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ABSTRACT

Low marine-phase survival of many Atlantic salmon (*Salmo salar*) populations is hindering productivity—and in some cases recovery—of the species, yet our understanding of the causal dynamics remains incomplete. Pop-up satellite archival tags were used to track fish captured in waters off West Greenland from September-April of 2010, 2011, and 2012 to gain insights into conditions experienced during their second year at sea. Migration dynamics, thermal habitat, and depth usage are described for 2 fish that retained their tags for the duration of the study. Predation of tagged fish was also inferred in 3 cases. Improving our understanding of this life stage is necessary to identify consistent patterns and potential survival bottlenecks, and to formulate effective marine management options to improve survival.

INTRODUCTION

Atlantic salmon (*Salmo salar*) populations in the North Atlantic are influenced by a complex mosaic of direct and indirect pressures, both natural and anthropogenic, during the freshwater and marine phases of their life cycle (Hansen and Quinn 1998; Parrish et al. 1998; Chaput 2012). While factors that regulate freshwater productivity are fairly well documented (Parrish et al. 1998), an understanding of factors that control marine productivity has been more elusive. However, survival during the marine phase is thought to have a greater influence on population abundance than survival during the freshwater phase (Reddin 1988; Pardo et al. 2021).

The marine phase has several life-history strategies determined by the duration spent at sea. Northern European populations generally spend more time at sea than North American and Southern European populations, which are typified by two primary strategies (Thorstad et al. 2011). Maiden 1-sea-winter (1SW) population segments remain at sea for 1 year before spawning while maiden 2-sea-winter (2SW) population segments remain at sea for 2 years before spawning. Maiden 2SW female spawners are considered the drivers of productivity in many populations because they are larger, more fecund (Chaput 2012; Halttunen et al. 2013), and they produce higher quality eggs, thereby generating more, higher quality offspring than their 1SW conspecifics (Cairns 2001). Accordingly, annual abundance patterns of many populations may be influenced differentially by complex interactions among the timing of maturation, marine mortality factors, and the variability of environmental drivers (Chaput 2012; Mills et al. 2013; Olmos et al. 2019). The abundance of many Atlantic salmon populations across the North Atlantic has been declining for several decades, largely the result of low marine productivity of maiden 2SW fish, and concern as to the viability of some populations without increases in the abundance of this important population segment is mounting (ICES 2019). Before management options to improve marine productivity can be considered, spatiotemporal usage patterns of the various life stages must be identified.

The marine migrations and distribution of Atlantic salmon can be coarsely assembled from previous fishery, survey, and research efforts. Mark-recapture programs using visual tags (e.g., Carlin tags, coded wire tags) have been employed to obtain coarse information on distribution, migration dynamics, and movement patterns of fish at sea (Jacobsen et al. 2012; Reddin et al. 2012). Advancements in passive electronic tag technology (i.e., acoustic technology) has enabled the collection of more detailed tracking information to better understand how ecological or environmental covariates may influence marine migration and survival (Rikardsen et al. 2008; Thorstad et al. 2013). However, the ability to collect information is reduced when fish move into offshore areas where complete and overlapping telemetry receiver coverage is impractical or when migration duration exceeds the battery life of the tags. In these situations, information can be collected over longer durations and distances with the use of data storage tags (DSTs). Larger study animals are generally required to accommodate internally implanted tags or externally harnessed tags, and the tags must be physically recovered to obtain the data (Thorstad et al. 2013). However, pop-up satellite archival tags (PSATs)—modified DSTs that communicate with satellites—eliminate the need for tag recovery to obtain data. Although larger animals are also required, this technology has been successfully used to obtain novel information on the marine phase dynamics of salmon that return to the sea after spawning (Lacroix, 2013; Hedger et al. 2017; Strøm et al. 2017; Rikardsen et al. 2021).

While the marine distribution of Atlantic salmon at sea is hypothesized to be driven by ocean currents and thermal conditions, particularly the location of the 4-8 °C isotherms (Reddin and Friedland 1993), the dearth of detailed spatiotemporal information on Atlantic salmon in the ocean has been recognized as a limitation to understanding the potential significance of various marine mortality sources (DFO 2015; NASCO 2015). Since an improved understanding of the ecology of eventual maiden 2SW spawners is necessary to determine the underlying factors that influence marine productivity, 25 animals were tagged with PSATs at the West Greenland feeding grounds from 2010-2012 to determine if obtaining high-quality data on this life stage (i.e., the immature 1SW adults at West Greenland that become maiden 2SW spawners the following year) was possible and to further develop fundamentally important questions about the marine migration of Atlantic salmon.

METHODS

Standard rate pop-up archival satellite tags (X-Tag, Microwave Telemetry, Inc., Columbia, MD, http://www.microwavetelemetry.com/fish/Xtag.cfm) measured and archived temperature, depth, and light levels at 2-minute intervals. An onboard processor used the light level data to estimate time of sunrise, sunset, and local noon, which was used to estimate daily geolocation position. The tags were programmed to release from the fish on April 1 the year following release (after ~7 months), after 4 days within a constant depth band of 3 m, or if the tag exceeded 1200 m depth. The expectation was that fish would be close to their natal rivers by April. Since tags must be in salt water to pop-off, the date was chosen because fish were thought to begin entering freshwater in early May. Tags were also programmed to pop-off after 4 days within a constant depth band of 3 m for several reasons: Since Atlantic salmon are thought to be largely surface oriented, this was considered sufficient to prevent premature pop-offs if they were alive and actively swimming but with limited vertical movement in the water column. If they were not actively moving after the 4-day delay within a narrow depth band, the assumption was that they would either be dead on the sea floor or floating on the surface. The 1200 m pop-off was an emergency release setting since this depth approaches the crush depth of the tag housing.

