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

Rune Knudsen^{1*} • Antti P. Eloranta^{2,3} • Anna Siwertsson¹ • Rachel A. Paterson⁴ • Michael Power⁵ •

Odd Terje Sandlund²

¹ UiT The Arctic University of Norway, Tromsø, Norway; ² The Norwegian Institute for Nature Research, Trondheim, Norway; ³ Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland; ⁴ School of Biosciences, Cardiff University, Cardiff, United Kingdom; ⁵ University of Waterloo, Waterloo, Canada

* R. Knudsen, Department of Arctic and Marine Biology, UiT The Arctic University of Norway, P.O. Box 6050, Langnes, NO-9037 Tromsø, Norway; Phone: (+47) 776-46037; e-mail: rune.knudsen@uit.no

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

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. 2017).
73 *Mysis* is an opossum shrimp native to Scandinavia, though previously absent from this Limingen
74 region of Norway (Spikkeland et al., 2016). *Mysis* show a pronounced diel vertical migration pattern,

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

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

92

93 **Material and methods**

94 **Study lake**

95 Lake Limingen (64°50'N, 13°13'E) is a large (surface area = 95.7 km²), deep (Z_{max} = 192 m, Z_{mean} =
96 87 m), dimictic, oligotrophic and relatively clear (Secchi depth = 9–12.7 m) lake situated at 418 m
97 a.s.l. in the north boreal vegetation zone of central Norway. Originally, the lake drained to the
98 Ångermanälven watercourse in northern Sweden, but after hydropower development in 1953 most of

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

106

107 Fish material

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

115 Individual Arctic charr were classified to one of three possible morphs based
116 on head and body morphology, maturation, and colouration following guidelines produced from
117 earlier studies of similar polymorphic populations (Skoglund et al., 2015; Simonsen et al., 2017). In
118 total, we sampled 178 Arctic charr from Limingen, with stomachs analysed from 171 individuals.
119 The catch per unit of effort (CPUE) was estimated as the number of fish caught per 100 m² gillnet
120 per night. A subsample of mature individuals from all three morphs was assessed for parasite
121 assemblages and sampled for stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). The numbers of each morph
122 included in the parasite and stable isotope sampling were: ‘normal’ morph ($n = 39$; mean \pm SD: $L_F =$

123 310.6 ± 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),
124 and ‘grey’ morph (n = 14; $L_F = 297.1 \pm 59.3$; age = 9.5 ± 3.4).

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

130

131 Diet

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

141

142

143 Parasites

144 All parasites from the body cavity, stomach, intestine, kidney, swim bladder, gills and eyes were
145 enumerated from sub-sampled fish (see Table 3 for more details). Most of the parasite taxa are
146 transmitted to Arctic charr via different prey items such as copepods (cestodes *Dibothriocephalus*

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).

161

162 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
 Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo

172 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
173 determined through the repeat analysis of internal laboratory standards calibrated against
174 International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen.

175

176 Statistical analyses

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

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

196 and parasite community composition, we used canonical correlation (vegan: CCorA, Oksanen et al.,
197 2017) of logit-transformed prey volumes and log-transformed abundances of trophically transmitted
198 parasites.

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

209

210 **Results**

211 Fish community, habitat preference and Arctic charr growth

212 Arctic charr was the dominant species ($n = 168$) in the benthic habitats (i.e., littoral and profundal),
213 whereas only nine ‘normal’ Arctic charr were caught in the pelagic zone (0.6 charr per 100 m² gillnet
214 area). Additionally, 34 brown trout, 68 minnows and one three-spined stickleback were caught from
215 the littoral zone. The CPUE of Arctic charr (overall mean: 3.8 fish per 100 m² benthic gillnet per
216 night) increased with depth from about 1.8 at 0-10 m, 2.2 at 10-20 m, 5.2 at 20-30 m to >8 at >30 m
217 depth. The ‘normal’ morph was most abundant in the upper water-column layers (Fig. 1a), down to

218 30 m depth (CPUE-range: 2-4.5). The ‘dwarf’ morph was most abundant at depths >20 m (CPUE:
219 >4), and the ‘grey’ morph was most abundant within the 30-50 m depth zone (CPUE: >2).

