

Thermal habitat of adult Atlantic salmon *Salmo salar* in a warming ocean

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Abstract

The year-round thermal habitat at sea for adult Atlantic salmon *Salmo salar* ($n = 49$) from northern Norway was investigated using archival tags over a 10 year study period. During their ocean feeding migration, the fish spent 90% of the time in waters with temperatures from 1.6–8.4°C. Daily mean temperatures ranged from –0.5 to 12.9°C, with daily temperature variation up to 9.6°C. Fish experienced the coldest water during winter (November–March) and the greatest thermal range during the first summer at sea (July–August). Trends in sea-surface temperatures influenced the thermal habitat of salmon during late summer and autumn (August–October), with fish experiencing warmer temperatures in warmer years. This pattern was absent during winter (November–March), when daily mean temperatures ranged from 3.4–5.0°C, in both colder and warmer years. The observations of a constant thermal habitat during winter in both warmer and colder years, may suggest that the ocean distribution of salmon is flexible and that individual migration routes could shift as a response to spatiotemporal alterations of favourable prey fields and ocean temperatures.

KEYWORDS

archival telemetry, Atlantic salmon, data-storage tags, North Atlantic Ocean, *Salmo salar*, temperature

1 | INTRODUCTION

Temperature has a strong influence on ectothermic fishes, as it affects their physiological performance, behaviour and spatial distribution (Fossheim *et al.*, 2015; Graham & Harrod, 2009). For the anadromous Atlantic salmon *Salmo salar* L. 1758, temperature affects growth and survival both in fresh water and at sea (Nicola *et al.*, 2018). The recent warming of the North Atlantic Ocean is linked to declines in salmon both in North America and Europe (Beaugrand & Reid, 2012; Mills *et al.*, 2013), potentially causing a northward expansion of their ocean range (Jensen *et al.*, 2014; Nielsen *et al.*, 2013).

While extensive information exists of the thermal niche of salmon in freshwater (Elliott & Elliott, 2010; Jonsson *et al.*, 2001), knowledge

of their thermal habitat at sea is less known. Sampling of salmon in the North Atlantic Ocean has documented that post-smolts inhabit diverse thermal habitats during the ocean feeding migration, mainly ranging between 4 and 12°C (Holm *et al.*, 2000; Reddin & Friedland, 1993; Sheehan *et al.*, 2012). In studies using archival tags, maiden salmon from Iceland spent most of the time in waters ranging from 7–11°C (Guðjónsson *et al.*, 2015), partly contrasting the thermal habitat of adults from Atlantic Canada that primarily inhabited waters with temperatures from 2–15°C during summer and autumn (Reddin *et al.*, 2004; Strøm *et al.*, 2017). The differences among studies suggests that the thermal habitat of salmon may depend on both geographical origin and life stage. However, as sampling at sea only provides snapshots of the thermal habitat and the data available from archival tags

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are either limited by tracking individuals for only parts of the marine phase or by small sample sizes, more information is needed in order to obtain a comprehensive understanding of the temperature individuals experience while at sea. The distribution of salmon also covers large geographic areas of the North Atlantic Ocean, with substantial variation in environmental conditions both between areas and between years. Hence, studies of the thermal habitat in different geographic areas and across multiple years would add to the overall understanding of the marine phase of Atlantic salmon.

Here, the thermal habitat of 49 adult salmon from northern Norway that spent c. 12 months at sea was quantified using archival tags. Fish were tagged over a 10 year period, enabling a comparison among years. The aim was to provide a comprehensive description of the thermal habitat of adult salmon during the entire ocean migration by describing seasonal trends in experienced temperature and investigate how annual variation in thermal conditions in the Northeast Atlantic Ocean affected the thermal habitat experienced during their ocean feeding migration.

2 | MATERIALS AND METHODS

The care and use of experimental animals complied with Norwegian animal welfare laws, guidelines and policies as approved by Norwegian Animal Research Authority and Norwegian Food Safety Authority (permit reference number 15950).