The care and use of experimental animals complied with Greenland animal welfare laws, guidelines, and policies as approved by the Greenland Institute of Natural Resources. Fish were collected south of Nuuk, Greenland, using several catch methods (i.e., gillnets, trolling, longline, and trap nets) with varying levels of effort and efficacy. After capture, fish were placed in a tank with clean seawater and examined for signs of capture stress (e.g., excessive scale loss, physical injury, lethargy, responsiveness). Fish judged to be in good physical condition were retained for tagging. In a separate tank, fish were anesthetized in a solution of MS-222 and seawater. When sedated, they were weighed (0.1 kg) and measured (0.5 cm). A small piece of fin tissue and several scales were collected for continent of origin and age determination, respectively (ICES 2019). The tags were attached to the fish with a custom harness system as described in Hedger et al. (2017). After tagging, fish recovered in a large tank of clean seawater.

Tag release and pop-off locations of host salmon that reached the April 1 pop-off date were determined via direct contact with the satellite, while interim positions were estimated by light-based geolocation. Final positions of the host salmon that did not reach the April 1 pop-off date were estimated through back-calculation to account for surface drift prior to transmission. This was necessary because tags that released early would have been floating at the surface for 4 days before the pop-off mechanism activated, thereby initiating data transmission and communication with the satellites. Each daily position estimate was generated by the tag-based software using estimates of sunrise, sunset, and local noon as measured by the onboard light sensor and internal clock. These estimates were cross-validated based on a set of migration rules and environmental metrics. First, the plausibility of all light-based geolocation positions between the tag release and tag pop-off were coarsely evaluated based on a migration rule that allowed movement of up to 86 km per day (i.e., continuous swimming at 1 $m \cdot s^{-1}$), and positions outside this daily radius were excluded (i.e., the location of the fish was somewhere within the radius). In situations where daily position estimates were either not transmitted or not received by the satellite system, the location radius increased additively. The longitude estimates for each day then defined the central axis of a 4°-wide search corridor from 50 °N to 85 °N, within which each tag's sea surface temperature (SST) estimates were matched against satellite-derived data from the National Centre for Ocean Forecasting's Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) database (https://podaac.jpl.nasa.gov/dataset/UKMO-L4HRfnd-GLOB-OSTIA). Locations with measured SST values that exceeded ± 0.5 °C of tag-derived SST data were excluded. Maximum depth recorded by the tag was then compared with bathymetry data (http://www.gebco.net/data_and_products/gridded_bathymetry_data) at potential positions to further exclude improbable position estimates. This resulted in daily fields of possible locations that matched environmental criteria. These daily positions were then refined in a forward-run step-wise process by which the possible locations for day n+1 were eliminated based on a 0.5 $m \cdot s^{-1}$ swimming speed rule from (a) the average latitude and longitude of plausible positions on day n (or the closest previous day on which matching positions were available) and (b) the pop-off location (Appendix I and II).

The final disposition of each fish was grouped into 1 of 3 categories based on the timing of tag pop-off and data transmission: *Timed release* (programmed pop-off date reached), *Early release* (programmed release date not reached), and *Unknown* (no data reported). A sub-group of *Early release*, the *Depredated* group, was identified by a combination of light level measurements and sunrise/sunset times, temperature changes, and/or abnormal changes in depth profiles compared to other fish. Eight tagged salmon were not included in the analysis because tags popped off after 7-30 days close to the release site and were considered compromised due to either capture (gillnet) or tagging-related stress (Table 1).

RESULTS

Twenty-five Atlantic salmon were tagged and released in September 2010 (n = 7), 2011 (n = 17), and 2012 (n = 1). Tagged fish originated from North America (n = 24) and Europe (n = 1), and were either immature 1-sea-winter (1SW; n = 22) or multi-sea-winter adults (MSW; n = 3), 2 of which were repeat spawners. Mean length (± SD) and weight (± SD) were 67.5 cm ± 5.3 and 3.95 kg ± 1.43, respectively, and were representative of the size distribution of the overall sampled West Greenland stock complex (ICES 2019). Tags were categorized among the *Timed release* (n=2), *Early release* (n = 8), *Depredated* (n = 3), and *Unknown* (n = 12) groups (Table 1). Data were obtained from 52% of the tags (n = 13), but none of the 25 tags were physically recovered. Pop-off locations of early releases were generally proximate to the release location over the West Greenland Shelf within 4 weeks post-release (Figure 1).

The tags from the *Timed release* group popped off after 186 (2011) and 200 (2010) days at large in the main basin of the Labrador Sea after traveling an estimated minimum distance of 5100 and 6400 km, respectively. Approximately 78% and 95% of the depth records from the two tags were in the top 10 m of the water column. The *Timed release* fish from 2010 (Figure 2a) moved north over shelf waters post-release where it maintained a largely surface orientation (i.e., approximately 78% of depth records were above 10 m) into the winter (Figure 2b). During this time, diving depth, likely constrained by the bathymetry of shelf waters, did not exceed 100 m. In February, when water temperatures fell steadily for several weeks to a minimum of -0.6 °C, the fish moved directly into the main Labrador Sea basin where it occasionally dove to 764 m during winter and spring until the tag popped off in the western Labrador Sea near the shelf break off northern Labrador. Conversely, the *Timed release* fish from 2011 moved to the south and east (Figure 3a) within 30 days post-release after encountering steadily declining water temperatures to a 1.2 °C minimum and maintained a largely surface orientation, while sporadic dives to depths of 672 m were recorded (Figure 3b) until the tag popped off in open North Atlantic waters. Evidence of diel diving behavior was inconclusive for these two fish; proportional use of depth below 10 m during daylight and night conditions was approximately 24% and 21%, respectively, for the fish released in 2010 and approximately 5% under both light conditions for the fish released in 2011. The fish released in 2010 occupied a thermal range between -0.6 and 6.5 °C (50% of the records below 4 °C; Figure 2c) while the fish released in 2011 occupied waters between 1.19 and 6.6 °C (27% of the records below 4 °C; Figure 3c). Overall, while both tags indicated thermal habitats less than 4 °C were routinely occupied, neither of the tags indicated Atlantic salmon experienced thermal conditions greater than 8 °C.

