Vol. 574: 127–140, 2017
https://doi.org/10.3354/meps12180

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published July 4

# Diving behaviour of Atlantic salmon at sea: effects of light regimes and temperature stratification

**Richard D. Hedger[1,2,*], Audun H. Rikardsen[2], John F. Strøm[2], David A. Righton[3], Eva B. Thorstad[1,2], Tor F. Næsje[1]**

[1]Norwegian Institute for Nature Research (NINA), 7485 Trondheim, Norway
[2]Department of Arctic and Marine Biology, University of Tromsø, 9037 Tromsø, Norway
[3]Centre for Environment, Fisheries and Aquaculture Science, NR33 0HT Lowestoft, UK

ABSTRACT: The diving behaviour of adult Atlantic salmon *Salmo salar* L. post-spawners in the Norwegian and Barents Seas was monitored with pop-up satellite archival tags (PSATs) and data storage tags (DSTs). Salmon from the 3 studied populations showed similar depth use patterns: tagged specimens spent most of their time near the surface (mean of 82% of the time at depths <10 m), with occasional short deep dives (>200 m depth, median time = 2.31 h; range = 0.18 to 22.5 h), the deepest recorded being 707 m. Increased use of greater depths occurred during daytime than night-time in the months between polar day and polar night (August to October). Diel change in depth use around the time of polar night (November to January) was weakest for the population (from the River Alta) that migrated furthest north. Diving was more frequent and shallower when the mixed layer was near the surface during the months of June to October. There was an increase in diving depth (>200 m) when the mixed layer extended to ~200 or 300 m in winter and spring (December to April). Deep diving consisted of 'U' shaped dives, possibly indicative of foraging. We hypothesise that seasonal light conditions, dependent on geographical location, affect Atlantic salmon diving, and that changes in diving depth may be due to seasonal differences in prey aggregation.

KEY WORDS: Continental shelf · Deep sea · Feeding · Fish · Migration · Arctic · North East Atlantic



## INTRODUCTION

Atlantic salmon *Salmo salar* L. are anadromous fish that undertake oceanic feeding migrations during post-smolt (early adult) and adult post-spawning life-stages (see Dadswell et al. 2010, Miller et al. 2014). They are opportunistic feeders at sea, with their main prey being fish larvae, small epipelagic and mesopelagic fishes, planktonic and large crustaceans, and squid (Hansen & Quinn 1998, Jacobsen & Hansen 2000, Rikardsen & Dempson 2011). In the North Atlantic, Atlantic salmon prey such as herring *Clupea harengus* L., sand eels *Ammodytes* spp., and amphipods have defined distributions, influenced by the North Atlantic current (Haugland et al. 2006). Thus, the geographic and depth distribution of Atlantic salmon within the North Atlantic may partly reflect that of their prey (Dadswell et al. 2010).

At sea, Atlantic salmon spend most of their time in the upper water column, diving aperiodically to greater depths (Jákupsstovu 1988, Lacroix 2013, Strøm et al. 2017). Dives to depths in excess of 100 m have been observed using telemetry for both post-smolt and post-spawned Atlantic salmon; however, this behaviour appears to be related to the stage of migration and the geographical area (Holm et al. 2006, Lacroix 2013, Godfrey et al. 2015, Guðjónsson et al. 2015). Diving may also be related to foraging and predator avoidance (Reddin et al. 2011). Reddin et al. (2004) proposed a model for energy optimisa-

*Corresponding author: richard.hedger@nina.no

tion by Atlantic salmon involving diving to cold water layers for foraging, and returning to warmer surface waters for digestion. Such thermal regulation has been observed for Pacific salmon *Oncorhynchus* spp. in temperate marine areas, with chum salmon *Oncorhynchus keta* observed diving into cooler layers, presumably to minimise energy use (Tanaka et al. 2000). However, there would seem to be little advantage to this behaviour in colder northern waters.

In this study, we examined the diving behaviour and activities of adult Atlantic salmon post-spawners in the Norwegian and Barents Seas using individuals from 3 populations originating from Norwegian rivers (the Orkla, Alta and Neiden), tagged with either pop-up satellite archival tags (PSATs) or data storage tags (DSTs). We compared long-term (monthly) and short-term (hourly) changes in depth use by individuals from the 3 populations to examine the influence of light regimes on depth use. We also examined diving for 13 individuals from the Alta population tagged with high resolution DSTs of 1 or 5 min intervals to examine the influence of light and thermal regimes on diving behaviour.

## MATERIALS AND METHODS

### Fish telemetry: PSATs and DSTs

Adult Atlantic salmon were sampled and tagged in 3 Norwegian rivers: the Orkla River (63.3° N, 9.7° E), the Alta River (70.0° N, 23.4° E), and the Neiden River (69.7° N, 29.4° E) (see Fig. 1). The Orkla and Alta Rivers discharge into the Norwegian Sea through Trondheimsfjord and Altafjord, respectively, and the Neiden River discharges into the Barents Sea through Neidenfjord. The Norwegian and Barents Seas are categorised as subarctic/Arctic seas, with sea surface temperatures ranging between ~15°C in summer and ~0°C in winter, and thermally stratified waters from July through September or October. Atlantic salmon were caught in the rivers by angling in late April to early May in the Orkla River, and from 10 to 22 May for the Alta and Neiden Rivers (no difference between years in terms of capture time) during their seaward migration period (see Halttunen et al. 2010). Mainly females were retained for tagging, as these generally have a higher survival in both the river and sea (Halttunen et al. 2013), but some males were also tagged (~7% of all tagged individuals). The salmon were kept in storage pens to allow acclimation to sea before they were anaesthetised for surgery (2-phenoxy-ethanol, 0.5 ml $l^{-1}$, mean anaesthetising time: 3 min). Each fish was cradled in a 25 cm diameter water-filled tube for tagging. The top half of this tube was removed to enable surgery, but the part surrounding the head of the individual undergoing surgery was kept intact to ensure that light intensity at the individual's eyes was minimised. The head and gills were kept submerged. Individuals from the Orkla and the Alta Rivers were tagged with either a PSAT or a DST, whereas all individuals from the Neiden River were tagged with PSATs (Table 1). All individuals were released between 3 May and 1 June.

PSATs (Microwave Telemetry) had a mass of 40 g and were 120 mm in length, 32 mm in diameter and had a 185 mm antenna. A PSAT was attached externally to each individual salmon by bridling the tag to 2 cushioned back-plates. Back-plates were wired through the dorsal musculature below the dorsal fin with 2 biocompatible plastic-coated stainless steel wires. The inside of the plates was surfaced with biocompatible silicon pads to reduce skin abrasion. A multifilament nylon thread attached each plate to the PSAT so that the tag streamed ~1 or 2 cm behind the dorsal fin. PSATs were programmed to pop-up (1) at a specified date (in most cases, after 156 d at sea), (2) if the PSAT crossed a maximum depth threshold (1200 m) to prevent tag destruction from high water pressure, or (3) if it registered a constant depth. Although PSATs recorded depth and temperature data at short intervals (~1 to 2 min), bandwidth limitations of data transmission to the satellite after pop-up allowed only a 15 min (or coarser) temporal resolution. The position of the PSATs at pop-up was registered by the ARGOS satellite positioning system. The limited battery life of PSATs precluded their use for long-term (>1 yr) study.

DSTs (Star-Oddi) were 39 mm long and 13 mm in diameter, and had a mass of 9.2 g. DSTs measured depth and temperature at a constant interval (1 to 30 min depending on the tag) over a long-term period (>1 yr). Each DST was inserted into the peritoneal cavity according to the method described in Rikardsen & Thorstad (2006). Recaptures in the DST program were dependent on fishers. An information sheet was sent to fishers in the fjords and attached rivers before the commencement of the fishing season each year explaining how to return the tag, with a reward of 1200 NOK (~$140 USD) for successful return.

