

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

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14  
15 **Abstract:** Niche diversification of polymorphic Arctic charr can be altered by multiple  
16 anthropogenic stressors. The opossum-shrimp (*Mysis relicta*) was introduced to compensate for  
17 reduced food resources for fish following hydropower operations in Lake Limingen, central Norway.  
18 Based on habitat use, stomach contents, stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) and trophically transmitted  
19 parasites, the zooplanktivorous upper water-column dwelling ‘normal’ morph was clearly trophically  
20 separated from two sympatric deep-water morphs (the ‘dwarf’ and the ‘grey’) that became more  
21 abundant with depth (>30m). *Mysis* dominated (50-60%) charr diets in deeper waters (>30m),  
22 irrespective of morph. *Mysis* and/or zooplankton prey groups caused high dietary overlap (>54%)  
23 between the ‘dwarf’ morph and the two other ‘normal’ and ‘grey’ morphs. After excluding *Mysis*,  
24 the dietary overlap dropped to 34% between the two profundal morphs, as the ‘dwarf’ fed largely on  
25 deep-water zoobenthos (39%), while the ‘grey’ morph fed on fish (59%). The time-integrated trophic  
26 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).

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 km<sup>2</sup>), deep ( $Z_{\text{max}} = 192$  m,  $Z_{\text{mean}} =$   
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 m<sup>2</sup> 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 ± SD:  $L_F =$   
124  $310.6 \pm 83.7$  mm; age =  $6.7 \pm 2.5$  years), ‘dwarf’ morph (n = 27;  $L_F = 173.9 \pm 31.7$ ; age =  $6.4 \pm 2.6$ ),  
125 and ‘grey’ morph (n = 14;  $L_F = 297.1 \pm 59.3$ ; age =  $9.5 \pm 3.4$ ).

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  $T$ ,  $L_\infty$  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

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

162

### 163 Stable isotopes

164 Stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) are commonly used to estimate the dietary  
165 sources (littoral *versus* pelagic carbon) and trophic position of organisms in lake food webs, as well  
166 as the intra- and inter-specific niche segregation of fish populations (e.g., Boecklen et al., 2011;  
167 Layman et al., 2012). Here, a small piece of dorsal muscle tissue, obtained posterior to the dorsal fin,  
168 was dissected from a subsample of fish and frozen at  $-20^{\circ}\text{C}$ . Tissue samples were dried at  $60^{\circ}\text{C}$  for  
169 48 hours and homogenised using a pestle and mortar. Approximately  $0.3 \pm 0.05$  mg of dried tissue  
170 was weighed and placed in tin capsules for analyses completed at the University of Waterloo,  
171 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  $\pm 0.2$  ‰ ( $\delta^{13}\text{C}$ ) and  $\pm 0.3$  ‰ ( $\delta^{15}\text{N}$ ) 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 m<sup>2</sup> 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 m<sup>2</sup> 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<sub>morph:age</sub>:  $F_{2,67} = 5.16$ ,  $p = 0.008$ ; 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<sub>morph</sub>:  $F_{2,70} = 4.70$ ,  $p = 0.012$ ; 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:  $\chi^2 = 10.69$ ,  $\text{df}$   
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

