1 **Contrasting patterns in trophic niche evolution of polymorphic Arctic charr**

2 **populations in two subarctic Norwegian lakes**

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25

26 **Abstract**

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28 Parallelism in trophic niches of polymorphic populations of Arctic charr was investigated in

29 two similar subarctic lakes, Tårnvatn and Skøvatn, in northern Norway. Analysis of eleven

30 microsatellite loci confirmed, respectively, the existence of three and two genetically

31 differentiated morphs. Three methods were used to describe their trophic niches: habitat

32 choice and stomach contents for the recent feeding behaviour, and trophically-transmitted

33 parasites and stable isotopes (δ^{13}C and δ^{15}N) as proxies for the longer term trophic niche

34 differences. The results showed a distinct segregation in trophic resource utilization of the

35 different morphs. Tårnvatn has three morphs: a littoral omnivorous (LO), a small-sized

36 profundal benthivorous (PB), and a large-sized profundal piscivorous (PP). In contrast, a

37 novel Arctic charr morph was discovered in Skøvatn: a small-sized profundal

38 zooplanktivorous-morph (PZ), which when compared to the sympatric LO-morph, had

39 distinct stable isotope values and a contrasting parasite community. A parallelism in habitat

40 choice and external morphology was found among the small-sized, deep-water morphs and

41 between the upper-water, omnivorous LO-morphs in both lakes. There was a no parallel

42 pattern in diet choice between the PB- and the PZ-morphs. These findings show how

43 evolution can produce diverse outcomes, even among systems with apparently similar

44 environmental and ecological conditions.

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46 Key-words: *Salvelinus alpinus*, polymorphism, genetic differences, trophic niche divergence,

47 stomach contents, stable isotope analyses, trophically transmitted parasites.

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55   **Introduction**

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57   A resource polymorphism is defined as the occurrence of distinct morphs specialized in

58   different resource use within a single species (Skúlason & Smith, 1995). Polymorphic

59   populations of several fish species have repeatedly been found in postglacial lakes, especially

60   within the genera *Salvelinus*, *Gasterosteus*, and *Coregonu*s (Skúlason & Smith, 1995; Skúlason

61   et al., 1999; Amundsen et al., 2008; Klemetsen, 2013). Since polymorphisms are considered to

62   be an important step in an ecologically induced speciation process (Wimberger, 1994;

63   Gíslason et al., 1999; Snorrason & Skúlason, 2004; Amundsen et al., 2008; Siwertsson et al.,

64   2013a), freshwater systems of recent origin are viewed as hotspots for investigating the

65   function and role of ecological components in divergent evolution (Schluter, 1996; Snorrason

66   & Skúlason, 2004; Klemetsen, 2010). Similar ecological niches and environments in many

67   isolated postglacial lakes have resulted in parallel adaptations in the morphology, behaviour,

68   physiology, and life-history traits of several fish species (Endler, 1986; Schluter, 2000),

69   including Arctic charr, *Salvelinus alpinus* (L.) (Skúlason & Smith, 1995; Klemetsen, 2010),

70   which is the target species of the present study.

71   The initial step in the evolutionary divergence of northern fishes has been suggested to

72   be competition for discrete habitats and food resources, which allow fish to specialize and

73   segregate in distinctive niches (Wimberger, 1994; Skúlason & Smith, 1995; Jonsson & Jonsson,

74   2001; Adams et al., 2003; Garduño-Paz & Adams, 2010). A repeatedly found pattern of trophic

75   niche segregation in postglacial lakes occurs along the benthic-pelagic resource axis, with

76 benthivorous morphs exploiting the littoral area, and planktivorous and/or piscivorous

77 morphs residing in the pelagic zone (Wimberger, 1994; Skúlason & Smith, 1995; Schluter,

78 1996; Sigursteinsdóttir & Kristjánsson, 2005). The degree of divergence within lakes varies

79 considerably, with containing completely reproductively isolated morphs (populations) and

80 other showing variable levels of reproductive isolation within a common species (Gíslason et

81 al., 1999; Skúlason et al., 1999; Hendry et al., 2009; Klemetsen, 2010). The frequent incidents

82 of parallel evolution observed in several fish taxa such as e.g. Arctic charr and three-spined

83 stickleback (*Gasterosteus aculeatus* L.), are considered strong evidence of ecologically induced

84 divergence, as they are unlikely to arise solely by genetic drift or other nonecological

85 mechanisms (Schluter & Nagel, 1995; Schluter, 1996, 2001; Nosil & Rundle, 2009; Kaeuffer et

86 al., 2012; Saltykova et al., 2017).

