

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

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## 17 **Abstract**

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

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

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## 36 Introduction

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

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

58 Boel et al. 2014), as well as beyond, to short- and long-distance coastal migration (del Villar-  
59 Guerra et al. 2013; Eldøy et al. 2015; Flaten et al. 2016). This migratory continuum has been  
60 observed in both first-time migrants (i.e., parr and smolts; del Villar-Guerra et al. 2013; Boel et  
61 al. 2014; Flaten et al. 2016), as well as veteran migrants (i.e., either mature or immature  
62 individuals that have previously completed a first summer feeding migration; Eldøy et al. 2015).  
63 While the drivers of the different migratory tactics remain obscure, especially for the marine  
64 migrations of veteran migrants (Drenner et al. 2012; Thorstad et al. 2016), previous studies of  
65 first-time migrants suggest that the choice of migratory tactic is a plastic response to individual  
66 physiological state, metabolic rate, and food availability (Wysujack et al. 2009). In experimental  
67 feeding studies, brown trout exposed to low food availability had lower pre-migratory body  
68 condition factors, which has been shown to influence the decision of first-time migrants to  
69 adopt anadromy, whereas higher-condition fish tended towards non-anadromy (Davidsen et al.  
70 2014; Olsson et al. 2006; Wysujack et al. 2008). Wysujack et al. (2008) similarly concluded that  
71 energetic state (i.e., body lipid content) close to the time of actual migration was likely  
72 responsible for the choice of migratory tactic. A recent telemetry study of the marine  
73 migrations of brown trout veteran migrants concluded that migratory decisions were likely  
74 influenced by body condition (Eldøy et al. 2015). However, the link between individual pre-  
75 migratory nutritional state and the spatio-temporal extent of subsequent marine habitat use by  
76 brown trout has not been well-defined (Aldvén and Davidsen 2017).

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

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

92 By providing enhanced growth opportunities, the marine environment is believed to  
93 support higher abundances and more productive brown trout populations (Thorstad et al.  
94 2016). Marine foraging, especially in areas where nutrient rich feeding opportunities are  
95 numerous (e.g., pelagic fish species, Davidsen et al. 2017), allows anadromous individuals to  
96 attain larger sizes than their freshwater resident counterparts, which for females translates to a  
97 higher fecundity-at-age (Jonsson and Jonsson 1993). Coupled with the higher prevalence of  
98 anadromy in females (as increased size represents a more direct fitness gain for females), it is  
99 likely that anadromous brown trout make important contributions to the species' population  
100 dynamics (Thorstad et al. 2016), although this has yet to be fully investigated. With the recent  
101 increase in marine mortality and decreased growth of anadromous brown trout due to

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

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

## 122 **Materials and methods**

### 123 **Study area and acoustic receiver array**

124 The study was conducted in the inter-connected, marine, Tosenfjord and Bindalsfjord  
125 (65.13°N, 12.13°E) in Nordland country, Norway (Fig. 1). Brown trout were captured from two  
126 different watercourses (i.e., freshwater systems): Åbjøra and Urvold. Both watercourses,  
127 situated ~14 km apart, drain into the Tosenfjord (~97 km<sup>2</sup>, maximum depth of ~550 m) which  
128 then leads to the Bindalsfjord (~91 km<sup>2</sup>, maximum depth of ~700 m) and finally to the Atlantic  
129 Ocean, located at ~33 km from Åbjøra and Urvold estuaries (defined as the interface between  
130 river mouth and fjord). During the study period, from April 8 – September 5, 2015 the surface  
131 salinity level (~1 m depth) of the Åbjøra estuary (i.e., Floet, station 69 in Fig. 1) and the outer-  
132 fjord (station 1) varied respectively from 0.0 – 28.6 ppt (mean = 9.4 ppt) and 4.8 – 33.5 ppt  
133 (mean = 20.0 ppt). Surface water temperature (~1 m depth) for those two sections of the fjord  
134 varied from 3.0 – 17.6 °C and 4.5 – 17.0 °C, respectively. The eastern section of Tosenfjord is  
135 similar to other inner-fjord areas in terms of depth, temperature, and surface salinity level that  
136 varies between ~0 – 34 ppt depending on areas, freshwater inputs, and tidal cycles.