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

348                   The relative importance of *Mysis* in the diet of the ‘grey’ morph is not typical  
349 for large-growing Arctic charr (but see Eloranta et al., 2015), although lake charr (*S. namaycush*)  
350 predate substantially on *Mysis* (e.g., Chavarie et al., 2016) particularly when introduced to  
351 oligotrophic lakes (e.g., Ellis et al., 2002). In Limingen, fish was an important prey for the ‘grey’  
352 morph, but not for the sympatric ‘normal’ and ‘dwarf’ morphs, indicating the position of ‘grey’  
353 Arctic charr as specialized piscivores (Adams et al., 1998; Power et al., 2005; Knudsen et al., 2016b;  
354 Moccetti et al. this volume). The inclusion of a specialized piscivore among lake-resident morphs is  
355 also found in other polymorphic *Salvelinus* spp. populations (Muir et al., 2016; Markevitch et al.,  
356 2018). Although the relatively high  $\delta^{15}\text{N}$  values of the ‘grey’ morph partly reflected their piscivorous  
357 diet, the morph was less clearly separated from the ‘dwarf’ morph than has been evident in studies of  
358 other profundal morph-pairs (Knudsen et al., 2016a; Moccetti et al., this volume). The ‘grey’ morph  
359 had a higher diversity of trophically transmitted parasites than ‘dwarf’ morph, likely passed on via  
360 prey fish as has been noted elsewhere (Siwertsson et al., 2016; Moccetti et al., this volume). The  
361 ‘grey’ morph also had aggregated high *Dibothriocephalus* spp. infections (a cestode able to re-  
362 establish in predatory fish; e.g., Curtis, 1984), as is often seen in other piscivorous *Salvelinus* spp.  
363 morphs (Frandsen et al., 1989; Butorina et al., 2008; Siwertsson et al., 2016, Moccetti et al., this  
364 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.,

415 2006; Knudsen et al., 2006; Klemetsen 2010; Præbel et al., 2013, 2016). Profundal morphs of Arctic  
416 charr have evidently inherited traits selected for surviving in cold, dark and nutrient-poor deep-water  
417 environments, including specific adaptations in trophic morphology, behavior and growth  
418 (Klemetsen et al., 2002, 2006; Knudsen et al., 2015). Other traits seem to a lesser degree to be under  
419 strong natural selection, such as temperature preference and vision capabilities (Siikavuopio et al.,  
420 2014; Kahilainen et al., 2016). Without appropriate knowledge of the occurrences of traits within and  
421 among populations of Arctic charr, and of northern lake resident fish in general, a full understanding  
422 of the functional biodiversity within these lakes will remain unknown. Functional diversity is an  
423 important component of biodiversity in northern lakes (Sandlund & Hesthagen, 2011) and its  
424 categorization is particularly important given the rapid anthropogenic induced environmental change  
425 that is altering ecosystems and biodiversity faster than the diversity can be inventoried (Reist et al.,  
426 2013).

427                   A second concern and challenge for management is to identify potential threats  
428 to these deep-water morphs that may reduce their abundance or even cause local extinction. There  
429 seems to be no population-specific, cold-water adaptations in deep-water Arctic charr morphs as they  
430 have the same estimated temperature preferences as those from Svalbard and most of Scandinavia  
431 (Larsson et al., 2005; Siikavuopio et al., 2014). Profundal morphs, however, tend to spawn later than  
432 sympatric upper water-column morphs, during the winter when lakes are normally ice-covered  
433 (Klemetsen et al., 1997; Smalås et al., 2017). The profundal zones in deep oligotrophic postglacial  
434 lakes are relatively stable environments, experiencing less variability in food supply and temperature  
435 regimes (e.g., Mousavi & Amundsen, 2012). Thus, populations inhabiting these lakes may be less  
436 affected by moderate global warming (Poesch et al., 2016), as they can thermally buffer in cold deep  
437 waters isolated from summer temperature stratification. Arctic charr populations that spawn in  
438 shallow areas may actively avoid the warm upper water-column layers during summer stratification  
439 (Murdoch & Power, 2012) but may alter spawning timing or habitat (e.g., Winfield et al., 2010;

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

446

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458

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736



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

Charr morph	# fish	Asymptotic length, $L_{\infty}$	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

738

739

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 <sup>1*</sup>
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; <sup>1</sup>see supplementary Table S1 for details.  $p < 0.05$ .