87 Arctic charr is considered to be a highly variable and plastic species, showing a myriad

88 of differences in coloration, morphology, ecology, and life history traits (Johnson, 1980;

89 Skúlason et al., 1999; Alexander & Adams, 2000; Jonsson & Jonsson, 2001; Klemetsen, 2010).

90 Polymorphic Arctic charr may represent two (e.g. Fjellfrøsvatn; Klemetsen et al., 1997), three

91 (e.g. Loch Rannoch; Adams et al., 1998), and even four (e.g. Thingvallavatn; Sandlund et al.,

92 1992) distinct morphs within a single lake (Smith & Skúlason, 1996; Jonsson & Jonsson, 2001;

93 Klemetsen, 2010; Jacobs et al., 2018). The evolution of phenotypic and ecological divergence

94 in Arctic charr has mediated the accumulation of genetic differences among the morphs both

95 when occurring as allopatric and polymorphic sympatric morphs (e.g. Gomez-Uchida et al.,

96 2008; Power et al., 2009; Præbel et al., 2016; Jacobs et al., 2018; O´Malley et al., 2019). Most

97 Arctic charr morphs are segregated along the littoral-pelagic axis, but deep-water living Arctic

98 charr morphs adapted to the profundal habitat have also been described in a few lakes

99 (Klemetsen, 2010; Markevich & Esin, 2018). The present study addresses the trophic niche

100   utilization of polymorphic Arctic charr populations in two subarctic lakes, with special

101   emphasis on the trophic ecology of profundal-dwelling morphs.

102   Two well-studied examples of profundal Arctic charr morphs are those in lakes

103   Fjellfrøsvatn and Skogsfjordvatn, northern Norway (Klemetsen et al., 1997; Knudsen et al.,

104   2006, 2016a,b; Amundsen et al., 2008; Smalås et al., 2013). In both lakes, there are two

105   distinct, replicated morphs: a littoral spawning omnivorous 'LO-morph' feeding on littoral

106   macrobenthos and zooplankton, and a small-sized profundal spawning benthivorous 'PB-

107   morph' that forages on soft-bottom benthic invertebrates (Klemetsen et al., 1997; Smalås et

108   al., 2013). Additionally, Skogsfjordvatn hosts a rare profundal spawning piscivorous 'PP-

109   morph' that feeds mostly on conspecific Arctic charr and, to a lesser extent, on three-spined

110   stickleback (Smalås et al., 2013; Knudsen et al., 2016b). Within each lake the different morphs

111   are clearly segregated in habitat and diet, as reflected by their stable isotope values and

112   parasite loads (e.g. Knudsen et al., 2016a, Siwertsson et al., 2016), and in life history strategies

113   and morphology (e.g. Smalås et al., 2013; Skoglund et al., 2015). The different morphs were

114   first classified on the basis of external morphological functional traits including: body and

115   head shape, eye and mouth size, and coloration (Knudsen et al., 2007; Skoglund et al., 2015;

116   Saltykova et al., 2017; Simonsen et al., 2017), and have subsequently been shown to be

117   reproductively isolated (Klemetsen et al., 1997; Smalås et al., 2017) and genetically distinct

118   based on microsatellite loci (Præbel et al., 2016; Simonsen et al., 2017).

119   Recent fish management surveys of additional northern Norwegian lakes have

120   suggested that lakes Tårnvatn and Skøvatn, similarly harbour polymorphic Arctic charr (three

121   and two putative morphs, respectively), with the varieties morphologically resembling those

122   described from Skogsfjordvatn and Fjellfrøsvatn. These preliminary observations suggest that

123   both Tårnvatn and Skøvatn harbour a normal growing LO-morph and potentially a small-

124   sized PB-morph. In addition, Tårnvatn appears to host a large-growing profundal piscivorous

morph similar to the PP-morph found in Skogsfjordvatn. The two lakes have similar fish

communities, are deep, dimictic, oligotrophic, and experience analogous subarctic climates

similar to Fjellfrøsvatn and Skogsfjordvatn. Although little was known about the ecology and

life history of the putative morphs in the two lakes, the same nomenclatures (i.e. LO, PB, PP)

were initially used to label the morphs in Tårnvatn and Skøvatn.

The primary goal of the present study was to explore any parallelism in the evolution

of sympatric Arctic charr morphs in Tårnvatn and Skøvatn. To establish whether the putative

morphs were genetically separated and the extent of divergence, the genetic differentiation

was examined using microsatellites and Bayesian clustering. The trophic ecology of the Arctic

charr morphs was then contrasted within and between the two lakes using stomach contents

to describe short-term resource use and trophically transmitted parasites and stable isotopes

analysis (SIA) to evaluate at longer, ecologically relevant time scales (Post, 2002; Knudsen et

al., 2011, 2014; Hayden et al., 2014). Further, any concordance with the sympatric morph

classifications reported from Fjellfrøsvatn and Skogsfjordvatn was assessed (Klemetsen et al.,