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

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

#### 149 **Capture, blood sampling and tagging**

150 A total of 32 brown trout veteran migrants were captured, sampled (i.e., for blood,  
151 measurements and scales), and tagged with an internal acoustic transmitter between April 9 -  
152 12, 2015 prior to their seaward feeding migration; 20 individuals from the tidal zone in river  
153 Åbjøra and 12 from lake Urvold (Table 1). At capture, veteran migrants were distinguished from  
154 smolts and parr based on size, which was later confirmed by scale readings. Fish were captured  
155 using a combination of angling (n=26) and gill netting (n=6; 35-42 mm mesh size), and efforts  
156 were made to reduce stress and the risk of injury by minimizing fight times and monitoring the  
157 gill net continuously (e.g., the net was pulled-in as soon as vibrations were felt). The average  
158 time-to-blood-sampling, as calculated from the first encounter with fishing gear, was similar for  
159 both methods;  $7:51 \pm 5:15$  min for angling and  $10:32 \pm 5:20$  min for gill netting (p-value = 0.29;  
160 Welch Two Sample t-test). Shortly after landing and prior to anaesthesia, ~2 ml blood samples  
161 were collected via caudal venipuncture from all fish (as described in Huston 1990). Samples  
162 were then placed in an ice-water slurry until processing. Following blood sampling, fish were  
163 kept for no more than 2 hours in a net cage situated in the river to allow recovery from capture  
164 and sampling before the tagging procedure. Prior to tagging, brown trout were anesthetized  
165 using 2-phenoxyethanol at a concentration of  $0.5 \text{ ml L}^{-1}$  water (SIGMA Chemical Co., USA).  
166 Depending on fish size, 69 kHz MP-9 (for fish between 310-390 mm in total length) or 69 kHz  
167 MP-13 acoustic transmitter (for fish between 400 to 720 mm in total length) were inserted in



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

#### 181 **Blood processing and triglycerides assay**

182         Within three hours of blood sampling, samples were centrifuged at 3300 g for 10  
183 minutes and the resultant plasma was collected and flash-frozen in dry ice before being  
184 transferred to a -80 °C freezer. Plasma triglyceride levels were assayed in duplicate using a  
185 commercially available colorimetric kit (Cayman Chemical Company, USA) and read at 530 nm  
186 with a BioTek Synergy HTX microplate reader (BioTek Instruments, Inc., USA), according to the  
187 manufacturer's standard procedure. The mean coefficient of variation between duplicates was  
188 3.9%.

#### 189 **DNA sex determination**

190 DNA was extracted from ethanol preserved fin clips with the QuickExtract kit (Epigen),  
191 according to manufacturer's protocol with the exception for the extraction volume, which was  
192 reduced to 150  $\mu$ l. Sex was determined by PCR amplification of a 200 pb fragment situated in the  
193 first intron of the male specific SDY gene, using the Salmo-sdY-F and Salmo sdY-R primers  
194 (Quéméré et al. 2014). The PCR was performed in 10  $\mu$ l reactions using the Qiagen Multiplex PCR  
195 kit. The following PCR profile was used: 95°C for 15 min, 11 cycles of touchdown PCR, 94°C for 30  
196 seconds, 63–52°C for 30 seconds, 72°C for 1 minute, followed by 25 cycles of 94°C for 30 seconds,  
197 52°C for 30 seconds, 72°C for 1 minute, with a final extension at 72°C for 10 minutes. Sex was  
198 scored by running the PCR products on 1% Agarose gels. Sex could be determined with  
199 confidence for all but one fish, so this individual had to be excluded from final models including  
200 sex as an explanatory variable.

## 201 **Data analysis**

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

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

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

234 41 and 42, as it had to cross that gate. Overall, out of a total of 203 gate-crossing events that  
235 occurred during the entire study period, individuals were detected on the gate 92% of the time.  
236 The detection efficiency (and location) of individual gates were as follow: 100% in Åbjøra  
237 estuary (stations 67 – 68, Fig. 1); 100% on Osane opening gate (stations 31 – 32); 91% on Terråk  
238 gate (stations 33 – 35); 100% on Sørfjord gate (stations 28 – 30); 100% on Bindalsfjord west  
239 gate (stations 11 – 13); 95% on Bindalsfjord east gate (stations 16 – 17); 86% on Tosenfjord  
240 outer gate (stations 40 – 42); 81% in Urvold estuary (stations 43 – 44); 100% on Tosenfjord  
241 central gate (stations 45 – 47); 100% on Tosenfjord east gate (stations 18 – 20); and 100% on  
242 Tosbotn gate (stations 26, 52, 53).

#### 243 *i. Riverine/lacustrine residency versus marine migration*

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

#### 255 *ii. Marine migratory tactics*

256           Once individuals were detected entering the fjord, fish from both populations were  
257 faced with similar habitat choices. Based on migratory distances and the areas of the fjord that  
258 were utilized, three different marine migratory tactics were identified (Fig. 1); i. short-distance  
259 migration (furthest detection <2 km from the river mouth; Fig. 2a); ii. long-distance/inner-fjord  
260 migration (furthest detection from ~13 to 28 km of the river mouth, without any detection on  
261 the outer receiver line, Fig. 2b); and iii. long-distance/outer-fjord migration (furthest detection  
262 >21 km from the river mouth and detected on the outer receiver line; Fig. 2c). To test the  
263 prediction that, within marine migrants, fish in poorer nutritional state (i.e., low body condition  
264 factor and depleted plasma triglyceride level) migrate further out in the marine environment,  
265 multinomial logistic regression models were performed (“multinom” package in R), suitable for  
266 nominal categorical response variable with three outcomes, here: short-distance, long-  
267 distance/inner-fjord, or long-distance/outer-fjord migration (Kwak and Clayton-Matthews 2002;  
268 Zuur et al. 2007a). The p-values of the regression coefficients were computed using Wald z-  
269 tests. Furthermore, to facilitate the interpretation of the model’s coefficients, changes in the  
270 predicted probabilities of adopting a given migratory tactic as a function of explanatory  
271 variables were calculated for each tactic using the “predict” function in R (Kwak and Clayton-  
272 Matthews 2002).

