



The effects of nutritional state, sex and body size on the marine migration behaviour of sea trout

S. H. Eldøy^{1,*}, X. Bordeleau^{2,3}, M. J. Lawrence^{4,5}, E. B. Thorstad⁶, A. G. Finstad¹,
F. G. Whoriskey⁷, G. T. Crossin², S. J. Cooke⁴, K. Aarestrup⁸, L. Rønning¹,
A. D. Sjørusen¹, J. G. Davidsen¹

¹Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, 7491 Trondheim, Norway

²Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4R2, Canada

³Maurice Lamontagne Institute, Department of Fisheries and Oceans Canada, 850 Route de la mer, Mont-Joli, QC G5H 3Z4, Canada

⁴Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, ON, K1S 5B6, Canada

⁵Department of Biological Sciences, University of Manitoba, Sifton Road, Winnipeg, MB R3T 2N2, Canada

⁶Norwegian Institute for Nature Research, 7485 Trondheim, Norway

⁷Ocean Tracking Network, Dalhousie University, 1355 Oxford Street, Halifax, NS B3H 4J1, Canada

⁸National Institute of Aquatic Resources, Technical University of Denmark, 8600 Silkeborg, Denmark

ABSTRACT: The sea trout (anadromous brown trout *Salmo trutta*) displays extensive among-individual variation in marine migration behaviour. We studied the migration behaviour of 286 sea trout (27–89 cm) tagged with acoustic transmitters in the spring, in 7 populations located in 2 distinct marine fjord systems in Norway. We examined whether individual nutritional state, sex and body size influenced marine migration behaviour in terms of (1) the decision to migrate to the sea or remain resident in freshwater and/or estuarine habitats, (2) seasonal timing of sea entry, (3) duration of the marine residency and (4) migration distance at sea from the home river. Most sea trout were in a poor nutritional state in the spring prior to migration. Sea trout with low body condition factors and low plasma triglyceride levels were more likely to migrate to sea, and low triglyceride levels were also associated with earlier sea entry. Poor body condition also increased the probability of individuals remaining at sea longer and migrating further offshore compared to fish in better condition. Females were more likely to migrate to the sea than males. Larger fish were also more likely to migrate to the sea instead of remaining in freshwater and estuaries, and dispersed over greater distances from the river than smaller fish. In conclusion, this study documented general trends across multiple populations and showed that nutritional state, sex and body size influence important aspects of the marine migration behaviour of sea trout.

KEY WORDS: Salmonid · Kelt · Post-spawning · Iteroparity · Fish migration · Feeding migration · Physiology

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1. INTRODUCTION

Migration behaviour is observed in a wide range of taxa (Dingle 2014). There are various proximate explanations for why animals migrate, but the ultimate reason is the optimization of individual growth and

survival in order to increase lifetime fitness (Dingle & Drake 2007). Throughout their lifetimes, individuals must continually allocate energy to various life-history activities, while balancing the metabolic demands for somatic growth, maturation and reproduction (Zera & Harshman 2001). Diadromy, which

*Corresponding author: sindre.eldoy@ntnu.no

refers to migrations between marine and freshwater habitats, is thought to have evolved because of differences in food availability between these habitats (Gross et al. 1988). Among the fish family Salmonidae, all species spawn in freshwater, but many are anadromous, which means individuals migrate to sea at some point in their lives to exploit the richer marine food resources (Jonsson & Jonsson 1993). Salmonid populations often consist of both freshwater-resident and sea-migrating individuals (i.e. partial migration, Chapman et al. 2012). Body size is positively correlated with fecundity within salmonids (Elliott 1995). Marine migration is advantageous if the fitness benefits of larger body size outweigh the cost of migration, including increased risk of mortality, disease and failure to reach spawning grounds (Klemetsen et al. 2003, Thorstad et al. 2016).

The brown trout *Salmo trutta* is a highly adaptable salmonid species, which through natural dispersal or human transport is found in all continents except Antarctica (MacCrimmon et al. 1970). Wide variation in environmental conditions and food availability influences the physiology of individuals, and further determines whether they migrate to sea (anadromous brown trout, hereafter referred to as sea trout) or remain freshwater resident (Forseth et al. 1999, Wysujack et al. 2009, Archer et al. 2020). After leaving freshwater, sea trout display plasticity in migratory tactics, with some individuals using nearshore and estuarine habitats, while others use marine areas more than 500 km away from their natal watercourse (Thorstad et al. 2016, Birnie-Gauvin et al. 2019b). However, variation in migration patterns and life history strategies is not fully understood, thus limiting our understanding of ecological and evolutionary dynamics of sea trout populations (Birnie-Gauvin et al. 2019b, Ferguson et al. 2019). Understanding the drivers of marine migration behaviour is crucial for evaluating the susceptibility of sea trout to large-scale climate change, and to human-induced stressors that can vary both temporally and spatially in coastal zone ecosystems (Thorstad et al. 2015, Nevoux et al. 2019). In general, migration is regarded as a biological phenomenon that is particularly sensitive to environmental change and anthropogenic disturbance (Wilcove & Wikelski 2008) such that it is important to understand how different taxa respond to such challenges (Lennox et al. 2016).

Energy status is known to impact migratory strategies of individual trout (Cucherousset et al. 2005, Boel et al. 2014, Bordeleau et al. 2018). For mature sea trout, reproduction is energetically expensive (Lien 1978, Jonsson & Jonsson 2005) and so they

must recondition between spawning events. In watercourses suitable for overwintering, sea trout can remain in the spawning river system throughout the winter after autumn spawning (Berg & Berg 1989, Östergren & Rivinoja 2008), but feeding and growth are usually limited in these oligotrophic systems. Post-spawned individuals are therefore in a generally poor nutritional state prior to the seaward migration in the spring (Jonsson & Jonsson 1998, Jonsson & Jonsson 2011a). How individual variation in energy status relates to variation in marine migration behaviour of sea trout is not well understood. Body condition factor, which is based on the relationship between body length and mass (i.e. the relative stoutness of fish), is commonly used as an index of somatic energy status in salmonids and other fishes, but might not always be a precise predictor of energy status (Weatherley & Gill 1983, Simpson 1992, Næsje et al. 2006). In addition to body condition factor, nutritional correlates derived from blood plasma samples can be used to assess the nutritional state of fishes. For salmonids, low levels of plasma triglycerides, total protein and calcium levels can indicate a poor nutritional state (Congleton & Wagner 2006), which has previously been observed to promote marine migratory decisions in brown trout and Atlantic salmon (Boel et al. 2014, Bordeleau et al. 2018, 2020). Elevated levels of cortisol, possibly due to low food availability, have previously been found to promote earlier seaward migration (Birnie-Gauvin et al. 2019a). These previous studies suggest that sea trout in poor nutritional state will display more risk-taking behaviour than individuals in better nutritional state in order to compensate for their depleted energy stores.

