individual information, it is uncertain to what extent this information is representative for the entire ocean phase. Consequently, detailed descriptions of horizontal movements could promote a greater understanding of the ongoing trends in population abundance, particularly if accompanied with information of individuals' behavioural ecology derived from vertical movement patterns and descriptions of the ocean mortality.

4 Summary of results

4.1 Revealing the full ocean migration of individual Atlantic salmon (paper I)

The horizontal migration and vertical behaviour of six post-spawned Atlantic salmon from the Alta River, Northern Norway, were studied using high-resolution data storage tags (DSTs) that recorded temperature, depth, and light intensity during the entire ocean migration. The method used for reconstructing individual migration routes and ocean distributions was a hidden Markov model (HMM). The HMM was designed to describe the ocean migration of Atlantic salmon originating from Arctic latitudes and allowed reconstruction of individuals' horizontal migration during periods when light-based geolocations were not feasible due to polar light regimes.

During their ocean residency, the six fish exhibited various migration routes with the overall distribution spanning Arctic areas from the eastern Barents Sea to areas off Jan Mayen Island (Figure 3). Four of the fish displayed a profound westward migration utilizing waters adjacent to Jan Mayen Island during winter, with two of these individuals migrating northwards towards Svalbard during summer and autumn. The remaining two fish migrated eastward and utilized the Barents Sea to a varying extent, with one fish displaying an exclusive utilization of the Barents Sea during the entire ocean migration. Overall, the Atlantic salmon displayed a pelagic behaviour, with all fish spending more than 83 % of their time in the uppermost 10 m of the water column, occasionally diving to depths exceeding 200 m. A strong seasonal trend was present in the diving intensity. This pattern was independent of individuals' spatial distribution, with more frequent diving during periods with extended daylight. In contrast, the diving depth did not follow any overall seasonal trend, but was positively correlated with the depth of the mixed layer.

Conclusions

1. The high fidelity towards ocean areas north of the Arctic Circle, suggests that the northernmost populations of European Atlantic salmon may utilize areas further north than previous thought, and particularly the importance of waters off the Jan Mayen Island may have been underestimated.
2. Despite this overall fidelity towards Arctic latitudes, Atlantic salmon from the Alta River displayed substantial variation in horizontal migration routes, suggesting that individuals from the same population may experience different ecological conditions during the ocean residency, which could contribute to within-population variation in growth and survival.
3. The seasonal variation in diving intensity, and spatial correlation between the diving depth and the depth of the mixed layer, indicate that the depth use of Atlantic salmon inhabiting areas with highly seasonal light regimes depends on both seasonality and dynamic oceanographic conditions.

4.2 Ocean migration of pop-up satellite archival tagged Atlantic salmon from the Miramichi River in Canada (paper II)

The ocean migration and depth use of 16 post-spawned Atlantic salmon from the Miramichi River, were investigated using pop-up satellite archival tags (PSATs) and acoustic transmitters. Individuals' horizontal migration was reconstructed using a hidden Markov model (HHM) in order to prevent movement onto land in areas with complex coastlines.

During their ocean migration, individuals exclusively utilized waters in the Gulf of St. Lawrence and the Labrador Sea, with two individuals returning to the river as consecutive spawners after spending the summer at sea. All fish primarily occupied surface waters, spending more than 67% of their time in the uppermost 10 m of the water column. When resident in the Gulf of St. Lawrence, individuals inhabited various regions, diving frequently during daylight hours, primarily to shallow depths. Eight of the fish exited the Gulf of St. Lawrence and entered the Labrador Sea through the Strait of Belle Isle (767 km from the river mouth) between June 27 and July 12, after 41 – 60 days at liberty. After exiting the Gulf of St. Lawrence, individuals utilized different waters extending from the Labrador Coast to the west coast of Greenland (Figure 3). This variation in spatial distributions was accompanied by differences in diving behaviour. Vertical movements resembled those in the Gulf of St. Lawrence when fish were distributed in coastal areas along the Labradors Shelf and off the west coast of Greenland. In contrast, when utilizing waters in the central Labrador Sea, the vertical behaviour was characterized by occasional deep dives to depths down to 909 m.

