Brown trout (*Salmo trutta* L. 1758) and Arctic charr (*Salvelinus alpinus* (L. 1758)) display different marine behaviour and feeding strategies in sympatry

J. G. Davidsen[1*], A. Halvorsen[2], S. H. Eldøy[1], E. B. Thorstad[3] & L. A. Vøllestad[2]

[1]NTNU University Museum, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

[2]University of Oslo, Department of Biosciences, Center for Ecological and Evolutionary Synthesis, P. O. Box 1066 Blindern, NO-0316 Oslo, Norway

[3]Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway.

*Corresponding author: Jan Grimsrud Davidsen, NTNU University Museum, Norwegian University of Science and Technology, NO-7491 Trondheim; Norway. Tel.: +47 922 66586; email: jan.davidsen@ntnu.no.

Running headline: Marine migration and feeding of anadromous brown trout and Arctic charr

27   **Abstract**

28   Brown trout (*Salmo trutta* L. 1758) and Arctic charr (*Salvelinus alpinus* (L. 1758)) tagged with

29   acoustic transmitters migrated from freshwater to the sea mainly in May and June, but with

30   large individual variation in migration timing. For *S. trutta*, large individuals (42-86 cm L_T)

31   migrated earlier in the season than small individuals (18-27 cm). For *S. alpinus*, no such pattern

32   was found, likely because of the small size range of tagged fish (28-41 cm). *S. trutta* stayed

33   longer at sea than *S. alpinus* (average two *vs*. one month). Early migrants of *S. trutta* stayed for

34   a shorter period at sea than late migrants, while no such pattern was observed for *S. alpinus*.

35   Large *S. trutta* moved quickly away from the river and spent average 3 days to reach a receiver

36   line 20 km from the river mouth, while small *S. trutta* and *S. alpinus* migrating that far spent 2-

37   3 weeks on the same distance. *S. trutta* utilized the entire fjord system and had a greater

38   proportion of long-distance migrants (> 20 km, 78% and 59 % of large and small *S. trutta*) than

39   *S. alpinus* (29%). *S. alpinus* mostly stayed in the inner fjord areas and none were recorded in

40   the outermost part of the fjord. The difference in use of marine areas may be caused by variation

41   in prey choice and spatial distribution of the preferred prey groups. Stable isotope analysis

42   showed that *S. trutta* had been feeding at a higher trophic level than *S. alpinus*. *S. trutta* had

43   mainly fed on marine fish and shrimps, while *S. alpinus* had large proportions of freshwater

44   invertebrates in the diet, suggesting that the estuary with benthos and amphipods drifting from

45   the river was an important feeding habitat for *S. alpinus*. In conclusion, major differences in

46   habitats use, migration patterns and feeding strategies were found between sympatric

47   anadromous *S. trutta* and *S. alpinus* while at sea.

48

49   **Key words**: acoustic telemetry, diet analyses, marine migrations, sea run Arctic charr, sea trout,

50   stable isotopes

Introduction

Animals in many taxa use migration between habitats as a strategy to increase individual growth, survival, and lifetime reproductive success (Dingle, 1996; Chapman *et al.*, 2011; Shaw, 2016). Some migratory fish move between salt- and freshwater during different parts of the life cycle, including many of the salmonids, such as brown trout (*Salmo trutta* L. 1758) and Arctic charr (*Salvelinus alpinus (*L. 1758*)*). *S. trutta* and *S. alpinus* spawn in freshwater and may remain in freshwater during their entire life. However, in populations having free access to the sea, it is common that some or all individuals undertake marine feeding migrations, followed by a return migration to the watercourse for spawning and/or overwintering (Klemetsen *et al.*, 2003).

Migration to better feeding grounds at sea is associated with increased growth (Gross *et al.*, 1988; Jonsson & Jonsson, 1997; Solomon, 2006) and thereby increased fecundity because number of eggs increases with body size and larger males become more successful when (Hendry *et al.*, 2004; Fleming *et al.*, 1996). However, migration may be costly by for example increased mortality rates and delayed maturation (Gross, 1987; Jonsson & Jonsson, 1993; Jensen *et al.*, 2019). Migrating is also energy demanding in terms of distance travelled, osmoregulation, and physiological processes that prepare the fish for life at sea (McDowall, 1988; Jonsson & Jonsson, 1993; Hendry *et al.*, 2004).

In previous studies, it has been observed that *S. trutta* typically migrate further than *S. alpinus* (Jonsson, 1989; Klemetsen et al., 2003), and stay longer at sea during the marine feeding migration (Berg and Berg, 1989a; Jensen et al., 2014; Bordeleau et al., 2018; Davidsen et al. 2018a). Both species are opportunistic generalist feeders, and their diet is expected to reflect changes in food availability, habitat, season, age, and size (Bridcut and Giller, 1995; Klemetsen et al., 2003). Also within the species, there is large variation among individuals and

76   populations in the duration and distance of the marine migration (McDowall, 1988; Klemetsen

77   *et al.*, 2003; Eldøy *et al.*, 2021). Individuals typically migrate to sea in spring or early summer

78   and return to the watercourse in late summer or fall, but there are many exceptions to this

79   pattern.

80   *S. alpinus* are usually slow-growing and late-maturing and may spend many years in

81   freshwater before their first migration to sea (Johnson, 1980; McDowall, 1988; Klemetsen *et*

82   *al.*, 2003). They usually overwinter in freshwater habitats. After their first marine migration,

83   most *S. alpinus* migrate annually until they reach first maturity, after which they may continue

84   to migrate annually or skip migrations for several years before migrating again (Johnson, 1980;

85   McDowall, 1988). In *S. trutta*, some individuals live most of the life at sea, some migrate to sea

86   and remain there for two or more years before returning, whereas others migrate to sea for only

87   a few weeks or months at a time (McDowall, 1988; Klemetsen *et al.*, 2003; Thorstad *et al.*,

88   2016).

89   The biology of both *S. trutta* and *S. alpinus* have been extensively studied, but most

90   studies focus on the freshwater part of the life cycle (ICES, 2013). The marine life of these

91   species is less studied, particularly in *S. alpinus*, despite the ecological, economic, and cultural

92   importance anadromous forms of these species represent. In recent decades, population declines

93   in both species have been observed across Europe, and deteriorating conditions in both marine

94   and freshwater environments have contributed to this (Svenning *et al.*, 2012; ICES, 2013;

95   Anon., 2022). In Northern Norway, anadromous populations of *S. alpinus*, *S. trutta* and Atlantic

96   salmon (*Salmo salar* L.1758) coexist, but in recent years recreational catches of *S. alpinus* have

97   decreased (Svenning *et al.*, 2016; Svenning *et al.*, 2021). Svenning *et al.* (2016) suggested that

98   juvenile Atlantic salmon may benefit from a warmer climate at the expense of the more cold-

99   water-adapted *S. alpinus*. In addition, these salmonid species are impacted negatively by a range

100   of human activities in coastal areas, in particular by Atlantic salmon farming and the spread of

101   salmon lice (*Lepeophtheirus salmonis* Krøyer 1837) (Thorstad *et al.*, 2015) and other pathogens

102   from these farms. The construction of harbours, roads and other installations, dredging, flood

103   control, boat traffic and other activities may also impact these species in the estuaries and near-

104   coastal areas. To be able to assess impacts and implement mitigation measures, it is necessary

105   to know the timing of migrations and habitat use of the affected species. In order to preserve

106   these species and their anadromous forms for the future, it is therefore crucial to understand

107   their behaviour at sea.

108   In this study, our aim was to compare marine migration patterns and feeding behaviour

109   of anadromous *S. trutta* and *S. alpinus* through studies of sympatric populations in northern

110   Norway. The hypothesis was that *S. alpinus* had migrations of shorter distance from the home

111   river, shorter duration of marine stays, and were feeding at a lower trophic level than *S. trutta.*

112   Acoustic telemetry was used to document migration timing, duration, distance travelled, and

113   space use of the fjord system, while stable isotope analysis was used to estimate important prey

114   groups for each species during the marine migration. The combined use of acoustic telemetry

115   and stable isotope analyses made it possible to link the behaviour observed during the marine

116   feeding migration with the general feeding habits of the two species.

117

118   <u>Materials and methods</u>

119   Study area

120   The study was conducted during 2016-2018 in a 51 km long North-Norwegian fjord system

121   (67°*N* 15°*E*, Figure 1), which consists of Saltdalsfjorden and Skjerstadfjorden. Eight Atlantic

122   salmon farms are located in the area (Figure 1). The Botnvassdraget watercourse is connected

123   to Saltdalsfjorden via the river Botnelva.

124   Water temperature and depth in river Botnelva (Figure 2), and temperature and salinity at

125   several receiver locations in the fjord (Supporting information, Figure 1) were recorded every

126   fourth hour by using depth-, temperature- and salinity data loggers (Star-Oddi, model DST

127   milli-TD, DST milli-CT).

128

129   Fish capture, tagging, and tracking

130   In total, 21 *S. alpinus* (5 females, 16 males) and 49 *S. trutta* (24 females, 18 males, seven

131   unknown gender) were captured for tagging in lake Botnvatnet and river Knallerdalselva.

132   Groups of large *S. trutta* were captured during spring and fall 2016 and *S. alpinus* during fall

133   2016 and 2017, by using fishing rods, gill nets (35-45 mm mesh size), dip nets and flashlights

134   for capture at night. Small *S. trutta* were capture during spring 2018 using fyke nets dedicated

135   to the capture of down migrating smolts. The fish were kept in holding nets until tagging (< 4

136   hours). Mean total length (L_T) was 332 mm (range 280-410) for *S. alpinus*, 204 mm (range 178-

137   268) for small *S. trutta* and 649 mm (range 420-860) for large *S. trutta* (Figure 3).