In this study, we tested the hypothesis that poor nutritional state promotes adoption of a more high-risk ocean migratory behaviour in sea trout in terms of timing, duration and migration distance. We used both body condition factor and blood plasma metabolites as measures of individuals' nutritional state. Migration behaviour in sea trout has also been observed to be influenced by sex (Pemberton 1976, Knutsen et al. 2004, Jensen et al. 2019) and body size (Jensen et al. 2014, Jonsson & Jonsson 2014). Hence, sex determined by genetic analyses and body size were also included in the analyses. We included 286 individual sea trout from 7 populations in 2 fjord systems in northern Norway in this study to test the general hypotheses that poor nutritional state, females and large size would promote initiation and greater extent of the marine migration. Specifically, we examined whether nutritional state, sex and body size (length) influenced (1) the tendency to migrate to the

sea or remain resident in freshwater and/or estuarine habitats, (2) the timing of sea entry, (3) the duration of the marine residency and (4) the distance moved out to sea from the river where the fish were tagged.

2. MATERIALS AND METHODS

2.1. Study site

This study was conducted in 2 Norwegian fjord systems in Nordland County, Skjerstadjorden (67° N) and Tosenfjorden (65° N) (Fig. 1), as part of 2 larger tracking studies, enabling sampling from 7 river systems. In Tosenfjorden, fish were captured and tagged in the period 4 May 2016 to 14 May 2017 in the Rivers Åbjøra and Urvold (Fig. 1). In Skjerstadjorden, fish were captured and tagged from 28 April 2016 to 15 June 2017 in the Rivers Saltdalselva, Botnvassdraget, Lakselva, Laksåga and Kosmovatnet (Fig. 1). Estuaries were defined as the transition zone between the freshwater and marine environment, where the water masses are expected to be brackish throughout the year. For all rivers, this included receivers that were deployed less than 600 m from the river mouth, except for River Saltdalselva, where receivers deployed up to 1 km from the river mouth were categorized as estuarine habitats.

In the Tosenfjorden study area, River Åbjøra has a 24 km stretch accessible for anadromous fish, and includes a large estuarine area influenced by the tide (about 1.6 km² of tidally affected surface area including shoreline areas inundated at high tide and the lower sections of the river including an estuarine pool), and Lake Åbjørvatnet (surface area of 4.8 km², 81 m above sea level). River Åbjøra is regulated for hydropower production and has a minimum discharge of 7 m³ s⁻¹. River Urvold has an average water discharge of 5 m³ s⁻¹, is not developed for hydropower production, and consists of a 200 m steep river stretch from the sea to Lake Urvoldvatnet (surface area of 0.6 km², 8.6 m above sea level). In the inner end of Lake Urvoldvatnet, River Urvold has a stretch of about 1 km accessible for anadromous fish. The estuary of River Urvold is small (about 0.002 km² of tidally influenced area inside the littoral zone) because the steep river drains straight into the open fjord.

In the Skjerstadjorden study area, River Saltdalselva is a large river with an average discharge of 55 m³ s⁻¹ and a 66 km stretch accessible for anadromous fish. Due to its large size, and relatively slow-

running areas in its lower part, River Saltdalselva has a comparatively large estuary (about 0.47 km² tidally influenced area inside the littoral zone). There is only 1 lake accessible for anadromous fish in River Saltdalselva, Lake Vassbotnvatn, which is located in a tributary. River Botnvassdraget has a 500 m steep river stretch to Lake Botnvatnet (12 m above sea level), and continues upstream of the lake, making a stretch of about 8 km accessible for anadromous fish. The confined estuary of River Botnvassdraget covers about 0.002 km² of tidally influenced area. River Lakselva has a stretch of about 7 km with no lakes accessible to anadromous fish, and has a tidally influenced surface area of about 0.08 km² in its estuarine area. River Laksåga has a stretch of about 6.5 km accessible for anadromous fish and drains into 2 large brackish-water lakes influenced by the sea (about 15 km² surface area). River Laksåga is regulated for hydropower purposes. River Kosmovatnet has a stretch of about 6 km accessible to anadromous fish, and drains into a brackish-water lake of about 8 km², separated from the sea by a 1 km narrow channel where the tide governs the direction of the current.

2.2. Capture and tagging of fish

A total of 286 sea trout, divided into 10 groups based on location and year (Table 1), were captured and tagged with individually coded acoustic transmitters (Thelma Biotel AS; 9 and 13 mm, expected battery life 10 to 24 mo, tag size depended on body size) during 2016 to 2018. Fish from River Åbjøra, River Kosmovatnet and River Laksåga were caught in the estuarine parts of the river systems. Fish from River Urvold were caught in Lake Urvold (freshwater), except for 13 individuals during spring 2017 (Table 1) that were caught in the river mouth. All fish caught in River Saltdalselva were caught in the river. The fish were captured by angling or by gillnets in the rivers, lakes and/or estuarine areas. Gill nets were continuously monitored and quickly tended when a fish was detected to minimize the time fish were entangled in the nets. The fish were released using scissors to cut the netting to prevent damage to the skin and gills. A non-lethal blood sample was drawn shortly after capture (maximum 5 ml blood per kg body mass, Lawrence et al. 2020). The fish were held in keep nets for up to 4 h before a transmitter was implanted.

Prior to tagging, each sea trout was anaesthetized for 4 min using 0.5 ml l⁻¹ 2-phenoxyethanol (EC No. 204-589-7, Sigma-Aldrich). For most fish, tags were

