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Nutritional correlates of spatio-temporal variations in the marine habitat use of brown trout, *Salmo trutta*, veteran migrants

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Abstract

The brown trout (*Salmo trutta*) is an iteroparous, anadromous salmonid that exhibits a complex continuum of feeding migration tactics, ranging from freshwater residency, to potamodromy, to estuarine migration, as well as short-to-long distance coastal migrations. While anadromous migrants are believed to play an important role in the species' population dynamics, little is known about the factors driving differences in the extent of individual marine habitat use. In this study, 32 brown trout veteran migrants were acoustically tagged prior to their seaward migration and sampled for indices of their nutritional state. Our findings suggest that: i. body condition factor differed amongst fish adopting different migratory tactics, with outer-fjord migrant being in poorer condition; and ii. within migratory groups, plasma triglyceride concentration was negatively correlated with the duration of marine residency. Results support the idea of condition-dependent migration in veteran migrants, with individual variation in nutritional state influencing the spatio-temporal aspects of marine habitat use. Furthermore, overall marine minimum survival during the summer feeding migration was 86%, the highest reported estimate for this life-stage.

Keywords: alternative migratory tactics, marine migrations, marine survival, plasma triglycerides, sea trout

36 Introduction

37 From an evolutionary point of view, migration can be regarded as an individual
38 adaptation to the changing requirements of life-histories and resource availabilities (Dingle
39 2006). As an individually expressed trait, migration can also be viewed as a syndrome, shaped
40 by natural selection, wherein correlated behavioural, physiological, morphological and other
41 traits combine to maximize fitness within particular life-history contexts (Dingle 2006, e.g.;
42 Peiman et al. 2017). As such, partial migration has been described in a variety of taxa, in which
43 variable proportions of a population are either migratory or non-migratory (Chapman et al.
44 2011). While differences in migratory strategies can have both environmental and genetic links,
45 the degree to which these contribute to an expressed migratory strategy can vary widely
46 (Pulido 2011). In anadromous brown trout (*Salmo trutta*) for example, little genetic variation
47 seems to exist among migrant and resident individuals living sympatrically (Hindar et al. 1991).
48 According to the conditional strategy concept, different tactics regulated by the same genotype
49 can be maintained within populations. This can occur when the migratory decisions and fitness
50 gained from alternative tactics depend primarily on individual phenotype, e.g., age, size, sex,
51 energetic state, etc. (Repka and Gross 1995).

52 The brown trout is a facultative anadromous, iteroparous salmonid species native to the
53 cold waters of Eurasia and North Africa. The species is socially and economically important, and
54 because of its high adaptability and phenotypic plasticity, it has been successfully introduced to
55 every continent except Antarctica (MacCrimmon and Marshall 1968). Within a population, the
56 species shows complex variation in its feeding migratory tactics, a continuum ranging from
57 freshwater residency, to potamodromy, and estuarine migration (Cucherousset et al. 2005;

Boel et al. 2014), as well as beyond, to short- and long-distance coastal migration (del Villar-Guerra et al. 2013; Eldøy et al. 2015; Flaten et al. 2016). This migratory continuum has been observed in both first-time migrants (i.e., parr and smolts; del Villar-Guerra et al. 2013; Boel et al. 2014; Flaten et al. 2016), as well as veteran migrants (i.e., either mature or immature individuals that have previously completed a first summer feeding migration; Eldøy et al. 2015). While the drivers of the different migratory tactics remain obscure, especially for the marine migrations of veteran migrants (Drenner et al. 2012; Thorstad et al. 2016), previous studies of first-time migrants suggest that the choice of migratory tactic is a plastic response to individual physiological state, metabolic rate, and food availability (Wysujack et al. 2009). In experimental feeding studies, brown trout exposed to low food availability had lower pre-migratory body condition factors, which has been shown to influence the decision of first-time migrants to adopt anadromy, whereas higher-condition fish tended towards non-anadromy (Davidsen et al. 2014; Olsson et al. 2006; Wysujack et al. 2008). Wysujack et al. (2008) similarly concluded that energetic state (i.e., body lipid content) close to the time of actual migration was likely responsible for the choice of migratory tactic. A recent telemetry study of the marine migrations of brown trout veteran migrants concluded that migratory decisions were likely influenced by body condition (Eldøy et al. 2015). However, the link between individual pre-migratory nutritional state and the spatio-temporal extent of subsequent marine habitat use by brown trout has not been well-defined (Aldvén and Davidsen 2017).

Following marine feeding migrations, mostly occurring in summer, anadromous brown trout usually return to freshwater to spawn and/or over-winter. During the winter, feeding opportunities in freshwater can be sparse, and so brown trout depend on somatic lipid stores

for survival, especially in post-spawned individuals (summarized in Jonsson and Jonsson 2011). Lipids stored in adipose and muscle tissues are catabolized and released into circulation as triglycerides. Triglycerides are delivered to target tissues, where hydrolysis (lipolysis) produces glycerol and free fatty acids, the major source of metabolic energy production in fish (Sargent et al. 2002). During starvation, plasma triglyceride concentration diminishes in an effort to sustain basal metabolic processes (Kakizawa et al. 1995). As such, plasma triglyceride concentration can be used as an indicator of nutritional status in many taxa including wild brown trout (Boel et al. 2014; Gauthey et al. 2015), and is therefore a good candidate parameter for testing hypotheses about condition-dependent models of migratory behaviour in wild animals. However, virtually nothing is known about how natural variation in pre-migratory levels of plasma triglycerides might affect the migratory decisions of brown trout veteran migrants.

By providing enhanced growth opportunities, the marine environment is believed to support higher abundances and more productive brown trout populations (Thorstad et al. 2016). Marine foraging, especially in areas where nutrient rich feeding opportunities are numerous (e.g., pelagic fish species, Davidsen et al. 2017), allows anadromous individuals to attain larger sizes than their freshwater resident counterparts, which for females translates to a higher fecundity-at-age (Jonsson and Jonsson 1993). Coupled with the higher prevalence of anadromy in females (as increased size represents a more direct fitness gain for females), it is likely that anadromous brown trout make important contributions to the species' population dynamics (Thorstad et al. 2016), although this has yet to be fully investigated. With the recent increase in marine mortality and decreased growth of anadromous brown trout due to

anthropogenic impacts on marine habitats (Thorstad et al. 2015), researchers have speculated that a reduction in the benefits of anadromy might favour selection for freshwater residency (Hendry et al. 2004; Thorstad et al. 2016). Better knowledge about the whereabouts of brown trout veteran migrants at sea and the endogenous factors affecting the extent of the marine migrations (e.g., distance and duration) will contribute to a fuller understanding of the drivers of marine habitat use of this important life-history stage. Such information is currently lacking but needed for improving current management and conservation actions.

To address these knowledge gaps, we combined acoustic telemetry and physiological sampling techniques within a fjord system in Northern Norway to quantify variation in migratory tactics and in the extent of marine habitat use of brown trout veteran migrants (e.g., duration of marine residency, distance travelled), as well as the influence of pre-migratory nutritional state (i.e., body condition factor, plasma triglyceride concentration). Utilizing this approach, we addressed the over-arching hypothesis that nutritional state underlies inter-individual differences in migratory behaviour. We tested the following predictions: i. individuals in poorer nutritional state (i.e., low body condition factor, low plasma triglyceride concentration) have a stronger tendency towards marine migration, and this tendency would be emphasized in females; ii. within marine migrants, fish in poorer nutritional state migrate further out; iii. fish in poorer nutritional state require more time in the marine environment to recondition; and iv. marine survival (i.e., to completion of the summer feeding migration) is lower for fish migrating to the outer reaches of the fjord.