Conclusions

1. The extended residency in the Gulf of St. Lawrence and the frequent diving behaviour displayed while present in the waters, suggest that post-spawned Atlantic salmon from the Miramichi River recondition in the Gulf of St. Lawrence.
2. The exclusive utilization of the Strait of Belle Isle as an entry point to the Labrador Sea, with fish exiting the Gulf of St. Lawrence primarily in early July, suggest that the Strait of Belle Isle is the principal migratory passage for Atlantic salmon from the Miramichi River.
3. The variation in migration routes displayed both in the Gulf of St. Lawrence and in the Labrador Sea, indicates that while the growth and survival of individual Atlantic salmon from the Miramichi River may be dependent on local foraging conditions, large oceanographic regions are likely important for the population’s overall success.

4. The observed variation in diving behaviour, from frequent shallow diving during daylight when present in the Gulf of St. Lawrence and in coastal regions of the Labrador Sea, to a more infrequent diving behaviour to greater depths when utilizing waters off the Labrador Shelf, suggest general behavioural modes associated with particular oceanographic environments.

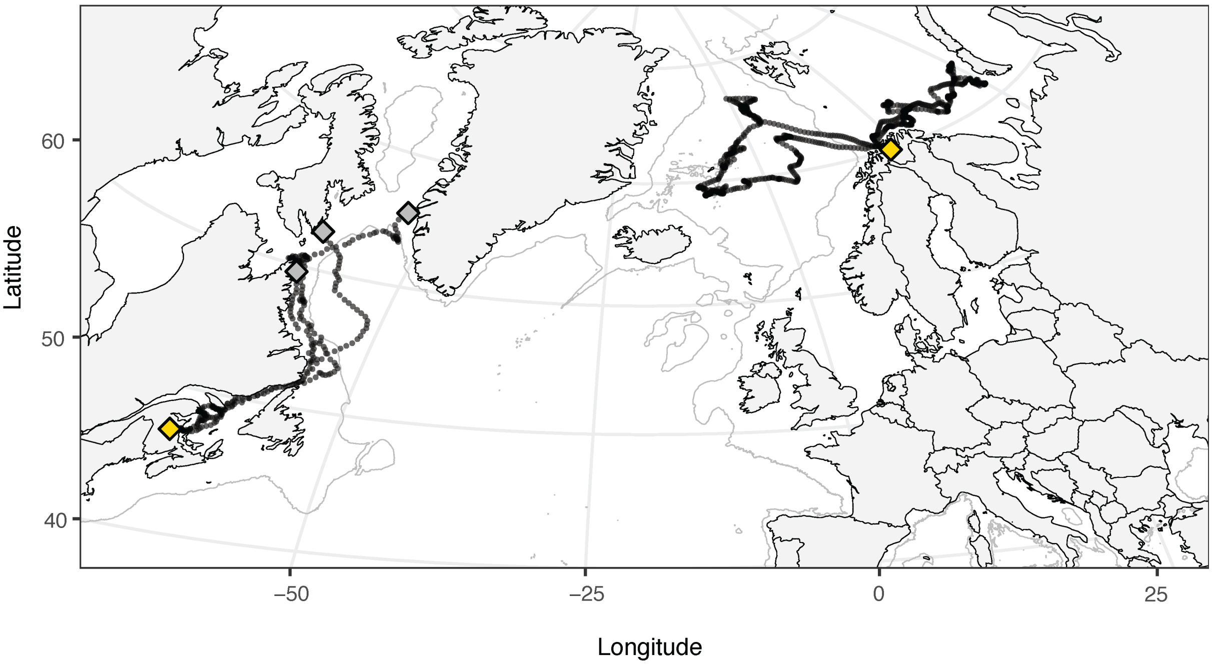

Figure 3: Examples of the ocean migration of Atlantic salmon from the Miramichi River (n = 3) tagged with pop-up satellite archival tags (PSATs) and from the Alta River (n = 2) tagged with data storage tags (DSTs). Yellow diamonds indicate the river locations, while grey diamonds indicate the end locations for the PSAT tagged fish. Grey lines indicate the 1000 m bathymetry contour.