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

229

230 Dietary niches

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

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

246

247 Parasite community composition

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

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

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

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

284

Stable isotopes

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

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

299

300 **Discussion**

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

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

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

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 Henriksen et al., this volume), 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,

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

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

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

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

409 For management of the scattered and unique deep-water morphs of Arctic
410 charr, it is important to obtain an overview of the occurrence of intra-lake divergence within
411 populations, describe their biological characteristics and determine the environmental prerequisites
412 for their occurrence. Based on recent ecological and genetic studies, deep-water morphs of Arctic
413 charr and whitefish are replicated in several locations and appear to originate locally (Østbye et al.,

414 2006; Knudsen et al., 2006; Klemetsen 2010; Præbel et al., 2013, 2016). Profundal morphs of Arctic
415 charr have evidently inherited traits selected for surviving in cold, dark and nutrient-poor deep-water
416 environments, including specific adaptations in trophic morphology, behavior and growth
417 (Klemetsen et al., 2002, 2006; Knudsen et al., 2015). Other traits seem to a lesser degree to be under
418 strong natural selection, such as temperature preference and vision capabilities (Siikavuopio et al.,
419 2014; Kahilainen et al., 2016). Without appropriate knowledge of the occurrences of traits within and
420 among populations of Arctic charr, and of northern lake resident fish in general, a full understanding
421 of the functional biodiversity within these lakes will remain unknown. Functional diversity is an
422 important component of biodiversity in northern lakes (Sandlund & Hesthagen, 2011) and its
423 categorization is particularly important given the rapid anthropogenic induced environmental change
424 that is altering ecosystems and biodiversity faster than the diversity can be inventoried (Reist et al.,
425 2013).

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

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

445

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457

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731

732

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

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

734

735

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

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

739 **Table 3.** Summary of life stage, infection site, intermediate host and trophic transmission status of parasite taxa from three Arctic charr morphs
740 ('normal', 'dwarf' and 'grey') in Limingen, central Norway. Prev = prevalence %; Abund = mean abundance \pm SE; stage (L = larval; A = adult),
741 infection site (v = viscera, i = intestine, k = kidney, sb = swim bladder, fg = fins/gills).

Parasite taxa	Stage	Site	Interm. host	Trophic transm.	'normal'		'dwarf'		'grey'		Contrasts ^{1*}
					Prev	Abund	Prev	Abund	Prev	Abund	
Trematoda											
<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	-

742 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
743 significant

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

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

748

749 **Figure legends:**

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

752

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

756

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

761

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

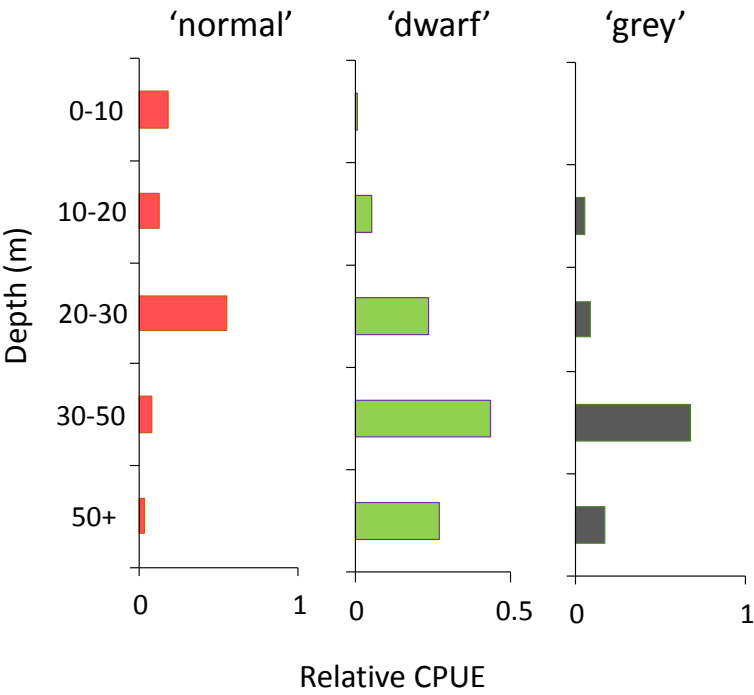
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768 **Figure 5.**a) Boxplots and b) a biplot showing differences in $\delta^{13}C$ and $\delta^{15}N$ values for the three Arctic
769 charr morphs: ‘normal’, ‘dwarf’ and ‘grey’ found in Limingen. The letters in a) indicate significant
770 differences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

771 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
772 trophic position of fish in the lake food web. Niche regions in b) are illustrated by ellipses containing
773 approximately 95% of the data points for each morph (Jackson et al., 2011).