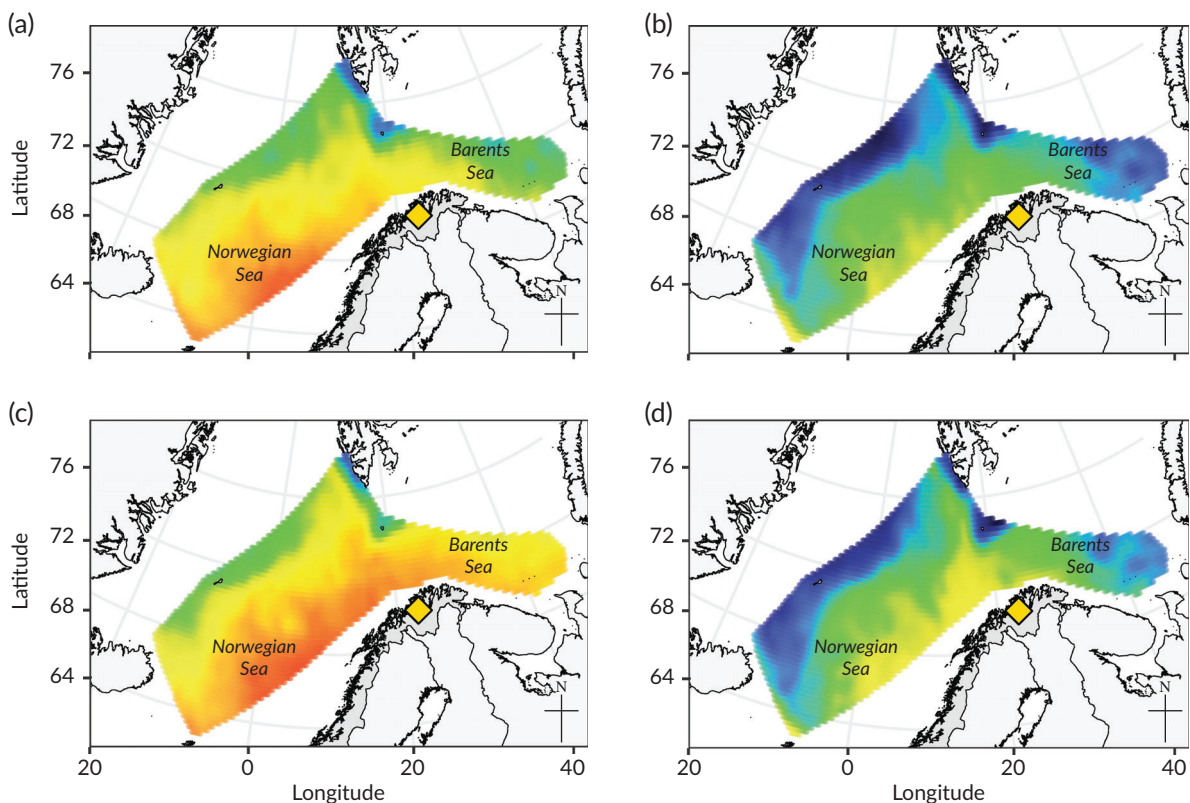


FIGURE 1 Maps with examples of monthly mean sea-surface temperatures in the assumed distribution range of *Salmo salar* from the Alta River based on Chittenden *et al.* (2013) and Strøm *et al.* (2018): (a) September 2010, (b) December 2010, (c) September 2011 and (d) December 2011. ♦, Location of the Alta River

2.1 | Tagging

Adult Atlantic salmon were sampled and tagged in the Alta River, northern Norway (70° N, 23.4° E), in May 2006–2015 after spawning the previous autumn. The Alta River discharges into the northern Norwegian Sea (Figure 1) and is a prized destination for recreational anglers due to its large-sized salmon. A total of 1044 salmon were tagged, with fork lengths (L_F) ranging from 51 to 121 cm (mean \pm SD = 90 \pm 13 cm). Fish were captured by angling and anaesthetised in an aqueous solution of 0.5 mL L⁻¹ 2-phenoxy ethanol prior to tagging. Tag type, tag sensors and temporal resolution of tag data varied among years (Table 1). In 2006–2007, tags equipped with a temperature sensor were attached externally, while in 2008–2015, tags recording temperature and depth were implanted into the body cavity of the fish (for details, see Rikardsen & Thorstad 2006; Strøm *et al.* 2018). Tags deployed in 2006 and 2007 failed to log data during the last months at sea, due limited battery capacity (Table 1).

2.2 | Data analyses

Of the 1044 tagged salmon, 49 fish were recaptured and killed with functioning tags after spending c. 1 year at sea (Table 1). At tagging, the recaptured fish had L_F ranging from 76–110 cm (mean \pm SD = 93.6 \pm 6.6 cm). All the recaptured fish had left the river shortly

TABLE 1 Overview of the number of tagged *Salmo salar* (*N*), the number of retrieved tags (*n*), tag producers, attachment methods, and previous analyses of the data set

Year	<i>N</i>	<i>n</i>	Tag producer	Tag sensors	Logging period	Attachment method	Previously published
2006	73	4	iButton	Temp (30 min)	June 06 – March 07	External ^a	c
2007	197	3	iButton	Temp (30 min)	June 07 – March 08	External ^a	c
2008	54	6	Star Oddi	Temp and depth (30 min)	June 08–July 09	Internal ^a	c and d
2009	60	3	Star Oddi	Temp and depth (30 min)	May 09–July 10	Internal ^a	d
2010	94	7	Star Oddi	Temp and depth (30 min)	May 10–June 11	Internal ^a	d
2011	67	5	Star Oddi	Temp and depth (30 min)	May 11–July 12	Internal ^a	d
2012	73	2	Star Oddi	Temp (30 min) and depth (10 min)	May 12–July 13	Internal ^a	d
2013	80	4	Star Oddi	Temp (15 min) and depth (5 min)	May 13–June 14	Internal ^a	d
	60	2	Lotek	Internal and external temp, depth, and light (30 s)		Internal ^b	b
2014	81	2	Star Oddi	Temp (15 min) and depth (5 min)	June 14 – July 15	Internal ^a	d
	61	2	Lotek	Internal and external temp, depth, and light (30 s)		Internal ^b	b
2015	68	7	Star Oddi	Temp (5 min) and depth (1 min)	May 15 – July 16	Internal ^a	d
	76	2	Lotek	Internal and external temp, depth, and light (30 s)		Internal ^b	b
Total	1044	49					

^aRikardsen and Thorstad, 2006.