4.3 Ocean predation and mortality of adult Atlantic salmon (paper III)

The ocean predation and mortality of post-spawned Atlantic salmon from populations spanning the species' distribution range were investigated by inferring mortalities based on data retrieved from pop-up satellite archival tags (PSATs). The total sample included Atlantic salmon from Canada, Denmark, Ireland, Norway, and Spain.

This study documented predation by various marine predators, including toothed whales, endothermic fish, and ectothermic fish. In addition, several unknown mortalities were observed. The estimated predation and total mortality rates were low for Atlantic salmon from northern Europe, with no confirmed predation of fish originating from Norway. This contrasted the Atlantic salmon from Canada, Spain, and Ireland, where higher predation and total mortality rates were estimated. Predation by Atlantic bluefin tuna (*Thunnus thynnus*) primarily occurred within the Gulf of St. Lawrence, while porbeagle (*Lamna nasus*) predation occurred both in the Gulf of St. Lawrence and in waters spanning from the west of the Irish Shelf to the Bay of Biscay. Predation by toothed whales and ectothermic fish was less common and occurred over greater geographical areas.

Conclusions

1. The observed predator diversity demonstrated that a variety of large aquatic animals might forage opportunistically on Atlantic salmon during their ocean migration.
2. Predation and mortality rates were highest for the Atlantic salmon with the most prominent population declines, and it is possible that mortality of post-spawned Atlantic salmon influence trends in population abundance if accompanied with low post-smolt survival.
3. The observed predation by endothermic fish on Atlantic salmon from the Gulf of St. Lawrence and southern Europe, might suggests that Atlantic bluefin tuna and porbeagle may be a substantial source of mortality for Atlantic salmon populations co-occurring with these species.

5 Discussion

This thesis provides novel information about the ocean migration of post-spawned Atlantic salmon from Northern Norway and the Gulf of St. Lawrence, by presenting the first simultaneous description of the detailed horizontal migration and vertical movements for several individuals from these regions. This information is, in combination with the new information of ocean predation and mortality also provided in this thesis, important for understanding the different ecological conditions individuals encounter while in the ocean.

5.1 Horizontal migration

For Atlantic salmon from Northern Norway, this thesis provides the first direct evidence of a fidelity towards Arctic areas throughout the ocean phase, with individual migration routes ranging from the eastern Barents Sea to the Jan Mayen Island (paper I). Similar results have been reported in two previous studies on the migration of post-spawned Atlantic salmon from the Alta River (Chittenden et al. 2013a, 2013b). However, these studies provided limited information of individuals' horizontal migration as they described the joint seasonal distribution of multiple fish tagged with data storage tags (DST) and the short-term migration of two individuals tagged with PSATs (Chittenden et al. 2013a, 2013b). In recent years, several studies have demonstrated that Atlantic salmon from Norway utilize areas in the northern Norwegian Sea (Rikardsen et al. 2008, Jensen et al. 2014, Hedger et al. 2017a). This indicates that the importance of northern parts of the Norwegian Sea has been underestimated in historical assessments of the ocean distribution for the northernmost populations, likely due to the absence of a high-sea fishery targeting Atlantic salmon in these areas. For Atlantic salmon from the Alta River, the observed fidelity towards areas adjacent to the Jan Mayen Island during winter, may suggest that these waters are of particular importance for overwintering (paper I).