### 273 *iii. Marine residency period*

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

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

#### 283 *iv. Marine survival*

284         The marine minimum survival was estimated from the initial number of fish that were  
285 detected entering the fjord system and the proportion of them that came back to the rivers,  
286 completing their summer marine migration (as indicated by detection at a river  
287 mouth/estuarine receiver conditional to later detection on upstream receivers). In addition to  
288 those fish, marine migrants that were detected returning to Åbjøra or Urvold estuary (stations  
289 67-69 in Åbjøra, and 43-44 in Urvold, Fig. 1) in late summer and fall were also deemed to have  
290 survived their marine summer feeding migration, despite not re-entering freshwater systems.  
291 These fish were assumed to be over-wintering in estuaries, as they were detected there  
292 through the fall and early winter. Marine migrants that presumably died or disappeared from  
293 the acoustic array through the summer might be the result of tag lost, technical failure of the  
294 tag, exhaustion of tag battery life, residency in uncovered areas, or animal mortality. To test the  
295 prediction that survival to completion of the summer feeding migration is lower for long-  
296 distance/outer-fjord migrants in comparison with other marine migratory tactics, binomial  
297 logistic regression models using the logit link were performed (“glm” function in R).

## 298 **Results**

### 299 **i. Riverine/lacustrine residency versus marine migration**

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

### 320 **ii. Marine migratory tactics**

321 For marine migrants (pooled sample of 9 fish from Åbjøra and 12 from Urvold), 3  
322 individuals (14%; 2 females and 1 male) were classified as short-distance migrants, 7 individuals  
323 (33%; 2 females and 5 males) were classified as long-distance/inner-fjord migrants, and 11  
324 individuals (52%; 6 females, 4 males, one unknown sex) were classified as long-distance/outer-  
325 fjord migrants (as summarized in Table 1). In assessing which factors might influence marine  
326 migratory decisions, the best fitting multinomial logistic model included body condition factor  
327 and sex as explanatory variables (Table 2). The other explanatory variables considered, i.e.,  
328 population, plasma triglycerides, length and mass, were not retained in the model during the  
329 stepwise process. Because population of origin was not retained as an influential explanatory  
330 variable, and in combination with the observation that a mix of fish from both populations were  
331 present in all three migratory tactics (Table 1), we pooled fish from both populations in a single  
332 model. In support of our second prediction, for long-distance migrants, the probability of outer-  
333 fjord migration decreased significantly with increasing body condition factor (-20.7 in the log  
334 odds of migrating to the outer-fjord following a one unit increase in body condition,  $p = 0.027$ ,  
335 Table 2). Thus, fish migrating to the outer part of the fjord were generally in the poorest  
336 condition prior to migration. Comparing sexes, for long-distance migrants, the log odds of  
337 migrating to the outer section of the fjord versus staying in the inner part increased by 3.15 for  
338 females, in which 75% (6/8) migrated to the outer section versus 44% (4/9) in males (although  
339 marginally non-significant at  $p = 0.058$ , Table 2). To facilitate interpretation, the predicted  
340 probabilities of adopting a given marine migratory tactic as a function of body condition factor  
341 and sex were calculated using the regression coefficients (Fig. 3). Body condition factor and sex  
342 mostly affected the probabilities of adopting the long-distance/outer-fjord versus long-  
343 distance/inner-fjord tactic, with no significant influence on the decision to undertake a short-