PSAT time-series were examined to identify if tagged Atlantic salmon had died due to predation or another reason. Adult Atlantic salmon at sea are typically eaten by whales *Cetacea* spp., seals *Phocidae* spp., sharks *Selachimorpha* spp., Atlantic bluefin

Table 1. Atlantic salmon from the Orkla, Alta, and Neiden Rivers tagged with pop-up satellite archival tags (PSATs) and data storage tags (DSTs). High and low temporal resolution DSTs are shown by H and L suffixes, respectively. n = sample size

| Population and tag type | Years | Released | | | Recovered | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | No. | Mean body length (cm) [range] | Mean body mass (kg) [range] | No. | Mean data length (d) | Mean body length (cm) [range] | Mean body mass (kg) [range] | Median recording interval (min) [n] |
| **Orkla** | | | | | | | | | |
| $PSAT_L$ | 2010 | 10 | 98 [88–114] | 6.7 [4.7–9.8] | 10 | 147 | 98 [88–114] | 6.7 [4.7–9.8] | 15 [3], 30 [7] |
| $DST_L$ | 2010 | 57 | 89 [71–107] | 4.8 [2.6–9.0] | 3 | 415 | 90 [87–94] | 4.9 [4.5–5.5] | 30 [3] |
| **Alta** | | | | | | | | | |
| $PSAT_L$ | 2008–2010 | 47 | 99 [92–112] | 7.2 [5.4–9.9] | 42 | 135 | 99 [92–112] | 7.3 [5.4–9.9] | 15 [18], 30 [13], 45 [1], 60 [10] |
| $DST_L$ | 2008–2012 | 348 | 92 [57–114] | 6.0 [1.4–13.0] | 22 | 407 | 92 [80–104] | 6.0 [4.0–9.0] | 10 [2], 30 [20] |
| $DST_H$ | 2013–2015 | 229 | 87 [56–112] | 5.2 [1.2–11.1] | 13 | 411 | 92 [79–99] | 5.4 [3.2–6.7] | 1 [7], 5 [6] |
| **Neiden** | | | | | | | | | |
| $PSAT_L$ | 2009–2010 | 16 | 91 [73–107] | 5.4 [2.8–9.8] | 14 | 104 | 92 [73–107] | 5.7 [2.9–9.8] | 15 [7], 30 [4], 60 [3] |

tuna *Thunnus thynnus*, skates *Rajidae* spp., and Atlantic halibut *Hippoglossus hippoglossus* (Joyce et al. 2002, Rikardsen et al. 2008, Lacroix 2014). As these species have depth-use and diving patterns that differ from Atlantic salmon, predation could be identified from an abrupt change in depth and diving pattern from that of Atlantic salmon. Temperatures indicative of the tag passing through the alimentary canal of an endothermic predator also indicated predation. A continuous reading of the tag at the sea bottom was taken to indicate that the Atlantic salmon individual was dead. PSAT data recorded after the identification of such a death point were removed from further analysis.

To avoid the data sampling interval causing bias in our analyses of behaviour, tag data were divided into 2 categories: low (≥10 min) and high (1 or 5 min) resolution. Both low and high resolution data were used for comparison of depth-use patterns among the populations (Orkla, Alta, and Neiden). High resolution data available for 13 Alta Atlantic salmon tagged with DSTs were used in a more detailed analysis of their diving behaviour. Low resolution data were not used to analyse diving behaviour because of the potential to not record short dives. Diving behaviour was examined only for individuals tagged with small, internally implanted DSTs to reduce the potential for introducing behavioural bias in diving behaviour which may be associated with large external PSATs (see Hedger et al. 2017).

## Comparison of populations (Orkla, Alta, and Neiden)

To evaluate if there were differences in maximum diving depth according to where the Atlantic salmon from the 3 populations had migrated, the maximum depth recorded leading up to pop-up (from the day of and day preceding pop-up) of the PSATs was compared with the water column depth at the site of pop-up. Water column depth was determined by cross-referencing the location of the tag (determined by ARGOS satellite positioning) with the water column depth of that location, obtained from the General Bathymetric Chart of the Ocean (GEBCO). Based on a maximum swimming distance of ~50 km $d^{-1}$ (see Lacroix 2013), the maximum fish depth recorded on the day of and day preceding pop-up will have occurred within 100 km of the position measured using the ARGOS system.

The depth distributions of the 3 populations were examined for temporal trends. Firstly, the depth frequency distribution, median, and maximum depth of Atlantic salmon from the 3 populations were examined for monthly changes. Hourly depth frequency distributions of the populations were examined seasonally from May to July (approximating polar day), August to October (the months between polar day and polar night), and November to January (approximating polar night)

### Diving behaviour of Alta Atlantic salmon tagged with high resolution DSTs

Mean absolute vertical velocity (vertical distance moved between tag depth registrations over tag registration interval) was calculated as a function of hour of day for 3 times of the year: May to July (polar day for the latitude of the Alta River), August to October (the months between polar day and polar night), and November to January (polar night).

Dives below the euphotic zone (>200 m depth) were examined with regard to diving and surfacing velocities, maximum diving depth, time length of dive, and change in temperature experienced. All dives (>25 m) and deep dives (> 200 m) were examined on a monthly basis to determine if there were long-term trends in relation to stratification, which could be indicative of a change in the availability of food. Stratification of the water column was defined as the depth of the mixed layer, determined from the operational TOPAZ4 Arctic Ocean system (data provided by the Copernicus Marine Environment Monitoring Service). The relationship between the depth of all dives (>25 m) and the depth of the mixed layer was determined using a generalised estimation equation (GEE) model (R function 'geeglm'; 'geepack' library), with clustering of data according to individual.

## RESULTS

Atlantic salmon migrated away from the coast to deep waters, as shown by the location of pop-up of PSATs (Fig. 1). Of all PSATs for which data could be recovered (66 out of 73 fish released; 90%), 47 (71%) popped-up due to constant pressure, 15 (23%) on the pre-set pop-up date, 3 were recaptured, and 1 measured a depth exceeding maximum threshold. Pop-ups resulting from registration of a constant depth or a depth greater than the maximum threshold occurred in 50% of the Orkla PSATs releases, 67% of the Alta PSAT releases and 100% of the Neiden PSAT releases. Pop-ups occurred from the end of May, several weeks after release, until April the following year. No seasonal differences for time of pop-up were apparent for the Orkla or Neiden populations; however, the Alta population had the greatest number of pop-ups in November and December. Recovery rates for DSTs, indicative of a return from the sea and recapture, were 5.2 and 6.1% for Orkla and Alta Atlantic salmon, respectively.

Recovered data, both for individuals tagged with PSATs and individuals tagged with DSTs, showed that the Atlantic salmon were pelagic, with occasional short forays into the water column. Atlantic salmon spent a mean of 81.6% of their time at depths <10 m (SD = 11.8%, min. = 20.8%, max. = 99.9%, n = 104 fish) and 87.8% of the time at depths <25 m (SD = 10.4%, min. = 20.8%, max. = 100%, n = 104). The salmon spent the majority of their time within the euphotic zone (<200 m depth) (mean = 98.6% of the time, SD = 1.41%, min. = 94.4%, max. = 100%, n = 104). Thirteen individuals (out of 104) did not dive deeper than 100 m and 26 did not dive deeper than 200 m. The greatest depth recorded for individuals from the Orkla River was 610.6 m (SD = 221.3, min. = 17.5, n = 13), 706.7 m (SD = 178.3, min. = 14.1, n = 77) for the Alta River and 347.0 m (SD = 113.1, min. = 21.5, n = 14) for the Neiden River.

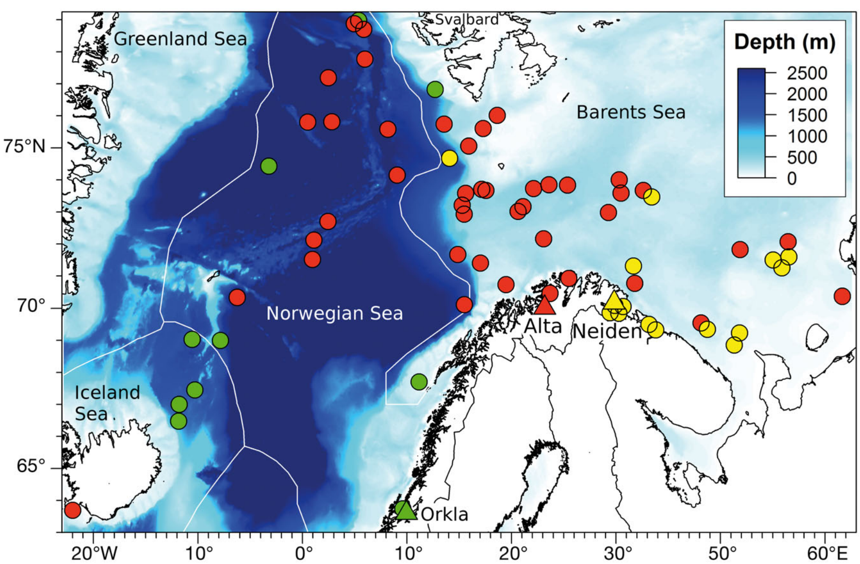


Fig. 1. Study area showing positions at pop-up (circles) of pop-up satellite archival tags (PSATs) that had been attached to Atlantic salmon from the Orkla (green), Alta (red), and Neiden (yellow) rivers, with places of release (triangles)