^bStrøm *et al.*, 2018.

^cChittenden *et al.*, 2013.

^dHedger *et al.*, 2017.

after tagging, with date of ocean entry ranging from May 9–July 5. In previous analyses using parts of this data set, the spatial distribution (Chittenden *et al.*, 2013; Strøm *et al.*, 2018) and depth use (Hedger *et al.*, 2017) of these individuals have been described (Table 1). Individual migration routes were reconstructed for six salmon tagged in 2013–2015, because they were fitted with tags that recorded light data, thus enabling light-based geolocation (Strøm *et al.* 2018, Table 1).

2.3 | Seasonal trends

Seasonal trends in temperature use were quantified by calculating the monthly probability density functions (PDF) of daily mean temperatures and by two sets of generalised additive mixed-effect models (GAMM) that included individual fish as random effects. In the first set of GAMMs, the seasonal change in daily mean temperature was investigated with day as the fixed smoothing term, daily mean depth and L_F at tagging as continuous fixed effects and year of tagging as a factorial fixed effect (Table 2). In the second set of GAMMs, changes in the weekly thermal range (difference between the maximum and minimum temperature) were investigated from late June in the year of tagging until early June the following year. Here, the most complex model included week as a fixed smoothing term, maximum depth and L_F at tagging as continuous fixed effects and year of tagging as a factorial fixed effect (Table 2). Tags deployed in 2006 and 2007 were omitted from the GAMMs, because these tags were not equipped with depth sensors (Table 1). All GAMMs included cubic regression splines using the *bam*-function from the *mgcv* package in R (Wood, 2011).

2.4 | Oceanographic conditions

To investigate how temperature trends in the North Atlantic Ocean affected the thermal habitat of salmon, the relationship between sea-surface temperature anomalies (SST anomalies) and daily mean temperatures was investigated during late summer and autumn (August–October) after the fish entered the ocean and during winter (November–March). Daily SST anomalies were defined as the difference between the observed SST and the mean SST from 1971–2000 (Reynolds *et al.*, 2007) and were acquired from the National Oceanic and Atmospheric Administration (NOAA) High Resolution SST data (<http://www.esrl.noaa.gov/psd/>). Daily mean SST anomalies were derived from the spatial domain most likely utilised by adult salmon from the Alta River (Figure 1; Chittenden *et al.* 2013, Strøm *et al.* 2018). Temperatures prior to August and after March were omitted from the analyses, because many of the salmon probably migrated through more coastal waters during these periods, which are more prone to errors in data derived from satellite imagery. To model the relationship between daily mean temperatures and SST anomalies, two sets of linear mixed-effect models (LMM) were entrained using the *nlme* package in R (Pinheiro *et al.*, 2018), for late summer and autumn and winter, respectively. The most complex LMMs included daily mean temperature as the response variable, mean daily SST anomalies and day as continuous fixed effects, year as a factorial fixed effect and individual fish as random effects on the model intercept. In both sets of models, day was initially formalised as a quadratic term (*i. e.*, second order polynomial) to account for potential non-linear relationships.

TABLE 2 Overview of the generalised additive mixed-effect models (GAMM) and linear mixed-effect models (LMM) used to quantify seasonal trends in thermal habitat and effects of sea-surface temperature anomalies on temperatures experienced by *Salmo salar*

Model type	Years	Response variable	Smoother	Fixed effects	Random effects (fish)	R ²
GAMM	2006–2015	Mean temperature	Day ^a	Mean depth ^a L _F Year	Intercept ^a Splines ^a	0.69
GAMM	2006–2015	Thermal range	Week ^a	Max depth ^a L _F Year	Intercept ^a Splines	0.47
LMM	2006–2015 (August–October)	Mean temperature		SST anomaly ^a Day ^a Day ² Year	Intercept ^a	0.29 (0.73)
LMM	2006–2015 (November–March)	Mean temperature		SST anomaly Day Day ² Year	Intercept ^a	0 (0.33)

^aModel terms included in the most parsimonious models; R², the adjusted R² for the GAMMs and the marginal R² for the LMMs, with the conditional R² given in the parenthesis.

All GAMMs and LMMs were corrected for temporal autocorrelation at the level of the individual fish, using a first-order autoregressive process that accounts for the immediately preceding value. Model selection was conducted using a backward selection strategy, where the optimal structure of the random effects was determined for the most complex model before fixed effects were removed in a sequential order until only explanatory model terms remained (Zuur *et al.*, 2013). For selection of the parsimonious GAMMs, model terms were selected based on their significance, while for the LMMs Bayesian information criterion (BIC) values were used to quantify model fit.

