

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

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13 Running headline: Physiological drivers for marine behaviour in sea trout *Salmo trutta*.

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19 ABSTRACT

20 The sea trout (anadromous brown trout, *Salmo trutta*) displays extensive among-individual
21 variation in marine migration behaviour. We studied the migration behaviour of 286 sea trout
22 (27-89 cm) tagged with acoustic transmitters in the spring, in seven populations located in
23 two distinct marine fjord systems in Norway. We examined whether individual nutritional
24 state, sex, and body size influenced marine migration behaviour in terms of *i.* the decision to
25 migrate to the sea or remain resident in freshwater and/or estuarine habitats, *ii.* seasonal

1 timing of sea entry, *iii.* duration of the marine residency, and *iv.* migration distance at sea
2 from the home river. Most sea trout were in a poor nutritional state in the spring prior to
3 migration. Sea trout with low body condition factors and low plasma triglyceride levels were
4 more likely to migrate to sea, and low triglyceride levels were also associated with earlier
5 sea-entry. Poor body condition also increased the probability of individuals remaining at sea
6 longer and migrating further offshore compared to fish in better condition. Females were
7 more likely to migrate to the sea than males. Larger fish were also more likely to migrate to
8 sea instead of remaining in freshwater and estuaries and dispersed over greater distances from
9 the river than smaller fish. In conclusion, this study documented general trends across
10 multiple populations and showed that nutritional state, sex and body size influence important
11 aspects of the marine migration behaviour of sea trout.

12

13 1. INTRODUCTION

14 Migration behaviour is observed in a wide range of taxa (Dingle 2014). There are various
15 proximate explanations for why animals migrate, but the ultimate reason is for the
16 optimization of individual growth and survival in order to increase lifetime fitness (Dingle &
17 Drake 2007). Throughout their lifetimes, individuals must continually allocate energy to
18 various life-history activities, while balancing the metabolic demands for somatic growth,
19 maturation, and reproduction (Zera & Harshman 2001). Diadromy, which refers to migrations
20 between marine and freshwater habitats, is thought to have evolved because of differences in
21 food availability between these habitats (Gross et al. 1988). Among the fish family
22 Salmonidae, all species spawn in freshwater, but many are anadromous, which means
23 individuals migrate to sea at some point in their lives to exploit the richer marine food
24 resources (Jonsson & Jonsson 1993). Salmonid populations often consist of both freshwater

1 resident and sea migrating individuals (i.e partial migration, Chapman et al. 2012). Body size
2 is positively correlated with fecundity within salmonids (Elliott 1995). Marine migration is
3 advantageous if the fitness benefits of larger body size outweighs the cost of migration,
4 including increased risk of mortality, disease and failure to reach spawning grounds
5 (Klemetsen et al. 2003, Thorstad et al. 2016).

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

24 Energy status is known to impact migratory strategies of individual trout
25 (Cucherousset et al. 2005, Boel et al. 2014, Bordeleau et al. 2018). For mature sea trout,

1 reproduction is energetically expensive (Lien 1978, Jonsson & Jonsson 2005), and so they
2 must recondition between spawning events. In watercourses suitable for overwintering, sea
3 trout can remain in the spawning river system throughout the winter after autumn spawning
4 (Berg & Berg 1989, Östergren & Rivinoja 2008), but in these oligotrophic systems feeding
5 and growth are usually limited. Post-spawned individuals are therefore in a generally poor
6 nutritional state prior to the seaward migration in the spring (Jonsson & Jonsson 1998,
7 Jonsson & Jonsson 2011a). How individual variation in energy status relates to variation in
8 marine migration behaviour of sea trout is not well understood. Body condition factor, which
9 is based on the relationship between body length and mass (i.e., the relative stoutness of fish),
10 is commonly used as an index of somatic energy status in salmonids and other fishes, but
11 might not always be a precise predictor of energy status (Weatherley & Gill 1983, Simpson
12 1992, Næsje et al. 2006). In addition to body condition factor, nutritional correlates derived
13 from blood plasma samples can be used to assess the nutritional state of fishes. For
14 salmonids, low levels of plasma triglycerides, total protein, and calcium levels can indicate
15 poor nutritional state (Congleton & Wagner 2006), which has previously been observed to
16 promote marine migratory decisions in brown trout and Atlantic salmon (Boel et al. 2014,
17 Bordeleau et al. 2018, Bordeleau et al. 2019). Elevated levels of cortisol possibly due to low
18 food availability, have previously been found to promote earlier seaward migration (Birnie-
19 Gauvin et al. 2019a). These previous studies suggest that sea trout in poor nutritional state
20 will display more risk-taking behaviour than individuals in better nutritional state in order to
21 compensate for their depleted energy stores.

22 In this study, we tested the hypothesis that poor nutritional state promotes adopting a
23 more high-risk ocean migratory behaviour in sea trout in terms of timing, duration and
24 migration distance. We used both body condition factor and blood plasma metabolites as
25 measures of individuals' nutritional state. Migration behaviour in sea trout has also been

1 observed to be influenced by sex (Pemberton 1976, Knutsen et al. 2004, Jensen et al. 2019)
2 and body size (Jensen et al. 2014, Jonsson & Jonsson 2014). Hence, sex determined by
3 genetic analyses and body size were also included in the analyses. We included 286
4 individual sea trout from seven populations in two fjord systems in Northern Norway in this
5 study to test the general hypotheses that poor nutritional state, females, and large size would
6 promote initiation and greater extent of the marine migration. Specifically, we examined
7 whether nutritional state, sex, and body size (length) influenced *i.* the tendency to migrate to
8 the sea or remain resident in freshwater and/or estuarine habitats, *ii.* the timing of sea entry,
9 *iii.* the duration of the marine residency, and *iv.* the distance moved out to sea from the river
10 where the fish were tagged.

11

12 2. MATERIAL & METHODS

13 2. 1 Study site

14 This study was conducted in two Norwegian fjord systems in Nordland County;
15 Skjerstadvfjorden (67°N) and Tosenfjorden (65°N) (Figure 1) as part of two larger tracking
16 studies, enabling sampling from seven river systems. In Tosenfjorden, fish were captured and
17 tagged in the period 27 March to 10 June in the Rivers Åbjøra and Urvold (Figure 1). In
18 Skjerstadvfjorden, fish were captured and tagged during 28 April to 15 June in the rivers
19 Saltdalselva, Botnvassdraget, Lakselva, Laksåga, and Kosmovatnet (Figure 1). Estuaries were
20 defined as the transition zone between the freshwater and marine environment, where the
21 water masses were expected to be brackish throughout the year. For all rivers, this included
22 receivers that were deployed less than 600 meters from the river mouth, except for River
23 Saltdalselva where receivers deployed up to 1 km from the river mouth were categorized as
24 estuarine habitats.