Materials and methods

Study area and acoustic receiver array

The study was conducted in the inter-connected, marine, Tosenfjord and Bindalsfjord (65.13°N, 12.13°E) in Nordland country, Norway (Fig. 1). Brown trout were captured from two different watercourses (i.e., freshwater systems): Åbjøra and Urvold. Both watercourses, situated ~14 km apart, drain into the Tosenfjord (~97 km², maximum depth of ~550 m) which then leads to the Bindalsfjord (~91 km², maximum depth of ~700 m) and finally to the Atlantic Ocean, located at ~33 km from Åbjøra and Urvold estuaries (defined as the interface between river mouth and fjord). During the study period, from April 8 – September 5, 2015 the surface salinity level (~1 m depth) of the Åbjøra estuary (i.e., Floet, station 69 in Fig. 1) and the outer-fjord (station 1) varied respectively from 0.0 – 28.6 ppt (mean = 9.4 ppt) and 4.8 – 33.5 ppt (mean = 20.0 ppt). Surface water temperature (~1 m depth) for those two sections of the fjord varied from 3.0 – 17.6 °C and 4.5 – 17.0 °C, respectively. The eastern section of Tosenfjord is similar to other inner-fjord areas in terms of depth, temperature, and surface salinity level that varies between ~0 – 34 ppt depending on areas, freshwater inputs, and tidal cycles.

In Åbjøra, the tagging site was located 2.7 km upstream of the river mouth (around station 65, Fig. 1). This area is situated in the tidal zone of the river with a surface salinity level that varied from 7.4 – 22.3 ppt (mean = 10.1 ppt) and water temperature from 2.7 – 16.7 °C during the study period, depending on tidal cycle and freshwater discharge. Spawning in the Åbjøra watercourse occurs in River Åbjøra and its tributaries (> 2 km upstream of the tagging area), while the lower part of the system includes deep pools and slow currents, and is consequently considered suitable overwintering habitat. In Urvold, the tagging site was situated in a freshwater lake, near the outlet (around station 61, Fig. 1). Lake Urvold has a surface area of ~0.6 km² and is ~80 m deep, which provides good overwintering habitat for brown trout. The

lake then drains into the fjord through a 0.2 km riverine stretch. Unlike Åbjøra, the transition from freshwater to the fjord is much more direct in Urvold due to the steepness of the short river section. In this watercourse, the main spawning site is located upstream of the lake.

Capture, blood sampling and tagging

A total of 32 brown trout veteran migrants were captured, sampled (i.e., for blood, measurements and scales), and tagged with an internal acoustic transmitter between April 9 - 12, 2015 prior to their seaward feeding migration; 20 individuals from the tidal zone in river Åbjøra and 12 from lake Urvold (Table 1). At capture, veteran migrants were distinguished from smolts and parr based on size, which was later confirmed by scale readings. Fish were captured using a combination of angling (n=26) and gill netting (n=6; 35-42 mm mesh size), and efforts were made to reduce stress and the risk of injury by minimizing fight times and monitoring the gill net continuously (e.g., the net was pulled-in as soon as vibrations were felt). The average time-to-blood-sampling, as calculated from the first encounter with fishing gear, was similar for both methods; $7:51 \pm 5:15$ min for angling and $10:32 \pm 5:20$ min for gill netting (p-value = 0.29; Welch Two Sample t-test). Shortly after landing and prior to anaesthesia, ~2 ml blood samples were collected via caudal venipuncture from all fish (as described in Huston 1990). Samples were then placed in an ice-water slurry until processing. Following blood sampling, fish were kept for no more than 2 hours in a net cage situated in the river to allow recovery from capture and sampling before the tagging procedure. Prior to tagging, brown trout were anesthetized using 2-phenoxyethanol at a concentration of 0.5 ml L^{-1} water (SIGMA Chemical Co., USA). Depending on fish size, 69 kHz MP-9 (for fish between 310-390 mm in total length) or 69 kHz MP-13 acoustic transmitter (for fish between 400 to 720 mm in total length) were inserted in

the abdominal cavity (nominal delay of 30 – 90 seconds, Thelma Biotel AS, Norway), according to standard operating procedures (as described in Cooke et al. 2011). MP-9 tags (5.2 g in air; estimated battery life of ~15 months) were 1.0 - 1.8% of fish total body mass, and MP-13 (11.8 g in air; estimated battery life of ~24 months) were 0.4 - 2.3% of fish total body mass. Immediately after surgical transmitter implant, fish were weighed and measured (i.e., total length), ~5-10 scales were sampled and stored for later aging, and a small adipose fin clip was collected for genetic sexual determination. Following tagging, the brown trout were released back at their respective capture site, and subsequently detected on an acoustic receiver array composed of 54 VR2W-69 kHz receivers (Vemco Ltd., Canada) deployed throughout the lakes, rivers, and marine fjords (Fig. 1). The array was established prior to the start of tagging and was in place until fall 2017 (although we are focusing on 2015 detections in the current study). The experimental procedures followed national ethical requirements and were approved by the Norwegian National Animal Research Authority (permit number: 7277).

Blood processing and triglycerides assay

Within three hours of blood sampling, samples were centrifuged at 3300 g for 10 minutes and the resultant plasma was collected and flash-frozen in dry ice before being transferred to a -80 °C freezer. Plasma triglyceride levels were assayed in duplicate using a commercially available colorimetric kit (Cayman Chemical Company, USA) and read at 530 nm with a BioTek Synergy HTX microplate reader (BioTek Instruments, Inc., USA), according to the manufacturer's standard procedure. The mean coefficient of variation between duplicates was 3.9%.

DNA sex determination

DNA was extracted from ethanol preserved fin clips with the QuickExtract kit (Epigen), according to manufacturer's protocol with the exception for the extraction volume, which was reduced to 150 μ l. Sex was determined by PCR amplification of a 200 pb fragment situated in the first intron of the male specific SDY gene, using the Salmo-sdY-F and Salmo sdY-R primers (Quéméré et al. 2014). The PCR was performed in 10 μ l reactions using the Qiagen Multiplex PCR kit. The following PCR profile was used: 95°C for 15 min, 11 cycles of touchdown PCR, 94°C for 30 seconds, 63–52°C for 30 seconds, 72°C for 1 minute, followed by 25 cycles of 94°C for 30 seconds, 52°C for 30 seconds, 72°C for 1 minute, with a final extension at 72°C for 10 minutes. Sex was scored by running the PCR products on 1% Agarose gels. Sex could be determined with confidence for all but one fish, so this individual had to be excluded from final models including sex as an explanatory variable.