Paper I provides the first evidence of exclusive utilization of the Barents Sea by individual Atlantic salmon. Utilization of the Barents Sea has previously been documented by ocean sampling surveys (SALSEA-Merge 2007), tag recoveries (Rikardsen et al. 2008), and archival tagging experiments (Chittenden et al. 2013a, Hedger et al. 2017a). Based on the pop-up positions of Atlantic salmon tagged with PSATs from three Norwegian river, it was documented that the fidelity towards the Barents Sea varied among populations (Hedger et al. 2017a). Atlantic salmon from the Alta River displayed a similar partial utilization as documented in paper I, using the Barents Sea to a greater extent than Atlantic salmon from Central Norway, for which pop-up positions occurred exclusively in the Norwegian Sea (Hedger et al. 2017a). In contrast, for Atlantic salmon from a river draining directly into the Barents Sea, most of the pop-up positions occurred within in this marginal sea (Hedger et al. 2017a). This spatial segregation is supported by the utilization of waters in proximity to the Irminger Sea for post-smolt from Iceland tagged with DSTs (Guðjónsson et al. 2015), indicating that the ocean distribution of European Atlantic salmon strongly depends on geographical origin (Jacobsen et al. 2012, Jensen et al. 2014). Based on this evidence, it is possible that the diverging trend in population abundance between southern and northern European stocks is linked to persistent differences in ocean migration (Vøllestad et al. 2009).

No previous archival tagging study has been performed on Atlantic salmon from the Miramichi River. However, a PSAT study was conducted in the Bay of Fundy, where post-spawned Atlantic salmon from three populations displayed different ocean migration strategies (Lacroix 2013). Fish from the inner bay mainly resided within the Bay of Fundy, while some fish from the outer bay migrated rapidly along the Scotian Shelf eventually entering the Labrador Sea, where they displayed a migration northward along the Labrador Shelf (Lacroix 2013). A similar coastal migration was also evident for several Atlantic salmon from the Miramichi River (paper

II). The fish also entered the Labrador Sea at approximately the same time of the year in the two studies (Lacroix 2013, paper II), suggesting that post-spawned Atlantic salmon from geographically separated North American populations experience similar ecological conditions during parts of their ocean migration.

The directed northward migration along the Labrador Coast observed by some of the tagged Atlantic salmon from the Miramichi River (paper II) and by fish from the outer Bay of Fundy (Lacroix 2013), implied movements against the prevailing south-flowing Labrador Current. For Atlantic salmon, it has been suggested, based on conventional tagging experiments on first time migrants, that individual migration routes follow the North Atlantic subpolar gyre (Dadswell et al. 2010). However, results from paper II and Lacroix (2013) question the general applicability of this hypothesis, indicating that while the migration of post-smolts may depend on oceanic gyre systems (Dadswell et al. 2010), the horizontal migration of post-spawned Atlantic salmon is more directly linked to other environmental cues.

This thesis provides the first direct measure of how individual migration routes vary during large parts of the ocean migration, documenting a substantial within-population variation in both studied populations (paper I and II). Previous studies on the ocean migration of Atlantic salmon using archival tags have been limited by either describing the joint spatial distribution for all individuals within a single year class (Chittenden et al. 2013b, Guðjónsson et al. 2015), or by insufficient number of long-term deployments (Chittenden et al. 2013a, Lacroix 2013). For the Atlantic salmon from the Alta River, the overall diversity in migration routes was profound, with some individuals residing in different oceanographic regions throughout their ocean residency (paper I). For Atlantic salmon from the Miramichi River, individuals displayed diverse horizontal migration patterns both in Gulf of St. Lawrence and in the Labrador Sea (paper II). This indicates that a diversification of migration routes is common for Atlantic salmon from the same river and life stage. Moreover, this suggests that while the growth and survival of individuals depend on distinct oceanographic regions, the success of the entire population success may be determined by ecological conditions across large ocean areas.

