Introduction of *Mysis relicta* (Mysida) reduces niche segregation between deep-water Arctic charr morphs

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Abstract: Niche diversification of polymorphic Arctic charr can be altered by multiple

anthropogenic stressors. The opossum-shrimp (*Mysis relicta*) was introduced to compensate for

reduced food resources for fish following hydropower operations in Lake Limingen, central Norway.

Based on habitat use, stomach contents, stable isotopes (δ^{13}C, δ^{15}N) and trophically transmitted

parasites, the zooplanktivorous upper water-column dwelling 'normal' morph was clearly trophically

separated from two sympatric deep-water morphs (the 'dwarf' and the 'grey') that became more

abundant with depth (>30m). *Mysis* dominated (50-60%) charr diets in deeper waters (>30m),

irrespective of morph. *Mysis* and/or zooplankton prey groups caused high dietary overlap (>54%)

between the 'dwarf' morph and the two other 'normal' and 'grey' morphs. After excluding *Mysis*,

the dietary overlap dropped to 34% between the two profundal morphs, as the 'dwarf' fed largely on

deep-water zoobenthos (39%), while the 'grey' morph fed on fish (59%). The time-integrated trophic

niche tracers (trophically transmitted parasites and stable isotopes) demonstrated only partial dietary

27 segregation between the two deep-water morphs. The high importance of *Mysis* in Arctic charr diets

28 may have reduced the ancestral niche segregation between the deep-water morphs and thereby

29 increased their resource competition and potential risk for hybridization.

30

31 **Keywords:** *Salvelinus alpinus*, polymorphism, ecological divergence, species introductions,

32 hydropower effects, parasite community, stable isotopes

33

34 **Introduction**

35 Ecologically induced speciation may lead to a continuum of evolutionary differences within and

36 among populations, with some groups being in the process of diversifying and others being

37 reproductively isolated (Schluter, 2000; Hendry et al., 2009). Post-glacial lakes are useful systems

38 for studying the impacts of biodiversity changes caused by environmental, ecological and human-

39 induced factors as they are semi-closed ecosystems with relatively well defined habitats that can host

40 polymorphic populations at different stages of evolutionary divergence (Schluter, 2000; Klemetsen,

41 2010; Hendry et al., 2017). Human activities may have large impacts on natural environments by

42 rapidly changing the direction of evolutionary developments and in some instances reverse the

43 evolutionary processes that promote increasing biodiversity (Hendry et al., 2017). Multiple

44 anthropogenic stressors in lake ecosystems, including pollution, commercial fishing and non-native

45 species introductions, have reversed speciation processes (Seehausen et al., 2008; Alexander et al.,

46 2017; Kuparinen & Festa-Bianchet, 2017). For example, reproductive breakdown has been observed

47 in newly differentiated native morph-pairs of whitefish (*Coregonus lavaretus*) and stickleback

48 (*Gasterosteus aculeatus*) following the introduction of competitive fish species or invasive crayfish

49 (Taylor et al., 2006; Velema et al., 2012; Baht et al., 2014).

In postglacial lakes, polymorphic fish populations often diverge along the benthic-pelagic resource axis (e.g., Schluter, 1996, 2000). Charr (*Salvelinus* spp.) is one of the few genera that is also found to diversify along the shallow *vs*. deep-water benthic resource axis (Knudsen et al., 2006; Klemetsen, 2010; Muir et al., 2016; Markevitch et al., 2018). Knowledge about deep-water (profundal) morphs of Arctic charr (*S. alpinus*) is still relatively limited, although they seem to occur across the entire Holarctic region (Klemetsen, 2010). The deep-water morphs are typically reproductively isolated from co-occurring littoral and pelagic morphs (Hindar et al., 1986; Westgaard et al., 2004; Simonsen et al., 2017). Moreover, they express heritable specialised physiological, behavioural, and morphological adaptations (Klemetsen et al., 2002, 2006; Knudsen et al., 2015) to effectively exploit (i.e., for foraging and mating) the deep-water niches (Knudsen et al. 2016a). Small-sized deep-water morphs feed mainly on benthic invertebrates whereas the few known, large-growing deep-water morphs are specialised piscivores (Knudsen et al. 2006, 2016b; Klemetsen et al. 2010; Power et al., 2009; Moccetti et al., this volume). Although the ecology of the deep-water morph has been studied, little is known about the potential impacts of multiple anthropogenic stressors (e.g., hydropower operations and the introduction of non-native species) on these deep-water morphs.

Lake Limingen, central Norway, has a polymorphic population of Arctic charr, consisting of three morphs: the upper-water 'normal' morph, the deep-water 'dwarf' morph, and the piscivorous 'grey' morph (Nyman et al., 1981; Aass et al., 2004). Following the damming of the lake in 1953 for hydropower production, brown trout (*Salmo trutta*) and Arctic charr population densities drastically declined (Aass et al., 2004; Gregersen et al., 2006). In 1969, *Mysis relicta* (hereafter *Mysis*) was introduced to compensate for reduced fish food resources and to mitigate the negative impacts of hydropower operations on fish and overall ecosystem productivity (cf. Hirsch et al. 2017). *Mysis* is an opossum shrimp native to Scandinavia, though previously absent from this Limingen region of Norway (Spikkeland et al., 2016). *Mysis* show a pronounced diel vertical migration pattern,

75 with nocturnal foraging on zooplankton in the upper water column potentially resulting in food

76 resource competition with zooplanktivorous Arctic charr (Moen & Langeland, 1989; Næsje et al.,

77 1991, Koksvik et al., 2009). In contrast, deep-water fish (e.g., burbot *Lota lota* and profundal Arctic

78 charr) may benefit from *Mysis* introductions through increased food availability (Langeland et al.,

79 1991; Næsje, 1995). Whilst introduced *Mysis* populations have become an important prey resource

80 for Arctic charr in Limingen and elsewhere (Garnås, 1986; Gregersen et al., 2006), detailed studies

81 of their impacts on trophic differentiation among sympatric Arctic charr morphs has been lacking.

82   In this study, we investigated the habitat use, diet, parasite infections and

83 stable isotope ratios (δ^{13}C, δ^{15}N) of the three sympatric Arctic charr morphs in Limingen. The aim of

84 the study was to explore the degree of niche overlap between the three sympatric Arctic charr

85 morphs about 50 years after the introduction of *Mysis*. We quantified niche overlap by using data on

86 habitat use and stomach contents (recent niche-use) and by analysing the occurrence of trophically

87 transmitted parasites and stable isotope values that reflect the temporally integrated trophic niches of

88 individual fish (Knudsen et al., 2011). We hypothesised that existing depth-habitat preferences for

89 the sympatric morphs would be maintained. However, due to damming and the introduction of

90 *Mysis*, we also hypothesised that prey resource use would overlap, particularly between the upper-

91 water 'normal' and the deep-water morphs.

92

93 **Material and methods**

94 Study lake

95 Lake Limingen (64°50'N, 13°13'E) is a large (surface area = 95.7 km^2), deep (Z_{max} = 192 m, Z_{mean} =

96 87 m), dimictic, oligotrophic and relatively clear (Secchi depth = 9–12.7 m) lake situated at 418 m

97 a.s.l. in the north boreal vegetation zone of central Norway. Originally, the lake drained to the

98 Ångermanälven watercourse in northern Sweden, but after hydropower development in 1953 most of

the water was diverted to the Namsen watershed in Trøndelag County, Norway (Sandlund et al.,

2017). Today, the lake is regulated with a maximum annual water level amplitude of 8.7 m. Spruce

forests with some birch dominate the riparian vegetation and there are only a few low-intensity farms

around the lake. In addition to the polymorphic Arctic charr, the lake has a small population of

brown trout, a littoral population of minnow (*Phoxinus phoxinus*; introduced in 1980s) and a very

sparse population of three-spined stickleback (introduction date unknown) (Aass et al., 2004;

Gregersen et al., 2006).

Fish material

Arctic charr were sampled in August 2016 with Nordic multi-mesh gill-nets consisting of 5 m panels

with 12 different knot-to-knot mesh sizes from 5 to 55 mm (Appelberg et al., 1995). The nets were

set in the littoral (1.5 m high benthic nets; 0-15 m depth), pelagic (6 m high offshore gill-nets set

from the surface; above 30 m depth), and profundal (1.5 m high benthic nets; at 20-50 m depth)

zones. Additional sampling with a pelagic pair trawl caught 63 'normal' morph Arctic charr. Fish

were weighed (closest 0.1 g) and measured (closest 1 mm, fork length, L_F). Otoliths were removed

for age determination.

