Diving and feeding of adult Atlantic salmon when migrating through the coastal zone in Norway

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Abstract Atlantic salmon post-spawners from a population in northern Norway were tagged with data storage tags ($N=773$), and the depth use and diving behaviour of recaptured individuals within the coastal zone were examined, both on their outward migration to sea ($N=44$) and their return to the natal river after overwintering at sea ($N=34$). In addition, the stomach contents of 909 returning adults caught in the fjord were examined to determine the extent to which, how recently and on what species they had fed. The tagged individuals migrated through surface waters and performed aperiodic dives, regardless of whether they were leaving the fjord as post-spawners (kelts) or returning after a winter or more at sea. However, diving behaviour differed between the fjord and outer coast. During both outward and return migration, dives when fish were likely in the fjord were shallower than on the outer coast. Deep dives of longer duration were more frequent on the outer coast than in the fjord. The stomach content analysis of salmon captured in the fjord did not show strong evidence of recent feeding: 58% of the salmon had empty stomachs, and most stomach contents were highly digested fish (mainly herring, but some capelin and unidentifiable species). We conclude that the inferred diving behaviour in the coastal zone, both on outward migration to sea and on return to the natal river, did not provide sufficient evidence of foraging within the water column, and hypothesize that diving in search for navigation cues is a more likely explanation.

Keywords Atlantic salmon · Coastal zone · Diving · Feeding

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Introduction

The Atlantic salmon (*Salmo salar* L.) is a culturally and economically important cold-water fish species (Liu et al. 2011; Ignatius and Haapasaari 2018) that serves as an indicator of freshwater and coastal ecosystem health (Lien et al. 2016). In contrast to Pacific salmon (*Oncorhynchus* sp.), which display a semelparous life-history strategy with individuals

dying shortly after spawning, Atlantic salmon are facultatively iteroparous and may spawn multiple times during their lifespan (Klemetsen et al. 2003). This bet-hedging strategy spreads the risk of reproductive failure over time and may enhance population resilience to environmental perturbations because the presence of larger-sized repeat spawners may sustain recruitment in years with low abundance of maiden spawners (Bordeleau et al. 2020). For Atlantic salmon, the success of iteroparity is dependent on the ability to transit fjords/estuaries to migrate between fresh water and marine feeding grounds.

Coastal areas are challenging environments for Atlantic salmon. Firstly, aggregations of marine predators may cause high mortality in both post-smolts (Thorstad et al. 2007) and larger adults (Lacroix 2014; Strøm et al. 2019). Secondly, there is increasing human activity in the coastal zone. Pathogen spill from open-net pen Atlantic salmon farming has been shown to impact post-smolt survival (Kristoffersen et al. 2018; Shephard and Gargan 2021). Anthropogenic stressors such as boat traffic (Codarin et al. 2009; Becker et al. 2013), pollution (Meador 2014), and the construction of infrastructure such as harbours or tidal and wind power plants (Bergstrom et al. 2014) impact marine fish, and it is possible that these factors may impact Atlantic salmon during their coastal migration. Being iteroparous, Atlantic salmon will be exposed to these conditions several times throughout their lifespan. Therefore, detailed knowledge about the behaviour of Atlantic salmon in coastal areas is essential for evaluating the impacts of different stressors and developing and evaluating mitigation measures designed to protect Atlantic salmon during migration through this challenging environment.

Diving and feeding are important behaviours within the coastal zone. However, there have been relatively few studies examining these behaviours in Atlantic salmon adults. A pop-up satellite tag (PSAT) study by Strøm et al. (2017) of outward migrating adults within the Gulf of St Lawrence found that they mainly migrated in near-surface waters with frequent shallow dives and that deep dives to > 50 m were rare. A PSAT study of returning adults in Scottish waters by Godfrey et al. (2015) found a similar preference for surface waters, alongside diving to an average depth of 64 m, and to a maximum of > 100 m. The reasons for diving by adult Atlantic salmon at sea are not fully understood, but it may be that diving behaviour is associated with searching for homing cues when returning through fjords (Davidsen et al. 2013), and feeding in more open waters (Strøm et al. 2017) and oceanic fronts (Rikardsen et al. 2021). Stomach contents of recaptured fish may provide information on whether they have fed and on what prey types they have selected, and may be used to infer reasons for diving behaviour (Rikardsen and Dempson 2011). Obtaining information on diets from stomach contents requires killing fish for sampling, and adult Atlantic salmon typically occur in low numbers so killing them for sampling prior to spawning is often not feasible or desirable. However, in Northern Norway, there are still areas with abundant Atlantic salmon populations, supporting a regular sea fishery and enabling the collection of fish stomach samples from the catch of local fishers.

The main aim of this study was to investigate the behaviour of adult Atlantic salmon during migration through the coastal zone. Specifically, we examined the coastal diving behaviour of Atlantic salmon adults, tagged with archival tags, during the initial and final phase of their ocean migration through a Norwegian fjord. In addition, a stomach content analysis of untagged adult Atlantic salmon captured by bag net fishers in the fjord during their return migration towards the river was conducted to determine if the prevalence and type of prey items could be used to infer the underlying causes for the observed diving behaviour of the tagged fish.

Method

The study was conducted in the coastal zone surrounding and including the Alta fjord on the northern coast of Norway (70.13°N, 23.08°E) (Fig. 1). The Alta fjord is a large sill fjord (length = 30 km, mean width = 7 km, maximum depth = 488 m, tidal range = 1.5–2.5 m) that flows into the Barents Sea ≈ 60 km from the mouth of its largest river (the River Alta) via the Stjernsund, Rognsund and Vargsund straits. The surface water layer of the fjord is strongly influenced by river discharge and may become brackish during summer (Skarðhamar et al. 2018). The fjord becomes thermally stratified in summer with a warm surface layer of ≈ 12–13 °C overlying a colder layer of < 10 °C at depths > 10 m in June/July. Surface