743 **Table 3.** Summary of life stage, infection site, intermediate host and trophic transmission status of parasite taxa from three Arctic charr morphs  
 744 ('normal', 'dwarf' and 'grey') in Limingen, central Norway. Prev = prevalence %; Abund = mean abundance  $\pm$  SE; stage (L = larval; A = adult),  
 745 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 <sup>1*</sup>
					Prev	Abund	Prev	Abund	Prev	Abund	
Trematoda											
<i>Apatemon</i> sp. <sup>#</sup>	L	e	snails, fish	No	60.0	1.3 $\pm$ 0.3	45.8	0.9 $\pm$ 0.3	57.1	1.6 $\pm$ 0.6	NS
<i>Crepidostomum</i> spp.	A	i	insect larvae	Yes	62.9	9.7 $\pm$ 2.2	37.5	0.8 $\pm$ 0.3	57.1	3.4 $\pm$ 1.7	normal > (dwarf = grey)
<i>Diplostomum</i> sp. <sup>#</sup>	L	e	snails, fish	No	45.7	2.9 $\pm$ 1.4	41.7	1.0 $\pm$ 0.3	64.3	1.3 $\pm$ 0.3	age
Cestoda											
<i>Cyathocephalus truncatus</i>	A	i	amphipods	Yes	2.9	0.9 $\pm$ 0.9	0	0	0	0	-
<i>Dibothriocephalus</i> spp.	L	v	copepods, fish	Yes	80.0	14.0 $\pm$ 5.0	65.2	18.9 $\pm$ 5.9	92.9	30.5 $\pm$ 11.4	NS
<i>Eubothrium salvelini</i>	A	i	copepods, fish	Yes	31.4	0.6 $\pm$ 0.2	4.2	0.04 $\pm$ 0.04	14.3	0.6 $\pm$ 0.4	-
<i>Proteocephalus</i> sp.	A	v	copepods, fish	Yes	77.1	25.4 $\pm$ 8.8	25.0	1.4 $\pm$ 0.8	35.7	0.6 $\pm$ 0.2	grey = (normal > dwarf); age
Nematoda											
<i>Cystidicola farionis</i>	A	sb	amphipods	Yes	20.0	1.5 $\pm$ 0.9	29.2	0.6 $\pm$ 0.2	50.0	1.4 $\pm$ 0.5	NS
Unidentified nematode	A	i	unknown	Yes	2.9	<0.01	4.2	0.04 $\pm$ 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 $\pm$ 0.2	4.2	0.04 $\pm$ 0.04	7.1	<0.01	-

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

747 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.

	<b>'normal'</b>	<b>'dwarf'</b>	<b>'grey'</b>
<b>'normal'</b>	-	14.5 [5 - 27]	10.1 [2 - 28]
<b>'dwarf'</b>	31.7 [9 - 59]	-	69.9 [46 - 91]
<b>'grey'</b>	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.

765

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:  $R^2_{adj}=0.30$ ,  $p<0.001$ ).

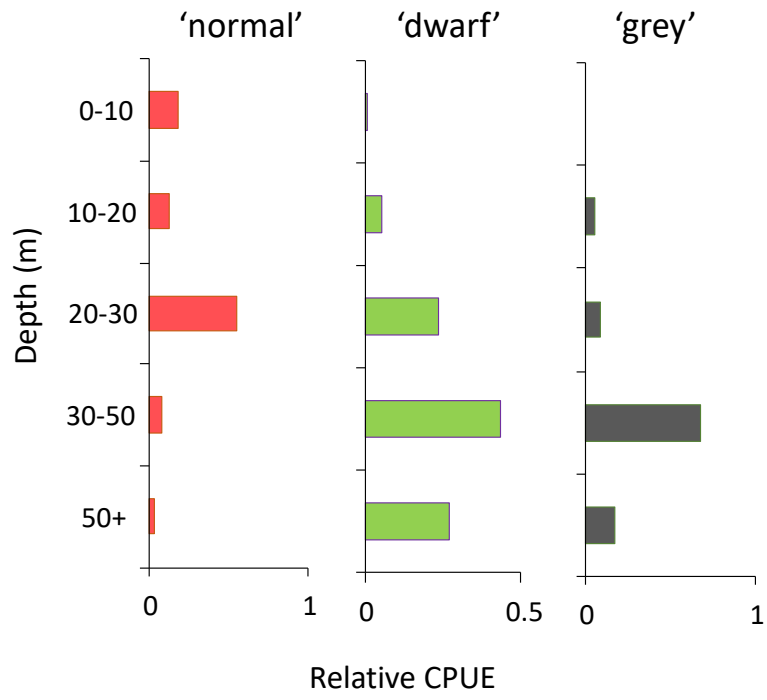
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772 **Figure 5.**a) Boxplots and b) a biplot showing differences in  $\delta^{13}C$  and  $\delta^{15}N$  values for the three Arctic  
773 charr morphs: ‘normal’, ‘dwarf’ and ‘grey’ found in Limingen. The letters in a) indicate significant  
774 differences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