Data analysis

Individual migratory behaviours can be classified into distinct tactics. First, brown trout are either riverine/lacustrine resident or marine migrant. Then, marine migrants could be further divided into groups depending on where and how far they migrated. To test the overarching hypothesis that nutritional state underlies inter-individual differences in migratory behaviour, statistical tests were performed to assess how individuals' characteristics influenced the different spatial and temporal aspects of migration, as well as survival (specific predictions are presented in the sections below). All individuals' morphological (i.e., length, mass, body condition factor) and physiological (i.e., plasma triglyceride concentration) characteristics, as well as sex and population of origin were considered as explanatory variables. However, due to limited sample sizes, final statistical models were limited to the inclusion of a maximum of two

explanatory variables. Selection of the best model for each aspect of individuals' migratory behaviour was determined using a forward stepwise approach (based on AIC values and comparison with a null model; Anderson et al. 2001). Body condition factor (i.e., Fulton's K) was calculated from the formula: $K = 100 \times \text{Mass [g]} \times \text{Total length [cm]}^{-3}$, following the observation that the regression coefficient of the mass-length relationship was 2.99 for tagged individuals, thus confirming the assumption of isometric growth. For each statistical model, we first verified that underlying assumptions were met. Out of 32 acoustically tagged individuals, four were excluded from further analyses due to abnormal patterns of detections: one transmitter was continuously detected on a single station (no. 63 in Fig. 1) for about five months before disappearing, two transmitters were not detected anywhere in the array after April 22nd, and one transmitter seems to have experienced technical failure as soon after release not a single detection was registered.

Potential false detections were first flagged using the "falseDetectionFilter" function of the "glatos" package in R, requiring a minimum of two detections from a given transmitter in a time span of 30 minutes at given receiver. Then, flagged detections that were legitimate were kept (i.e., subsequent detections on other receivers located nearby) and others were deleted. To evaluate the detection efficiencies of various portions of the acoustic array, we examined 11 receiver gates, where spacing between receivers was 400 m and the distance from shore to the nearest receivers was 200 m. We calculated the percentage of events in which an individual was detected on a gate when crossing from one side to the other (as revealed from detections on other receivers). For example, in Fig. 1, if a fish was first detected on station 43 and then on station 16, we controlled if that fish was properly detected on the gate formed by stations 40,

41 and 42, as it had to cross that gate. Overall, out of a total of 203 gate-crossing events that occurred during the entire study period, individuals were detected on the gate 92% of the time. The detection efficiency (and location) of individual gates were as follow: 100% in Åbjøra estuary (stations 67 – 68, Fig. 1); 100% on Osane opening gate (stations 31 – 32); 91% on Terråk gate (stations 33 – 35); 100% on Sørfjord gate (stations 28 – 30); 100% on Bindalsfjord west gate (stations 11 – 13); 95% on Bindalsfjord east gate (stations 16 – 17); 86% on Tosenfjord outer gate (stations 40 – 42); 81% in Urvold estuary (stations 43 – 44); 100% on Tosenfjord central gate (stations 45 – 47); 100% on Tosenfjord east gate (stations 18 – 20); and 100% on Tosbotn gate (stations 26, 52, 53).

i. Riverine/lacustrine residency versus marine migration

In Åbjøra, the tidal zone of the river offers a brackish environment in which some individuals may decide to stay into to feed. While these fish are not true freshwater resident, they were regrouped as riverine “resident” to be distinguish from marine migrants that ventured into the fjord system. In Urvold, however, the transition from freshwater to the brackish waters of the fjord is much more direct and fish can either decide to reside within the freshwater lake or to move into the fjord, and were unlikely to reside in the short river section. For this reason, models were developed separately for each population. To test the prediction that individuals in poorer nutritional state (i.e., low body condition factor and depleted plasma triglyceride level) have a stronger tendency towards marine migration, binomial logistic regression models using the logit link were performed (“glm” function in R; two outcomes: staying in the river/lake, or migrating to the fjord/marine environment).

ii. Marine migratory tactics

Once individuals were detected entering the fjord, fish from both populations were faced with similar habitat choices. Based on migratory distances and the areas of the fjord that were utilized, three different marine migratory tactics were identified (Fig. 1); i. short-distance migration (furthest detection <2 km from the river mouth; Fig. 2a); ii. long-distance/inner-fjord migration (furthest detection from ~13 to 28 km of the river mouth, without any detection on the outer receiver line, Fig. 2b); and iii. long-distance/outer-fjord migration (furthest detection >21 km from the river mouth and detected on the outer receiver line; Fig. 2c). To test the prediction that, within marine migrants, fish in poorer nutritional state (i.e., low body condition factor and depleted plasma triglyceride level) migrate further out in the marine environment, multinomial logistic regression models were performed (“multinom” package in R), suitable for nominal categorical response variable with three outcomes, here: short-distance, long-distance/inner-fjord, or long-distance/outer-fjord migration (Kwak and Clayton-Matthews 2002; Zuur et al. 2007a). The p-values of the regression coefficients were computed using Wald z-tests. Furthermore, to facilitate the interpretation of the model’s coefficients, changes in the predicted probabilities of adopting a given migratory tactic as a function of explanatory variables were calculated for each tactic using the “predict” function in R (Kwak and Clayton-Matthews 2002).

iii. Marine residency period

The marine residency period could be calculated for a total 14 individuals (5 fish from Åbjøra and 9 from Urvold) that were detected entering the fjord in the spring and returning to the rivers later in the summer. For those fish, the marine residency period started at the time of first detection at a river mouth/estuarine receiver (stations 67-68 in Åbjøra, and 43-44 in

Urvold, Fig. 1) and ended at the time of last detection at a river mouth/estuarine receiver (conditional to later detection on upstream receiver, station 63 in Åbjøra, and 61 in Urvold). To test the prediction that fish with low body condition factor and depleted plasma triglyceride level would remain in the marine environment for longer periods of time, general linear regression models were performed (“lm” function in R).

iv. Marine survival

The marine minimum survival was estimated from the initial number of fish that were detected entering the fjord system and the proportion of them that came back to the rivers, completing their summer marine migration (as indicated by detection at a river mouth/estuarine receiver conditional to later detection on upstream receivers). In addition to those fish, marine migrants that were detected returning to Åbjøra or Urvold estuary (stations 67-69 in Åbjøra, and 43-44 in Urvold, Fig. 1) in late summer and fall were also deemed to have survived their marine summer feeding migration, despite not re-entering freshwater systems. These fish were assumed to be over-wintering in estuaries, as they were detected there through the fall and early winter. Marine migrants that presumably died or disappeared from the acoustic array through the summer might be the result of tag lost, technical failure of the tag, exhaustion of tag battery life, residency in uncovered areas, or animal mortality. To test the prediction that survival to completion of the summer feeding migration is lower for long-distance/outer-fjord migrants in comparison with other marine migratory tactics, binomial logistic regression models using the logit link were performed (“glm” function in R).