3 | RESULTS

3.1 | Seasonal trends

During the ocean migration, Atlantic salmon experienced temperatures ranging from -0.9 to 15.8°C and 90% of the recorded temperatures were between 1.6 and 8.4°C (Figure 2). Individuals' minimum temperatures ranged from -0.9 to 3.0°C and maximum temperatures from 9.3 to 15.8°C . Daily mean temperatures experienced by the fish ranged from -0.5 to 12.9°C (mean \pm SD = $5.4 \pm 2.0^{\circ}\text{C}$). The monthly probability density functions of daily mean temperatures revealed a clear seasonal trend (Figure 3). Daily mean temperatures were highest in July, when the range from the first to the third quartile was 6.7 – 8.9°C , before they gradually decreased until November (Figure 3). From November until March, the daily mean temperatures were stable, ranging primarily from 3.4 to 5.0°C (Figure 3). This seasonal pattern, with the lowest temperatures during winter, was confirmed by the GAMMs with daily mean temperatures as the response variable (Figure 4). The parsimonious model included a significant effect of day as a smoothing term (EDF = 8.1, $P < 0.001$), a negative effect of daily mean depth

($t = -62.23$, $P < 0.001$) and individual fish as random effects both on the model's intercept (EDF = 35.1, $P < 0.001$) and regression splines (EDF = 33.4, $P < 0.001$; Table 2), indicating some individual differences (Figure 2). While the effect of mean depth on daily mean temperatures was small ($\beta \pm \text{SE} = -0.0060 \pm 0.0001$), it was still considered as a relevant predictor variable because daily mean depths ranged from 0.3 to 562 m (mean \pm SD = 18.9 ± 35.9), thus corresponding to a 0.6°C decrease in daily mean temperature 100 m^{-1} .

Daily differences between the maximum and minimum temperatures experienced by the fish ranged from 0.0 – 9.6°C (mean \pm SD = $1.3 \pm 1.2^{\circ}\text{C}$), with the greatest thermal range experienced during the first summer at sea (Figure 4). This was confirmed by the GAMMs with thermal range as the response variable. Here, the parsimonious model included a significant effect of week as a smoothing term (EDF = 8.2, $P < 0.001$), maximum depth as a continuous fixed effect ($Z = 23.8$, $P < 0.001$) and individual fish as random effects on the model's intercept (EDF = 28.6, $P < 0.001$; Table 2). Despite the effect of maximum depth on individuals' thermal range being small ($\beta \pm \text{SE} = 0.0040 \pm 0.0002$), it was considered important given the range of depths utilised by the tagged fish. While at sea, the salmon utilised depths ranging from 0–740 m and the thermal range was predicted to increase by 0.4°C 100 m^{-1} according to the model. In both sets of GAMMs, year and L_F at tagging were excluded as fixed effects (Table 2).

3.2 | Oceanographic conditions

From August to March, the mean SST anomalies in the assumed distribution area ranged between -0.8 and 1.7°C (mean \pm SD = $0.8 \pm 0.4^{\circ}\text{C}$), with sea-surface temperatures varying both within and among years (Figure 1). SST anomalies had a significant effect on daily mean temperatures experienced by the fish during summer and