138   The fish were anaesthetized in a solution of phenoxy-ethanol (EEC No 204 589-7, 0.5

139   mL per L of water). Total length (L_T,) and mass of the fish were measured. The tag was

140   inserted into the body cavity through a 1.5-2.0 cm long incision on the ventral surface of the

141   fish, anterior to the pelvic girdle. The incision was closed by 2-3 sutures (Resolon 3/0). Six

142   tags of different sizes were used (Supporting information, Table A), and the tag chosen for

143   any individual fish was based on the L_T of the fish. A Carlin tag (Carlin, 1955) was attached

144   below the dorsal fin of fish > 270mm to inform fishers that the fish was tagged. The fish were

145   released once normal swimming behaviour was regained, at the capture site. The care and use

146   of field-sampled animals complied with the Government of Norway animal welfare laws,

147   guidelines and policies as approved by the Norwegian Food Safety Authority (permit

148   18/67706). All methods are reported in accordance with ARRIVE guidelines.

149   In total, 85 acoustic receivers (Vemco Inc., Canada, models VR2, VR2W and VR2W-

150   AR) were used to track tagged fish; 81 in the fjord and four in the watercourses

151 Botnvassdraget, Misvær, Lakså, and Sulitjelma (Figure 1). The receivers were deployed at

152 0.5-3.0 m depth in freshwater and 5 meters depth in the fjord, except a few at 50-150 m depth.

153 In 2018, 22 of the receivers had built-in pinger tags (Vemco model VR2-W-AR). Recordings

154 of signals from these tags by neighbouring receivers indicated a detection range for receivers

155 of 200-400 meters. The detection efficiency of the second outermost receiver line was 100%,

156 based on all ten *S. trutta* recorded at the outermost receiver line being recorded also at this

157 line (Figure 1). All telemetry data were uploaded to the Ocean Tracking Network

158 (https://members.oceantrack.org/OTN/projects) and European Tracking Network data

159 warehouses (https://www.lifewatch.be/etn/)

160

161 Isotope analyses

162 A trap was installed in the outlet of Lake Botnvatnet (Figure 1) to record the return of tagged

163 and untagged fish during 26.06-19.08.2017. A total of 26 *S. alpinus* (9 males, 11 females, 6

164 unknown sex; 17 immature, 6 mature, 3 unknown maturity) and 110 *S. trutta* (51 males, 47

165 females, 12 unknown sex; 103 immature, 6 mature, 1 unknown maturity) sampled from the

166 trap were stored at -18 °C for six months prior to further analyses. After thawing in the lab,

167 approximately 1 cm^3 of muscle tissue from the area behind the dorsal fin and above the lateral

168 line was extracted and used for stable isotope analysis.

169 Total length (L_T) was smaller for *S. alpinus* (mean 276 mm, range 204-390, sd = 35.93; n

170 = 26) than *S. trutta* (mean 336 mm, range 185-720, sd = 98.51; n = 110) (Wilcoxon rank sum

171 test, W = 1021; p < 0.01). Mean body mass was 209 g (range 66-599, sd = 101.58; n = 25) for

172 *S. alpinus* and 479 g (range 27-2292, sd = 455.81; n = 117) for *S. trutta*. Mean age was 5.4

173 years (range 4-8, sd = 0.91) for *S. alpinus* and 4.3 years (range 3-10, sd = 1.17) for *S. trutta* (see

174 Supporting information, Figure B).

175

176   To determine the marine diet of *S. alpinus* and *S. trutta* based on stable isotope levels in

177   sampled fish, potential prey species (see Supporting information, Table B) were collected for

178   stable isotope analyses in Skjerstadfjorden 5-8 June and 21-23 August 2018. In June, hauls with

179   a fine mesh seine net were conducted from the beach near the outlet of Botnvassdraget.

180   Captured prey species included three-spined stickleback (*Gasterosteus aculeatus* L. 1758), sand

181   gobies (*Pomatoschistus minutus* (Pallas 1770)), sand shrimps (*Crangon sp.)*, amphipods

182   (Amphipoda), European plaice (*Pleuronectes platessa* L. 1758), and common dab (*Limanda*

183   *limanda* (L. 1758)). In August, bottom gillnets (6-25 mm mesh size) in near-shore areas were

184   used to capture prey species. These included saithe (*Pollachius virens* (L. 1758)), Atlantic

185   herring (*Clupea harengus* L. 1758), Atlantic mackerel (*Scomber scombrus* L. 1758), Atlantic

186   cod (*Gadus morhua* L. 1758), haddock (*Melanogrammus aeglefinus* (L. 1758)), and lesser sand

187   eel (*Ammodytes tobianus* L. 1758). Larger fish were captured in the fjord using rods to sample

188   additional prey species from their stomachs. Krill (Euphausiacea) and crabs (*Hyas* sp.) were

189   sampled from stomachs of Atlantic cod, while krill and flying insects were found in *S. alpinus*

190   and *S. trutta* stomachs. The prey items collected were identified to the lowest taxonomic group

191   possible. Up to about 1 cm^3 of tissue was collected from each specimen, but due to small prey

192   sizes, samples were often smaller. For larger crustaceans, the exoskeleton was removed and the

193   tissue inside used as the sample. For smaller specimens, the whole body was included in the

194   analysis.

195   Each sample was dried in aluminium foil in a drying oven for 48 hours and subsequently

196   crushed to a fine powder using a mortar. Approximately 1 mg of sample was weighed up for

197   analysis and placed in 5×9 mm tin containers. Each container was placed in a "Thermo

198   Scientific FLASH 2000 HT Elemental Analyzer" with columns set up for "NC with Flash

199   IRMS". The samples were burned with O_2 in a carrier gas of He, at 1020°C. NO_x was reduced

200   to N_2 with Cu at 680°C. The products were then separated in a glass column and transferred to

201   a "Thermo Electron DELTA V Advantage IRMS" via a "Thermo Fisher Scientific Confo IV

202   Universal Interface" for analysis of carbon and nitrogen isotope ratios, as described by

203   Davidsen *et al.*, (2018b). Carbon and nitrogen stable isotope compositions were measured as

204   the ratio of the heavier isotope to the lighter isotope ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) and reported in

205   standard delta (δ) notation as parts per thousand (per mil, ‰) relative to internationally defined

206   standards for carbon (Vienna Pee Dee Belemnite; Craig, 1953) and nitrogen (Ambient Inhalable

207   Reservoir; Mariotti, 1983). Every third sample run was a gelatine fish mix with already known

208   variables (G7041 GelatineFish), and the first and last samples in a series of 32 were empty

209   control samples.

210   Scales were used for age determination of individual *S. trutta* (Dahl, 1910; Lea, 1910).

211   For *S. alpinus*, age was estimated from sagittal annuli counts following Grainger (1953).

212   All scales and otoliths were analysed independently by two persons. If there was disagreement

213   in the age determination, the lowest age estimate was used in analyses.

214

215   Data analyses

216   Detections of tagged fish from April 2016 – October 2018 were analysed. Data from the

217   receiver in Botnvassdraget were filtered to reduce the risk of recording false IDs resulting from

218   several fish residing within the range of the receiver at the same time, by excluding detections

219   that were not followed by a second detection of the same tag ID within 10 minutes. Transmitters

220   consistently detected at the same receiver for more than a week, indicating tag expulsion or fish

221   mortality, were excluded. Eleven *S. trutta* that disappeared within three days of fjord entry were

222   excluded from analyses, because they either returned to freshwater without being recorded,

223   died, or tags were expelled or malfunctioning.

224   Duration of the marine migration was estimated from the first detection of the fish by a

225   receiver in the fjord to the last detection by the receiver closest to the watercourse (or first

226   detection in fresh water if not recorded there). If a fish had its last detection outside another

227   watercourse, it was assumed to have travelled up that watercourse, and that detection was used

228   as the last detection in the fjord. If a fish returned to a watercourse several times during the

229   season, the time spent in the watercourse was subtracted from the overall duration of the marine

230   migration.

231   Each fish was classified as either a short-, medium-, or long-distance migrant. Short-

232   distance migrants were fish recorded at, but never beyond, the closest receiver line to the

233   watercourse (line 1, Figure 1), i.e., fish that travelled about 2-5 km from the river. Medium-

234   distance migrants were fish recorded beyond line 1, but never at or past line 2, i.e., fish that

235   travelled about 5-20 km. Long-distance migrants were fish recorded at or past receiver line 2,

236   which was the last line that crossed the main body of the fjord system, i.e., fish that travelled >

237   ~20 km.

238   Statistical analyses were conducted in RStudio (RStudio Team, 2016). When comparing

239   mean values between *S. alpinus* and *S. trutta*, the Welch two-sample t-test was used when the

240   assumption of normality was met, and the Wilcoxon rank sum test when not. Correlations were

241   examined using Pearson's product-moment correlation (normality) and Spearman's correlation

242   test (non-normality). Normality was tested for by using functions ggqqplot(), ggdensity(),

243   plotNormalHistogram(), and shapiro.test() in packages dplyr (Wickham et al., 2018), ggpubr

244   (Kassambara, 2018), and rcompanion (Mangiafico, 2019). To test if there was a difference in

245   the proportions of short-, medium-, and long-distance migrants between the two species, a χ^2-

246   contingency test was used.

247   The stable isotope data were analysed by using the simmr-package in RStudio (Parnell,

248   2016; RStudio Team, 2016). simmr is a stable isotope mixing model based on the siar-package

249   (Parnell and Jackson, 2013). Stable isotope mixing models are often used to quantify source

250   contributions to a mixture (Phillips et al 2005). Prey δ^{15}N- and δ^{13}C-values were corrected for

251   trophic enrichment using fractionation factors of 3.23 and 1.03 for *S. trutta* (Jensen *et al.*, 2012)

252   and 3.80 and 0.66 for *S. alpinus* (Linnebjerg et al., 2016; Søreide et al., 2006). In addition to

253   the 14 groups of marine prey collected in the study area, isotopic values from five groups of

254   freshwater prey were extracted from existing literature (Eloranta et al., 2010; Hayden et al.,

255   2013). The 19 groups of prey were further assembled into 10 groups used in the analyses, which

256   were flying insects, freshwater zooplankton, freshwater profundal benthos, freshwater littoral

257   benthos, freshwater amphipods, marine amphipods, marine shrimp, marine crabs, marine krill,

258   and marine fish.