Results

299 i. Riverine/lacustrine residency versus marine migration

300 Out of the 20 brown trout tagged in Åbjøra, four individuals had to be removed from the
301 analysis as their migratory decision could not be identified with confidence (as described
302 previously). From those remaining (n=16), 7 individuals (44%) opted to reside in the tidal zone
303 in the river for the summer, moving in and out of Floet but never entering the fjord (Table 1). In
304 contrast, 9 individuals (56%) moved out of the river between April 10th and May 29th (median of
305 May 2nd) migrating into the fjord. The prediction that individuals in poorer nutritional state (i.e.,
306 low body condition factor and depleted plasma triglyceride level) would have a stronger
307 tendency towards marine migration was not supported by our results, as the null model had a
308 lower AIC value than alternative models. In addition, no statistically significant morphological
309 differences (i.e., length and mass) were found between riverine resident and marine migrants
310 (p-values > 0.31; Welch Two Sample t-tests). However, as expected, females tended to migrate
311 into the fjord in higher proportion than males, as 8 out of 11 females (73%) left the river
312 compared to only 1 out of 5 males (20%) (p = 0.070 for sex; binomial logistic regression),
313 although marginally non-significant - which, considering the effect size, is likely due to small
314 sample size. In contrast to Åbjøra, all 12 brown trout tagged in freshwater, near the outlet of
315 Lake Urvold, migrated into the fjord to feed in the marine environment irrespective of sex,
316 morphology and physiology. Those individuals migrated into the fjord between April 25th and
317 May 15th (median of May 10th). As all fish from this population migrated, we could not test the
318 hypothesis that individuals in poorer nutritional state would have a stronger tendency towards
319 anadromy.

320 ii. Marine migratory tactics

For marine migrants (pooled sample of 9 fish from Åbjøra and 12 from Urvold), 3 individuals (14%; 2 females and 1 male) were classified as short-distance migrants, 7 individuals (33%; 2 females and 5 males) were classified as long-distance/inner-fjord migrants, and 11 individuals (52%; 6 females, 4 males, one unknown sex) were classified as long-distance/outer-fjord migrants (as summarized in Table 1). In assessing which factors might influence marine migratory decisions, the best fitting multinomial logistic model included body condition factor and sex as explanatory variables (Table 2). The other explanatory variables considered, i.e., population, plasma triglycerides, length and mass, were not retained in the model during the stepwise process. Because population of origin was not retained as an influential explanatory variable, and in combination with the observation that a mix of fish from both populations were present in all three migratory tactics (Table 1), we pooled fish from both populations in a single model. In support of our second prediction, for long-distance migrants, the probability of outer-fjord migration decreased significantly with increasing body condition factor (-20.7 in the log odds of migrating to the outer-fjord following a one unit increase in body condition, $p = 0.027$, Table 2). Thus, fish migrating to the outer part of the fjord were generally in the poorest condition prior to migration. Comparing sexes, for long-distance migrants, the log odds of migrating to the outer section of the fjord versus staying in the inner part increased by 3.15 for females, in which 75% (6/8) migrated to the outer section versus 44% (4/9) in males (although marginally non-significant at $p = 0.058$, Table 2). To facilitate interpretation, the predicted probabilities of adopting a given marine migratory tactic as a function of body condition factor and sex were calculated using the regression coefficients (Fig. 3). Body condition factor and sex mostly affected the probabilities of adopting the long-distance/outer-fjord versus long-distance/inner-fjord tactic, with no significant influence on the decision to undertake a short-

distance marine migration (Table 2). However, we interpret the latter result with caution due to the low number of short-distance marine migrants. Moreover, following the observation that no significant morphological and physiological differences (i.e., in length, mass, body condition factor, and plasma triglyceride level) existed between long-distance/inner-fjord and short-distance migrants (p -values > 0.68 ; Welch Two Sample t -tests), the two tactics were pooled to take a closer look at what might be driving the decision to migrate to the outer section of the fjord (reducing the tests to only two marine migratory outcomes: outer-fjord versus inner-fjord migrants). In this analysis, female outer-fjord migrants had significantly lower body condition factor prior to migration compared to inner-fjord migrants (0.79 ± 0.05 vs 0.92 ± 0.05 , $p = 0.006$, Welch Two Sample t -test, Fig. 4). A similar, but non-significant difference in body condition was observed in males. Pooling both sexes, outer-fjord migrants had significantly lower body condition (0.75 ± 0.09) than inner-fjord migrants (0.87 ± 0.10 , $p = 0.005$, non-parametric Mann–Whitney U test). While male outer-fjord migrants were significantly smaller than inner-fjord migrants (433 ± 59 mm versus 576 ± 100 mm, $p = 0.022$, Welch Two Sample t -test), females showed the opposite tendency with outer-fjord migrants being generally larger (range: 400–640 mm) than inner-fjord migrants (range: 310–445 mm, although the difference in mean length was not significant, Fig. 4). Supporting the assumption that plasma triglyceride concentration is informative of individuals' post-winter/pre-migratory nutritional state, body condition factor and plasma triglycerides were correlated at $r = 0.45$ ($p = 0.009$). Interestingly, females displayed a negative correlation between length and pre-migratory body condition factor ($r = -0.57$, $p = 0.02$), and similarly between length and plasma triglyceride concentration ($r = -0.48$, $p = 0.06$), so that larger females were generally found in poorer pre-migratory

condition. This negative relationship between body condition factor and length was not observed in males.

iii. Marine residency period

Of the individuals that were detected entering the fjord in the spring ($N = 21$), a total of 14 individuals (5 from Åbjøra and 9 from Urvold) came back to the river/lake later in the spring or during the summer (May 23rd to July 16th; median of July 4th). Individuals' marine residency period varied between 32 and 83 days (average of 59 days). Looking at the factors that might explain inter-individual variance in the marine residency period, the best fitting linear regression model included plasma triglyceride concentration and marine migratory tactic (Table 3; multiple $R^2 = 0.60$). All other potential explanatory variables (population of origin, body condition factor, length, mass, and simple interactions) were not retained in the model during the stepwise process. This, combined with the fact that no significant differences existed in the marine residency period between fish from the two study populations ($p > 0.20$; Welch Two Sample t-test), allowed us to pool fish from the two populations. Out of the 14 individuals that came back to freshwater, 7 were long-distance/outer-fjord migrants, 6 were long-distance/inner-fjord migrants, and only one was a short-distance migrant. In order to meet the assumptions of general linear regression models (i.e., independence, normality of residuals, homoscedasticity, and balanced influence of individual observations), the short-distance migratory tactic ($N = 1$) had to be removed from the final model as it had high leverage (hat value 3.5-fold greater than the average, "hatvalue" function in R) which led to a deviation from normality (Zuur et al. 2007b). In support of our third prediction, within migratory groups, the duration of marine residency was negatively correlated with pre-migration plasma triglyceride

concentration (Table 3), such that depleted individuals generally spent more time in the marine environment (~24 more days for a decrease of 1 mmol L^{-1} in triglyceride level). In addition, long-distance/inner-fjord migrants spent on average 69.2 ± 11 days in the marine environment, ~15 days more than long-distance/outer-fjord migrants (54.6 ± 16 days), a significant difference controlling for the effect of plasma triglyceride level (Table 3; Fig. 5). The only short-distance migrant for which marine residency could be calculated spent only 35 days there (Table 1).