778

779 **Fig. 1a**

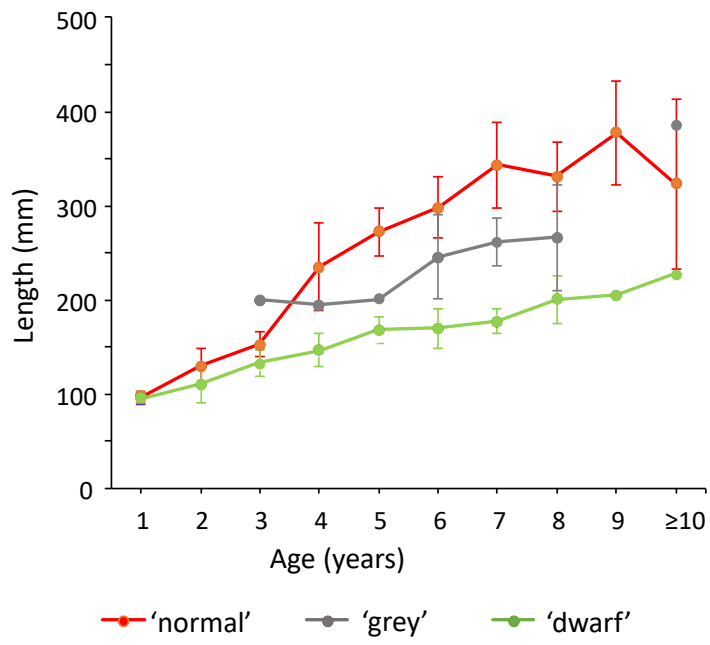


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783 **Fig. 1b.**



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Figure 2a)

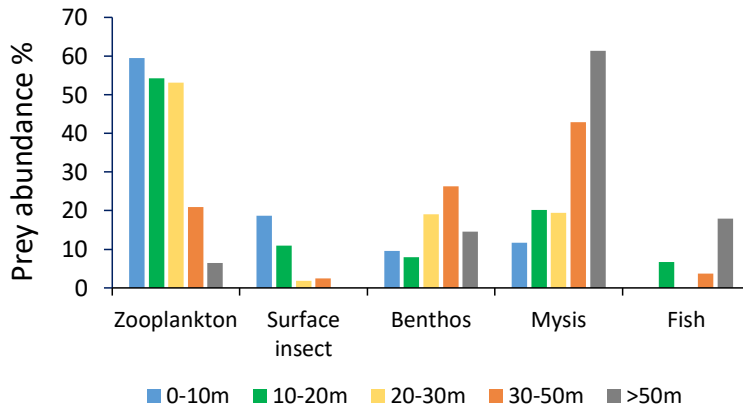
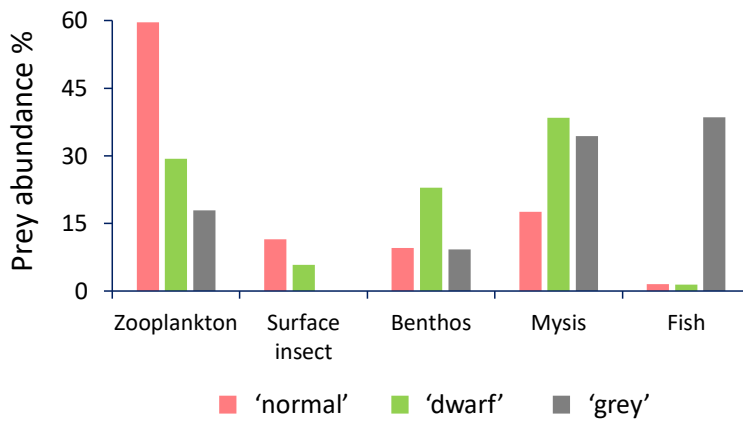