774

775 **Fig. 1a**



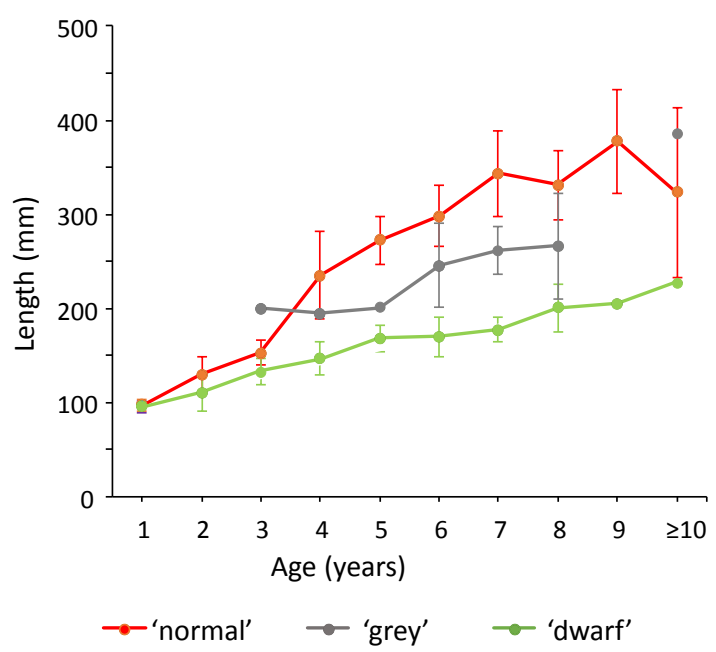
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780 **Fig. 1b.**



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Figure 2a)