iv. Marine survival

Out of a total of 21 veteran migrants that were detected entering the fjord in the spring, seven were not detected coming back to freshwater. Of those, four individuals (i.e., three females and one male) were presumed to have survived but opted for over-wintering in the marine environment as they were detected in estuaries in the fall and winter (summarized in Table 1), apparently deciding to skip spawning. Those three females were generally smaller (range: 310-420 mm) than the five females that had migrated back to freshwater (range: 405-640 mm), and were possibly still immature (Klemetsen et al. 2003). For the remaining three individuals that neither returned to freshwater nor over-wintered in estuaries, two disappeared from the array (as they were last detected in late May/early June in the outer section of the fjord, and were never heard from again despite the array remaining in place until fall 2017) and one was continuously detected on a single receiver for >6 months starting in mid-June. Minimum marine survival through the summer feeding migration was thus estimated at 86%, as at least 18 out of 21 individuals that migrated out into the fjord survived to return to freshwater, or were detected in estuaries in the fall and winter. In partial support of our fourth prediction, all three fish that presumably died or disappeared at in the marine environment

were long-distance migrants, with significantly lower body condition factor (0.75 ± 0.02) than the average marine migrant (0.82 ± 0.12 , $p = 0.048$; Welch Two Sample t-test), implying a 73% minimum survival for this marine migratory tactic ($N = 11$) versus 100% survival for the other two tactics ($N = 10$). However, no morphological or physiological individual characteristics, nor sex, population or marine migratory tactics statistically influenced the probability of marine survival, as the null model had lower AIC value than alternative binomial models.

Discussion

Our findings support the over-arching hypothesis that pre-migratory nutritional state, as indicated by body condition factor and plasma triglyceride concentration, is correlated with spatio-temporal variations in the marine habitat use of brown trout veteran migrants. They also bring some support to the general belief that females are more inclined to migrate to the marine environment.

We found that, after a winter in freshwater, female trout from the Åbjøra watershed showed a higher tendency than males to leave the river and migrate into the fjord in spring. This higher tendency of females towards anadromy is commonly observed in facultative anadromous salmonid populations, and is believed to be driven by the strong relationship between body size and fecundity, with the productivity of the marine environment sustaining faster growth (reviewed in Jonsson and Jonsson 1993). Previous work on the migratory behaviour of brown trout post-smolts suggest a condition-dependent migration, with low body condition factor generally promoting anadromy (Davidsen et al. 2014; Olsson et al. 2006; Wysujack et al. 2008), but not always (del Villar-Guerra et al. 2013; Boel et al. 2014). Despite our first prediction that poorer nutritional state would promote marine migration, no

432 significant differences in body condition factor and plasma triglyceride concentration were
433 observed between riverine/lacustrine residents and marine migrants.

434 However, among brown trout that initiated marine migrations, body condition factor
435 differed between migratory tactics. As predicted, brown trout in the poorest relative body
436 condition were those most likely to migrate to the outer section of the fjord, where nutrient
437 rich foraging opportunities are presumably more abundant (e.g., increased dependence upon
438 pelagic fishes, Davidsen et al. 2017), and a greater proportion of female (77%), than male long-
439 distance migrants (44%), opted for this tactic then the alternative inner-fjord tactic. While fish
440 of various sizes migrated to the outer reaches of the fjord, female long-distance/outer-fjord
441 migrants were generally larger than female inner-fjord migrants. Interestingly, females
442 displayed negative correlations between length and pre-migratory body condition factor as well
443 as triglyceride concentration, so that larger females were generally found in poorer pre-
444 migratory condition and were more likely to migrate to the outer-fjord. This negative
445 relationship between body condition factor and length was not observed in males. By
446 comparing immature brown trout, with first-time and repeat-spawners of both sexes, Berg et
447 al. (1998) showed that lipid and protein depletion through the spawning season increased with
448 size in female, but not male. Accordingly, while the energy content of immature individuals
449 increased, the specific energy content of spawning females decreased with length due to
450 increased reproductive investments (Berg et al. 1998). While it was shown that anadromous
451 female brown trout invest more into reproduction than resident counterparts (Elliott 1988;
452 Jonsson and Jonsson 1997), which affects post-spawning nutritional state, our findings suggest
453 that the costs of reproduction might influence future migratory decision by affecting the extent

of individual marine habitat use the following year. Larger, depleted females might be migrating further to sea in an attempt to recondition themselves more effectively and offset the costs of reproduction. However, while the variation in weight and plasma metabolites through spawning is reflective of energy investment to reproduction (Gauthey et al. 2015), post-spawning nutritional state alone, as measured in the current study, is not necessarily directly representative of reproductive investment. As such, the link between reproductive investment, post-spawning condition, and subsequent migratory decision is an area requiring further investigation.

In contrast to those initiating outer-fjord migrations, brown trout remaining within the inner-fjord tended to be in better overall condition. Interestingly, these inner-fjord migrants spent significantly more time in the marine environment than outer-fjord migrants (Table 3; Fig. 5). Anadromous trout (brown trout and Arctic charr), both first-time and veteran migrants, generally experience a rapid initial growth phase in the marine environment, which is probably a result of energetic reconditioning after winter-depletion in freshwater (e.g., compensatory growth; Berg and Berg 1987, 1989; Rikardsen et al. 2004). Fish then migrate back to safer freshwater habitats once marine growth potential diminishes later in the season in Northern Norway (Berg and Berg 1987, 1989; Rikardsen et al. 2004). If migration to the outer-fjord was expressly for the purpose of energetic reconditioning for those incurring the greatest costs of reproduction, then it might seem counter-intuitive that they should spend less time there foraging compared to trout in the inner-fjord. This might, however, simply indicate that trout in the outer-fjord need less time to recondition because they are in an area where energy-rich pelagic fish prey are presumably more abundant (see also Eldøy et al. 2015; Davidsen et al.

2017), although there could also be risks associated with migration to the outer-fjord that might limit their time there, such as predation (Lyse et al. 1998) and sea lice parasitism (Thorstad et al. 2015). Within migratory groups that travelled to similar areas of the fjords, marine residency time was negatively correlated with plasma triglyceride levels so that fish with depleted circulating lipid levels spent more time in the marine environment, perhaps reflecting higher nutritional requirements (Table 3; Fig. 5). The duration of the marine residency period is thus probably influenced by individual lipid depletion (or nutritional requirements), and by the relative productivity of the marine habitat to which the fish migrate. As revealed from the significant positive correlation with body condition, plasma triglyceride concentration is believed to reflect post-winter, pre-migratory nutritional condition in these fish that were captured in early spring. Collectively, our findings suggest a condition-dependent migratory tactic in brown trout veteran migrants, in which an individual's pre-migratory nutritional state influences its spatio-temporal use of the marine environment.

In the current study, the survival of marine migrants was estimated at 86% (18 of 21). This is slightly higher than previously reported marine survival estimates of 29-85%, for this life-stage (Jensen 1968; Jonsson and Jonsson 2009; Jensen et al. 2014; only including post-spawners in Aarestrup et al. 2015). Interestingly, mortality only occurred among those fish that migrated to the outer fjord. Although sample sizes are small, this might reflect the idea that long-distance migration to more pelagic habitats might be a riskier tactic undertaken by fish in poorer pre-migratory nutritional condition. This tendency for fish in poorer post-spawning/pre-migratory nutritional condition to opt for a riskier migratory tactic has also been observed in Atlantic salmon, in the form of differential migratory timing. Halttunen et al. (2013) showed that salmon

from the Alta River with lower body condition factors following spawning initiated their seaward migration earlier, and likely encountered unfavorable environmental condition at sea.