259   Results

260   Migration timing and duration of the marine migration

261   All tagged fish (21 *S. alpinus* and 49 *S. trutta*) were at some point recorded in the fjord (table

262   1). Of these, 20 *S. trutta* and 9 *S. alpinus* were recorded to return to the watercourse after the

263   marine migration.

264   Median date of sea entry was 28 May (range 1 May-6 July) for large *S. trutta*, 17 June (range

265   30 May-12 July) for small *S. trutta* and 5 June (range 8 May-1 June) for *S. alpinus*, all years

266   combined (table 1). Median date of return to freshwater was 5 August (range 18 July-29

267   September) for large *S. trutta*, 29 August (range 4 July–8 September) for small *S. trutta* and 29

268   July (range 12 June-27 September) for *S. alpinus*, all years combined (table 1).

269   When including individuals with last recording other places than in Lake Botnvassdraget,

270   large *S. trutta* spent median average of 65 days in the fjord (2016 and 2017 combined; n = 27;

271   range = 6-121; SD = 31), while small *S. trutta* spent median average 56 days (n = 22; range =

272   11-116; SD = 29). *S. alpinus* spent median average of 31 days (2017 and 2018 combined; n =

273   21; range = 4-112; SD = 31). Large and small *S. trutta* spent significantly longer time in the

274   fjord than *S. alpinus* (Welch t-test, $p < 0.01$ and $p < 0.05$, Figure 4), while there was no

275   difference between large and small *S. trutta* ($p > 0.05$).

276   The timing of sea entry was not correlated with fish L_T for large *S. trutta* (Spearman's

277   rank correlation; rho = -0.31; p > 0.05), small *S. trutta* (rho = -0.29; p > 0.05) nor *S. alpinus*

278   (rho = -0.21; p > 0.05), but large *S. trutta* entered the sea earlier than small *S. trutta* (Welch t-

279   test, p < 0.01). There was no difference in time of sea entry between large trout and *S. alpinus*

280   (Welch t-test, p > 0.05). Migration duration was negatively correlated with timing of outward

281   migration for small *S. trutta* (rho = -0.57; p < 0.01), but not for large *S. trutta* (rho=-0.25; p >

282   0.05) nor *S. alpinus* (rho = -0.22; p > 0.05).

283

284   Migration distance and use of the fjord system

285   Among the large *S. trutta*, 21 (78%) were long-distance migrants, 4 (15%) medium-distance

286   migrants, and 2 (7%) short-distance migrants (table 1). Among the small *S. trutta*, 13 (59%)

287   were long-distance migrants, 6 (27%) medium-distance migrants, and 3 (14%) short-distance

288   migrants. Among the *S. alpinus*, 6 (29%) were long-distance migrants, 9 medium-distance

289   migrants (43%), and 6 short-distance migrants (29%). A larger proportion of *S. trutta* (large

290   and small combined) than *S. alpinus* undertook long-distance migrations (χ^2 contingency test,

291   χ^2 = 9.4; df = 2; p < 0.01). Large *S. trutta* defined as long-distance migrants spent on average

292   2.9 (± 2.9) days to reach the defined boundary qualifying them for long-distance migration

293   (20 km), while small *S. trutta* spent on average 18.5 (± 8.3) days and *S. alpinus* on average of

294   13.3 days (± 8.7) on the same stretch. In general, *S. trutta* utilized the entire fjord system and

295   was frequently recorded by receivers in the outer regions, whereas *S. alpinus* mostly utilized

296   the inner areas and were never registered at the outermost receiver lines.

297

298   Stable isotope analysis

299   *S. alpinus* and *S. trutta* had significantly different isotope signatures (Wilcoxon rank sum test

300    $\delta^{15}N$; W = 112; p < 0.001, and $\delta^{13}C$; W = 136; p < 0.001), although with some overlap between

301   individuals (Figure 5). *S. alpinus* had a mean δ^{15}N isotopic value of 9.1‰ (range 6.6‰ to

302   11.9‰) and a mean δ^{13}C of -23.2‰ (range -27.1‰ to -20.7‰). *S. trutta* had mean δ^{15}N of

303   12.3‰ (range 6.9‰ to 15.0‰) and mean δ^{13}C of -20.2‰ (range -26.2‰ to -19.2‰, Figure 5).

304   *S. alpinus* had a diet dominated by freshwater littoral benthos and freshwater amphipods, while

305   *S. trutta* had a diet dominated by marine shrimps and fish (Figure 6).

306   There was a positive correlation between δ^{15}N-values and L_T (Spearman's correlation;

307   rho = 0.67; p < 0.001, Figure 7). When separating the species, the correlation was still

308   significant for *S. trutta* (rho = 0.75; p < 0.001), but not for *S. alpinus* (rho = -0.32; p > 0.05). If

309   looking only at low-δ^{15}N individuals (those with δ^{15}N < 12‰, which includes all *S. alpinus*),

310   there was no difference between the two species in terms of body length (L_T) (Wilcoxon rank

311   sum test; W = 563; p > 0.05), but even within this comparable size group, *S. trutta* had more

312   enriched δ^{15}N-values than *S. alpinus* (W = 112; p < 0.001).

313

314   <u>Discussion</u>

315   This study of sympatric *S. trutta* and *S. alpinus* showed differences in habitat use, migration

316   patterns and feeding strategies between the species during their marine migration. *S. alpinus*

317   generally stayed in the estuary and fjord areas close to the river mouth, and had a diet dominated

318   by freshwater invertebrates and amphipods drifting from the river, whereas *S. trutta* utilized the

319   entire fjord system and were to a large extent recorded in the outer part of the fjord and had a

320   piscivorous and marine diet. However, there was large individual variation in migration patterns

321   and diet for both species, demonstrating the large flexibility in behaviour of both *S. trutta* and

322   *S. alpinus*. Individuals of both species migrated from the river to the fjord in May and June and

323   returned to the watershed in late summer or autumn, which is a typical behaviour of *S. trutta*

324   and *S. alpinus* in Northern Norway (Berg and Berg, 1989a; Jensen et al, 2020). Some *S. trutta*

325   are known to overwinter in seawater, but do so more commonly further south in the

326   distributional range (e.g. Knutsen et al. 2004). Osmoregulation efficiency may be poor in cold

327   water for many salmonids (Berg and Berg, 1989b; Finstad et al., 1989), and *S. alpinus* have

328   only been observed to overwinter in estuaries if they do not have access to a lake (Jensen and

329   Rikardsen, 2008).

330   *S. alpinus* generally spent a shorter time at sea than *S. trutta*, although both species

331   showed large individual variation in date of sea entry and freshwater return. The duration of the

332   marine migration of approximately two months for *S. trutta* was in accordance with results from

333   other studies in northern Norway, and also these other studies found that *S. alpinus* stayed for

334   a shorter time period in the sea than *S. trutta* (Berg and Berg, 1989a; Jensen et al., 2014;

335   Bordeleau et al., 2018; Davidsen et al. 2018a). However, the duration of the marine migration

336   for *S. alpinus* in this study of approximately one month was shorter than observed in some of

337   the previous studies (Berg and Berg 1989b, Jensen et al. 2014), which may be due to differences

338   among watersheds, size groups of fish, and environmental conditions in the sea, which may

339   also vary between years.

340   There was a larger proportion of long-distance migrants among *S. trutta* than *S. alpinus*,

341   independent of individual body size, and *S. trutta* were frequently recorded by the outermost

342   receivers in the fjord system, 20-40 km from the river mouth. Large *S. trutta* spent on average

343   3 days reaching the receiver line 20 km from the river mouth, whereas *S. alpinus* and small *S.*

344   *trutta* migrating that far spent 2-3 weeks reaching the same distance. It might be that large *S.*

345   *trutta* aimed directly for a more pelagic piscivorous lifestyle in the outer fjord system than the

346   smaller *S. trutta* and *S. alpinus*. The stable isotope analysis indicated that *S. trutta* were

347   generally more piscivorous than *S. alpinus*, independent of body size. Feeding opportunities

348   might therefore be important in determining distance travelled in the fjord by *S. trutta*, because

349   they are likely to seek out areas with a high occurrence of fish to prey on.

350   *S. trutta* had higher δ^{15}N- and δ^{13}C-values than *S. alpinus*, according to the isotope

351   analysis. A higher δ^{15}N- value indicates feeding at a higher trophic level, while a higher δ^{13}C-

352   value indicates marine as opposed to freshwater feeding (Fuller et al., 2012; Hobson, 1999; Van

353   der Zanden and Rasmussen, 1999). The results suggest that *S. trutta* had a marine diet consisting

354   mainly of fish and shrimps, while *S. alpinus* had a freshwater diet consisting of littoral benthos

355   and amphipods. Stomach contents additionally showed that both *S. trutta* and *S. alpinus* had

356   been feeding on surface insects, fish, and crustaceans prior to capture (Halvorsen, 2019).

357   The diet of *S. trutta* as shown in this study is in accordance with other studies that have

358   found fish, crustaceans, polychaetas, and surface insects to be important prey groups for this

359   species at sea (Davidsen et al., 2017; Knutsen et al., 2001; Lyse et al., 1998). More surprising

360   is the finding that *S. alpinus* had been feeding on freshwater species. All individuals examined

361   were presumed to be anadromous individuals returning from a marine feeding migration.