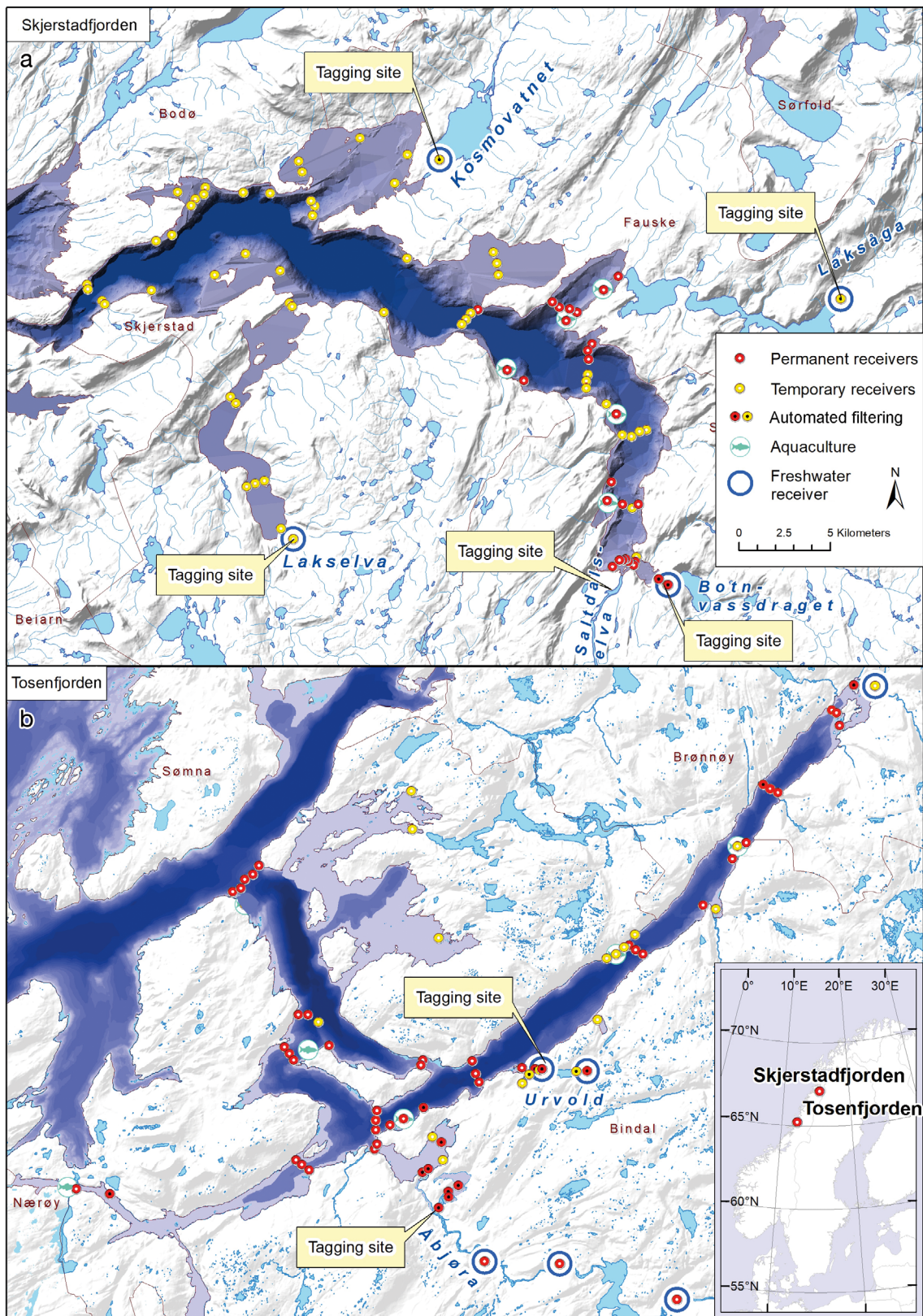


Fig. 1. Study areas in the 2 fjords, (a) Skjerstadvfjorden and (b) Tosenfjorden. Automated filtering: receivers where automatic data filtering was applied to remove false detections. Light blue indicates watercourses. Purple to deep blue indicates the depth of estuarine and marine habitats

Table 1. Description of fjord, watercourse, tracking year, number of individuals, date of tagging, and the mean \pm SD (range) sea trout body size and body mass. Dates given as dd/mm/yy

Site	Watercourse	Tracking year	Tagging date	n	Body size (mm)	Body mass (g)
Tosenfjorden	Åbjøra	2016	21/05/2016–26/05/2016	23	405 \pm 62 (290–520)	705 \pm 269 (240–1280)
Tosenfjorden	Åbjøra	2017	27/03/2017–29/03/2017	37	451 \pm 58 (350–560)	847 \pm 318 (400–1540)
Tosenfjorden	Urvold	2016	04/05/2016–10/06/2016	24	415 \pm 81 (270–620)	639 \pm 401 (160–1940)
Tosenfjorden	Urvold	2017	19/04/2017–14/05/2017	46	463 \pm 98 (330–730)	949 \pm 816 (290–4550)
Skjerstadjorden	Botnvassdraget	2016	01/05/2016–20/05/2016	21	574 \pm 164 (300–850)	2068 \pm 1812 (200–5800)
Skjerstadjorden	Kosmovatnet	2017	11/05/2017–15/06/2017	19	379 \pm 71 (275–470)	531 \pm 284 (180–990)
Skjerstadjorden	Laksåga	2017	30/05/2017–31/05/2017	34	384 \pm 78 (290–630)	538 \pm 447 (180–2590)
Skjerstadjorden	Lakselva	2017	02/05/2017–09/05/2017	13	442 \pm 53 (360–520)	902 \pm 377 (410–1580)
Skjerstadjorden	Saltdalselva	2016	28/04/2016–30/04/2016	40	520 \pm 157 (360–860)	1574 \pm 1611 (350–5600)
Skjerstadjorden	Saltdalselva	2018	01/05/2018–10/05/2018	29	637 \pm 113 (450–890)	2459 \pm 1626 (830–8400)

inserted through a 1.5 to 3 cm incision in the body cavity (Cooke et al. 2011, Eldøy et al. 2015). For the fish tagged in River Åbjøra in 2017 (Table 1), the transmitters were externally attached using a wire through the dorsum about 1 cm below the dorsal fin, with a silicone plate between the tag and the fish and a plastic plate on the opposite side of the dorsum to prevent erosion of skin and flesh. The sea trout were subsequently placed in a holding tank until recovery from anaesthesia and released into a slow-flowing area as close to the capture location as possible. The experimental procedures were approved by the Norwegian National Animal Research Authority (permission numbers 2015/8518, 1614092 and 18/67706).

2.3. Fish tracking

The tagged sea trout were tracked using 74 acoustic receivers in Tosenfjorden and 82 acoustic receivers in Skjerstadjorden (Vemco models: VR2, VR2-W and VR2-AR). The fish in Tosenfjorden were tracked from May 2016 to December 2017, while the fish tagged in Skjerstadjorden were tracked from May 2017 to December 2018, although not all receivers were operative throughout these periods (Fig. 1).

Tracking data were filtered for false registrations generated by code collisions with simultaneously transmitting tags, or by noise in the environment (Pincock 2012). After empirically assessing the frequency of false detections (i.e. a receiver reported detection of an unused transmitter ID) recorded by each receiver, automated filtering was applied to 16 receivers in Tosenfjorden and 4 receivers in Skjerstadjorden (see Fig. 1 for filtered receiver locations). The filter required that a tagged sea trout had to

be registered at least 2 times by a receiver within a 10 min time period to be accepted as a true registration, and resulted in removal of 68 682 of 2 191 047 detections (3.1%) in Tosenfjorden and 2402 of 594 345 detections (0.4%) in Skjerstadjorden. The data were subsequently visually inspected by plotting a timeline of all recordings for each fish, and registrations that did not fit with the overall migration track of each fish were also removed (i.e. detections suggesting unrealistic migration speed and/or passing multiple receiver gates without detection).

2.4. Processing and analysing blood samples

Blood samples were stored in tubes and immediately placed in an ice-water bath for up to 3 h before being centrifuged at $1163 \times g$ for 10 min. Blood plasma was flash-frozen in a liquid nitrogen dry shipper and subsequently stored at -80°C until biochemical analyses could be carried out. Plasma triglyceride levels were assessed in duplicates using the manufacturer's suggested protocols with a commercially available colorimetric kit (Cayman Chemical Company). Total plasma protein levels were determined using a Bradford's assay (Bradford 1976, Kruger 2009) with commercial reagents (Bio-Rad Laboratories). Plasma Ca^{2+} concentrations were determined using flame spectrophotometry (Varian Spectra AA 220FS, Varian) for a single replicate. Due to the limited volume of blood that could be taken from each fish (see Lawrence et al. 2020), there was not enough blood for all individuals to run all biochemical assays. Therefore, 214 fish were tested for blood plasma triglycerides, 204 fish were tested for blood plasma protein and 185 fish for blood plasma calcium.