25 In the Tosenfjorden study area, River Åbjøra has 24 km of river stretch available for

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

11 In the Skjerstadvfjorden study area, River Saltdalselva is a large river with average
12 discharge of 55 m³/s and 66 km of river stretch available for anadromous fish. Due to its large
13 size, and relatively slow-running areas in its lower part, River Saltdalselva has a relatively
14 large estuary (about 0.47 km² tidal influenced areas inside the littoral zone). There is only one
15 lake available for anadromous fish in River Saltdalselva, Lake Vassbotnvatn, which is located
16 in a tributary. River Botnvassdraget has a 500 m steep river stretch to Lake Botnvatnet (12 m
17 above the sea), and continues upstream of the lake, making about 8 km of river stretch
18 available for anadromous fish. River Botnvassdraget's confined estuary covers about 0.002
19 km² of tidal influenced area. River Lakselva has about 7 km of river stretch with no lakes
20 available to anadromous fish, and has a tidally influenced surface area of about 0.08 km² in
21 its estuarine area. River Laksåga has about 6.5 km of river stretch available for anadromous
22 fish and drains into two large brackish-water lakes influenced by the sea (about 15 km²
23 surface area). River Laksåga is regulated for hydropower purposes. River Kosmovatnet has
24 about 6 km of river stretch available to anadromous fish, and drains into a brackish-water

1 lake of about 8 km², separated from the sea by a 1 km narrow channel where the tide governs
2 the direction of the current.

3 2.2. Capture and tagging of fish

4 A total of 286 sea trout, divided into 10 groups based on location and year (Table 1), were
5 captured and tagged with individually coded acoustic transmitters (Thelma Biotel AS; 9 mm
6 and 13 mm, expected battery life 10-24 months, tag size depended on body size) during
7 2016-2018. Fish from River Åbjøra, River Kosmovatnet and River Laksåga were caught, in
8 the estuarine parts of the river systems. Fish from River Urvold were caught in Lake Urvold
9 (freshwater), except for 13 individuals during spring 2017 (Table 1) that were caught in the
10 river mouth. All fish caught in River Saltdalselva were caught in the river. The fish were
11 captured by angling or by gillnets in the rivers, lakes and/or estuarine areas. Gill nets were
12 continuously monitored and quickly tended when a fish was detected to minimize the time
13 fish were entangled in the nets, and the fish were released using scissors to cut the netting to
14 prevent damage to the skin and gills. A non-lethal blood sample was drawn shortly after
15 capture (max 5 ml blood per kg body mass, Lawrence *et al.*, 2020). The fish were held in
16 keep nets for up to four hours before they had a transmitters implanted.

17 Prior to tagging, each sea trout was anesthetized for 4 minutes using 0.5 ml⁻¹ 2-
18 phenoxy-ethanol (EC No. 204-589-7, Sigma-Aldrich, USA). For most fish, tags were inserted
19 through a 1.5-3 cm incision in the body cavity (Cooke *et al.* 2011, Eldøy *et al.* 2015). For the
20 fish tagged in River Åbjøra in 2017 (Table 1), the transmitters were externally attached using
21 a wire through the dorsum about 1 cm below the dorsal fin, with a silicone plate between the
22 tag and the fish and a plastic plate on the opposite side of the dorsum to prevent erosion on
23 skin and flesh. The sea trout were subsequently placed in a holding tank until recovery from
24 anaesthesia and released in a slow flowing area as close to the capture location as possible.

1 The experimental procedures were approved by the Norwegian National Animal Research
2 Authority (permission number 2015/8518, 1614092 & 18/67706).

3 2.3 Fish tracking

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

9 Tracking data were filtered for false registrations generated by code collisions with
10 simultaneously transmitting tags, or by noise in the environment (Pincock 2012). After
11 empirically assessing the frequency of false detections (i.e., a receiver reported detection of
12 an unused transmitter ID) recorded by each receiver, automated filtering was applied to 16
13 receivers in Tosenfjorden, and 4 receivers in Skjerstadjorden (see Figure 1 for filtered
14 receiver locations). The filter required that a tagged sea trout had to be registered at least two
15 times by a receiver within a 10-minute time period to be accepted as a true registration, and
16 resulted in removal of 68 682 of 2 191 047 detections (3.1%) in Tosenfjorden and 2 402 of
17 594 345 detections (0.4%) in Skjerstadjorden. The data were subsequently visually inspected
18 by plotting a timeline of all recordings for each fish, and registrations that did not fit with the
19 overall migration track of each fish were also removed (i.e. detections suggesting unrealistic
20 migration speed and/or passing multiple receiver gates without detection).

21 2.4 Processing and analysing blood samples

22 Blood samples were stored in tubes and immediately placed in an ice water bath for up to 3
23 hours before being centrifuged at 1163g for 10 min. Blood plasma was flash-frozen in a
24 liquid nitrogen dry shipper and subsequently stored at -80 °C until biochemical analyses
25 could be carried out. Plasma triglyceride levels were assessed in duplicates using the

1 manufacturer's suggested protocols with a commercially available colorimetric kit (Cayman
2 Chemical Company, USA). Total plasma protein levels were determined using a Bradford's
3 assay (Bradford 1976, Kruger 2009) using commercial reagents (Bio-Rad Laboratories
4 (Canada) Ltd., Mississauga, ON, Canada). Plasma Ca²⁺ concentrations were determined
5 using flame spectrophotometry (Varian Spectra AA 220FS, Varian Inc., Palo Alto, CA, USA)
6 for a single replicate. Due to the limited volume of blood that could be taken from each fish
7 (see Lawrence *et al.* 2020), there was not enough blood for all individuals to run all
8 biochemical assays. Therefore, 214 fish were tested for blood plasma triglycerides, 204 fish
9 were tested for blood plasma protein and 185 fish were tested for blood plasma calcium.