362   Muscle tissue is a metabolically active tissue that will equilibrate to diet within the order of a

363   few months in rapidly growing salmonids (Perga and Gerdeaux, 2005; Tieszen et al., 1983;

364   Trueman et al., 2005). For anadromous individuals of *S. trutta* and *S. alpinus*, this would

365   typically reflect the summer period of somatic growth, which is the period when most of the

366   growth occurs (Perga and Gerdeaux, 2005). Although the telemetry data showed that some

367   individuals of *S. alpinus* performed long-distance migrations, the majority of the *S. alpinus*

368   remained in the inner parts of the fjord system, near the estuary of the home river or

369   neighbouring rivers, as also found in a study by Atencio *et al*., (2021). In addition to containing

370   both marine and estuarine species, estuaries often contain freshwater species having drifted

371   down with the currents from the river (e.g. Roper et al., 1983). It is therefore possible that *S.*

372   *alpinus* feed on freshwater species when they are in the estuary. The *S. alpinus* sampled for

373   stable isotopes may have moved to the estuary for a short time period before returning, which

374   is sometimes observed for immature *S. alpinus* (Johnson, 1980).

375   Both *S. trutta* and *S. alpinus* are opportunistic generalist feeders whose diets are expected

376   to reflect changes in food availability, habitat, season, age, and size (Bridcut and Giller, 1995;

377   Klemetsen et al., 2003; Knutsen et al., 2001). *S. alpinus* sampled for stable isotopes were

378   significantly smaller than the *S. trutta*. Moreover, both *S. trutta* and *S. alpinus* sampled for

379   stable isotopes were smaller than *S. trutta* and *S. alpinus* tagged for telemetry (60 mm shorter

380   on average for *S. alpinus*). Feeding is typically size-dependent for fish, and fish in particular is

381   known to become an increasingly important food item as individuals grow larger (Amundsen,

382   1994; Damsgård, 1993; Davidsen et al., 2017). Observed differences in isotopic values might

383   therefore be a reflection of a difference in size.

384   It is common for δ^{15}N-values to increase with size, as larger individuals usually feed

385   higher up in the food chain than do smaller ones (an increase of ~3‰ per trophic level is

386   commonly observed; e.g. Fuller et al., 2012; Schoeninger and DeNiro, 1984). However, no

387   pattern of increased δ^{15}N-values with size was observed for *S. alpinus* in this study, possibly

388   due to the small size range of fish caught. All *S. alpinus* were smaller than 400 mm and had a

389   δ^{15}N-value less than 12. When comparing *S. alpinus* with *S. trutta* of equal body length ($L_T <$

390   400 mm), eliminating body size as a factor explaining the observed differences between the

391   species, *S. trutta* had still a higher δ^{15}N-value than *S. alpinus*. A difference in feeding behaviour

392   between the two species, even when comparing fish of similar body length, is therefore

393   apparent, with *S. trutta* feeding higher up in the food chain than *S. alpinus*. When found in

394   sympatry in freshwater, it is commonly observed that *S. trutta* are more piscivorous and

395   typically begin to feed on fish at a smaller size than *S. alpinus* (e.g. 130 mm contra 160 mm in

396   freshwater in Björnsson, 2001; L'Abée-Lund et al., 1992). Stomach content analysis did,

397   however, show that some *S. alpinus* had been feeding on fish prior to capture (Halvorsen, 2019),

398   even though this was not apparent in the stable isotope analysis. *S. trutta* movement patterns in

399   the fjord system indicated that piscivorous food conditions might be poor in the innermost,

400   near-estuarine parts of the fjord. *S. alpinus* can exploit lower trophic levels if abundance of

401   suitable prey fish is low, including plankton and littoral hyperbenthos (Grønvik and Klemetsen,

402   1987).

403   Only isotopes of carbon and nitrogen were used for analysis in this study, and ideally the

404   simmr-model should have been run with only three food groups (Phillips et al., 2014). However,

405   both *S. trutta* and *S. alpinus* are generalist feeders, and the final count of food groups ended up

406   at ten in the present study. This makes the analysis less accurate when it comes to the individual

407   food groups, and the emphasis should be on the separation of a more marine *S. trutta* diet at a

408   higher tropic level as opposed to a more freshwater *S. alpinus* diet at a lower tropic level.

409   Additionally, some food groups may have been important parts of the diet but not included in

410   our samples, like freshwater sticklebacks and marine zooplankton and benthos.

411   *S. alpinus* had an overall return-rate to the watershed after the marine migration of 43%

412   and *S. trutta* of 41%. Berg and Jonsson (1990), found higher minimum annual survival rates of

413   large *S. alpinus* and *S. trutta* in the Vardnes River (57% and 50%, respectively). However,

414   survival may vary greatly between watercourses, and return rates between 15%-86% have been

415   reported for large *S. trutta* in different studies (Bordeleau et al., 2018; Jonsson and Jonsson,

416   2009; Kristensen et al., 2019). Mortality at sea is typically highest soon after the fish enter the

417   marine environment as smolts (Jensen et al., 2017; Klemetsen et al., 2003; Thorstad et al.,

418   2016), and subsequently decrease as the fish get larger (Jensen et al., 2022). This was also

419   shown in the present study, and the return rate of the small *S. trutta* (36%) was similar to first-

420   time migrants of *S. trutta* from the Vardnes River (37%, Berg and Jonsson, 1990).

421   Combined, the telemetry results and the feeding analyses in the present study suggest that

422   species-specific differences in prey choice may have influenced the observed habitat use and

423   marine migratory strategies of *S. trutta* and *S. alpinus*. For *S. trutta*, also size-specific

424   differences in habitat use and migration patterns were found. Such differences in prey choice

425 and area use of the marine coastal habitat may cause human activities, which are known to vary

426 in both time and space, to influence the species and size groups differently. This should be taken

427 into consideration when working towards the conservation of these species.

428

438

439 **Contributions**

440 J.G.D. designed the study; J.G.D., A.H., S.H.E., E.B.T. and L.A.V. conceived the idea for the

441 manuscript. J.G.D., A.H. and S.H.E. conducted the field work and analyzed the data and

442 E.B.T. and L.A.V interpreted the results. J.G.D. and A.H. wrote the manuscript with input

443 from S.H.E., E.B.T. and L.A.V. All authors reviewed and approved the manuscript.