1997; Knudsen et al., 2006, 2016a,b; Amundsen et al., 2008; Smalås et al., 2013; Præbel et al.,

2016; Simonsen et al., 2017). Four hypotheses were addressed. Firstly, we hypothesised that

the sympatric Arctic charr morphs in both lakes were genetically differentiated. Secondly, we

hypothesised that the sympatric Arctic charr morphs would show trophic niche divergence in

habitat and diet within each of the two study lakes, with the divergence being stable over time

(i.e., similar based on gut contents, parasite community and SIA). Thirdly, it was hypothesised

that the Arctic charr morphs display evolutionary parallelism when compared to morphs

known to exist in Fjellfrøsvatn and Skogsfjordvatn (Knudsen et al., 2016a, Siwertsson et al.,

2016), with the LO-morphs showing a generalist foraging behaviour and feeding on pelagic

zooplankton and littoral benthos, and the small-sized deep-water morphs specializing in

feeding on profundal soft-bottom macroinvertebrates. Finally, it was hypothesised that the

150   putative PP-morph in Tårnvatn would exhibit a distinctive piscivorous feeding strategy,

151   preying upon small-sized charr (i.e. cannibalism) in the profundal habitat.

152

153   **Material and methods**

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155   *Study area description and field sampling*

156   Tårnvatn and Skøvatn are subarctic lakes situated at 107 and 180 m, respectively, above sea

157   level at 69°N in northern Norway. They have surface areas of 3.2 and 6.2 km² and maximum

158   depths of 53 and 119 m, respectively. Both lakes are dimictic, oligotrophic, and are usually

159   icebound from December to May. The linear distance between the two water bodies is about

160   33 km. Tårnvatn has a very simple fish community, consisting entirely of land-locked Arctic

161   charr and brown trout (*Salmo trutta* L.). Skøvatn is an open system directly connected to sea

162   with a 14 km long unobstructed river and hosts mostly resident Arctic charr and brown trout,

163   but also small stocks of anadromous Arctic charr, brown trout, and Atlantic salmon (*Salmo*

164   *salar*). The Secchi disk transparency was measured to be approximately 8 and 10 m in

165   Tårnvatn and Skøvatn, respectively. The euphotic depth (<1% of surface light) was estimated

166   as two times the Secchi disk-depths and was standardized to 15 m in both lakes.

167   Fishing was conducted during the lake turnover period in late October 2016 in the

168   littoral (1.5 m high benthic nets, 0 – 10 m depth), profundal (1.5 m high benthic nets, 15 – 35

169   m depth), and pelagic habitats (6 m high floating nets set offshore above 35 m depth) using

170   multi-mesh gillnets 40 m long with mesh sizes from 10 to 45 mm (knot to knot) set overnight

171   (see details in Smalås et al., 2013). The number of multi-mesh benthic nets used to survey the

172   littoral and profundal habitats was respectively four and six in Tårnvatn, and six and four in

173   Skøvatn. Two multi-mesh floating nets were set out in the pelagic zone in Tårnvatn, whereas,

174   in Skøvatn, the pelagic zone was omitted from the sampling due to unfavourable weather

conditions. Additionally, standard sized nets having only a single mesh size (6, 8, 10, 12, 20, 25, 30, 40 mm) were used to increase sample sizes of all morphs in both lakes. The habitat use of the different Arctic charr morphs was assessed based on catch per unit effort (CPUE expressed as number of fish caught per 100 m^2 multi-mesh gill-net per night) in the different habitats.

All Arctic charr were classified into different morph groups according to their external morphology (e.g., head and body shape and colour). The morphological characterization of the different morphs was based on criteria developed from previous studies of polymorphic charr in northern Norway (Klemetsen et al., 1997; Skoglund et al., 2015; Saltykova et al., 2017). In Tårnvatn, individuals were sorted into three distinct morphs (LO, PB, and PP), and in Skøvatn, into two morphs (LO and PB) (see Appendix Figs. 1, 2). The LO-morph adult fish had typical Arctic charr breeding coloration with a red-orange abdomen, a generally silvered dorsal area, and paired fins edged in white. The head, mouth, and eyes were relatively small compared to the body size. Juvenile fish generally displayed parr marks along the lateral sides of the body. The PB-morph had a small and deep body, with a relatively large head and a blunt snout, and round, big eyes. The colouration of the PB-morphs differed between the two lakes. In Tårnvatn, the mature PB-morph charr had a pale yellow-brown coloration with a brass hue, usually with very pale parr marks. In contrast, the PB-morph in Skøvatn had clear parr marks and a more silvery body colour. The PP-morph in Tårnvatn had a slender elongated body shape, a robust, large, pointed head with sharp teeth on the palate and the tongue. The head, caudal fin, and back were very dark, with shades of grey and black. The abdomen and the flanks were generally opaque orange in colour, with white bordered paired fins similar to the LO-morph.