Of 13 tags that reported data, 8 detached from fish for unknown reasons, and the data from the tags offered few clues as to why. However, 3 fish were hypothesized *Depredated* (Figure 1) after approximately three weeks at large (Figure 4a-f). Prior to being consumed, these fish maintained swimming and depth profiles consistent with *Timed release* fish. Hypothesized ingestion was identified by several indicators: 1) the tag estimated sunset at an unexpected time and total darkness for an extended duration, 2) depth profiles changed drastically compared to the previous data points, and 3) the temperature profile changed abruptly relative to previous ambient temperatures. After hypothesized expulsion, all three tags ascended directly to the surface and recorded 4 days of constant depth (i.e., 0 m)—indicating the tags were no longer attached to the fish—before data transmission.

DISCUSSION

The marine migration and distribution patterns of Atlantic salmon are hypothesized to be driven partially by ocean currents and thermal conditions, particularly the location of the 4 °C isotherm (Reddin and Friedland 1993). Overall, the primary thermal habitat used by fish in the current study (2-6 °C) was skewed toward the lower end of the reported range for the species in the Labrador Sea based on research surveys (approximately 4-10 °C; Reddin and Friedland 1993), and there was no indication the two Atlantic salmon in the *Timed release* group entered water above 8 °C. This discrepancy may be the result of a spatiotemporal mismatch between the research surveys and PSAT deployments (particularly given the low sample size in this study) but suggests that the over-wintering habitat of Atlantic salmon during the second year at sea may be larger than previously documented, consistent with Atlantic salmon in the Eastern North Atlantic (Strøm et al. 2019). Increasing the sample size in the future will greatly facilitate a more robust description of Atlantic salmon thermal habitat and constraints to their marine distribution.

Fish also appeared to initiate their migration away from the West Greenland feeding grounds upon encountering steadily decreasing water temperatures over short durations (2-3 weeks), albeit at different times of the year and at different minimum temperatures (February and October at -0.6 °C and 1.2 °C, respectively) but more consistent with current studies (Strøm et al. 2020). Whether migrations away from the energy-rich feeding grounds were in response to factors such as cumulative thermal experience, a rate of temperature decline, a minimum temperature threshold, proximity to advancing sea ice, or in response to temperature-mediated biological processes (e.g., metabolism, lipid storage) is not known. A more complete understanding of how thermal habitat and energy dynamics influence marine usage patterns of Atlantic salmon at the West Greenland feeding grounds and in the over-wintering area in the Labrador Sea is a knowledge gap that must be addressed to inform Atlantic salmon population abundance projections in the North Atlantic.

Individually tagged Atlantic salmon were primarily surface oriented, overall spending 87% of their time in the top 10 m of the water column, similar to both emigrating post-smolts (Renkawitz et al. 2012) and kelts in the Northwest Atlantic (Reddin et al. 2004; Reddin et al. 2011; Lacroix 2013; Strøm et al. 2017; Rikardsen et al. 2021). Diving behavior was likely constrained by available water depth over the shelf and was similar to findings reported for kelts in the Northwest Atlantic (Reddin et al. 2004; Strøm et al. 2017). When over shelf waters, fish tended to use depths between 10 and 75 m, presumably searching for and feeding on shoals of their primary prey—capelin (*Mallotus villosus*), amphipods (*Themisto compressa*), and Boreo-Atlantic armhook squid (*Gonatus fabricii*)—to accumulate and store lipid reserves for use over the winter and into the spring (Renkawitz et al. 2015). Conversely, while in the Labrador Sea basin, fish maintained a primarily surface orientation (i.e., within 5 m of the surface), except for periodic diving forays to depths of up to 760 m that sometimes lasted for over 24 hours. It has been suggested that deep diving behavior in marine Atlantic salmon in open waters could be a predator avoidance behavior, a temperature regulation strategy (Godfrey et al. 2015), and a deep ocean energy-maintenance strategy in which salmon feed on lipid-rich mesopelagic prey (e.g., squid, barracudina, lanternfish; Lear 1980) in deep water and return to surface waters to maximize metabolic activity and energy assimilation (Reddin et al. 2004). Vertical movements were not obviously associated with strict diurnal cycles in this study, in contrast to Atlantic salmon in different areas of the ocean (Hedger et al. 2017), at different times of the year, and at different life stages (Strøm et al. 2017).

Known predators of Atlantic salmon in the ocean include large marine mammals, endothermic and ectothermic sharks and other piscivorous fish (Bigelow and Schroeder 1953; Lacroix 2014; Strøm et al. 2019). However, given the absence of significant temperature increases, and that regular dive patterns reflective of surface breathing were not detected, candidate predators such as marine mammals and endothermic sharks and fishes were eliminated for the 3 hypothesized *Depredated* tags. The hypothesized predator of one Atlantic salmon was an Atlantic halibut (*Hippoglossus hippoglossus*; Bigelow and Schroeder 1953). While typically a demersal species, they are known to occasionally feed in the water column (Stokesbury et al. 2005; Vollen et al. 2008) where an Atlantic salmon in this study was hypothesized consumed based on the depth and light level records (Figure 4 a, b). At the time of hypothesized consumption during the middle of the day at a depth of 38 m of water, well within the photic zone, the tag abruptly measured total darkness, suggesting the tag was inside a predator. The tag then recorded an uninterrupted descent to 226 m, a rapid and sustained temperature change from 2 to 5 °C, and appeared relatively sessile for several days, as suggested by what appeared to be cyclic tidal influences on the depths recorded by the tag. Several rapid ascents and descents were recorded just before the hypothesized tag expulsion (inferred by the sudden resumption of light measurement).