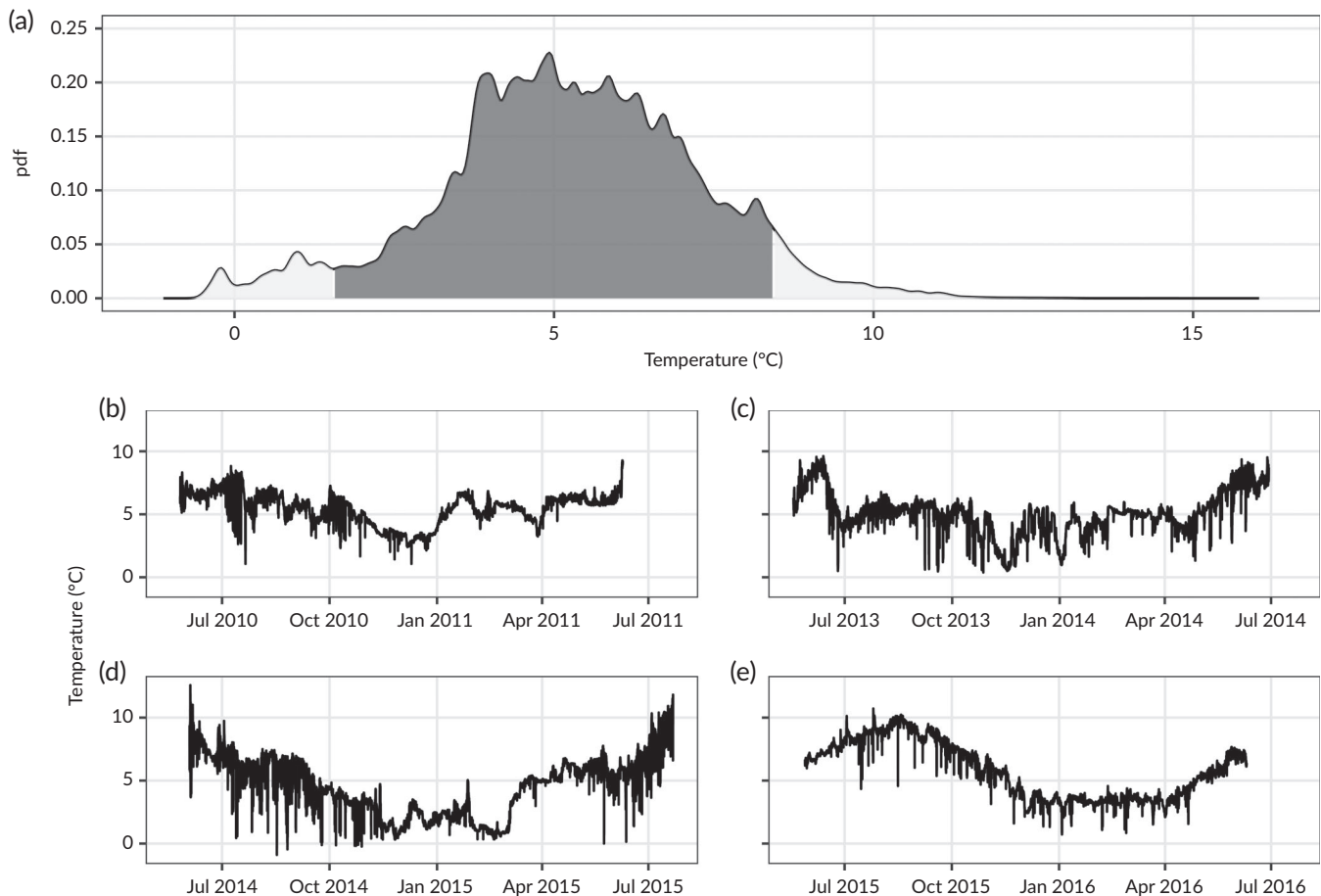


FIGURE 2 Water temperatures experienced by *Salmo salar* tagged with temperature-sensing archival tags ($n = 49$). (a) Probability density function (PDF) of all recorded temperatures from the returned tags. ■, The area between the 5th and 95th percentile (*i.e.*, 90% of the observations). (b)–(e) Examples of complete temperature profiles of individual fish

autumn (August–October), with the parsimonious model including SST anomaly ($\beta \pm SE = 0.43 \pm 0.08$) and day ($\beta \pm SE = -0.04 \pm 0.001$) as fixed effects and random effects of individual fish on the model's intercept (Table 2). In contrast, an overall relationship between SST anomalies and daily mean temperatures experienced by the fish was absent during winter (November–March), with the random effect model providing the best fit to the data (Table 2).

4 | DISCUSSION

The ocean temperatures experienced by Atlantic salmon in this study, with most temperature recordings ranging from 1.6–8.4°C, documented residency in colder waters than indicated in previous studies, where salmon have primarily been recorded in waters with temperatures between 5 and 15°C (Table 3). For anadromous salmonids, thermal preference in the ocean has been shown to be size-dependent, with larger individuals inhabiting colder waters (Morita *et al.*, 2010). While there was no effect of body size on temperatures experienced by individual fish in the present study, it is possible that the overall large size of the repeat ocean migrants may partially explain the lower temperatures observed here compared with

previous studies of salmon post-smolts (Table 3), thus indicating some differences in ocean distribution among life stages. However, similar temperatures to those recorded here were documented for both repeat ocean migrants and large maiden salmon in the Labrador Sea during autumn and winter in studies using archival tags (Strøm *et al.* 2017; T.F. Sheehan pers. comm.). This, in combination with recent catches of maiden salmon in cold waters at 78° N (Jensen *et al.*, 2014), suggest that the temperatures recorded in the present study might be representative of the thermal habitat during autumn and winter for salmon that inhabits northern parts of their ocean distribution range.

Daily mean temperature experienced by the fish varied cyclically during the ocean migration, with the coldest temperatures recorded during winter. A similar seasonal pattern was observed for maiden fish from Iceland tagged as smolts, which similar to the repeat ocean migrants in the present study spent *c.* 1 year at sea (Guðjónsson *et al.*, 2015). This suggests that a cyclic trend in thermal habitat consistent with the seasonal variation in temperatures in the North Atlantic Ocean may be typical for salmon of different life-stages.