### Comparison of populations (Orkla, Alta, and Neiden)

The Atlantic salmon from the different populations migrated to different areas (Fig. 1), which appeared to influence the likelihood of deep dives. Pop-ups from the Orkla population mainly occurred in the western Norwegian Sea around the Mid-Atlantic ridge between Iceland and Svalbard. Pop-ups from the Alta population occurred in 2 regions: (1) along the Mid-Atlantic ridge, nearer to Svalbard than Iceland and (2) in the Barents Sea. Pop-ups from the Neiden population occurred in the Barents Sea, with the exception of 2 individuals that migrated northward to Svalbard. Near the time of pop-up (day of and day preceding pop-up), dive depths depended on geographical location. Individuals within the Barents Sea (east of 15° E) dived to significantly greater depths (median = 120 m, min. = 0 m, max. = 519 m, n = 31) than those in deeper waters, offshore in the Norwegian Sea (west of 15° E) (median = 2 m, min. = 0 m, max. = 196 m, n = 20) (Wilcoxon rank sum test, $W = 211$, $p = 0.028$).

Long-term (monthly) and short-term (diel) trends in depth use were evident in all 3 populations. Atlantic salmon from the Alta and the Orkla spent more time at depths >5 m during the summer months of July to October, less during the autumn and winter months of November to February, and then more again during the spring months of March to May (Fig. 2, upper panels). Individuals from the Neiden population only provided data until January following release, but showed a similar pattern of greater

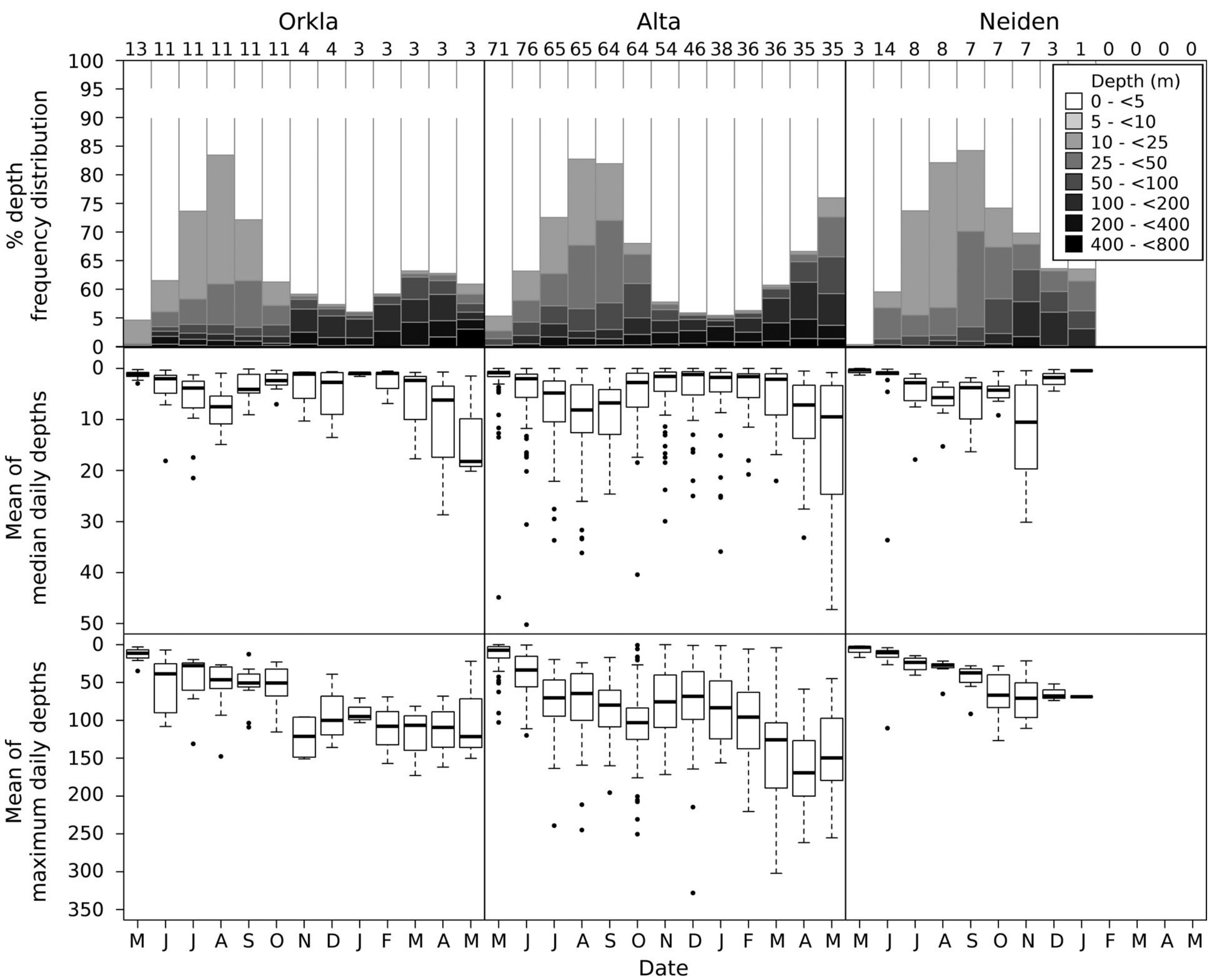


Fig. 2. Depth use of all tagged Atlantic salmon from the Orkla, Alta, and Neiden rivers according to month from release: percentage depth frequency distribution (upper panels), median depth (middle panels), and maximum depth (lower panels). Data from the Neiden tag-group were not available after January the year after release. Percentage depth frequency distributions are determined for each individual, and a mean of individual percentage frequency distributions is shown. Median and maximum depths were determined on a daily basis, and the means of these calculated per month are shown. Numbers of individuals used in the estimate are shown above each bar

occupancy of depths >5 m during summer than winter. Median depths were mostly within the upper 10 m of the water column, but a seasonal trend was present, with shallower median depths immediately after sea entry (May) and during winter (December to February) than in summer, followed by a return to deeper median depths (for the Alta and the Orkla individuals) in the following spring (Fig. 2, middle panels). Dive depth increased as the salmon migrated away from their release points, and Orkla and Alta individuals typically dived to 100 or 200 m from March the year after release (Fig. 2, lower panels).

Diel patterns in depth use depended on time of year (Fig. 3). In the first few months after release (May to July, where there was polar day at high latitudes), there was no diel trend in depth use. However, diel trends were evident later (August to October, where there was a mixed daytime/night-time regime),with greater depths being registered from 06:00 to 18:00 h than from 18:00 to 16:00 h (as measured by the clock, calibrated to the position of release). Even later (November to January, where there was polar night at high latitudes), this diel behaviour was apparent, but the period of use of greater depths was confined to a shorter number of hours during the day. Changes in depth use according to hour of day from November to January were smallest for individuals from the River Alta.

## Diving behaviour of Alta Atlantic salmon tagged with high resolution DSTs

Vertical movements were greater during day than night (Fig. 4); however, the tendency to exhibit diel patterns was strongly dependent upon time of year.