5.2 Vertical movements

Vertical movements in pelagic fishes are likely governed by multiple ecological and physiological functions, including foraging behaviour, orientation, thermoregulation, and predator avoidance (Wilson and Block 2009, Thums et al. 2012, Braun et al. 2015, Righton et al. 2016). Diel vertical movement patterns, with either more frequent diving during daylight hours or a consistent deeper depth distribution during the day, are for many pelagic fish species associated with foraging (Walli et al. 2009, Campana et al. 2011, Dewar et al. 2011, Francis et al. 2015). For Atlantic salmon, repetitive diving associated with daylight has previously been observed in archival tagged post-spawned fish from Newfoundland, Bay of Fundy, and Norway (Reddin et al. 2011, Lacroix 2013, Hedger et al. 2017a). This behaviour has been documented as the principal behavioural mode of consecutive spawners (Reddin et al. 2004, 2011, paper II). Since these fish spend most of their ocean migration reconditioning, it is likely a suitable proxy for foraging. Repetitive diving during the day has also been observed in studies of first-time migrants (Holm et al. 2006, Reddin et al. 2006, Guðjónsson et al. 2015), indicating that this particular behaviour is a common foraging strategy across life stages and habitats.

Frequent diving in the upper part of the water column was observed during prolonged periods of the ocean migration, indicating that Atlantic salmon from both the Alta and the Miramichi River depended on extensive geographical areas for reconditioning (paper I and II). For Atlantic salmon from the Miramichi River, a clear diel pattern in diving behaviour was present when the fish were distributed in the Gulf of St. Lawrence and in coastal waters off Labrador and West Greenland (paper II). However, for fish that migrated to the central Labrador Sea, the vertical movements shifted to a more surface-oriented behaviour, accompanied by occasional deep dives (paper II). This suggests that vertical movement patterns of Atlantic salmon in the Labrador Sea were highly influenced by the oceanographic environment, which was further supported by the reversion to the diving behaviour displayed in the Gulf of St. Lawrence for the fish that later migrated towards coastal areas (paper II). These results contrasted the vertical movements of fish from the Alta River, where the diving frequency followed a clear seasonal trend, with a decreased diving intensity during the polar night period, independent of individuals' spatial distribution (paper I). A similar seasonal trend was found by Hedger et al. (2017a), indicating that the seasonal variation in the northeast Atlantic Ocean is an important determinant for the vertical movement patterns in this population.

In contrast to the diving intensity, a seasonal trend was absent in the diving depth for Atlantic salmon from the Alta River, with diving depth correlating with the depth of the mixed layer (paper I). Thermocline characteristics are known to influence the depth use of pelagic teleost and for bluefin tuna (*Thunnus* spp.), it has been postulated that individuals focus their diving around the mixed-layer depth in order to enhance foraging, because prey tend to aggregate around the thermocline (Walli et al. 2009, Furukawa et al. 2014). Whether or not a similar causal relationship is influencing the diving behaviour of Atlantic salmon is somewhat speculative. However, as a comparable pattern was documented in a previous study on Atlantic salmon from the Alta river (Hedger et al. 2017a), it is likely that the depth use is at least partially governed by the characteristics of the mixed layer. This suggests that while the diving intensity of Atlantic salmon inhabiting polar regions is primarily influenced by large scale seasonal factors, certain aspects of the vertical movement patters are linked to spatial-specific oceanographic features.

While the deep dives displayed in the northeast Atlantic Ocean are seemingly linked to foraging around the depth of the mixed layer (paper I), the governing mechanisms for the prolonged periods of deep diving displayed by the Atlantic salmon distributed in the central Labrador Sea are uncertain, as the relationship between vertical movement parameters and oceanographic conditions was not explicitly addressed (paper II). For Atlantic salmon, it has previously been suggested that deep dives are either indicative of searching for environmental cues associated with transition phases (Lacroix 2013), or foraging (Hedger et al. 2017a). Flexible foraging strategies have been inferred from changes in vertical movement patterns for several migratory pelagic fishes, and the ability to adapt to different ecological conditions is considered an important prerequisite for species that migrate across contrasting habitats (Walli et al. 2009, Humphries et al. 2010, Sims et al. 2012, Queiroz et al. 2017). For Atlantic salmon distributed in the central Labrador Sea, it likely that the observed shift in vertical movement patterns reflects individuals' ability to forage on a variety of prey species and that the deep dives are at least partially associated with feeding. This is supported by evidence of foraging on deep water prey by individuals residing over oceanic depths in the Labrador Sea (Templeman 1967, Rikardsen and Dempson 2011).