A seasonal trend was also evident in the weekly thermal range, with smaller differences between maximum and minimum

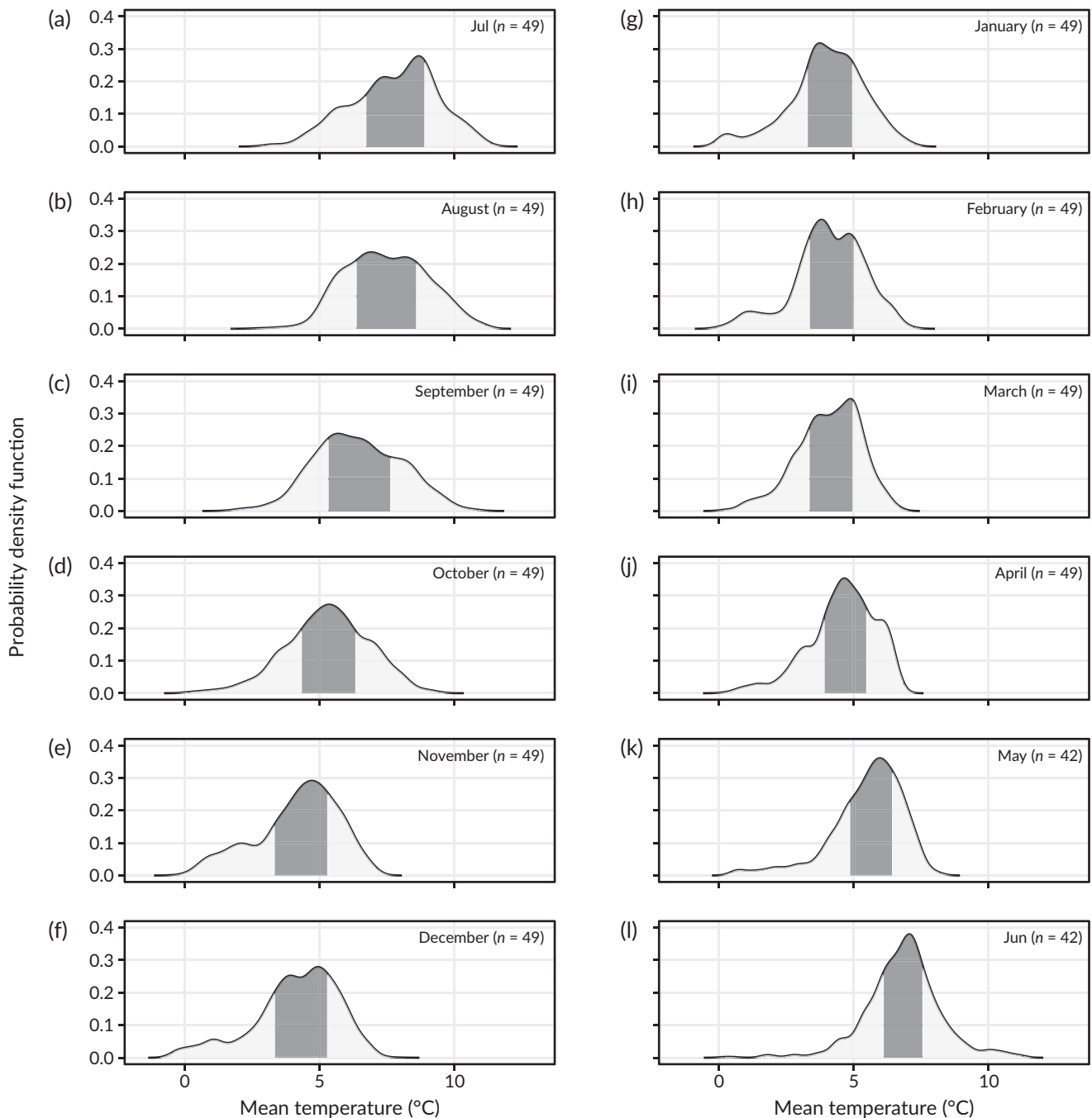


FIGURE 3 Seasonal trends in daily mean temperatures for *Salmo salar* tagged with temperature-sensing archival tags ($n = 49$). (a)–(l) Monthly probability density functions of daily mean temperatures from July in the year of tagging to June in the year of return. ■, The area between the 1st and 3rd quartile (i.e., 50% of the observations); n , tagged fish sample size

temperatures in winter than in late summer. Using data from some of the fish included here, Hedger *et al.* (2017) and Strøm *et al.* (2018) found that the diving behaviour varied during the ocean feeding migration, with fish diving less frequently and to greater depths during the winter months. This behavioural shift correlated with seasonal changes in light availability at high latitudes and with the deepening of the thermocline (Hedger *et al.*, 2017; Strøm *et al.*, 2018), indicating that the seasonal trend in thermal range is influenced by both behavioural changes and environmental variation.

Variation in ocean temperatures among years affected the temperatures experienced by salmon during the first summer and autumn, with fish occupying warmer waters in warmer years during this time of the season. This is direct evidence that changes in oceanographic conditions affect the thermal habitat of salmon and may suggest that a continued warming of the North Atlantic Ocean will further increase the temperatures experienced during summer and autumn. For Atlantic salmon, temperature-induced changes in marine ecosystems are partly linked to the ongoing population declines, with several correlative studies linking the reduction in growth and survival of European