Fig. 1 Map of study area, showing the Alta Fjord. Bathymetry data source: Kartverket (https://dybdedata.kartverket.no)
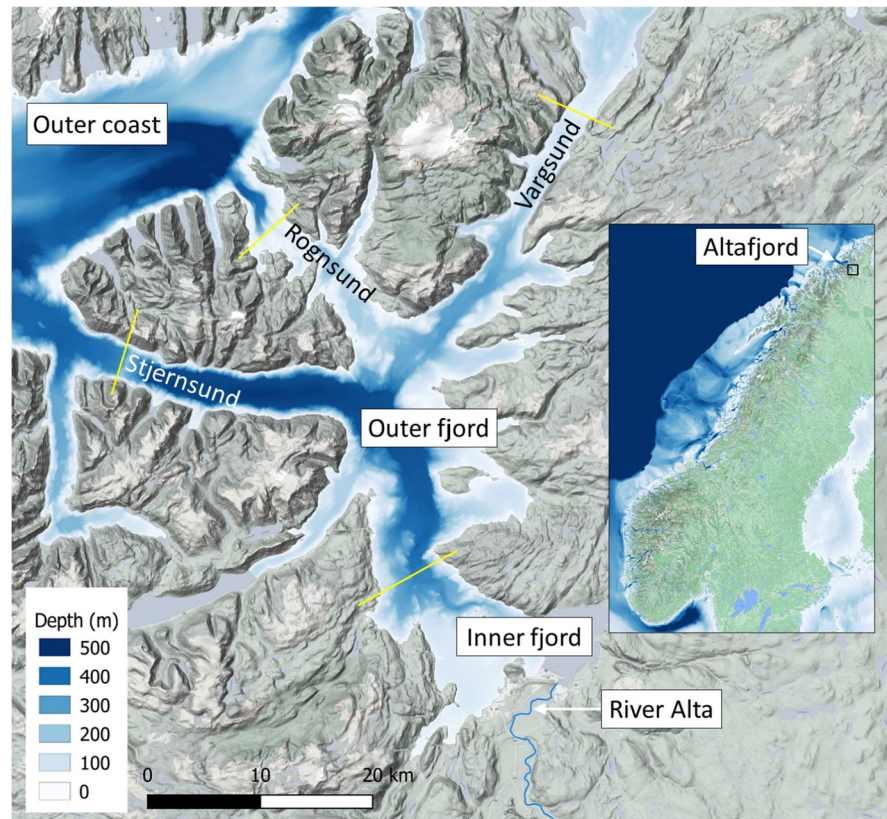
temperature patterns within the fjord are complex and suggest horizontal recirculation.

The study consisted of two parts: (1) a tagging study using data storage tags which archived information on depth use and diving behaviour of Atlantic salmon adults migrating through the Alta fjord coastal zone both on outrun and return and (2) a stomach contents study of untagged adults captured in the fjord that were returning for spawning, which provided information on the prevalence of feeding and the prey species.

Tagging study

Capture, tagging, release and recapture

From 2008 to 2015, 773 post-spawned adult Atlantic salmon from the River Alta were tagged with data storage tags. Post-spawners were captured in the river after ice break-up in May of each year by angling using spoon bait (two hook lures with the barbs removed so as to minimize fish damage). Larger individuals (mean body length = 92 cm, range = 55–121 cm; mean body mass = 6.0 kg, range = 1.2–13.8 kg; mean condition factor, K = 0.75, range = 0.49–1.59) were selected for tagging to minimize the tagging effects on the probabilities of survival and subsequent recovery, so tagged individuals were predominantly female (93% of those tagged) due to their larger size relative to males in this river (Halttunen et al. 2010).

Each post-spawner selected for tagging was placed in a holding tank and anesthetized in an aqueous solution of 0.5 ml 2-phenoxy ethanol l^{-1} (EC No 204–589-7, Sigma Chemical Co., St Louis, Missouri, USA). Once anesthetized, it was placed in a tagging tube that was partly filled with freshwater so that the mouth and gills were submerged, a lateral cut (≈2–2.5 cm long) was made through its ventral surface posterior to the pelvic girdle, and a tag was inserted into its body cavity. Several tag types were used. A total of 576 post-spawners were tagged with data storage tags supplied by Star Oddi, Reykjavik, Iceland (www.star-oddi.com): either (1) *DST milli*: 39.4 × 13 mm, 9.2 g in air; or (2) *DST centi*:

46×15 mm, 19 g in air. These tags recorded depths at intervals of 1, 5, 10 or 30 min, depending upon year of tagging, and recorded body temperatures concurrently with depth, except for the tags measuring depth at a 1-min interval which recorded temperature every 5 min. An additional 197 individuals were tagged with *Geo* data storage tags supplied by Lotek Wireless Inc., Ontario, Canada (www.lotek.com): *LAT2810L*, 44×13 mm, 13 g in air. These recorded depth and temperature (both the internal body temperature of the fish and the external temperature of the surrounding water) at a 30-s interval. Fish were also tagged externally with Carlin identification tags (Floy tag, Mervin Manufacturing Inc., Seattle, Washington, USA) to ensure easier identification on return. The handling and tagging procedure for each post-spawner took approximately six minutes. After tagging, post-spawners were released into the River Alta, except for in 2009 when post-spawners were released directly into the fjord at the river mouth to avoid potential negative effects of an expected large flood in the river (Table 1).

Recapture of tagged Atlantic salmon was done by fishers (bag net fishing in Alta fjord or angling in the Alta River) who had been informed of the tagging project and offered a monetary reward for each returned tag. Recaptures occurred in both the fjord and along the nearby coast (Note, recapture location

in one returning adult was not registered due to error). Of the 773 tagged Atlantic salmon released, 45 were recaptured: three on out migration and 42 after a winter or more at sea. One tag had failed to record temperature, hindering identification of time of sea entry, so data from this tag were discarded. This left tag data for 44 post-spawners. Of the 42 tags captured after a winter or more at sea, eight tags were discarded due to infrequent or incomplete measurements of depth and temperature before recapture, leaving tag data for 34 returning adults (Supplementary table 1).

Data analyses

Parts of the data series when the tagged Atlantic salmon were not in sea water (before release or after recapture, or within the River Alta) were identified and removed. Tag registrations within the river were identified by a consistent diurnal temperature pattern of daytime warming and night-time cooling of $\approx 1–3$ °C, as opposed to those in sea water which did not show such a pattern. Tags were calibrated at a 10 m depth from several hours before tagging. However, some tags "drifted" in their depth recordings, and depths were adjusted by subtracting the shallowest depth recorded on the assumption that this depth represented the fish surfacing.

Table 1 Characteristics of recaptured tagged Atlantic salmon

Tag resolution	Release year	Measurement interval (mins) (N = number recaptured)	Characteristics on release		
			Mean length (cm) (min.–max.)	Mean body mass (kg) (min.–max.)	Mean condition factor (min.–max.)
Low	2008	30 ($N=6$)[Ŧ]	95.7 (93–104)	6.7 (5.8–8)	0.76 (0.71–0.91)
	2009	30 ($N=3$)[Ŧ]	91.0 (84–98)	6.5 (6.5–6.5)	0.89 (0.69–1.10)
	2010	30 ($N=7$)[Ŧ]	89.9 (83–99)	5.6 (4.3–7)	0.77 (0.72–0.79)
	2011	30 ($N=7$)[Ŧ]	93.6 (85–105)	6.5 (4.7–9)	0.79 (0.72–0.84)
	2012	10 ($N=1$)[Ŧ]	85.0	4.0	0.65
	2013	5 ($N=4$)[Ŧ]	91.5 (90–93)	5.7 (5.2–5.9)	0.74 (0.71–0.77)
	2014	5 ($N=3$)[Ŧ]	93.0 (91–96)	5.5 (5.2–5.9)	0.68 (0.67–0.70)
High	2015	1 ($N=7$)[Ŧ]	92.9 (79–99)	5.6 (3.2–7.2)	0.69 (0.60–0.78)
	2013	0.5 ($N=2$)[*]	95.5 (93–98)	5.8 (5.3–6.3)	0.66 (0.66–0.67)
	2014	0.5 ($N=2$)[*]	102.5 (95–110)	8.0 (6.0–9.9)	0.72 (0.70–0.74)
	2015	0.5 ($N=2$)[*]	101.0 (95–105)	6.9 (5.9–7.8)	0.72 (0.67–0.76)