Genetic analyses

200   To establish the extent of genetic divergence among the morphs in Tårnvatn and Skøvatn, a

201   small sample of gill-lamella was cut out from each fish and stored in 96 % ethanol. DNA was

202   extracted using an E-Z96 Tissue DNA Kit (OMEGA Bio-tek®) following manufacturer

203   instructions. A total of 133 individuals were included in the genetic analysis (Table 1). Eleven

204   microsatellite loci were amplified in two multiplex polymerase chain reactions (PCR) using

205   forward labelled primers (Appendix Table 1). The PCRs consisted of 1.25 µl QIAGEN®

206   Multiplex PCR Master Mix, 0.25 µl primer mix (multiplex panel Sal_Mp1 or 2), 0.5 µl water,

207   and 5-10 ng template DNA. The general PCR profile for all multiplex reactions was: 95°C for

208   15 min followed by 25 cycles of 94°C for 30 s, Ta for 3 mins, and 72°C for 1 min, with a final

209   60°C extension for 30 min, where Ta was 60ºC and 55ºC for Sal_Mp1 and 2, respectively. The

210   analysis included 3 % blank and 3 % replicate samples, which were blank or matched to the

211   original samples, respectively. The PCR products were separated on an ABI 3130XL

212   Automated Genetic Analyzer (Applied Biosystems) using LIZ500 as an internal standard, and

213   the alleles were scored using the GeneMapper 3.7 software (Applied Biosystems). Each

214   genotype was automatically binned in predefined allelic bins by the GeneMapper software

215   and verified by visual inspection.

216   Departures from Hardy-Weinberg equilibrium (HWE) among loci within populations

217   and among populations, and linkage disequilibrium (LD) among loci within populations were

218   estimated using GENEPOP 4.0 (Rousset, 2007). All pair-wise estimates were corrected using

219   Bonferroni corrections (Rice, 1989). The locus Sco204 was removed from the subsequent

220   analysis as it was consistently linked with Sco218 across all populations, and with Sco220 in

221   TvPP and SvLO, and with SMM22 in SvLO. Hence, all subsequent estimates were based on

222   variation at 10 microsatellite loci. Summary statistics for each locus per population were

223   estimated in GenAlEx 6.5 (Peakall & Smouse, 2006) (Appendix Table 2).

224   The genetic divergence between morphs within lakes was estimated by F_{ST} (Weir &

225   Cockerham, 1984) and tested for statistical significance using 10,000 bootstraps in ARLEQUIN

226   3.5.1.2 (Excoffier & Lischer, 2010). Divergence among morphs within lakes was inferred using

227   Bayesian clustering as implemented in STRUCTURE 2.3.4 (Pritchard et al., 2000; Hubisz et al.,

228   2009). The most likely number of populations (K) and their admixture (q) within each lake

229   was estimated using a model assuming admixture and correlated allele frequencies. The

230   LOCPRIOR option was used to assist the clustering as recommended by the software

231   documentation in situations with weak genetic divergence among populations in the dataset.

232   The model was tested with 50,000 - 150,000 burn-ins and Markov chain Monte Carlo (MCMC)

233   replicates from 100,000 to 300,000. The optimal condition considering computational time

234   versus model convergence was found to be 100,000 burn-ins and 200,000 MCMCs. The

235   analysis was repeated 10 times for each K and the most likely K per lake was estimated by

236   assessing the mean LnP(K) and ΔK as implemented in STRUCTURE HARVESTER (Earl &

237   vonHoldt, 2012).

238

239   *Diet composition*

240   Stomachs were removed and stored in 70% ethanol. The number of empty stomachs was low

241   in both lakes (19.1% and 6.6% in Tårnvatn and Skøvatn, respectively). Prey items were

242   identified and sorted to the lowest practical taxonomic groups, and their contribution to the

243   total stomach fullness was evaluated (0-100%) following Amundsen (1995). A total of 12

244   different prey types were identified in the 180 stomachs analysed for both lakes (see

245   Appendix Table 4 for details). Rarefaction curves indicated that sample sizes in this study

246   produced a good approximation of the diet diversity for the different morphs (Appendix Fig.