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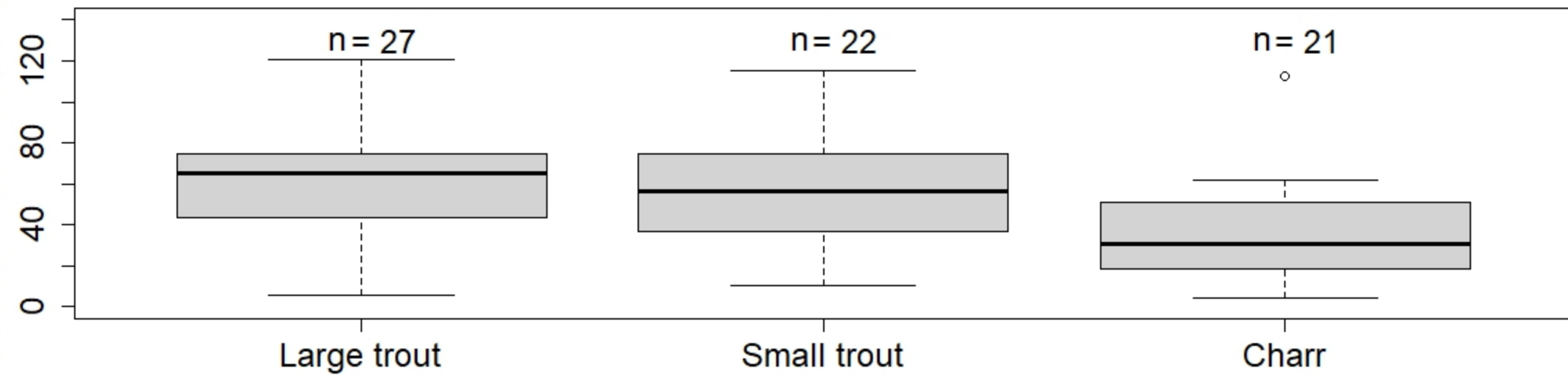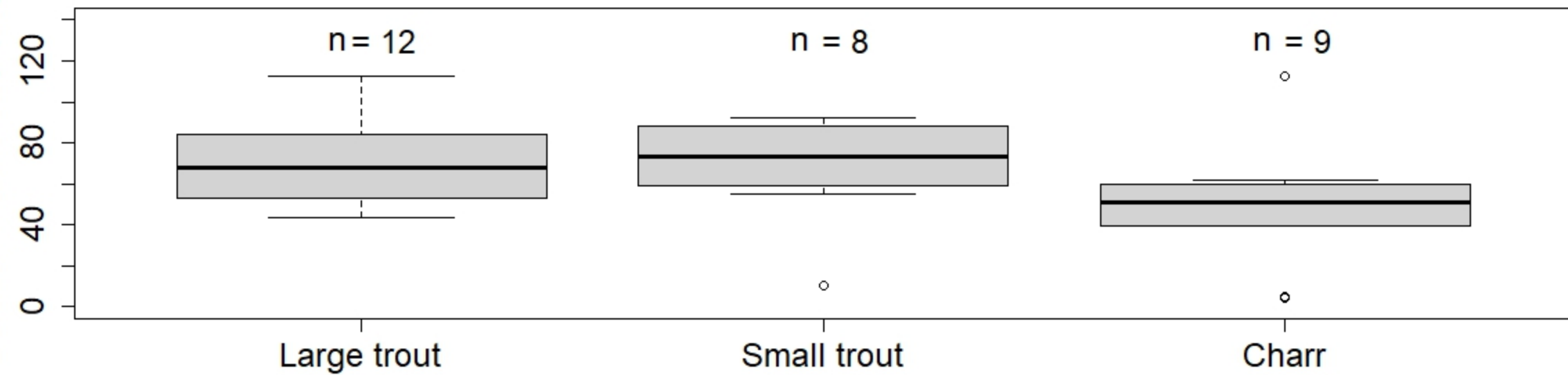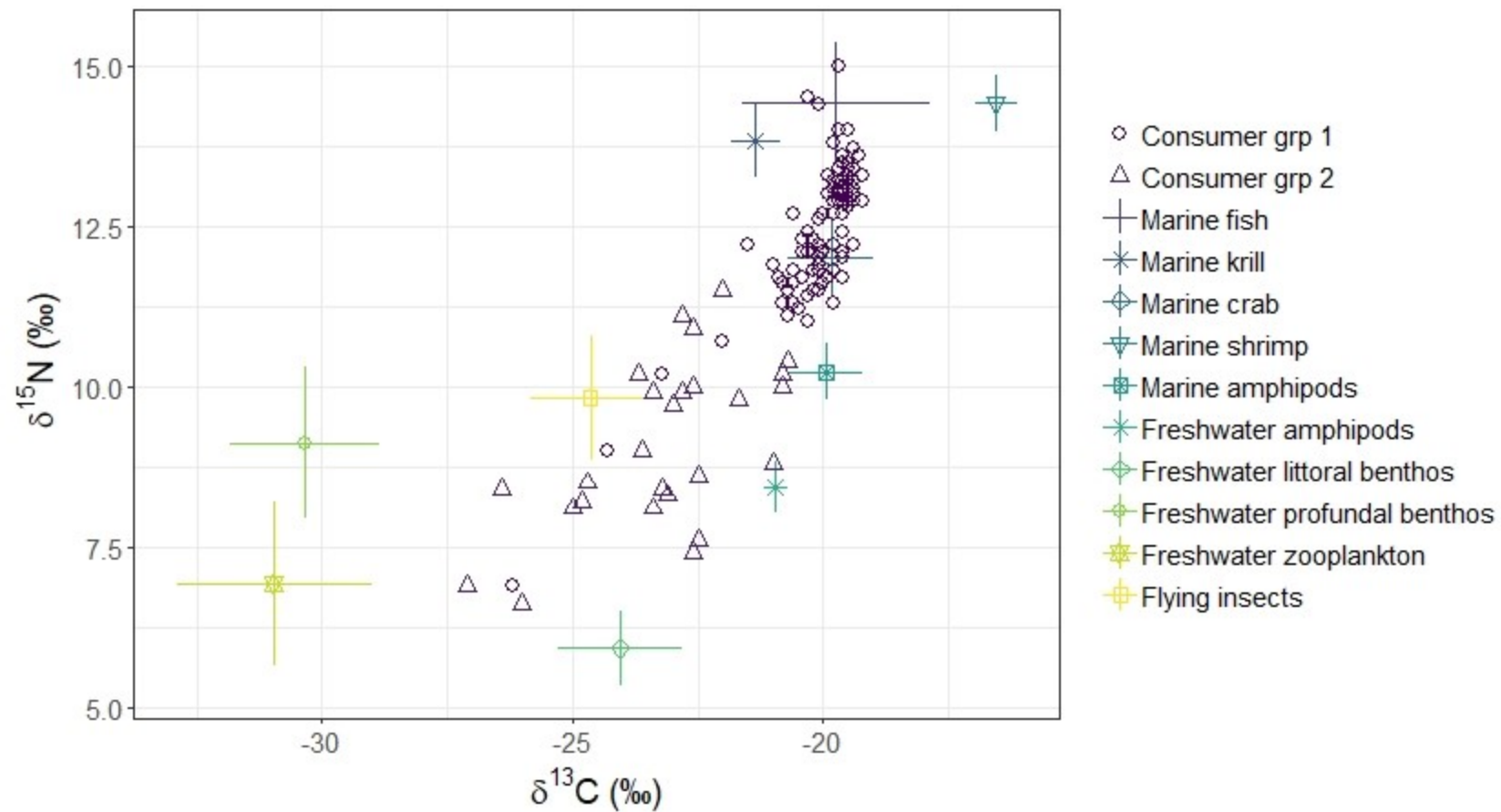
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657