2.5. Determining the sex of individuals

DNA samples from adipose fin clips taken at the time of tagging and preserved in ethanol were used to genetically determine the sex of the sea trout. DNA was extracted using the QuickExtract kit (Epigen) using the manufacturer's protocol but with extraction volume reduced to 150 μ l. Using 10 μ l reactions of the Qiagen Multiplex PCR kit and Salmo-sdY-F and Samo sdYR primers, PCR amplification was applied to a 200 base pair fragment from the first intron of the male-specific SDY gene (Quéméré et al. 2014). PCR steps for denaturation, annealing and extension were: incubation at 95°C for 15 min, 11 cycles of touchdown PCR, held at 94°C for 30 s, 63 to 52°C for 30 s, then 72°C for 1 min followed by 25 cycles at 94°C for 30 s, 52°C for 30 s, 72°C for 1 min and a final extension at 72°C for 10 min. Sex was determined by running PCR products in 1 % agarose gels.

2.6. Migrating to the sea vs. remaining in freshwater and estuaries

The trout either remained resident in the habitat where they were captured and tagged (river, lake and estuarine habitats), or migrated to the fjord. Individual sea trout were considered sea migrants if they were recorded by any marine receiver except those categorized as estuarine of the river where they were tagged. Fish that we lost track of shortly after tagging, or which showed a 'permanent residency' at a particular receiver indicative of mortality or tag loss within the receiver's detection range were excluded from statistical analyses ($n = 7$).

2.7. Timing of sea entry and duration of the marine migration

The timing of sea entry was calculated for all individuals that were recorded leaving the freshwater and estuarine areas of the watercourse where they were tagged. It was recorded as the first detection of a tagged fish in the estuary for the Rivers Urvold, Saltdalselva and Botnvassdraget. In River Åbjøra, the timing of sea entry was defined as the time of the last recorded detection in the river's estuary, provided the fish was subsequently detected by a receiver in the fjord. For the fish tagged in Laksåga, the time of sea entry was defined as the time of first detection by a receiver in the fjord. The different definitions for timing of sea entry were due to logistical and hydro-

logic constraints that required different approaches to receiver deployment in the estuarine areas of the different watercourses. Fish tagged in Rivers Lakselva and Kosmovatnet were excluded from these analyses due to small sample sizes ($n \leq 2$).

Residence time at sea was calculated as the period between the time a fish entered the sea to its last detection in the sea prior to entering the river during the first year of tracking. In River Åbjøra, the sea journey was considered to have ended at the last detection at a receiver deployed in the river mouth, provided that detection was followed by subsequent detections within the watercourse. In some cases, sea trout transitioned between freshwater and marine habitats multiple times within a year. Time spent in the freshwater habitat between migrations to the sea was not included in the total marine migration time. Fish tagged in Lakselva and Kosmovatnet were excluded from the analyses of residence time at sea due to a low sample size ($n = 1$). At these sites, most tagged fish stayed in the river and estuary.

2.8. Maximum migration distance at sea

For marine migrants, the maximum migration distance at sea from the river mouth was calculated for the fish from the Rivers Åbjøra, Urvold, Saltdalselva, Botnvassdraget and Laksåga. Because receivers were only deployed in the inner part of Skjerstadjorden in 2016, the fish tagged in Skjerstadjorden in 2016 were excluded from the analyses of migration distance. The maximum migration distance for each fish was calculated as the distance from the receiver deployed closest to the mouth of the river in which the fish were tagged to the furthestmost receiver at sea where the fish was recorded. This was done by estimating the shortest migration route avoiding land, using the 'costDistance' function in the gdistance R package (van Etten 2018). Fish that were not detected after 20 July of the year of tagging (which was the date corresponding to the upper 95 % percentile for reaching maximum distance for fish observed returning to watercourses), that were not last observed returning to freshwater, or that were last observed at the outer arrays of receivers in the fjord were not included in the maximum migration distance analysis ($n = 21$).

2.9. Statistical analyses

To test for effects of nutritional state, sex and body size (natural length) on migratory behaviour, we

used a set of generalized mixed effect models. The behavioural traits that were used as response variables were either binomial (migrated or did not migrate) or continuous and normally distributed (timing, duration and distance of sea migration). Independent variables (fixed explanatory effects) were sex, body size and nutritional state (body condition and blood plasma triglycerides). Tagging years were nested within populations (watercourse) and used as random effects. We did not aim to investigate which of the nutritional state variables employed were the best proxies. As such, we fitted 1 full model for each of the nutritional state variables (i.e. the nutritional state variables were used simultaneously in a full model). As all nutritional indicators were found to be correlated, and to simplify the presentation and interpretation of results in this study, modelling using blood plasma protein and blood plasma calcium was excluded from the manuscript, but can be found in Tables S1–S8 in the Supplement at www.int-res.com/articles/suppl/m665p185_supp.pdf. This approach allowed us to avoid issues with co-linearity among nutritional indicators.

All statistical analyses were conducted in R Studio version 1.2.1335 (RStudio Team 2019) and R version 3.5.3 (R Core Team 2019) with the 'glmer' function in the 'lme4' R package (Bates et al. 2015) for the model with a binomial dependent variable. The 'lme' function in the nlme R package (Pinheiro et al. 2018) was used for models with normally distributed dependent variables. Collinearity within models was checked using the 'check_collinearity' function in the performance R package (Lüdtke et al. 2020), and collinearity was found to be low (variance inflation factor [VIF] ≤ 1.09). All variables were standardized prior to modelling using the 'scale' function in the R 'base' package. Blood plasma triglycerides values were log-transformed in order to stabilize variance. Body condition factor was calculated from the formula $K = 100 \times \text{mass (g)} \times \text{total length (cm)}^{-3.028}$, as the regression coefficient of the mass–length relationship was 3.028 for the tagged individuals. Model selection was conducted using Akaike's information criterion (AIC), with the ' dredge ' function in the MuMIn R package (Barton 2013). In cases when model selection left us with support for multiple alternative models ($\Delta\text{AIC} < 2$), conditional model averaging was applied, using all alternative models ($\Delta\text{AIC} < 4$) to estimate the coefficients of the explanatory variables. Kruskal-Wallis tests were applied for comparisons among groups of tagged fish (based on tagging year and population) in terms of body size, body condition factor, blood plasma triglycerides,

blood plasma protein and blood plasma calcium. Spearman's correlation tests were applied to test for correlations between pairs of nutritional indicators (body condition factor, blood plasma triglycerides, blood plasma protein and blood plasma calcium). For visualization purposes, linear regression lines were fitted to the relationships among nutritional correlates (see Fig. 3) using the 'geom_smooth' function in the ggplot2 R package (Wickham 2016). Spearman's correlation tests were applied to test for correlations between behavioural traits (timing of sea entry, marine residency and marine migration distance).

The raw tracking dataset on individual fish generated and analysed during the current study is uploaded to the Ocean Tracking Network data system (www.oceantrackingnetwork.org).