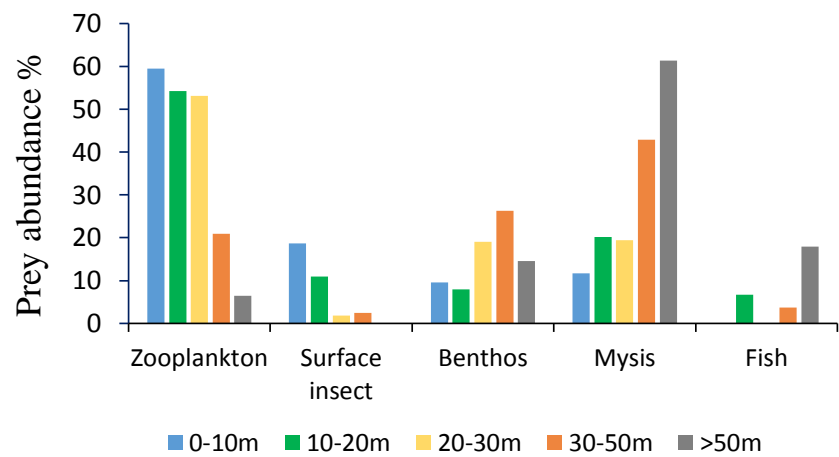
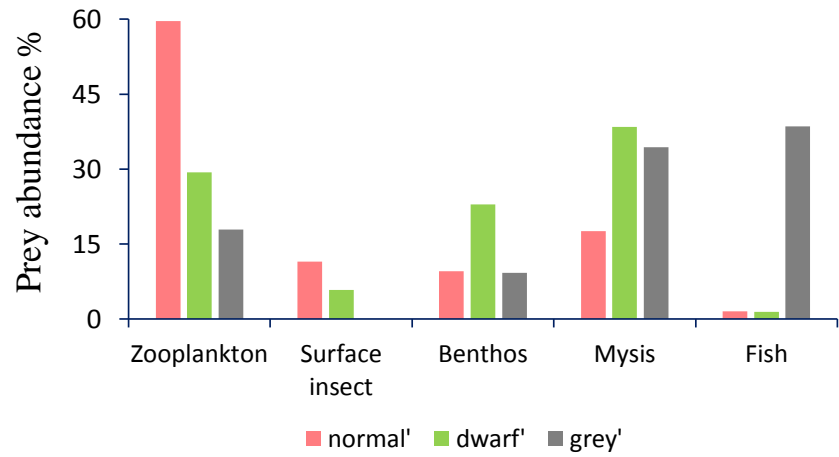
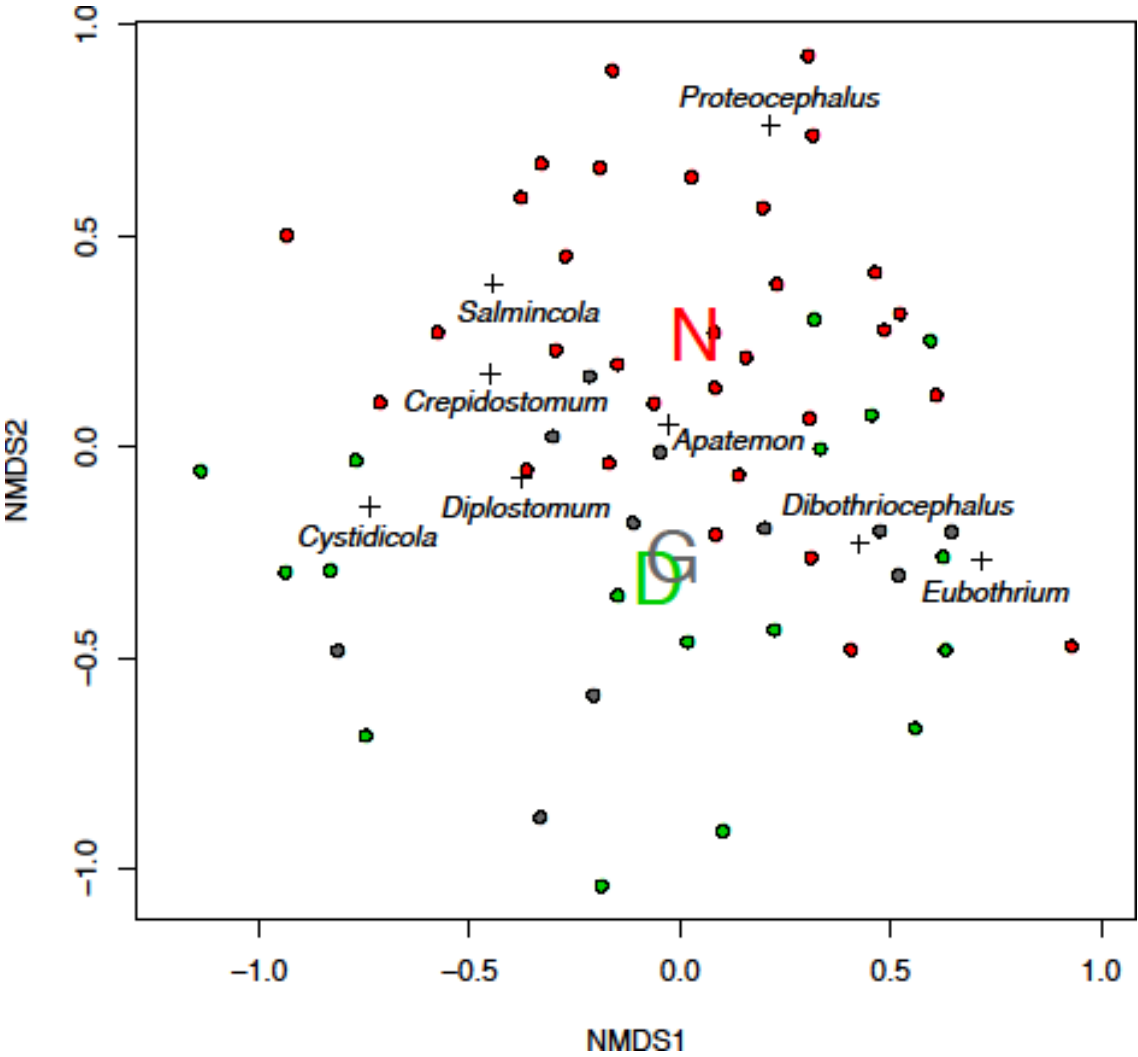