H. hippoglossus occasionally exhibit periods of limited vertical movement for extended periods of time (Peklova et al. 2015), as suggested by the evidence from the tag data. While *H. hippoglossus* predation has not been documented for Atlantic salmon previously, the Pacific halibut (*Hippoglossus stenolepis*), similar in size to *H. hippoglossus*, has been documented to feed on Pacific salmonid adults (Best and St. Pierre 1986). Additionally, the Greenland shark (*Somniosus microcephalus*), an occasional predator of Atlantic salmon in the wasters off Greenland (MacNeil et al. 2012), was a hypothesized predator of another fish in this study. After consuming the salmon near the surface (Figure 4 c, d), the shark descended to depths of 1000-1200 m where it moved actively in a pattern consistent with known movement patterns of the species (Campana et al. 2015). The tag of the third consumed fish was rapidly egested at depth (i.e., within several hours) by the hypothesized predator precluding inference as to predator type based on the tag data (Figure 4 e, f).

The animals tagged in this study likely represent the lower limit of the suitable size range for tagging with the currently available technology. PSATs, due to their size, drag, and slight positive buoyancy, can reduce the dive frequency of Atlantic salmon adults and result in shallower dive profiles compared to individuals tagged with smaller DSTs (Hedger et al. 2017). However, these results demonstrate that fish can retain these tags for at least 7 months, indicating the method is suitable for longer term studies and potentially on smaller animals as tag technology improves and tag size is reduced. This study provides the first detailed glimpse into the poorly understood marine phase dynamics of eventual maiden 2SW at a time and in a location where high levels of mortality may be constraining population abundances in the North Atlantic. While efforts to obtain basic information on marine phase Atlantic salmon are filling knowledge gaps, our understanding of the open ocean life of Atlantic salmon is far from comprehensive and remains a research priority (DFO 2015; NASCO 2015; ICES 2019) given the disproportionate effect marine productivity has on abundance.

While capable of occupying deep depths and making deep diving forays, immature Atlantic salmon adults (maiden 1SW) in the waters off West Greenland and in the Labrador Sea are surface oriented. Thermal habitats occupied are cooler than expected and usage areas may be more spatially expansive and varied than previously documented. Additionally, data suggest Atlantic salmon are susceptible to predation off the coast of West Greenland. Building a foundation of knowledge based on basic yet fundamental information about the immature adult life stage is an essential step in understanding the ecology and marine phase dynamics of eventual maiden 2SW spawning segments of North Atlantic populations.

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Table 1. Disposition of 25 Atlantic salmon tagged with PSATs at West Greenland during autumn 2010-2012. The *Timed release* group retained the tags until the programmed pop-off date, the *Depredated* group was hypothesized to be consumed by a large predator, and the *Early release* group popped off for unknown reasons after 3-26 days. The *Unknown* group either never transmitted data or transmissions were not received by the satellite system.

Year	Timed Release	Depredated	Early Release	Unknown
2010	1	1	2	3
2011	1	2	6	8
2012	-	-	-	1
Total	**2**	**3**	**8**	**12**