3. RESULTS

3.1. Characteristics of tagged fish

The results were based on 286 trout (165 females, 121 males, i.e. 58 % females, 42 % males) with a body size ranging from 270 to 890 mm (mean = 471 mm, SD = 129 mm) (Fig. 2). The fish were divided into 10 groups based on the river and year in which they were tagged. The proportion of females within these groups varied between 38 and 78 % (Fig. 2). There were significant differences in body condition factor among the groups (Kruskal-Wallis test; $n = 286$, $p < 0.001$, Fig. 2). Average concentrations of the nutritional metabolites (pooled samples for all fish from all rivers) derived from blood plasma sampling were 0.71 mmol l⁻¹ triglycerides (SD = 0.85, range = 0.004–4.36), 25.03 mg ml⁻¹ of protein (SD = 5.70, range = 8.87–45.85) and 3.21 mmol l⁻¹ of calcium (SD = 0.43, range = 1.94–5.56) among the groups (Fig. 2). However, there were significant differences among the groups in concentrations of blood plasma triglycerides (Kruskal-Wallis test; $n = 214$, $p < 0.001$), plasma protein ($n = 204$, $p < 0.001$) and plasma calcium ($n = 185$, $p < 0.001$, Fig. 2).

3.2. Correlations between the nutritional indicators

There were significant positive correlations between all the measured variables reflecting nutritional state (Fig. S1 in the Supplement). There was a positive correlation between body condition factor and (1) log-transformed blood plasma triglycerides (Spearman's correlation; $n = 214$, $r_s = 0.36$, $p < 0.001$),

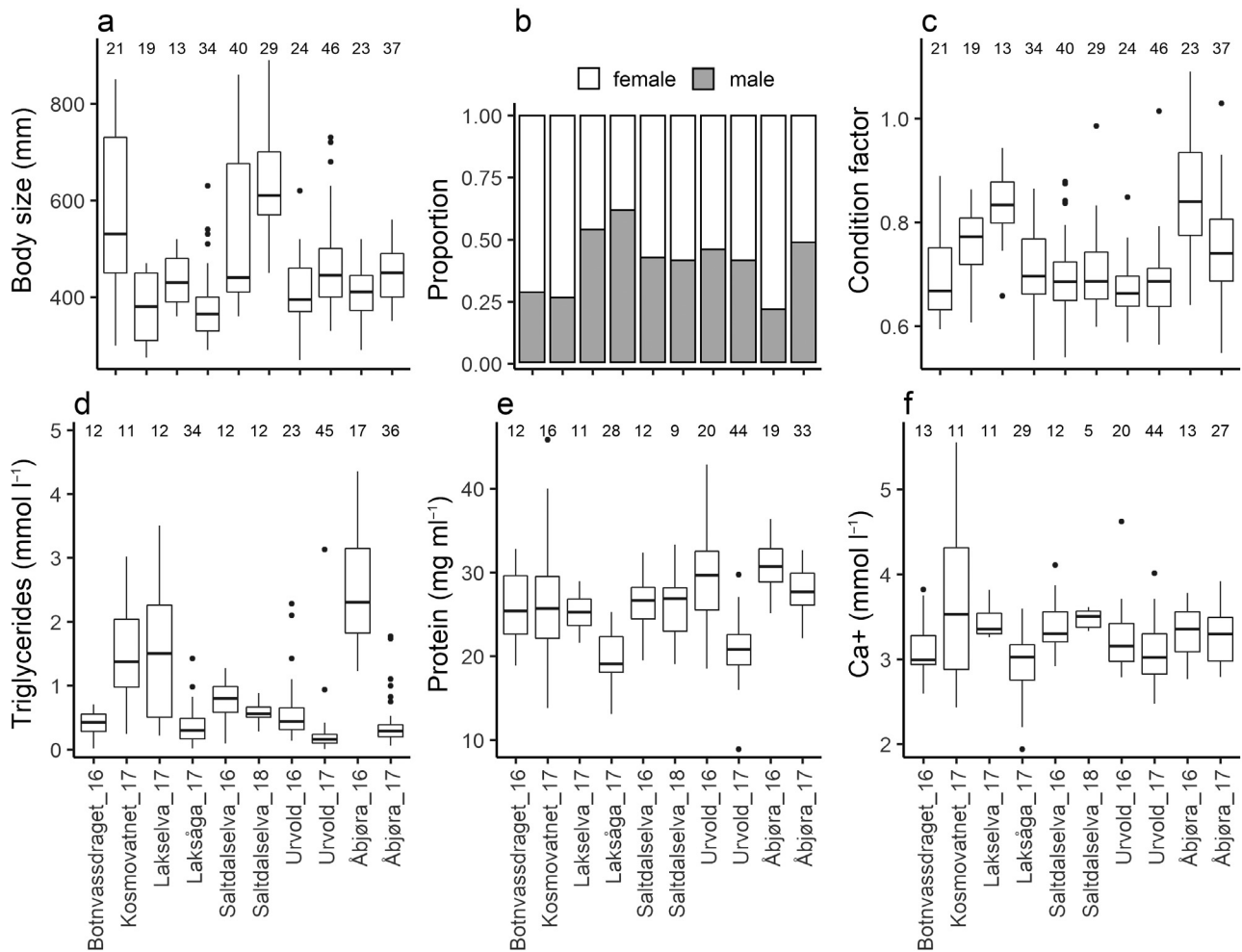


Fig. 2. (a) Body size, (b) sex (proportion of males and females in each group), (c) body condition factor, (d) blood plasma triglycerides, (e) blood plasma proteins and (f) blood plasma calcium for the groups of tagged fish (location and year in which the groups were tagged are indicated on the x-axes). The box plots show the interquartile range (boxes), median (horizontal line), the 5th and 95th percentiles (whiskers) and outliers (dots), with number of individuals in each group denoted at the top of the panels

(2) blood plasma protein ($n = 204$, $r_s = 0.42$, $p < 0.001$) and (3) plasma calcium ($n = 185$, $r_s = 0.23$, $p < 0.001$). There were positive correlations between the log-transformed blood plasma triglycerides and both blood plasma protein ($n = 194$, $r_s = 0.45$, $p < 0.001$) and blood plasma calcium ($n = 178$, $r_s = 0.31$, $p < 0.001$). There was also a positive correlation between blood plasma protein and blood plasma calcium ($n = 173$, $r_s = 0.60$, $p < 0.001$).

3.3. Migration to the sea or continued residence in freshwater and estuaries

Of the 286 tagged trout, 173 individuals migrated to the sea, while 106 individuals remained in fresh-

water and estuaries during the rest of the year. For 7 individuals, migratory decision could not be determined due to absence of detections, or detection records suggesting mortality, tag loss or tag malfunction. Overall, the models (see below) suggested that the fish migrating to the sea had greater body sizes than those remaining in freshwater, that females had a greater tendency to migrate to the sea than males, and that those migrating had lower body condition factors and lower blood plasma triglyceride levels than individuals remaining resident (Figs. 3 & 4, Tables S1 & S2).