Individual Arctic charr were classified to one of three possible morphs based

on head and body morphology, maturation, and colouration following guidelines produced from

earlier studies of similar polymorphic populations (Skoglund et al., 2015; Simonsen et al., 2017). In

total, we sampled 178 Arctic charr from Limingen, with stomachs analysed from 171 individuals.

The catch per unit of effort (CPUE) was estimated as the number of fish caught per 100 m^2 gillnet

per night. A subsample of mature individuals from all three morphs was assessed for parasite

assemblages and sampled for stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$). The numbers of each morph

included in the parasite and stable isotope sampling were: 'normal' morph (n = 39; mean ± SD: L_F =

123   310.6 ± 83.7 mm; age = 6.7 ± 2.5 years), 'dwarf' morph (n = 27; L_F = 173.9 ± 31.7; age = 6.4 ± 2.6),

124   and 'grey' morph (n = 14; L_F = 297.1 ± 59.3; age = 9.5 ± 3.4).

125   Growth differences among morphs were described by mean length-at-age

126   using a modified von Bertalanffy growth model (Roff, 1984): $L_T = L_\infty * (1 - (exp(- k * A_T)$, where

127   L_T is fish body length at time T, L_∞ is the asymptotic fish length, k is the growth coefficient, and A_T is

128   the age at time T. This simplified model has been shown to work well with inland polymorphic

129   salmonids (Jonsson et al., 1988).

130

131   Diet

132   Prey items from fish stomachs were preserved in ethanol and later identified to the lowest feasible

133   taxonomic level (23 different prey taxa in total) and subsequently sorted into five main categories: i)

134   zooplankton (e.g., *Daphnia*, *Bosmina*, *Holopedium, Bythotrephes*, copepods), ii) surface insects

135   (adult insects), iii) benthos (e.g., snails, clams, insect larvae, benthic crustaceans), iv) *Mysis*, and v)

136   fish. The contribution of each prey category to the diet was estimated by visual determination of the

137   stomach fullness using a percentage scale ranging from empty (0%) to full (100%) (prey abundance;

138   Amundsen et al., 1996). Among morph dietary overlap was quantified for all prey categories using

139   Schoener's (1970) similarity index, which is commonly considered high when the overlap exceeds

140   60% (Wallace, 1981).

141

142

143   Parasites

144   All parasites from the body cavity, stomach, intestine, kidney, swim bladder, gills and eyes were

145   enumerated from sub-sampled fish (see Table 3 for more details). Most of the parasite taxa are

146   transmitted to Arctic charr via different prey items such as copepods (cestodes *Dibothriocephalus*

147   spp., *Proteocephalus* sp. and *Eubothrium salvelini*), insect larvae (trematodes *Crepidostomum* spp.),

148   and the benthic amphipod *Gammarus lacustris* (cestode *Cyathocephalus truncatus*, nematode

149   *Cystidicola farionis*, and Acanthocephalan sp.). *Mysis* may also transmit the swim bladder nematode

150   *C. farionis* (Black & Lankester, 1980), however, the intermediate host for this parasite is currently

151   unknown. All taxa, except *Dibothriocephalus* spp., utilize Arctic charr as the final host (see Table 3

152   for further details). Larval *Dibothriocephalus* spp. (former *Diphyllobothrium* spp., see

153   Waeschenbach et al., 2017) are able to use fish as parathenic hosts and re-establish in piscivorous

154   individuals (Curtis, 1984), which also may be the case for *Eubothrium* sp. (Williams & Jones, 1994).

155   Additionally, three parasite taxa are non-trophically transmitted to the fish, either from other fish,

156   i.e., the parasitic gill crustacean (*Salmincola edwardsii*), or via trematode larvae released from

157   intermediate snail hosts, i.e., *Diplostomum* sp. and *Apatemon* sp. We quantified parasite prevalence

158   (percentage of hosts infected by the parasite) and abundance (number of parasites *per* host) following

159   methods outlined in Bush et al. (1997). The exceptions were *Diplostomum* sp. and *Apatemon* sp., for

160   which the prevalence and abundance were estimated from a single eye (at random).

161

162   Stable isotopes

163   Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) are commonly used to estimate the dietary

164   sources (littoral *versus* pelagic carbon) and trophic position of organisms in lake food webs, as well

165   as the intra- and inter-specific niche segregation of fish populations (e.g., Boecklen et al., 2011;

166   Layman et al., 2012). Here, a small piece of dorsal muscle tissue, obtained posterior to the dorsal fin,

167   was dissected from a subsample of fish and frozen at $-20°$C. Tissue samples were dried at $60°$C for

168   48 hours and homogenised using a pestle and mortar. Approximately 0.3 ± 0.05 mg of dried tissue

169   was weighed and placed in tin capsules for analyses completed at the University of Waterloo,

170   Canada, on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo

171   Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo

172   Erba, Milan, Italy). The machine analytical precision of ± 0.2 ‰ (δ^{13}C) and ± 0.3 ‰ (δ^{15}N) was

173   determined through the repeat analysis of internal laboratory standards calibrated against

174   International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen.

175

176   Statistical analyses

177   All statistical analyses were computed using R (version 3.4.2, R Core Team 2017). Differences in the

178   number of parasite taxa among morphs were compared using a general linear model fitted with a

179   Gaussian distribution family. Differences in total parasite abundance and the abundance of each

180   parasite taxon among charr morphs were examined using a series of generalized linear models, with

181   the exception of five rare taxa (*C. truncatus*, *E. salvelini*, *S. edwardsii*, Acanthocephalan sp.,

182   unidentified nematode), which were excluded from further analysis. Generalized linear models were

183   fitted with a quasipoisson distribution and log-link function due to the over-dispersion of abundance

184   data. Fish age (years) was included as a continuous fixed factor in all general and generalized linear

185   models to account for the influence of varying host age on parasite abundance and richness. Potential

186   outliers were identified by graphically examining the raw data and by running models with and

187   without outliers to assess their influence on model outcomes. Analysis of variance was used to assess

188   whether the interaction term between morph and age provided additional explanatory power over the

189   simpler additive model. Contrast analyses were constructed for each final model set by varying the

190   base morph (intercept) to assess the significance of differences between morph pairs.

191   Multivariate analyses were conducted using the package vegan (version 2.5-2,

192   Oksanen et al., 2017). Parasite community composition differences among morphs were visualized

193   by using individual Arctic charr in a non-metric multidimensional scaling analysis (NMDS) based on

194   Bray-Curtis dissimilarities of log-transformed parasite abundances, including both trophically and

195   directly transmitted parasite species. To visualize and explore the correlation between individual diet

196   and parasite community composition, we used canonical correlation (vegan: CCorA, Oksanen et al.,

197   2017) of logit-transformed prey volumes and log-transformed abundances of trophically transmitted

198   parasites.

199   Non-parametric Kruskal-Wallis tests, followed by pairwise comparisons with

200   Mann-Whitney U-tests, were used to evaluate the significance of differences in $\delta^{13}C$ (reflecting

201   littoral *vs.* pelagic resource use) and $\delta^{15}N$ (reflecting trophic position) values among the three charr

202   morphs. Isotopic niche overlaps were calculated between all pairs of morphs using the probabilistic

203   method developed by Swanson et al. (2015), available in the R-package nicheROVER (Lysy et al.,

204   2014). In this method, a Bayesian approach is employed to produce 95% probability niche regions

205   and directional estimates of pairwise niche overlap. Niche overlap is defined as posterior

206   probabilities that an individual of one morph falls within the niche region (95%) of the other morph.

207   Potential outliers were identified graphically from the raw data, and two outliers were removed to

208   ensure better fit to multivariate normal distribution of the data.

209

210   **Results**

211   Fish community, habitat preference and Arctic charr growth

212   Arctic charr was the dominant species (n =168) in the benthic habitats (i.e., littoral and profundal),

213   whereas only nine 'normal' Arctic charr were caught in the pelagic zone (0.6 charr per 100 m^2 gillnet

214   area). Additionally, 34 brown trout, 68 minnows and one three-spined stickleback were caught from

215   the littoral zone. The CPUE of Arctic charr (overall mean: 3.8 fish per 100 m^2 benthic gillnet per

216   night) increased with depth from about 1.8 at 0-10 m, 2.2 at 10-20 m, 5.2 at 20-30 m to >8 at >30 m

217   depth. The 'normal' morph was most abundant in the upper water-column layers (Fig. 1a), down to

218   30 m depth (CPUE-range: 2-4.5). The 'dwarf' morph was most abundant at depths >20 m (CPUE:

219   >4), and the 'grey' morph was most abundant within the 30-50 m depth zone (CPUE: >2).

220   Length-at-age differed among the morphs, with significant differences in mean

221   length (t-tests, $p<0.05$) observed between 'normal' and profundal 'dwarf' morphs for each age-class

222   between four and nine years (Fig. 1b). Estimated von Bertalanffy growth models indicated greater

223   asymptotic lengths for the 'normal' and 'grey' morphs as compared with the 'dwarf' morph, with

224   non-overlapping confidence intervals indicating significantly different maximal sizes for all morphs.

225   Growth rate (k) similarly differed among the morphs as indicated by non-overlapping confidence

226   intervals, being lower in the 'normal' and 'grey' morphs and highest in 'dwarf' morph (Table 1). It

227   should be noted that the precision of parameter estimates for the 'grey' morph was possibly affected

228   by the smaller number of fish available for estimating model parameters.

229

230   Dietary niches

231   Generally, the abundance (%) of *Mysis* in charr stomach contents increased with depth, independent

232   of the morph considered (Fig. 2a), being about 10% in upper water column (0-10 m) and >60% in

233   deep waters (>50 m). In contrast, the diet of all Arctic charr captured in the uppermost water column

234   (<30 m depth) was dominated by zooplankton (>53%) and surface insects (>20%). *Mysis* constituted

235   18% of the diet of the 'normal' morph, 35% of the 'grey' morph diet and 39% of the 'dwarf' morph

236   diet (Fig 2b). The 'dwarf' morph consumed zooplankton (29%) and benthos (23%), in addition to

237   *Mysis*. The 'dwarf' morph ate much less *Daphnia* and *Bythotrephes*, but approximately equal

238   amounts of *Bosmina* and *Holopedium* when compared with the 'normal' morph. The 'grey' morph

239   relied more heavily on fish (38%) than the other morphs, which had less than 1.5% fish in their

240   stomachs. Common consumption of *Mysis* and/or zooplankton prey groups caused a relatively high

241   dietary overlap (54-56%) between the 'dwarf' morph and the two other morphs when considering all

242 prey groups (23 taxa). Dietary overlap was lower (41%) between the 'normal' and the 'grey' morph.

243 After removing *Mysis* as a prey group, the dietary overlap dropped to 34% between the two deep-

244 water morphs, as the 'dwarf' morph fed mainly on zooplankton (49%) and deep-water zoobenthos

245 (39%), while the 'grey' morph fed mainly on fish (59%).

246

247 Parasite community composition

248 A total of 11 parasite taxa were found, including eight trophically transmitted parasites, one directly

249 transmitted parasite (*S. edwardsii*) and two trematode taxa (*Diplostomum* sp. and *Apatemon* sp.)

250 transmitted from snail intermediate hosts. Taxon richness increased with host age for both 'normal'

251 and 'dwarf' morphs, whereas age did not influence parasite taxon richness in the piscivorous 'grey'

252 morph (GLM$_{morph:age}$: $F_{2,67} = 5.16$, $p = 0.008$; Tables 2 and S1). Total parasite abundance was

253 significantly higher in the 'normal' morph compared to the 'dwarf' morph, while the piscivorous

254 'grey' morph had intermediate infection levels (GLM$_{morph}$: $F_{2,70} = 4.70$, $p = 0.012$; Tables 2 and S1).

255 Parasite community composition in individual Arctic charr appeared to be

256 more similar in the two profundal morphs compared to the 'normal' morph (Fig. 3). Of the three

257 parasite taxa non-trophically transmitted to charr, *Diplostomum* sp. and *Apatemon* sp. were the most

258 prevalent among morphs (~40-65 %), whereas *S. edwardsii* tended to occur in the 'normal' charr

259 morph (20 %). The abundance of non-trophically transmitted parasites was consistently low (< 3

260 individual parasites per fish) and did not differ among morphs, although there was a positive

261 relationship between *Diplostomum* sp. abundance and charr age (Tables 3, S2). Of the trophically

262 transmitted parasites, the upper water-column 'normal' morph had the highest prevalence for five of

263 eight parasite taxa, and the remaining three parasite taxa were most prevalent in the piscivorous

264 'grey' morph. Two *Gammarus* transmitted taxa, *C. truncatus* and *Acanthocephala* sp., were

265 restricted to 'normal' charr morphs only. *Dibothriocephalus* spp. cestode larvae were the most

266   prevalent trophically transmitted parasite and occurred in similar abundances in all morphs (Tables 3,

267   S2). The copepod-transmitted taxa, i.e. *Proteocephalus* sp. and *Eubothrium* sp., were more prevalent

268   in the 'normal' morph than in the deep-water charr morphs. *Proteocephalus* sp. abundance was

269   greater in the 'normal' morph than in the 'dwarf' morph, with the abundance of this parasite

270   declining with charr age (Tables 3, S2). The swim bladder nematode *C. farionis* was found most

271   often in the piscivorous 'grey' morph, although it was in consistently low abundance in all charr

272   morphs (Table 3).

273   The community composition of trophically transmitted parasites in individual

274   charr was significantly explained, albeit moderately, by the diet composition of the individual

275   (Canonical Correlation R^2adj = 0.30, p < 0.001; Fig. 4). Thus, when visualizing both the most recent

276   diet (stomach contents) and the temporally-integrated characterization of resource use as measured

277   by trophically transmitted parasites, all morphs appeared to have different trophic niches (Fig. 4).

278   The two deep-water morphs were located closest to each other, indicating they have more similar

279   trophic niches. The 'normal' morph was more separated (Fig. 4) and associated with higher

280   infections of *Proteocephalus* sp. and *Crepidostomum* spp. as a result of feeding on a different

281   assemblage of zooplankton species and insect larvae than the 'dwarf' or 'grey' morphs. The 'grey' and

282   'dwarf' morphs were mainly associated with infections of *Dibothriocephalus* spp. and *C. farionis*,

283   linked to feeding on *Mysis*, mussels, chironomid larvae, and fish.

284

285   Stable isotopes

286   The three Arctic charr morphs showed significant differences in $\delta^{13}C$ (Kruskal-Wallis: χ^2 = 10.69, df

287   = 2, p = 0.005) and $\delta^{15}N$ (χ^2 = 42.93, df = 2, p < 0.001) values. The 'normal' morph had significantly

288   lower (i.e., more pelagic) $\delta^{13}C$ values than the 'grey' morph (Mann-Whitney pairwise comparison: p

289   = 0.002), whereas the other between-morph differences in $\delta^{13}C$ were non-significant (p = 0.07–0.09).

290 The 'normal' morph showed variable but significantly lower δ^{15}N values than either the 'dwarf' or

291 'grey' morphs (Mann-Whitney pairwise comparisons; $p < 0.001$; Figure 5a) and was separated from

292 both by approximately one trophic level (i.e., ~3 ‰). In contrast, the 'dwarf' and 'grey' morphs did

293 not differ in δ^{15}N (Mann-Whitney pairwise comparisons; p -=0.268), although 'grey' morph

294 individuals tended to have higher δ^{15}N values consistent with piscivorous feeding. Isotopic niche

295 overlap analyses showed that the 'dwarf' and 'grey' morphs had high probabilities of sharing the

296 same niche region (70% and 76%), while they had lower probabilities of overlapping with the

297 'normal' morph (32% and 25%) (Table 4; Fig 5b). The 'normal' morph had the lowest probabilities

298 of overlapping with either of the profundal morphs (14% and 10%) (Table 4).

299

Discussion

301 We observed a partial niche segregation between the three sympatric Arctic charr morphs in

302 Limingen, with the clearest segregation being between the upper water-column zooplanktivorous

303 'normal' morph and the two profundal morphs, the 'dwarf' and the piscivorous 'grey' morphs.

304 Although we do not have directly comparable data from each of the morphs before the *Mysis*

305 introduction (Gregersen et al., 2006), our results suggest that the *Mysis* introduction has reduced

306 niche segregation between the three sympatric Arctic charr morphs as a result of common

307 exploitation of this resource, with the strongest impacts being on the two deep-water morphs. The

308 temporally integrated trophic tracers (parasite fauna and stable isotope values) pointed to a further

309 partial dietary segregation between the two Arctic charr morphs with identical deep-water

310 preferences, with the 'dwarf' and 'grey' morphs supplementing a *Mysis*-based diet with benthic prey

311 and fish, respectively. The reduced trophic segregation has increased the apparent ecological

312 similarity between the morphs and has the potential to enhance the probability for increased

313 competitive interactions and hybridization.

314   A corresponding trophic segregation between the 'normal' morph and the

315 sympatric profundal morphs occurs in some other polymorphic lakes (Knudsen et al., 2006, 2016a;

316 Amundsen et al., 2008; Moccetti et al., this volume). In Arctic charr, a zooplanktivorous diet is

317 generally found in southern Scandinavian lakes (e.g., L'Abée-Lund et al., 1993; Sandlund et al.,

318 2016; Jensen et al., 2017; Paterson et al., this volume), in lakes regulated for hydropower production

319 (e.g., Hirsch et al., 2017), and in northern lakes with benthivorous competitors (e.g., Skoglund et al.,

320 2013; Eloranta et al., 2013). In northern lakes with deep-water morphs, the upper water-column

321 'normal' Arctic charr morph may also include littoral resources in the diet (Knudsen et al., 2010,

322 2016a; Eloranta et al., 2013; Moccetti et al., this volume). In Limingen, however, the benthic

323 resources in shallow littoral areas are restricted due to water level fluctuations that reduce littoral

324 zone productivity(e.g., Hirsch et al., 2017) and the occupancy of available shallow areas by abundant

325 minnows and a few brown trout (Aass et al., 2004; Gregersen et al., 2006). Low presence of littoral

326 benthos in the diet of the 'normal' morph is supported by low infection by the few parasite species

327 transmitted from benthic prey (i.e., *Crepidostomum* sp.), as also been observed in other studies in this

328 geographic region (Paterson et al., 2018; Paterson et al., this volume).

329   The small-sized deep-water 'dwarf' morph included both zooplankton and

330 *Mysis* in the diet, resulting in a relatively high dietary overlap between the 'normal' and 'grey'

331 morphs. Small-sized deep-water Arctic charr morphs typically specialize on soft-bottom benthos

332 (Hindar & Jonsson, 1982; Knudsen et al., 2006, 2016a,b; Hooker et al., 2016; Moccetti et al., this

333 volume), as do profundal whitefish morphs (Harrod et al., 2010; Præbel et al., 2013; Siwertsson et

334 al., 2013) and brown trout (Piggott et al., 2018). In Limingen, excluding *Mysis* consumption reduced

335 the apparent dietary overlap between the two profundal morphs, with consumption of prey resources

336 other than *Mysis* pointing to a more distinct benthivorous dietary niche for the 'dwarf' morph.

337 Although separation into morph groupings was not reported, zoobenthos were noticeably more

338 common in the diet of Arctic charr prior to the *Mysis* introduction (Gregersen et al., 2006). The

339   introduction of *Mysis* may have induced a dietary shift by the 'dwarf' morph towards a more pelagic

340   diet as a result of the diel vertical migration of *Mysis* within the water column. The 'dwarf' morph

341   also had significantly higher $\delta^{15}N$ values and less diverse parasite fauna when compared to the

342   'normal' morph in Limingen and nearby lakes (Paterson et al., 2018; Paterson et al., this volume), as

343   has been reported for other polymorphic Arctic charr lakes (Knudsen et al., 1997, 2016a; Siwertsson

344   et al., 2016). Despite the apparently large dietary overlap, the above suggests that the 'dwarf' morph

345   has a less unique benthivorous diet in Limingen than in other lakes (see also Mocchetti et al., this

346   volume).

347   The relative importance of *Mysis* in the diet of the 'grey' morph is not typical

348   for large-growing Arctic charr (but see Henriksen et al., this volume), although lake charr (*S.*

349   *namaycush*) predate substantially on *Mysis* (e.g., Chavarie et al., 2016) particularly when introduced

350   to oligotrophic lakes (e.g., Ellis et al., 2002). In Limingen, fish was an important prey for the 'grey'

351   morph, but not for the sympatric 'normal' and 'dwarf' morphs, indicating the position of 'grey'

352   Arctic charr as specialized piscivores (Adams et al., 1998; Power et al., 2005; Knudsen et al., 2016b;

353   Moccetti et al. this volume). The inclusion of a specialized piscivore among lake-resident morphs is

354   also found in other polymorphic *Salvelinus* spp. populations (Muir et al., 2016; Markevitch et al.,

355   2018). Although the relatively high $\delta^{15}N$ values of the 'grey' morph partly reflected their piscivorous

356   diet, the morph was less clearly separated from the 'dwarf' morph than has been evident in studies of

357   other profundal morph-pairs (Knudsen et al., 2016a; Moccetti et al., this volume). The 'grey' morph

358   had a higher diversity of trophically transmitted parasites than 'dwarf' morph, likely passed on via

359   prey fish as has been noted elsewhere (Siwertsson et al., 2016; Moccetti et al., this volume). The

360   'grey' morph also had aggregated high *Dibothriocephalus* spp. infections (a cestode able to re-

361   establish in predatory fish; e.g., Curtis, 1984), as is often seen in other piscivorous *Salvelinus* spp.

362   morphs (Frandsen et al., 1989; Butorina et al., 2008; Siwertsson et al., 2016, Moccetti et al., this

363   volume). However, the parasite data also suggests abundant ingestion of *Mysis* by the 'grey' morph,

as *C. farionis* (a swim-bladder nematode potentially transmitted by mysids; Black & Lankester, 1980) were most frequent in the 'grey' morph. Overall, the parasite results (i.e., community structure and/or abundance) described here support previous conclusions that piscivorous predators are exposed to a portfolio of parasite species that differ from those found in sympatric invertebrate feeding morphs (Siwertsson et al., 2016; Moccetti et al., this volume).

The profundal 'grey' and 'dwarf' morphs in Limingen also showed greater similarity in diets and growth rates than the sympatric deep-water benthivorous and piscivorous charr morphs found elsewhere (Smalås et al., 2013; Knudsen et al., 2016a,b; Moccetti et al., this volume), likely as a result of *Mysis* consumption as has been noted for lake trout feeding on introduced *Mysis* in Flathead Lake, Montana (Ellis et al., 2002). The introduced *Mysis* is also one of the main reasons for the high dietary overlap, which was similarly reflected in the overlap in isotopic niches and parasite fauna between the deep-water Arctic charr morphs. When present, *Mysis* may dominate the diet of benthic and pelagic Arctic charr in Scandinavian lakes in all seasons, but especially during winter when zooplankton are scarce (Garnås, 1986; Næsje, 1995; Hammar, 2014). Introduction of *Mysis* in polymorphic Arctic charr lakes may therefore diminish the ecological segregation between sympatric morph pairs and alter the local selection regimes. Whilst there is no information regarding reproductive isolation (e.g., time and place of spawning) for Limingen Arctic charr, the morphs are thought to be genetically different (Nyman et al., 1981). In several other post-glacial lakes, upper water-column morphs of Arctic charr and whitefish are genetically different from their sympatric benthivorous deep-water morphs, as well as from resident piscivorous morphs (Verspoor et al., 2010; Præbel et al., 2013, 2016; Siwertsson et al., 2013; Simonsen et al., 2017; Moccetti et al., this volume). The 'normal' morph in Limingen differ from the other two sympatric morphs in terms of habitat depth, whereas the two deep-water morphs segregate in terms of piscivory; yet, all three morphs prey on the introduced *Mysis*. Thus, reliance on *Mysis* clearly reduces the niche segregation between the morphs as a result of its impacts on energy flow pathways through the lake food web

389   (e.g., Ellis et al., 2002). Ecological convergence (e.g., similarity in diet) as observed in the present

390   'dwarf' and 'grey' morphs, may even promote hybridization. The "reverse speciation" process

391   (increased hybridization) among native fish morphs has been reported from other lakes where the

392   introduction of non-native competitors or potential prey have impaired ecological segregation (e.g.,

393   Taylor et al., 2006; Vonlanthen et al., 2012; Baht et al., 2014).

394   Multiple human-induced stressors are evident in Limingen and common in

395   many Scandinavian freshwater systems (Hirsh et al., 2017). Hydropower-induced water level

396   fluctuations provided the initial environmental stressor that reduced littoral benthic food resources

397   for fish (Gregersen et al., 2006). Another human-induced ecosystem stressor was the introduction of

398   Eurasian minnow, a typical shallow-water benthivorous resource competitor for salmonids

399   (Borgstrøm et al., 2010; Museth et al., 2010). Finally, the introduction of *Mysis* may have further

400   altered the niche use of the 'normal' morph through increased competition for zooplankton resources

401   (Langeland et al., 1991). There is generally little understanding about how multiple human-induced

402   stressors may affect relatively simple postglacial lake ecosystems such as Limingen, and no

403   information exists on how cumulative stressors can affect the evolutionary processes structuring

404   polymorphic Arctic charr populations (Sandlund & Hesthagen, 2011). By introducing *Mysis* into a

405   lake ecosystem with a littoral zone impaired by hydropower operations, the evolutionary selection

406   regimes appear to have been modified, which may in turn induce a breakdown of the reproductive

407   isolation between established morphs as a result of increasing the functional ecological similarity

408   among the morphs.

409   For management of the scattered and unique deep-water morphs of Arctic

410   charr, it is important to obtain an overview of the occurrence of intra-lake divergence within

411   populations, describe their biological characteristics and determine the environmental prerequisites

412   for their occurrence. Based on recent ecological and genetic studies, deep-water morphs of Arctic

413   charr and whitefish are replicated in several locations and appear to originate locally (Østbye et al.,

2006; Knudsen et al., 2006; Klemetsen 2010; Præbel et al., 2013, 2016). Profundal morphs of Arctic

charr have evidently inherited traits selected for surviving in cold, dark and nutrient–poor deep-water

environments, including specific adaptations in trophic morphology, behavior and growth

(Klemetsen et al., 2002, 2006; Knudsen et al., 2015). Other traits seem to a lesser degree to be under

strong natural selection, such as temperature preference and vision capabilities (Siikavuopio et al.,

2014; Kahilainen et al., 2016). Without appropriate knowledge of the occurrences of traits within and

among populations of Arctic charr, and of northern lake resident fish in general, a full understanding

of the functional biodiversity within these lakes will remain unknown. Functional diversity is an

important component of biodiversity in northern lakes (Sandlund & Hesthagen, 2011) and its

categorization is particularly important given the rapid anthropogenic induced environmental change

that is altering ecosystems and biodiversity faster than the diversity can be inventoried (Reist et al.,

2013).

A second concern and challenge for management is to identify potential threats

to these deep-water morphs that may reduce their abundance or even cause local extinction. There

seems to be no population-specific, cold-water adaptations in deep-water Arctic charr morphs as they

have the same estimated temperature preferences as those from Svalbard and most of Scandinavia

(Larsson et al., 2005; Siikavuopio et al., 2014). Profundal morphs, however, tend to spawn later than

sympatric upper water-column morphs, during the winter when lakes are normally ice-covered

(Klemetsen et al., 1997; Smalås et al., 2017). The profundal zones in deep oligotrophic postglacial

lakes are relatively stable environments, experiencing less variability in food supply and temperature

regimes (e.g., Mousavi & Amundsen, 2012). Thus, populations inhabiting these lakes may be less

affected by moderate global warming (Poesch et al., 2016), as they can thermally buffer in cold deep

waters isolated from summer temperature stratification. Arctic charr populations that spawn in

shallow areas may actively avoid the warm upper water-column layers during summer stratification

(Murdoch & Power, 2012) but may alter spawning timing or habitat (e.g., Winfield et al., 2010;

439 Jeppesen et al., 2012). Thus, upper water-column morphs may be more severely affected by an

440 accumulation of anthropogenic -induced stressors, e.g., climate change and hydropower-induced

441 water level fluctuations. Furthermore, if whole lake ecosystems are significantly modified, there may

442 be cascading ecological consequences even for deep-water morphs, as has been suggested by the

443 data from Limingen. This may include an increased risk of hybridization between morph-pairs that

444 will eventually reduce the intraspecific biodiversity apparent in many Scandinavian lakes.

445

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732

733 **Table 1**. von Bertalanffy growth parameters for the three Arctic charr morphs found in Limingen.

Charr morph	# fish	Asymptotic length, L_∞	SE	95% C.I. (lower and upper bound)	Growth coefficient, k	SE	95% C.I. (lower and upper bound)
'normal'	132	496.2	36.2	424.5 – 567.7	0.14	0.02	0.11 – 0.18
'dwarf'	81	196.2	6.2	183.8 – 208.5	0.39	0.03	0.32 – 0.45
'grey'	18	360.3	38.7	278.3 – 442.4	0.20	0.05	0.08 – 0.31

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735

736 **Table 2.** Summary of parasite infection in the three Arctic charr morphs ('normal', 'dwarf' and

737 'grey') from Limingen, central Norway. Values are mean ± SE.

	'normal' n=35	'dwarf' n=24	'grey' n=14	Contrast[1][*]
Taxa richness	4.1 ± 0.3	2.5 ± 0.3	3.9 ± 0.3	(normal:age = dwarf:age) ≠ grey:age
Total abundance*	56.9 ± 9.1	23.0 ± 5.7	39.6 ± 11.0	(normal > dwarf) = grey

738 [*] summary of inter-morph contrast analyses; [1]see supplementary Table S1 for details. p < 0.05.

739 **Table 3.** Summary of life stage, infection site, intermediate host and trophic transmission status of parasite taxa from three Arctic charr morphs

740 ('normal', 'dwarf' and 'grey') in Limingen, central Norway. Prev = prevalence %; Abund = mean abundance ± SE; stage (L = larval; A = adult),

741 infection site (v = viscera, i = intestine, k = kidney, sb = swim bladder, fg = fins/gills).

Parasite taxa	Stage	Site	Interm. host	Trophic transm.	'normal		'dwarf'		'grey'		Contrasts[1][*]
					Prev	Abund	Prev	Abund	Prev	Abund	
Trematoda											
Apatemon sp.[#]	L	e	snails, fish	No	60.0	1.3 ± 0.3	45.8	0.9 ± 0.3	57.1	1.6 ± 0.6	NS
Crepidostomum spp.	A	i	insect larvae	Yes	62.9	9.7 ± 2.2	37.5	0.8 ± 0.3	57.1	3.4 ± 1.7	normal > (dwarf = grey)
Diplostomum sp.[#]	L	e	snails, fish	No	45.7	2.9 ± 1.4	41.7	1.0 ± 0.3	64.3	1.3 ± 03	age
Cestoda											
Cyathocephalus truncatus	A	i	amphipods	Yes	2.9	0.9 ± 0.9	0	0	0	0	-
Dibothriocephalus spp.	L	v	copepods, fish	Yes	80.0	14.0 ± 5.0	65.2	18.9 ± 5.9	92.9	30.5 ± 11.4	NS
Eubothrium salvelini	A	i	copepods, fish	Yes	31.4	0.6 ± 0.2	4.2	0.04 ± 0.04	14.3	0.6 ± 0.4	-
Proteocephalus sp.	A	v	copepods, fish	Yes	77.1	25.4 ± 8.8	25.0	1.4 ± 0.8	35.7	0.6 ± 0.2	grey = (normal > dwarf); age
Nematoda											
Cystidicola farionis	A	sb	amphipods	Yes	20.0	1.5 ± 0.9	29.2	0.6 ± 0.2	50.0	1.4 ± 0.5	NS
Unidentified nematode	A	i	unknown	Yes	2.9	<0.01	4.2	0.04 ± 0.04	7.1	<0.01	-
Acanthocephala											
Acanthocephalan sp.	A	i	amphipods	Yes	2.9	<0.01	0	0	0	0	-
Copepoda											
Salmincola edwardsii	A	fg	none	No	20.0	0.5 ± 0.2	4.2	0.04 ± 0.04	7.1	<0.01	-

742 Notes: # prevalence and abundance estimated from single eye; [*] summary of inter-morph contrast analyses; [1]see supplementary Table S2 for details. P < 0.05, NS – not

743 significant

744　**Table 4.** Probabilistic niche overlap calculated from nicheRover using the 95% niche regions

745　between each pair of Arctic charr morphs from Limingen (Swanson et al., 2015). Mean [range 95%

746　credibility interval] probability (%) of finding an individual of the morph in the row within the niche

747　region of the morph in the column.

	'normal'	**'dwarf'**	**'grey'**
'normal'	-	14.5 [5 - 27]	10.1 [2 - 28]
'dwarf'	31.7 [9 - 59]	-	69.9 [46 - 91]
'grey'	25.5 [2 - 65]	76.1 [51 - 95]	-

748

Figure legends:

Figure 1. a) Habitat choice (relative CPUE %) and b) growth (mean ±SD) of the 'normal' (red),

'dwarf' (green) and 'grey' (grey) morphs of Arctic charr found in Limingen.

Figure 2. The diet (prey abundance, %) of the a) Arctic charr along a gradient of increasing capture

depth and b) of different morphs 'normal' (red), 'dwarf' (green) and 'grey' (grey) morphs found in

Limingen.

Figure 3. Parasite community composition for the three morphs of Arctic charr, the 'normal' (red),

the 'dwarf' (green) and 'grey' (grey) found in Limingen, visualized using Nonmetric

multidimensional scaling based on Bray-Curtis dissimilarities of parasite infra-communities (n=59;

stress: 0.23). Letters denote the mean for each morph.

Figure 4. The relation between the most recent trophic niche (stomach content, blue text) and

community composition of trophically transmitted parasites representing a temporally integrated

trophic niche (red text) in 58 individuals of the three Arctic charr morphs found in Limingen:

'normal' (red), 'dwarf' (green) and 'grey' (grey) morph. Letters denote the mean for each morph

(Canonical correlation: R^2adj=0.30, p<0.001).

Figure 5.a) Boxplots and b) a biplot showing differences in $\delta^{13}C$ and $\delta^{15}N$ values for the three Arctic

charr morphs: 'normal', 'dwarf' and 'grey" found in Limingen. The letters in a) indicate significant

differences (p < 0.05) in pairwise comparisons, based on Mann-Whitney U-tests. The $\delta^{13}C$ values

771   reflect littoral (low δ^{13}C) *versus* pelagic (high δ^{13}C) resource use by fish, whereas δ^{15}N values reflect

772   trophic position of fish in the lake food web. Niche regions in b) are illustrated by ellipses containing

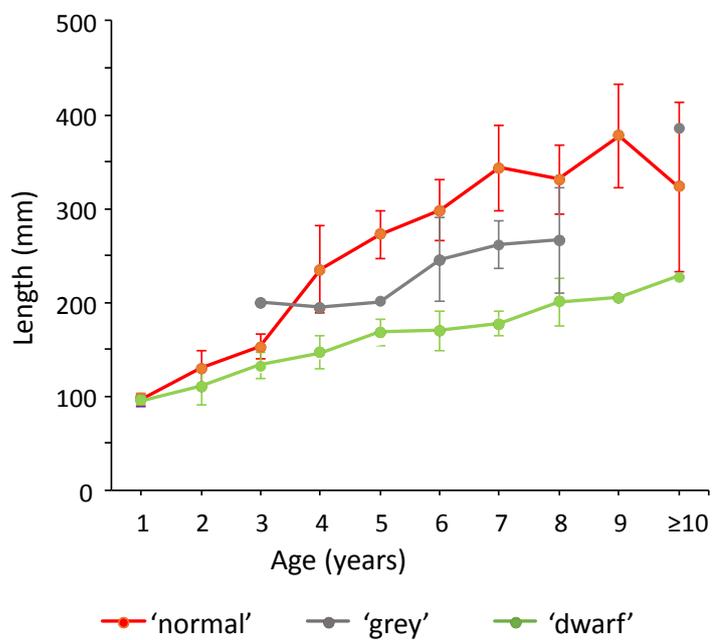773   approximately 95% of the data points for each morph (Jackson et al., 2011).

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Fig. 1a

Fig. 1b.

785 **Fig. 2**
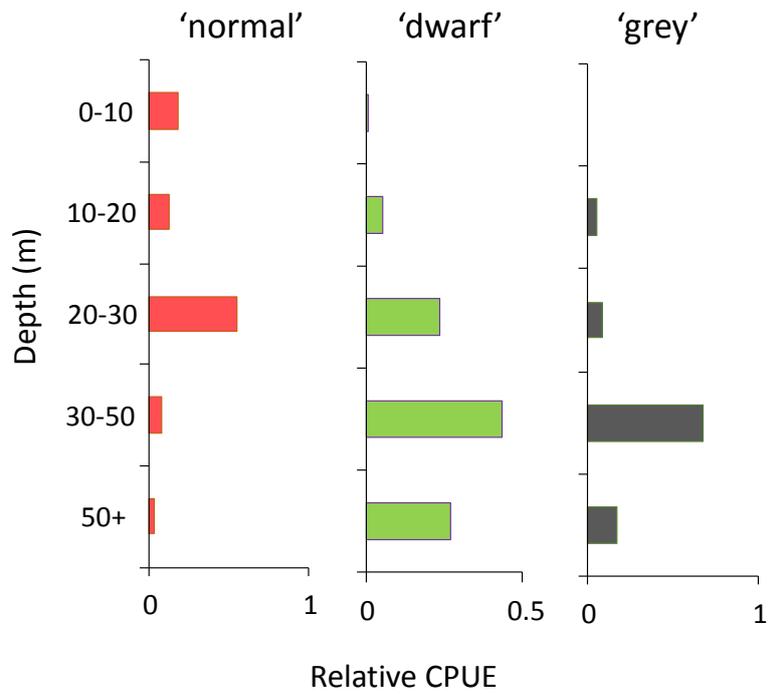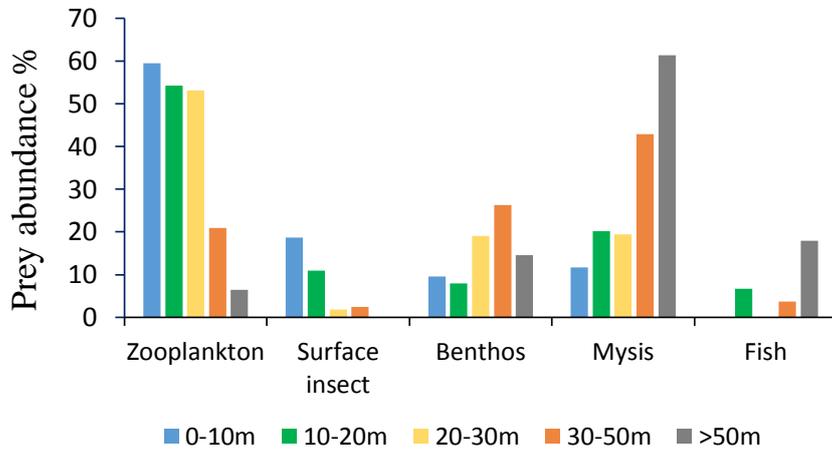
Figure 2a)

Figure 2b)
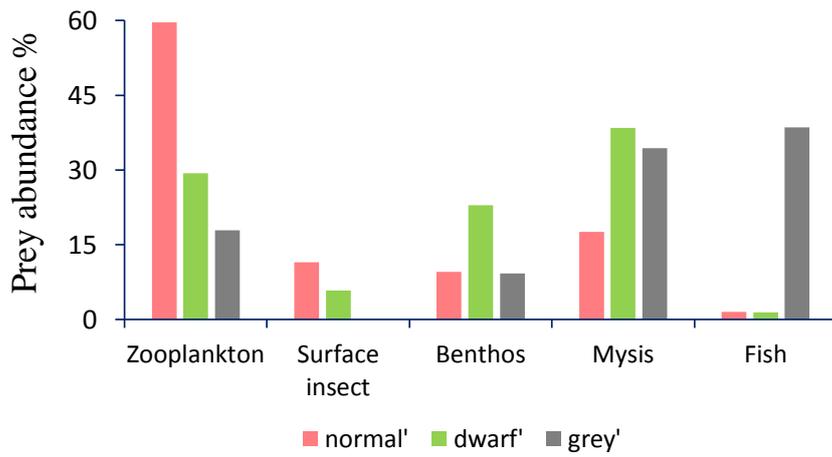
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Fig. 3
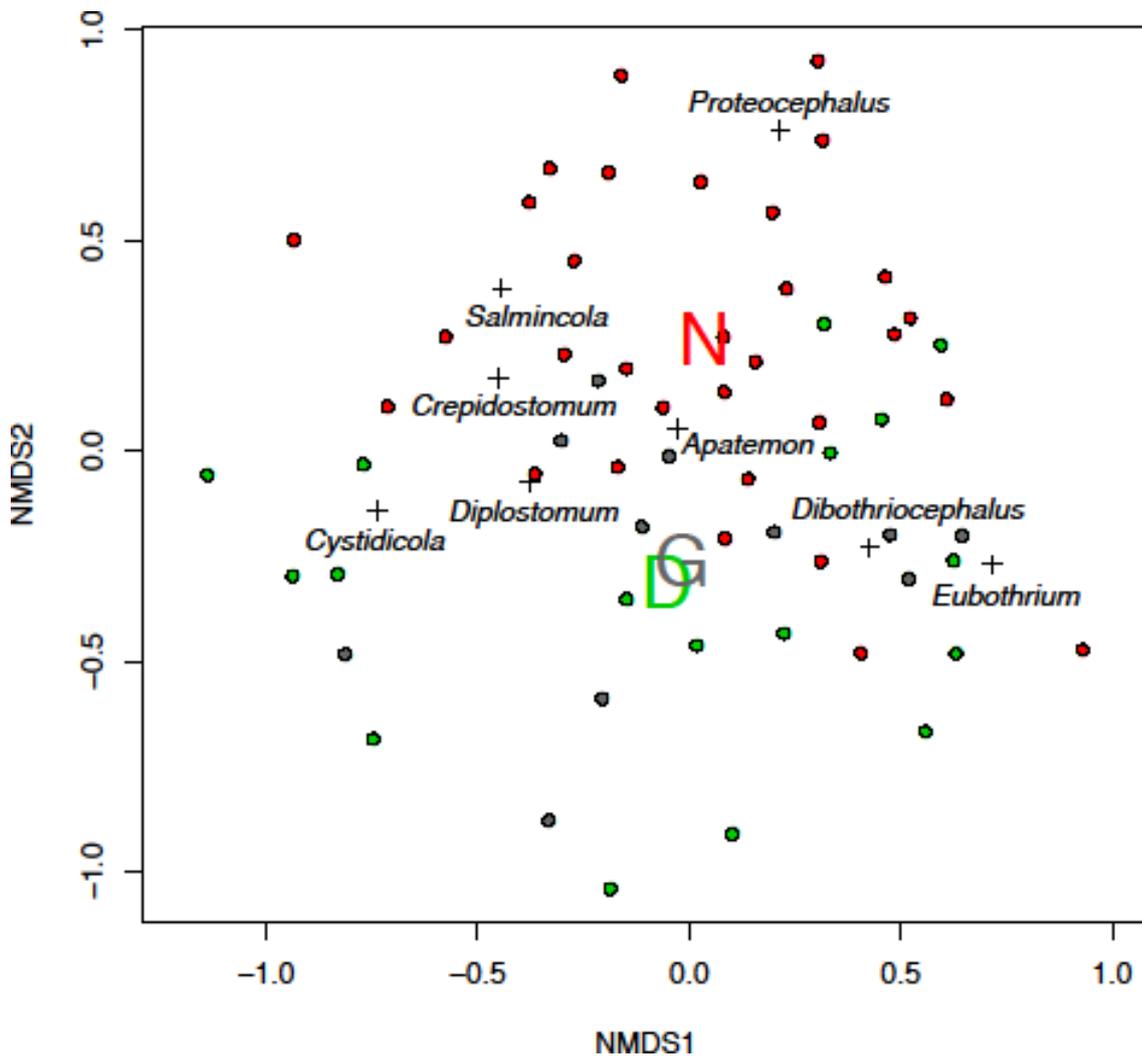
Fig. 4
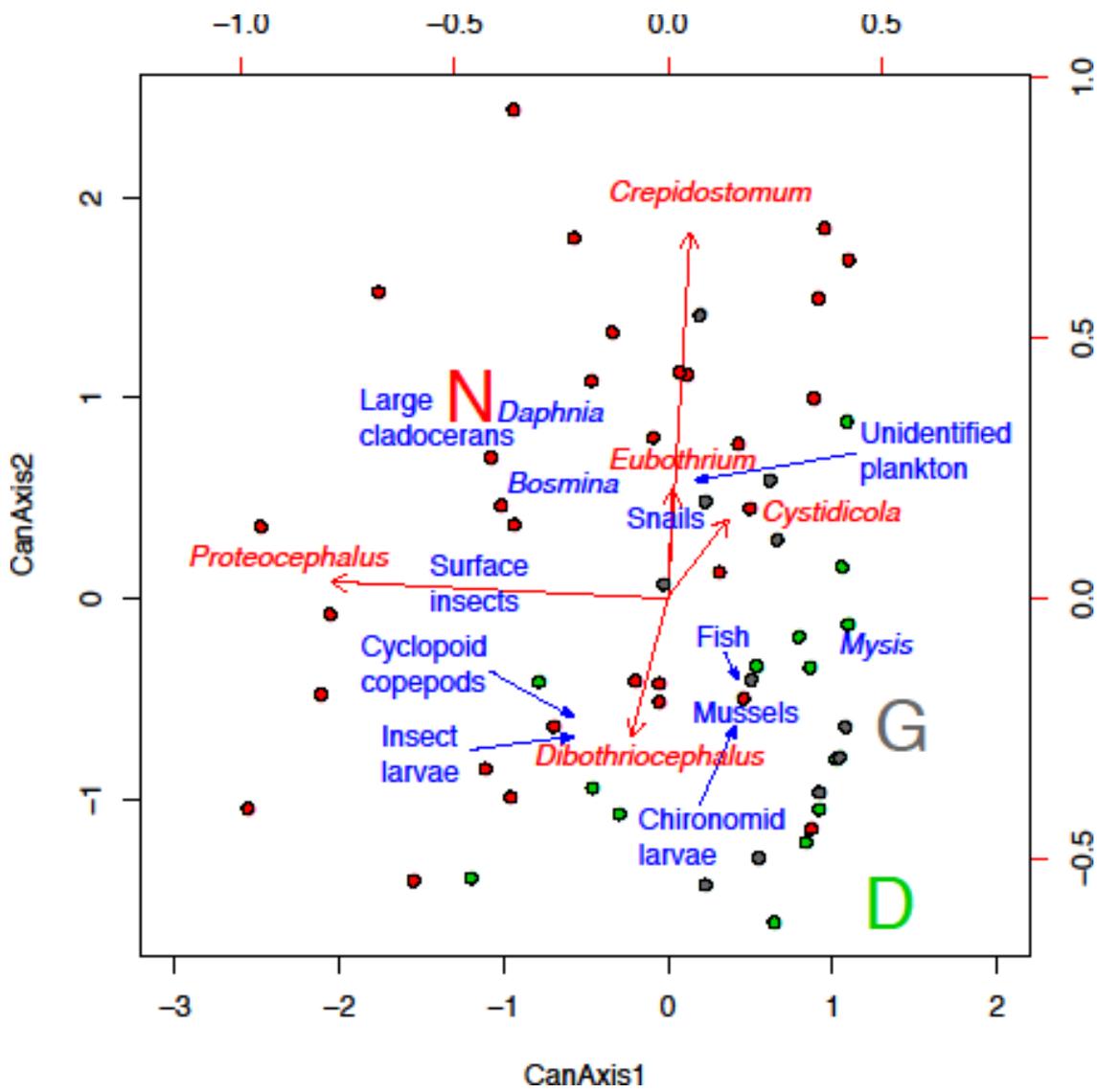
810 **Fig. 5 a).**

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814   **b)**

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818 **Table S1.** Influence of morph and age (years) on parasite taxa richness and total abundance (number