[Ŧ]Star Oddi tags

[*]Lotek Geo tags

Depth use and diving behaviour of the post-spawners and returning adults were analyzed according to time since release (on outward migration for post-spawners) or time before recapture (for returning adults) on the rationale that this would indicate their probable location relative to the river mouth and fjord. Previous studies have shown rapid migration through the fjord. Halttunen et al. (2009) found a mean post-spawner transit time of 33 h on outmigration through the 30 km length of the fjord, and Davidsen et al. (2013) identified a mean migration speed of returning adults through the fjord of 9.7 km day^{-1} (range 0.7–33.1 km day^{-1}) corresponding to a transit time of several days through the fjord. Based on the progression speeds from these studies, fish on day 1 after entry into the sea were assumed to be mainly in the inner fjord (0–15 km from river mouth), fish on day 2–3 were assumed to be mainly in the outer fjord (15–60 km from river mouth, ending at the outer mouth of the straits), and fish on day 4–14 were assumed to be mainly on the outer coast (> 60 km from river mouth, Fig. 1). Time-series data further than 14 days outside of sea entry or before recapture were omitted from further analysis as they most likely represented times when the fish were in the deep sea, and outside the scope of this study (see Strøm et al. 2018).

For all post-spawners, trends in depth use and diving were examined as a function of time since sea entry. Data from all tags ($N = 44$) were used to obtain depth composition and maximum daily depth, providing information on what parts of the water column the fish were using, and the approximate maximum depths to which fish dived. For the fish tagged with high-resolution tags ($N = 13$, measurement interval ≤ 1 min), it was possible to obtain more detailed metrics of the diving behaviour (dives being defined as a movement from the surface ≤ 5 m to a deeper depth with a subsequent return to the surface), even for short dives that may have been missed with a low sample resolution. Trends were examined using linear mixed-effects models (R function *lmer{lmerTest}*). Four models were fitted with the following response variables: (1) maximum daily depth (m) (all tags); (2) dive depth (m) (high-resolution tags); (3) dive frequency (N day^{-1}) (high-resolution tags); and (4) dive duration (min) (high-resolution tags). Individual fish were used as the random effect, and models were fitted using

random slopes and fixed intercepts. Random slopes allowed analysis of whether trends were consistent among individuals; fixed intercepts were used to ensure convergence for models that included random slopes. To ensure appropriate residual distributions, response variables were log-transformed prior to model fitting. For maximum daily depth and dive frequency, the predictor variable was day after sea entry (1, 2, 3,… 14). For dive depth and dive duration, the predictor variable was the fractional day after sea entry on initiation of the dive. Dives of the fish tagged with high-resolution tags were further analyzed by comparing descent and ascent speeds using a Wilcoxon signed-rank test (R function wilcox-test{stats}) as differences in speed might suggest underlying behavioural mechanisms. Finally, registered temperatures (both internal and external) of the six Geo tags were examined to determine if the tagged fish were diving into colder waters (from the external temperatures) and if the temperature change on diving was great enough to affect internal body temperature.

For all returning adults where capture location had been recorded ($N = 33$), depth distributions and maximum recorded depths in the final 24 h at sea were analyzed with respect to recapture zone—(1) outer coast or (2) fjord or river—using Wilcoxon tests. Longitudinal trends in maximum daily depth, dive depth, dive frequency and dive duration were examined in the same way as for post-spawners using linear mixed-effects models, but with regard to time before recapture rather than after sea entry. Descent and ascent speeds were also compared for the high resolution tags, and registered temperatures of the Geo tags were examined in the same way as for post-spawners.

Stomach contents study   Feeding by adult Atlantic salmon in and proximate to the fjord during return migration was investigated by examining the stomach contents of 909 individuals which had been captured in the fjord by local bag net fishers (May to September, 2008–2010). Captured individuals had a median body length of 76 cm (range = 50–130 cm), a median body mass of 4.2 kg (range = 1.0–20.2 kg) and a median condition factor of 1.0 (range = 0.49–1.66). Individuals captured in May and June tended to be larger (median body length = 95.5 cm, median body mass = 9.4 kg, $N = 309$) than those captured

in July to September (median body length = 62 cm, median body mass = 2.5 kg, $N = 585$): note, capture month was unavailable for 15 fish. To determine a potential effect of fish characteristics on whether they had recently fed, the probability of a stomach containing one or more prey items was modelled as a function of body mass, body length, condition factor, and day of year of capture using generalized linear modelling (R function *glm{stats}*) with a binomial family ($N = 884$; 25 fish were omitted due to an unregistered day of year of capture). A range of models was fitted including either body mass (M) or length (L) and different additive combinations with condition factor (K) and/or day of year of capture (D): (1) M, (2) M + K, (3) M + D, (4) M + K + D, (5) L, (6) L + K, (7) L + D, (8) L + K + D. The optimal model was selected based on the AIC value. Stomach contents were also analyzed with regard to the degree of digestion of prey items ($N = 810$ prey items across 374 Atlantic salmon), and the prey type. The degree of digestion was examined according to Atlantic salmon body length to see if there was a size effect on how recently the fish had fed. Degree of digestion was characterized as (1) undigested; (2) partly digested, where some skin was digested but the head was mostly intact; (3) mostly digested, where most skin and flesh was digested and the head was partially digested; (4) highly digested, where only vertebrae and some flesh remained; or (5) almost completely digested. A test of equal proportions (R function prop.test{stats}) was done to compare small (body length < 80 cm) and large (≥ 80 cm) Atlantic salmon in terms of stomach content digestion (undigested to mostly digested versus highly to almost completely digested).

Results

Post-spawners released in the river entered the fjord during early summer (median date of entry = June 5, range = May 7–July 29, $N = 44$). Returning adults with full tag data records were recaptured in the fjord and river during mid- to late summer (median date of recapture = June 27, range = June 6–July 30, $N = 34$) 1 year after release.

Depth use and diving behaviour of post-spawners during outward migration

Post-spawners migrated through surface waters in the fjord and outer coast, spending > 90% of their time at depths < 5 m on the first day after sea entry, and between ≈75 and > 90% of their time at these depths on subsequent days (Fig. 2A). The average of the individual median depths was 1.5 m (range = 0.3–6.0 m, $N = 44$). Maximum daily depths generally increased with time at sea (Fig. 2B; Table 2). However, this relationship varied according to the individual, and nearly 20% of post-spawners (8 out of 44) showed a reduction in maximum daily depth with time at sea (Supplementary Fig. 1). On day 1, when post-spawners were likely in the inner fjord, the median of their daily maximum depths recorded was ≈16 m; this increased to ≈18 m (day 2–3), and ≈28 m (day 3–14).