Figure 2b)



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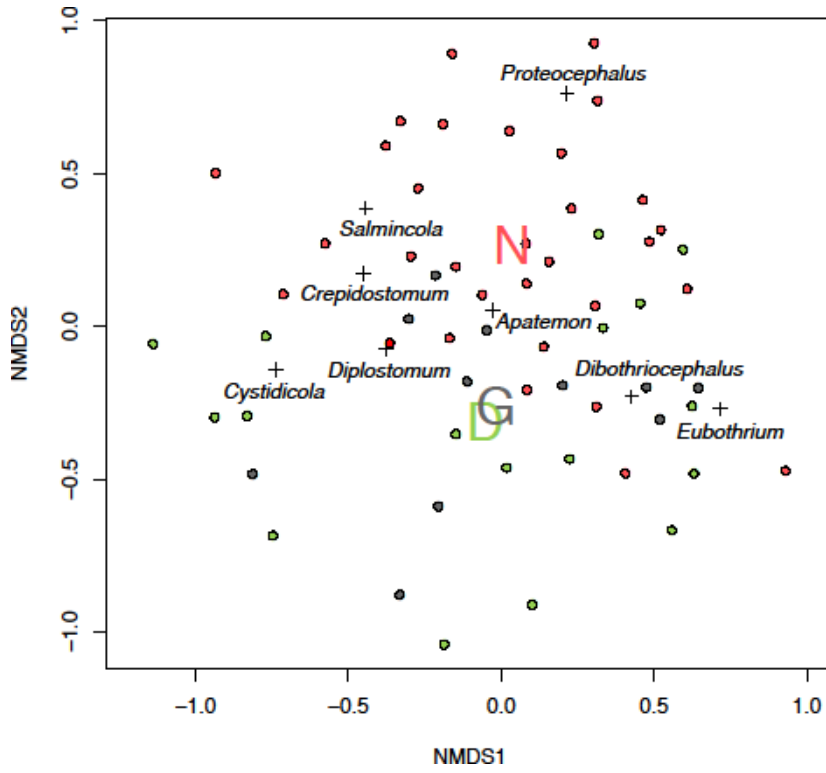
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795 **Fig. 3**

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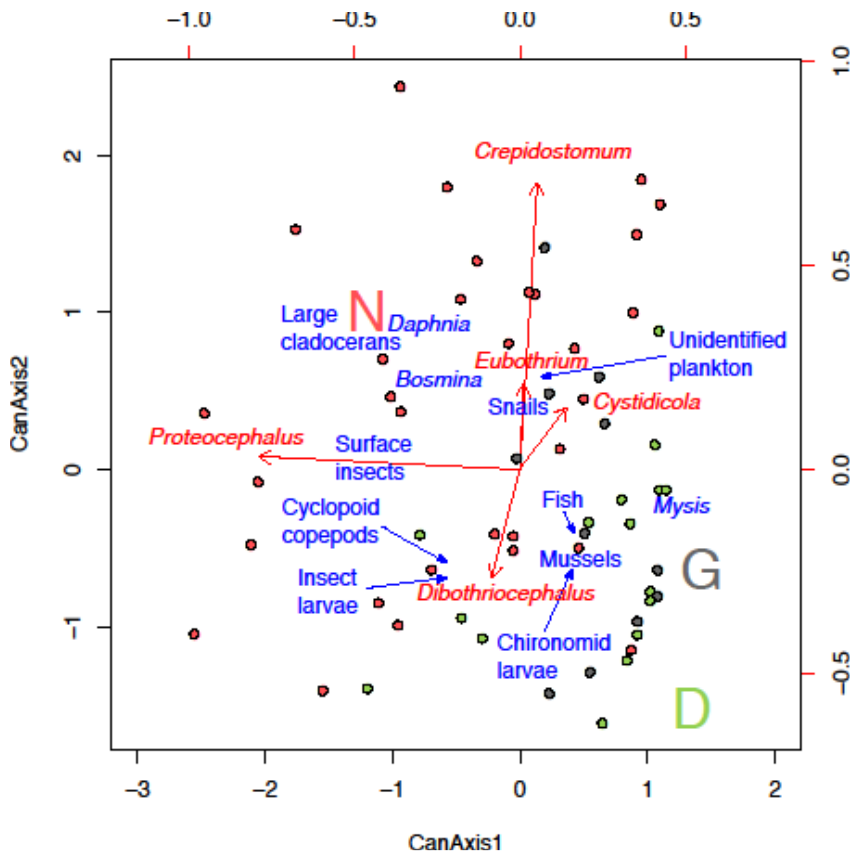
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808 **Fig. 4**