5.3 Ocean predation and mortality

The unique feature of pop-up satellite tags (PSATs) to provide data from dead fish has facilitated investigations of predator-prey interactions for numerous fish species (Béguer-Pon et al. 2012, Lacroix 2014, Cosgrove et al. 2015, Amilhat et al. 2016, Tolentino et al. 2017). In this thesis, predation by toothed whales, various ectothermic fish, Atlantic bluefin tuna, and porbeagle was inferred, in addition to several unknown mortalities (paper III). This predator diversity indicates that various large marine animals may forage on Atlantic salmon.

While predation by toothed whales and ectotherm fish was distributed over large geographic areas, affecting several of the studied populations, predation by endothermic fish was largely confined to Atlantic salmon from Canada and Spain (paper III). In the northwest Atlantic Ocean, several predation events by both Atlantic bluefin tuna and porbeagle were recorded in the Gulf of St. Lawrence (paper III). This contrasts to the pattern in the northeast Atlantic Ocean, where porbeagle was the most likely predator species in all predation events that occurred in proximity to the Irish Shelf and Bay of Biscay (paper III). A high predation pressure from Atlantic bluefin tuna and porbeagle was also recorded for post-spawned Atlantic salmon from the Bay of Fundy (Lacroix 2014), suggesting that predation by endothermic fish is common for populations co-occurring with Atlantic bluefin tuna and porbeagle.

Overall, the predation and mortality rates were highest for the Canadian, Irish, and Spanish Atlantic salmon, with fewer mortalities recorded for the northern European Atlantic salmon, and no confirmed predation events observed for the Norwegian populations. It has previously been suggested that the predation on post-spawned Atlantic salmon could impede the recovery of vulnerable populations (Lacroix 2014). As the overall trend in ocean mortality observed in paper III, coincides with the ongoing population declines, which are more profound for the southernmost stocks (ICES 2017), it is possible that a persistent low survival of post-spawned adults may act as an additive stressor to already vulnerable populations.

The use of PSATs for estimating marine mortality may be problematic for several species, as tag effects could increase the mortality (Jepsen et al. 2015). In this thesis, extensive efforts were made to prevent potential tag effects by only tagging fish considered of sufficient size and in a good overall condition. While this selective tagging may theoretically cause an underestimation of the natural mortality of post-spawned adults, it is more likely that the tagging increases the vulnerability to predation, due the physical impediment of being tagged. In paper III, the estimated predation and mortality rates were highest for the populations comprising of post-spawned Atlantic salmon of smaller relative size, indicating that the natural mortality may be somewhat overestimated. However, as no size difference was detected within populations between fish that died and fish that were alive throughout the deployment period, (paper III), it is likely that at least some of the differences in predation and mortality rates reflect contrasting mortality regimes.

6 Where do we go from here?

The principal problem with the existing archival tagging studies on Atlantic salmon is the lack of information on the ocean migration of first-time migrants. For Atlantic salmon, marine growth and survival of post-smolts are among the principal factors controlling population trends (Friedland et al. 2009, Chaput 2012). With the exception of two published studies (Reddin et al. 2006, Guðjónsson et al. 2015), little detailed information exists of the ocean migration and behaviour of this life stage. This lack of knowledge is primarily due to the small size of post-smolts, which eliminates the use pop-up satellite archival tags (PSATs), making small data storage tags (DSTs) the only option. However, the high natural mortality of maiden Atlantic salmon result in low recapture rates (Reddin et al. 2006, Guðjónsson et al. 2015). One way to circumvent this problem is to capture and tag maiden fish with PSATs at their ocean feeding grounds, when they have reached a sufficient size for tagging. While such studies will provide important information about the ocean migration of first time migrants, knowledge about maiden Atlantic salmon's migratory behaviour during the initial marine phase will still be missing. Consequently, without further miniaturization of PSATs or extensive tagging of post-smolts with DSTs, large parts of the ocean migration of maiden fish will have to be inferred by assuming that their movements mirror that of post-spawned individuals.