10 2.5 Determining the sex of individuals

11 DNA samples from adipose fin clips taken at the time of tagging and preserved in ethanol
12 were used to genetically determine the sex of the sea trout. DNA was extracted using the
13 QuickExtract kit (Epigen) using the manufacturer's protocol but with extraction volume
14 reduced to 150 µl. Using 10 µl reactions of the Qiagen Multiplex PCR kit and Salmo-sdY-F
15 and Samo sdYR primers, PCR amplification was applied to a 200 base pair fragment from the
16 first intron of the male-specific SDY gene (Quéméré *et al.* 2014). PCR steps for denaturation,
17 annealing and extension were: incubation at 95 °C for 15 min, 11 cycles of touchdown PCR,
18 held at 94 °C for 30 s, 63-52 °C for 30 s, then 72 °C for 1 min followed by 25 cycles at 94 °C
19 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
20 determined by running PCR products in 1% agarose gels.

21 2.6 Migrating to the sea vs. remaining in freshwater and estuaries

22 The trout could remain resident in the habitat where they were captured and tagged (river,
23 lake and estuarine habitats), or migrate to the fjord. Individual sea trout were considered sea
24 migrants if they were recorded by any marine receiver except those categorized as estuarine

1 of the river where they were tagged. Fish that we lost track of shortly after tagging, or which
2 showed a “permanent residency” at a particular receiver indicative of mortality or tag loss
3 within the receiver’s detection range were excluded from statistical analyses ($n = 7$).

4 2.7 Timing of sea entry and duration of the marine migration

5 The timing of sea entry was calculated for all individuals that were recorded leaving the
6 freshwater and estuarine areas of the watercourse where they were tagged. The timing of sea
7 entry was recorded as the first detection of a tagged fish in the estuary for Rivers Urvold,
8 Saltdalselva and Botnvassdraget. In River Åbjøra, the timing of sea entry was defined as the
9 time of the last recorded detection in the river’s estuary, provided the fish was subsequently
10 detected by a receiver in the fjord. For the fish tagged in Laksåga, the time of sea entry was
11 defined as the time of first detection by a receiver in the fjord. The different definitions for
12 timing of sea entry were due to logistical and hydrologic constraints that required different
13 approaches to receiver deployment in the estuarine areas of the different watercourses. Fish
14 tagged in rivers Lakselva and Kosmovatnet were excluded from these analyses due to small
15 sample sizes ($n \leq 2$).

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

1 2.8 Maximum migration distance at sea

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

15 2.9 Statistical analyses

16 To test for effects of nutritional state, sex and body size (natural length) on migratory
17 behaviour, we used a set of generalized mixed effect models. The behavioural traits that were
18 used as response variables were either binomial (migrated or did not migrate) or continuous
19 and normally distributed (timing, duration and distance of sea migration). Independent
20 variables (fixed explanatory effects) were sex, body size and nutritional state (body condition
21 and blood plasma triglycerides). Tagging years were nested within populations (watercourse)
22 and used as random effects. We did not aim to investigate which of the nutritional state
23 variables employed were the best proxies. As such, we fitted one full model for each of the
24 nutritional state variables (i.e. the nutritional state variables were used simultaneously in a
25 full model). As all nutritional indicators were found to be correlated, and to simplify the

1 presentation and interpretation of results in this study, modelling using blood plasma protein
2 and blood plasma triglycerides was excluded from the manuscript, but can be found in
3 Appendices 1 – 8. This approach allowed us to avoid issues with co-linearity among
4 nutritional indicators.

5 All statistical analyses were conducted in R Studio version 1.2.1335 (RStudio Team
6 2019) and R version 3.5.3 (R Core Team 2019) with the ‘glmer’ function in the ‘lme4’ R
7 package (Bates et al. 2015) for the model with a binomial dependent variable. The ‘lme’
8 function in the nlme R package (Pinheiro et al. 2018) was used for models with normally
9 distributed dependent variables. Collinearity within models was checked using the
10 ‘check_collinearity’ function in the performance R package (Lüdtke et al. 2020), and
11 collinearity was found to be low ($VIF \leq 1.09$). All variables were standardised prior to
12 modelling using the ‘scale’ function in the R ‘base’ package. Blood plasma triglycerides
13 values were log-transformed in order to stabilise variance. Body condition factor was
14 calculated from the formula $K = 100 \times \text{mass (g)} \times \text{total length (cm)}^{-3.028}$, as the regression
15 coefficient of the mass-length relationship was 3.028 for the tagged individuals. Model
16 selection was conducted using Akaike information criterion (AIC) (Anderson *et al.*, 2001),
17 with the ‘dredge’ function in the MuMIn R package (Barton, 2019). In cases when model
18 selection left us with support for multiple alternative models ($\Delta AIC < 2$), conditional model
19 averaging was applied, using all alternative models ($\Delta AIC < 4$) to estimate the coefficients
20 of the explanatory variables. Kruskal-Wallis-tests were applied for comparisons among
21 groups of tagged fish (based on tagging year and population) in terms of body size, body
22 condition factor, blood plasma triglycerides, blood plasma protein and blood plasma calcium.
23 Spearman correlation tests were applied to test for correlations between pairs of nutritional
24 indicators (body condition factor, blood plasma triglycerides, blood plasma protein and blood
25 plasma calcium). For visualization purposes, linear regression lines were fitted to the

1 relationships among nutritional correlates in Figure 3 using the ‘geom_smooth’ function in
2 the ggplot2 R package (Wickham 2016). Spearman correlation tests were applied to test for
3 correlations between behavioural traits (timing of sea entry, marine residency and marine
4 migration distance).

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

8

9

10 3. RESULTS

11 3.1 Characteristics of tagged fish

12 The results were based on 286 trout (165 females, 121 males, i.e. 58% females, 42% males)
13 with a body size ranging from 270 to 890 mm (mean = 471 mm, SD = 129 mm) (Figure 2).

14 The fish were divided into ten groups based on the river and year they were tagged. The
15 proportion of females within these groups varied between 38% and 78% (Figure 2). There
16 were significant differences in body condition factor among the groups (Kruskal-Wallis test n
17 = 286, $P < 0.001$, Figure 2). Average concentrations of the nutritional metabolites (pooled
18 samples for all fish from all rivers) derived from blood plasma sampling were 0.71 mmol l⁻¹
19 triglycerides (SD = 0.85, range 0.004-4.36), 25.03 mg ml⁻¹ of protein (SD = 5.70, range 8.87-
20 45.85) and 3.21 mmol l⁻¹ of calcium (SD = 0.43, range = 1.94-5.56) among the groups
21 (Figure 2). However, there were significant differences among the groups in concentrations
22 of blood plasma triglycerides (Kruskal-Wallis test; $n = 214$, $P < 0.001$), plasma protein ($n =$
23 204, $P < 0.001$) and plasma Calcium ($n = 185$, $P < 0.001$, Figure 2).