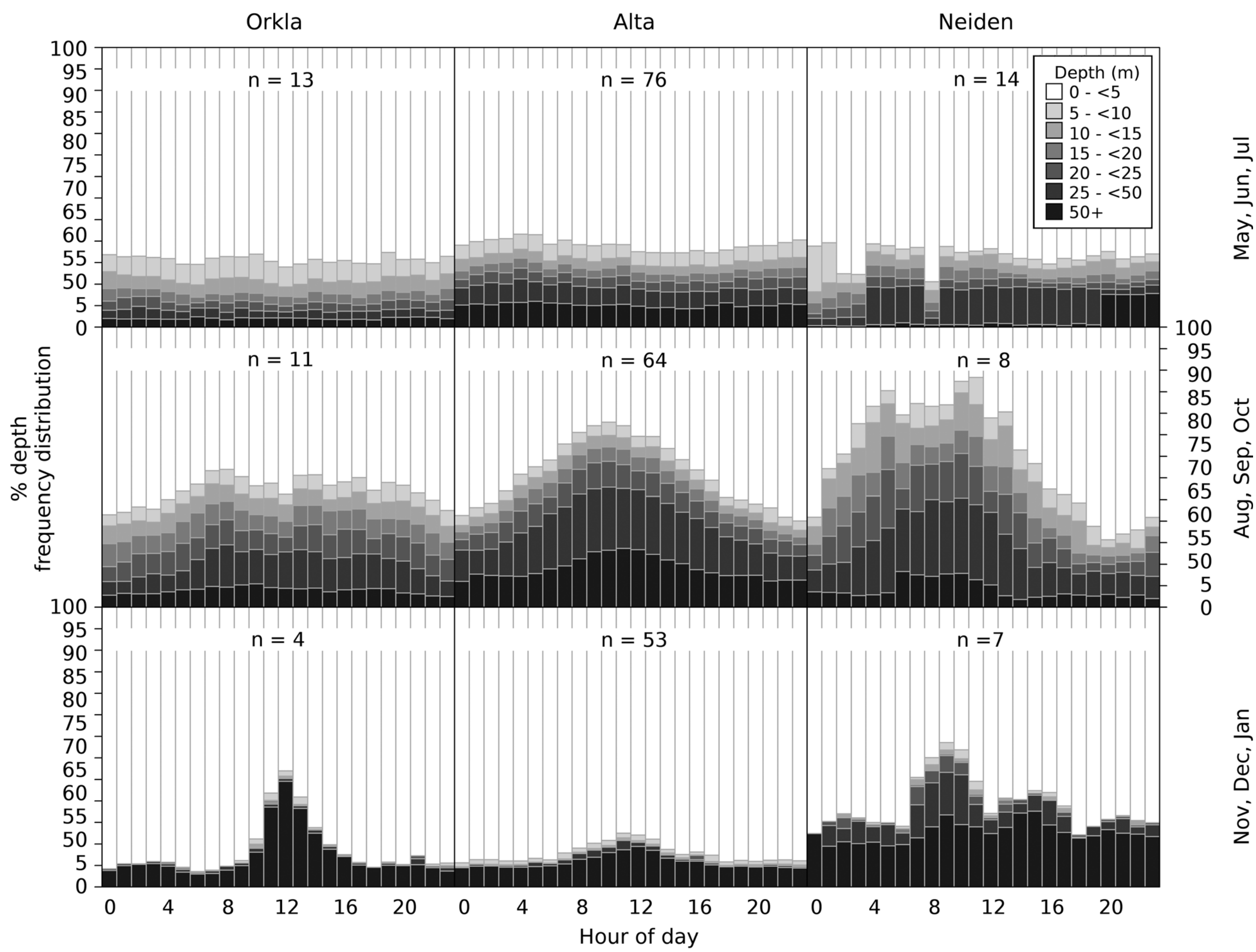


Fig. 3. Percentage depth frequency distribution of tagged Atlantic salmon from the Orkla, Alta, and Neiden Rivers according to hour of day for May to July (upper panels), August to October (middle panels), and November to January (lower panels). Hour of day is calibrated to the position of release. Percentage depth frequency distributions are determined for each individual, and a mean of individual percentage frequency distributions is shown. The actual time of day experienced by the salmon will be offset by +1 h for every 15° the individual moves eastward and −1 h for every 15° westward

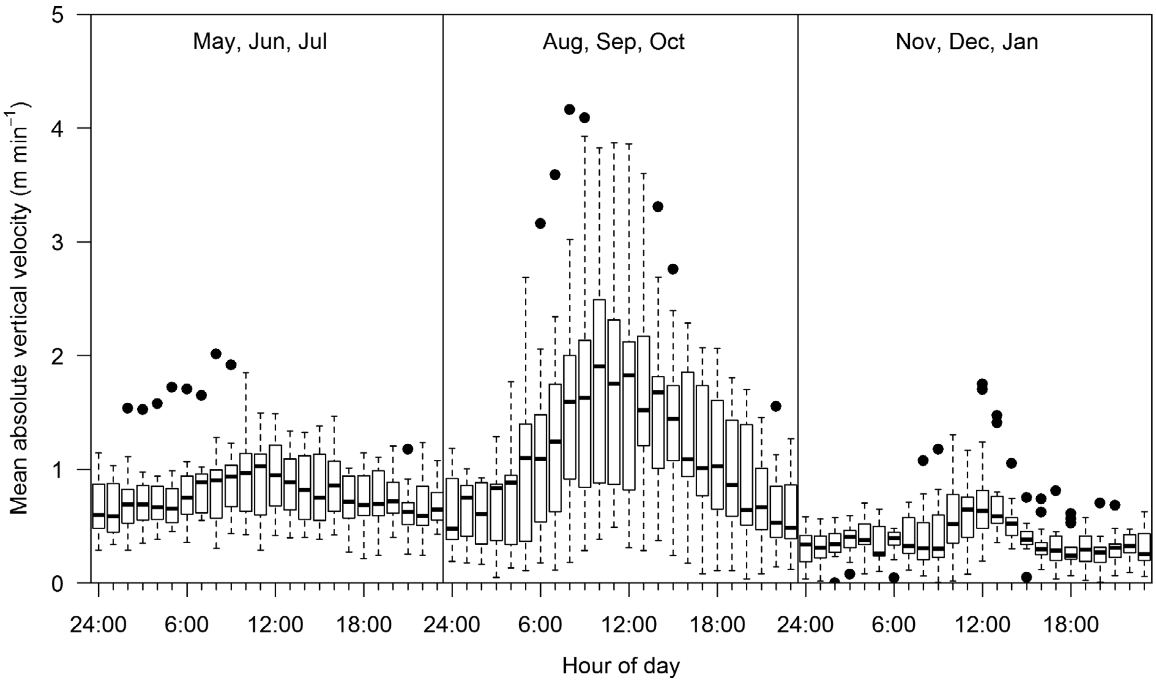


Fig. 4. Absolute vertical velocity of 13 Atlantic salmon from the River Alta carrying high temporal resolution data storage tags (DSTs)

During times approximating the polar day and polar night for the latitudes of the River Alta and northwards, there was a much weaker diel pattern than during the season between polar day and night. When Atlantic salmon experienced a 24 h day–night cycle, mean vertical velocities ranged from ~0.5 m min$^{-1}$ at 24:00 h to ~1.65 m min$^{-1}$ at 12:00 h (from the tag clock calibrated to position of release).

Visual inspection showed that most deep dives (>200 m) followed a 'U' shape (~42.1 % of deep dives) rather than a 'V' shape pattern, with an initial rapid descent, followed by a period of time lingering at depth, concluding with a rapid ascent to the surface (Fig. 5a). Diving velocities were ~0.5 m s$^{-1}$ near the dive's initiation and declined to 0 m s$^{-1}$ over a period of ~20 to 30 min as the trough of the dive was approached. There was typically little vertical movement at depth until the individual accelerated towards the surface to finish the dive. Some dives showed a skewed 'U' shape in which there was a slight surfacing trend before the individual rapidly swam towards the surface (~22.2 % of total dives) (Fig. 5b). A smaller number of dives showed a 'U' shape in which the individual dived with an initial rapid descent, before a slow approach of the trough of the dive (~7.6 % of total dives). Other dives showed more complex patterns. Some were generally 'U' shaped but involved multiple short-term vertical movements around the trough of the dive (~22.0 % of total dives) (Fig. 5c). Others involved occupancy of a distinct sill depth, where the individual remained for an extended time before or after diving to deeper depths (~6.2 % of total dives) (Fig. 5d).

Overall, the descending phase was significantly faster than the ascending phase (Wilcoxon signed rank test, $V = 91$, $p < 0.001$, n = 13 fish) (Fig. 6a). The mean of individual descent velocities was 0.20 m s$^{-1}$ (range = 0.11 to 0.35 m s$^{-1}$, n = 13), and on ascent, 0.10 m s$^{-1}$ (range = 0.05 to 0.18 m s$^{-1}$, n = 13). The proportion of deep dives was inversely proportional to the dive depth, with only 1.8 % of dives to >600 m depth (Fig. 6b). Deep diving events lasted for several hours (median time = 2.31 h, range = 0.18 to 22.5 h, SD = 2.03 h) (Fig. 6c). Diving typically involved relatively small decreases in temperature (median = 0.4°C, max. = 5.8°C) (Fig. 6d).