247   3). The different prey types were divided into five categories: zooplankton (limnetic

248   cladocerans and copepods), littoral benthos (gastropods, larvae of stoneflies, caddisflies, and

249   fish eggs), *Gammarus lacustris* (littoral amphipod), profundal benthos (chironomid larvae,

250 *Pisidium* sp. mussels and *Acanthocyclops* sp. benthic copepods), and fish (Arctic charr). The

251 proportion of each prey type in the diet was estimated as percent prey abundance following

252 Amundsen et al. (1996). Dietary niche overlap between the different Arctic charr morphs was

253 quantified using Schoener's (1970) similarity index. To visualize the diet of individual Arctic

254 charr in the two lakes, a non-metric multidimensional scaling analysis (NMDS) based on the

255 Bray-Curtis index of similarity was computed using relative prey abundance. The analysis was

256 executed using the vegan package (Oksanen et al., 2013) in R version 3.3.1. (R Core Team,

257 2016). For the NMDS analysis, the LO- and PP-morph individuals were divided in two size

258 groups to explore possible ontogenetic diet shifts. In the LO-morph, the division of small (<16

259 cm) and large (>16 cm) individuals was based on the onset of maturation sizes for the LO-

260 morph observed, 17 cm and 16 cm, respectively for Tårnvatn and Skøvatn (Kjær, 2018). The

261 size-group division was also compared with that reported for earlier studies of polymorphic

262 Arctic charr populations in the same region (Amundsen et al., 2008; Knudsen et al., 2016a)

263 that contrasted the trophic niche of adult small-sized profundal morphs with juveniles of the

264 upper-water (LO) morph. The threshold size for the PP-morph in Tårnvatn was set at 20 cm

265 based on the piscivorous diet shift size reported for the PP-morph in Skogsfjordvatn

266 (Knudsen et al., 2016b).

267

268 *Parasite communities*

269 Past diet was inferred from trophically transmitted parasites in a subset of Arctic charr from

270 each morph. Trophically transmitted parasites reside in specific prey types, and are ingested

271 together with the prey. These parasites can live in the Arctic charr host for months or years

272 (depending of the parasite life expectancy, Table 4) and act as tracers of long-term feeding

273 patterns (Knudsen et al., 1996; Knudsen et al., 2008). For the purposes of this study,

274 particularly relevant parasites were transmitted to Arctic charr by the amphipod *G. lacustris*

275 (the cestode *Cyathocephalus truncatus*), insect larvae (the trematodes *Crepidostomum* spp.

276 and *Phyllodistomum umblae*) and different species of pelagic copepods (the cestodes

277 *Eubothrium salvelini*, *Proteocephalus* sp., and *Dibothriocephalus* spp.) (Knudsen, 1995;

278 Knudsen et al., 1997, 2007, 2014; Jonsson & Jonsson, 2001; Siwertsson et al., 2016). All

279 parasite species are in the adult stage in the Arctic charr except for larval *Dibothriocephalus*

280 spp. (former *Diphyllobothrium* spp., see Waeschenbach et al., 2017). Prevalence (i.e.

281 proportion of individuals infected in a host morph) and abundance (i.e. average number of

282 parasites in host fish from a given morph) were calculated for each parasite species following

283 Bush et al. (1997). Rarefaction curves indicated that sample sizes in this study produced a

284 good approximation of the parasite diversity for the different morphs (Appendix Fig. 4).

285 Individual species richness of trophically transmitted parasites is related to the diet niche

286 width, since utilization of a larger range of different prey types is associated with higher

287 infection risks from a multitude of food transmitted parasites. Thus, differences in individual

288 parasite species richness between morphs were tested using non-parametric Mann-Whitney

289 U tests to account for non-normality. Differences between morphs in the abundance of single

290 parasite species were tested using generalized linear models (GLMs), specifying Poisson

291 distributions typically used for count data. Whenever pairwise tests were performed, a

292 Bonferroni correction was applied (Rice, 1989) such that for all tests when comparing

293 morphs within the two lakes (four pairwise comparisons) a P-value < 0.0125 was considered

294 statistically significant.

295

296 *Stable isotope analysis*

297 For stable isotope analyses a muscle tissue sample from each fish was cut from the dorsal area

298 posterior to the dorsal fin and above the lateral line and immediately frozen. Littoral

299 zoobenthos (*G. lacustris*, insect larvae, and snails) and pelagic zooplankton samples from both

300 lakes were collected and used to explore baseline differences in stable isotope values between

301 the major lake habitats (Fig. 6). Zooplankton sampling from the whole water column was

302 carried out using a plankton net (diameter 26 cm, mesh size 90 μm) hauled three times

303 vertically from a depth of 15 m to the surface. Benthic littoral macroinvertebrates were

304 sampled using a benthos hand square net. Both zooplankton and littoral benthos samples

305 were immediately frozen. Littoral benthos samples were sorted into *G. lacustris*, Megaloptera,

306 Ephemeroptera, Trichoptera, Plecoptera, Chironomidae, and molluscs. Only the soft body

307 tissue of molluscs was prepared for analyses. Samples were dried at 60°C for 24 hours,

308 homogenised using mortar and pestle, and weighed (0.3 ± 0.05 mg) into tin capsules. The

309 analyses were performed at the University of Waterloo, Canada, on a Delta Plus Continuous