24 3.2 Correlations between the nutritional indicators

1 There were significant positive correlations between all the measured variables reflecting
2 nutritional state (Appendix 1). There was a positive correlation between body condition
3 factor and 1) log transformed blood plasma triglycerides (Spearman's correlation; $n = 214$, r_s
4 $= 0.36$, $P < 0.001$), 2) blood plasma protein ($n = 204$, $r_s = 0.42$, $P < 0.001$), and 3) plasma
5 calcium ($n = 185$, $r_s = 0.23$, $P < 0.001$). There were positive correlations between the log
6 transformed blood plasma triglycerides and both blood plasma protein ($n = 194$, $r_s = 0.45$, P
7 < 0.001) and blood plasma calcium ($n = 178$, $r_s = 0.31$, $P < 0.001$). There was also a positive
8 correlation between blood plasma protein and blood plasma calcium ($n = 173$, $r_s = 0.60$, $P <$
9 0.001).

10 3.3 To migrate to the sea or stay in freshwater and estuaries

11 Of the 286 tagged trout, 173 individuals migrated to the sea, while 106 individuals remained
12 in freshwater and estuaries during the rest of the year. For 7 individuals, migratory decision
13 could not be determined due to absence of detections, or detection records suggesting
14 mortality, tag loss or tag malfunction. Overall, the models (see below) suggested that the fish
15 migrating to the sea had greater body sizes than those remaining in freshwater, that females
16 had a greater tendency to migrate to the sea than males, and that those migrating had lower
17 body condition factors and lower blood plasma triglyceride levels than individuals remaining
18 resident (Figure 3 and 4, Appendix 2 and 3).

19 Using body condition factor as the nutritional indicator, a model for migratory
20 decision which included condition factor, sex and body size, and an alternative model
21 excluding sex, were of equally good ($\Delta AIC = 0.62$, Appendix 2). Conditional model
22 averaging indicated that body size had the strongest effect on migratory decision, followed by
23 condition factor and sex, respectively (Figure 3, Appendix 3).

24 Using plasma triglycerides as nutritional indicator, the model on migratory decision
25 which included sex and body size was the best model ($\Delta AIC 2.22$ to second best model;

1 Appendix 2). The model estimates showed that sex had the strongest effect on migratory
2 decision, followed by body size and blood plasma triglycerides, respectively (Figure 4,
3 Appendix 3).

4

5

6 3.4 Timing of sea entry

7 Timing of sea entry could be determined for 161 individuals. There were four models with Δ
8 $AIC < 2$ (Appendix 4) for the timing of sea entry, including the null model, when using body
9 condition factor as a nutritional indicator. Here, the model averaging estimates generally
10 suggested limited effects of all explanatory variables (Figure 3, Appendix 5).

11 Three equally well supported models for timing of sea entry were identified when
12 using plasma triglycerides as the nutritional indicator ($\Delta AIC = 1.89$, Appendix 4). The model
13 averaging estimates indicated that sea trout with higher plasma triglyceride levels entered the
14 sea later in the season, while the effect of sex and body size on timing of sea entry was
15 limited (Figure 4, Appendix 5).

16

17

18 3.5 Marine residence time

19 The marine residence times could be determined for 74 individuals. Three equally well
20 supported models for the marine residence time were identified when using body condition
21 factor as the nutritional indicator ($\Delta AIC = 1.65$, Appendix 6). The model estimates from
22 conditional model averaging showed that condition factor had the strongest effect on marine
23 residence time, showing that sea trout with lower condition factors spent longer times at sea
24 (Figure 3, Appendix 7).

1 There were four models with $\Delta AIC < 2$ (Appendix 6) for the marine residence time,
2 including the null model, when using body plasma triglycerides as the nutritional indicator.
3 Conditional model averaging for these models showed that the standard errors exceeded the
4 estimated effects of the explanatory variables (Figure 4, Appendix 7).

5 There was a significant negative correlation between timing of sea entry and marine
6 residence time (Spearman's correlation; $n = 80$, $P < 0.001$), where fish entering the sea earlier
7 spent more time at sea.

8

9 3.6 Maximum migration distance in the sea

10 Maximum migration distance could be determined for 111 individuals. The full model on
11 migration distance, which included condition factor, sex and body size, and an alternative
12 model excluding sex, were equally well supported ($\Delta AIC = 1.97$, Appendix 8). Model
13 averaging showed that larger fish and fish with lower body condition factors migrated further
14 out in the marine habitat, and that sex had limited effect on the migration distance (Figure 3,
15 Appendix 9).

16 The migration distance model selection process where blood plasma triglyceride was
17 used as nutritional indicator found that a model only including body size and an alternative
18 model including body size and sex were equally well supported ($\Delta AIC = 1.73$, Appendix 8).
19 Here, model conditional averaging showed that larger fish tended to migrate further out to sea
20 than smaller fish, while sex and blood triglycerides had limited effect on the migration
21 distance (Figure 4, Appendix 9).

22 The maximum migration distance at sea was not correlated with the timing of sea
23 entry (Spearman's correlation; $n = 167$, $P = 0.89$) or the duration of the marine residency ($n =$
24 69 , $P = 0.49$).

25

1 4 DISCUSSION

2 Overall, nutritional state, sex and body size (length) influenced the marine migration
3 behaviour of sea trout from the seven study populations in two distinct fjord systems in
4 northern Norway. Sea trout with poor body conditions and low triglyceride levels tended to
5 leave the river and estuaries and migrate to the sea, and individuals with low triglyceride
6 levels migrated to the sea earlier. Fish with poor body condition prior to the migration
7 remained at sea for a longer time-period and migrated further out in the fjords than fish in
8 better condition. Although all the nutritional indicators were found to be highly correlated,
9 this study suggests that measuring both body condition and blood plasma metabolites gave a
10 better evaluation of the nutritional state of the individuals and the impacts of nutritional state
11 on behaviour. While body condition results from the balance between energy intake vs.
12 expenditure over time frames of weeks or months, blood plasma triglycerides have previously
13 been observed to change in response to food intake over much shorter time scales (Sheridan
14 1988, Congleton & Wagner 2006).