Dive depth increased with time across the 14 days following sea entry for fish tagged with high-resolution tags ($N = 13$) (Table 2). This relationship was shown by 92% of fish (12 out of 13) (Supplementary Fig. 1). Dive frequency was greatest on fjord entry (day 1, median = 34 dives day^{-1}, range = 0–171, $N = 13$), and declined far offshore on day 14 (median = 5 dive day^{-1}, range = 0–134, $N = 13$) (Fig. 2C). However, there was not a significant trend over the 14 days (Table 2). Dives were generally of short duration (mean = 2–3 min) throughout the 14 days monitored (Fig. 2D), and there was not a consistent change in dive duration with time after sea entry (Table 2). Post-spawners showed a range of diving behaviours, both during the first 3 days of sea entry, when they were likely in the fjord (Fig. 3) and later when they were more likely to be in the outer coast (Supplementary Fig. 2). For example the salmon with tag B1093 remained near the surface and did not dive deeper than 100 m until 9 days after sea entry, whereas the salmon with tag Geo1574 dived deeper than 100 m on the first day after entry. There was no difference between vertical speed on descent (mean = 0.07 m s^{-1}) and vertical speed on ascent (mean = 0.06 m s^{-1}) (Wilcoxon signed-rank test, $p = 0.25$). Measurements of water temperature by the Geo tags within the first 14 days after entry showed that fish were generally diving into colder waters (mean reduction = 0.46 °C from surface to dive trough). There was a negligible change in body

Fig. 2 Depth patterns of post-spawners according to time after sea entry: **A** depth composition, **B** maximum depth, **C** dive frequency, and **D** mean dive duration. **A** and **B** show data for all post-spawners ($N=44$); **C** and **D** show data for post-spawners tagged with high-resolution tags ($N=13$)
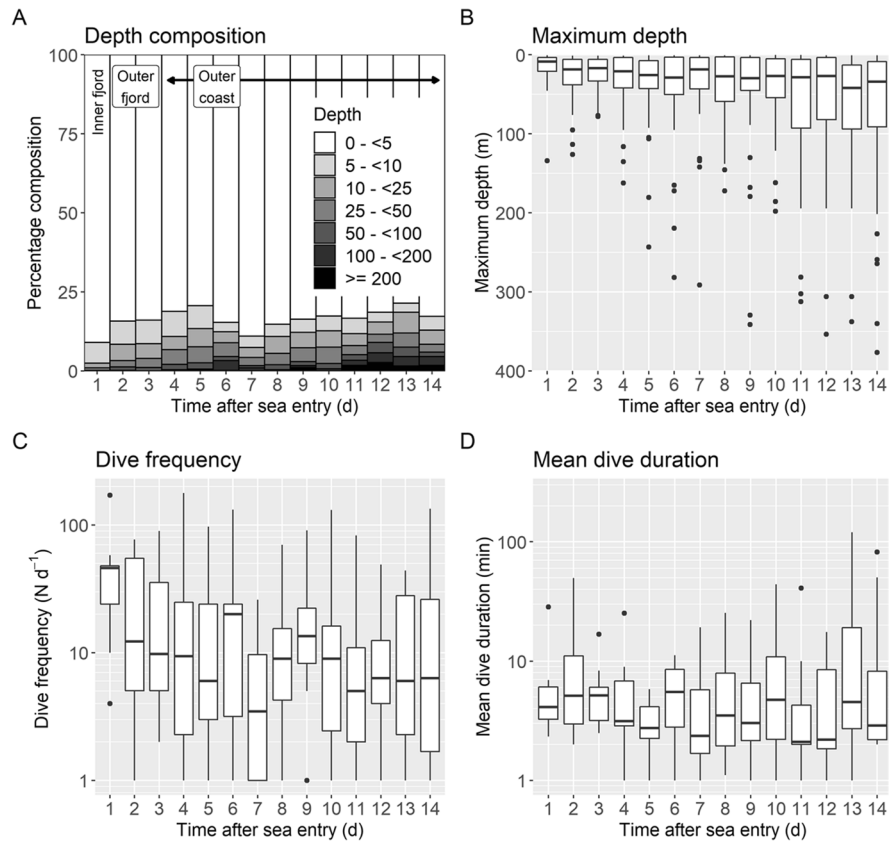

Table 2 Relationship between maximum daily depth, dive depth, dive frequency and dive duration and time after sea entry for post-spawners and time before recapture/return for returning adults as determined by mixed modelling. For maximum daily depth and dive frequency, time is measured in integer days (1, 2, 3,…14); for dive depth and dive duration, time is expressed as a fractional day since sea entry or before recapture/return, equivalent to the initiation of the dive. Significant fixed effects are shown in bold

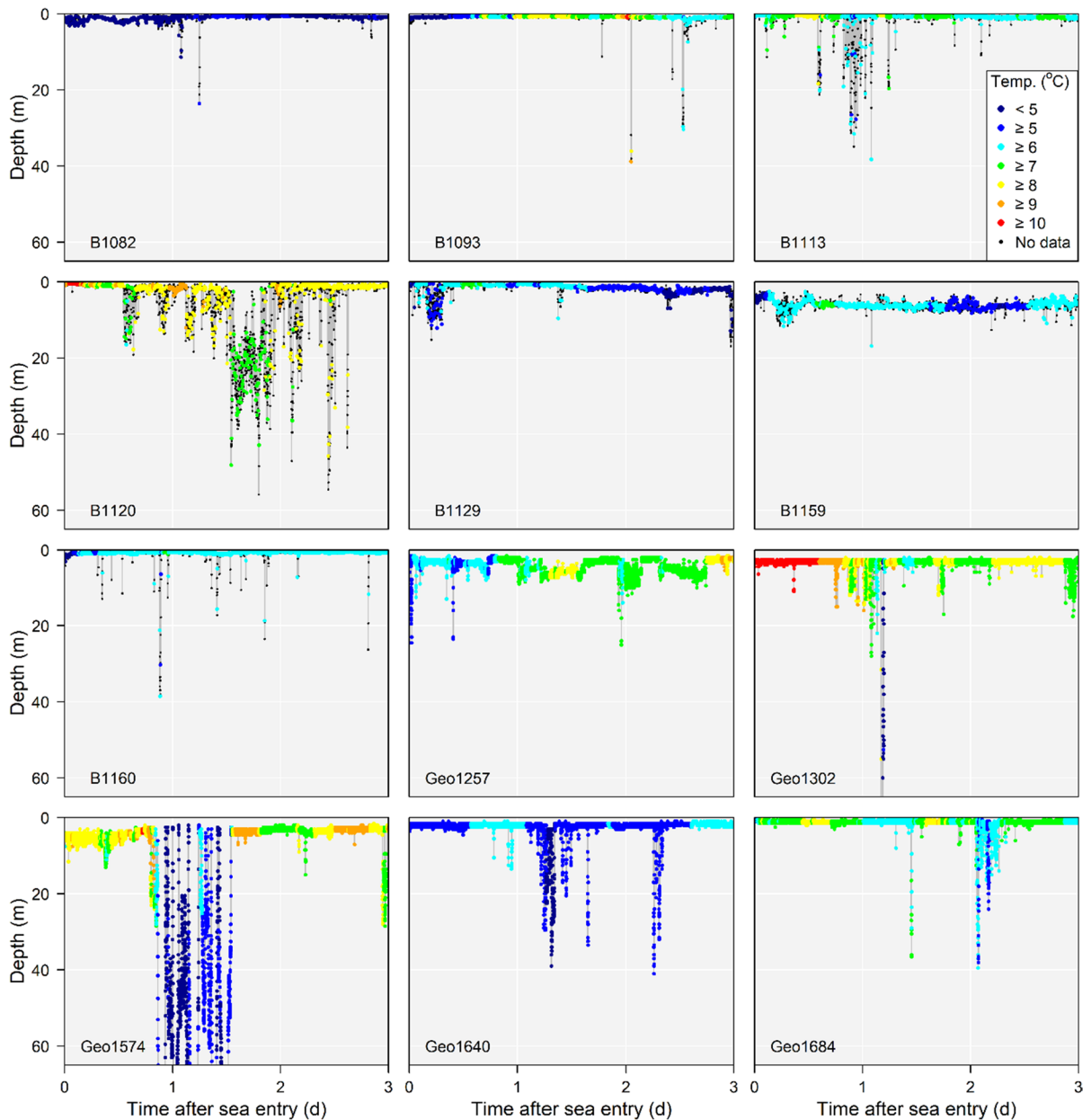| Post-spawners						
Response	**Predictor**	**Estimate**	**SE**	**Df**	**t value**	**Pr(>|t|)**
Maximum daily depth (m)	(Intercept)	2.521	0.098	571.00	25.64	<0.001
	Time after entry	0.057	0.018	91.57	3.18	**0.002**
Dive depth (m)	(Intercept)	2.094	0.017	3419.41	125.83	<0.001
	Time after entry	0.050	0.013	12.34	3.82	**0.002**
Dive frequency (N day⁻¹)	(Intercept)	2.466	0.188	168.00	13.13	<0.001
	Time after entry	−0.055	0.032	29.25	−1.71	0.099
Dive duration (min)	(Intercept)	1.098	0.033	3423.20	32.94	<0.001
	Time after entry	0.018	0.019	13.46	0.94	0.365
Returning adults						
Response	**Response**	**Estimate**	**SE**	**Df**	**t value**	**Pr(>|t|)**
Maximum daily depth (m)	(Intercept)	2.918	0.083	441.00	35.09	<0.001
	Time before rec/ret	0.069	0.017	58.08	3.987	**<0.001**
Dive depth (m)	(Intercept)	2.285	0.013	6980.55	179.70	<0.001
	Time before rec/ret	0.044	0.009	12.51	4.64	**0.001**
Dive frequency (N day⁻¹)	(Intercept)	3.421	0.165	168.00	20.72	<0.001
	Time before rec/ret	−0.037	0.029	26.85	−1.26	0.218
Dive duration (min)	(Intercept)	0.655	0.021	6984.94	30.73	<0.001
	Time before rec/ret	0.069	0.01	13.04	6.56	**<0.001**

Fig. 3 Depths and internal temperatures of post-spawners tagged with high-resolution tags in the first 3 days after sea entry. Note, the fish with tag number Geo1565, which did not dive in this period, has been omitted. Depths shown have a cut-off at 65 m, and exclude parts of some dives by the fish with tag number Geo1574 and Geo1302

temperature on diving registered by these tags (mean reduction = 0.01 °C), so dives were not of a sufficient duration to cool the fish to ambient water temperature.

Depth use and diving behaviour of returning adults

Returning adults recaptured outside the fjord had occupied greater depths in the final 24 h at sea than those recaptured within the fjord or river, spending less time in surface waters (depth < 5 m) and having

greater maximum depths (Fig. 4). However, there was a large individual variation; therefore, differences in depth distribution according to recapture zone were not significant (Wilcoxon tests, $p > 0.05$). Returning adults, similar to post-spawners migrated through surface waters in the outer coast and fjord, spending $> 75\%$ of their time at depths < 5 m (Fig. 5A). The average of the individual median depths was 2.6 m (range $= 0.5$–22.6 m, $N = 34$). Maximum daily depths registered tended to decline with proximity to capture in the sea or return to the river (Fig. 5B; Table 2): 85% of fish (29 out of 34) showed

Fig. 4 Depths in final 24 h at sea of returning adults according to recapture zone (outer coast $N = 8$, fjord or river $N = 25$): **A** depth distribution and **B** maximum registered depth. Note that one individual has been excluded due to an unregistered recapture location
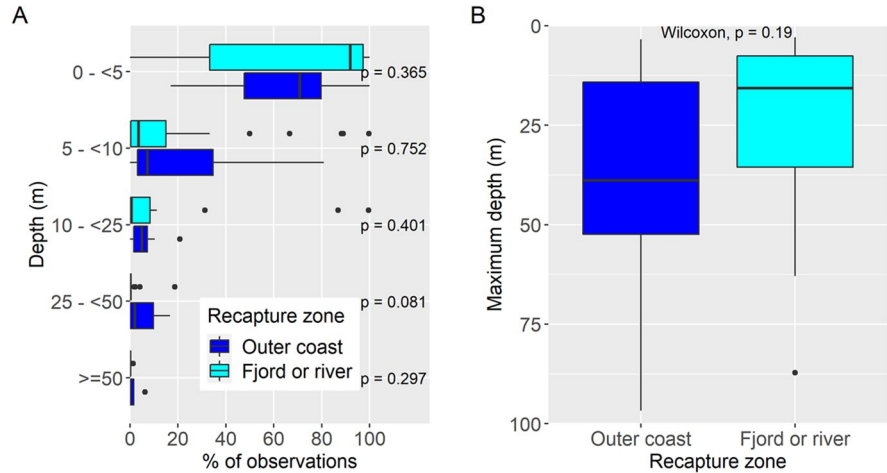
Fig. 5 Depth patterns of returning adults according to time before recapture/return to river: **A** depth composition, **B** maximum depth, **C** dive frequency, and **D** mean dive duration. **A** and **B** show data for all returning adults ($N = 34$); **C** and **D** show data for returning adults tagged with high-resolution tags ($N = 13$)
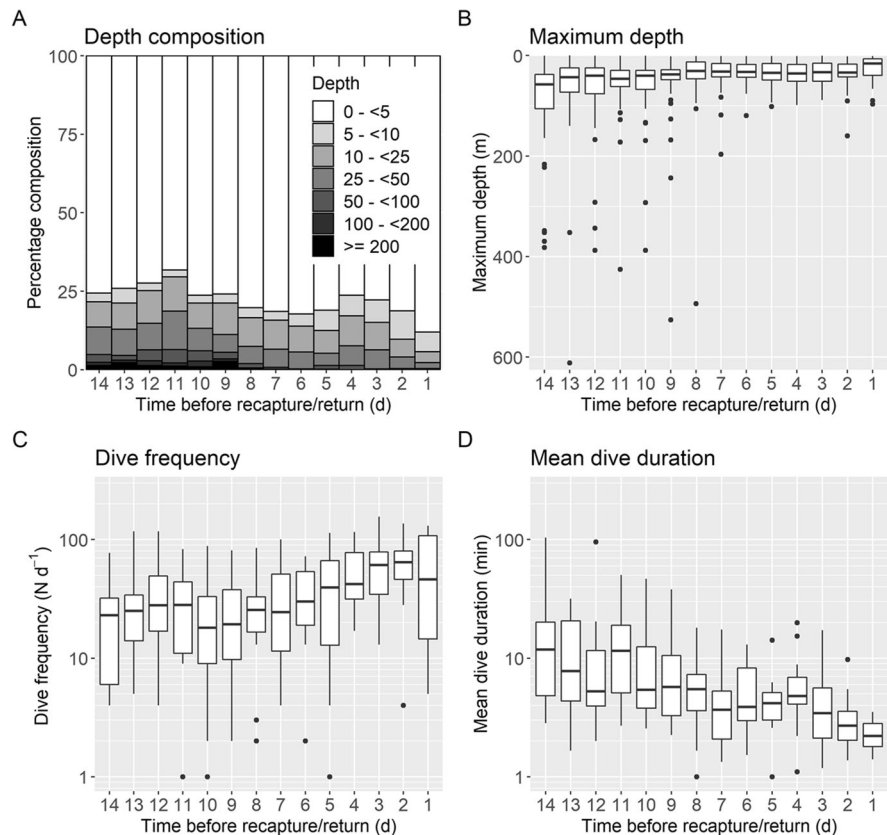
this pattern (Supplementary Fig. 1). For example, from day 4–14, when returning adults were likely offshore, the median of daily maximum depths was ≈38 m, with one individual diving to ≈650 m. In contrast, on day 2–3, the median had declined to 33 m, and on day 1 (within 24 h before recapture or return), the median was ≈16 m with the deepest dive registered being ≈100 m.

For returning adults, tagged with high-resolution tags ($N = 13$), dive depth decreased with proximity to recapture/return (Table 2), a relationship shown by 92% of fish (12 out of 13) (Supplementary Fig. 1). Similar to during out migration, there was no significant temporal trend in dive frequency on return (Fig. 5C; Table 2). However, the average diving rate in the last 14 days at sea (mean = 38.4 dives day^{-1}, range = 10.6–74.7, $N = 13$) was approximately twice that on out migration during the first 14 days after sea entry (mean = 18.82 dives day^{-1}, range = 2.1–59.4, $N = 13$). Diving behaviour was characterized by shorter dives with proximity to recapture/return (Fig. 5D; Table 2) for all individuals with high-resolution tags (Supplementary Fig. 1). Diving behaviour on return also showed wide individual variation (Fig. 6; Supplementary Fig. 3). For example, B1093 did not dive deeper than 8 m in the 14 days before recapture, whereas the other 12 returning adults showed multiple deeper dives. There was no difference between speed on descent (mean = 0.11 m s^{-1}) and speed on ascent (mean = 0.11 m s^{-1}) (Wilcoxon signed-rank test, $p = 0.97$). Similar to post-spawners on out migration, returning adults were diving into slightly colder waters (mean reduction = 0.49 °C for the 14 days at sea preceding recapture/return for the fish tagged with Geo tags), but dives were short enough that there was a negligible change in body temperature on diving (mean reduction = 0.01 °C).

Stomach contents of returning adults

Of 909 captured Atlantic salmon, 58% ($N = 530$) had empty stomachs, and only 5% ($N = 50$) had stomachs > 90% full (Fig. 7A). Most stomachs that contained prey only had one or two prey items (50% and 21% of stomachs with prey, respectively), but one stomach contained 17 items. Models of the probability of an Atlantic salmon having prey in its stomach fitted to body length had lower AIC values (AIC = 1075.7–1080.6) than those fitted to body mass (AIC = 1089.2–1095.5). The model with body length and day of year as predictors had the lowest AIC value (Supplementary table 2). The probability of an Atlantic salmon stomach containing prey decreased with increasing salmon body length (Fig. 7B) ($p < 0.001$), ranging from ≈0.71 at a body length of 50 cm to ≈0.05 at a body length of 130 cm for individuals captured on day of year 192 (the median day of capture). The probability of the stomach containing prey also decreased with day of year, but the relationship was only marginally significant ($p = 0.021$).

Most prey items were at least partly digested (> 98%). The stomach contents of larger Atlantic salmon tended to be more digested than those of smaller Atlantic salmon (Fig. 7C). For example, ≈70% of prey items were highly or almost completely digested in Atlantic salmon with a body length of ≥ 80 cm, as opposed to ≈24% of prey items in Atlantic salmon < 80 cm in body length (Test of equal proportions, $p < 0.001$). Among the prey items, the two identifiable fish species were herring (*Clupea harengus*) (46% of prey items) and capelin (*Mallotus villosus*) (6% of prey items). The remaining prey items (48%) were too digested for fish species to be identifiable.

Discussion

The tagged adult Atlantic salmon migrated through surface waters and performed aperiodic dives, both on outward migration and return. Dives were generally shallow (≈10–40 m) and of short duration (2–3 min). This pattern is consistent with previous studies, both for post-spawners (Halttunen et al. 2009) and returning adults (Godfrey et al. 2015). However, diving behaviour changed over time, during both outward and return migration, and dives within the first day after entering the fjord and in the day before recapture/return (likely mainly within the fjord) were generally shallower than those further away from entry or recapture/return (likely further out to sea).

Post-spawners are energy-depleted fish (Jonsson et al. 1991; Halttunen et al. 2013) that likely need to start feeding soon after sea entry, but also appear to be motivated to migrate rapidly through fjords (see Halttunen et al. 2009). Atlantic salmon are opportunistic feeders that may feed on a large variety of food
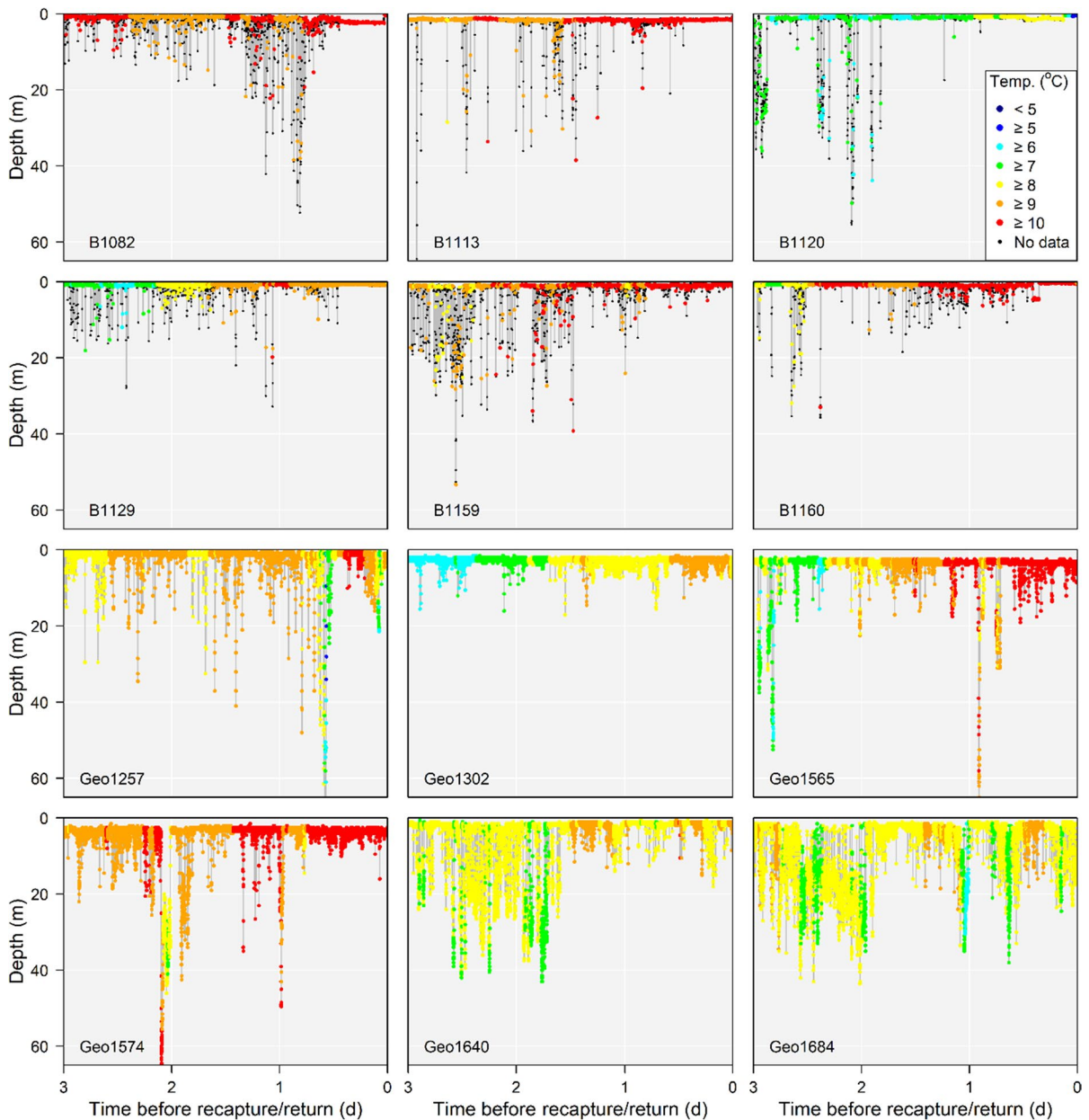
Fig. 6 Depths and internal temperatures of returning adults tagged with high-resolution tags in the last 3 days before recapture/return to river. Note, the fish with tag number B1093, which did not dive in this period, has been omitted. Depths shown have a cut-off at 65 m, and exclude parts of some dives by the fish with tag number B1113, Geo1257, Geo1565, and Geo1574

items (Rikardsen and Dempson 2011), and adults may feed both close to the surface and in deeper water. In general, sea productivity is greater near the surface where primary production is concentrated; therefore, the likelihood of encountering food during

migration without actively foraging may be greater near the surface than in deeper waters. The short-dive times observed within the fjord in the current study were not consistent with the longer-lasting 'U' shaped dives that have been hypothesized to indicate foraging

Fig. 7 Stomach contents of Atlantic salmon captured in Alta fjord: **A** Stomach volume occupied by food (%) (N = 909); **B** probability of stomach containing one or more prey items as a function of Atlantic salmon body length, as modelled by a generalized linear model (model 7, Supplementary table 2); **C** digestion rating of stomach prey items (N = 810) as a function of Atlantic salmon body length. In **B**, the curve shown is for median date of capture (day of year = 192)
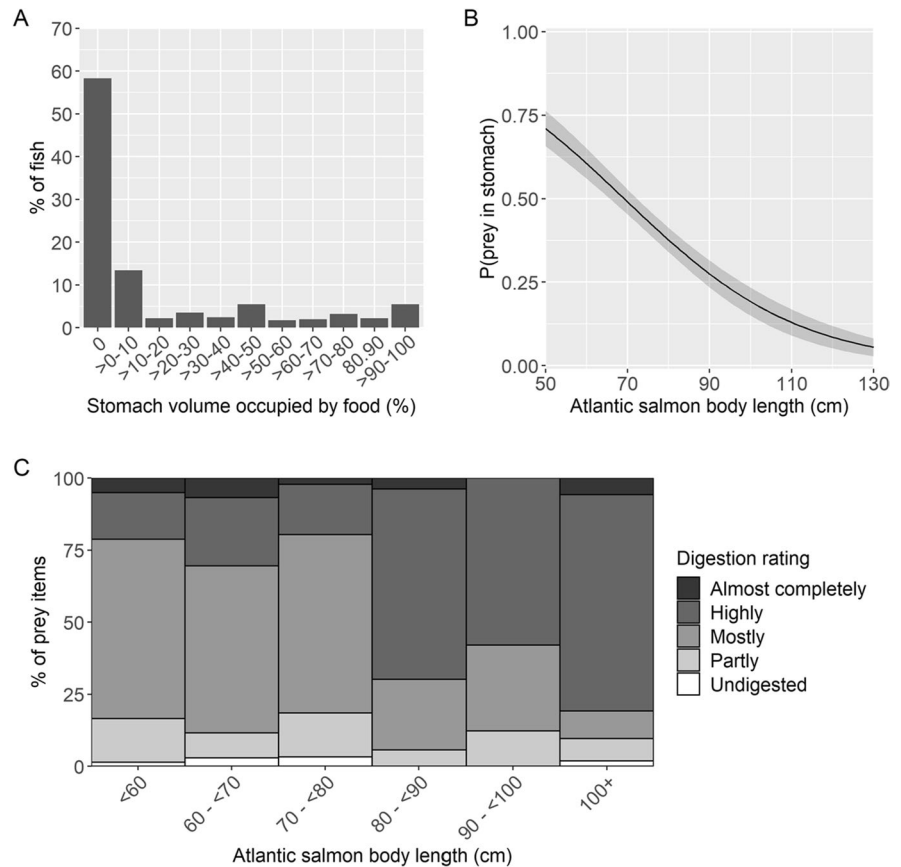
by fish at sea (Wilson and Block 2010; Hedger et al. 2017). Hence, swimming mostly near the surface, as recorded in this study, may be a beneficial strategy for rapid migration while increasing the likelihood of finding the occasional prey without expending time and energy foraging within the water column.