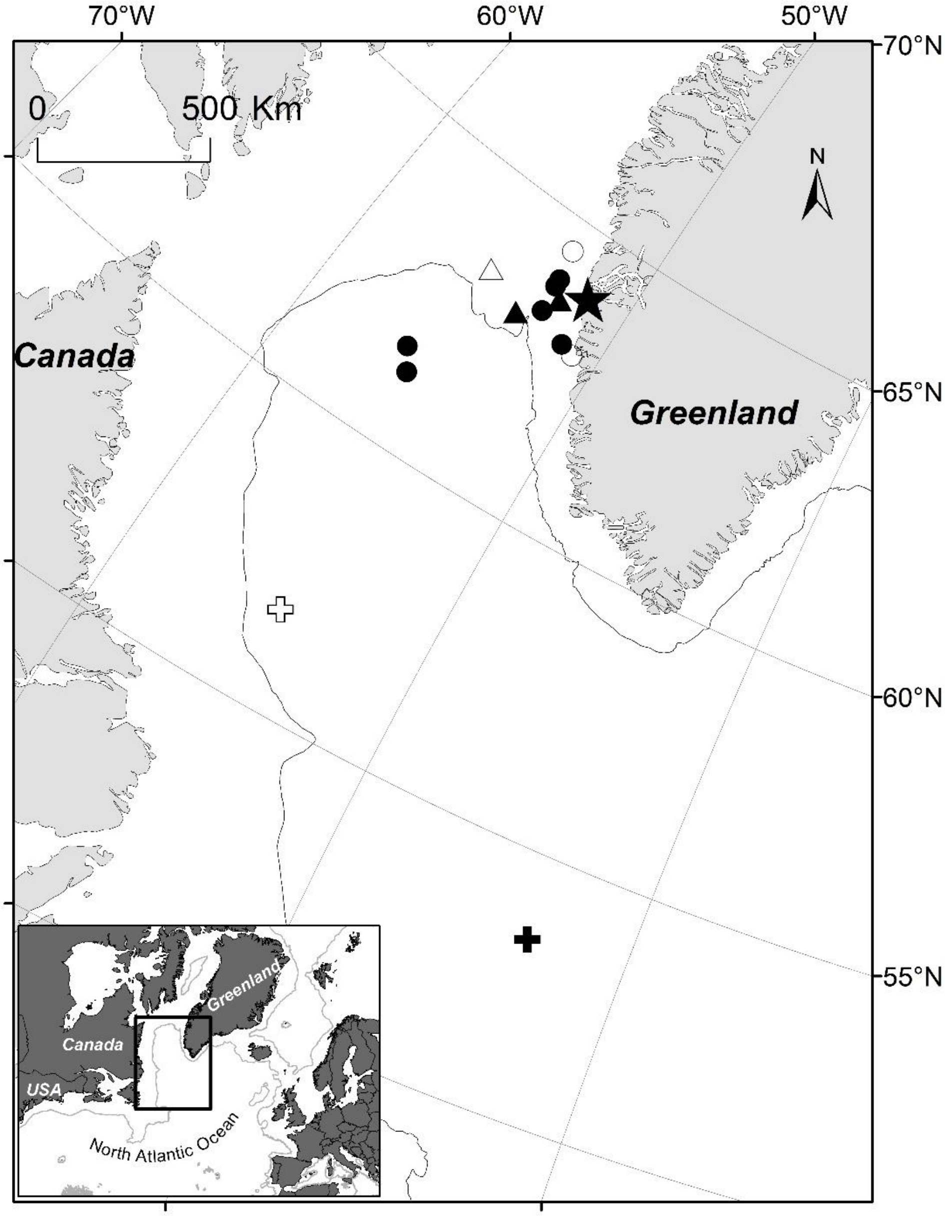

Figure 1. **Locations of** ***Timed release*** **(crosses),** ***Early release*** **(circles), and hypothesized** ***Depredated*** **Atlantic salmon (triangles). Filled and unfilled symbols represent 2011 and 2010 pop-off locations, respectively. The black star indicates the release location while the solid lines indicate the continental shelf break (~350 to 400 m depth).**

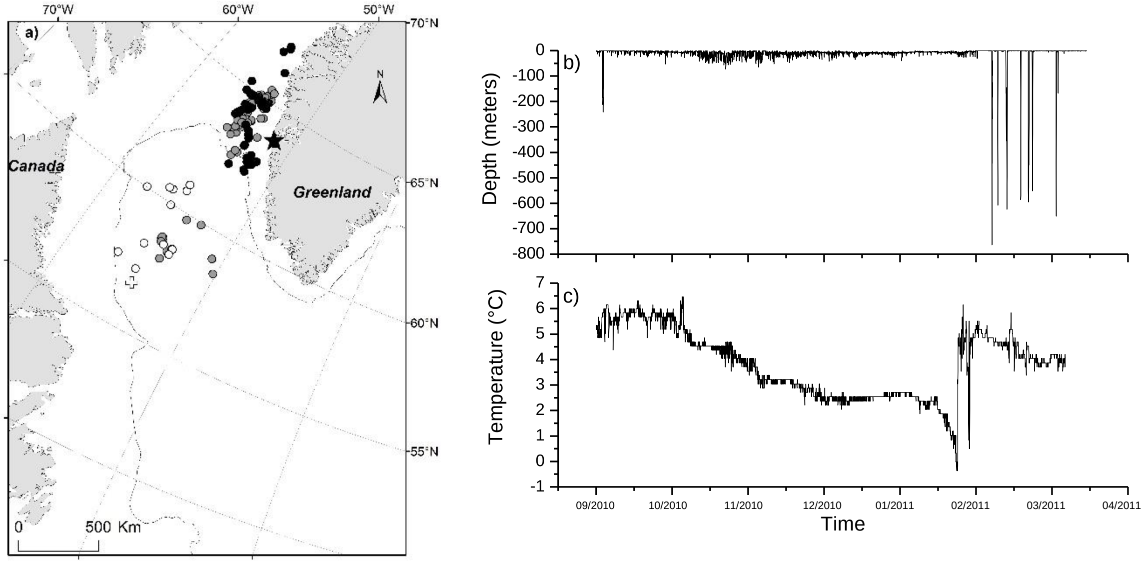

Figure 2. Validated geolocation positions (a), depth profile (b), and temperature profile (c) of an Atlantic salmon released near Nuuk, Greenland from autumn 2010 to spring 2011. The black star represents the release location, and the circle shadings represent position by season (autumn: September-November (black), winter: December-February (gray), and spring: March-April (white)). The open cross indicates the pop-up location while the solid lines indicate the continental shelf break (~350 to 400m depth).

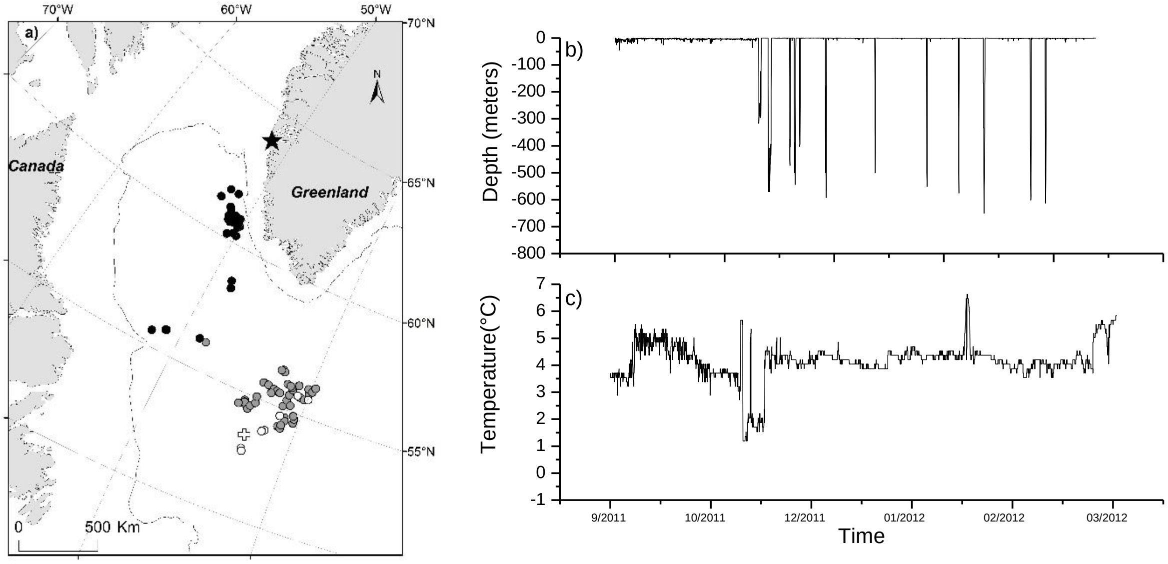

Figure 3. Validated geolocation positions (a), depth (b), and temperature profile (c) of an Atlantic salmon released near Nuuk, Greenland, from autumn 2011 to spring 2012. The black star represents the release location, and the circle shadings represent position by season (autumn: September-November (black), winter: December-February (gray), and spring: March-April (white)). The open cross indicates the pop-up location while the solid line indicates the continental shelf break (~350 to 400 m depth).