15 Migrating to the marine environment is believed to provide better feeding
16 opportunities and potentially increased growth and reproductive capacity (Klemetsen et al.
17 2003, Thorstad et al. 2016) because of the higher productivity in marine habitats than
18 freshwater habitats in high latitude areas (Gross et al. 1988). On the other hand, energetic
19 costs related to migration and osmoregulation, the risk of predation, disease, or other factors
20 that could prevent a migratory individual from returning to freshwater spawning grounds are
21 all risk factors presumed to be higher when an individual migrates to the sea (Thorstad et al.
22 2015, Jensen et al. 2019). In this study, the observed effects of nutritional state on sea trout
23 migratory behaviour suggest that individuals in a poor nutritional state tend to engage in
24 riskier migration behaviour than fish in a better nutritional state. The results from this study
25 also suggest that individuals in a poor nutritional state were energetically limited in

1 freshwater, tipping the cost vs. benefit trade-off in favour of migration. In a previous study,
2 Boel *et al.* (2014) found that sea trout with poor body condition were most likely to migrate
3 towards the sea. Davidsen *et al.* (2014) observed that starved hatchery-reared sea trout
4 released to the wild utilized sea habitat to a greater extent than well fed hatchery fish, which
5 tended to remain in the lower parts of the river and estuarine areas to which they were
6 released. The observed relationship between nutritional state and timing of sea entry is also
7 consistent with previous studies on reconditioning post-spawn Atlantic salmon *S. salar* which
8 exhibited earlier sea entry for individuals in poor body condition (Halttunen *et al.* 2018,
9 Bordeleau *et al.* 2019). Birnie-Gauvin *et al.* (2019a) showed that elevated baseline cortisol
10 levels, possibly in response to nutritional need, were associated with earlier migration
11 towards the sea for post-spawned sea trout. Interestingly, we observed a stronger effect of
12 blood plasma triglycerides levels than of body condition factor on the timing of sea entry.
13 This may suggest behavioural response to nutritional need, as acute triglyceride deprivation
14 was a strong predictor for migratory initiation. Alternatively, it may suggest that
15 opportunistic feeding in the freshwater or estuarine habitats during early spring may
16 recondition nutritional state and delay the initiation of marine migration.

17 Once migration has occurred, sea trout with poor body condition factors tended to
18 spend more time at sea and migrate further out in the marine habitat, possibly reflecting a
19 greater need to recondition compared to individuals with better body condition factors. There
20 was a significant relationship between timing of sea entry and duration of marine residency,
21 where fish that migrated early resided longer at sea. The prolonged residency at sea may
22 enable sea trout to recondition for the next spawning and overwintering season but may also
23 include higher risk of mortality as marine habitats often have greater abundance of potential
24 predators. A previous study by Haraldstad *et al.* (2018) showed that post-spawned sea trout in
25 poor body condition were more likely to skip spawning the following season compared to

1 individuals in better body condition. Bordeleau *et al.* (2018) reported that the pre-migratory
2 level of blood plasma triglycerides was negatively correlated with the duration of marine
3 residency in veteran sea trout migrants. According to previous studies, sea trout with a low
4 body condition tended to migrate further out to sea compared with individuals in a better
5 body condition (Davidsen *et al.* 2014, Eldøy *et al.* 2015, Bordeleau *et al.* 2018). In the present
6 study, differences in characteristics of the near marine habitats among the multiple sites we
7 studied probably impacted how far the sea trout from the various rivers needed to migrate to
8 meet their metabolic demands. No correlation was found between migration distance and
9 timing of marine entry or marine residence time.

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

21 Although the nutritional status of most fish in the study was poor, there was large
22 variation in nutritional state both among individuals and groups of fish. There may be several
23 reasons for this, including differences in nutritional state after the previous growth season,
24 energy investment in previous spawning, overwintering conditions, metabolic rate and
25 feeding activity (Midwood *et al.* 2015, Auer *et al.* 2016). Some individuals had elevated

1 nutritional indicators indicative of a better nutritional status. These individuals mainly
2 belonged to the groups of fish tagged in the estuarine habitats of River Åbjøra, River
3 Lakselva and the Kosmovatnet watercourse. For these fish, elevated blood plasma
4 triglyceride level was the most obvious signal. This might suggest that the fish had started
5 feeding prior to tagging, because triglycerides become elevated a few hours after feeding
6 (Sheridan 1988), and a previous laboratory experiment documented that blood plasma
7 triglycerides recovered quickly when refeeding began after a starvation period in rainbow
8 trout *Oncorhynchus mykiss* (Congleton & Wagner 2006). Common for these groups of tagged
9 fish was that they were captured and tagged in lower parts of watercourses which have
10 relatively large estuarine areas likely suitable for opportunistic feeding during early spring.

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

21 The models in the present study provided limited support for the influence of sex on
22 migration timing, duration and distance migrated at sea. Some previous studies have reported
23 that male sea trout tended to migrate earlier (Jensen 1968, Östergren & Rivinoja 2008), while
24 others at different sites have suggested an earlier migration timing for females (Berg & Berg
25 1989). Berg & Berg (1989) also observed that females had a longer duration of marine

1 residency than males. Bordeleau *et al.* (2018) found that females migrated further from the
2 river than males and were more likely to migrate to the outer fjord areas of Tosenfjorden.
3 Although the reasons female and males differed in their migration patterns among these
4 different sites remain obscure, it suggests that a combination of local environmental
5 conditions and population characteristics may plays an important role for the trade-off
6 mechanisms shaping the migratory decisions of individuals within sea trout populations. This
7 plasticity is one of the reasons the species has been so successful.

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

23 In conclusion, despite the large individual and among-group variation observed in
24 both nutritional state and migratory behaviour, this study showed that sex, body size and pre-
25 migratory nutritional state strongly influenced the migratory patterns of sea trout. Anadromy

1 is considered a quantitative threshold trait, where environmental thresholds for triggering
2 behavioural responses are genetically determined (Ferguson 2006, Ferguson et al. 2019).
3 Previous studies have suggested that the migratory behaviour of brown trout is a continuum
4 of behavioural responses to the environmental cues experienced by the individuals in coastal
5 trout populations (Cucherousset et al. 2005, Boel et al. 2014, Villar-Guerra et al. 2014).
6 However, the importance of different factors affecting the pre-migratory nutritional state, and
7 the influence of carry-over effects are poorly understood (O'Connor et al. 2014). For
8 example, it is unknown how the success of a previous feeding migration interacts with
9 spawning investment and over-wintering conditions to determine the nutritional state and
10 subsequent marine migrations of post-spawned, veteran sea trout migrants (Bordeleau 2019).
11 As shown by Jensen et al. (2020), life history patterns or decisions adopted early in life may
12 persist throughout an individual's lifetime, and significantly affect the animal's lifetime
13 fitness. Jensen et al. (2020) showed that early migrants continued to migrate early throughout
14 their life time, had better growth, and a larger lifetime fecundity. This suggests that
15 individuals developing under favourable conditions will gain fitness benefits throughout their
16 lifetime. Jensen et al. (2020) therefore concluded that individuals that experience
17 environmental conditions as juveniles in freshwater and/or with genes that contribute to a
18 large smolt size and early smolt migration may benefit preferentially from growth
19 opportunities in the sea, and the benefits of the early adoption of anadromy enables them to
20 continue with early and longer migrations during following years. However, the fact that sea
21 trout populations do not evolve to contain exclusively early migrants highlights again that
22 there are costs that counterbalance the strategy.