Anadromous migrants, and especially females, are believed to play an important role in brown trout population dynamics due to their increased growth potential at in the marine environment and higher reproductive investments (Thorstad et al. 2016). However, large inter-individual variation exists in the spatial and temporal extent of the marine habitat use of anadromous migrants. Our results showed that the pre-migratory nutritional state of veteran migrants differed among marine migratory tactics and was associated with the duration of marine residency period. Future research efforts investigating the benefits and costs of different marine migratory tactics in veteran migrants (in terms of survival, growth and fecundity) would contribute to a better understanding of the evolution of the brown trout migratory continuum. Assessing how much intra-individual variability exists in the migratory decisions of individuals tracked through multiple consecutive marine feeding migrations, as it relate to differences in environmental conditions, would also provide novel and highly useful information in the face of rapidly changing environmental conditions.

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523 **References**

- 524 Aarestrup, K., Baktoft, H., Thorstad, E.B., Svendsen, J.C., Höjesjö, J., and Koed, A. 2015. Survival
525 and progression rates of anadromous brown trout kelts *Salmo trutta* during downstream
526 migration in freshwater and at sea. *Mar. Ecol. Prog. Ser.* **535**(July): 185–195.
527 doi:10.3354/meps11407.
- 528 Aldvén, D., and Davidsen, J.G. 2017. Marine migrations of sea trout (*Salmo trutta*). *In* Sea
529 Trout: Science & Management: Proceedings of the 2nd International Sea Trout
530 Symposium. *Edited by* G. Harris. Troubador Publishing Ltd. pp. 288–297.
- 531 Anderson, D.R., Link, W. a, Johnson, D.H., Burnham, K.P., and Press, A. 2001. Suggestions for
532 presenting the results of data analyses. *J. Wildl. Manage.* **65**(3): 373–378.
533 doi:10.2307/3803088.
- 534 Berg, O.K., and Berg, M. 1987. The seasonal pattern of growth of the sea trout (*Salmo trutta* L.)
535 from the Vardnes river in northern Norway. *Aquaculture* **62**(2): 143–152.
536 doi:10.1016/0044-8486(87)90318-8.
- 537 Berg, O.K., and Berg, M. 1989. Sea Growth and Time of Migration of Anadromous Arctic Char (*Salvelinus alpinus*)
538 from the Vardnes River, in Northern Norway. *Can. J. Fish. Aquat. Sci.*
539 **46**(6): 955–960. doi:10.1139/f89-123.
- 540 Berg, O.K., Thronæs, E., and Bremset, G. 1998. Energetics and survival of virgin and repeat
541 spawning brown trout (*Salmo trutta*). *Can. J. Fish. Aquat. Sci.* **55**(1): 47–53.

- doi:10.1139/cjfas-55-1-47.
- Boel, M., Aarestrup, K., Baktoft, H., Larsen, T., Søndergaard Madsen, S., Malte, H., Skov, C., Svendsen, J.C., and Koed, A. 2014. The physiological basis of the migration continuum in brown trout (*Salmo trutta*). *Physiol. Biochem. Zool.* **87**(2): 334–45. doi:10.1086/674869.
- Chapman, B.B., Brönmark, C., Nilsson, J.Å., and Hansson, L.A. 2011. The ecology and evolution of partial migration. *Oikos* **120**(12): 1764–1775. doi:10.1111/j.1600-0706.2011.20131.x.
- Cooke, S.J., Murchie, S., Mc Connachie, S., and Goldberg, T. 2011. Standardized surgical procedures for the implantation of electronic tags in key Great Lakes fishes. Technical Report. Great Lakes Fishery Commission, Ann Arbor, MI.
- Cucherousset, J., Ombredane, D., Charles, K., Marchand, F., and Bagliniere, J.L. 2005. A Continuum of Life History Tactics in a Brown Trout *Salmo Trutta* Population. *Can. J. Aquat. Sci.* **1610**: 1600–1610. doi:10.1139/f05-057.
- Davidson, J.G., Daverdin, M., Sjørnsen, A.D., Rønning, L., Arnekleiv, J. V., and Koksvik, J.I. 2014. Does reduced feeding prior to release improve the marine migration of hatchery brown trout *Salmo trutta* smolts? *J. Fish Biol.* **85**(6): 1992–2002. doi:10.1111/jfb.12485.
- Davidson, J.G., Knudsen, R., Power, M., Sjørnsen, A.D., Rønning, L., Hårsaker, K., Næsje, T.F., and Arnekleiv, J. V. 2017. Trophic niche similarity among sea trout *Salmo trutta* in central Norway investigated using different time-integrated trophic tracers. **26**: 217–227.
- Dingle, H. 2006. Animal migration: Is there a common migratory syndrome? *J. Ornithol.* **147**(2): 212–220. doi:10.1007/s10336-005-0052-2.
- Drenner, S.M., Clark, T.D., Whitney, C.K., Martins, E.G., Cooke, S.J., and Hinch, S.G. 2012. A Synthesis of Tagging Studies Examining the Behaviour and Survival of Anadromous Salmonids in Marine Environments. **7**(3): 1–13. doi:10.1371/journal.pone.0031311.

- 565 Eldøy, S.H., Davidsen, J.G., Thorstad, E.B., Whoriskey, F., Aarestrup, K., Næsje, T.F., Rønning, L.,
566 Sjursen, A.D., Rikardsen, A.H., Arnekleiv, J.V., and Jonsson, B. 2015. Marine migration and
567 habitat use of anadromous brown trout (*Salmo trutta*). Can. J. Fish. Aquat. Sci. **72**(9):
568 1366–1378. doi:10.1139/cjfas-2014-0560.
- 569 Elliott, J.M. 1988. Growth, size, biomass and production in contrasting populations of trout
570 *Salmo trutta* in two Lake District streams. J. Anim. Ecol. **57**(1): 49–60. doi:10.2307/4762.
- 571 Flaten, A.C., Davidsen, J.G., Thorstad, E.B., Whoriskey, F., Rønning, L., Sjursen, A.D., Rikardsen,
572 A.H., and Arnekleiv, J. V. 2016. The first months at sea: marine migration and habitat use
573 of sea trout *Salmo trutta* post-smolts. J. Fish Biol. **89**(3): 1624–1640.
574 doi:10.1111/jfb.13065.
- 575 Gauthey, Z., Freychet, M., Manicki, A., Herman, A., Lepais, O., Panserat, S., Elosgi, A., Tentelier,
576 C., and Labonne, J. 2015. The concentration of plasma metabolites varies throughout
577 reproduction and affects offspring number in wild brown trout (*Salmo trutta*). Comp.
578 Biochem. Physiol. Part A **184**: 90–96. doi:10.1016/j.cbpa.2015.01.025.
- 579 Halttunen, E., Lovisa, J., Jensen, A., Næsje, T.F., Davidsen, J.G., Thorstad, E.B., Chittenden, C.M.,
580 Hamel, S., Primicerio, R., and Rikardsen, A.H. 2013. State-dependent migratory timing of
581 postspawned Atlantic salmon. Can. J. Aquat. Sci. **1071**(9037): 1063–1071.
- 582 Hendry, A.P., Bohlin, T., Jonsson, B., and Berg, O.K. 2004. To sea or not to sea? *In* Evolution
583 illuminated: Salmon and their relatives. Edited by A.P. Hendry and S.C. Stearns. Oxford
584 University Press. Oxford, UK. pp. 92–125.
- 585 Hindar, K., Jonsson, B., Ryman, N., and Ståhl, G. 1991. Genetic relationships among landlocked,
586 resident, and anadromous Brown Trout, *Salmo trutta* L. Heredity (Edinb). **66**(1): 83–91.
587 doi:10.1038/hdy.1991.11.