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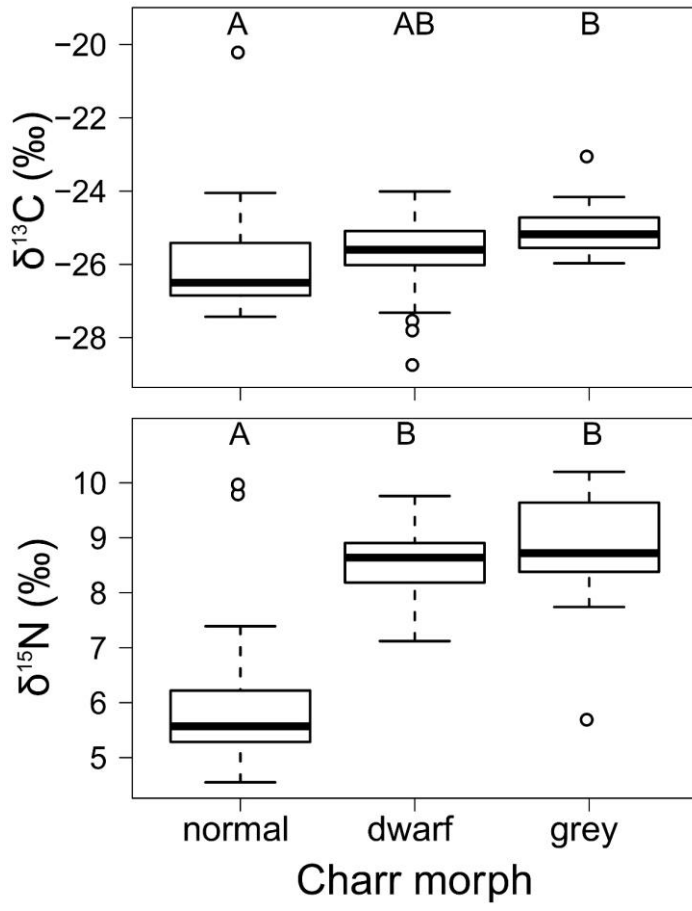
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819 **Fig. 5 a).**