344 distance marine migration (Table 2). However, we interpret the latter result with caution due to  
345 the low number of short-distance marine migrants. Moreover, following the observation that  
346 no significant morphological and physiological differences (i.e., in length, mass, body condition  
347 factor, and plasma triglyceride level) existed between long-distance/inner-fjord and short-  
348 distance migrants ( $p$ -values  $> 0.68$ ; Welch Two Sample  $t$ -tests), the two tactics were pooled to  
349 take a closer look at what might be driving the decision to migrate to the outer section of the  
350 fjord (reducing the tests to only two marine migratory outcomes: outer-fjord versus inner-fjord  
351 migrants). In this analysis, female outer-fjord migrants had significantly lower body condition  
352 factor prior to migration compared to inner-fjord migrants ( $0.79 \pm 0.05$  vs  $0.92 \pm 0.05$ ,  $p =$   
353  $0.006$ , Welch Two Sample  $t$ -test, Fig. 4). A similar, but non-significant difference in body  
354 condition was observed in males. Pooling both sexes, outer-fjord migrants had significantly  
355 lower body condition ( $0.75 \pm 0.09$ ) than inner-fjord migrants ( $0.87 \pm 0.10$ ,  $p = 0.005$ , non-  
356 parametric Mann–Whitney  $U$  test). While male outer-fjord migrants were significantly smaller  
357 than inner-fjord migrants ( $433 \pm 59$  mm versus  $576 \pm 100$  mm,  $p = 0.022$ , Welch Two Sample  $t$ -  
358 test), females showed the opposite tendency with outer-fjord migrants being generally larger  
359 (range: 400-640 mm) than inner-fjord migrants (range: 310-445 mm, although the difference in  
360 mean length was not significant, Fig. 4). Supporting the assumption that plasma triglyceride  
361 concentration is informative of individuals' post-winter/pre-migratory nutritional state, body  
362 condition factor and plasma triglycerides were correlated at  $r = 0.45$  ( $p = 0.009$ ). Interestingly,  
363 females displayed a negative correlation between length and pre-migratory body condition  
364 factor ( $r = -0.57$ ,  $p = 0.02$ ), and similarly between length and plasma triglyceride concentration  
365 ( $r = -0.48$ ,  $p = 0.06$ ), so that larger females were generally found in poorer pre-migratory

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

### 368 **iii. Marine residency period**

369 Of the individuals that were detected entering the fjord in the spring (N = 21), a total of  
370 14 individuals (5 from Åbjøra and 9 from Urvold) came back to the river/lake later in the spring  
371 or during the summer (May 23<sup>rd</sup> to July 16<sup>th</sup>; median of July 4<sup>th</sup>). Individuals' marine residency  
372 period varied between 32 and 83 days (average of 59 days). Looking at the factors that might  
373 explain inter-individual variance in the marine residency period, the best fitting linear  
374 regression model included plasma triglyceride concentration and marine migratory tactic (Table  
375 3; multiple  $R^2 = 0.60$ ). All other potential explanatory variables (population of origin, body  
376 condition factor, length, mass, and simple interactions) were not retained in the model during  
377 the stepwise process. This, combined with the fact that no significant differences existed in the  
378 marine residency period between fish from the two study populations ( $p > 0.20$ ; Welch Two  
379 Sample t-test), allowed us to pool fish from the two populations. Out of the 14 individuals that  
380 came back to freshwater, 7 were long-distance/outer-fjord migrants, 6 were long-  
381 distance/inner-fjord migrants, and only one was a short-distance migrant. In order to meet the  
382 assumptions of general linear regression models (i.e., independence, normality of residuals,  
383 homoscedasticity, and balanced influence of individual observations), the short-distance  
384 migratory tactic (N = 1) had to be removed from the final model as it had high leverage (hat  
385 value 3.5-fold greater than the average, "hatvalue" function in R) which led to a deviation from  
386 normality (Zuur et al. 2007b). In support of our third prediction, within migratory groups, the  
387 duration of marine residency was negatively correlated with pre-migration plasma triglyceride

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

#### 394 **iv. Marine survival**

395 Out of a total of 21 veteran migrants that were detected entering the fjord in the spring,  
396 seven were not detected coming back to freshwater. Of those, four individuals (i.e., three  
397 females and one male) were presumed to have survived but opted for over-wintering in the  
398 marine environment as they were detected in estuaries in the fall and winter (summarized in  
399 Table 1), apparently deciding to skip spawning. Those three females were generally smaller  
400 (range: 310-420 mm) than the five females that had migrated back to freshwater (range: 405-  
401 640 mm), and were possibly still immature (Klemetsen et al. 2003). For the remaining three  
402 individuals that neither returned to freshwater nor over-wintered in estuaries, two disappeared  
403 from the array (as they were last detected in late May/early June in the outer section of the  
404 fjord, and were never heard from again despite the array remaining in place until fall 2017) and  
405 one was continuously detected on a single receiver for  $>6$  months starting in mid-June.  
406 Minimum marine survival through the summer feeding migration was thus estimated at 86%, as  
407 at least 18 out of 21 individuals that migrated out into the fjord survived to return to  
408 freshwater, or were detected in estuaries in the fall and winter. In partial support of our fourth  
409 prediction, all three fish that presumably died or disappeared at in the marine environment

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

## 416 **Discussion**

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

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

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

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

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

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

476 2017), although there could also be risks associated with migration to the outer-fjord that  
477 might limit their time there, such as predation (Lyse et al. 1998) and sea lice parasitism  
478 (Thorstad et al. 2015). Within migratory groups that travelled to similar areas of the fjords,  
479 marine residency time was negatively correlated with plasma triglyceride levels so that fish with  
480 depleted circulating lipid levels spent more time in the marine environment, perhaps reflecting  
481 higher nutritional requirements (Table 3; Fig. 5). The duration of the marine residency period is  
482 thus probably influenced by individual lipid depletion (or nutritional requirements), and by the  
483 relative productivity of the marine habitat to which the fish migrate. As revealed from the  
484 significant positive correlation with body condition, plasma triglyceride concentration is  
485 believed to reflect post-winter, pre-migratory nutritional condition in these fish that were  
486 captured in early spring. Collectively, our findings suggest a condition-dependent migratory  
487 tactic in brown trout veteran migrants, in which an individual's pre-migratory nutritional state  
488 influences its spatio-temporal use of the marine environment.