Deep diving events were aperiodic and the time between successive deep dives was highly positively skewed, with more than 20 % of surfacing events from a deep dive followed by a subsequent deep dive less than 15 min later. However, a similar percentage of surfacing events involved the individual remaining at the surface for more than 2 d, with one individual staying there for 74 d between deep dives. Some individuals occasionally spent long periods on the surface without performing deep dives, followed by multiple successive deep dives. Atlantic salmon exhibited both shallow and deep dives throughout the

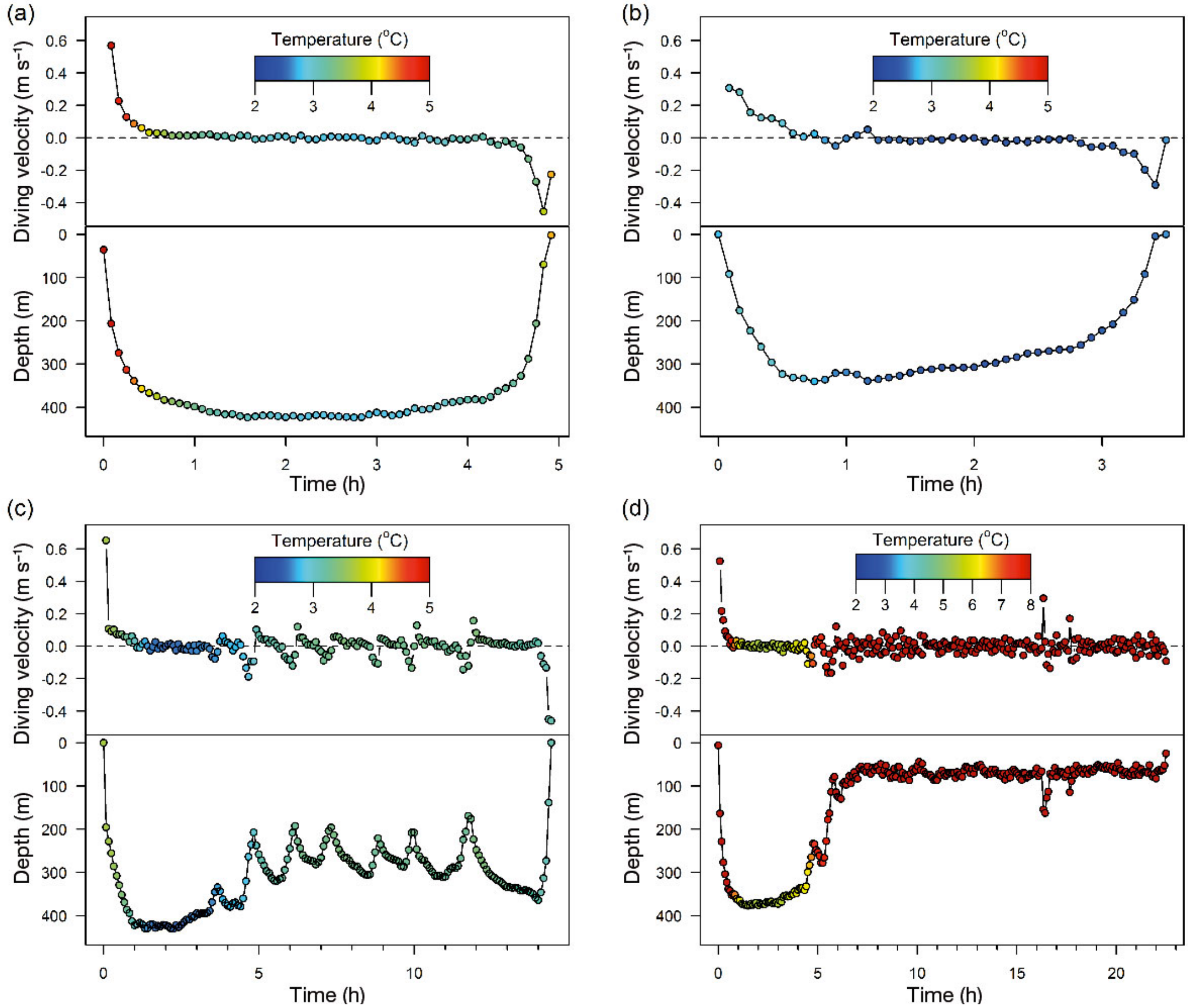


Fig. 5. Deep dive characteristics (>200 m) for selected Atlantic salmon from the River Alta carrying data storage tags (DSTs): (a) 'U' shaped pattern; (b) skewed 'U' shape pattern; (c) movement to depth with multiple depth fluctuations before surfacing; and (d) movement to depth followed by sustained presence as a shallower depth before surfacing. Positive diving velocities indicate the descending phase, and negative diving velocities indicate the ascending phase

year, but the overall diving pattern was associated with changes in the mixed layer depth (Fig. 7a).

When the mixed layer was near the surface (depth <50 m, June to October), most dives were relatively shallow; when the depth of the mixed layer increased (depth 150 to 250 m, mid-November to May), dives tended to be deeper. Diving depth (Fig. 7b) increased with the depth of mixed layer (GEE, $p < 0.001$, cluster $n = 13$). The diving rate showed a similar seasonal pattern. The rate of all dives >25 m was strongly related to time of year, with diving rate being greatest in summer (peaking in August and September), and lowest during winter (reaching a minimum in December) (Fig. 7c). In contrast, the rate of deep dives (>200 m) was greater during winter (when the mixed layer depth had deepened) than during summer.

## DISCUSSION

This study used 2 different tag types — PSATs and DSTs — to elucidate diving behaviour in tagged Atlantic salmon individuals from 3 populations. The use of the different tag types was not consistent among the populations, with ~71% (Orkla), ~55% (Alta) and 100% (Neiden) of individuals being tagged with PSATs rather than DSTs. Given this, it is necessary to