Figure 2b)



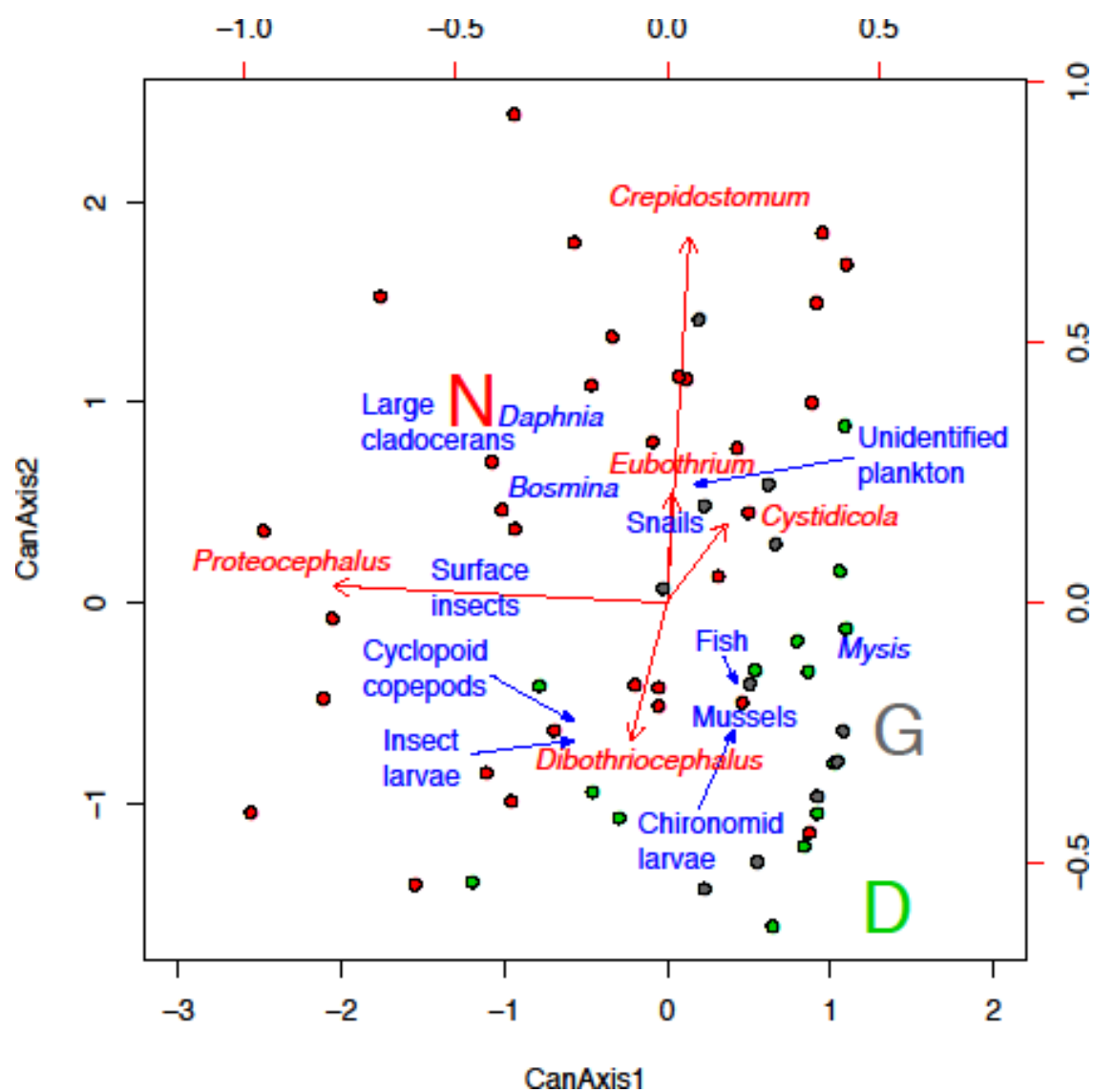
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792 **Fig. 3**