310 Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled

311 to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an

312 analytical precision of ± 0.2 ‰ ($\delta^{13}C$) and ± 0.3 ‰ ($\delta^{15}N$). Analytical accuracy was

313 established through the repeat analysis of internal laboratory standards calibrated against

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

315 Analytical precision was established by the repeat analysis of one in ten samples. All results

316 were reported in conventional delta notation (δ) relative to international standard Vienna

317 Peedee Belemnite, VPBD, for $\delta^{13}C$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}N$ (Mariotti,

318 1983). As tissue samples had C:N values < 4, lipids were neither extracted nor corrected for

319 using mathematical models (Jardine et al., 2013). Due to the non-normality of stable isotope

320 values, Kruskal-Wallis and pair-wise Mann-Whitney U tests were used to statistically test for

321 differences in $\delta^{13}C$ and $\delta^{15}N$ values among the morphs within the two lakes. Whenever

322 pairwise tests were performed, a Bonferroni correction was applied (Rice, 1989).

323 **Results**

Genetic analyses

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The five samples of morphs were all in HWE (Table 1), and none of the loci displayed

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deviation from HWE after Bonferroni corrections. Ten of 225 pairwise comparisons showed

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significant LD, but only one (OMM1105 vs SMM22 in SvLO) of 225 remained significant after

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Bonferroni corrections. The number of alleles per morph varied from one (Sco215 in SvLO,

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TvLO, TvPP, and TvPB) to 19 in SvLO (Sco218) (Appendix Table 2). The genetic variation

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(expected heterozygosity, H_e) of the Arctic charr morphs was higher in Skøvatn (H_e = 0.729-

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0.739) than in Tårnvatn (H_e = 0.593-0.693), and none of the morph samples displayed

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significant inbreeding signatures (Table 1).

333

In Tårnvatn, the LO-morph displayed F_{ST}s of 0.134 (P<0.001) and 0.121 (P<0.001)

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compared to the PB and PP-morphs, respectively (Table 2). The genetic divergence between

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the PP- and PB- morphs was lower (F_{ST} = 0.042), but significant (P<0.001). The STRUCTURE

336

analysis identified K = 2 or K = 3 clusters in Tårnvatn (Fig. 1a, b). In both cases, the LO-morph

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formed its own cluster, where PB- and PP-morphs grouped together for K =2 (Fig. 1a). The

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groupings revealed by STRUCTURE followed the visual phenotypic classification of

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individuals completed in the field. The two morphs in Skøvatn showed a significant genetic

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divergence with an F_{ST} value of 0.041 (Table 2). The result was supported by the STRUCTURE

341

analysis, which clustered the morphs in two separate clusters according to their phenotype

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(Fig. 1c).

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344

Habitat and diet

345

In Tårnvatn, the LO-morph (mean length ± S.D.: 20.6 ± 5.6 cm) was caught in all three

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habitats, but at highest densities in littoral and pelagic areas (CPUE: 16.7 and 31.7,

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respectively; Table 3). The diet of the LO-morph in Tårnvatn included chiefly zooplankton

348

(exclusively cladocerans) and some littoral benthos, with *G. lacustris* as the main benthic prey (Fig. 2, Appendix Table 4). All individuals of the PB- and PP- morphs were caught at depths > 15 m in Tårnvatn (Table 3). The PB-morph (mean length ± S.D.: 14.0 ± 5.6 cm) largely exploited profundal benthic prey groups, mostly chironomid larvae (Fig. 2, Appendix Table 4). The PP-morph (mean length ± S.D.: 26.0 ± 11.8 cm) in Tårnvatn exhibited a broad diet including profundal benthos, *G. lacustris*, and a notable (18 %) proportion of small-sized Arctic charr (Fig. 2, Appendix Table 4). The PP-morph had a high dietary similarity when compared with the PB-morph in the same lake (54 %). In contrast, the diet of the LO- and PP-, and the LO- and PB- morphs in Tårnvatn were distinct (26 % and 29 % diet overlap, respectively).

In Skøvatn, all the LO-morph individuals were caught in littoral habitat (Table 3). The LO-morph (mean length ± S.D.: 18.5 ± 6.5 cm) had a wide diet comprised of zooplankton (cladocerans) and littoral benthos, with *G. lacustris* constituting the largest single benthic prey item (47%) (Fig. 2, Appendix Table 4). In contrast, the PB-morph in Skøvatn (mean length ± S.D.: 9.5 ± 1.7 cm) had highest CPUE in the profundal habitat (Table 3) and fed mainly on zooplankton, particularly on the cladocerans *Bosmina* and *Daphnia* spp. (Fig. 2, Appendix Table 4). The dietary overlap between the two morphs in Skøvatn was 49 % (Schoener's similarity index).