23 While at sea, sea trout commonly reside in habitats heavily affected by human activity
24 (Nevoux et al. 2019). Salmon lice infestation related to open cage farming of Atlantic salmon
25 was recently evaluated as the biggest threat for Norwegian sea trout stocks (Norwegian

1 Scientific Advisory Committee for Atlantic Salmon 2019) . Serra-Llinares *et al.* (2020)
2 documented that sea trout infested with salmon lice altered their migration behaviour and
3 experienced increased mortality. The results of the present study, where fish in poor
4 nutritional state seemed to migrate to the sea earlier and spent more time at sea, suggest that
5 fish in poor nutritional state may display behavioural patterns that make them especially
6 vulnerable to such negative anthropogenic factors at sea. This is both because their longer
7 stay at sea increases the risk of being infested by salmon lice, and because they migrate to
8 areas with high salinity favourable for sea lice instead of remaining in brackish water areas
9 where the lice do not survive well. The links between migration behaviour, human induced
10 stressors and reproductive success throughout the lifetime of sea trout remain obscure. Future
11 studies examining the link between marine migration behaviour and reproductive investment
12 over consecutive years are therefore advocated.

13

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9

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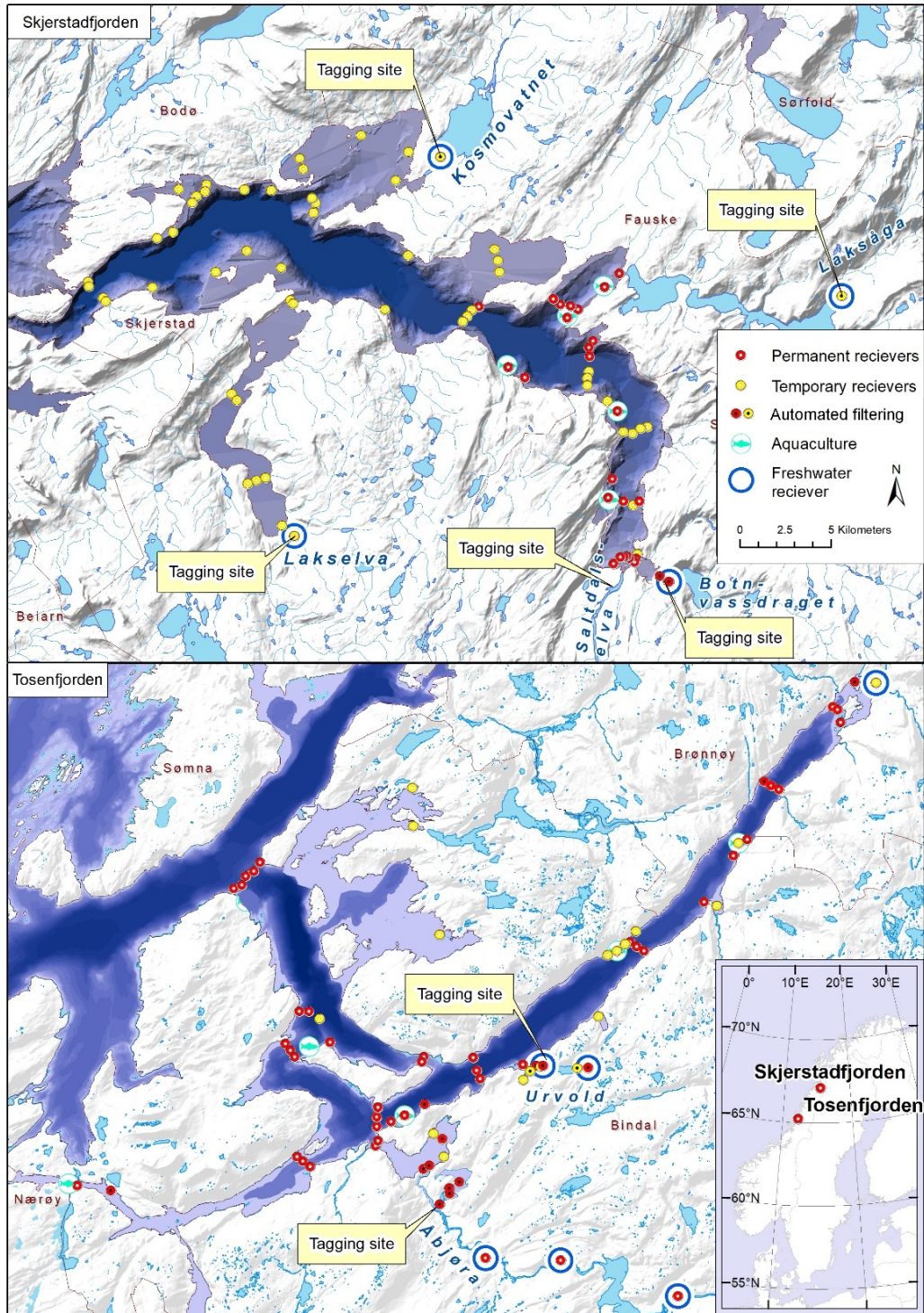
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1 Table 1: Description of fjord, watercourse, tracking year, number of individuals, date
 2 of tagging and mean (\pm SD) sea trout body size (mm) and body mass (g)

3 .