802 Fig. 4

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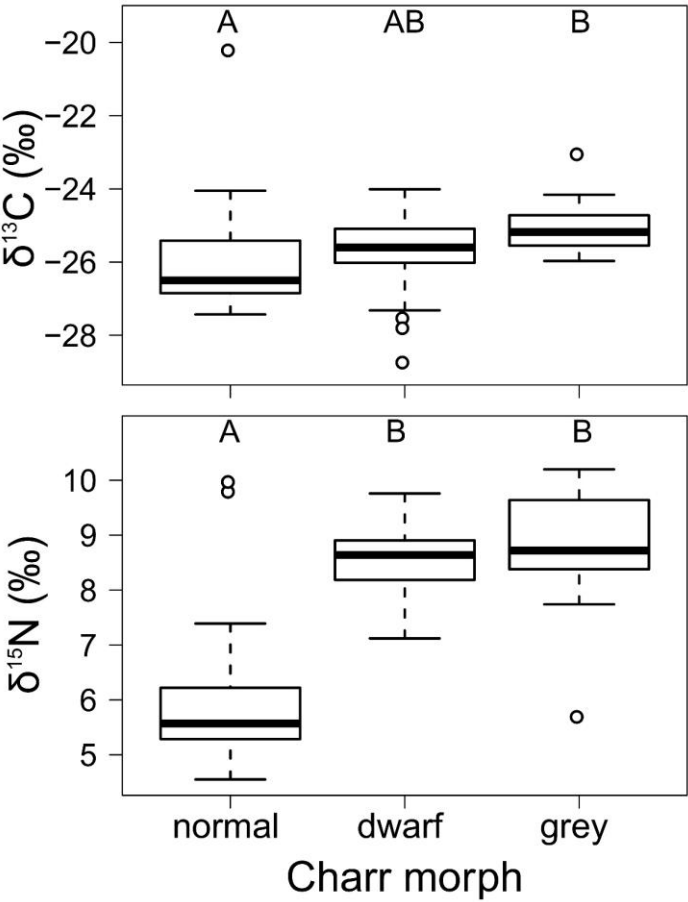
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810 **Fig. 5 a).**

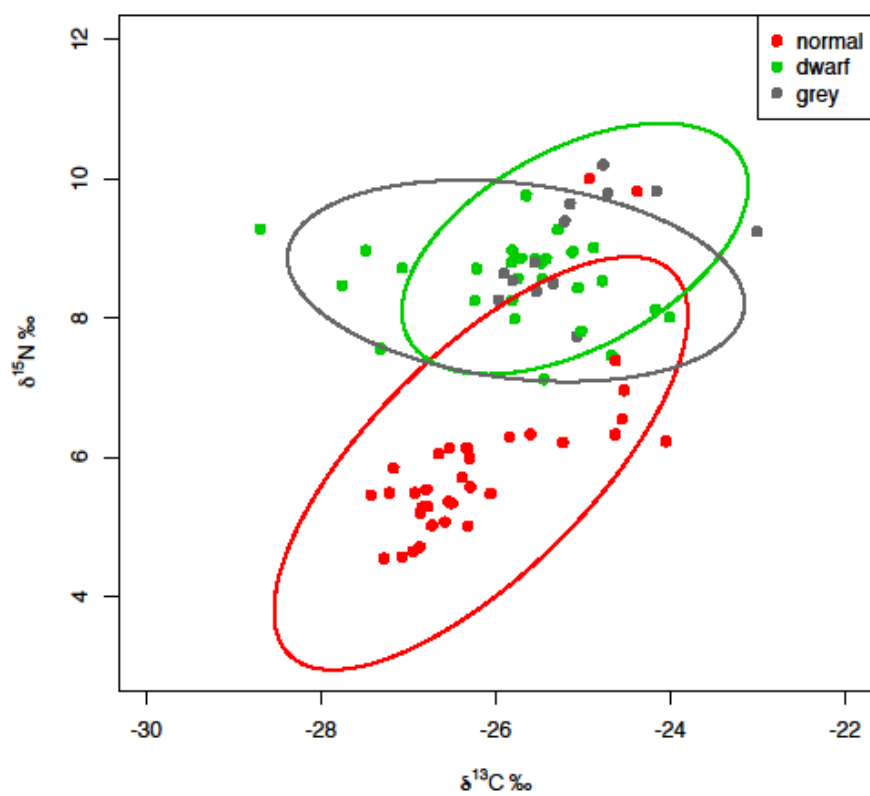


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814 **b)**



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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

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

822

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

825

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