When comparing the analogous morphs from the two lakes, the LO-morphs had the highest diet niche similarity of 53 % (Fig. 2). Nevertheless, the two LO-morphs had different ontogenetic dietary patterns in the two lakes (Fig. 3). In Tårnvatn, there was little difference in diet between small (< 16 cm) and large (> 16 cm) individuals. In contrast, in Skøvatn there was a clear shift from a zooplanktivorous feeding behaviour in the small fish towards a mixed diet composed of benthic prey and zooplankton in the large individuals (Fig. 3). The two small-sized deep-water PB-morphs, on the other hand, revealed contrasting feeding strategies

374   in the two lakes with low dietary similarity (29 %) (Figs. 2, 3, Appendix Table 4). The PB-

375   morph in Skøvatn had the highest dietary similarity with the small LO-morphs from both

376   lakes, feeding mainly on cladocerans (Fig. 3). The two PB-morphs showed no signs of

377   ontogenetic dietary changes. The Tårnvatn PP-morph diet was distinctly different between

378   small and large size-classes (Fig. 3). The small PP-morph (< 20 cm) almost exclusively

379   consumed profundal benthos and had diet similar to the PB-morph in Tårnvatn (Fig. 3). The

380   larger individuals (> 20 cm) relied predominantly on *G. lacustris* and fish, having the most

381   distinctive diet of all the studied morphs (Fig. 3).

382

383   *Parasite communities*

384   In total, six different food-borne parasite genera were recorded in Arctic charr in both lakes,

385   including four cestodes (pelagically-transmitted *Dibothriocephalus* spp., *E. salvelini*, and

386   *Proteocephalus* sp., and littoral *C. truncatus*) and two littoral benthic-transmitted trematodes

387   (*Crepidostomum* spp. and *P. umblae*). No nematodes were found in any fish. All morphs in the

388   two lakes harboured all six trophically transmitted parasites taxa.

389   In Tårnvatn, the PB-morph had the lowest parasite richness (mean number ± S.E.: 2.0 ±

390   0.2; Mann-Whitney U test: P < 0.001) (Fig. 4), whereas there was no significant difference in

391   the number of parasite species between the LO- (3.7 ± 0.2) and PP- (3.4 ± 0.2) morphs (Mann-

392   Whitney U test: P = 0.378) (Fig. 4). The prevalence in the LO- and PP- morphs was high for

393   most of the parasite species, especially for *Dibothriocephalus* spp., *Crepidostomum* spp. and *E.*

394   *salvelini* (Table 4). In contrast, the PB-morph had a low prevalence for all parasites, except for

395   *Crepidostomum* spp., which infected a high proportion of individuals (Table 4). In Tårnvatn,

396   the PP-morph had the highest total parasite abundance (mean number ± S.E.: 129.1 ± 37.7),

397   followed by the LO-morph (67.9 ± 16.2), whereas the PB-morph had the lowest (35.3 ± 16.2).

398   The LO-morph had the highest abundance of *P. umblae* and *Proteocephalus* sp. (GLMs: P <

399 0.001), whereas the PP-morph had the highest infection of *C. truncatus*, *Crepidostomum* spp.,

400 *E. salvelini*, and *Dibothriocephalus* spp. (GLMs: P < 0.001) (Fig. 5). In contrast, the PB-morph

401 had low abundance for most of the parasites, with the lowest infections of *Proteocephalus* sp.,

402 *E. salvelini* and *Dibothriocephalus* spp. (GLMs: P < 0.001) (Fig. 5).

403   The LO-morph in Skøvatn had the highest parasite richness, harbouring up to six

404 different parasites genera in one individual (mean number ± S.E.: 3.3 ± 0.3 S.E.) (Mann-

405 Whitney U test: P < 0.001) (Fig. 4). In contrast, a lower parasite richness (1.5 ± 0.2) with a

406 maximum of four parasite taxa was recorded in the PB-morph (Fig. 4). In Skøvatn, the LO-

407 morph in general had a high parasite prevalence, with the greatest occurrence of

408 *Dibothriocephalus* spp. and *Crepidostomum* spp. (Table 4). In contrast, the PB-morph showed a

409 lower prevalence than the LO-morph for all parasites except for *Dibothriocephalus* spp., which

410 was more frequently present in the PB-morph (Table 4). The LO-morph had a higher parasite

411 abundance (mean number ± S.E.: 118.7 ± 33.6) compared to the PB-morph (67.9 ± 17.4). In

412 Skøvatn, the highest mean abundance in the LO-morph was found for *Crepidostomum* spp.,

413 followed by *Dibothriocephalus* spp., *C. truncatus*, and *P. umblae*, whereas the infection rate was

414 very low for *E. salvelini* and *Proteocephalus* sp. (Fig. 5). On the other hand, the PB-morph

415 generally had low infection levels, with significantly lower abundance for all parasites species

416 (GLM: P < 0.001), except *Proteocephalus* sp. (GLM: P = 0.791) and *Dibothriocephalus* spp. (Fig.