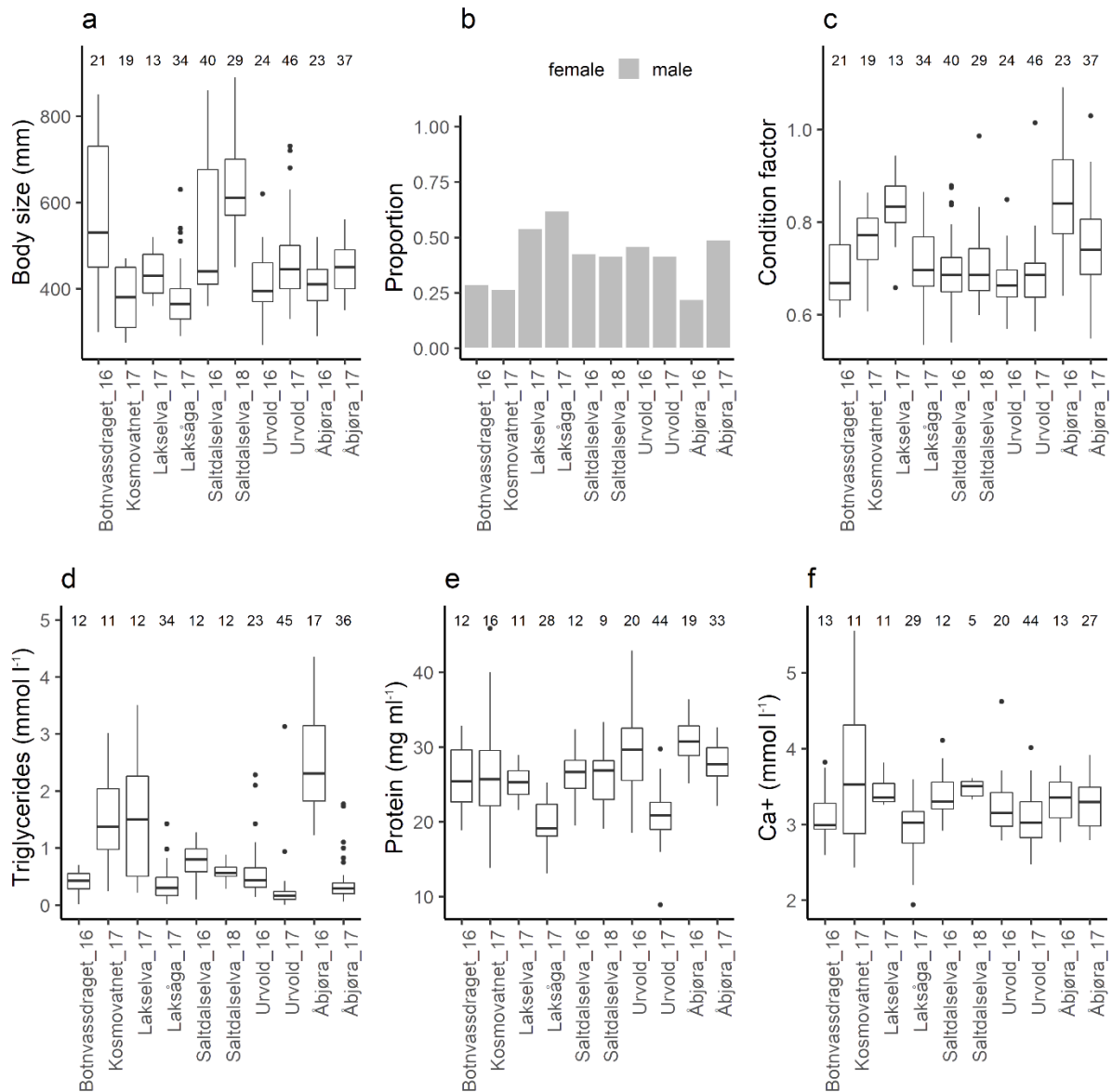
Site	Watercourse	Tracking			Body size (mm)	Body Mass (g)
		year	Tagging date	<i>n</i>		
Tosenfjorden	Åbjøra	2016	21/05/2016–	23	405 \pm 62	705 \pm 269
			26/05/2016		(290-520)	(240-1280)
Tosenfjorden	Åbjøra	2017	27/03/2017–	37	451 \pm 58	847 \pm 318
			29/03/2017		(350-560)	(400-1540)
Tosenfjorden	Urvoll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

4



1

2 Figure 1: Map over the study areas in the two fjords Skjerstadvfjorden (upper) and
 3 Tosenfjorden (lower), with tagging sites and receiver positions indicated. “Automated
 4 filtering” indicates receivers where automatic data filtering was applied to remove false
 5 detections. Light blue water surface indicates watercourses. Purple to deep blue surface
 6 colour indicate the depth of estuarine and marine habitats.