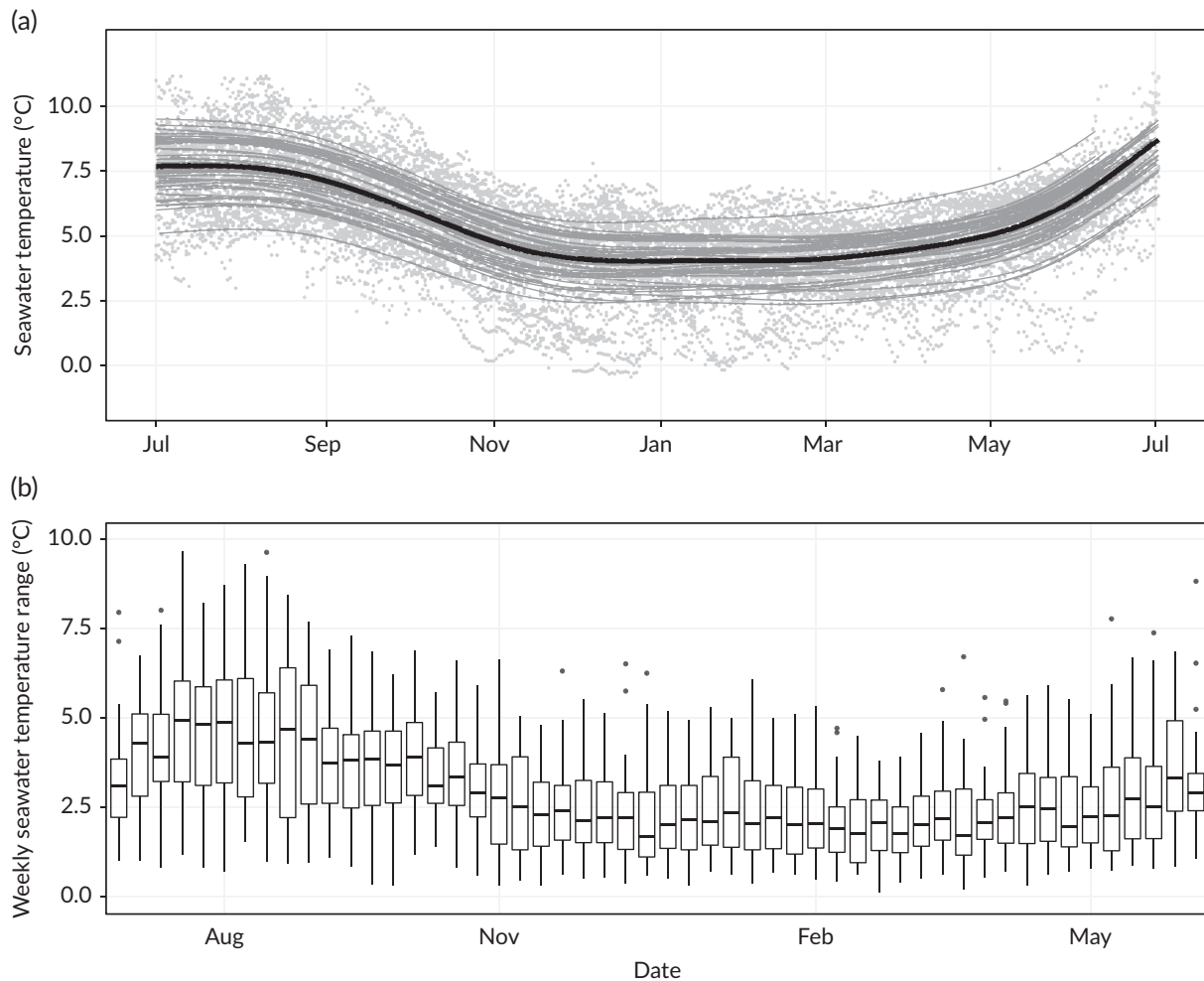


FIGURE 4 Seasonal trends in water temperatures experienced by *Salmo salar* tagged with temperature and depth sensing archival tags ($n = 42$). (a) Daily mean temperatures, with individual smoothers (—, —) and overall smoother (—; effect of day, EDF = 8.1, $P < 0.001$). (b) Boxplots (—, median; □, interquartile range; —, 95% of range; O, outliers) of weekly thermal range (difference between maximum and minimum temperature) from late June in the year of tagging until early June the following year

post-smolts to increased ocean temperatures during the first summer at sea (Friedland *et al.*, 2009, 2014). While the current study only described the thermal habitat of adult fish, the relationship between available ocean temperatures and the experienced thermal habitat during summer and autumn may be representative also for first-time migrants.