Using body condition factor as the nutritional indicator, a model for migratory decision which included condition factor, sex and body size, and an alternative model excluding sex, were equally good

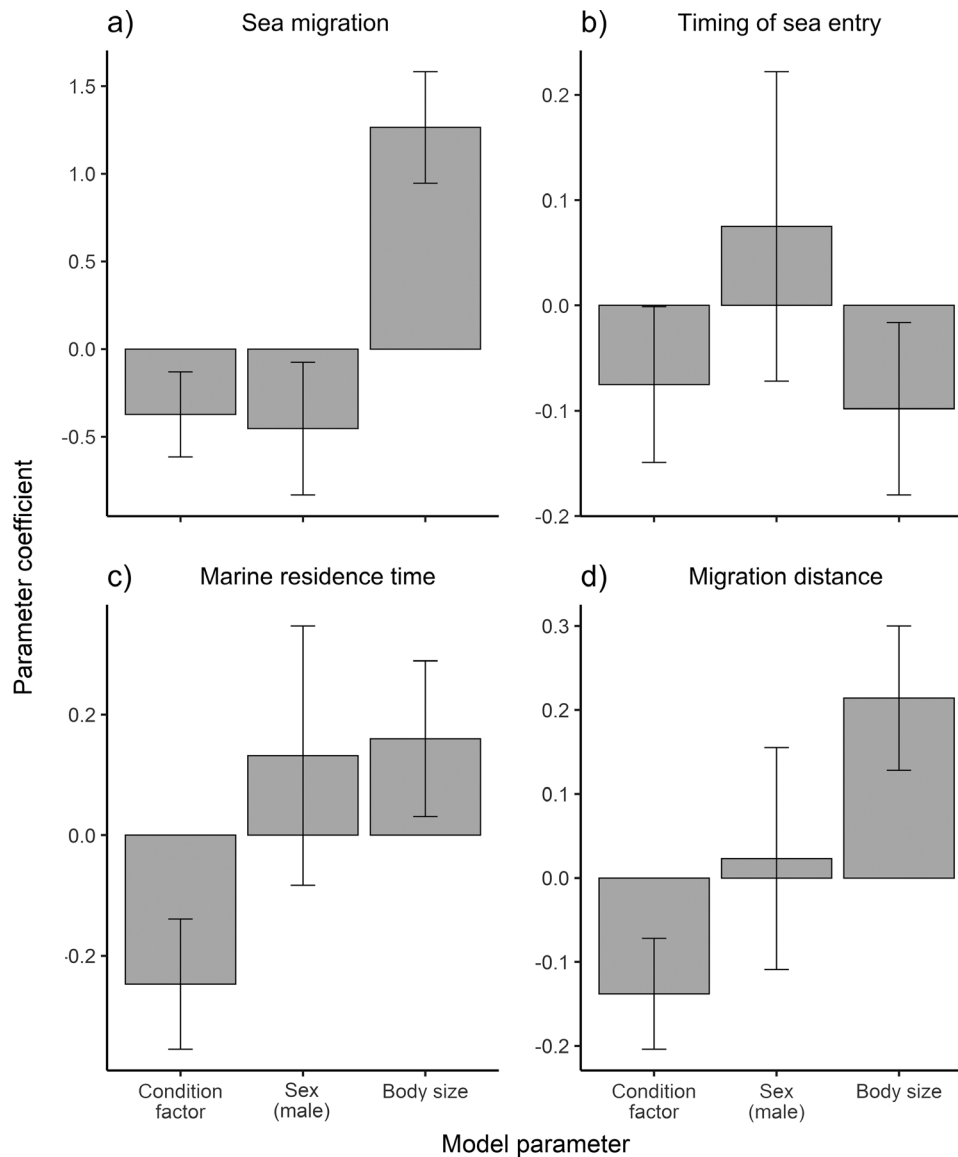


Fig. 3. Estimated effect of body condition factor, sex (male) and body size on the (a) decision to migrate to sea, (b) timing of sea entry, (c) marine residence time and (d) migration distance at sea. The bar plots show the estimated parameter coefficients and their standard error (whiskers) for the best fitted model ($\Delta\text{AIC} < 2$) or from conditional model averaging (including models with $\Delta\text{AIC} < 4$) where model selection identified multiple models with similar support

($\Delta\text{AIC} = 0.62$, Table S1). Conditional model averaging indicated that body size had the strongest effect on migratory decision, followed by condition factor and sex, respectively (Fig. 3, Table S2).

Using plasma triglycerides as nutritional indicator, the model on migratory decision which included sex and body size was the best model ($\Delta\text{AIC} = 2.22$ to second best model; Table S1). The model estimates showed that sex had the strongest effect on migratory decision, followed by body size and blood plasma triglycerides, respectively (Fig. 4, Table S2).

3.4. Timing of sea entry

Timing of sea entry was determined for 161 individuals. There were 4 models with $\Delta\text{AIC} < 2$ (Table S3) for the timing of sea entry, including the null model, when using body condition factor as a nutritional indicator. Here, the model averaging estimates generally suggested limited effects of all explanatory variables (Fig. 3, Table S4).

Three equally well supported models for timing of sea entry were identified when using plasma triglycerides as the nutritional indicator ($\Delta\text{AIC} = 1.89$,