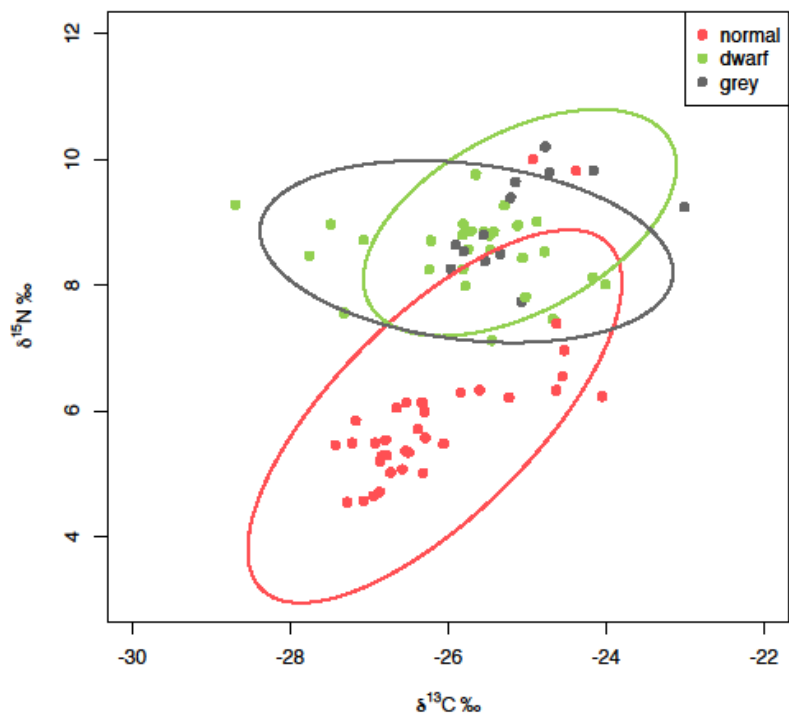
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823 **b)**

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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	<b>intercept</b>	2.45	0.82	3.00	<b>0.004</b>	
			'dwarf'	-1.35	1.11	-1.22	0.227	
			'grey'	3.38	1.38	2.45	<b>0.017</b>	
			<b>age</b>	0.23	0.11	2.05	<b>0.044</b>	
			'dwarf':age	-0.001	0.15	-0.01	0.995	
			'grey':age	-0.43	0.16	-2.78	<b>0.007</b>	
			'dwarf'	intercept	1.10	0.75	1.47	0.147
				'grey'	4.73	1.34	3.54	<b>&lt;0.001</b>
	<b>age</b>	0.22		0.11	2.07	<b>0.042</b>		
	'grey':age	-0.43		0.15	-2.79	<b>0.007</b>		
	Total abundance	'normal'	simple	<b>intercept</b>	4.03	0.38	10.50	<b>&lt;0.001</b>
				'dwarf'	-0.91	0.32	-2.81	<b>0.006</b>
'grey'				-0.37	0.34	-1.08	0.286	
age				0.001	0.05	0.03	0.978	
'dwarf'		<b>intercept</b>	3.12	0.43	7.31	<b>&lt;0.001</b>		
		'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>
<b>Trematoda</b>						
<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'	<b>intercept</b>	1.51	0.55	2.77	<b>0.007</b>
		<b>'dwarf'</b>	-2.45	0.79	-3.08	<b>0.003</b>
		<b>'grey'</b>	-1.33	0.56	-2.38	<b>0.020</b>
		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'	<b>intercept</b>	-0.85	0.49	-1.74	<b>0.086</b>
		'dwarf'	0.10	0.36	0.28	0.783
		'grey'	-0.07	0.44	-0.17	0.869
		<b>age</b>	0.12	0.06	2.08	<b>0.042</b>
	'dwarf'	intercept	-0.75	0.49	-1.53	0.130
		'grey'	-0.17	0.46	-0.37	0.711
<b>Cestoda</b>						
<i>Dibothriocephalus</i> spp.	'normal'	<b>intercept</b>	2.09	0.62	3.40	<b>0.001</b>
		'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'	<b>intercept</b>	2.44	0.60	4.06	<b>&lt;0.001</b>
		'grey'	0.24	0.55	0.43	0.667
<i>Proteocephalus</i> sp.	'normal'	<b>intercept</b>	5.59	0.96	5.84	<b>&lt;0.001</b>
		<b>'dwarf'</b>	-3.22	1.29	-2.49	<b>0.015</b>
		'grey'	-3.22	2.61	-1.23	0.223
		<b>age</b>	-0.36	0.16	-2.34	<b>0.022</b>
	'dwarf'	intercept	2.37	1.47	1.61	0.113
		'grey'	0.003	2.91	0.001	0.999
<b>Nematoda</b>						
<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

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

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