Trophic ecology of piscivorous Arctic charr (*Salvelinus alpinus* (L.)) in subarctic lakes with contrasting food-web structures

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Abstract The trophic ecology of piscivorous Arctic charr (*Salvelinus alpinus* (L.); charr) in the food webs of large subarctic lakes is not well understood. We assessed charr diets, parasites, growth, maturity, and stable isotope ratios in Fennoscandian subarctic lakes dominated by monomorphic or polymorphic whitefish (*Coregonus lavaretus* (L.)) populations. Charr density was low in all lakes, except in profundal habitats. Charr shifted to piscivory at small size (16–25 cm total length) and consumed a range of prey fish sizes (2–25 cm). Cannibalism was observed in a few individuals from one monomorphic whitefish lake. Charr matured at 37–51 cm (5–8 years old), grew to 52–74 cm maximum observed length and 47–83 cm asymptotic length. Charr increased total area of convex hull and core stable isotopic diversity area of the fish community by 51-98% and 44-51% in monomorphic whitefish lakes, but only 8–11% and 7–10% in polymorphic whitefish lakes. The difference was due to increasing food-chain length in monomorphic whitefish lakes, whereas reliance on littoral carbon did not change. Charr were the top piscivores in monomorphic whitefish lakes, but played a less important role in polymorphic whitefish lakes, which contained a more diverse predator fauna.

Keywords: diet; food-chain length; polymorphism; predation; stable isotopes; whitefish morphs

Introduction

Piscivorous fish play a pivotal role in lake food webs by influencing behavioral decisions of individual prey, size structure of prey populations and ecosystem-level energy flows (Ferrari et al., 2009; Gallagher et al., 2017). They may exert direct top-down, as well as indirect behavioral control of prey populations, with subsequent cascading effects on lake food webs (Kahilainen et al., 2009; Jensen et al., 2015; Thomas et al., 2017). In addition, the high mobility of top consumers is important for food webs as it allows pelagic and benthic food-web compartments to be linked (Vander Zanden & Vadeboncouer, 2002; Eloranta et al., 2015a). Large subarctic lakes are fueled by both benthic and pelagic energetic pathways associated with specialist species or morphs, and they could be especially valuable systems for assessing the role of top predators in food webs. The ecology and role of large piscivorous Arctic charr (*Salvelinus alpinus* (L.)) in community and food-web processes in different types of subarctic lakes has remained poorly studied. This likely reflects a limited number of Scandinavian lakes supporting large-bodied piscivorous Arctic charr, as is the case with large piscivorous (ferox) brown trout (*Salmo trutta* L.) (Campbell, 1979). For example, only a few lakes in subarctic Finnish Lapland contain large-bodied Arctic charr populations (Seppovaara, 1969).

Arctic charr is the world's northernmost freshwater fish, being well adapted to cold water, and dominant in freshwater ecosystems with low species diversity throughout the Arctic (Klemetsen, et al., 2003; Elliott & Elliott, 2010). Arctic charr are highly plastic, utilizing contrasting habitats and forming distinct freshwater, river, or anadromous populations, as well as polymorphic populations throughout their core distribution area (Klemetsen, 2013). However, Arctic charr are sensitive to impaired water quality and increased resource competition with other fishes, making them highly vulnerable to climate warming, increasing productivity, and interactions with invasive species (Lehtonen 1998; Elliott & Elliott 2010; Rolls et al., 2017). In this respect, large multispecies subarctic lakes at the edge of the species' core distribution area may provide insights

65 into the current role of Arctic charr in these systems and aid the evaluation of the food-web level

66 consequences of local extinction.

67

68 To adequately assess the role of top predators in specific food webs, predator ecology must be

69 considered in the context of the relative abundance of prey and their size distribution (e.g. Jensen

70 et al., 2008). Despite the development of modern stable isotope, fatty acid, and DNA bar-coding

71 methods, stomach content analyses remain crucial for quantifying the diet and ontogenetic diet

72 shifts of the large predatory fish (Nielsen et al., 2018). A combined approach using both stable

73 isotopes and diet allows for quantification of the trophic location of target species in a food web,

74 as well as the relative abundance of prey fish in the diet, the number of prey fish in stomachs,

75 and prey size for estimating the predation window for different prey species (Clark & Levy,

76 1988; Kahilainen & Lehtonen, 2003; Hrabik et al., 2006). Moreover, such detailed knowledge of

77 prey species consumed is key for understanding food-borne parasite infections in predators

78 (Hammar, 2000; Henriksen et al., 2016; Hammar et al., 2018). Due to the complementary nature

79 of different analyses of resource use, application of multiple methods is the best approach for

80 achieving a deeper understanding of predator-prey interactions, community structure, and energy

81 flows in lake ecosystems.

82

83 Combined use of stable carbon and nitrogen isotopes and stomach content analyses have been

84 especially useful in subarctic lakes, where these methods provide good resolution of

85 differentiation between benthic and pelagic energetic pathways (Eloranta et al., 2010, 2015a).

86 Furthermore, stable isotopes can be effectively used to separate invertebrate baselines from all

87 three principal habitats (littoral, pelagic and profundal) in large and deep subarctic lakes (Harrod

88 et al., 2010). The relatively low number of species in subarctic lakes facilitates the stable isotope

89 assessment of species or morph niches, in addition to community and food-web size (Thomas et

90 al., 2016, 2017). Small subarctic lakes are generally driven by energy derived from benthic algae

91   (e.g. Sierszen et al., 2003; Karlsson & Byström, 2005). This is reflected in high littoral reliance

92   of Arctic charr in small lakes, whereas the species increases use of pelagic habitats and prey in

93   larger lakes (Eloranta et al., 2015a). The relatively narrow dietary and isotopic niche of deep-

94   water (profundal) Arctic charr is expected to result from strong interspecific resource competition

95   in multispecies lakes, and is potentially further reinforced by the cold-water preference of Arctic

96   charr (Kahilainen & Lehtonen, 2002; Sandlund et al., 2016; Hammar et al., 2018).

97

98   Subarctic Fennoscandian lakes with multiple piscivore and forage fish species provide excellent

99   opportunities to study the role of Arctic charr in food webs. Large lakes (>10 km^2 in Finnish

100   Lapland) are deep enough to contain distinct littoral, pelagic, and profundal habitats, each of

101   which is dominated by coregonid fishes providing prey for piscivores such as Arctic charr

102   (Kahilainen & Lehtonen, 2003; Thomas et al., 2017). Whitefish (*Coregonus lavaretus* (L.)) are

103   ubiquitous in the region and they have commonly diverged into benthic and pelagic morphs

104   (Harrod et al., 2010). A few larger lakes have up to four whitefish morphs (Kahilainen et al.,

105   2014; Thomas et al., 2016; Kahilainen et al., 2017). The occurrence of monomorphic and

106   polymorphic whitefish lakes in the same region provides an opportunity to assess the importance

107   of Arctic charr in different kinds of food webs. Besides whitefish, several other putative

108   competitor fish species from both the invertebrate-feeding and piscivorous foraging guilds

109   coexist with Arctic charr (Thomas et al., 2017).

110

111   Here, we used a large dataset from three pairs of subarctic lakes in northern Fennoscandia hosting

112   contrasting multispecies fish communities. Two lakes have Arctic charr and monomorphic

113   whitefish, two lakes have Arctic charr and polymorphic whitefish, and two lakes have non-Arctic

114   charr piscivores with mono- and polymorphic whitefish (Thomas et al., 2017). Here, we adressed

115   two broad objectives: the first was to evaluate the general role of Arctic charr in different types

116   of whitefish dominated lake food webs (based on habitat, diet, prey size, parasites, growth and

117   maturation), and the second was to compare stable isotope food-web metrics in lakes with and

118   without Arctic charr. Specifically, we tested two predictions: (1) the diet, life-history traits and

119   parasite load of Arctic charr will reflect their position as apex predators in subarctic lake food

120   webs and (2) as Arctic charr are located at the top of the food chain, their presence will increase

121   the overall size of the food-web as estimated with stable isotope analyses.

122

123   **Methods**

124   Study lakes

125   All six oligotrophic, clear-water, subarctic study lakes are located in Finnish Lapland (Fig. 1,

126   Table 1). Arctic charr (hereafter charr) inhabit Lakes Kilpisjärvi, Rahajärvi, Muddusjärvi and

127   Inarijärvi, but not Lakes Vuontisjärvi and Paadarjärvi (hereafter shortened without "lake" or

128   "järvi", the Finnish word for lake), which were used as controls for food-web analyses. Charr

129   naturally reproduce in four charr lakes, but are currently supplemented by stocking in Inari, and

130   have been stocked historically in Muddus and Raha. In the latter two lakes, stocked charr were

131   relatively easy to exclude from analyses based on their large size, deteriorated fins and adipose

132   fin-clipping. In Inari, charr are stocked mainly in their first year of life (0+; circa 5-8 cm of total

133   length) and cannot be as easily identified as adults. Thus our data may contain stocked

134   individuals. All six lakes are multispecies systems dominated by coregonid fishes (Kahilainen et

135   al., 2017; Thomas et al., 2017). Kilpis, Raha and Vuontis have only a single whitefish morph,

136   whereas Muddus, Inari, and Paadar contain four sympatric morphs (Thomas et al., 2017).

137   Monomorphic lakes only support populations of the large sparsely rakered (LSR) whitefish that

138   use all principal habitat types, including littoral, pelagic and profundal zones (Harrod et al.,

139   2010). In lakes with polymorphic whitefish, LSR whitefish use littoral habitat, small sparsely

140   rakered (SSR) whitefish use the profundal zone, whereas the densely rakered (DR) and large

141   densely rakered (LDR) whitefish use the pelagic zone as their main foraging habitat (Kahilainen

142 et al., 2014, Thomas et al., 2016; Kahilainen et al., 2017). The non-native pelagic planktivorous

143 coregonid, vendace (*Coregonus albula* L.) has been stocked in Inari and Raha, where it currently

144 forms a part of the pelagic fish community (Kahilainen et al., 2011; Thomas et al., 2016). In

145 Inari, piscivorous lake trout (*Salvelinus namaycush* Mitchill) and land-locked salmon (*Salmo*

146 *salar* m. sebago L.) have been introduced and currently make a relatively limited contribution to

147 the fish community (Eloranta et al., 2015b). In all study lakes, whitefish are an important prey

148 for piscivorous fish (Thomas et al., 2017).

149

150 Sampling of fish and invertebrates

151 Due to the low abundance of charr in most study lakes, we combined data from open water

152 season sampling over several years and used multiple gears to increase sample sizes (see Table

153 1 and 2 for details of sampling gear, years and efforts). Sampling of the entire fish community

154 was conducted with gill-net series comprised of eight 30 m long and 1.8 m high nets with knot-

155 to-knot mesh sizes of 12, 15, 20, 25, 30, 35, 45 and 60 mm (Table 1). This method generally

156 captures fish with total length range of 9-65 cm. Predatory fish samples were supplemented by

157 large-mesh gill net series composed of five 5 m high and 60 m long nets with knot-to-knot mesh

158 sizes of 35, 40, 45, 50 and 55 mm (Kahilainen & Lehtonen, 2002; Table 2). Gill-nets were set in

159 littoral, pelagic and profundal habitats in the evening and lifted the following morning with total

160 soak times of ~12 hours. Fish were immediately killed after removal from the gill-net with a

161 sharp blow to the head that caused immediate unconsciousness followed by death. The gill-net

162 catch was held on ice and later processed in the laboratory.

163 Benthic invertebrates were sampled with an Ekman grab (area 272 cm^2) along a transect from

164 lake shore areas (1 m depth) towards the deepest areas. Profundal sampling was limited to 40 m

165 depth, except in Vuontis, where the deepest point of the lake was 30 m (Table 1). Each sampling

166 depth (1, 2, 3, 5, 10, 15, 20, 30 and 40 m) included three replicates located around 10 m apart.

167 Samples were immediately sieved through a 500 µm mesh and remaining animals and sediment

168 were stored in a plastic bucket filled with water. In the field laboratory, benthic animals were

169 sorted to the lowest feasible taxonomic level (varying from species to genus). Sorted samples

170 were stored frozen (−20 °C) in 2 ml plastic tubes. Zooplankton were sampled by vertical hauls

171 through the uppermost 20 m of the water column using a plankton net (diameter = 25 cm, mesh

172 size = 50 µm). This sampling station was located near the deepest sampling point of the benthic

173 transect so as to collect pelagic plankton at their main distribution depths. Zooplankton samples

174 were first stored in a one-liter bucket and then transported to the laboratory for further sieving

175 through a 50 µm mesh to remove extra lake water. Remaining samples consisting of both

176 cladocerans and copepods were stored in 2 ml plastic tubes and frozen at −20 °C.

177

178 Fish processing

179 Each fish was identified to species: whitefish were identified to morph based on differences in

180 body, head, and gill raker characteristics (see next paragraph). Total length (± 1 mm) and blotted

181 wet mass (± 0.1 g) were recorded. From subsamples of fish (target sample size of 30 individuals

182 per species), a piece of white muscle tissue posterior to the dorsal fin was dissected, stored in a

183 2 ml plastic tube and frozen at −20 °C for stable isotope analysis (SIA). The body cavity of charr

184 was also opened to determine sex and maturity (0 = immature, 1 = mature). Sagittal otoliths were

185 removed from charr for age estimation done by examining whole otoliths submerged in distilled

186 water under a microscope. Stomach contents of charr were quantified using a modified points

187 method (Swynnerton & Worthington, 1940), where stomach fullness was first visually classified

188 from 0 (empty) to 10 (maximum full). Prey items were then identified to the lowest feasible

189 taxonomic level and their relative contribution to total fullness was visually estimated. For

190 undeteriorated prey fish, total length was estimated (± 1 mm).

191 We identified whitefish morphs whenever possible: intermediate-sized SSR whitefish have a

192 pronounced downward pointing snout and low number of short and bent gill rakers; large-sized

193 LSR whitefish have a downward pointing mouth and intermediate number of short gill rakers;

194 large-sized LDR have a slightly pointed head, longer upper jaw and high number of relatively

195 long gill rakers; and small-sized DR whitefish have a pointed head, equal jaw length and high

196 number of long gill rakers (Kahilainen & Østbye, 2006; Harrod et al., 2010; Kahilainen et al.,

197 2017). Unlike whitefish, vendace have a longer lower jaw and very high number of longer and

198 finer gill rakers (Kahilainen et al., 2011).

199 The charr shift to piscivory was calculated by excluding data from empty stomachs and coding

200 prey containing stomachs as either 0 (only invertebrates) or 1 (fish or fish and invertebrates). In

201 addition, the normal Levins' B dietary breadth index (Levins, 1968), mean stomach fullness, and

202 number of empty stomachs were reported for each charr population. Finally, *Diphyllobothrium*

203 spp. cysts from the oesophagus and stomach wall of charr were counted from Inari, Kilpis and

204 Raha. This copepod-transmitted parasite is capable of being re-established from planktivorous

205 prey fish to charr, and thus their abundance is correlated with the intensity of piscivory (Hammar,

206 2000; Henriksen et al., 2016). For parasites, we calculated the mean infection intensity

207 (abundance as cysts/individual) and prevalence of infection (percentage of host individuals

208 infected).

209

210 Stable isotope analysis

211 Frozen fish and invertebrate samples were freeze-dried for 48 hours at −50°C or oven dried for

212 48 hours at 60°C. Samples were then ground to a fine powder, weighed (0.5–1.0 mg) and

213 encapsulated in tin cups. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios were measured

214 using an elemental analyzer connected to an isotope flow mass spectrometer at Max Planck

215 Institute for Limnology (Germany), University of Jyväskylä (Finland), University of New

216 Brunswick (SINLAB; Canada), or University of California Davis (SIF; US). All laboratories

217 used their own internal laboratory standards, calibrated with international standards, Vienna

218 PeeDee Belemnite for $\delta^{13}C$ and atmospheric nitrogen for $\delta^{15}N$. Analytical precision at all

219 laboratories was <0.3 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ based on repeated analyses of internal standards.

220 Charr may have a high lipid content in subarctic lakes (Kahilainen et al., 2016; Thomas et al.,

221 2016), so we arithmetically lipid-corrected carbon values using elemental C:N values (Kiljunen

222 et al., 2006).

223

224 Statistical analysis

225 *Prediction 1*: The trophic ecology of charr was assessed using biological metrics. A non-linear

226 von Bertalanffy growth model was used to estimate growth rate and asymptotic length (von

227 Bertalanffy, 1938). Probit regression was used to estimate length and age at 50% maturity, and

228 the size at which charr shifted to piscivory. Differences in mean sizes of prey in charr stomachs

229 were tested with ANOVA, followed by pairwise comparisons with Tukey's HSD tests. Statistical

230 significance was set to $P < 0.05$. Analyses were conducted using SYSTAT 11.0 (Systat Software

231 Inc., Chicago, IL, USA).

232 *Prediction 2*: The position and role of charr in lake food webs were assessed using stable

233 isotopes. Previously published stable isotope-based food-web data were reanalyzed (Thomas et

234 al., 2017). Inter-lake variation in stable isotope data was removed by transforming $\delta^{13}C$ values

235 into littoral reliance and $\delta^{15}N$ values into trophic position estimates using littoral benthic

236 macroinvertebrates and pelagic zooplankton as isotopic end-members and baselines (Karlsson &

237 Byström, 2005). Layman metrics, including littoral reliance (LR) range, trophic position (TP)

238 range, total area of convex hull (TA), mean distance to centroid (CD), mean nearest neighbor

239 distance (NND), and standard deviation of nearest neighbor distance (SDNND), and the core

240 stable isotopic diversity area of the fish community (SEAc) were used to assess how community-

241 level isotopic metrics differed between lakes with and without charr (Layman et al., 2007;

242 Jackson et al., 2011; Thomas et al., 2016). Food-web analyses were conducted using the Stable

243 Isotope Bayesian Ellipses in R (SIBER; Jackson et al., 2011) package version 3.4.1 (R

244 Development Core Team, 2017).

245

246

247 **Results**

248 Prediction 1: Population structure and biometrics data

249 Charr density was relatively low in all study lakes and ranged from 0.1% in Muddus to 7.6% in

250 Inari (Table 1). The profundal zone was the most important feeding habitat for charr (54.5–

251 100%), and charr were absent from the pelagic zone catches, except in Kilpis, where 2.5% of all

252 charr were captured from pelagic habitats (Table 2). Charr in all lakes attained a large size, with

253 maximum observed total length ranging from 51.5 to 74.3 cm (Table 2). Mean total length and

254 mass of charr were larger in Kilpis (42.6 cm, 1163 g) than in the other charr lakes, whereas the

255 lowest mean age was observed in Inari (Table 2). Asymptotic length ranged 46.8–83.4 cm and

256 growth rate (k) ranged 0.11–0.46, respectively (Table 2). Size at sexual maturity followed the

257 same pattern as asymptotic length: charr in Raha and Muddus reached maturity at a smaller size

258 than conspecifics in Inari and Kilpis (Table 2). Age at sexual maturity was higher in Kilpis and

259 Raha with monomorphic whitefish than Muddus and Inari with polymorphic whitefish. Charr

260 shifted to piscivory at a length of 15.9–24.8 cm and the smallest individual fish (11.2 cm) with

261 fish prey in its stomach was found in Inari (Table 2). Mean prey length differed among lakes

262 (ANOVA, $F_{3,318} = 15.8$, $p < 0.05$), and was larger in Muddus (12.4 cm) than in the other lakes

263 (Tukey's HSD tests, $p < 0.05$). Prey length ranged 1.9–25.2 cm. The smallest prey were

264 ninespined stickleback (*Pungitius pungitius* (L.)), whereas the largest were LSR whitefish (Table

265 2).

Fish prey contributed significantly to diets of charr of all sizes (Table 3), with coregonid fishes being important prey for charr. In monomorphic whitefish lakes, small piscivorous charr initially consumed small-bodied fish, such as alpine bullhead, *Cottus poecilopus* Heckel, (Kilpis) or ninespined stickleback, (Raha), and later shifted to larger sized LSR whitefish (Tables 2 and 3). Cannibalism was only observed in Kilpis, where four charr had consumed conspecifics. In lakes with polymorphic whitefish populations, piscivorous charr shifted diets from ninespined sticklebacks to pelagic coregonids, vendace or DR whitefish (Inari), or as in Muddus fed directly on DR whitefish throughout life (Tables 2 and 3). Preference for specific fish prey led to relatively low dietary breath (Levins B) that generally decreased with length, especially in Kilpis and Raha that had monomorphic whitefish where large charr preyed heavily on LSR whitefish (Table 3). Abundance and prevalence of *Diphyllobothrium* spp. cysts in charr increased with size. The trend was more pronounced in Kilpis and Raha with monomorphic whitefish than in Inari with polymorphic whitefish (Table 3).

Prediction 2: Stable isotopes and food webs

Charr occupied the highest trophic position in all lakes, with $\delta^{15}N$ values ranging from 10‰ to 12‰, and with $\delta^{13}C$ values ranging from −27‰ to −24‰ (Fig. 2; Table 4). In Kilpis and Raha (charr and monomorphic whitefish), charr were clearly the sole top predators, whereas in Inari and Muddus (charr with polymorphic whitefish) other piscivores shared the high trophic position with charr (Fig. 2). In the two control lakes without charr (Vuontis and Paadar), brown trout, pike, and burbot were at the top positions in the food web, with $\delta^{15}N$ values varying between 8‰ and 10‰, and $\delta^{13}C$ values ranging from −27‰ to −24‰. Mean littoral reliance (LR) of charr ranged from 30% to 60%, while estimated trophic position (TP) ranged from 3.8 to 4.4, but estimates did not differ between mono- or polymorphic whitefish lakes (Fig. 3).

290   Inclusion of charr increased food-chain length by 17.5–50.5% in monomorphic whitefish lakes

291   and by 2.2–13.9% in polymorphic whitefish lakes, whereas littoral reliance was not affected by

292   charr inclusion in any lake (Fig. 3, Table 5). The total fish community area (TA) increased by

293   51–97.6% and the core stable isotopic diversity area of fish community (SEA_c) increased by

294   44.4–50.6% in lakes with monomorphic whitefish, but only 8.1–10.9% and 6.7–9.5% in lakes

295   with polymorphic whitefish, when charr were included in the fish community (Table 5).

296   Inclusion of charr also increased mean distance to centroid (CD) in all lakes, whereas mean

297   nearest neighbor distance (NND) increased in lakes with monomorphic whitefish and decreased

298   in lakes with polymorphic whitefish populations (Table 5). Lakes without charr (Vuontis and

299   Paadar) had variable TA and SEA_c, but did not have food-chain lengths as long as lakes with

300   charr (Fig. 3, Table 5).

301

302   **Discussion**

303   Our results showed that charr shifted to piscivory at small size, grew to large asymptotic length,

304   matured late, almost exclusively consumed fish prey, and fed on a wide range of prey sizes. The

305   monomorphic whitefish lakes seemed to have more directed energy flow and based on diet,

306   parasite and stable isotope results had food chains linking invertebrates to LSR whitefish to charr.

307   Comparisons of the total area of the convex hull and the core stable isotopic diversity area of the

308   fish community demonstrated that charr increased the overall isotopic area of the fish community

309   by increasing food-chain length, especially in monomorphic whitefish lakes where charr was

310   clearly the top consumer. In polymorphic whitefish lakes hosting many piscivores, the food-web

311   structuring effects of charr were less pronounced.

312

313

Charr as a part of diverse fish communities

Charr populations studied here had relatively low densities, and mainly inhabited deep profundal habitats. All the fish communities examined here were dominated by coregonid fishes, which contributed more than 60% (numerical abundance) of the fish catch. Whitefish was the most abundant coregonid, which is a well-known resource competitor for charr due to its more efficient zooplanktivory (Svärdson, 1976; Sandlund et al., 2010; Jensen et al., 2017). In Muddus and Inari, whitefish have diverged into morphs spanning across littoral, pelagic, and profundal zones, thereby reducing invertebrate prey resources (Kahilainen et al., 2017). Resource competition of juvenile charr with polymorphic whitefish for both pelagic and benthic invertebrates is likely intense in these lakes, at least during summer months. However, lakes of this size typically support a more a diverse range of prey species of vary body size, further complicating trophic interactions. This may open an avenue for a small proportion of charr to make a shift to piscivory, ultimately allowing them to prey on their whitefish competitors, further increasing the complexity of interactions between the two species in these systems.In addition, large lakes are generally cold-water environments, where charr may benefit compared to whitefish due to its better growth potential at low temperatures (Siikavuopio et al., 2010). We acknowledge that in small lakes with limited habitat and prey availability, whitefish introductions can be deleterious to charr populations (Svärdson, 1976). In three of the charr lakes, littoral habitats had abundant populations of Eurasian perch (*Perca fluviatilis* L.) and grayling (*Thymallus thymallus* (L.)), which are both likely resource competitors for juvenile charr (Eloranta et al., 2011; Sandlund et al., 2010, 2016). Furthermore, pelagic and littoral habitats, especially in polymorphic lakes, contained piscivorous brown trout that are direct competitors for large charr (Kahilainen & Lehtonen, 2002; Thomas et al., 2017). All charr lakes also hosted pike (*Esox lucius* L.) and burbot (*Lota lota* (L.)) that potentially prey on charr (Svärdson, 1976, Byström et al., 2007; Knudsen et al., 2010). Obviously the high resource competition and

339   predation regimes may have contributed to low charr density in the littoral and pelagic zones,

340   and induced a shift by charr to profundal habitats in these lakes.

341

342   Prediction 1: Large-bodied charr as a piscivore in multispecies fish communities

343   Availability of several small-bodied prey fishes likely facilitated the population-level shift of

344   charr to piscivory at 15–25 cm total length. This length at the shift to piscivory is within the range

345   found in other charr lakes, as well as those found in other piscivorous salmonids (L'Abee-Lund

346   et al., 1992; Amundsen, 1994; Mittelbach & Persson, 1998). The shift to piscivory in all studied

347   char lakes was associated with fast growth, large maximum size, and late maturation age. In charr

348   lakes, especially in Kilpis, charr growth and maturation size were more similar to the situation

349   found in warmer lakes at lower latitudes, where charr rely on vendace and smelt (*Osmerus*

350   *eperlanus* L.) as principal prey resources (Hammar, 2014; Hammar et al., 2018). These prey

351   species were not present or native in our subarctic study lakes, in which whitefish was an

352   important food source for all populations. While the mean prey size was typically <10 cm, some

353   fish consumed larger prey (up to 25 cm), which were typically whitefish as has been observed in

354   previous studies of charr diet in multispecies lakes (Amundsen 1994; Hammar, 2014; Hammar

355   et al., 2018).

356

357   Small charr preferred small-bodied prey fish, such as alpine bullhead and ninespined stickleback.

358   Based on charr diets, these species are potentially abundant in lakes, but their abundance cannot

359   be assessed from gill net catches due to their small size, slow swimming speed, and low

360   catchability (Malinen et al., 2014). At a larger size, charr used the most available prey fish,

361   namely coregonid fishes (Eloranta et al., 2015b). The pelagic density of coregonid prey ranged

362   from 80 LSR whitefish per hectare in Kilpis up to 670 DR whitefish per hectare in Muddus

363   (Malinen et al., 2014). In Inari and Raha, pelagic prey-fish density, vendace, whitefish, and their

364   hybrids, reached 390 per hectare in both lakes (Kahilainen et al., 2011; Malinen et al., 2014;

365   Thomas et al., 2016). Prey selection of the most abundant prey in multispecies lakes is typical

366   for charr (Amundsen, 1994; Kahilainen & Lehtonen, 2002; Hammar et al., 2018). However,

367   because charr preferred benthic habitat in all lakes, pelagic prey fish density may not directly

368   reflect benthic prey availability, especially of benthic LSR whitefish that could be better assessed

369   using gill net CPUE (Malinen et al. 2014). While cannibalism by charr is common, especially in

370   small lakes with low species diversity, cannibalism was only observed in Kilpis, perhaps because

371   other prey species are generally more abundant and profitable to feed on in multispecies lakes

372   (Amundsen, 1994; Kahilainen & Lehtonen, 2003; Eloranta et al., 2015a). Strict selection of one

373   or two abundant prey species was also evident based on the generally narrow dietary breadth of

374   charr.

375

376   A strong preference for LSR whitefish prey in monomorphic whitefish systems was also

377   indicated by rapidly increasing numbers of *Diphyllobothrium* spp. cysts in the stomach wall of

378   piscivorous charr. This parasite can re-establish infections in salmonid top predators after being

379   ingested in its original coregonid host (Hammar, 2000; Henriksen et al., 2016). Parasite

380   abundance was higher in charr foraging on monomorphic LSR whitefish in Kilpis and Raha (this

381   study, Kahilainen et al., 2011; Hayden et al. 2014), as compared to Inari, where charr fed on a

382   larger variety of prey fishes. This reflects a more direct energy flow from copepods to LSR

383   whitefish, and finally to charr, in monomorphic whitefish systems, as compared to the case in

384   polymorphic whitefish lakes that have more complex prey fish communities and food-web

385   structures. From a parasite transmission point of view, generalist monomorphic whitefish provide

386   a straight pathway to the next trophic level through charr, whereas in polymorphic systems,

387   several potential intermediate hosts are available, so the probability of parasites encountering a

388   final avian host (gulls and divers) is likely lower. Specialist zooplanktivores in polymorphic

whitefish lakes, such as pelagic whitefish morphs and vendace, could also be more resistant to *Diphyllobothrium* spp. infections because their parasite abundance and prevalence was generally much lower than observed for LSR whitefish in monomorphic lakes (Kahilainen et al. 2011; Hayden et al., 2014).

Prediction 2: The role of piscivorous charr in lake food webs

Stable isotopes indicated that charr were the only, or among the main top consumers, in all charr lakes. In lakes with monomorphic whitefish, inclusion of charr clearly increased total area and core isotopic diversity area of the whole fish community relative to Muddus and Inari with polymorphic whitefish populations. The latter lakes had many other predators (e.g. brown trout, burbot, pike, and lake trout) with similar trophic positions to charr, and as a result exclusion of charr did not substantially alter the isotopic niche areas of these fish communities. The difference between lake types was also evident from contrasting patterns of nearest-neighbor distances that were higher in lakes with monomorphic whitefish than in lakes with polymorphic whitefish. This indicates that polymorphic lakes not only have more piscivorous species sharing the top consumer position with charr, but also a wider array of prey fish (species or ecomorphs). Simpler monomorphic whitefish lakes therefore seem to have more direct food chains than those in polymorphic whitefish systems. Food-chain length was also generally shorter in lakes without charr. For example, Vuontis (monomorphic whitefish population) has many predators (pike, burbot and brown trout) sharing the top consumer position, and thus energy flow is less direct. In contrast, Paadar (polymorphic whitefish) showed less consistent patterns of piscivores, the overall food-web shape was more horizontal than vertical, and there were multiple energy flow pathways.

Our food-web data suggest that the role of large charr as top consumer varies in different lake types. The role as apex predator seems to be most pronounced in Kilpis and Raha, which are both deep lakes with simple prey fish communities dominated by monomorphic LSR whitefish. These lakes have limited littoral foraging or spawning habitat available for competing piscivores such as pike and brown trout. Top-down regulation by charr is likely strong in both lakes, inducing strong fluctuations of LSR whitefish populations (Kahilainen et al., 2011; Hayden et al., 2014). Piscivory by cold-water adapted charr, can be an important source of mortality in late winter and spring when they are more active than their main prey, i.e. LSR whitefish (Siikavuopio et al. 2010). The deep and cold subarctic lakes with monomorphic whitefish have zooplankton communities dominated by copepods, and sheltered soft-sediment habitats harboring abundant benthic macroinvertebrate sources are scarce. Such lake ecosystems reduce the opportunities for morph divergence (Harrod et al. 2010; Hayden et al. 2014). These low diversity conditions have resulted in more direct energy flow in the food web. They are also prone to population fluctuations across different trophic levels (copepods, LSR whitefish, charr and parasites), making them highly unstable over time as is typical for many Arctic ecosystems (e.g. Hanski et al. 1991; Jepsen et al. 2008). In contrast, higher diversity systems, such as lakes with polymorphic whitefish, have more links and various energy flow pathways to top consumers, making them less prone to fluctuations (MacArthur, 1955; Hutchinson, 1959; Polis & Strong, 1996). Lakes with polymorphic whitefish are associated with a more diverse piscivore fish assemblages within which individuals commonly attain large body-sizes, suggesting that ecological speciation by whitefish has food-web consequences (Thomas et al. 2017). Potentially, the divergence of prey could promote the divergence of predators (Brodersen et al., 2018), but testing this assumption would require considerable research, particularly in large lakes with high habitat availability.

Climate change implications and future of large charr

438 Climate warming is occurring markedly faster in subarctic and Arctic regions than the global

439 average (Rolls et al., 2017). Climate change is associated with increased nutrient inputs to lakes

440 from surrounding catchments, and invasions by new warm- and turbid-water adapted species

441 have been related to probable local extinction of charr (Hayden et al., 2017). Such invasions are

442 likely important in both high and low diversity systems because the addition of new key species,

443 like vendace, can have considerable ecosystem-level consequences (Bøhn et al. 2008; Kahilainen

444 et al. 2011; Thomas et al. 2016). Increased lake temperature and productivity are also expected

445 to reduce oxygen concentrations in the profundal zone, thereby further squeezing the niche space

446 of charr (Lehtonen, 1996; Guzzo et al., 2017). In addition, polymorphic fish populations are

447 especially susceptible to eutrophication and new species invasions that often lead to local

448 extinction via reverse speciation (Taylor et al., 2006; Vonlanthen et al., 2012; Bhat et al., 2014).

449 All these combined stressors could change the oligotrophic top-down controlled lake ecosystems

450 with long food-chains to bottom-up controlled systems with shorter food chains where fish

451 communities are exclusively dominated by abundant, small-sized, warm-adapted non-salmonid

452 species (Hayden et. al., 2017).

453

454 Conclusions

455 Large piscivorous charr are important apex predators in multispecies subarctic communities.

456 They have an especially important functional role in the species-poor lakes with simple food

457 webs, which are often dominated by monomorphic whitefish. In these lakes, exclusion of charr

458 reduced the stable isotopic area of the fish community by reducing the food-chain length,

459 whereas such effects were less pronounced in systems with more diverse fish fauna (polymorphic

460 whitefish lakes). However, more detailed long-term studies in both lake types are needed for a

461 detailed assessment of the top-down role of charr in whitefish dominated systems. Assessments

462 of how divergence of one species affects other trophic levels, including potential divergence, are

463 also needed. The overall low abundance of charr in the fish communities studied here suggests

464 that management control of new stressors, such as land-use change, introductions or the invasions

465 of new species will be needed to maintain the remaining large-bodied charr populations in

466 subarctic Scandinavia. Moreover, understanding the role of charr in subarctic lakes at present

467 may help to better predict how such systems could change if charr were to become locally extinct

468 as a result of climate change or other anthropogenic factors.

469

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Table 1. Lake type (mono-WF=monomorphic whitefish, poly-WF=polymorphic whitefish), location, morphological properties, water chemistry and numerical proportion of different fish species present in the study lakes, based on multi-mesh (12-60 mm) gill net catches (height 1.8 m) in the three major habitats in each lake. Fishing effort refers to the number of sampling occasions with two gill net series (1.8 m high and 5 m high). Compensation depth refers to the water column depth, where 1% of surface light was maintained, denoting the border between the littoral and profundal zones. Percentage of profundal is the proportion of this habitat to the total lake surface area. The abbreviations for whitefish morphs are: LSR=large sparsely rakered whitefish, DR=densely rakered whitefish, LDR= large densely rakered whitefish, and SSR=small sparsely rakered whitefish. Minus sign (-) refers to absence and plus sign (+) presence of species in the lake, based on all used fishing methods and stomach content analyses. Note that Vuontis and Paadar are not inhabited by charr.

Parameter	Kilpis	Raha	Muddus	Inari	Vuontis	Paadar
Lake type	Charr and mono-WF	Charr and mono-WF	Charr and poly-WF	Charr and poly-WF	No charr, mono-WF	No charr, poly-WF
Location	69°00'N, 20°49'E	68°45'N, 27°17'E	69°00'N, 26°50'E	68°58'N, 27°40'E	69°01'N 27°04'E	68°52'N, 26°35'E
Area (km^2)	37	23	48	32*	11	21
Altitude (m a.s.l.)	473	132	146	118	151	144
Max depth (m)	57	46	73	40*	31	56
Mean depth (m)	19.4	14.1	8.5	14.5	6.5	11.7
Tot P (μgl^{-1})*	3	4	4	5	5	7
Tot N (μgl^{-1})*	100	100	160	150	180	160
Compensation depth (m)	10	9	7	8	12	5
Percentage profundal (%)	71	57	41	40	20	62
Fishing effort (1.8 m net series)	69	18	30	14	14	42
Fishing effort (5 m net series)	47	18	329	27	23	10
Arctic charr (%)	4.3	3.3	0.1	7.6	-	-
LSR whitefish (%)	88.8	57.7	15.3	10.5	90.4	22.7
DR whitefish (%)	-	-	49.8	13.1	-	43.7
SSR whitefish (%)	-	-	15.6	30.4	-	22.0
LDR whitefish (%)	-	-	2.5	1.8	-	2.0
Vendace (%)	-	9.6	-	24.3	-	-
Perch (%)	-	26.8	14.2	10.9	8.7	5.6
Brown trout (%)	1.4	0.5	1.1	1.0	0.2	1.4
Burbot (%)	3.4	1.4	0.6	0.2	0.2	1.8
Pike (%)	0.1	0.6	0.7	0.1	0.4	0.1
Grayling (%)	0.9	0.2	0.1	+	0.1	0.5
Minnow (%)	0.8	+	+	+	+	0.1
Alpine bullhead (%)	0.3	-	-	-	-	-
Ninespined stickleback (%)	-	+	+	+	+	+
Threespined stickleback (%)	-	+	+	+	+	+
Lake trout (%)	-	-	-	+	-	-
Landlocked salmon (%)	-	-	-	+	-	-

*area and max depth of sampled site are from Nanguvuono bay.

Table 2. Biological metrics of charr (mean ± 95% CL). Lake type (mono-WF=monomorphic whitefish, poly-WF=polymorphic whitefish), sample size, proportion of females, size and condition, capture habitat of charr samples, von Bertalanffy growth modelling results, sexual maturation, total length at shift to piscivory, range of prey total length and mean total lengths.

Parameter	Kilpis	Raha	Muddus	Inari
Lake type	Charr and mono-WF	Charr and mono-WF	Charr and poly-WF	Charr and poly-WF
Sampling years	2002, 2005,2006, 2009, 2010, 2011, 2012	2005	1999-2002, 2004-2007, 2011	2009-2010
Number of charr	159	66	164	108
Mean total length (cm)	42.6±2.5	33.3±2.5	39.1±1.1	29.9±3.1
Total length range (cm)	13-74.3	13.6-51.5	15-59.3	11.2-70
Mean weight (g)	1163.3±187.4	401.3±74.5	576.5±49.6	545.9±139.6
Weight range (g)	14.2-5525	16.3-1296.6	23-2368.4	9.7-4234
Mean age (years)	6.8±0.3	7.5±0.7	6.7±0.2	4.1±0.5
Age range (years)	1-12	2-13	3-9	1-9
Profundal (%)	84.9	98.3	54.5	100
Littoral (%)	12.6	1.7	45.5	0
Pelagic (%)	2.5	0	0	0
Growth rate (k; vonBertalanffy)	0.14±0.01	0.22±0.01	0.46±0.02	0.11±0.01
Asymptotic length (L_∞)	83.4±1.7	46.8±0.9	48.8±0.5	79.4±3.4
t_0	1.32	0.9	3.0	-0.54
Age at sexual maturity (50%)	8.3±0.9	8.6±1.6	5.9±0.3	6.7±1
Length at sexual maturity (50%)	50.8±2.5	37.2±4.8	36.6±1.1	43.9±4.7
Shift to piscivory length (50%)	15.9±5.6	24.8±3.6	17.6±6.1	16.5±5.8
Length range of charr with fish prey in their stomachs (cm)	15.0-70.4	19.7-51.5	16.2-51.0	11.2-54
Mean prey length (cm)	9.4±0.9	9.6±1.4	12.4±0.6	7.6±1.6
Range of prey size (cm)	1.9-25.2	2.5-18.1	5.5-24	1.9-17.2
Mean number of fish in stomach	2.8±0.9	2.5±0.6	2.1±0.4	2.2±1.0
Number of fish in stomach range	0-21	0-9	0-8	0-21
Coregonus sp. (mean±95%CL;range)	-	11.1±3.1;6.5-17;	12.5±1.2;5.5-21;	13.5±1.8; 7-17.2
LSR whitefish	12.1±1.1;5.6-25.2	12.7±1.4;6.5-19	13.9±3.6;7-24	-
DR whitefish	-	-	12.2±0.6;4-15.1	10.5
Vendace	-	10.7±4.3;8-15	-	7.8±1.3;6.2-14.5
Ninespined stickleback	-	3.2±0.3;2.5-4.7	-	2.8±0.3;1.9-4.5
Alpine bullhead	5.0±0.3;1.9-7	-	-	-
Arctic charr	12.9±1.9;11.3-15.2	-	-	-
Burbot	18.1	-	5.5	-
Perch	-	-	11	-

687 Table 3. The proportion (%) of different prey categories in the diet of different total length

688 categories (cm) of charr in the study lakes. Abbreviations: BMI=benthic macroinvertebrates,

689 LSR=large sparsely rakered, DR=densely rakered, Levins B= Levins dietary breadth, empty (%)

690 = proportion of empty stomachs, SF=stomach fullness (scale 0=empty, 10=maximum full),

691 n=number of studied stomachs, *Diphyllobothrium* cysts=mean number of cysts in stomach wall,

692 prevalence=proportion of individuals infected. Please note that in Muddus, *Diphyllobothrium*

693 spp. parasites were not counted. Kilpis and Raha have charr and monomorphic whitefish,

694 whereas Muddus and Inari have charr and polymorphic whitefish.

Prey category and diet related calculations	Kilpis			Raha			Muddus			Inari		
	<20	20-39	>40	<20	20-39	>40	<20	20-39	>40	<20	20-39	>40
Zooplankton	37.3	0	0	53.4	6.4	0	13.3	0	0	15.4	0.9	0
BMI	11.5	3.4	0.6	18.9	9.5	0.6	6.7	3.2	0.4	38.7	4.6	0.2
Vendace	0	0	0	0	6.4	3.9	0	0	0	0	34.7	30.0
Unidentified fish	7.7	11.7	4.6	0	2.1	8.4	0	0.9	0	9.4	22.7	5.4
Perch	0	0	0	0	0	0	0	0	1.1	0	0	0
LSR whitefish	14.5	61.3	69.7	0	46.0	68.8	0	4.5	10.6	0	0	0
Coregonus spp.	0	0	0	0	23.2	18.2	13.3	40.6	26.8	0	34.7	57.9
Ninespined stickleback	0	0	0	27.7	6.4	0	0	0	0	36.4	2.3	0
DR whitefish	0	0	0	0	0	0	66.7	50.9	60.3	0	0	6.4
Burbot	0	0	4.2	0	0	0	0	0	0.8	0	0	0
Alpine bullhead	29.0	9.2	19.3	0	0	0	0	0	0	0	0	0
Arctic charr	0	14.3	1.5	0	0	0	0	0	0	0	0	0
Proportion of fish (%)	51.3	96.6	99.4	27.7	84.1	99.4	80	96.8	99.6	45.9	94.4	99.8
Levins B	3.8	2.4	1.9	2.5	3.5	1.9	2.1	2.3	2.2	3.2	3.4	2.3
Empty (%)	22.7	25.6	54.2	16.7	5.1	0	0	34.7	37.4	14.9	38.1	60
mean SF	2.8	2.8	2.1	3.9	4.8	5.1	3.8	3.0	3.2	2.8	2.1	1.2
n	22	43	94	12	39	15	4	75	83	47	21	40
Diphyllobothrium cysts	4.2	49	95.8	0.4	23	38.2	-	-	-	0	4.8	15.6
Prevalence (%)	54.6	100	100	41.7	87.2	100	-	-	-	0	42.9	92.5

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702   Table 4. Sample sizes of different fish species used in stable isotope analyses.

Species	Kilpis	Raha	Muddus	Inari	Vuontis	Paadar
Lake type	Charr and mono-WF	Charr and mono-WF	Charr and poly-WF	Charr and poly-WF	No charr and mono-WF	No charr and poly-WF
Alpine bullhead	17	–	–	–	–	–
Arctic charr	30	30	14	30	–	–
Brown trout	21	30	30	30	19	30
Burbot	30	13	20	30	21	9
Grayling	26	–	23	27	8	7
Lake trout	–	–	–	30	–	–
Minnow	12	–	–	–	–	–
Ninespined stickleback	–	–	–	30	5	9
Perch	–	30	30	30	30	30
Pike	30	6	30	25	28	3
DR whitefish	–	–	30	30	–	30
LDR whitefish	–	–	30	30	–	30
LSR whitefish	120	105	30	30	80	30
SSR whitefish	–	–	30	30	–	30
Vendace	–	30	–	30	–	–
Total sample size	286	244	267	382	191	208

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Table 5: Food-web metrics derived from stable isotope data (Layman et al. 2007, Jackson et al. 2011) including trophic position (TP) range, littoral reliance (LR) range, total convex hull area (TA), mean distance to centroid (CD), mean nearest neighbor distance (NND) and standard deviation of mean nearest neighbor distance (SDNND) and core stable isotopic diversity area of fish community (SEAc). In charr lakes, we included values to represent estimates including (Charr) and discounting charr (No charr) and the resulting proportional difference in values (%). Kilpis and Raha host charr and monomorphic whitefish populations, in contrast to Inari and Muddus which host charr and polymorphic whitefish populations. Vuontis (monomorphic whitefish) and Paadar (polymorphic whitefish) are lakes lacking charr and are presented as control lakes.

Metric	Kilpis			Raha			Inari			Muddus			Vuontis	Paadar
	No charr	Charr	Δ%	No charr	Charr	Δ%	No charr	Charr	Δ%	No Charr	Charr	Δ%	No Charr	No Charr
TP range	0.75	1.12	50.5	0.74	0.87	17.5	1.22	1.25	2.2	0.97	1.10	13.9	1.04	0.54
LR range	0.55	0.55	0.0	0.40	0.40	0.0	0.67	0.67	0.0	0.57	0.57	0.0	0.45	0.83
TA	0.21	0.32	51.0	0.10	0.19	97.6	0.48	0.52	8.1	0.33	0.36	10.9	0.23	0.27
CD	0.25	0.33	34.9	0.28	0.31	10.9	0.35	0.38	8.6	0.35	0.39	12.0	0.42	0.35
NND	0.18	0.20	8.6	0.15	0.16	9.1	0.18	0.17	-6.9	0.18	0.16	-11.5	0.18	0.22
SDNND	0.15	0.14	-6.9	0.07	0.07	6.6	0.11	0.07	-35.4	0.12	0.10	-12.7	0.14	0.09
SEAc	0.16	0.23	44.4	0.09	0.14	50.6	0.25	0.27	6.7	0.22	0.24	9.5	0.20	0.24

Figure captions


Figure 1. Map of northern Fennoscandian (A) showing the location of study lakes in western (B) and eastern (C) Finnish Lapland. The number in the parentheses after lake name refers to type of fish population: 1 = charr and monomorphic whitefish populations, 2 = charr and polymorphic whitefish populations, 3 = no charr and monomorphic whitefish populations and 4 = no charr and polymorphic whitefish populations.

Figure 2. Stable isotope bi-plot data showing mean ± SD values of the littoral benthic macroinvertebrates (LBMI), zooplankton (ZPL) and profundal benthic macroinvertebrates (PBMI). Ellipses show the core isotopic area of different fish species and are presented with abbreviations: AC=Arctic charr, LT=lake trout, P=pike, B=burbot, BT=brown trout, PE=perch, G=grayling, SB=ninespined stickleback, AB=alpine bullhead, V=vendace, M=minnow, LSR=large sparsely rakered whitefish, LDR=large densely rakered whitefish, SSR=small sparsely rakered whitefish, DR= densely rakered whitefish. Kilpis and Raha have charr and monomorphic whitefish, Muddus and Inari have charr and polymorphic whitefish and control lakes Vuontis (monomorphic whitefish) and Paadar (polymorphic whitefish) do not have charr in the fish community.

Figure 3. Stable isotopic diversity of the fish communities based on total area (convex hull) and core area (ellipse) with (black line) or without (gray line) including the data for charr. Each point represents the mean value for one fish species. Kilpis and Raha have charr with monomorphic whitefish, but Muddus and Inari have charr with polymorphic whitefish. Please note that Vuontis (monomorphic whitefish) and Paadar (polymorphic whitefish) are not inhabited by charr and presented as control lakes.
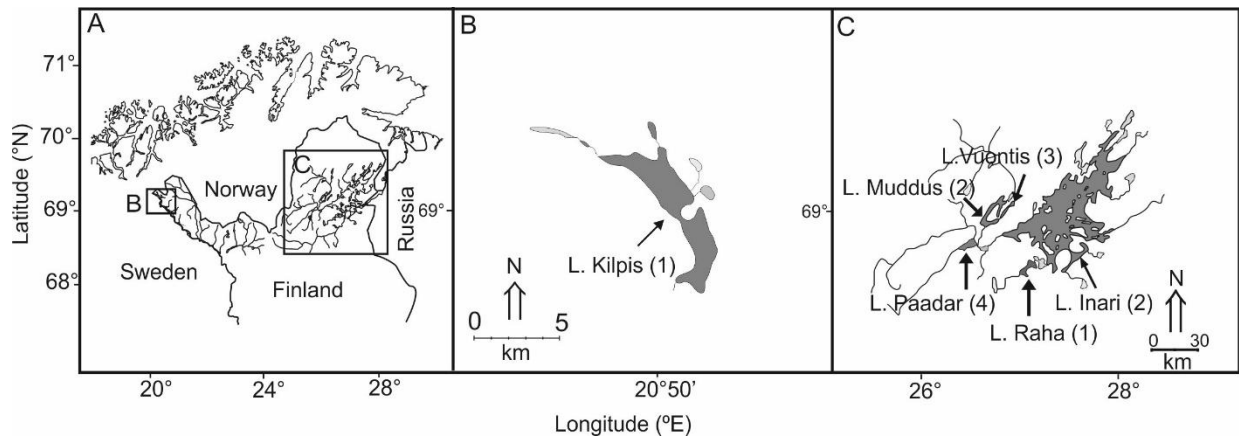
Figure 1.

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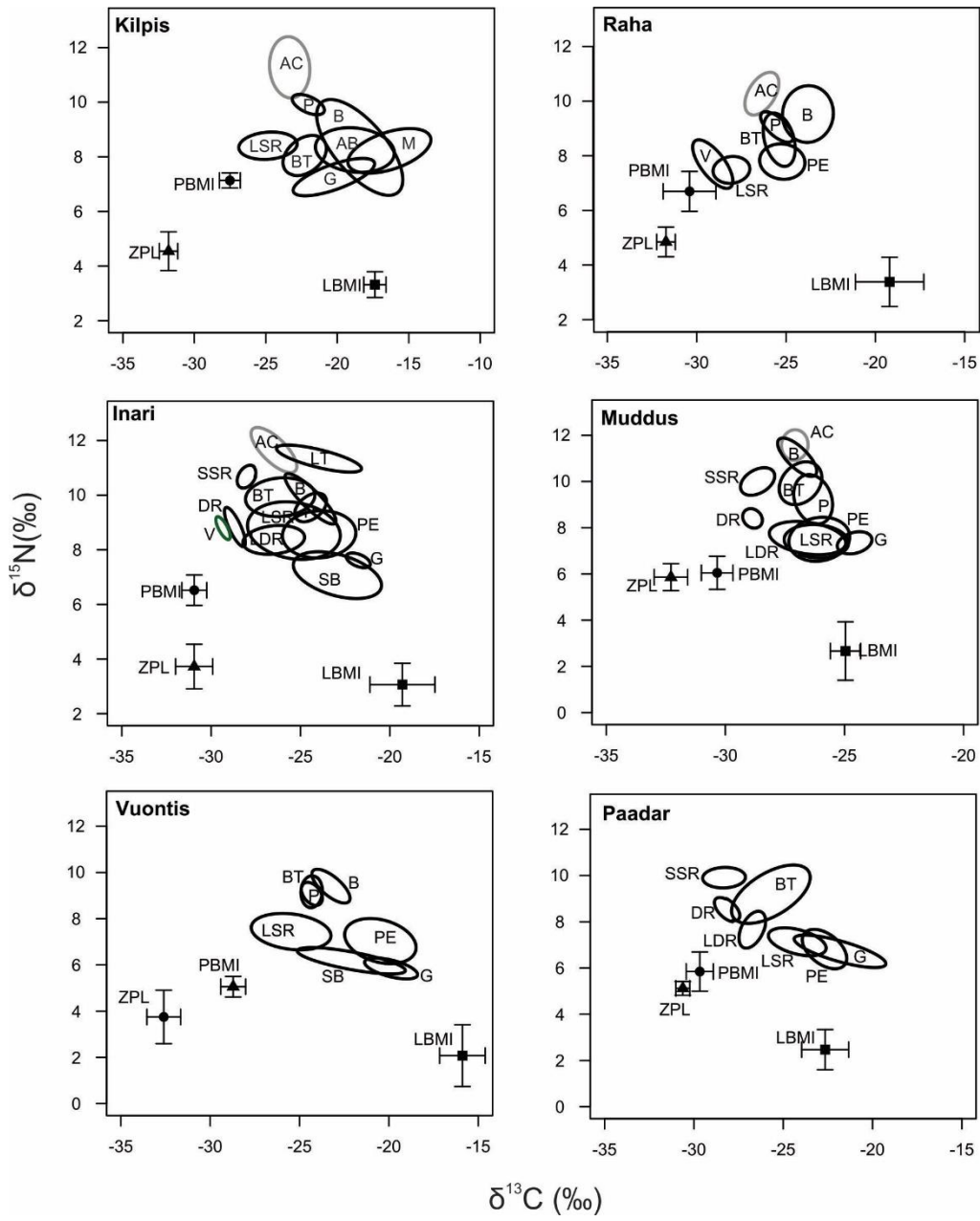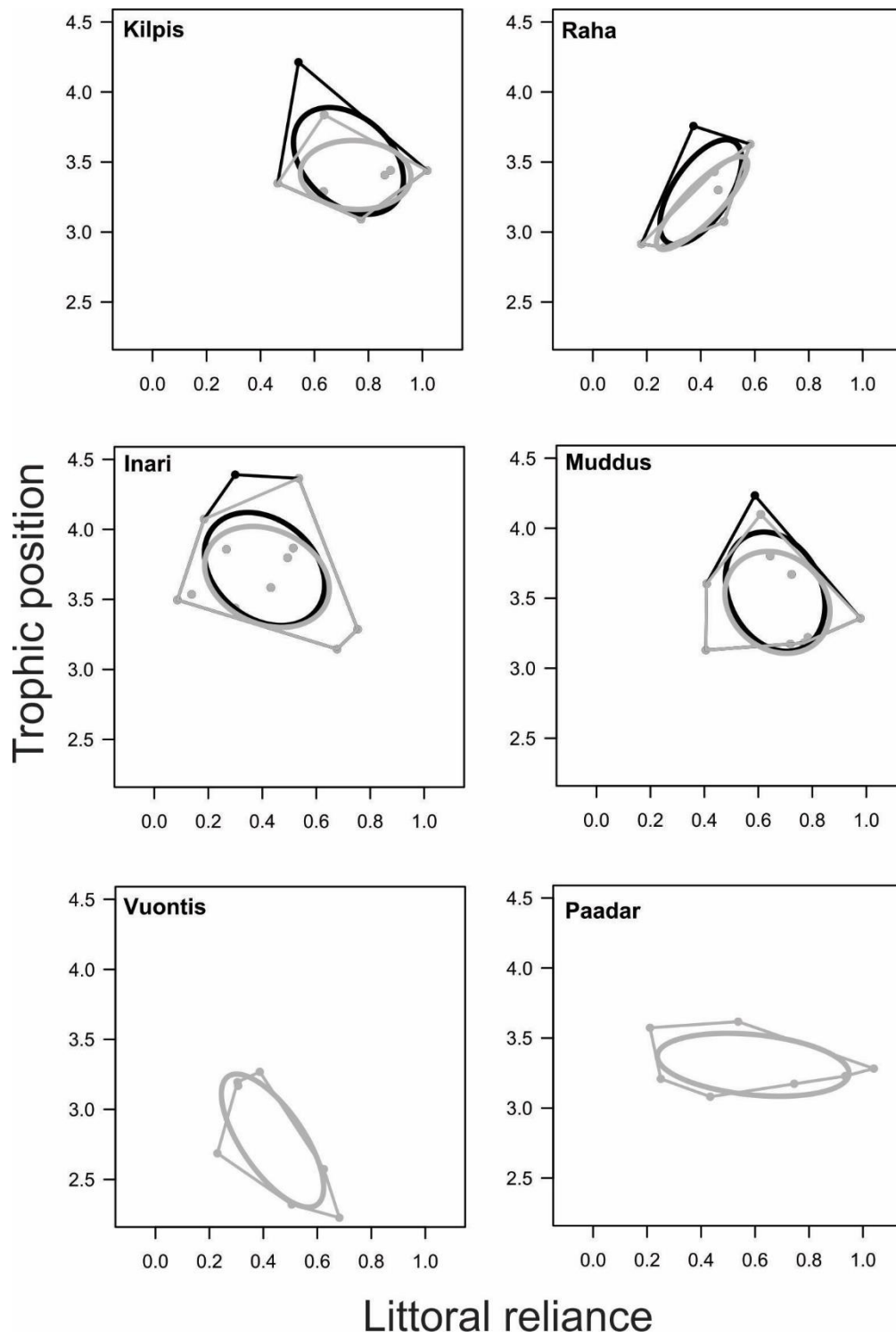
752   Figure 3.