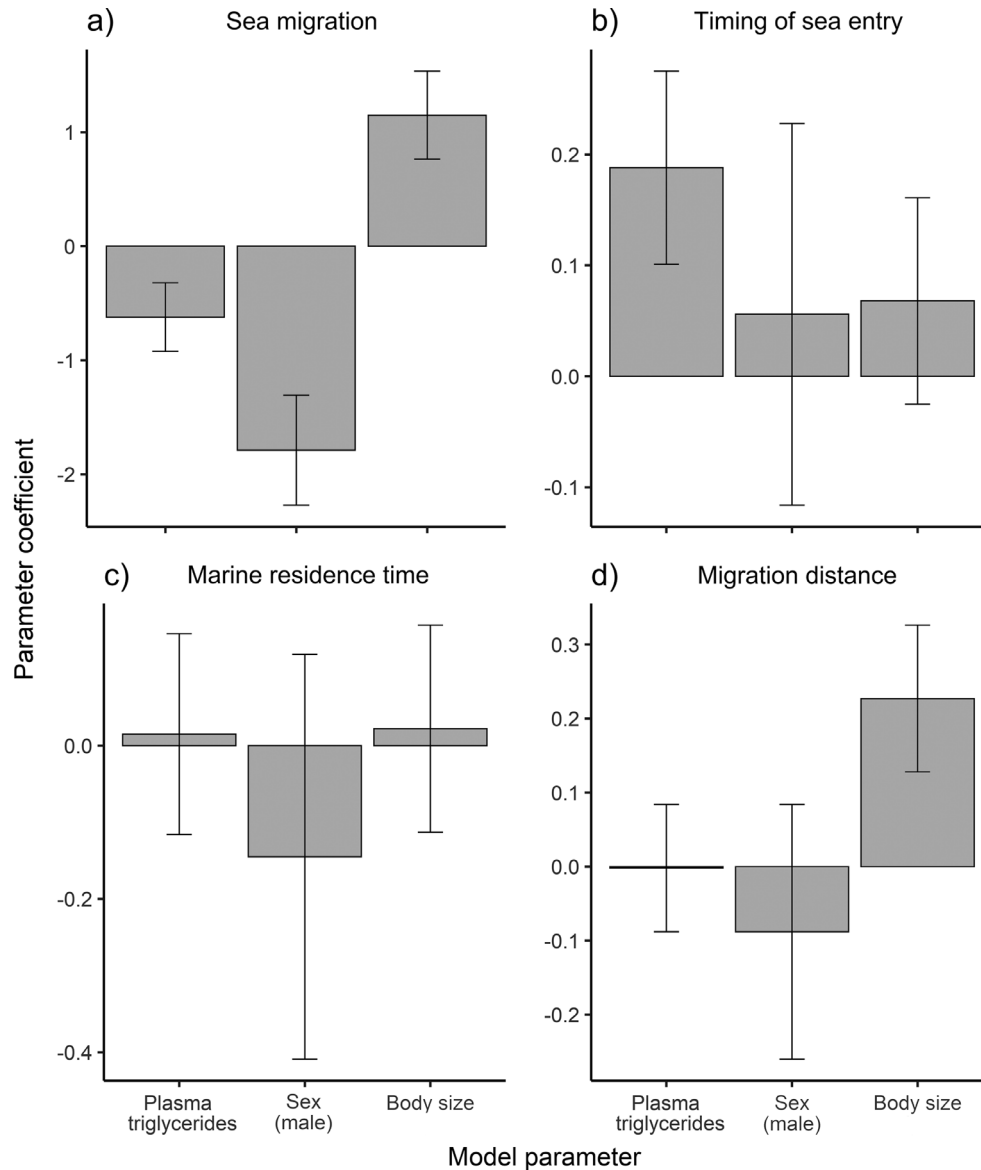


Fig. 4. Estimated effect of plasma triglycerides, sex (male) and body size on the (a) decision to migrate to sea, (b) timing of sea entry, (c) marine residence time and (d) migration distance at sea. See Fig. 3 legend for details of bar plots

Table S3). The model averaging estimates indicated that sea trout with higher plasma triglyceride levels entered the sea later in the season, while the effect of sex and body size on timing of sea entry was limited (Fig. 4, Table S4).

3.5. Marine residence time

The marine residence times were determined for 74 individuals. Three equally well supported models for the marine residence time were identified when using body condition factor as the nutritional indicator ($\Delta AIC = 1.65$, Table S5). The model estimates

from conditional model averaging demonstrated that condition factor had the strongest effect on marine residence time, showing that sea trout with lower condition factors spent longer times at sea (Fig. 3, Table S6).

There were 4 models with $\Delta AIC < 2$ (Table S5) for the marine residence time, including the null model, when using body plasma triglycerides as the nutritional indicator. Conditional model averaging for these models showed that the standard errors exceeded the estimated effects of the explanatory variables (Fig. 4, Table S6).

There was a significant negative correlation between timing of sea entry and marine residence

time (Spearman's correlation; $n = 80$, $p < 0.001$), where fish entering the sea earlier spent more time at sea.

3.6. Maximum migration distance in the sea

Maximum migration distance was determined for 111 individuals. The full model on migration distance, which included condition factor, sex and body size, and an alternative model excluding sex, were equally well supported ($\Delta AIC = 1.97$, Table S7). Model averaging showed that larger fish and fish with lower body condition factors migrated further out in the marine habitat, and that sex had limited effect on the migration distance (Fig. 3, Table S8).

The migration distance model selection process where blood plasma triglyceride was used as the nutritional indicator found that a model including only body size and an alternative model including body size and sex were equally well supported ($\Delta AIC = 1.73$, Table S7). Here, model conditional averaging showed that larger fish tended to migrate further out to sea than smaller fish, while sex and blood triglycerides had limited effect on the migration distance (Fig. 4, Table S8).

The maximum migration distance at sea was not correlated with the timing of sea entry (Spearman's correlation; $n = 167$, $p = 0.89$) or the duration of marine residency ($n = 69$, $p = 0.49$).

4. DISCUSSION

Overall, nutritional state, sex and body size (length) influenced the marine migration behaviour of sea trout from the 7 study populations in 2 distinct fjord systems in northern Norway. Sea trout with poor body conditions and low triglyceride levels tended to leave the river and estuaries and migrate to the sea, and individuals with low triglyceride levels migrated to the sea earlier. Fish with poor body condition prior to migration remained at sea for a longer time-period and migrated further out in the fjords than fish in better condition. Although all the nutritional indicators were found to be highly correlated, this study suggests that measuring both body condition and blood plasma metabolites gave a better evaluation of the nutritional state of the individuals and the impacts of nutritional state on behaviour. While body condition results from the balance between energy intake and expenditure over time frames of weeks or months, blood plasma triglyc-

erides have previously been observed to change in response to food intake over much shorter time scales (Sheridan 1988, Congleton & Wagner 2006).

Migrating to the marine environment is believed to provide better feeding opportunities and potentially increased growth and reproductive capacity (Klemetsen et al. 2003, Thorstad et al. 2016) because of the higher productivity in marine habitats than freshwater habitats in high latitude areas (Gross et al. 1988). On the other hand, energetic costs related to migration and osmoregulation, the risk of predation and disease, and other factors that could prevent a migratory individual from returning to freshwater spawning grounds are all risk factors presumed to be higher when an individual migrates to the sea (Thorstad et al. 2015, Jensen et al. 2019). In the present study, the observed effects of nutritional state on sea trout migratory behaviour suggest that individuals in a poor nutritional state tend to engage in riskier migration behaviour than fish in a better nutritional state. The results from this study also suggest that individuals in a poor nutritional state were energetically limited in freshwater, tipping the cost vs. benefit trade-off in favour of migration. In a previous study, Boel et al. (2014) found that sea trout with poor body condition were most likely to migrate towards the sea. Davidsen et al. (2014) observed that starved hatchery-reared sea trout released to the wild utilized sea habitat to a greater extent than well-fed hatchery fish, which tended to remain in the lower parts of the river and estuarine areas in which they were released. The observed relationship between nutritional state and timing of sea entry is also consistent with previous studies on reconditioning post-spawn Atlantic salmon *Salmo salar*, which exhibited earlier sea entry for individuals in poor body condition (Halttunen et al. 2018, Bordeleau et al. 2020). Birnie-Gauvin et al. (2019a) showed that elevated baseline cortisol levels, possibly in response to nutritional need, were associated with earlier migration towards the sea for post-spawned sea trout. Interestingly, we observed a stronger effect of blood plasma triglycerides levels than of body condition factor on the timing of sea entry. This may suggest a behavioural response to nutritional need, as acute triglyceride deprivation was a strong predictor for migratory initiation. Alternatively, it may suggest that opportunistic feeding in the freshwater or estuarine habitats during early spring may recondition nutritional state and delay the initiation of marine migration.

Once migration had occurred, sea trout with poor body condition factors tended to spend more time at sea and migrate further out into the marine habitat,

possibly reflecting a greater need to recondition compared to individuals with better body condition factors. There was a significant relationship between timing of sea entry and duration of marine residency, where fish that migrated early resided longer at sea. The prolonged residency at sea may enable sea trout to recondition for the next spawning and overwintering season but may also include higher risk of mortality, as marine habitats often have a greater abundance of potential predators. A previous study by Haraldstad et al. (2018) showed that post-spawned sea trout in poor body condition were more likely to skip spawning the following season compared to individuals in better body condition. Bordeleau et al. (2018) reported that the pre-migratory level of blood plasma triglycerides was negatively correlated with the duration of marine residency in veteran sea trout migrants. According to previous studies, sea trout with a low body condition tended to migrate further out to sea compared with individuals in a better body condition (Davidsen et al. 2014, Eldøy et al. 2015, Bordeleau et al. 2018). In the present study, differences in characteristics of the near marine habitats among the multiple sites we studied probably impacted how far the sea trout from the various rivers needed to migrate to meet their metabolic demands. No correlation was found between migration distance and timing of marine entry or marine residence time.