A 2017

B 2018
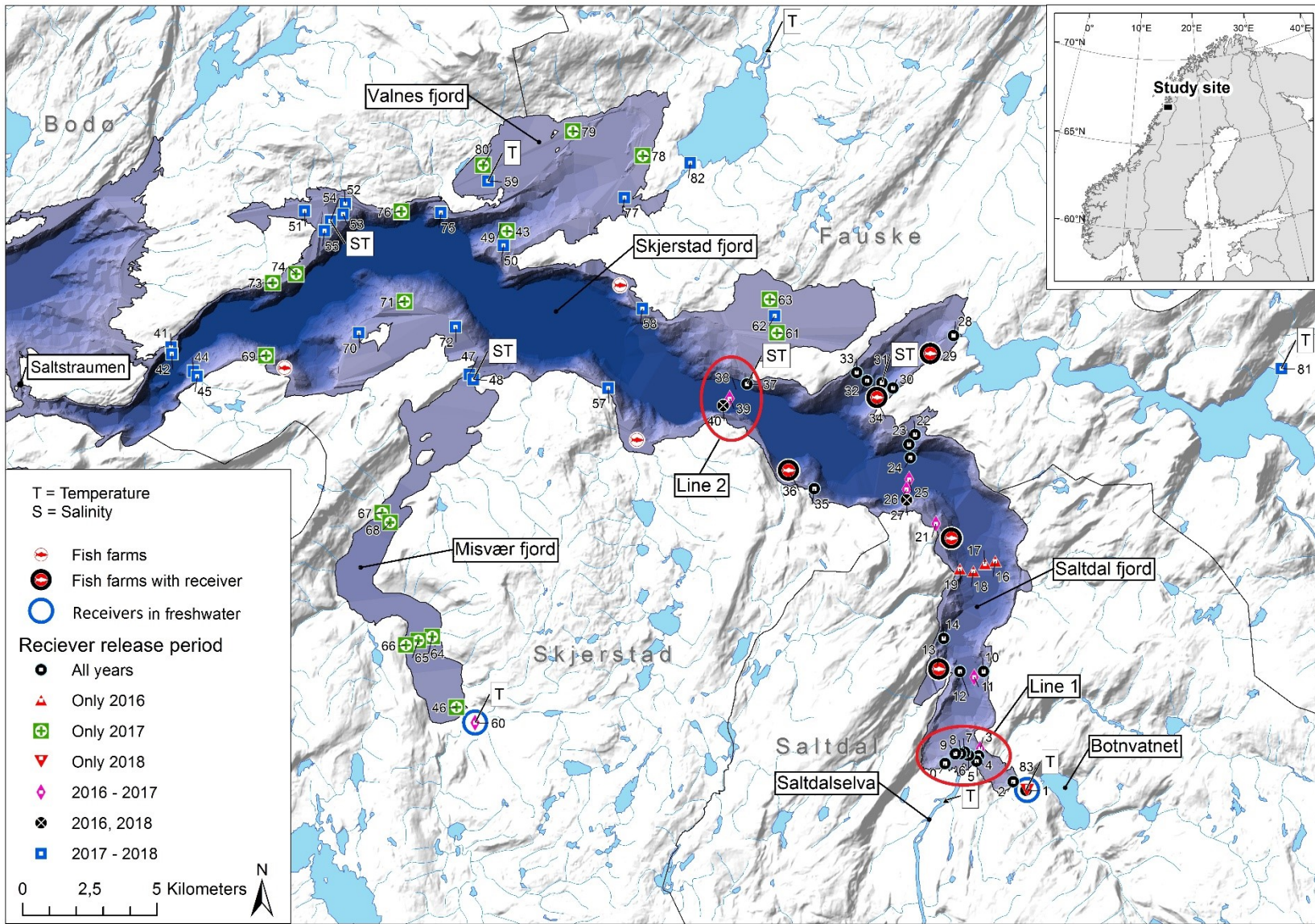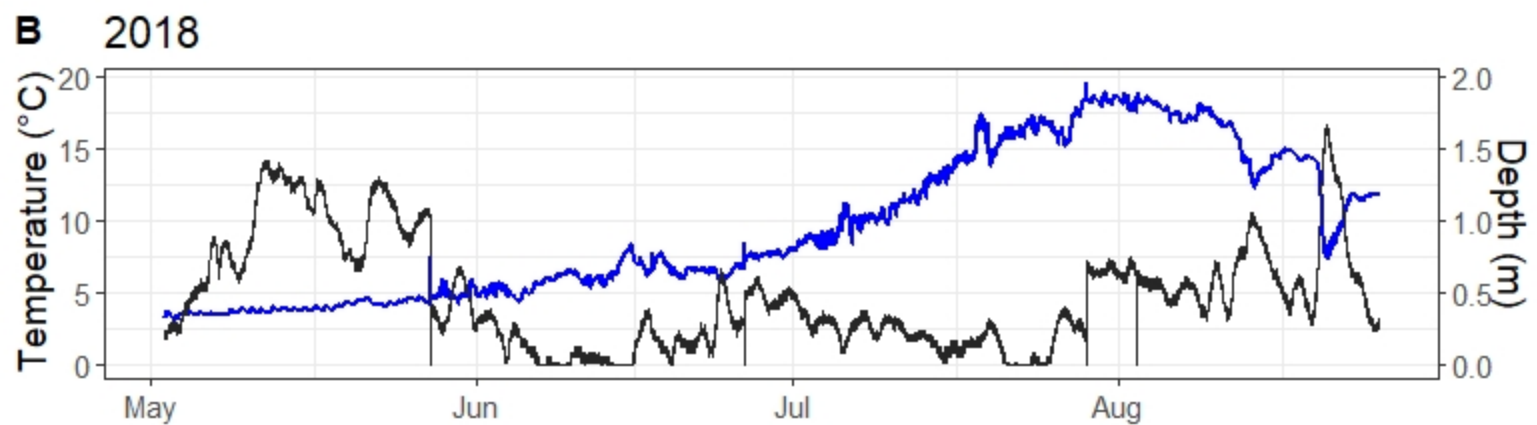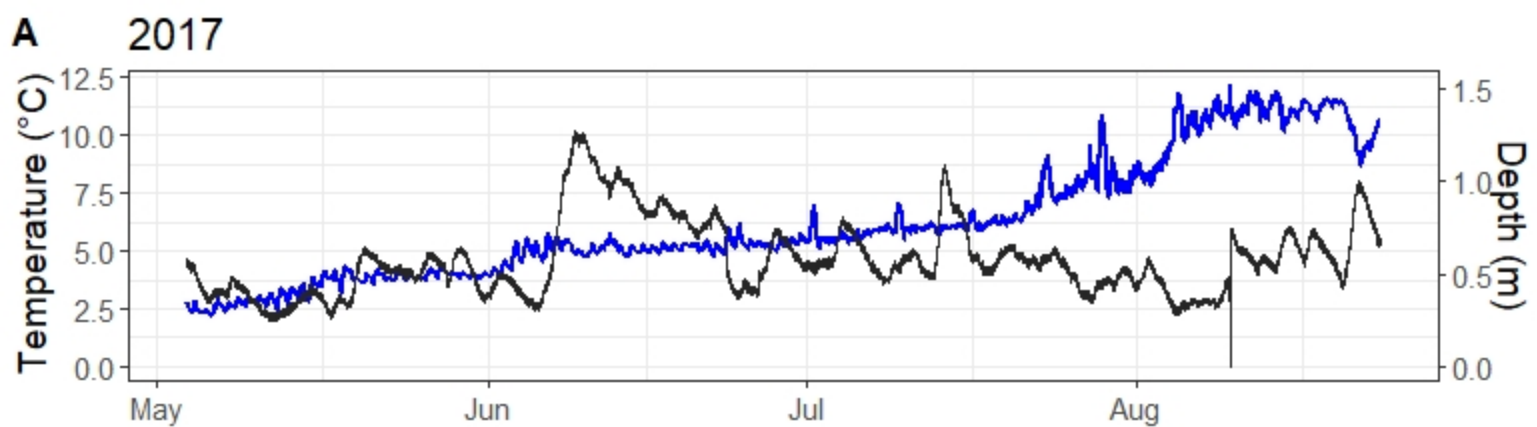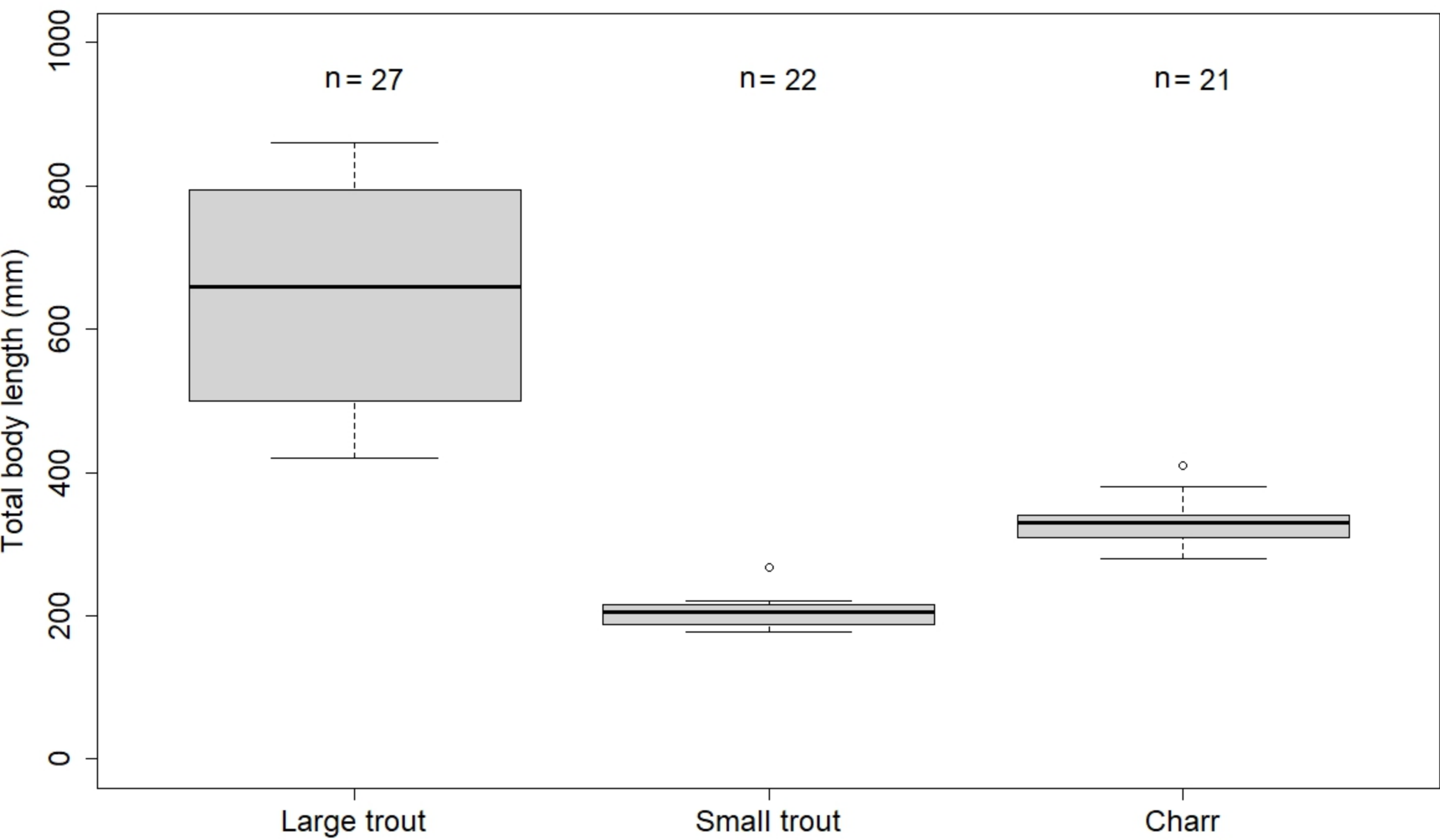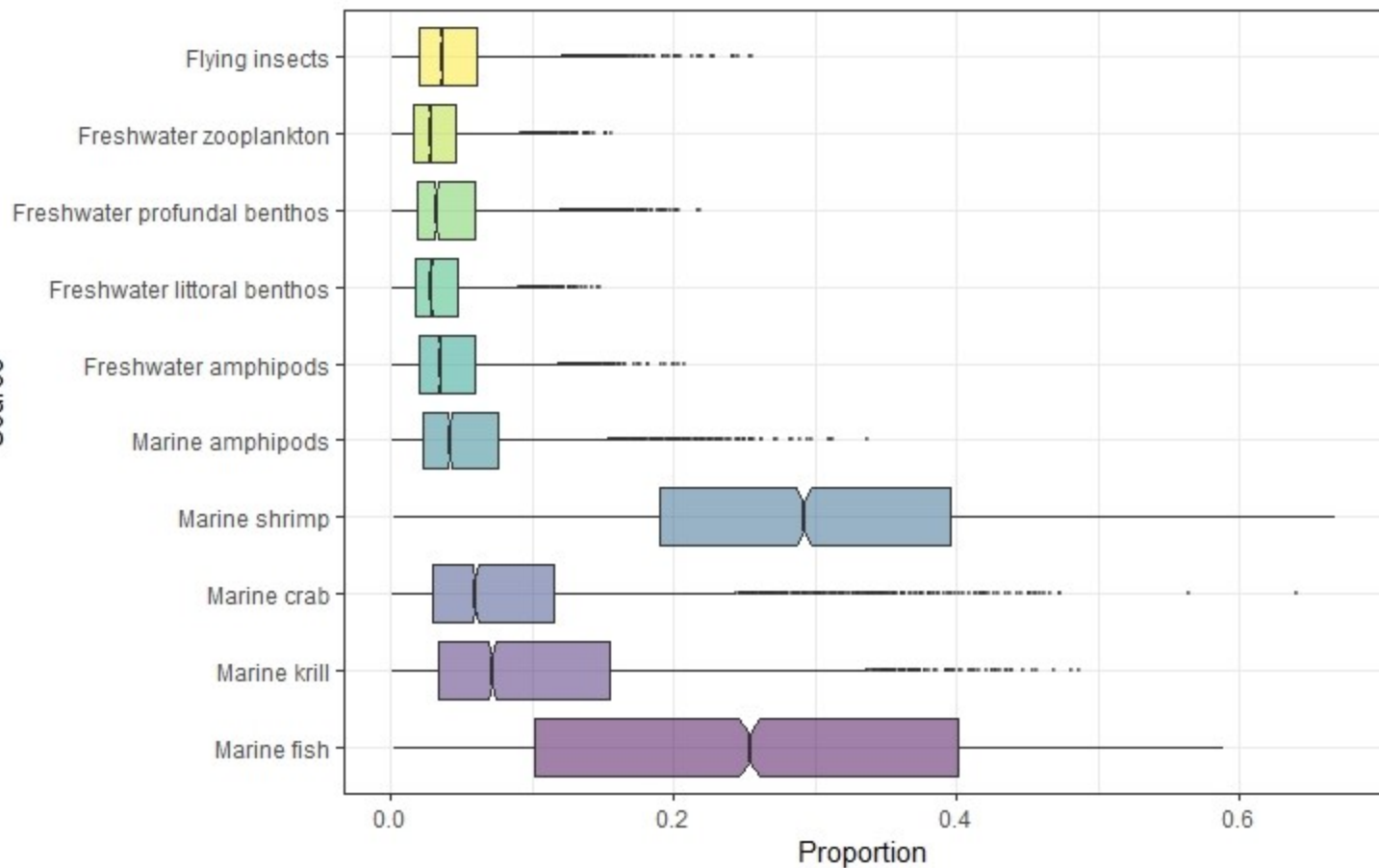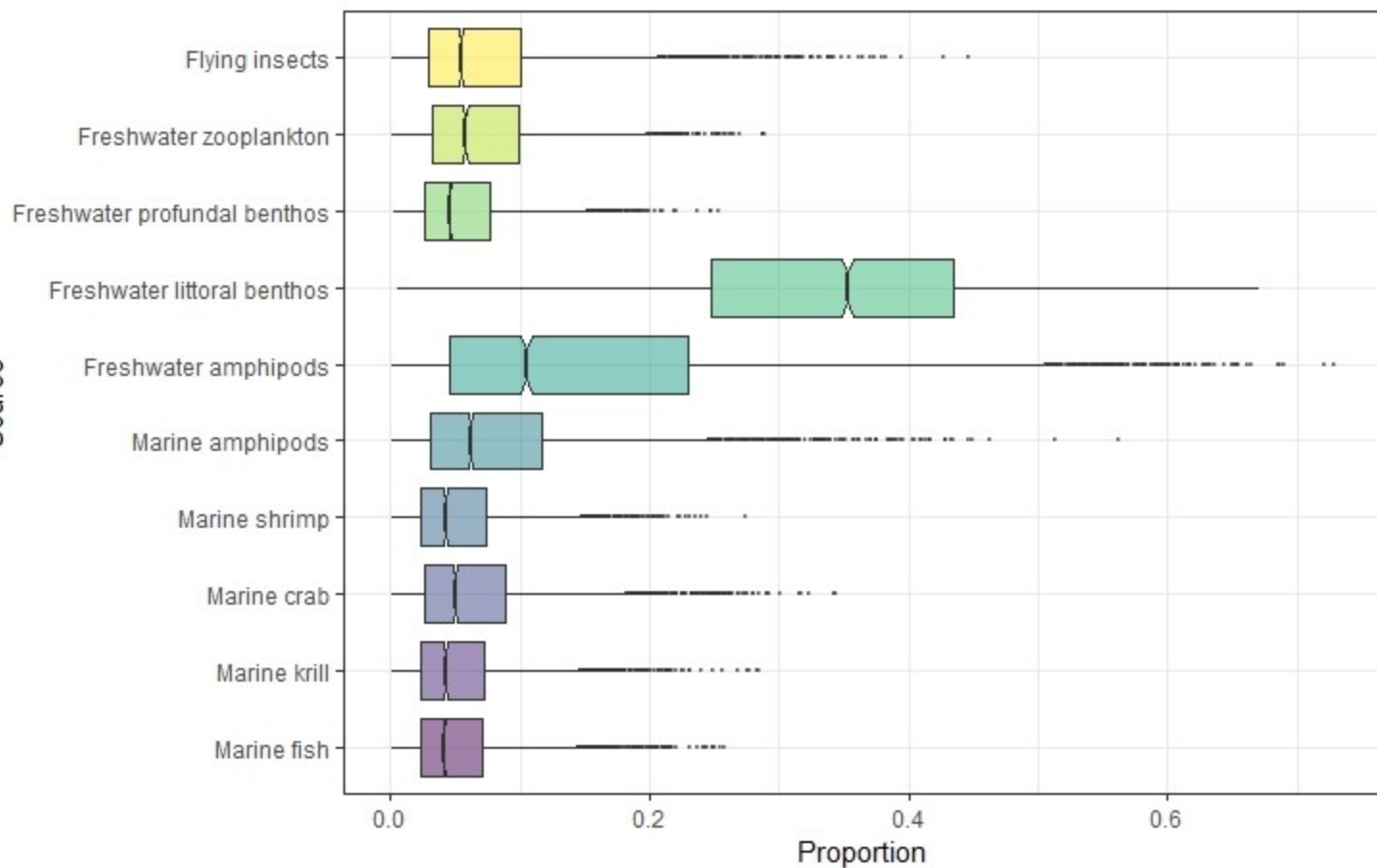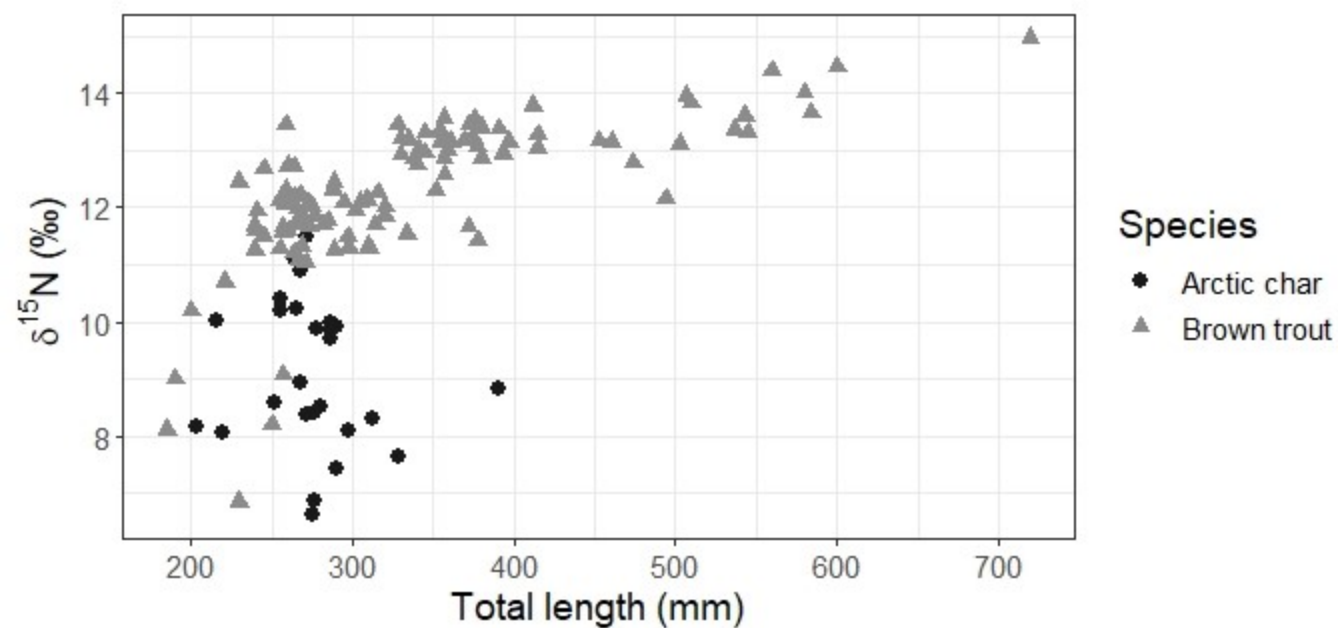
Figure captions:

Table 1: Timing (date and distribution) of seaward and return migration of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in Lake Botnvassdraget and the proportion of short/medium/long distance migrants.

Figure 1. The study area showing the positions of acoustic receivers used for tracking tagged fish and the time period they were in operation. The location of temperature and salinity loggers, and fish farms with and without acoustic receivers, are also shown. Red circles indicate lines of acoustic receivers used in the analyses. The location of Botnvassdraget (Lake Botnvatnet and River Knallerdalselva), the neighbouring river Saltdalselva, and Saltstraumen are also shown.

Figure 2. Water temperature (blue line) and water depth (black line) as an indication of water discharge in river Botnelva during May-September 2017 (A) and 2018 (B).

Figure 3. Total body length (L_T) of tagged fish. Trout: brown trout (*S. trutta)*. Charr: Arctic charr (*S. alpinus)*. The box-and-whisker plots show the median values (bold lines), the interquartile ranges (boxes), the 5th and 95th percentiles (whiskers) and outliers (dots). Numbers above each plot indicate sample size of each group.

Figure 4: Duration of the marine migration for large and small brown trout (*Salmo trutta*), and Arctic charr (*Salvelinus alpinus*) during 2016-2018. Upper panel: based on individuals returning to the water course where they were tagged and fish with last recording other places. Lower panel: Based on individuals returning to the watercourse where they were tagged only.

The box-and-whisker plots show the median values (bold lines), the interquartile ranges (boxes), the 5th and 95th percentiles, and outliers (dots). n = sample size.

Figure 5: Isospace plot for brown trout (*Salmo trutta*; Consumer grp 1 - circles), Arctic charr (*Salvelinus alpinus*; Consumer group 2 - triangles), and 10 prey groups based on carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values. Symbols represent the average mean isotopic value of each group, while lines represent standard deviations. Values were corrected for trophic enrichment.

Figure 6: The proportion of estimated prey groups of Arctic charr (*S. alpinus*; upper panel) and brown trout (*S. trutta*; lower panel), based on simmr-analyses.

Figure 7: Total body length (L_T, in mm) plotted against δ^{15}N-values for Arctic charr (*S. alpinus*; black circles) and brown trout *(S. trutta;* grey triangles). δ^{15}N-value increased with body size for *S. trutta* but not for *S. alpinus*.