The stomach contents of adult Atlantic salmon captured in the fjord indicated little feeding during the last phase of the return migration, which would concur with a lack of foraging through diving within the fjord. Nearly two-thirds of fish had empty stomachs. The stomach evacuation rate in Atlantic salmon is in the order of 1–3 days. Storebakken et al. (1999) reported an 88% evacuation within 24 h for small salmon individuals (body mass = 0.15–0.30 kg) at a temperature of 9 °C. A near 100% evacuation within 3 days has been reported for smolts at temperatures of 6–18 °C (Handeland et al. 2008) and adults at temperatures of 4–5 °C (Waagbo et al. 2017). Available temperature data from the fjord, measured daily at a fish farm at a depth of 3 m in June–August 2008

and 2009, were comparable with these temperatures: median = 9.8 °C (range = 5.5–13.6 °C) (note, data from 2010 were unavailable). Therefore, similar stomach evacuation rates can be expected for the captured Atlantic salmon in the current study. Given this, it can be inferred that nearly two-thirds of captured individuals did not feed within a period of several days before recapture.

The likelihood of an Atlantic salmon individual having prey in its stomach decreased with body size and the digestion level of prey items increased with its body size, suggesting that larger individuals may have stopped feeding earlier during the return migration than smaller individuals. The fact that the size of individuals captured in the fjord later in the year (July–September) was smaller than those captured earlier (May–June) suggests that larger individuals were swimming through the fjord to return to the river earlier in the year. Early return to rivers may be beneficial, because the ocean may be a more dangerous place to stay than rivers due to predators (Strøm et al.

2019). At the same time, early return implies a longer period without food intake since adult Atlantic salmon largely stop feeding when they enter rivers. It might be that large individuals already have sufficient energy reserves for spawning and survival by early-spring, whereas smaller individuals have more to gain by continued feeding at sea: smaller individuals have lower energy reserves and higher maintenance requirements per unit mass, so have greater need to gain mass for survival and reproduction on return to freshwater.

For the Atlantic salmon that did have food remains in their stomachs, identified prey types were exclusively fish species (mainly herring) rather than other potential prey types (e.g. crustaceans, squids, amphipods). The absence of any other prey types implies that they were not major recent sources of prey. Atlantic salmon feed opportunistically at sea but become more specialized as they return (MacKenzie et al. 2012) and Atlantic salmon may select fish over other prey types (Jacobsen and Hansen 2000; Rikardsen and Dempson 2011). Identified prey species in the current study were herring and capelin (89% and 11% of identified prey items, respectively). Herring has been commonly observed as a food source for Atlantic salmon in the NE Atlantic, in Icelandic waters (Sturlaugsson 2000), in the Norwegian Sea off Northern Norway (Grønvik and Klemetsen 1987; Aykanat et al. 2020) and in the Northern Baltic (Salminen et al. 2001), but capelin has also been observed as a prey type for Atlantic salmon (Hansen and Pethon 1985; Aykanat et al. 2020). Herring is more commonly found in the Norwegian Sea (Vogel et al. 2021), while the larger capelin commonly feeds in the more northern Barents Sea, except during spawning on the Norwegian continental shelf in March–April. Capelin die soon after spawning, so their importance as prey for Atlantic salmon diminishes throughout summer (Rasmussen 2012). Predation on mainly herring by returning Atlantic salmon was consistent with the salmon feeding on them when migrating through surface or near-surface waters, or during their longer-lasting dives on the outer coast towards the periphery of the Norwegian Sea. The absence of benthic species such as crustaceans or sand eels, *Ammodytes marinus*, which Atlantic salmon are known to feed on, coupled with the fact that maximum recorded depths were generally shallow (≈10–40 m), suggests that they were not diving to the seabed (depths typically ≈ 100–400 m within the fjord) for foraging.

Alternative reasons for diving may be energy conservation, thermoregulation or navigation. It is possible for fish to conserve energy by gently gliding during descents before rapid active swimming on ascents to the surface (Kawabe et al. 2004; Gleiss et al. 2011). However, the Atlantic salmon of the current study showed a wide range of diving patterns, and average vertical speeds of descent were similar to those of ascent, so there was no strong evidence to suggest that this was occurring, either on out migration or return. Thermoregulation has been suggested as an influence on diving (Reddin et al. 2004). However, this is also not likely to be a primary cause of diving in the current study because depth-dependent variation in temperature was too small for this to provide a thermoregulatory advantage, evident from the fact that changes in internal body temperature during dives were negligible. Diving for the purpose of navigation is possible, involving individuals exploring different layers within the water column to find cues for navigating out of the fjord and back to the natal river. Atlantic salmon return to their natal river with a high precision, and seemingly use cues sequentially learned during outward migration to orient through near-coastal and fjord areas to locate the natal river (Hansen et al. 1993). The Atlantic salmon did not dive to depths consistent with them interacting with the fjord bottom. However, we speculate that diving may be associated with exploring water layers. This may be particularly important for the type of fjord considered, which is influenced by wind-induced surface currents that may affect longitudinal gradients in surface water properties, and which becomes stratified in summer such that there is a warmer, lower salinity 5–10 m surface layer overlying cooler and more saline waters (Skarðhamar et al. 2018).

Conclusion

Adult Atlantic salmon migrating through a fjord showed a wide range of individual behaviours, both on out migration as post-spawners and on return to the natal river. The diving behaviour of post-spawners was characterized by frequent, shallow dives on entering the fjord, which changed to deeper dives further out in coastal waters. That of returning adults was characterized by shorter and shallower dives as they approached the fjord and river. Most adults

captured in the fjord and nearby coast by bag net fishers had not fed in the days immediately before recapture, suggesting that feeding in the fjord and nearby coastal waters was rare. Those which had fed preyed exclusively on epipelagic fish species (mainly herring, and some capelin). Given the general lack of feeding, and lack of evidence of feeding on demersal species, it can be inferred that the short, frequent diving is not strong evidence of feeding within fjords. Based on the lack of alternative explanations for diving, it can be hypothesized that the diving recorded during entry into the fjord from the river, and during return from sea, may be mainly for the purpose of finding navigation cues within a vertically stratified fjord that is characterized by complex horizontal circulation patterns.

Availability of data and material Data are available on request.

Code availability R code is available on request.

Declarations

Ethics approval All handling and tagging was conducted according to the Norwegian regulations on treatment and welfare of animals (Directive 2010/63/EU of the European Parliament).

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no or competing interests.

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