As expected, there were significant positive correlations among all measured nutritional indicators. A previous laboratory experiment by Congleton & Wagner (2006) documented low levels of blood plasma triglycerides, blood plasma protein and blood plasma calcium in starved juvenile salmonids. Overall nutritional state is determined by net differences between energy intake and energy expenditure over periods of weeks or months (Congleton & Wagner 2006). Poor nutritional state could likely be explained by limited feeding while overwintering, and for fish that have reproduced, also by the energy expenditure during spawning the previous autumn (Bordeleau et al. 2018). The energy investment in spawning can be substantial for brown trout (Jonsson & Jonsson 2011b). In Lake Vangsvatnet in Norway, Jonsson & Gravem (1985) documented that immature migrants fed little while in freshwater and that mature migrants stopped feeding after the spawning season.

Although the nutritional status of most fish in the study was poor, there was large variation in nutritional state both among individuals and among groups of fish. There may be several reasons for this, including differences in nutritional state after the

previous growth season, energy investment in previous spawning, overwintering conditions, metabolic rate and feeding activity (Midwood et al. 2015, Auer et al. 2016). Some individuals had elevated nutritional indicators indicative of a better nutritional status. These individuals mainly belonged to the groups of fish tagged in the estuarine habitats of River Åbjøra, River Lakselva and the Kosmovatnet watercourse. For these fish, elevated blood plasma triglyceride level was the most obvious signal. This suggests that the fish had started feeding prior to tagging, because triglycerides become elevated a few hours after feeding (Sheridan 1988), and a previous laboratory experiment documented that blood plasma triglycerides recovered quickly in rainbow trout *Oncorhynchus mykiss* when refeeding began after a starvation period (Congleton & Wagner 2006). Common for these groups of tagged fish was that they were captured and tagged in lower parts of watercourses which have relatively large estuarine areas likely suitable for opportunistic feeding during early spring.

Females were more likely to migrate to the sea than males, instead of remaining in the freshwater and estuarine areas of the river where they were tagged. Previous studies with this species have also noted that females are more likely to migrate than males (Pemberton 1976, Knutsen et al. 2004, Jensen et al. 2019). In a study in Tosenfjorden, Bordeleau et al. (2018) found that females in the Åbjøra watercourse were more likely to leave the estuarine areas than males. This is likely caused by a greater benefit of increased feeding opportunities for females than males due to the strong correlation between female body size and the number of eggs the female can produce (Elliott 1995). Sexual bias in migratory behaviours is a well known phenomenon that has previously been observed in a range of salmonid species (reviewed by Dodson et al. 2013).

The models in the present study provided limited support for the influence of sex on migration timing, duration and distance migrated at sea. Some previous studies have reported that male sea trout tended to migrate earlier (Jensen 1968, Östergren & Rivinoja 2008), while others at different sites have suggested an earlier migration timing for females (Berg & Berg 1989). Berg & Berg (1989) also observed that females had a longer duration of marine residency than males. Bordeleau et al. (2018) found that females migrated further from the river than males and were more likely to migrate to the outer fjord areas of Tosenfjorden. Although the reasons females and males differed in their migration patterns among

these different sites remain obscure, the results of these studies suggest that a combination of local environmental conditions and population characteristics may play an important role for the trade-off mechanisms shaping the migratory decisions of individuals within sea trout populations. This plasticity is one of the reasons why the species has been so successful.

Larger fish of both sexes were more likely to migrate to the sea and migrated greater distances at sea than smaller fish. These tendencies are likely driven by the need of larger individuals to find more prey of larger size than the smaller fish, larger fish being less susceptible to predation than smaller fish and possibly larger fish being more powerful swimmers (Dill 1983, Klemetsen et al. 2003). Individual sea trout tend to repeat their migratory patterns among successive years (Eldøy et al. 2019) although some studies suggest that iteroparous salmonids may reduce their migration distances as they become larger and older (Svärdson & Fagerström 1982, Bond et al. 2015). The earlier seaward migration of large fish observed in the present study is similar to the timing observed in previous studies (Pemberton 1976, Bohlin et al. 1996, Jonsson & Jonsson 2009). The positive correlation we noted between body size and the duration of the marine migration is also consistent with previous work (Eldøy et al. 2015). However, the tendency we found for larger fish to migrate further out to sea compared to smaller individuals has only been noted in a few of the previous studies on this species (e.g. Berg & Berg 1989, Jensen et al. 2014, Jonsson & Jonsson 2014).

In conclusion, despite the large individual and among-group variation observed in both nutritional state and migratory behaviour, the present study showed that sex, body size and pre-migratory nutritional state strongly influenced the migratory patterns of sea trout. Anadromy is considered a quantitative threshold trait, where environmental thresholds for triggering behavioural responses are genetically determined (Ferguson 2006, Ferguson et al. 2019). Previous studies have suggested that the migratory behaviour of brown trout is a continuum of behavioural responses to the environmental cues experienced by the individuals in coastal trout populations (Cucherousset et al. 2005, Boel et al. 2014, del Villar-Guerra et al. 2014). However, the importance of different factors affecting the pre-migratory nutritional state and the influence of carry-over effects are poorly understood (O'Connor et al. 2014). For example, it is unknown how the success of a previous feeding migration interacts with spawning investment and over-wintering conditions to determine the

nutritional state and subsequent marine migrations of post-spawned, veteran sea trout migrants (Bordeleau 2019). As shown by Jensen et al. (2020), life history patterns or decisions adopted early in life may persist throughout an individual's lifetime and significantly affect the animal's lifetime fitness. Jensen et al. (2020) showed that early migrants continued to migrate early throughout their lifetime, and had better growth and a larger lifetime fecundity. This suggests that individuals developing under favourable conditions will gain fitness benefits throughout their lifetime. Jensen et al. (2020) therefore concluded that individuals that experience favourable environmental conditions as juveniles in freshwater and/or with genes that contribute to a large smolt size and early smolt migration may benefit preferentially from growth opportunities in the sea, and the benefits of the early adoption of anadromy enables them to continue with early and longer migrations during following years. However, the fact that sea trout populations do not evolve to contain exclusively early migrants highlights again that there are costs that counterbalance the strategy.

While at sea, sea trout commonly reside in habitats heavily affected by human activity (Nevoux et al. 2019). Salmon lice infestation related to open cage farming of Atlantic salmon was recently evaluated as the biggest threat for Norwegian sea trout stocks (Norwegian Scientific Advisory Committee for Atlantic Salmon 2019). Serra-Llinares et al. (2020) documented that sea trout infested with salmon lice altered their migration behaviour and experienced increased mortality. The results of the present study, where fish in poor nutritional state seemed to migrate to the sea earlier and spent more time at sea, suggest that fish in poor nutritional state may display behavioural patterns that make them especially vulnerable to such negative anthropogenic factors at sea. This is both because their longer stay at sea increases the risk of being infested by salmon lice, and because they migrate to areas with high salinity favourable for sea lice instead of remaining in brackish water areas where the lice do not survive well. The links between migration behaviour, human-induced stressors and reproductive success throughout the lifetime of sea trout remain obscure. Future studies examining the link between marine migration behaviour and reproductive investment over consecutive years are therefore advocated.

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