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

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

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

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- 653

654 **Tables**

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

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

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



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

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

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

680	Explanatory variable	Coefficient	SE	t-statistic	p-value
681					
682	Intercept	67.5	5.9	11.5	$4.5 \times 10^{-7}$
683	Migratory tactic				
684	Long-dist./in	15.3	5.8	2.6	0.025
685					
686	Triglycerides (mmol L <sup>-1</sup> )	-23.7	8.0	-3.0	0.015

687 Multiple R<sup>2</sup> = 0.60

## 688 **Figures**

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

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

703

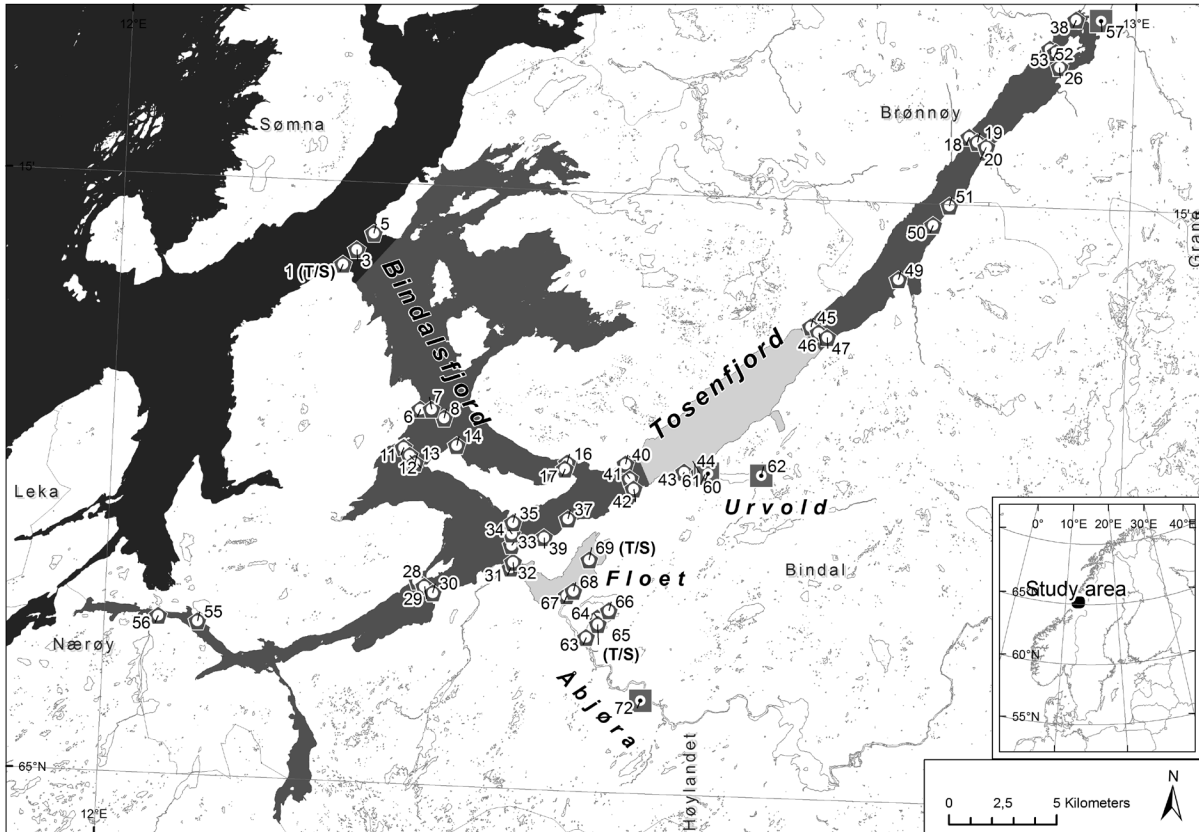
704 Fig. 3. Predicted probabilities of adopting a given marine migratory tactics as a function of body  
705 condition factor and sex, as calculated from the regression coefficients (information presented  
706 in Table 2). The shaded areas represent the 95% confidence intervals.