1   Table 1:

|	Large *S. trutta* 2016	Large *S. trutta* 2017	Small *S. trutta* 2018	Large *S. trutta* 2016 and 2017	*S. alpinus* 2017 and 2018
Date outward migration	*n* = 14 median = 29 May range = 1 May-6 July IQR = 27	*n* = 13 median = 28 May range = 20 May-8 June IQR = 12	*n* = 22 median = 17.06.2018 range = 30 May-12 July IQR = 6	*n* = 27 median = 28 May range = 1 May-6 July IQR = 10	*n* = 21 median = 5 June range = 8 May-16 June IQR = 2
Distribution outward migration (percentage individuals per month)	57% May 36% June 7% July	69% May 31% June	5% May 82% June 14% July	63% May 33% June 4% July	19% May 81% June
Date return migration	*n* = 6, median = 11 August range = 18 July-29 September IQR = 45	*n* = 6, median = 7 August range = 20 July-20 September IQR = 24	*n* = 8, median = 29 August range = 4 July-8 September IQR = 12	*n* = 12, median = 5 August range = 18 July-29 September IQR = 39	*n* = 9, median = 29 July range = 12 June -27 September IQR = 33
Distribution return migration (percentage individuals per month)	50% July 17% August 33% September	33% July 50% August 17% September	13% July 50% August 38% September	42% July 33% August 25% September	22% June 44% July 22% August 11% September
Proportion short/medium/long distance migrants	14% short 29% medium 57% long	0% short 0% medium 100% long	14% short 27% medium 59% long	7% short 15% medium 78% long	29% short 43% medium 29% long

2

Supporting information

3   Figure A: Salinity and temperature in the fjord system

4   Salinity and temperature were measured at several receiver locations in the fjord during 2017-

5   2018. Recordings from two stations, one in the outer area (station 54, plot B and C, Figure A)

6   and one in the inner area of the Skjerstad fjord (station 31, plot A, Figure A), are plotted in

7   Figure A. Overall, summer temperatures were higher in 2018 than in 2017. Peak temperatures

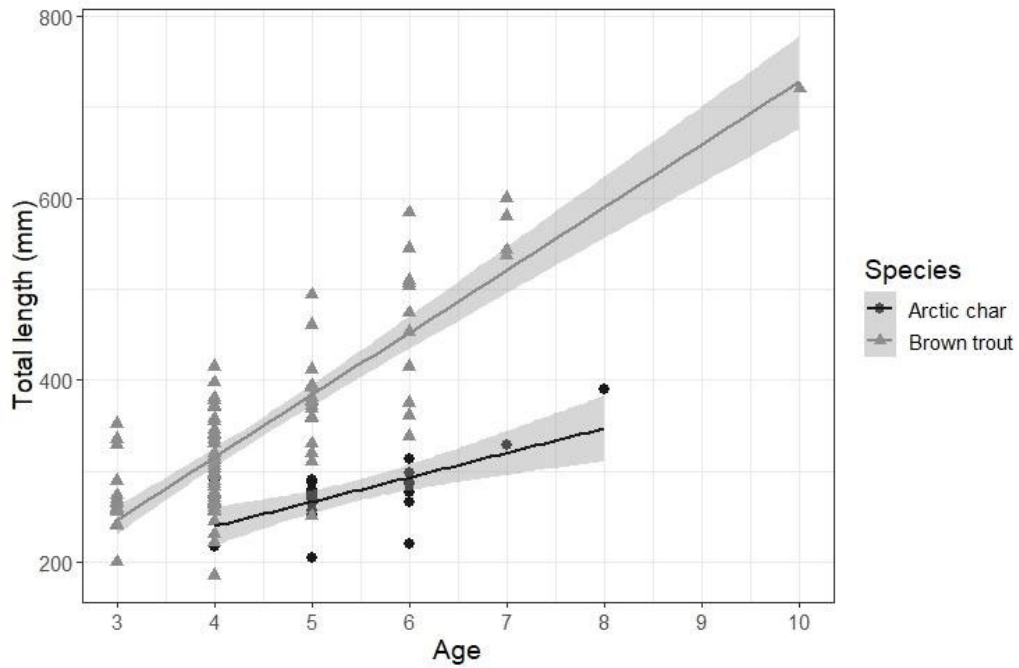8   occurred in late July/early August both years. Salinity was typically lowest in June/July.

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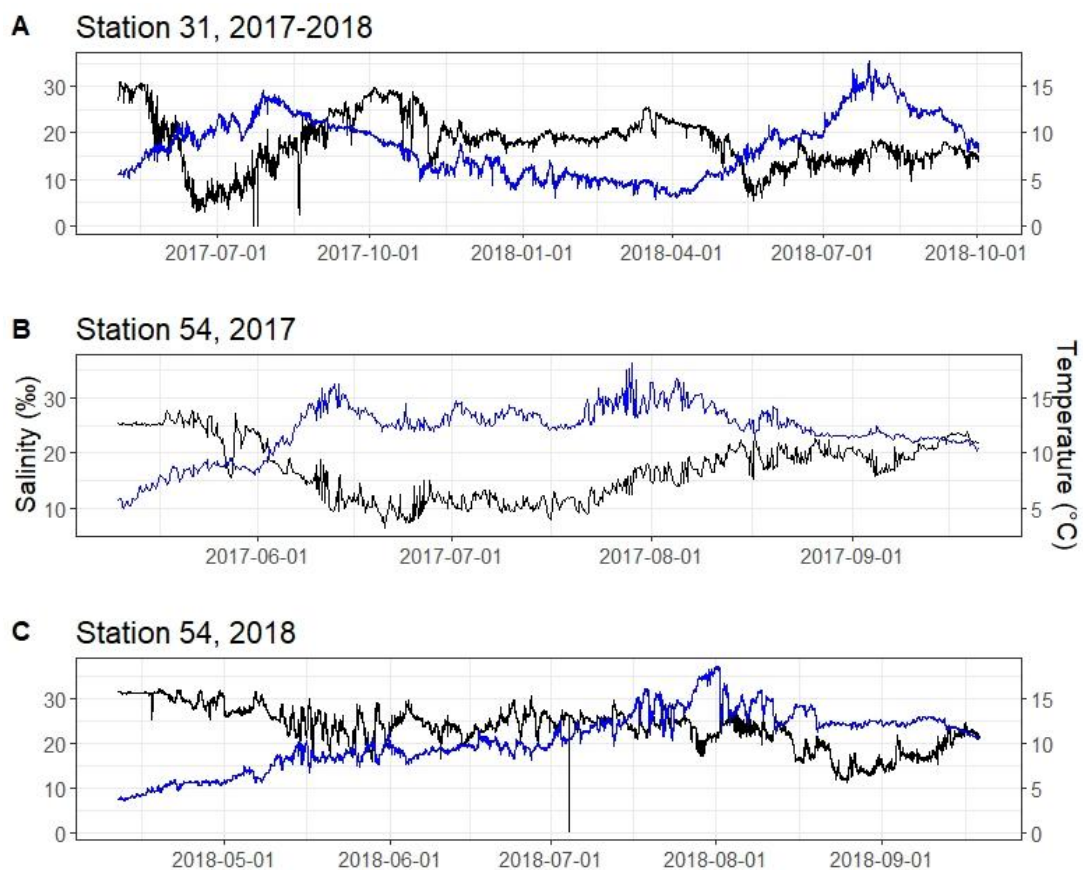
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11   Figure A. Measurements of temperature (blue line) and salinity (black line) at two different

12   stations in the fjord system; station 31 (plot A) and station 54 (plot B and C) (see Figure 2.1).

13   Recordings were made in 2017 and 2018.

14

15 Figure B. Growth curves of fish included in stable isotope analyses. Age and body length at

16 age was estimated from scales of brown trout (*S. trutta*, grey triangles) and otoliths from

17 Arctic charr (*S. alpinus*, black circles). Growth is represented by the projected regression lines

18 (+ 95% confidence intervals) and is seen to be slower for *S. alpinus* than for *S. trutta*.

19 Additionally, at any given age, *S. trutta* was typically larger than *S. alpinus*.

20

21

22 Table A. Overview of acoustic transmitters used in the study (69kHz), and number of fish

23 tagged with each tag model. Transmitter pulse intervals varied randomly between 30-90

24 seconds. Signal output is given as decibel (dB) with the standard reference level for sound in

25 water (re 1μPa) at 1 meter depth.

Model	Weight (g, air)	Diameter (mm)	Length (mm)	Battery life (months)	Output (dB re 1μPa @1m)	# fish (brown trout /Arctic charr)
ID-LP7	1.9	7.3	18	5	139	22/0
ID-MP9L	5.3	9	29	15	146	9/21
DT-LP13	9.7	13	31	24	150	18/0

26

27

28   Table B. Prey items sampled for stable isotope analysis, including number of individuals

29   caught per prey item, capture method, and date of capture. Isotopic values of some prey items

30   had to be collected from existing literature, as they were not sampled specifically for this

31   study. Habitat of each prey item is also noted as marine (M) or freshwater (F).

Prey	#	Capture method	Date of capture	Marine/ Freshwater
Amphipoda	5	Seine net	06.06.2018	M
Atlantic cod (*Gadus morhua*)	7	Bottom net	21-23.08.2018	M
Atlantic herring (*Clupea harengus*)	2	Bottom net	22.08.2018	M
Atlantic mackerel (*Scomber scombrus*)	2	Bottom net	22.08.2018	M
Common dab (*Limanda limanda*)	3	Seine net	06.06.2018	M
European plaice (*Pleuronectes platessa*)	1	Seine net	06.06.2018	M
Flying insects	4	From stomach samples of brown trout and Arctic charr	–	F
Gammarus lacustris	–	From literature (Eloranta et al., 2010)	–	F

Haddock (*Melanogrammus aeglefinus*)	1	Bottom net	22.08.2018	M
Hyas sp.	3	Found in the stomach of an Atlantic cod	23.08.2018	M
Krill (Euphausiacea)	8	Found in the stomachs of other fish	–	M
Lesser sand eel (*Ammodytes tobianus*)	1	Bottom net	23.08.2018	M
Littoral benthic animals	–	From literature (Hayden et al., 2013)	–	F
Profundal benthic animals	–	From literature (Hayden et al., 2013)	–	F
Sand goby (*Pomatoschistus minutus*)	5	Seine net/bottom net	06.06.2018/ 21-23.08.2018	M
Sand shrimp (*Crangon crangon*)	5	Seine net	06.06.2018	M
Saithe (*Pollachius virens*)	1 0	Bottom net	21-23.08.2018	M
Three-spined stickleback (*Gasterosteus aculeatus*)	5	Seine net/bottom net	06.06.2018/ 21-23.08.2018	M
Zooplankton	–	From literature (Hayden et al., 2013)	–	F

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