- 588 Huston, A.H. 1990. Blood and circulation. *In* Methods for Fish Biology. *Edited by* C.B. Schreck
589 and P.B. Moyle. American Fisheries Society. pp. 273–343.
- 590 Jensen, J.L.A., Rikardsen, A.H., Thorstad, E.B., Suhr, A.H., Davidsen, J.G., and Primicerio, R. 2014.
591 Water temperatures influence the marine area use of *Salvelinus alpinus* and *Salmo trutta*.
592 J. Fish Biol. **84**(6): 1640–1653. doi:10.1111/jfb.12366.
- 593 Jensen, K.W. 1968. Seatrout (*Salmo trutta* L.) of the River Istra, western Norway. Rep. Inst.
594 Freshw. Res. (48): 1187–1213.
- 595 Jonsson, B., and Jonsson, N. 1993. Partial migration: niche shift versus sexual maturation in
596 fishes. Rev. Fish Biol. Fish. **3**(4): 348–365. doi:10.1007/BF00043384.
- 597 Jonsson, B., and Jonsson, N. 2009. Migratory timing, marine survival and growth of anadromous
598 brown trout *Salmo trutta* in the River Imsa, Norway. J. Fish Biol. **74**(3): 621–638.
599 doi:10.1111/j.1095-8649.2008.02152.x.
- 600 Jonsson, B., and Jonsson, N. 2011. Maturation and spawning. *In* Ecology of Atlantic Salmon and
601 Brown Trout. Springer. pp. 327–414. doi:10.1007/978-94-007-1189-1.
- 602 Jonsson, N., and Jonsson, B. 1997. Energy allocation in polymorphic Brown Trout. Funct. Ecol.
603 **11**(3): 310–317. doi:10.1046/j.1365-2435.1997.00083.x.
- 604 Kakizawa, S., Kaneko, T., Hasegawa, S., and Hirano, T. 1995. Effects of feeding, fasting,
605 background adaptation, acute stress, and exhaustive exercise on the plasma somatolactin
606 concentrations in rainbow trout. doi:10.1006/gcen.1995.1054.
- 607 Klemetsen, a, P-a, A., Jb, D., Jonsson, B., Jonsson, N., O'Connell, M., and Mortensen, E. 2003.
608 Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus*
609 *alpinus* (L.): a review of aspects of their life histories. Ecol. Freshw. Fish **12**: 1–59.
- 610 Kwak, C., and Clayton-Matthews, A. 2002. Multinomial Logistic Regression. Nurs. Res. **51**(6):

- 611 404–410. doi:10.1097/00006199-200211000-00009.
- 612 Lyse, A.A., Stefansson, S.O., and Fernö, A. 1998. Behaviour and diet of sea trout post-smolts in a
613 Norwegian fjord system. *J. Fish Biol.* **52**(923): 923–936. doi:10.1006/jfbi.1998.0641.
- 614 MacCrimmon, H.R., and Marshall, T.L. 1968. World distribution of brown trout *Salmo trutta*. *J.*
615 *Fish. Res. Board Canada* **25**(12): 2527–2548.
- 616 Olsson, I.C., Greenberg, L.A., Bergman, E., and Wysujack, K. 2006. Environmentally induced
617 migration: The importance of food. *Ecol. Lett.* **9**(6): 645–651. doi:10.1111/j.1461-
618 0248.2006.00909.x.
- 619 Peiman, K.S., Birnie-Gauvin, K., Larsen, M.H., Colborne, S.F., Gilmour, K.M., Aarestrup, K.,
620 Willmore, W.G., and Cooke, S.J. 2017. Morphological, physiological and dietary covariation
621 in migratory and resident adult brown trout (*Salmo trutta*). *Zoology*.
622 doi:10.1016/j.zool.2017.07.002.
- 623 Pulido, F. 2011. Evolutionary genetics of partial migration - the threshold model of migration
624 revis(it)ed. *Oikos* **120**(12): 1776–1783. doi:10.1111/j.1600-0706.2011.19844.x.
- 625 Quéméré, E., Perrier, C., Besnard, A.-L., Evanno, G., Baglinière, J.-L., Guiguen, Y., and Launey, S.
626 2014. An improved PCR-based method for faster sex determination in brown trout (*Salmo*
627 *trutta*) and Atlantic salmon (*Salmo salar*). *Conserv. Genet. Resour.* **6**(4): 825–827.
628 doi:10.1007/s12686-014-0259-8.
- 629 Repka, J., and Gross, M.R. 1995. The evolutionarily stable strategy under individual condition
630 and tactic frequency. *J. Theor. Biol.* **176**(1): 27–31. doi:10.1006/jtbi.1995.0172.
- 631 Rikardsen, A.H., Thorpe, J.E., and Dempson, J.P. 2004. Modeling the life history variation of
632 Arctic charr. *Ecol. Freshw. Fish* **13**: 305–311. doi:10.1111/j.1600-0633.2004.00070.x.
- 633 Sargent, J., Tocher, D., and Bell, J. 2002. The lipids. *In* *Fish nutrition. Edited by* R.W. Halver, J.E.,

- 634 Hardy. Academic Press. pp. 181–257.
- 635 Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kålås,
636 S., Berg, M., and Finstad, B. 2015. Effects of salmon lice *Lepeophtheirus salmonis* on wild
637 sea trout *salmo trutta* - A literature review. *Aquac. Environ. Interact.* **7**(2): 91–113.
638 doi:10.3354/aei00142.
- 639 Thorstad, E.B., Todd, C.D., Uglem, I., Bjørn, P.A., Gargan, P.G., Vollset, K.W., Halttunen, E., Kålås,
640 S., Berg, M., and Finstad, B. 2016. Marine life of the sea trout. *Mar. Biol.* **163**(3): 47.
641 Springer Berlin Heidelberg. doi:10.1007/s00227-016-2820-3.
- 642 del Villar-Guerra, D., Aarestrup, K., Skov, C., and Koed, A. 2013. Marine migrations in
643 anadromous brown trout (*Salmo trutta*). Fjord residency as a possible alternative in the
644 continuum of migration to the open sea. *Ecol. Freshw. Fish*: 594–603.
645 doi:10.1111/eff.12110.
- 646 Wysujack, K., Greenberg, L.A., Bergman, E., and Olsson, I.C. 2009. The role of the environment
647 in partial migration: Food availability affects the adoption of a migratory tactic in brown
648 trout *Salmo trutta*. *Ecol. Freshw. Fish* **18**(1): 52–59. doi:10.1111/j.1600-0633.2008.00322.x.
- 649 Zuur, A.F., Ieno, E.N., and Smith, G.M. 2007a. Univariate tree models. *In* *Analysing Ecological*
650 *Data*. Springer. pp. 143–162. doi:10.1016/B978-0-12-387667-6.00013-0.
- 651 Zuur, A.F., Ieno, E.N., and Smith, G.M. 2007b. Linear regression. *In* *Analysing Ecological Data*.
652 Springer. pp. 49–78. doi:10.1016/B978-0-12-387667-6.00013-0.
- 653

654 **Tables**

655 Table 1. Summary of the migratory behaviour of tagged fish (N = 32). The Information is filtered
656 by migratory tactic: riverine/lacustrine residents (N = 7), short-distance migrants (N = 3), long-
657 distance/inner-fjord migrants (N = 7), long-distance/outer-fjord migrants (N = 11), and 4 NA's.