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

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

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

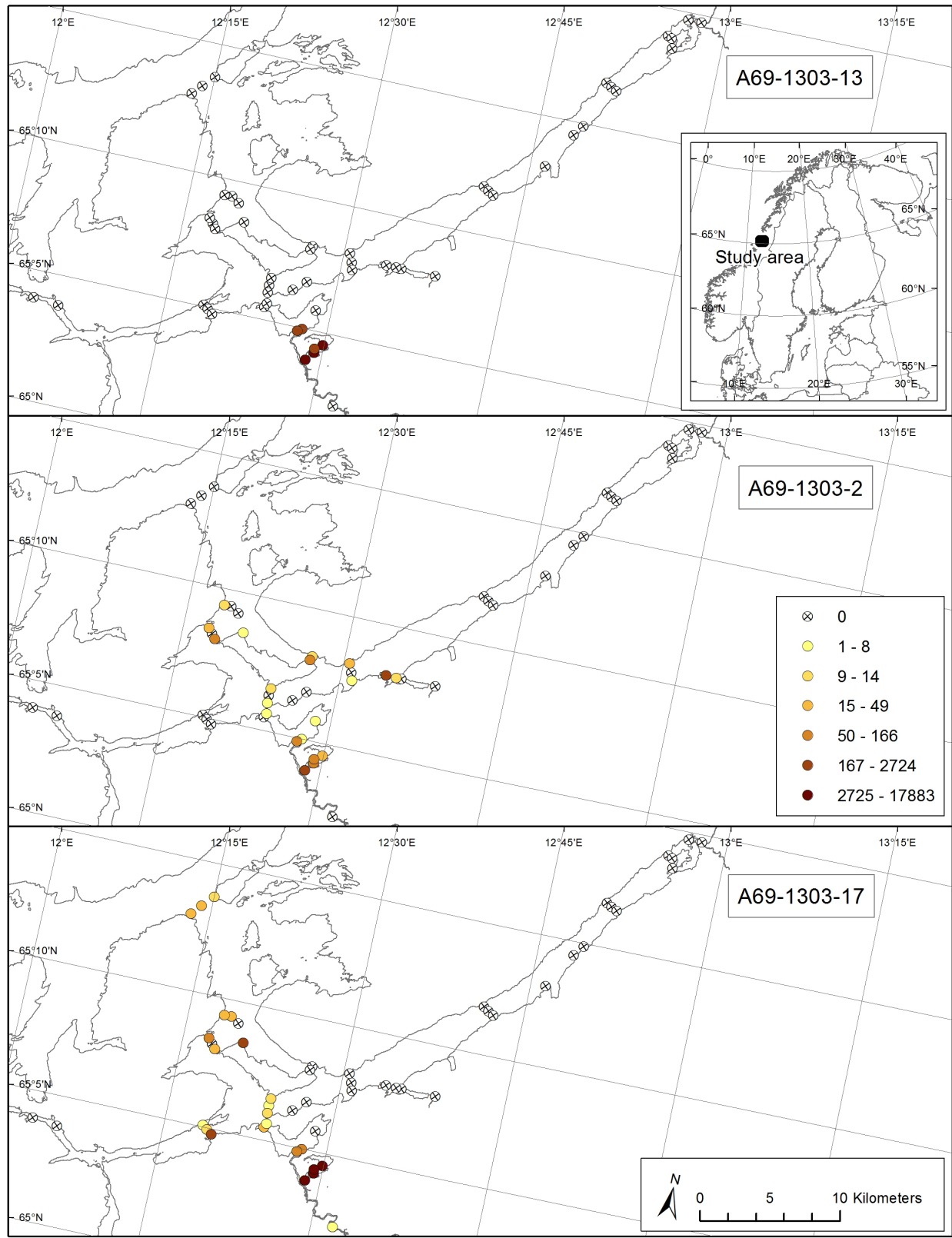
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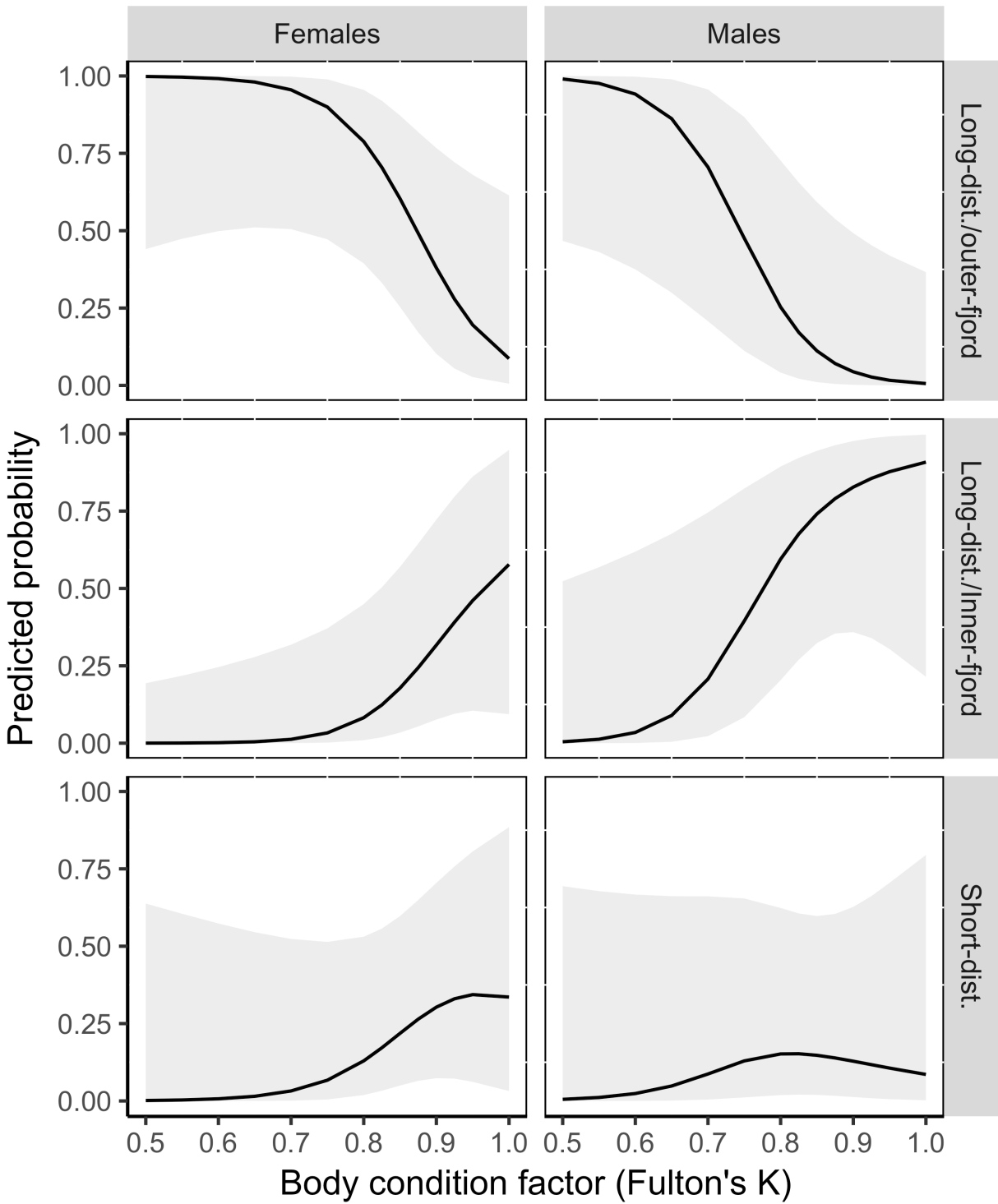
720 Figure 1:

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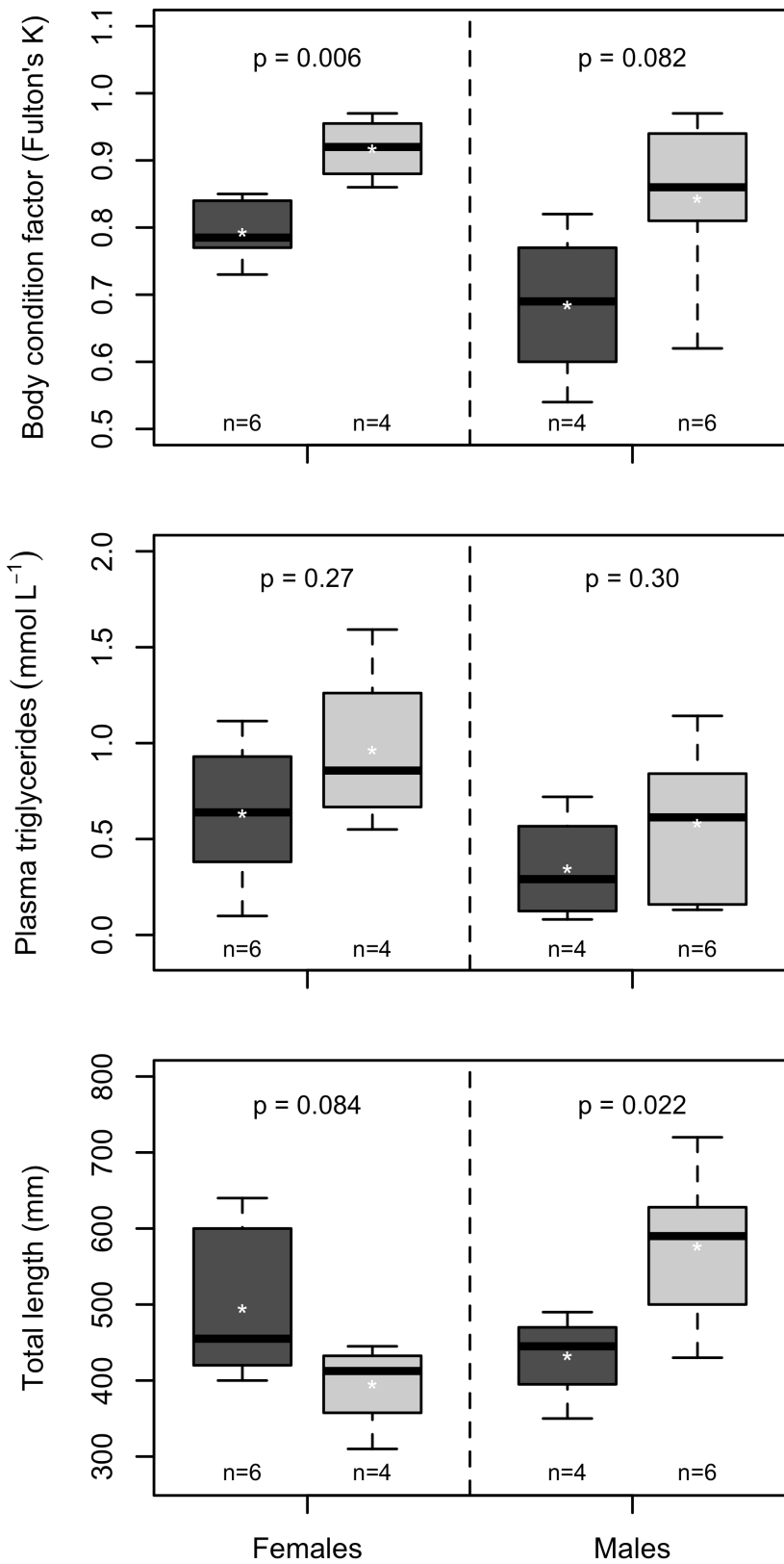
723 Figure 2:



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725 Figure 3:

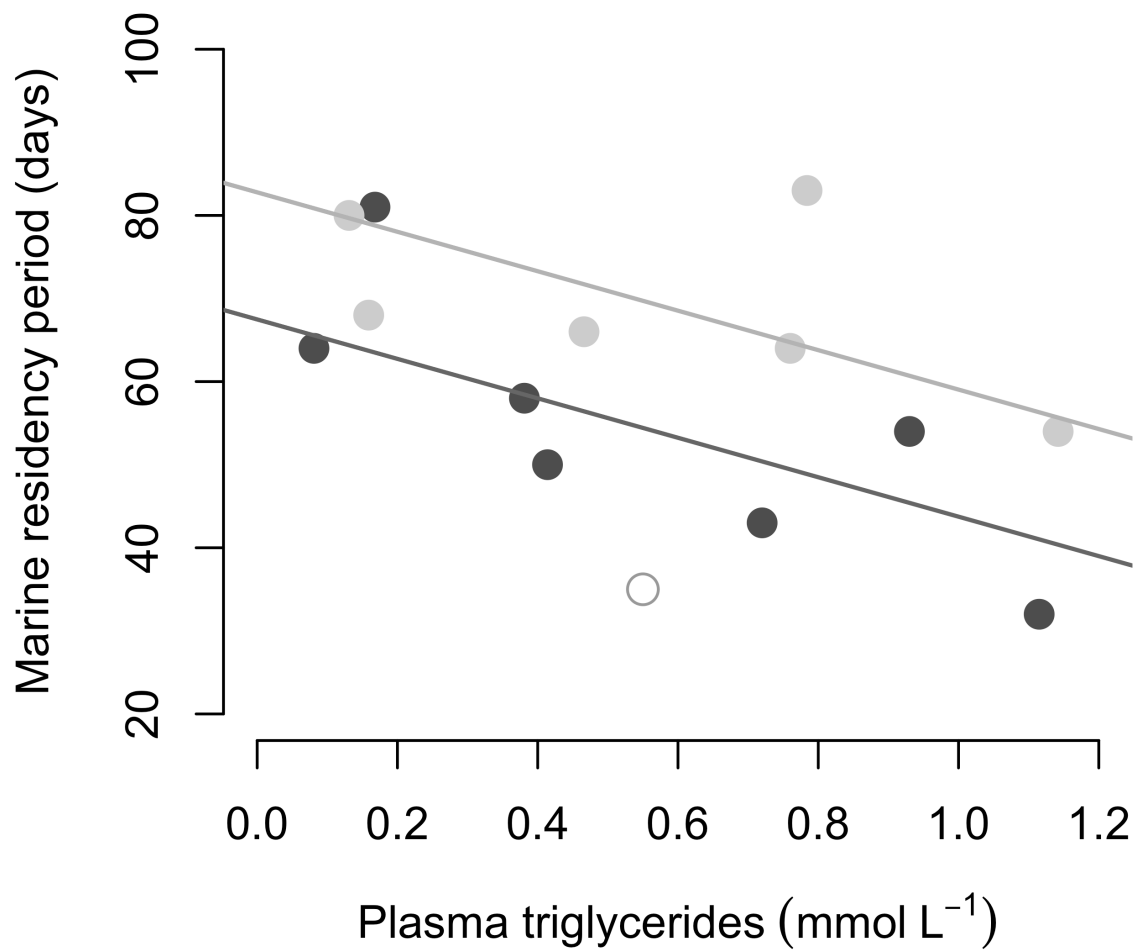
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728 Figure 4:





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730 Figure 5: