

**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 ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) 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

segregation between the two deep-water morphs. The high importance of *Mysis* in Arctic charr diets may have reduced the ancestral niche segregation between the deep-water morphs and thereby increased their resource competition and potential risk for hybridization.

Keywords: *Salvelinus alpinus*, polymorphism, ecological divergence, species introductions, hydropower effects, parasite community, stable isotopes

Introduction

Ecologically induced speciation may lead to a continuum of evolutionary differences within and among populations, with some groups being in the process of diversifying and others being reproductively isolated (Schluter, 2000; Hendry et al., 2009). Post-glacial lakes are useful systems for studying the impacts of biodiversity changes caused by environmental, ecological and human-induced factors as they are semi-closed ecosystems with relatively well defined habitats that can host polymorphic populations at different stages of evolutionary divergence (Schluter, 2000; Klemetsen, 2010; Hendry et al., 2017). Human activities may have large impacts on natural environments by rapidly changing the direction of evolutionary developments and in some instances reverse the evolutionary processes that promote increasing biodiversity (Hendry et al., 2017). Multiple anthropogenic stressors in lake ecosystems, including pollution, commercial fishing and non-native species introductions, have reversed speciation processes (Seehausen et al., 2008; Alexander et al., 2017; Kuparinen & Festa-Bianchet, 2017). For example, reproductive breakdown has been observed in newly differentiated native morph-pairs of whitefish (*Coregonus lavaretus*) and stickleback (*Gasterosteus aculeatus*) following the introduction of competitive fish species or invasive crayfish (Taylor et al., 2006; Velema et al., 2012; Baht et al., 2014).

50 In postglacial lakes, polymorphic fish populations often diverge along the
51 benthic-pelagic resource axis (e.g., Schluter, 1996, 2000). Charr (*Salvelinus* spp.) is one of the few
52 genera that is also found to diversify along the shallow vs. deep-water benthic resource axis
53 (Knudsen et al., 2006; Klemetsen, 2010; Muir et al., 2016; Markevitch et al., 2018). Knowledge
54 about deep-water (profundal) morphs of Arctic charr (*S. alpinus*) is still relatively limited, although
55 they seem to occur across the entire Holarctic region (Klemetsen, 2010). The deep-water morphs are
56 typically reproductively isolated from co-occurring littoral and pelagic morphs (Hindar et al., 1986;
57 Westgaard et al., 2004; Simonsen et al., 2017). Moreover, they express heritable specialised
58 physiological, behavioural, and morphological adaptations (Klemetsen et al., 2002, 2006; Knudsen et
59 al., 2015) to effectively exploit (i.e., for foraging and mating) the deep-water niches (Knudsen et al.
60 2016a). Small-sized deep-water morphs feed mainly on benthic invertebrates whereas the few
61 known, large-growing deep-water morphs are specialised piscivores (Knudsen et al. 2006, 2016b;
62 Klemetsen et al. 2010; Power et al., 2009; Moccetti et al., this volume). Although the ecology of the
63 deep-water morph has been studied, little is known about the potential impacts of multiple
64 anthropogenic stressors (e.g., hydropower operations and the introduction of non-native species) on
65 these deep-water morphs.

66 Lake Limingen, central Norway, has a polymorphic population of Arctic charr,
67 consisting of three morphs: the upper-water ‘normal’ morph, the deep-water ‘dwarf’ morph, and the
68 piscivorous ‘grey’ morph (Nyman et al., 1981; Aass et al., 2004). Following the damming of the lake
69 in 1953 for hydropower production, brown trout (*Salmo trutta*) and Arctic charr population densities
70 drastically declined (Aass et al., 2004; Gregersen et al., 2006). In 1969, *Mysis relicta* (hereafter
71 *Mysis*) was introduced to compensate for reduced fish food resources and to mitigate the negative
72 impacts of hydropower operations on fish and overall ecosystem productivity (cf. Hirsch et al.,
73 2017). *Mysis* is an opossum shrimp native to Scandinavia, though previously absent from this
74 Limingen region of Norway (Spikkeland et al., 2016). *Mysis* show a pronounced diel vertical

75 migration pattern, with nocturnal foraging on zooplankton in the upper water column potentially
76 resulting in food resource competition with zooplanktivorous Arctic charr (Moen & Langeland,
77 1989; Næsje et al., 1991, Koksvik et al., 2009). In contrast, deep-water fish (e.g., burbot *Lota lota*
78 and profundal Arctic charr) may benefit from *Mysis* introductions through increased food availability
79 (Langeland et al., 1991; Næsje, 1995). Whilst introduced *Mysis* populations have become an
80 important prey resource for Arctic charr in Limingen and elsewhere (Garnås, 1986; Gregersen et al.,
81 2006), detailed studies of their impacts on trophic differentiation among sympatric Arctic charr
82 morphs has been lacking.

83 In this study, we investigated the habitat use, diet, parasite infections and
84 stable isotope ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of the three sympatric Arctic charr morphs in Limingen. The aim of
85 the study was to explore the degree of niche overlap between the three sympatric Arctic charr
86 morphs about 50 years after the introduction of *Mysis*. We quantified niche overlap by using data on
87 habitat use and stomach contents (recent niche-use) and by analysing the occurrence of trophically
88 transmitted parasites and stable isotope values that reflect the temporally integrated trophic niches of
89 individual fish (Knudsen et al., 2011). We hypothesised that existing depth-habitat preferences for
90 the sympatric morphs would be maintained. However, due to damming and the introduction of
91 *Mysis*, we also hypothesised that prey resource use would overlap, particularly between the upper-
92 water ‘normal’ and the deep-water morphs.

93

94 **Material and methods**

95 **Study lake**

96 Lake Limingen (64°50’N, 13°13’E) is a large (surface area = 95.7 km²), deep (Z_{max} = 192 m, Z_{mean} =
97 87 m), dimictic, oligotrophic and relatively clear (Secchi depth = 9–12.7 m) lake situated at 418 m
98 a.s.l. in the north boreal vegetation zone of central Norway. Originally, the lake drained to the

99 Ångermanälven watercourse in northern Sweden, but after hydropower development in 1953 most of
100 the water was diverted to the Namsen watershed in Trøndelag County, Norway (Sandlund et al.,
101 2017). Today, the lake is regulated with a maximum annual water level amplitude of 8.7 m. Spruce
102 forests with some birch dominate the riparian vegetation and there are only a few low-intensity farms
103 around the lake. In addition to the polymorphic Arctic charr, the lake has a small population of
104 brown trout, a littoral population of minnow (*Phoxinus phoxinus*; introduced in 1980s) and a very
105 sparse population of three-spined stickleback (introduction date unknown) (Aass et al., 2004;
106 Gregersen et al., 2006).

107

108 Fish material

109 Arctic charr were sampled in August 2016 with Nordic multi-mesh gill-nets consisting of 5 m panels
110 with 12 different knot-to-knot mesh sizes from 5 to 55 mm (Appelberg et al., 1995). The nets were
111 set in the littoral (1.5 m high benthic nets; 0-15 m depth), pelagic (6 m high offshore gill-nets set
112 from the surface; above 30 m depth), and profundal (1.5 m high benthic nets; at 20-50 m depth)
113 zones. Additional sampling with a pelagic pair trawl caught 63 ‘normal’ morph Arctic charr (see
114 details in Sandlund et al., 2017). Fish were weighed (closest 0.1 g) and measured (closest 1 mm, fork
115 length, L_F). Otoliths were removed for age determination.

116 Individual Arctic charr were classified to one of three possible morphs based
117 on head and body morphology, maturation, and colouration following guidelines produced from
118 earlier studies of similar polymorphic populations (Skoglund et al., 2015; Simonsen et al., 2017). In
119 total, we sampled 178 Arctic charr from Limingen, with stomachs analysed from 171 individuals.
120 The catch per unit of effort (CPUE) was estimated as the number of fish caught per 100 m² gillnet
121 per night. A subsample of mature individuals from all three morphs was assessed for parasite
122 assemblages and sampled for stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). The numbers of each morph

123 included in the parasite and stable isotope sampling were: ‘normal’ morph (n = 39; mean \pm SD: $L_F =$
124 310.6 ± 83.7 mm; age = 6.7 ± 2.5 years), ‘dwarf’ morph (n = 27; $L_F = 173.9 \pm 31.7$; age = 6.4 ± 2.6),
125 and ‘grey’ morph (n = 14; $L_F = 297.1 \pm 59.3$; age = 9.5 ± 3.4).

126 Growth differences among morphs were described by mean length-at-age
127 using a modified von Bertalanffy growth model (Roff, 1984): $L_T = L_\infty * (1 - (\exp(-k * A_T)))$, where
128 L_T is fish body length at time T , L_∞ is the asymptotic fish length, k is the growth coefficient, and A_T is
129 the age at time T . This simplified model has been shown to work well with inland polymorphic
130 salmonids (Jonsson et al., 1988).

131

132 Diet

133 Prey items from fish stomachs were preserved in ethanol and later identified to the lowest feasible
134 taxonomic level (23 different prey taxa in total) and subsequently sorted into five main categories: i)
135 zooplankton (e.g., *Daphnia*, *Bosmina*, *Holopedium*, *Bythotrephes*, copepods), ii) surface insects
136 (adult insects), iii) benthos (e.g., snails, clams, insect larvae, benthic crustaceans), iv) *Mysis*, and v)
137 fish. The contribution of each prey category to the diet was estimated by visual determination of the
138 stomach fullness using a percentage scale ranging from empty (0%) to full (100%) (prey abundance;
139 Amundsen et al., 1996). Among morph dietary overlap was quantified for all prey categories using
140 Schoener’s (1970) similarity index, which is commonly considered high when the overlap exceeds
141 60% (Wallace, 1981).

142

143

144 Parasites

145 All parasites from the body cavity, stomach, intestine, kidney, swim bladder, gills and eyes were
146 enumerated from sub-sampled fish (see Table 3 for more details). Most of the parasite taxa are

transmitted to Arctic charr via different prey items such as copepods (cestodes *Dibothriocephalus* spp., *Proteocephalus* sp. and *Eubothrium salvelini*), insect larvae (trematodes *Crepidostomum* spp.), and the benthic amphipod *Gammarus lacustris* (cestode *Cyathocephalus truncatus*, nematode *Cystidicola farionis*, and Acanthocephalan sp.). *Mysis* may also transmit the swim bladder nematode *C. farionis* (Black & Lankester, 1980), however, the intermediate host for this parasite is currently unknown. All taxa, except *Dibothriocephalus* spp., utilize Arctic charr as the final host (see Table 3 for further details). Larval *Dibothriocephalus* spp. (former *Diphyllbothrium* spp., see Waeschenbach et al., 2017) are able to use fish as parathenic hosts and re-establish in piscivorous individuals (Curtis, 1984), which also may be the case for *Eubothrium* sp. (Williams & Jones, 1994). Additionally, three parasite taxa are non-trophically transmitted to the fish, either from other fish, i.e., the parasitic gill crustacean (*Salmincola edwardsii*), or via trematode larvae released from intermediate snail hosts, i.e., *Diplostomum* sp. and *Apatemon* sp. We quantified parasite prevalence (percentage of hosts infected by the parasite) and abundance (number of parasites *per* host) following methods outlined in Bush et al. (1997). The exceptions were *Diplostomum* sp. and *Apatemon* sp., for which the prevalence and abundance were estimated from a single eye (at random).

162

163 Stable isotopes

Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are commonly used to estimate the dietary sources (littoral *versus* pelagic carbon) and trophic position of organisms in lake food webs, as well as the intra- and inter-specific niche segregation of fish populations (e.g., Boecklen et al., 2011; Layman et al., 2012). Here, a small piece of dorsal muscle tissue, obtained posterior to the dorsal fin, was dissected from a subsample of fish and frozen at -20°C . Tissue samples were dried at 60°C for 48 hours and homogenised using a pestle and mortar. Approximately 0.3 ± 0.05 mg of dried tissue was weighed and placed in tin capsules for analyses completed at the University of Waterloo, Canada, on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo

172 Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo
173 Erba, Milan, Italy). The machine analytical precision of $\pm 0.2\text{ ‰}$ ($\delta^{13}\text{C}$) and $\pm 0.3\text{ ‰}$ ($\delta^{15}\text{N}$) was
174 determined through the repeat analysis of internal laboratory standards calibrated against
175 International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen.

176

177 Statistical analyses

178 All statistical analyses were computed using R (version 3.4.2, R Core Team 2017). Differences in the
179 number of parasite taxa among morphs were compared using a general linear model fitted with a
180 Gaussian distribution family. Differences in total parasite abundance and the abundance of each
181 parasite taxon among charr morphs were examined using a series of generalized linear models, with
182 the exception of five rare taxa (*C. truncatus*, *E. salvelini*, *S. edwardsii*, Acanthocephalan sp.,
183 unidentified nematode), which were excluded from further analysis. Generalized linear models were
184 fitted with a quasipoisson distribution and log-link function due to the over-dispersion of abundance
185 data. Fish age (years) was included as a continuous fixed factor in all general and generalized linear
186 models to account for the influence of varying host age on parasite abundance and richness. Potential
187 outliers were identified by graphically examining the raw data and by running models with and
188 without outliers to assess their influence on model outcomes. Analysis of variance was used to assess
189 whether the interaction term between morph and age provided additional explanatory power over the
190 simpler additive model. Contrast analyses were constructed for each final model set by varying the
191 base morph (intercept) to assess the significance of differences between morph pairs.

192 Multivariate analyses were conducted using the package vegan (version 2.5-2,
193 Oksanen et al., 2017). Parasite community composition differences among morphs were visualized
194 by using individual Arctic charr in a non-metric multidimensional scaling analysis (NMDS) based on
195 Bray-Curtis dissimilarities of log-transformed parasite abundances, including both trophically and

196 directly transmitted parasite species. To visualize and explore the correlation between individual diet
197 and parasite community composition, we used canonical correlation (vegan: CCorA, Oksanen et al.,
198 2017) of logit-transformed prey volumes and log-transformed abundances of trophically transmitted
199 parasites.

200 Non-parametric Kruskal-Wallis tests, followed by pairwise comparisons with
201 Mann-Whitney U-tests, were used to evaluate the significance of differences in $\delta^{13}\text{C}$ (reflecting
202 littoral *vs.* pelagic resource use) and $\delta^{15}\text{N}$ (reflecting trophic position) values among the three charr
203 morphs. Isotopic niche overlaps were calculated between all pairs of morphs using the probabilistic
204 method developed by Swanson et al. (2015), available in the R-package nicheROVER (Lysy et al.,
205 2014). In this method, a Bayesian approach is employed to produce 95% probability niche regions
206 and directional estimates of pairwise niche overlap. Niche overlap is defined as posterior
207 probabilities that an individual of one morph falls within the niche region (95%) of the other morph.
208 Potential outliers were identified graphically from the raw data, and two outliers were removed to
209 ensure better fit to multivariate normal distribution of the data.

210

211 **Results**

212 Fish community, habitat preference and Arctic charr growth

213 Arctic charr was the dominant species ($n = 168$) in the benthic habitats (i.e., littoral and profundal),
214 whereas only nine ‘normal’ Arctic charr were caught in the pelagic zone (0.6 charr per 100 m² gillnet
215 area). Additionally, 34 brown trout, 68 minnows and one three-spined stickleback were caught from
216 the littoral zone. The CPUE of Arctic charr (overall mean: 3.8 fish per 100 m² benthic gillnet per
217 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
218 depth. The ‘normal’ morph was most abundant in the upper water-column layers (Fig. 1a), down to

219 30 m depth (CPUE-range: 2-4.5). The ‘dwarf’ morph was most abundant at depths >20 m (CPUE:
220 >4), and the ‘grey’ morph was most abundant within the 30-50 m depth zone (CPUE: >2).

221 Length-at-age differed among the morphs, with significant differences in mean
222 length (t-tests, $p < 0.05$) observed between ‘normal’ and profundal ‘dwarf’ morphs for each age-class
223 between four and nine years (Fig. 1b). Estimated von Bertalanffy growth models indicated greater
224 asymptotic lengths for the ‘normal’ and ‘grey’ morphs as compared with the ‘dwarf’ morph, with
225 non-overlapping confidence intervals indicating significantly different maximal sizes for all morphs.
226 Growth rate (k) similarly differed among the morphs as indicated by non-overlapping confidence
227 intervals, being lower in the ‘normal’ and ‘grey’ morphs and highest in ‘dwarf’ morph (Table 1). It
228 should be noted that the precision of parameter estimates for the ‘grey’ morph was possibly affected
229 by the smaller number of fish available for estimating model parameters.

230

231 Dietary niches

232 Generally, the abundance (%) of *Mysis* in charr stomach contents increased with depth, independent
233 of the morph considered (Fig. 2a), being about 10% in upper water column (0-10 m) and >60% in
234 deep waters (>50 m). In contrast, the diet of all Arctic charr captured in the uppermost water column
235 (<30 m depth) was dominated by zooplankton (>53%) and surface insects (>20%). *Mysis* constituted
236 18% of the diet of the ‘normal’ morph, 35% of the ‘grey’ morph diet and 39% of the ‘dwarf’ morph
237 diet (Fig 2b). The ‘dwarf’ morph consumed zooplankton (29%) and benthos (23%), in addition to
238 *Mysis*. The ‘dwarf’ morph ate much less *Daphnia* and *Bythotrephes*, but approximately equal
239 amounts of *Bosmina* and *Holopedium* when compared with the ‘normal’ morph. The ‘grey’ morph
240 relied more heavily on fish (38%) than the other morphs, which had less than 1.5% fish in their
241 stomachs. Common consumption of *Mysis* and/or zooplankton prey groups caused a relatively high
242 dietary overlap (54-56%) between the ‘dwarf’ morph and the two other morphs when considering all

243 prey groups (23 taxa). Dietary overlap was lower (41%) between the ‘normal’ and the ‘grey’ morph.
244 After removing *Mysis* as a prey group, the dietary overlap dropped to 34% between the two deep-
245 water morphs, as the ‘dwarf’ morph fed mainly on zooplankton (49%) and deep-water zoobenthos
246 (39%), while the ‘grey’ morph fed mainly on fish (59%).

247

248 Parasite community composition

249 A total of 11 parasite taxa were found, including eight trophically transmitted parasites, one directly
250 transmitted parasite (*S. edwardsii*) and two trematode taxa (*Diplostomum* sp. and *Apatemon* sp.)
251 transmitted from snail intermediate hosts. Taxon richness increased with host age for both ‘normal’
252 and ‘dwarf’ morphs, whereas age did not influence parasite taxon richness in the piscivorous ‘grey’
253 morph (GLM_{morph:age}: $F_{2,67} = 5.16$, $p = 0.008$; Tables 2 and S1). Total parasite abundance was
254 significantly higher in the ‘normal’ morph compared to the ‘dwarf’ morph, while the piscivorous
255 ‘grey’ morph had intermediate infection levels (GLM_{morph}: $F_{2,70} = 4.70$, $p = 0.012$; Tables 2 and S1).

256 Parasite community composition in individual Arctic charr appeared to be
257 more similar in the two profundal morphs compared to the ‘normal’ morph (Fig. 3). Of the three
258 parasite taxa non-trophically transmitted to charr, *Diplostomum* sp. and *Apatemon* sp. were the most
259 prevalent among morphs (~40-65 %), whereas *S. edwardsii* tended to occur in the ‘normal’ charr
260 morph (20 %). The abundance of non-trophically transmitted parasites was consistently low (< 3
261 individual parasites per fish) and did not differ among morphs, although there was a positive
262 relationship between *Diplostomum* sp. abundance and charr age (Tables 3, S2). Of the trophically
263 transmitted parasites, the upper water-column ‘normal’ morph had the highest prevalence for five of
264 eight parasite taxa, and the remaining three parasite taxa were most prevalent in the piscivorous
265 ‘grey’ morph. Two *Gammarus* transmitted taxa, *C. truncatus* and *Acanthocephala* sp., were
266 restricted to ‘normal’ charr morphs only. *Dibothriocephalus* spp. cestode larvae were the most

267 prevalent trophically transmitted parasite and occurred in similar abundances in all morphs (Tables 3,
268 S2). The copepod-transmitted taxa, i.e. *Proteocephalus* sp. and *Eubothrium* sp., were more prevalent
269 in the ‘normal’ morph than in the deep-water charr morphs. *Proteocephalus* sp. abundance was
270 greater in the ‘normal’ morph than in the ‘dwarf’ morph, with the abundance of this parasite
271 declining with charr age (Tables 3, S2). The swim bladder nematode *C. farionis* was found most
272 often in the piscivorous ‘grey’ morph, although it was in consistently low abundance in all charr
273 morphs (Table 3).

274 The community composition of trophically transmitted parasites in individual
275 charr was significantly explained, albeit moderately, by the diet composition of the individual
276 (Canonical Correlation $R^2_{\text{adj}} = 0.30$, $p < 0.001$; Fig. 4). Thus, when visualizing both the most recent
277 diet (stomach contents) and the temporally-integrated characterization of resource use as measured
278 by trophically transmitted parasites, all morphs appeared to have different trophic niches (Fig. 4).
279 The two deep-water morphs were located closest to each other, indicating they have more similar
280 trophic niches. The ‘normal’ morph was more separated (Fig. 4) and associated with higher
281 infections of *Proteocephalus* sp. and *Crepidostomum* spp. as a result of feeding on a different
282 assemblage of zooplankton species and insect larvae than the ‘dwarf’ or ‘grey’ morphs. The ‘grey’ and
283 ‘dwarf’ morphs were mainly associated with infections of *Dibothriocephalus* spp. and *C. farionis*,
284 linked to feeding on *Mysis*, mussels, chironomid larvae, and fish.

285

286 Stable isotopes

287 The three Arctic charr morphs showed significant differences in $\delta^{13}\text{C}$ (Kruskal-Wallis: $\chi^2 = 10.69$, df
288 $= 2$, $p = 0.005$) and $\delta^{15}\text{N}$ ($\chi^2 = 42.93$, $\text{df} = 2$, $p < 0.001$) values. The ‘normal’ morph had significantly
289 lower (i.e., more pelagic) $\delta^{13}\text{C}$ values than the ‘grey’ morph (Mann-Whitney pairwise comparison: p
290 $= 0.002$), whereas the other between-morph differences in $\delta^{13}\text{C}$ were non-significant ($p = 0.07\text{--}0.09$).

291 The ‘normal’ morph showed variable but significantly lower $\delta^{15}\text{N}$ values than either the ‘dwarf’ or
292 ‘grey’ morphs (Mann-Whitney pairwise comparisons; $p < 0.001$; Figure 5a) and was separated from
293 both by approximately one trophic level (i.e., $\sim 3\%$). In contrast, the ‘dwarf’ and ‘grey’ morphs did
294 not differ in $\delta^{15}\text{N}$ (Mann-Whitney pairwise comparisons; $p = 0.268$), although ‘grey’ morph
295 individuals tended to have higher $\delta^{15}\text{N}$ values consistent with piscivorous feeding. Isotopic niche
296 overlap analyses showed that the ‘dwarf’ and ‘grey’ morphs had high probabilities of sharing the
297 same niche region (70% and 76%), while they had lower probabilities of overlapping with the
298 ‘normal’ morph (32% and 25%) (Table 4; Fig 5b). The ‘normal’ morph had the lowest probabilities
299 of overlapping with either of the profundal morphs (14% and 10%) (Table 4).

300

301 Discussion

302 We observed a partial niche segregation between the three sympatric Arctic charr morphs in
303 Limingen, with the clearest segregation being between the upper water-column zooplanktivorous
304 ‘normal’ morph and the two profundal morphs, the ‘dwarf’ and the piscivorous ‘grey’ morphs.
305 Although we do not have directly comparable data from each of the morphs before the *Mysis*
306 introduction (Gregersen et al., 2006), our results suggest that the *Mysis* introduction has reduced
307 niche segregation between the three sympatric Arctic charr morphs as a result of common
308 exploitation of this resource, with the strongest impacts being on the two deep-water morphs. The
309 temporally integrated trophic tracers (parasite fauna and stable isotope values) pointed to a further
310 partial dietary segregation between the two Arctic charr morphs with identical deep-water
311 preferences, with the ‘dwarf’ and ‘grey’ morphs supplementing a *Mysis*-based diet with benthic prey
312 and fish, respectively. The reduced trophic segregation has increased the apparent ecological
313 similarity between the morphs and has the potential to enhance the probability for increased
314 competitive interactions and hybridization.

315 A corresponding trophic segregation between the ‘normal’ morph and the
316 sympatric profundal morphs occurs in some other polymorphic lakes (Knudsen et al., 2006, 2016a;
317 Amundsen et al., 2008; Moccetti et al., this volume). In Arctic charr, a zooplanktivorous diet is
318 generally found in southern Scandinavian lakes (e.g., L’Abée-Lund et al., 1993; Sandlund et al.,
319 2016; Jensen et al., 2017; Paterson et al., this volume), in lakes regulated for hydropower production
320 (e.g., Hirsch et al., 2017), and in northern lakes with benthivorous competitors (e.g., Skoglund et al.,
321 2013; Eloranta et al., 2013). In northern lakes with deep-water morphs, the upper water-column
322 ‘normal’ Arctic charr morph may also include littoral resources in the diet (Knudsen et al., 2010,
323 2016a; Eloranta et al., 2013; Moccetti et al., this volume). In Limingen, however, the benthic
324 resources in shallow littoral areas are restricted due to water level fluctuations that reduce littoral
325 zone productivity (e.g., Hirsch et al., 2017) and the occupancy of available shallow areas by
326 abundant minnows and a few brown trout (Aass et al., 2004; Gregersen et al., 2006). Low presence
327 of littoral benthos in the diet of the ‘normal’ morph is supported by low infection by the few parasite
328 species transmitted from benthic prey (i.e., *Crepidostomum* sp.), as also been observed in other
329 studies in this geographic region (Paterson et al., 2018; Paterson et al., this volume).

330 The small-sized deep-water ‘dwarf’ morph included both zooplankton and
331 *Mysis* in the diet, resulting in a relatively high dietary overlap between the ‘normal’ and ‘grey’
332 morphs. Small-sized deep-water Arctic charr morphs typically specialize on soft-bottom benthos
333 (Hindar & Jonsson, 1982; Knudsen et al., 2006, 2016a,b; Hooker et al., 2016; Moccetti et al., this
334 volume), as do profundal whitefish morphs (Harrod et al., 2010; Præbel et al., 2013; Siwertsson et
335 al., 2013) and brown trout (Piggott et al., 2018). In Limingen, excluding *Mysis* consumption reduced
336 the apparent dietary overlap between the two profundal morphs, with consumption of prey resources
337 other than *Mysis* pointing to a more distinct benthivorous dietary niche for the ‘dwarf’ morph.
338 Although separation into morph groupings was not reported, zoobenthos were noticeably more
339 common in the diet of Arctic charr prior to the *Mysis* introduction (Gregersen et al., 2006). The

introduction of *Mysis* may have induced a dietary shift by the ‘dwarf’ morph towards a more pelagic diet as a result of the diel vertical migration of *Mysis* within the water column. The ‘dwarf’ morph also had significantly higher $\delta^{15}\text{N}$ values and less diverse parasite fauna when compared to the ‘normal’ morph in Limingen and nearby lakes (Paterson et al., 2018; Paterson et al., this volume), as has been reported for other polymorphic Arctic charr lakes (Knudsen et al., 1997, 2016a; Siwertsson et al., 2016). Despite the apparently large dietary overlap, the above suggests that the ‘dwarf’ morph has a less unique benthivorous diet in Limingen than in other lakes (see also Moccetti et al., this volume).

The relative importance of *Mysis* in the diet of the ‘grey’ morph is not typical for large-growing Arctic charr (but see Eloranta et al., 2015), although lake charr (*S. namaycush*) predate substantially on *Mysis* (e.g., Chavarie et al., 2016) particularly when introduced to oligotrophic lakes (e.g., Ellis et al., 2002). In Limingen, fish was an important prey for the ‘grey’ morph, but not for the sympatric ‘normal’ and ‘dwarf’ morphs, indicating the position of ‘grey’ Arctic charr as specialized piscivores (Adams et al., 1998; Power et al., 2005; Knudsen et al., 2016b; Moccetti et al. this volume). The inclusion of a specialized piscivore among lake-resident morphs is also found in other polymorphic *Salvelinus* spp. populations (Muir et al., 2016; Markevitch et al., 2018). Although the relatively high $\delta^{15}\text{N}$ values of the ‘grey’ morph partly reflected their piscivorous diet, the morph was less clearly separated from the ‘dwarf’ morph than has been evident in studies of other profundal morph-pairs (Knudsen et al., 2016a; Moccetti et al., this volume). The ‘grey’ morph had a higher diversity of trophically transmitted parasites than ‘dwarf’ morph, likely passed on via prey fish as has been noted elsewhere (Siwertsson et al., 2016; Moccetti et al., this volume). The ‘grey’ morph also had aggregated high *Dibothriocephalus* spp. infections (a cestode able to re-establish in predatory fish; e.g., Curtis, 1984), as is often seen in other piscivorous *Salvelinus* spp. morphs (Frandsen et al., 1989; Butorina et al., 2008; Siwertsson et al., 2016; Moccetti et al., this volume). However, the parasite data also suggests abundant ingestion of *Mysis* by the ‘grey’ morph,

365 as *C. farionis* (a swim-bladder nematode potentially transmitted by mysids; Black & Lankester,
366 1980) were most frequent in the ‘grey’ morph. Overall, the parasite results (i.e., community structure
367 and/or abundance) described here support previous conclusions that piscivorous predators are
368 exposed to a portfolio of parasite species that differ from those found in sympatric invertebrate
369 feeding morphs (Siwertsson et al., 2016; Moccetti et al., this volume).

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

390 (e.g., Ellis et al., 2002). Ecological convergence (e.g., similarity in diet) as observed in the present
391 ‘dwarf’ and ‘grey’ morphs, may even promote hybridization. The “reverse speciation” process
392 (increased hybridization) among native fish morphs has been reported from other lakes where the
393 introduction of non-native competitors or potential prey have impaired ecological segregation (e.g.,
394 Taylor et al., 2006; Vonlanthen et al., 2012; Baht et al., 2014).

395 Multiple human-induced stressors are evident in Limingen and common in
396 many Scandinavian freshwater systems (Hirsh et al., 2017). Hydropower-induced water level
397 fluctuations provided the initial environmental stressor that reduced littoral benthic food resources
398 for fish (Gregersen et al., 2006). Another human-induced ecosystem stressor was the introduction of
399 Eurasian minnow, a typical shallow-water benthivorous resource competitor for salmonids
400 (Borgstrøm et al., 2010; Museth et al., 2010). Finally, the introduction of *Mysis* may have further
401 altered the niche use of the ‘normal’ morph through increased competition for zooplankton resources
402 (Langeland et al., 1991). There is generally little understanding about how multiple human-induced
403 stressors may affect relatively simple postglacial lake ecosystems such as Limingen, and no
404 information exists on how cumulative stressors can affect the evolutionary processes structuring
405 polymorphic Arctic charr populations (Sandlund & Hesthagen, 2011). By introducing *Mysis* into a
406 lake ecosystem with a littoral zone impaired by hydropower operations, the evolutionary selection
407 regimes appear to have been modified, which may in turn induce a breakdown of the reproductive
408 isolation between established morphs as a result of increasing the functional ecological similarity
409 among the morphs.

410 For management of the scattered and unique deep-water morphs of Arctic
411 charr, it is important to obtain an overview of the occurrence of intra-lake divergence within
412 populations, describe their biological characteristics and determine the environmental prerequisites
413 for their occurrence. Based on recent ecological and genetic studies, deep-water morphs of Arctic
414 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;

Jeppesen et al., 2012). Thus, upper water-column morphs may be more severely affected by an accumulation of anthropogenic-induced stressors, e.g., climate change and hydropower-induced water level fluctuations. Furthermore, if whole lake ecosystems are significantly modified, there may be cascading ecological consequences even for deep-water morphs, as has been suggested by the data from Limingen. This may include an increased risk of hybridization between morph-pairs that will eventually reduce the intraspecific biodiversity apparent in many Scandinavian lakes.

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735

736

737 **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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740 **Table 2.** Summary of parasite infection in the three Arctic charr morphs ('normal', 'dwarf' and
 741 'grey') from Limingen, central Norway. Values are mean \pm SE.

	'normal' n=35	'dwarf' n=24	'grey' n=14	Contrast ^{1*}
Taxa richness	4.1 \pm 0.3	2.5 \pm 0.3	3.9 \pm 0.3	(normal:age = dwarf:age) \neq grey:age
Total abundance*	56.9 \pm 9.1	23.0 \pm 5.7	39.6 \pm 11.0	(normal > dwarf) = grey

742 ^{*} summary of inter-morph contrast analyses; ¹see supplementary Table S1 for details. p < 0.05.

Table 3. Summary of life stage, infection site, intermediate host and trophic transmission status of parasite taxa from three Arctic charr morphs ('normal', 'dwarf' and 'grey') in Limingen, central Norway. Prev = prevalence %; Abund = mean abundance \pm SE; stage (L = larval; A = adult), 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											
<i>Apatemon</i> 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
<i>Crepidostomum</i> 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)
<i>Diplostomum</i> sp. [#]	L	e	snails, fish	No	45.7	2.9 ± 1.4	41.7	1.0 ± 0.3	64.3	1.3 ± 0.3	age
Cestoda											
<i>Cyathocephalus truncatus</i>	A	i	amphipods	Yes	2.9	0.9 ± 0.9	0	0	0	0	-
<i>Dibothriocephalus</i> 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
<i>Eubothrium salvelini</i>	A	i	copepods, fish	Yes	31.4	0.6 ± 0.2	4.2	0.04 ± 0.04	14.3	0.6 ± 0.4	-
<i>Proteocephalus</i> 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											
<i>Cystidicola farionis</i>	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											
<i>Salmincola edwardsii</i>	A	fg	none	No	20.0	0.5 ± 0.2	4.2	0.04 ± 0.04	7.1	<0.01	-

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

748 **Table 4.** Probabilistic niche overlap calculated from nicheRover using the 95% niche regions
 749 between each pair of Arctic charr morphs from Limingen (Swanson et al., 2015). Mean [range 95%
 750 credibility interval] probability (%) of finding an individual of the morph in the row within the niche
 751 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]	-

752

753 **Figure legends:**

754 **Figure 1.** a) Habitat choice (relative CPUE %) and b) growth (mean \pm SD) of the ‘normal’ (red),
755 ‘dwarf’ (green) and ‘grey’ (grey) morphs of Arctic charr found in Limingen.

756

757 **Figure 2.** The diet (prey abundance, %) of the a) Arctic charr along a gradient of increasing capture
758 depth and b) of different morphs ‘normal’ (red), ‘dwarf’ (green) and ‘grey’ (grey) morphs found in
759 Limingen.

760

761 **Figure 3.** Parasite community composition for the three morphs of Arctic charr, the ‘normal’ (red),
762 the ‘dwarf’ (green) and ‘grey’ (grey) found in Limingen, visualized using Nonmetric
763 multidimensional scaling based on Bray-Curtis dissimilarities of parasite infra-communities (n=59;
764 stress: 0.23). Letters denote the mean for each morph.

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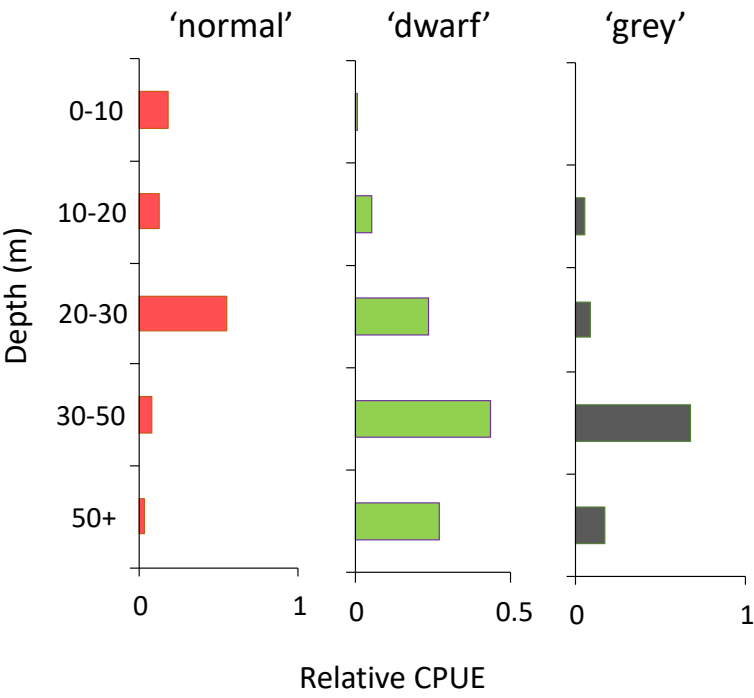
766 **Figure 4.** The relation between the most recent trophic niche (stomach content, blue text) and
767 community composition of trophically transmitted parasites representing a temporally integrated
768 trophic niche (red text) in 58 individuals of the three Arctic charr morphs found in Limingen:
769 ‘normal’ (red), ‘dwarf’ (green) and ‘grey’ (grey) morph. Letters denote the mean for each morph
770 (Canonical correlation: $R^2_{adj}=0.30$, $p<0.001$).

771

772 **Figure 5.**a) Boxplots and b) a biplot showing differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the three Arctic
773 charr morphs: ‘normal’, ‘dwarf’ and ‘grey’ found in Limingen. The letters in a) indicate significant
774 differences ($p < 0.05$) in pairwise comparisons, based on Mann-Whitney U-tests. The $\delta^{13}\text{C}$ values

775 reflect littoral (low $\delta^{13}\text{C}$) *versus* pelagic (high $\delta^{13}\text{C}$) resource use by fish, whereas $\delta^{15}\text{N}$ values reflect
776 trophic position of fish in the lake food web. Niche regions in b) are illustrated by ellipses containing
777 approximately 95% of the data points for each morph (Jackson et al., 2011).

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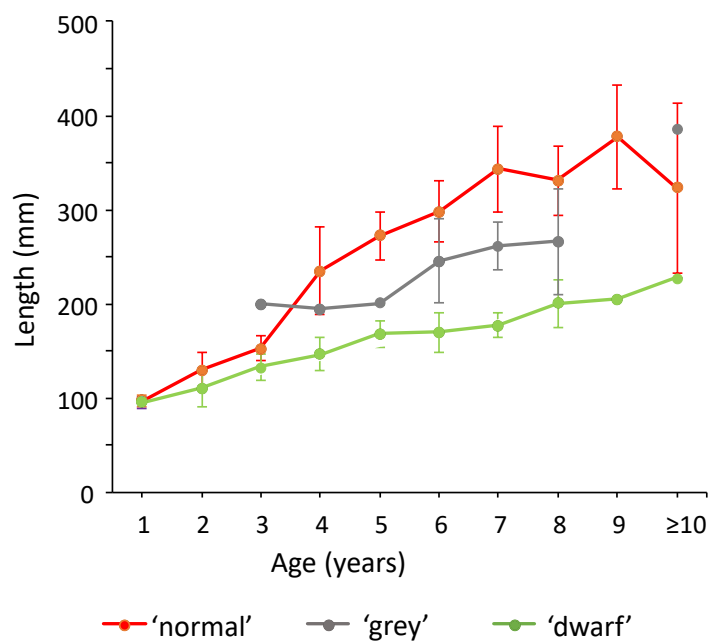


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783 **Fig. 1b.**



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Figure 2a)

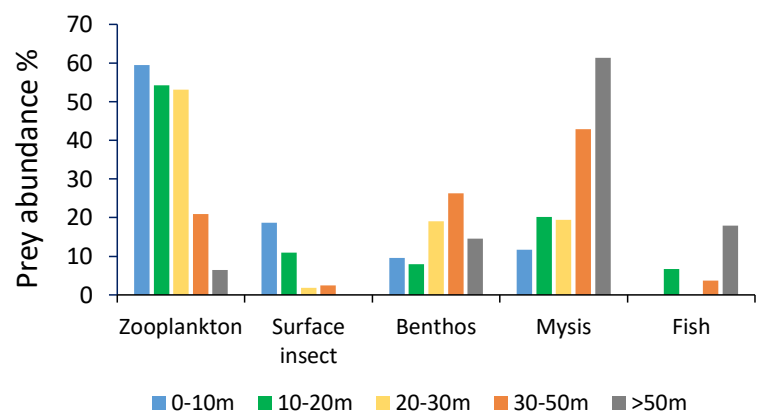
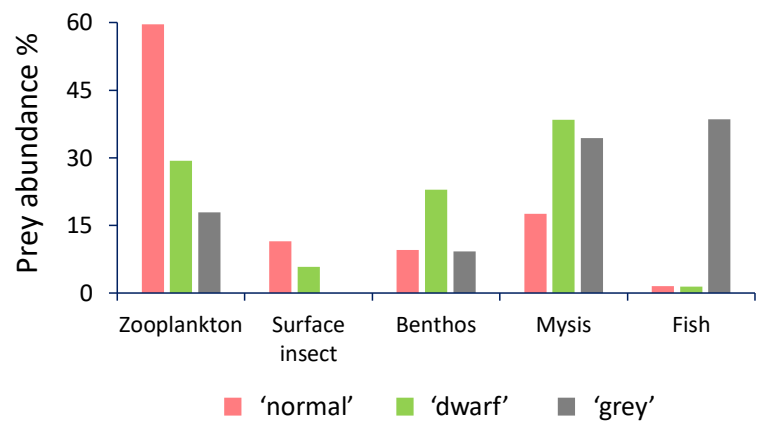


Figure 2b)



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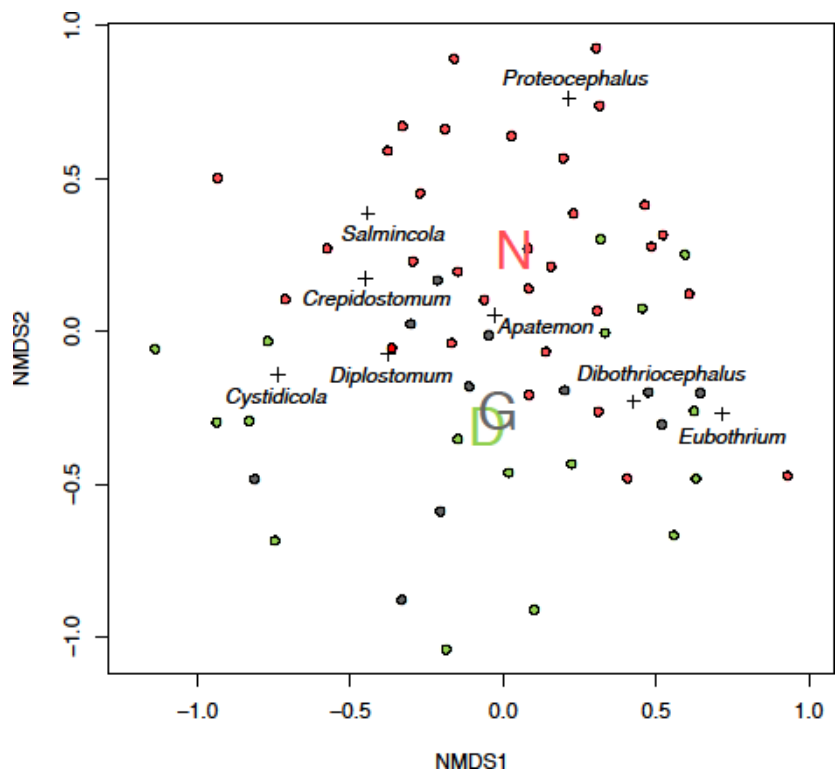
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795 **Fig. 3**

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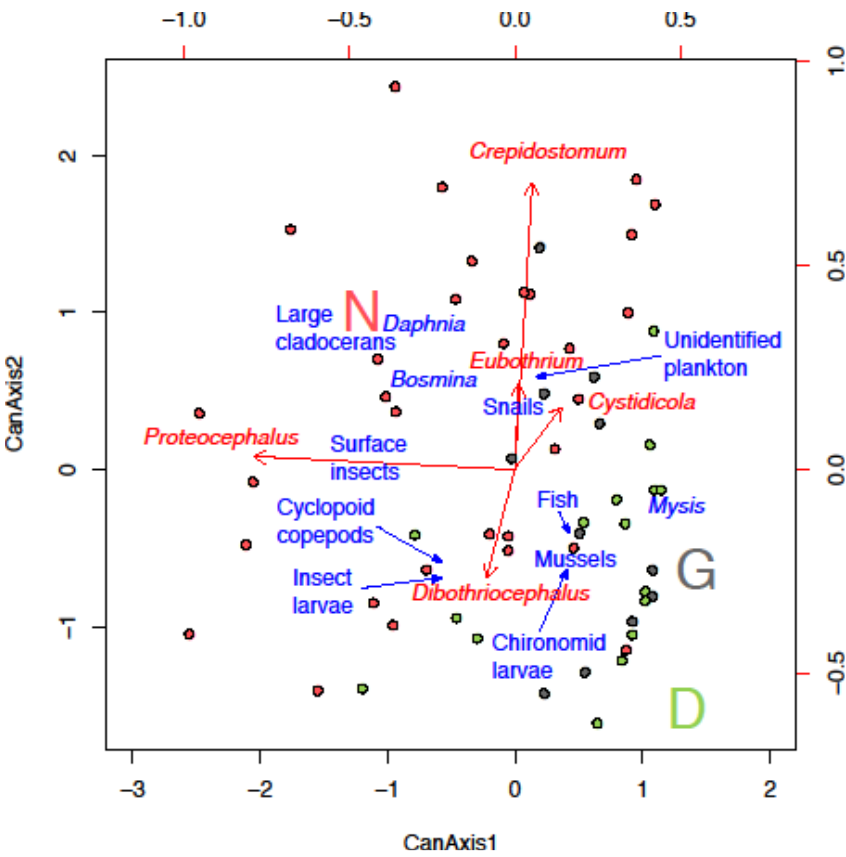
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808 **Fig. 4**

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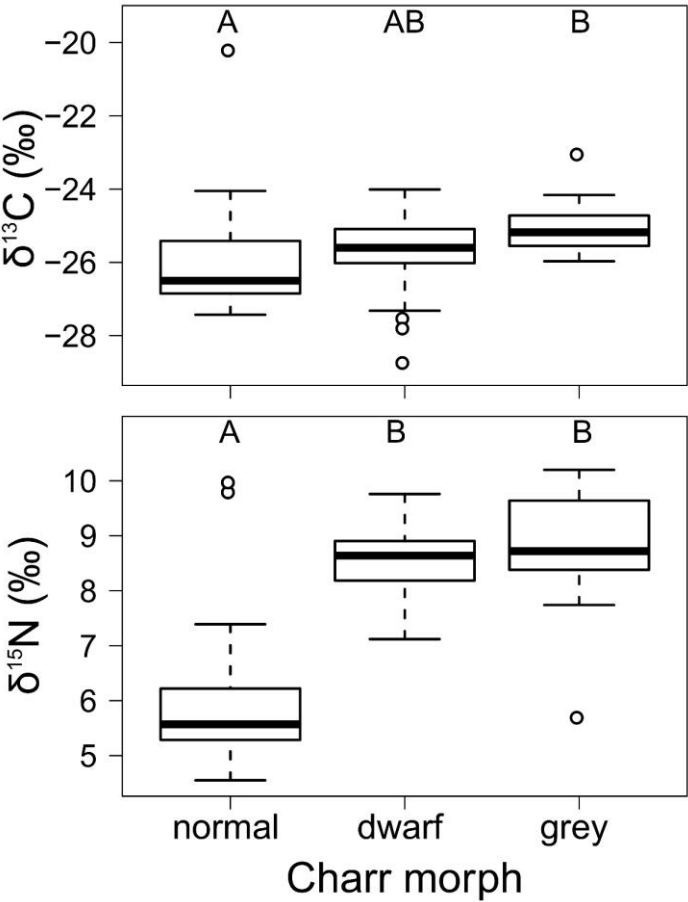
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819 **Fig. 5 a).**



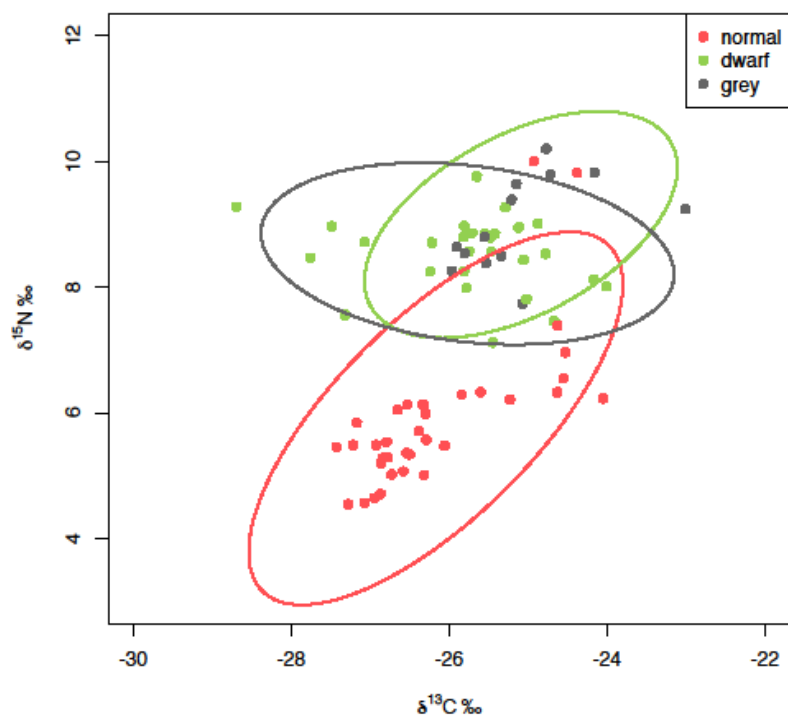
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823 **b)**

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Table S1. Influence of morph and age (years) on parasite taxa richness and total abundance (number of individual parasites) infecting Arctic charr in Limingen, Norway.

Index	Morph	Model type*	Parameter	Contrast	SE	<i>t</i> value	<i>P</i>
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

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

833

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

836

Parasites taxa	Morph	Parameter	Contrast	SE	<i>t</i> value	<i>P</i>
Trematoda						
<i>Apatemon</i> 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
<i>Crepidostomum</i> 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
<i>Diplostomum</i> 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						
<i>Dibothriocephalus</i> 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
<i>Proteocephalus</i> 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						
<i>Cystidicola farionis</i>	'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

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

838