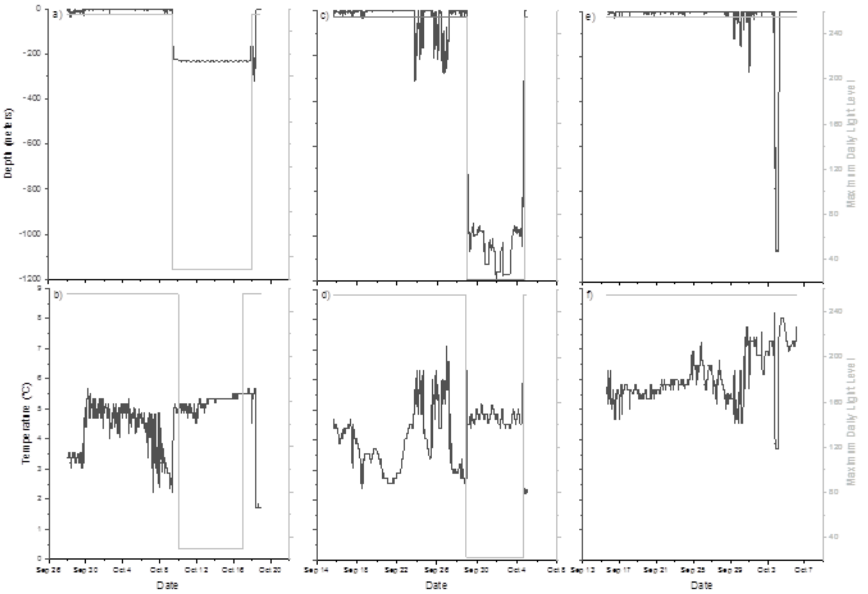

Figure 4. Depth (meters), temperature (°C), and maximum daily light level (<4×10−5 lux at 555 nm, scaled) profiles of Atlantic salmon tagged off the coast of West Greenland with PSATs that were believed depredated by Atlantic halibut (a & b) and Greenland shark (c & d). Identification of a potential predator for one hypothesized predation event (e & f) was precluded because of a lack of data caused by a seemingly rapidly egested tag.

APPENDIX I

Average daily geolocation position estimates of an Atlantic salmon tagged with a PSAT in 2010 (Tag ID 85520). Maximum depth, and minimum and maximum daily water temperatures recorded by PSAT are also presented. This Atlantic salmon was at the surface every day (i.e., minimum daily depth).

Date (year-month-day)	Ave. Daily Longitude	Ave. Daily Latitude	Max. Daily Depth (m)	Min. Daily Temp. (°C)	Max. Daily Temp. (°C)
2010-9-19	-52.01	62.76	32.3	4.9	6.2
2010-9-20	-52.23	62.81	10.8	5.7	6.0
2010-9-21	-52.43	62.76	26.9	5.3	6.0
2010-9-23	-51.83	62.95	16.1	5.5	6.0
2010-9-24	-52.05	62.86	10.8	5.8	6.3
2010-9-25	-51.80	62.96	16.1	5.7	6.2
2010-9-26	-52.11	62.75	21.5	5.3	6.0
2010-9-27	-52.45	63.05	26.9	4.9	5.8
2010-9-29	-53.72	63.73	16.1	5.3	6.2
2010-10-1	-53.53	63.60	32.3	5.0	6.0
2010-10-2	-53.38	63.51	48.4	4.9	6.0
2010-10-3	-53.32	63.23	26.9	5.2	6.0
2010-10-5	-53.54	62.35	21.5	5.0	5.8
2010-10-6	-52.61	62.88	32.3	4.9	5.7
2010-10-7	-52.30	62.46	37.7	4.9	6.2
2010-10-8	-52.19	62.42	37.7	5.0	6.5
2010-10-11	-54.19	63.85	43.0	4.7	5.3
2010-10-14	-54.09	66.13	32.3	4.5	5.2
2010-10-16	-54.95	66.92	75.3	4.5	4.7
2010-10-18	-55.05	66.99	64.6	4.4	4.7
2010-10-22	-55.29	66.70	53.8	4.5	4.7
2010-10-27	-55.91	65.22	53.8	4.2	4.5
2010-10-28	-55.35	64.83	69.9	4.4	4.5
2010-10-29	-55.38	64.84	59.2	4.2	4.5
2010-10-31	-55.20	64.43	75.3	3.9	4.7
2010-11-1	-54.76	64.33	69.9	3.7	4.7
2010-11-2	-55.38	63.96	80.7	3.9	4.7
2010-11-3	-55.30	64.05	69.9	3.5	4.7
2010-11-5	-55.19	64.16	48.4	3.9	4.5
2010-11-6	-55.22	64.08	102.2	3.9	4.4
2010-11-8	-55.04	64.43	59.2	3.7	4.2
2010-11-9	-54.88	64.34	86.1	3.7	4.2
2010-11-12	-54.59	64.46	69.9	3.4	4.2
2010-11-16	-54.90	64.43	59.2	3.4	4.0
2010-11-23	-54.51	64.81	59.2	3.0	3.9
2010-11-24	-53.67	64.94	48.4	2.9	3.4
2010-11-25	-54.18	64.89	48.4	2.9	3.4
2010-11-26	-54.63	64.91	59.2	2.7	3.4

Date (year-month-day)	Ave. Daily Longitude	Ave. Daily Latitude	Max. Daily Depth (m)	Min. Daily Temp. (°C)	Max. Daily Temp. (°C)
2010-11-27	-55.81	64.87	48.4	3.0	3.5
2010-11-28	-55.14	64.85	37.7	3.2	3.4
2010-11-29	-54.03	64.73	32.3	3.0	3.2
2010-11-30	-53.58	64.74	48.4	3.0	3.2
2010-12-1	-53.76	64.68	59.2	3.0	3.2
2010-12-2	-54.82	64.54	59.2	2.9	3.2
2010-12-3	-54.24	64.89	48.4	3.0	3.2
2010-12-5	-53.97	64.81	53.8	3.0	3.2
2010-12-6	-54.16	64.84	37.7	3.0	3.2
2010-12-7	-54.55	64.83	21.5	2.7	3.2
2010-12-8	-54.09	64.87	59.2	2.7	3.2
2010-12-9	-53.89	64.89	37.7	2.9	3.2
2010-12-11	-53.60	65.06	48.4	2.7	3.0
2010-12-12	-53.95	65.24	53.8	2.5	3.0
2010-12-13	-54.10	65.38	53.8	2.0	3.0
2010-12-16	-54.50	64.84	43.0	2.7	3.0
2010-12-17	-54.57	65.04	32.3	2.5	3.0
2010-12-19	-53.76	65.33	59.2	2.4	3.0
2010-12-20	-54.12	65.10	59.2	2.2	3.0
2010-12-21	-54.18	65.03	48.4	2.0	2.9
2010-12-22	-54.75	64.95	37.7	2.0	2.9
2010-12-23	-55.01	64.56	37.7	2.2	2.5
2010-12-24	-54.78	64.62	26.9	2.4	2.7
2010-12-25	-54.81	64.44	32.3	2.2	2.5
2010-12-26	-54.65	64.24	21.5	1.9	2.5
2010-12-27	-54.28	64.02	53.8	1.9	2.7
2010-12-28	-53.99	64.06	37.7	2.0	2.7
2010-12-29	-53.31	64.39	32.3	2.2	2.5
2010-12-30	-54.05	64.09	32.3	2.0	2.5
2010-12-31	-54.54	63.95	21.5	2.2	2.5
2011-1-1	-54.47	63.99	21.5	2.0	2.5
2011-1-3	-54.76	63.79	21.5	2.4	2.7
2011-1-4	-54.48	64.01	43.0	2.4	2.7
2011-1-5	-54.70	63.84	32.3	2.5	2.7
2011-1-6	-54.83	63.76	21.5	2.4	2.7
2011-1-7	-54.57	63.88	21.5	2.5	2.7
2011-1-8	-54.64	63.96	43.0	2.4	2.7
2011-1-9	-54.75	63.63	26.9	2.4	2.7
2011-1-10	-54.63	63.58	26.9	2.4	2.7
2011-1-11	-54.45	63.43	26.9	2.5	2.7
2011-1-12	-54.95	63.46	26.9	2.2	2.7
2011-1-13	-54.71	63.60	21.5	2.4	2.7
2011-1-14	-54.39	63.66	26.9	2.4	2.5
2011-1-16	-53.78	62.66	16.1	2.0	2.5

Date (year-month-day)	**Ave. Daily Longitude**	**Ave. Daily Latitude**	**Max. Daily Depth (m)**	**Min. Daily Temp. (°C)**	**Max. Daily Temp. (°C)**
2011-1-17	-53.50	62.87	26.9	1.9	2.4
2011-1-18	-53.71	62.88	21.5	2.0	2.4
2011-1-21	-54.72	63.26	21.5	2.4	2.5
2011-1-22	-55.25	63.39	32.3	2.0	2.5
2011-1-23	-54.64	63.68	16.1	2.2	2.5
2011-1-25	-54.78	63.60	32.3	1.9	2.0
2011-1-26	-54.94	63.81	21.5	1.7	2.0
2011-1-27	-54.14	63.94	32.3	1.4	1.9
2011-1-28	-53.47	64.34	32.3	1.0	1.9
2011-1-30	-54.56	63.83	37.7	1.0	1.7
2011-2-1	-52.84	63.70	53.8	0.7	1.2
2011-2-3	-53.34	63.20	69.9	0.0	1.2
2011-2-8	-53.83	59.79	5.4	3.0	5.0
2011-2-10	-52.75	59.92	521.8	4.2	6.2
2011-2-13	-54.01	58.06	640.2	0.5	5.8
2011-2-14	-53.80	58.41	16.1	4.0	5.0
2011-2-16	-53.85	58.43	591.7	5.0	5.7
2011-2-17	-54.55	58.78	629.4	4.9	5.5
2011-2-18	-54.66	58.74	5.4	4.9	5.2
2011-2-19	-54.66	58.80	5.4	4.7	5.3
2011-2-20	-54.56	58.63	10.8	4.7	5.3
2011-2-23	-50.80	59.04	5.4	4.5	4.9
2011-2-25	-50.19	58.56	629.4	4.4	4.9
2011-3-2	-56.66	57.46	607.9	4.5	4.9
2011-3-5	-54.28	58.58	5.4	4.5	5.0
2011-3-7	-53.63	58.60	10.8	3.5	4.9
2011-3-8	-53.57	58.59	16.1	4.0	4.7
2011-3-9	-53.60	58.36	5.4	3.9	4.7
2011-3-15	-55.90	60.46	5.4	3.7	4.4
2011-3-16	-56.17	60.45	694.0	3.9	4.2
2011-3-18	-54.99	60.69	21.5	3.7	4.2
2011-3-20	-55.04	60.93	26.9	3.7	3.9
2011-3-23	-55.39	59.95	5.4	3.9	4.0
2011-3-25	-57.54	60.01	26.9	3.7	4.2
2011-3-28	-55.49	58.25	5.4	3.5	4.2
2011-3-30	-55.05	57.27	5.4	3.9	4.2

APPENDIX II

Average daily geolocation position estimates of an Atlantic salmon tagged with a PSAT in 2011 (Tag ID 107100). Maximum depth, and minimum and maximum daily water temperatures recorded by PSAT are also presented. This Atlantic salmon was at the surface every day (i.e., minimum daily depth).

Date (year-month-day)	Ave. Daily Longitude	Ave. Daily Latitude	Max. Daily Depth (m)	Min. Daily Temp. (°C)	Max. Daily Temp. (°C)
2011-9-28	-51.58	63.96	69.9	2.7	3.9
2011-9-30	-52.17	61.65	26.9	3.0	4.2
2011-10-1	-51.32	61.00	16.1	3.2	5.5
2011-10-2	-50.64	60.70	21.5	4.2	5.5
2011-10-3	-50.52	60.79	16.1	4.2	5.2
2011-10-4	-50.94	60.61	10.8	4.4	5.3
2011-10-6	-50.97	60.74	21.5	4.2	5.3
2011-10-7	-50.78	60.64	26.9	3.5	5.2
2011-10-8	-51.49	61.09	21.5	3.5	5.0
2011-10-11	-51.28	60.80	16.1	3.4	4.9
2011-10-12	-50.80	60.91	10.8	4.0	5.5
2011-10-13	-50.37	60.89	10.8	3.2	4.4
2011-10-14	-50.38	60.71	32.3	2.9	4.2
2011-10-15	-50.32	60.63	26.9	3.4	4.2
2011-10-16	-50.19	60.60	21.5	2.9	4.0
2011-10-17	-50.13	60.64	21.5	2.9	4.0
2011-10-18	-50.24	60.57	16.1	3.0	3.9
2011-10-19	-50.70	60.18	10.8	3.4	3.9
2011-10-20	-50.01	60.27	10.8	3.0	3.9
2011-10-21	-50.31	60.30	5.4	2.9	3.7
2011-10-22	-51.16	60.65	16.1	2.2	3.9
2011-10-25	-52.52	61.25	37.7	2.5	3.2
2011-11-4	-51.48	61.65	10.8	1.5	2.4
2011-11-9	-48.45	58.44	5.4	4.4	4.7
2011-11-11	-48.66	58.71	473.4	3.7	4.9
2011-11-19	-51.93	55.60	5.4	3.9	4.4
2011-11-20	-51.06	55.87	5.4	4.0	4.5
2011-11-21	-51.11	55.86	0.0	4.2	4.4
2011-11-29	-48.75	56.17	10.8	3.9	4.0
2011-12-1	-48.25	56.14	5.4	4.0	4.5
2011-12-8	-43.36	55.68	0.0	4.2	4.5
2011-12-9	-42.99	55.66	10.8	4.4	4.5
2011-12-10	-42.52	55.59	21.5	4.2	4.5
2011-12-11	-42.28	55.56	16.1	4.4	4.4
2011-12-13	-42.42	56.46	5.4	4.2	4.4
2011-12-15	-42.27	56.40	5.4	4.2	4.9
2011-12-16	-42.54	56.42	10.8	4.0	4.4
2011-12-23	-44.09	54.74	10.8	4.0	4.2

Date (year-month-day)	**Ave. Daily Longitude**	**Ave. Daily Latitude**	**Max. Daily Depth (m)**	**Min. Daily Temp. (°C)**	**Max. Daily Temp. (°C)**
2011-12-24	-44.06	54.67	5.4	3.9	4.2
2011-12-25	-44.07	54.60	5.4	3.9	4.0
2011-12-26	-44.06	54.65	16.1	3.9	4.0
2011-12-27	-44.42	54.53	5.4	3.9	4.0
2011-12-29	-43.69	54.45	0.0	3.9	4.2
2011-12-30	-43.60	54.61	10.8	3.9	4.0
2011-12-31	-43.34	54.79	16.1	3.9	3.9
2012-1-1	-43.41	55.05	26.9	3.9	4.0
2012-1-4	-41.30	54.25	26.9	4.4	4.5
2012-1-7	-41.06	54.69	10.8	4.2	4.4
2012-1-9	-40.98	54.55	10.8	4.0	4.5
2012-1-10	-40.36	54.59	586.4	4.2	4.7
2012-1-12	-40.38	54.76	21.5	4.4	4.5
2012-1-13	-40.51	54.87	5.4	4.0	4.4
2012-1-17	-40.56	55.68	5.4	4.4	4.4
2012-1-19	-40.05	55.95	5.4	4.2	4.5
2012-1-20	-40.21	56.12	5.4	4.4	4.5
2012-1-21	-39.89	56.06	650.9	4.0	4.7
2012-1-22	-39.76	56.25	559.5	4.2	4.9
2012-1-23	-40.94	56.11	10.8	4.2	4.5
2012-1-24	-41.20	55.82	10.8	4.2	4.5
2012-1-30	-41.08	54.21	5.4	4.4	4.5
2012-1-31	-41.10	54.35	10.8	4.0	4.4
2012-2-3	-41.48	55.09	5.4	4.0	4.2
2012-2-5	-41.36	55.38	10.8	3.7	4.0
2012-2-7	-41.36	55.60	10.8	3.7	4.0
2012-2-8	-41.24	55.85	10.8	4.0	4.2
2012-2-12	-41.74	55.99	10.8	3.5	3.9
2012-2-13	-41.36	55.92	10.8	3.5	4.0
2012-2-14	-41.49	55.97	5.4	3.9	4.2
2012-2-18	-41.00	55.22	10.8	4.2	4.2
2012-2-22	-42.59	55.42	634.8	3.5	4.4
2012-2-26	-42.02	55.55	10.8	3.7	4.2
2012-2-29	-40.26	55.65	667.1	3.5	4.0
2012-3-4	-41.42	54.69	48.4	3.9	4.2
2012-3-9	-39.96	55.71	0.0	3.9	4.2
2012-3-10	-40.77	55.71	5.4	4.0	4.5
2012-3-16	-42.03	53.90	5.4	3.9	4.4
2012-3-17	-42.19	53.83	0.0	3.9	4.2
2012-3-18	-42.19	53.82	16.1	3.7	4.0
2012-3-22	-43.06	52.87	26.9	4.9	5.5
2012-3-23	-42.97	52.77	5.4	5.3	5.7
2012-4-1	-43.20	53.43	0.7	6.0	6.6

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