In contrast to the positive relationship between SST anomalies and daily mean temperatures experienced by the fish during summer and autumn, a correlation between temperatures in the assumed distribution range and individuals' thermal habitat was absent during winter. From November to March, the tagged salmon resided in areas with waters temperatures ranging between 3.4 and 5°C in both warmer and colder years, indicating a strong fidelity towards waters with these temperatures during large part of their ocean migration. Factors controlling habitat selection in salmon were not addressed here, but it is likely that the habitat use was influenced by prey availability instead of by water temperatures *per se*, or by a combination of these factors. During their

ocean migration, the tagged fish experienced temperatures well within their critical limits (Elliott & Elliott, 2010), but far below temperatures that optimise growth at excess food rations at sea (Handeland *et al.*, 2008). For ectothermic fishes, the temperatures at which somatic growth are highest gradually decline as food rations and food intake decrease (Jobling, 1997). Thus, the observed thermal habitat may be influenced by interactions between the spatiotemporal distribution of prey and ocean temperatures, with salmon inhabiting waters that enhance growth both in terms of maximising overlap with favourable prey fields and minimising metabolic cost during periods of low prey availability. Moreover, since evidence of population-specific thermal adaptations is lacking for salmon (Anttila *et al.*, 2014; Jonsson *et al.*, 2001), it is possible that a similar interaction affects the temperatures experienced by individuals across the North Atlantic Ocean and that differences in thermal habitat among populations utilising different areas at sea (Table 3) are mainly influenced by local variation in prey fields and ocean temperatures.

TABLE 3 Overview of the thermal habitat of *Salmo salar* in various ocean areas derived from previously published studies and personal communication

Study	Method	Tagging location	Ocean area	Duration	Life-stage	Range (°C)	90th percentile (°C)
Reddin <i>et al.</i> , 2004	Archival tagging	Newfoundland	Gulf of St. Lawrence and Labrador Sea	May–September	Adults	0–25	3.9–17.3 (90%) ^a
Reddin <i>et al.</i> , 2006	Archival tagging	Newfoundland	Labrador Sea	May–June	Maiden	> 0–20	8–15 (90%)
Holm <i>et al.</i> , 2006	Archival tagging	Norwegian Sea	Norwegian Sea	April–August	Maiden	5–16	–
Reddin <i>et al.</i> , 2011	Archival tagging	Newfoundland	Labrador Sea	May–August	Adults	> 0–20	3.8–14.1 (90%) ^a
Lacroix, 2013	Archival tagging	Bay of Fundy	Bay of Fundy, Gulf of Maine, Labrador Sea	November–August	Adults	> 0–16	–
Guðjónsson <i>et al.</i> , 2015	Archival tagging	Iceland	Irminger Sea	Full migration	Maiden	5–16	7.1–11.5 (90%) ^a
Strøm <i>et al.</i> , 2017	Archival tagging	Gulf of St. Lawrence	Gulf of St. Lawrence	May–July	Adults	0–17.9	4.9–12.8 (90%)
Strøm <i>et al.</i> , 2017	Archival tagging	Gulf of St. Lawrence	Labrador Sea	June–October	Adults	–1.3 to 14.9	2.2–9.6 (90%)
T.F. Sheehan pers. comm.	Archival tagging	West Greenland	Labrador Sea	September–April	Maiden	–0.4 to 7.8	2.4–5.8 (90%)
This study	Archival tagging	Northern Norway	Norwegian and Barents Sea	Full migration	Adults	–0.9 to 15.8	1.6 to 8.4 (90%)
Reddin and Friedland, 1993	Sampling surveys	–	Labrador Sea	All year	Maiden	3–13	–
Holm <i>et al.</i> , 2000	Sampling surveys	–	Norwegian and Barents Sea	May–Sep	Maiden	3–13	–
Sheehan <i>et al.</i> , 2012	Sampling surveys	–	Labrador Sea	Aug–Sep	Maiden	5–13	–
Minke-Martin <i>et al.</i> , 2015	Otolith-derived	–	West Greenland	Summer	Maiden	0–19	–

^a90th percentiles were not stated in the publications but obtained from personal communication.

Changes in ocean temperatures have led to shifts in the spatial distribution for a diversity of marine fish species (Cheung *et al.*, 2015; Fosshem *et al.*, 2015). Owing to the magnitude of the ongoing ocean warming, a similar trend may also present for anadromous salmonids that perform long-distant ocean feeding migrations (Nielsen *et al.*, 2013). Based on recent catches of salmon in waters previously considered as north of the species' northernmost limit, a northward expansion of the ocean distribution has been suggested (Jensen *et al.*, 2014). Compared with other marine fishes, where a northward displacement is well documented, detailed knowledge of the historical ocean distribution of salmon is limited, with most information originating from fisheries off the Faroe Islands and west Greenland (Jacobsen *et al.*, 2012; Reddin *et al.*, 2012) and sampling of post-smolts in the Norwegian and Labrador Sea (Holm *et al.*, 2000; Reddin & Friedland, 1993). Recent studies using archival tags have revealed novel aspects of individuals' spatial distribution (Hedger *et al.*, 2017; Strøm *et al.*, 2017, 2018) and the suggestion of a northward expansion may therefore be an artefact due to lack of detailed historical information. However, the observations of a constant thermal habitat during winter in both warmer and colder years in the present study, may suggest that the ocean distribution of salmon is flexible and

that individual migration routes could shift as a response to changes in the North Atlantic Ocean.

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AUTHOR CONTRIBUTIONS

A.H.R. designed the sampling. J.F.S. and E.B.T. conceived the idea for the manuscript. J.F.S. analysed the data. J.F.S. led the writing of the manuscript, with contribution from E.B.T and A.H.R. All authors approved the final version of the manuscript.

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