819 of individual parasites) infecting Arctic charr in Limingen, Norway.
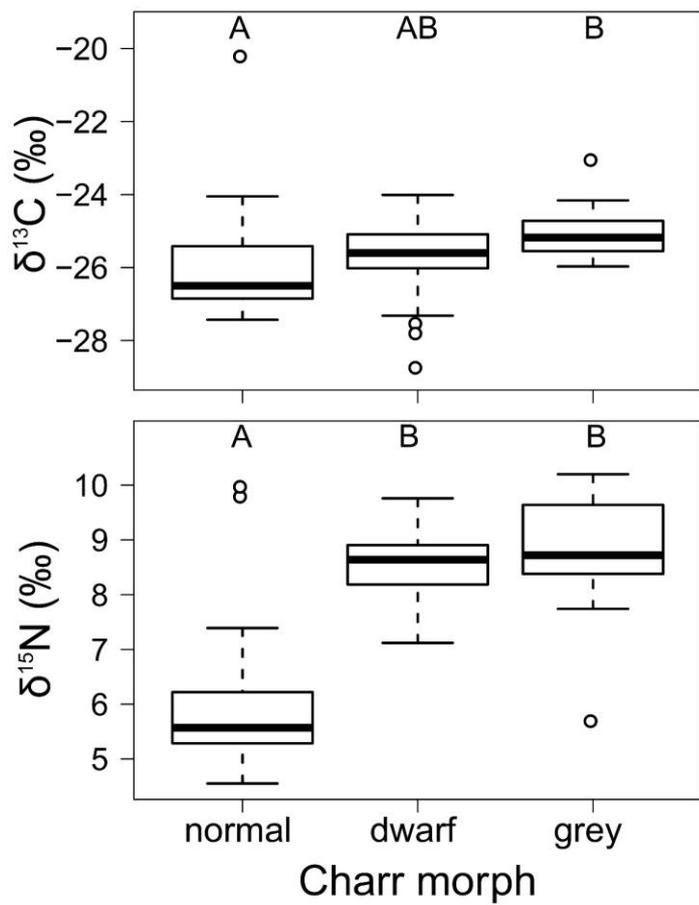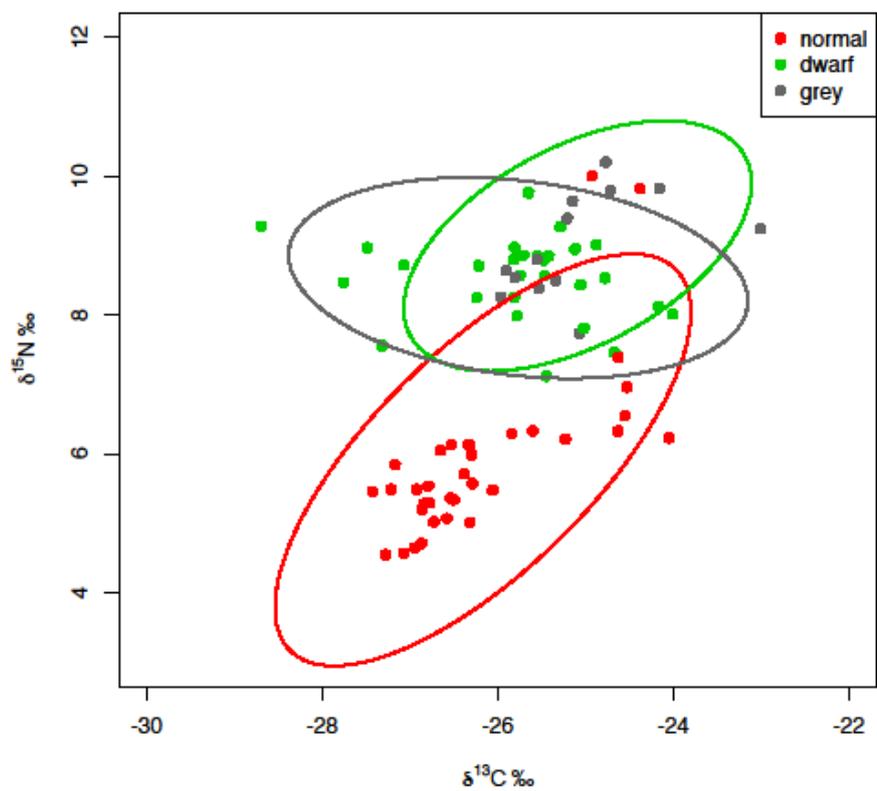
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Index	Morph	Model type*	Parameter	Contrast	SE	*t* value	*P*
Taxa richness	'normal'	complex	**intercept**	2.45	0.82	3.00	**0.004**
			'dwarf'	-1.35	1.11	-1.22	0.227
			'grey'	3.38	1.38	2.45	**0.017**
			age	0.23	0.11	2.05	**0.044**
			'dwarf':age	-0.001	0.15	-0.01	0.995
			'grey':age	-0.43	0.16	-2.78	**0.007**
	'dwarf'		intercept	1.10	0.75	1.47	0.147
			'grey'	4.73	1.34	3.54	**<0.001**
			age	0.22	0.11	2.07	**0.042**
			'grey':age	-0.43	0.15	-2.79	**0.007**
Total abundance	'normal'	simple	**intercept**	4.03	0.38	10.50	**<0.001**
			'dwarf'	-0.91	0.32	-2.81	**0.006**
			'grey'	-0.37	0.34	-1.08	0.286
			age	0.001	0.05	0.03	0.978
	'dwarf'		**intercept**	3.12	0.43	7.31	**<0.001**
			'grey'	0.54	0.43	1.26	0.213

821 Note; *model type: complex (interaction between fixed factors).

822

Table S2. Influence of morph and age (years) on the abundance of parasite taxa infecting Arctic
charr in Limingen, central Norway.

Parasites taxa	Morph	Parameter	Contrast	SE	*t* value	*P*
Trematoda						
Apatemon sp.	'normal'	intercept	0.96	0.54	1.79	0.078
		'dwarf'	-0.50	0.42	-1.21	0.230
		'grey'	0.40	0.42	0.96	0.340
		age	-0.10	0.07	-1.33	0.187
	'dwarf'	intercept	0.46	0.54	0.84	0.405
		'grey'	0.91	0.51	1.78	0.080
Crepidostomum spp.	'normal'	**intercept**	1.51	0.55	2.77	**0.007**
		'dwarf'	-2.45	0.79	-3.08	**0.003**
		'grey'	-1.33	0.56	-2.38	**0.020**
		age	0.10	0.07	1.55	0.127
	'dwarf'	intercept	-0.94	0.91	-1.03	0.305
		'grey'	1.12	0.94	1.19	0.238
Diplostomum sp.	'normal'	**intercept**	-0.85	0.49	-1.74	**0.086**
		'dwarf'	0.10	0.36	0.28	0.783
		'grey'	-0.07	0.44	-0.17	0.869
		age	0.12	0.06	2.08	**0.042**
	'dwarf'	intercept	-0.75	0.49	-1.53	0.130
		'grey'	-0.17	0.46	-0.37	0.711
Cestoda						
Dibothriocephalus spp.	'normal'	**intercept**	2.09	0.62	3.40	**0.001**
		'dwarf'	0.34	0.48	0.72	0.477
		'grey'	0.58	0.52	1.11	0.270
		age	0.08	0.07	1.07	0.287
	'dwarf'	**intercept**	2.44	0.60	4.06	**<0.001**
		'grey'	0.24	0.55	0.43	0.667
Proteocephalus sp.	'normal'	**intercept**	5.59	0.96	5.84	**<0.001**
		'dwarf'	-3.22	1.29	-2.49	**0.015**
		'grey'	-3.22	2.61	-1.23	0.223
		age	-0.36	0.16	-2.34	**0.022**
	'dwarf'	intercept	2.37	1.47	1.61	0.113
		'grey'	0.003	2.91	0.001	0.999
Nematoda						
Cystidicola farionis	'normal'	intercept	-0.15	1.02	-0.15	0.880
		'dwarf'	-0.92	0.92	-1.01	0.317
		'grey'	-0.29	0.88	-0.33	0.742

	age	0.08	0.12	0.65	0.518
'dwarf'	intercept	-1.08	1.19	-0.91	0.368
	'grey'	0.63	1.14	0.55	0.581

826