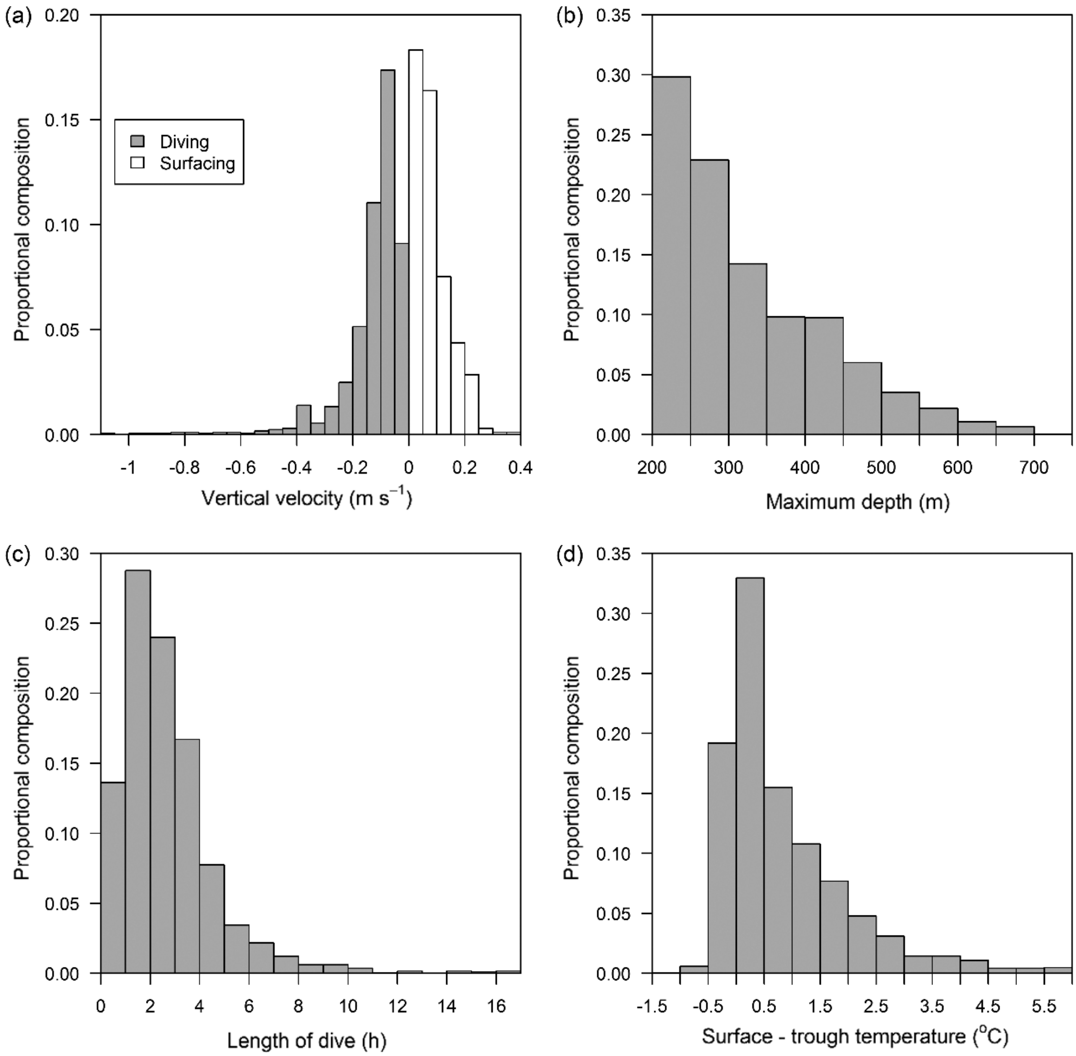


Fig. 6. Characteristics of the deep dives (>200 m) by 13 Atlantic salmon from the River Alta carrying high temporal resolution data storage tags (DSTs): (a) diving velocity; (b) maximum depth; (c) length of dive; and (d) difference between surface and trough (maximum depth) temperatures

consider the potential for tag effects biasing results of the study. Hedger et al. (2017) showed that although depth distributions among Atlantic salmon individuals tagged with PSATs were broadly similar to those of individuals tagged with DSTs, those tagged with PSATs tended to dive to shallower depths and dived less frequently than those tagged with DSTs. This may have slightly biased our estimates of overall depth distributions when comparing populations. However, the consistency in seasonal trends in depth behaviour among populations in the current study suggests that a mix of tags may still be applied effectively to compare populations. For analysis of environmental influences on diving behaviour, the current study focused on the high resolution DSTs, so differential tag effects were not an issue.

### Consistency among populations

Atlantic salmon from the 3 populations showed similar depth use and diving patterns during their marine migration. Firstly, all populations showed a trend of increasing use of subsurface waters (depth >5 m) from release until late summer (August), followed by a return to greater occupancy of surface waters in winter (December to February). Secondly, all populations showed similar changes in diel patterns, with no diel variation during May to July, and increased use of greater depths during the daytime between August and October. During November through January, the Alta population showed little diel pattern, whereas there was more use of greater depths for ~4 h around 12:00 h (using the tag clock

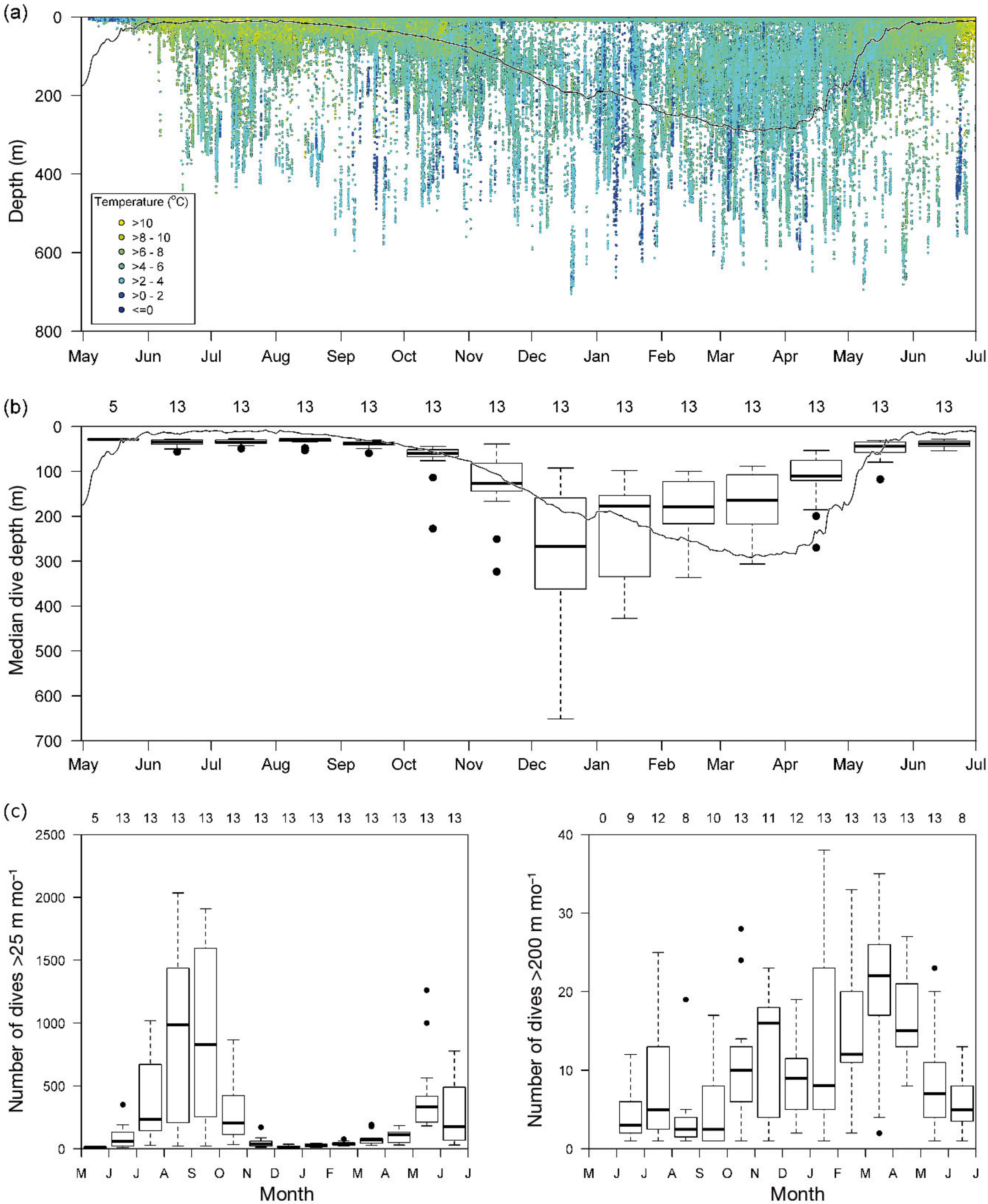


Fig. 7. Long-term trend of diving behaviour of 13 Atlantic salmon from the River Alta carrying high temporal resolution data storage tags (DSTs): (a) depth and temperature versus time; (b) median depth of dives where depth >25 m; and (c) total number of dives (depth >25 m) and number of deep dives (depth >200 m). The depth of the mixed layer (solid line), calculated for a convex polygon encompassing all pop-up locations for these individuals, has been superimposed on (a) and (b) (obtained from the Operational Mercator Global Ocean Analysis and Forecast System through the Copernicus Marine Environment Service). In (b) and (c) numbers above each box show the number of individuals

calibrated to position of release) for the Orkla population.

Although the Atlantic salmon came from 3 different populations, they were migrating to waters that were similar in terms of surface temperature and depth of the mixed layer, so it is not that surprising that they showed similarities. In comparison, stocks of North American Atlantic salmon have shown different diving patterns (Reddin et al. 2011, Lacroix 2013, Strøm et al. 2017) which may be related to differences in environmental conditions between the current study and those conducted in North American locations.

### Trends in depth use and diving among populations

Atlantic salmon behaviour in the initial phase of sea migration was not dominated by deep dives. There was little diving in the first month after release despite the fact that fjord and coastal zone depths could exceed several hundred metres. This is consistent with results from previous studies of Atlantic salmon kelts and post-smolts, both in the North West Atlantic and the North East Atlantic, showing swimming through the near surface layers and a lack of deep diving (LaBar et al. 1978, Davidsen et al. 2008, Halttunen et al. 2009, Guðjónsson et al. 2015). Diet studies of Atlantic salmon in the fjords of this study show that Atlantic salmon post-smolts feed almost exclusively on fish (Rikardsen et al. 2004). Post-smolts of other salmonids — Arctic charr *Salvelinus alpinus* L. and sea trout *Salmo trutta* L. — in the Altafjord have been found to feed pelagically on herring (Rikardsen & Amundsen 2005) when the prey were abundant. Given that adult Atlantic salmon in the current study were in poor condition on first entering the sea (median condition factor, $K = 0.74$), it can be expected that they would have had the impetus to feed. Thus, we propose that they were feeding pelagically in the first month at sea during the transit away from the coast when prey were available.