Tag_ID	Pop.	TL	Sex	Marine	Migratory	Marine res.	Marine	Over-
		(mm)		migration	tactic	(days)	survival	winter
A69-1303-13	Åbjøra	540	M	0	Resident	0	NA	NA
A69-1303-01	Åbjøra	390	F	0	Resident	0	NA	NA
A69-1303-14	Åbjøra	430	M	0	Resident	0	NA	NA
A69-1303-15	Åbjøra	430	F	0	Resident	0	NA	NA
A69-1303-16	Åbjøra	485	M	0	Resident	0	NA	NA
A69-1303-33	Åbjøra	490	M	0	Resident	0	NA	NA
A69-1303-35	Åbjøra	530	F	0	Resident	0	NA	NA
A69-1303-23	Åbjøra	420	F	1	Short mig.	NA	1	Estuary
A69-1303-19	Åbjøra	405	F	1	Short mig.	35	1	River/lake
A69-1303-29	Urvold	590	M	1	Short mig.	NA	1	Estuary
A69-1303-11	Åbjøra	445	F	1	Long/in mig.	83	1	River/lake
A69-1303-02	Åbjøra	310	F	1	Long/in mig.	NA	1	Estuary
A69-1303-31	Urvold	500	M	1	Long/in mig.	54	1	River/lake
A69-1303-30	Urvold	720	M	1	Long/in mig.	66	1	River/lake
A69-1303-28	Urvold	628	M	1	Long/in mig.	80	1	River/lake
A69-1303-27	Urvold	430	M	1	Long/in mig.	64	1	River/lake
A69-1303-25	Urvold	590	M	1	Long/in mig.	68	1	River/lake

32

A69-1303-17	Åbjøra	430	F	1	Long/out mig.	32	1	River/lake
A69-1303-20	Åbjøra	490	M	1	Long/out mig.	43	1	River/lake
A69-1303-21	Åbjøra	600	F	1	Long/out mig.	58	1	River/lake
A69-1303-22	Åbjøra	420	F	1	Long/out mig.	NA	0	Dead at sea
A69-1303-34	Åbjøra	400	F	1	Long/out mig.	NA	1	Estuary
A69-1303-05	Urvold	350	M	1	Long/out mig.	81	1	River/lake
A69-1303-32	Urvold	640	F	1	Long/out mig.	54	1	River/lake
A69-1303-22498	Urvold	480	F	1	Long/out mig.	NA	0	Dead at sea
A69-1303-22497	Urvold	560	NA	1	Long/out mig.	NA	0	Dead at sea
A69-1303-26	Urvold	450	M	1	Long/out mig.	50	1	River/lake
A69-1303-24	Urvold	440	M	1	Long/out mig.	64	1	River/lake
A69-1303-12	Åbjøra	490	F	NA	NA	NA	NA	NA
A69-1303-03	Åbjøra	310	F	NA	NA	NA	NA	NA
A69-1303-04	Åbjøra	320	M	NA	NA	NA	NA	NA
A69-1303-18	Åbjøra	430	F	NA	NA	NA	NA	NA

Table 2. Output of the best fitting multinomial logistic regression model of the log odds of adopting a given marine migratory tactic versus an alternative tactic (3 outcomes; short-distance, long-distance/inner-fjord, and long-distance/outer-fjord migrants) as a function of body condition factor (*K*) and sex.

Migratory tactics comparison		Coefficient	SE	p-value
Long/Out vs Long/In				
	<i>K</i>	-20.7	9.4	0.027
	Sex (F)	3.2	1.7	0.058
Long/Out vs Short				
	<i>K</i>	-15.6	9.7	0.108
	Sex (F)	1.3	1.8	0.460
Long/In vs Short				
	<i>K</i>	5.0	9.5	0.592
	Sex (F)	-1.8	1.6	0.247

Table 3. Output of the best fitting general linear regression model of individuals' marine residency period (in days) as a function of plasma triglyceride concentration and marine migratory tactics, 2 outcomes: long-distance/inner-fjord, and long-distance/outer-fjord migrants (baseline outcome).

Explanatory variable	Coefficient	SE	t-statistic	p-value
Intercept	67.5	5.9	11.5	4.5×10^{-7}
Migratory tactic				
Long-dist./in	15.3	5.8	2.6	0.025
Triglycerides (mmol L ⁻¹)	-23.7	8.0	-3.0	0.015

Multiple R² = 0.60

Figures

Fig. 1. Map of the acoustic array deployed (N = 54 receivers). Receivers deployed in freshwater are represented by squares and those deployed in brackish or saltwater are represented by pentagons. The different coloured areas of the fjords represent the different marine migratory strategies: short-distance in pale grey (two areas; for Åbjøra and Urvold fish), long-distance/inner-fjord in dark grey, and long-distance/outer-fjord in black. Temperature and salinity loggers (T/S) were deployed on stations 1, 65 and 69. The tagging site was located around station 65 in Åbjøra, and in the lake around station 61 in Urvold. Map data: Norge Digitalt – Statens kartverk.

Fig. 2. Example of observed individuals' marine migratory tactics: a) short-distance migrant; b) long-distance/inner-fjord migrant; and c) long-distance/outer-fjord migrant. The dots represent the position of each acoustic receivers: white crossed dots for receivers on which the individual was not detected; and from yellow to red for receivers on which it was detected (the colour reflecting the number of detections that were registered for that individual on each receivers). Map data: Norge Digitalt – Statens kartverk.

Fig. 3. Predicted probabilities of adopting a given marine migratory tactics as a function of body condition factor and sex, as calculated from the regression coefficients (information presented in Table 2). The shaded areas represent the 95% confidence intervals.

Fig. 4. Comparisons of body condition factor, plasma triglyceride concentration, and total length in brown trout adopting an outer-fjord (long-distance) in black versus inner-fjord marine

709 migration tactic in grey (short and long-distance combined). The boxplots show median (black
710 lines) and mean values (white dots), as well as the interquartile ranges (boxes) and the 5th and
711 95th percentiles (whiskers). Comparisons were made using Welch Two Sample t-tests.

712 Fig. 5. Marine residency period as a function of pre-migration plasma triglyceride level and
713 marine migratory tactics: long-distance/outer-fjord migrants in black; and long-distance/inner-
714 fjord migrants in grey (regression coefficients and p-values can be found in Table 3). The hollow
715 symbol represents the only short-distance migrant for which marine residency period could be
716 calculated. However, this individual was excluded from the analysis for reasons described
717 previously.

Draft

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952x1143mm (72 x 72 DPI)

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