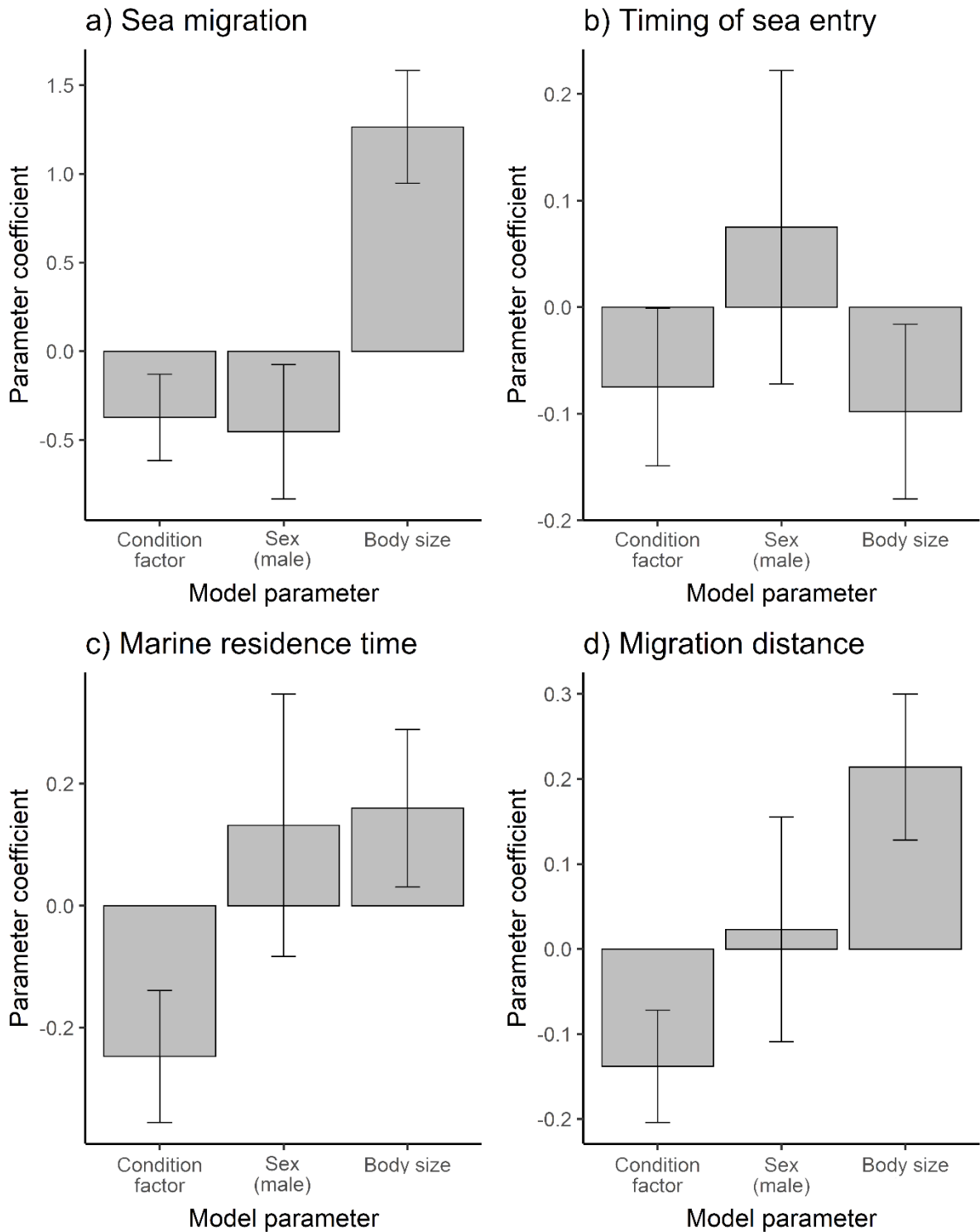


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2 Figure 2: Sex (a), body size (mm) (b), body condition factor (c), blood plasma triglycerides
 3 (d), blood plasma proteins (e) and blood plasma calcium (f) for the study's groups of tagged
 4 fish (location and year of tagging for the groups indicated on the x-axes). The stacked bar
 5 plots (a) shows the proportion of males and females in each group. The box plots show the
 6 interquartile range (boxes), median (horizontal line in boxes), the 5th and 95th percentiles
 7 (whiskers) and outliers (dots), with number of individuals in each group denoted at the top of
 8 the panels.

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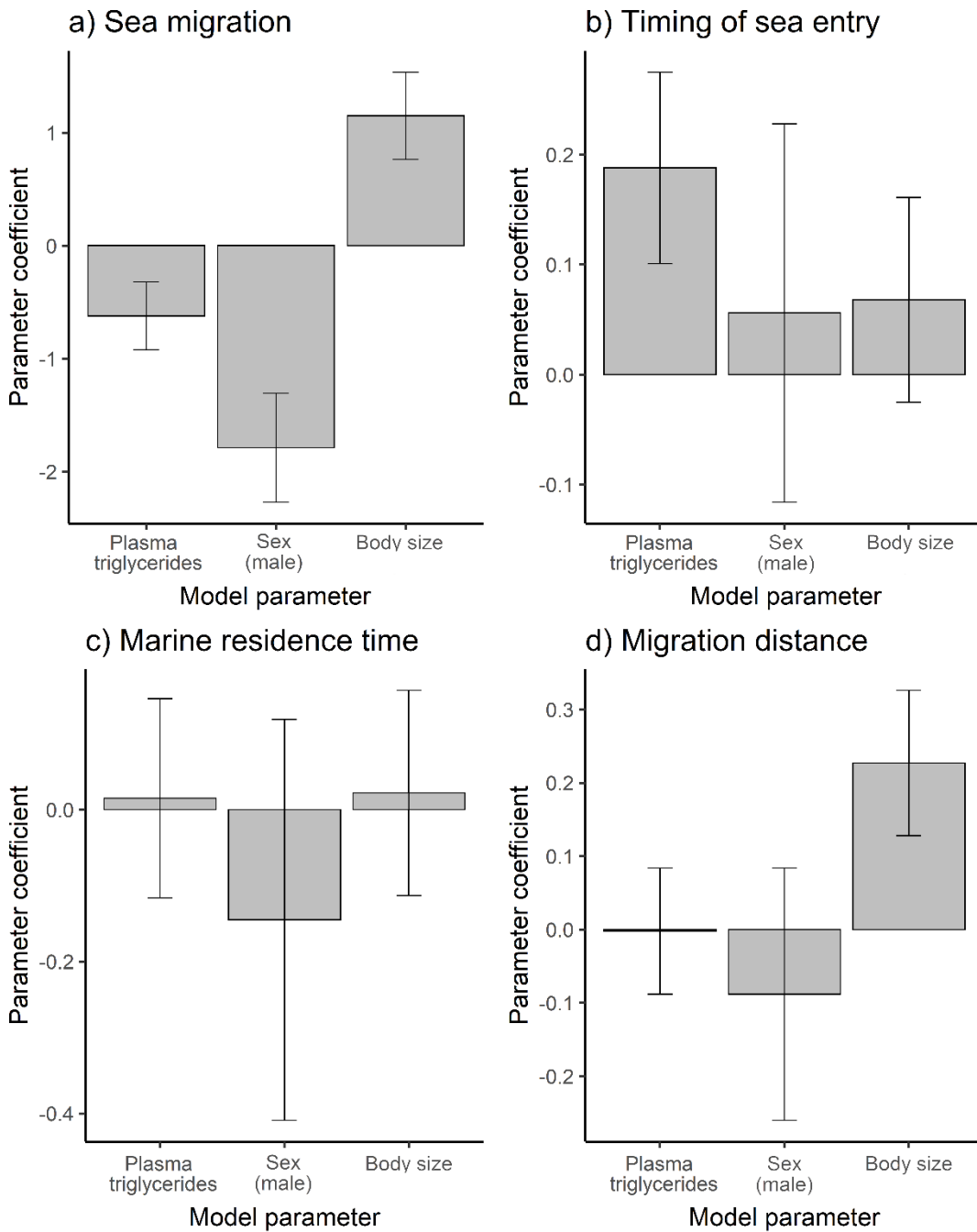
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2 Figure 3: Estimated effect of body condition factor, sex (male) and body size on the decision
 3 to migrate to sea (a), timing of sea entry (b), marine residence time (c) and migration distance
 4 at sea (d). The bar plots show the estimated parameter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

1



2

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

9

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