Further from release, some individuals did show occasional dives (depths of 200 to 400 m) in summer (June to August) (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m574p127_supp.pdf). This suggests they had moved off the continental shelf into the Norwegian Sea. Lacroix (2013) observed deep dives when post-spawners crossed the deep Laurentian Channel or migrated to the edge of the continental shelf, and hypothesised that they may have been looking for a thermal refuge or orientation cues, or feeding in highly productive upwelling water at the continental shelf edge. Given that deep dives at this time are rare, occasional events, we hypothesise that this is an example of exploratory and orienteering behaviour rather than foraging behaviour, triggered by the Atlantic salmon moving from coastal to deeper waters.

In the winter and spring following release, the Atlantic salmon began diving deeper. Greater maximum depths were observed for all populations in winter, and for the Orkla and Alta individuals tagged with DSTs that had extended coverage, into the spring. In addition, the frequency of deep diving increased for the Alta Atlantic salmon tagged with high resolution DSTs. Atlantic salmon in the deep sea have been shown to feed on the mesopelagic community, both in the NW Atlantic (Lear 1972) and the NE Atlantic (Hansen & Pethon 1985). This may be the cause of the deep dives shown in the current study. Near the time of pop-up, Atlantic salmon which had migrated to the deeper part of the Norwegian Sea (from the Orkla and one-third of the Alta population) dived within the water, but to shallower depths than those that migrated to the shallow Barents Sea (from the Neiden and two-thirds of those from the Alta population). Differences in diving depths may indicate different feeding behaviours. Prey fish for adult Atlantic salmon, including herring, capelin *Mallotus villosus*, and sand eel (Haugland et al. 2006, Rikardsen & Dempson 2011, Renkawitz et al. 2015), are found throughout the Norwegian and Barents Seas (see Jakobsen & Ozhigi 2011), but there is limited information on how their distributions change spatially and temporally, so it is difficult to relate the diving behaviours of Atlantic salmon in these seas to differences in prey availability. Some of the deep dives within the Barents Sea preceding pop-up were deep enough that they may have been diving to the sea bottom, so the salmon could also have been feeding on benthic prey items. However, the ability for Atlantic salmon to quickly migrate allowed for the possibility that they could have been diving in deeper waters before a pop-up took place at a relatively shallow location.

### Environmental influences on diving

Short- and long-term changes in the depth frequency distribution of all populations, and in the vertical velocities of the Alta Atlantic salmon tagged with high resolution DSTs, are likely associated with changes in light. Adult Atlantic salmon at sea have been shown to dive more during daytime than night-time and/or occupy nearer surface waters during night-time (Holm et al. 2006, Reddin et al. 2011, Renkawitz et al. 2012, Lacroix 2013). Atlantic salmon from all rivers in the current study showed a diel pattern of depth occupancy that was attenuated during polar day and polar night. Depth did not change according to hour of day from May to July, during the polar day. Thus, the lack of diel changes in depth use during this period may be related to the small diel variation in light intensity. Later in the year (August to October), periods of night-time began to return, which was associated with increased use of greater depths during daylight. Later in the winter (November to January), PSAT data suggest that Atlantic salmon from all 3 populations were in northern latitudes. During this time, the length of both daylight and twilight were short, which was associated with shorter periods (~4 h) of use of greater depths for the Orkla and Neiden Atlantic salmon. When the daytime lasted a short period, the greatest depth use of Neiden Atlantic salmon occurred 4 h earlier than noon at the local time of the River Neiden (for which the tag clock was set). Therefore, if they were diving during the brightest conditions around noon during the short winter day, it is likely that Neiden Atlantic salmon had moved ~60° east of the release site. Of the 3 populations, the Alta Atlantic salmon exhibited the least difference in depth according to time of day during winter. This suggests that the Alta Atlantic salmon were at latitudes with smaller daily differences in light intensity, i.e. were farther north. The Alta Atlantic salmon tagged with high resolution DSTs showed a similar pattern. Vertical movements for the Alta Atlantic salmon were greatest between August and October, when there was greatest diel contrast in illumination. These vertical movements would be consistent with visual foraging during the daytime period.

Diel variation in depth use by Atlantic salmon may be directly affected by variation in light conditions creating opportunities for visual foraging. Indirect effects of light are also possible if they feed on prey that have diel vertical migrations. Atlantic salmon are able to feed in the dark, as evident from their feeding in darkness under ice cover (Finstad et al. 2004). However, foraging would likely be more efficient if they can use their visual sense. Therefore, the depth at which Atlantic salmon feed may be a function of prey location and relative visual feeding efficiency. If most prey were deeper in the water column, occupancy of greater depths would be expected during brighter periods of the day (see Reddin et al. 2011) when Atlantic salmon can use their vision to forage, which would concur with the seasonal/diel depth patterns observed in this study.

Diving behaviour was probably not related to suboptimal summer or winter thermal conditions. Reddin et al. (2011) proposed that during stratification in summer, Atlantic salmon dive for short periods of time to catch prey despite cold suboptimal conditions, and return to the surface to digest prey. Lacroix (2013) hypothesised that adult Atlantic salmon avoided the surface layer in the Labrador Sea during winter because supercooling caused surface temperatures to fall below a critical threshold of −0.76°C (see Saunders 1986, Fletcher et al. 1988). However, neither of these conditions were observed in our study. It was rare for Atlantic salmon to dive into temperatures below the critical threshold, and the temperature change during dives was not great, with ~87% of dives never involving a reduction in temperature of >2°C. Median surface (depth <5 m) temperatures during winter (December to January) were 3.6, 4.3, and 5.2°C for Orkla, Alta, and Neiden populations, respectively, so Atlantic salmon were not experiencing supercooling near the surface. This was because variation between winter and summer in terms of sea surface temperature is less for the North East Atlantic, where this study was based, than that for the North West Atlantic. Thus, the difference between Atlantic salmon behaviour in this study and that of Reddin et al. (2011) and Lacroix (2013) may be due to the different environments. It is also unlikely that diving behaviour was influenced by low oxygen levels in the mesopelagic. Hypoxia in Atlantic salmon occurs at dissolved oxygen (DO) levels below 6 mg $l^{-1}$ (Burt et al. 2013). Predictions by the TOPAZ4 Arctic Ocean Biogeochemistry Analysis and Forecast always showed DO levels greater than 8 mg $l^{-1}$ throughout the mesopelagic in the Norwegian and Barents Sea, so Atlantic salmon in the current study were not diving into conditions likely to induce hypoxia.

Changes in the frequency and diving depth of Alta Atlantic salmon tagged with high resolution DSTs coincided with changes in stratification, with frequent shallow dives during near-surface stratification, and a reduction in the rate of shallow dives but an increase in the rate of deep dives when the mixed layer extended to a depth of several hundred metres. Diving has been related to stratification in other marine fishes. Walli et al. (2009), for example, found that Atlantic bluefin tuna showed preference for surface layers when in strongly stratified waters, spent less time above the thermocline when in weakly stratified waters, and dived to depths that were positively related to the depth of the thermocline. They speculated that strong thermal stratification may facilitate prey detection and improve the chance of successful feeding. Atlantic salmon in the current study dived to deep waters only after a relatively long period at sea. The delay may be related to the deepening of the mixed layer and consequent changes in prey aggregation. Deep (>200 m) diving exhibited by Alta Atlantic salmon with high resolution DSTs was characterised by relatively infrequent and short duration 'U'-shaped dives. These 'U' shaped dives have been hypothesised to be indicative of foraging behaviour in bluefin tuna (Wilson & Block 2009), and this may be the case for the adult Atlantic salmon in the current study.

## CONCLUSIONS

Diel and seasonal patterns in depth use and diving were broadly consistent among groups of tagged Atlantic salmon in the northern part of the North East Atlantic. This was manifested as use of greater depths during daylight on a daily time scale. Seasonally, this involved use of deeper depths in summer, more use of nearer-surface depths at the onset of winter, and a return to more use of deeper depths in late winter and spring with a concurrent increase in deep dives (>200 m) into the water column. The diel effect was likely associated with changes in the light regime, as suggested by transitions in behaviour between polar day and polar night. The seasonal pattern of deep diving may have been influenced by seasonal trends in the depth of the mixed layer, which we hypothesise affects diving behaviour by aggregating sources of prey.