Due to the limited prior knowledge about the ocean migration of Atlantic salmon, the existing archival tagging studies have been largely confined to describing "where the fish moved" and "what they did" while at liberty. While there are still geographical regions where such descriptive information is needed, new studies should aim to formalize and test ecological hypotheses in combination with further quantification of the ocean migration. For Atlantic salmon, hypothesis-driven studies should explicitly aim to test how environmental factors govern individual movement regimes. To obtain a greater understanding of the fine-scale behavioural ecology, individuals' diving behaviour should be analysed in an environmental context, by further testing of how patterns in depth use vary between different oceanographic regions. This could enable explicit identification of oceanographic characteristics present in key marine habitats. Moreover, the functionality of different vertical movement patterns should be further explored by investigating dive shapes, which are considered a suitable proxy for the underlying behaviour in pelagic fishes (Wilson and Block 2009, Howey et al. 2016, Queiroz et al. 2017). In particular, disentangling the functionality of deep diving would enhance our overall understanding of Atlantic salmon's movement ecology, because this behaviour is commonly observed, but poorly understood.

While studies on how depth use correlate with environmental conditions will undoubtedly enhance our knowledge about the behavioural ecology of Atlantic salmon, investigating the drivers for horizontal migration is perhaps of even greater importance. Greater knowledge of how biotic and abiotic factors impact individual migration routes could improve our understanding of Atlantic salmon's ecology in the ocean and their spatial overlap with potential prey and predators. A recent study on the migration of ocean sunfish (*Mola mola*) revealed temperature as the principal driver for horizontal movements, with individuals residing in high productive frontal areas for extended periods (Sousa et al. 2016). Similar results have also been suggested for other migratory fishes (Walli et al. 2009, Braun et al. 2015) and for Atlantic salmon, explicit utilization of frontal waters is likely common (Jacobsen et al. 2012, Chittenden et al. 2013b). However, to what extent the thermal preference directly influences individuals' ocean distribution compared to other oceanographic features, such as food availability, salinity, and gyre systems, is not well known. To this end, archival tags that log environmental variables other than temperature are needed. This would enable simultaneous testing of the impact of multiple oceanographic variables on the horizontal migration of Atlantic salmon and facilitate predictions of annual variability in ocean distribution, particularly if accompanied by improved biological and physical data from important areas.

Although the ocean mortality of post-spawned Atlantic salmon has been quantified both in this thesis (paper III) and in a previous archival tagging study (Lacroix 2014), there is still a great need for more information on the extent and causes of the mortality and predation experienced by different populations while at sea. As previous archival tagging programs on Atlantic salmon have been conducted with the primary aim of studying migration, tagging experiments with the principal objective of studying mortality are therefore desired. These studies should deploy simpler low-cost PSATs that are designed for studying mortality (e.g. Goldsmith et al. 2017), as this would promote larger samples and more robust estimates of the ocean mortality. Such studies could provide an understanding of whether the ocean mortality of post-spawned adults influences trends in population abundance across different regions.

Despite archival tags being the only tool that can provide detailed information about the ocean migration of individuals, they should not be considered the only method to study the ocean distribution of Atlantic salmon. Archival tags are expensive, and future studies should aim to complement data obtained from archival tagging experiments with other methods. In addition to supplement data obtained from archival tags with data from ongoing sampling surveys, archival tagging studies should be combined with assessments of the ocean distribution using microchemical analyses (MacKenzie et al. 2011), which could provide more robust estimates of population-specific migration routes. This information could then be implemented in simulation studies of ocean migration routes (e.g. Mork et al. 2012, Byron and Burke 2014), in order to predict potential distribution shifts due to ongoing changes in the ocean.

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