*Acknowledgements*. We thank the Tromsø Research Foundation (supported by Trond Mohn), the Norwegian Research Council (project 221400/E40), Alta Laksefiskeri Interessentskap and the University of Tromsø for financial support to the Salmotrack-project during the period 2008-2017.

## LITERATURE CITED

Burt K, Hamoutene D, Perez-Casanova J, Gamperl AK, Volkoff H (2013) The effect of intermittent hypoxia on growth, appetite and some aspects of the immune response of Atlantic salmon (*Salmo salar*). Aquacult Res 45:124–137

Dadswell MJ, Spares AD, Reader JM, Stokesbury MJW (2010) The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the 'merry-go-round' hypothesis. J Fish Biol 77:435–467

Davidsen JG, Manel-la NP, Okland F, Diserud OH and others (2008) Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. J Fish Biol 73:1065–1074

Finstad AG, Forseth T, Næsje TF, Ugedal O (2004) The importance of ice cover for energy turnover in juvenile Atlantic salmon. J Anim Ecol 73:959–966

Fletcher GL, Kao MH, Dempson JB (1988) Lethal freezing temperatures of Arctic char and other salmonids in the presence of ice. Aquaculture 71:369–378

Godfrey J, Stewart D, Middlemas S, Armstrong J (2015) Depth use and migratory behaviour of homing Atlantic salmon (*Salmo salar*) in Scottish coastal waters. ICES J Mar Sci 72:568–575

Guðjónsson S, Einarsson SM, Jónsson IR, Guðbrandsson J (2015) Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar*) as inferred from recoveries of data storage tags. Can J Fish Aquat Sci 72:1087–1098

Halttunen E, Rikardsen A, Davidsen J, Thorstad E, Dempson J (2009) Survival, migration speed and swimming depth of Atlantic salmon kelts during sea entry and fjord migration. In: Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J (eds) Reviews: methods and technologies in fish biology and fisheries, Vol 9. Tagging and tracking of marine animals with electronic devices. Springer, Dordrecht, p 35–49

Halttunen E, Rikardsen AH, Thorstad EB, Naesje TF, Jensen JLA, Aas O (2010) Impact of catch-and-release practices on behavior and mortality of Atlantic salmon (*Salmo salar* L.) kelts. Fish Res 105:141–147

Halttunen E, Jensen JLA, Naesje TF, Davidsen JG and others (2013) State-dependent migratory timing of post-spawned Atlantic salmon (*Salmo salar*). Can J Fish Aquat Sci 70:1063–1071

Hansen LP, Pethon P (1985) The food of Atlantic salmon, *Salmo salar* L., caught by long-line in northern Norwegian waters. J Fish Biol 26:553–562

Hansen L, Quinn T (1998) The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. Can J Fish Aquat Sci 55(Suppl 1): 104–118

Haugland M, Holst JC, Holm M, Hansen LP (2006) Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. ICES J Mar Sci 63:1488–1500

Hedger RD, Rikardsen AH, Thorstad EB (2017) Pop-up satellite archival tag effects on the diving behaviour, growth and survival of adult Atlantic salmon *Salmo salar* at sea. J Fish Biol 90:294–310

Holm M, Jacobsen J, Sturlaugsson J, Holst J (2006) Behaviour of Atlantic salmon (*Salmo salar* L.) recorded by data storage tags in the NE Atlantic — implications for interception by pelagic trawls. ICES ASC CM 2006/Q:12

Jacobsen JA, Hansen LP (2000) Feeding habits of Atlantic salmon at different life stages at sea. In: Mills D (ed) The ocean life of Atlantic salmon: environmental and biological factors influencing survival. Wiley-Blackwell, Oxford, p 170–192

Jakobsen T, Ozhigi V (2011) The Barents Sea: ecosystem, resources, management. Half a century of Russian–Norwegian Cooperation. Tapir Academic Press, Trondheim

Jákupsstovu SH (1988) Exploitation and migration of salmon in Faroese waters. In: Mills D, Piggins D (eds) Atlantic salmon: planning for the future. Croom Helm, London, p 458–482

Joyce WN, Campana SE, Natanson LJ, Kohler NE, Pratt HL, Jensen CF (2002) Analysis of stomach contents of the

porbeagle shark (*Lamna nasus* Bonnaterre) in the northwest Atlantic. ICES J Mar Sci 59:1263–1269
LaBar GW, McCleave JD, Fried SM (1978) Seaward migration of hatchery-reared Atlantic salmon (*Salmo salar*) smolts in the Penobscot River estuary, Maine: open water movements. J Cons Cons Int Explor Mer 38:257–269
Lacroix GL (2013) Population-specific ranges of oceanic migration for adult Atlantic salmon (*Salmo salar*) documented using pop-up satellite archival tags. Can J Fish Aquat Sci 70:1011–1030
Lacroix GL (2014) Large pelagic predators could jeopardize the recovery of endangered Atlantic salmon. Can J Fish Aquat Sci 71:343–350
Lear WH (1972) Food and feeding of Atlantic salmon in coastal areas and over oceanic depths. Res Bull (Int Comm Northwest Atl Fish) 9:27–39
Miller AS, Miller TJ, Mills KE, Sheehan TF (2014) Retrospective analysis of Atlantic salmon (*Salmo salar*) marine growth and condition in the northwest Atlantic based on tag-recovery data. Fish Oceanogr 23:103–115
Reddin DG, Friedland KD, Downton P, Dempson JB, Mullins CC (2004) Thermal habitat experienced by Atlantic salmon (*Salmo salar* L.) kelts in coastal Newfoundland waters. Fish Oceanogr 13:24–35
Reddin DG, Downton P, Fleming IA, Hansen LP, Mahon A (2011) Behavioural ecology at sea of Atlantic salmon (*Salmo salar* L.) kelts from a Newfoundland (Canada) river. Fish Oceanogr 20:174–191
Renkawitz MD, Sheehan TF, Goulette GS (2012) Swimming depth, behavior, and survival of Atlantic salmon postsmolts in Penobscot Bay, Maine. Trans Am Fish Soc 141: 1219–1229
Renkawitz MD, Sheehan TF, Dixon HJ, Nygaard R (2015) Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. Mar Ecol Prog Ser 538: 197–211
Rikardsen AH, Amundsen PA (2005) Pelagic marine feeding of Arctic charr and sea trout. J Fish Biol 66:1163–1166
Rikardsen AH, Dempson JB (2011) Dietary life-support: the food and feeding of Atlantic salmon at sea. In: Aas Ø, Einum S, Klemetsen A, Skurdal J (eds) Atlantic salmon ecology. Wiley-Blackwell, Oxford, p 115–143
Rikardsen AH, Thorstad EB (2006) External attachment of data storage tags increases probability of being recaptured in nets compared to internal tagging. J Fish Biol 68: 963–968
Rikardsen AH, Haugland M, Bjorn PA, Finstad B and others (2004) Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. J Fish Biol 64:1655–1679
Rikardsen AH, Hansen LP, Jensen AJ, Vollen T, Finstad B (2008) Do Norwegian Atlantic salmon feed in the northern Barents Sea? Tag recoveries from 70 to 78° N. J Fish Biol 72:1792–1798
Saunders R (1986) The thermal biology of Atlantic salmon: influence of temperature on salmon culture with particular reference to constraints imposed by low temperature (*Salmo salar*). Report – Institute of Freshwater Research, Book 63, Drottningholm, p 77–90
Strøm J, Thorstad E, Chafe G, Sørbye S, Righton D, 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
Tanaka H, Takagi Y, Naito Y (2000) Behavioural thermoregulation of chum salmon during homing migration in coastal waters. J Exp Biol 203:1825–1833
Walli A, Teo SLH, Boustany A, Farwell CJ and others (2009) Seasonal movements, aggregations and diving behavior of Atlantic bluefin tuna (*Thunnus thynnus*) revealed with archival tags. PLOS ONE 4:e6151
Wilson SG, Block BA (2009) Habitat use in Atlantic bluefin tuna *Thunnus thynnus* inferred from diving behavior. Endang Species Res 10:355–367

*Editorial responsibility: Alejandro Gallego, Aberdeen, UK*

*Submitted: January 19, 2017; Accepted: May 4, 2017*
*Proofs received from author(s): June 20, 2017*