417 5). The abundance of *Dibothriocephalus* spp. was higher in the PB-morph than in the LO-

418 morph (GLM: P < 0.001) (Fig. 5).

419   Parasite species richness was similar across lakes between the two LO- morphs (Mann-

420 Whitney U test: P = 0.231) and PB-morphs (Mann-Whitney U test: P = 0.061) (Fig. 4).

421 Nevertheless, the LO- and PB- morphs in Tårnvatn had a lower total parasite abundance than

422 the corresponding morphs in Skøvatn. A similar pattern of prevalence for the LO-morphs was

423 observed in the two lakes, with the majority of fish infected by *Dibothriocephalus* spp. and

424   *Crepidostomum* spp. However, the LO-morph in Tårnvatn showed a greater occurrence of

425   pelagically-transmitted parasites, but a lower prevalence of the *G. lacustris*-transmitted *C.*

426   *truncatus* (Table 4). The PB-morph in Tårnvatn had a higher prevalence than the PB-morph in

427   Skøvatn for all parasites, except for *Dibothriocephalus* spp., which was more prevalent in

428   Skøvatn (Table 4). The two LO-morphs had significant differences in the abundance of all

429   parasites species (GLM: P < 0.001) except for *Dibothriocephalus* spp. (GLM: P = 0.700) (Fig. 5).

430   The PB-morph in Skøvatn had a higher abundance of *Dibothriocephalus* spp. than the PB-

431   morph in Tårnvatn (GLM: P < 0.001), but lower abundances of *C. truncatus*, *Crepidostomum*

432   spp. and *Proteocephalus* sp. (GLM: P < 0.001) (Fig. 5). The abundances of the other parasite

433   species were not significantly different (GLMs: P > 0.060) (Fig. 5).

434

435   *Stable isotope analysis*

436   There were significant differences in the stable isotope values among the morphs in Tårnvatn

437   (Kruskal-Wallis tests: P < 0.001). The PB- and PP-morphs had similar $\delta^{13}C$ mean values

438   (Mann-Whitney U test: P = 0.015), but higher compared to the sympatric LO-morph (Mann-

439   Whitney U tests: P ≤ 0.0125) (Fig. 6a; Appendix Table 4). The LO-morph had the lowest $\delta^{15}N$

440   values (Mann-Whitney U test: P < 0.001) in comparison to the other morphs, which were

441   similar (Mann-Whitney U test: P = 0.339) (Fig. 6a; Appendix Table 4).

442   In Skøvatn, the LO-morph had significantly higher $\delta^{13}C$ values than the sympatric PB-

443   morph (Mann-Whitney U test: P < 0.005), but lower $\delta^{15}N$ (Mann-Whitney U test: P < 0.001)

444   (Fig. 6b; Appendix Table 4).

445

446

447   **Discussion**

448

449   As predicted, all the sympatric Arctic charr morphs in the two lakes were genetically

450   differentiated. In both lakes, genetic differences were evident between the LO- and the co-

451   occurring profundal morphs as has been noted in earlier studies of analogous morph-pairs in

452   Fjellfrøsvatn and Skogsfjordvatn (Præbel et al., 2016; Simonsen et al., 2017). The genetic

453   differentiation was weaker, but still highly significant between the PB- and PP-morphs in

454   Tårnvatn. Collectively, the results show that an intra-lacustrine divergence of the Arctic charr

455   morphs is ongoing in both lakes and that all morphs can be genetically discriminated. There

456   was also a clear separation in the trophic niches (habitat and diet) between the upper-water

457   column (LO-morph) and profundal morphs within each lake. Niche segregation among the

458   Arctic charr morphs in both Tårnvatn and Skøvatn was also supported by the differences

459   between the temporally integrated trophic tracers (stable isotopes and parasites), that

460   pointed to the persistence of trophic niche segregation over the ecologically relevant time

461   scales of months (stable isotopes) or years (parasites). The resulting weight of evidence

462   provided by the genetic differences, the clear trophic segregation, and life-history patterns

463   (Kjær, 2018) strongly suggests the existence of two distinct deep-water morphs in Tårnvatn

464   and one in Skøvatn. However, while the LO-morphs appeared to have similar trophic niches in

465   both lakes, the PB-morphs were strikingly different. Although similar in appearance, life

466   histories (Kjær, 2018), and habitat preference, the PB-morph in Skøvatn was feeding mainly

467   on zooplankton while in Tårnvatn they were feeding on profundal benthos like in other lakes

468   in the region (Klemetsen, 2010; Knudsen et al., 2016a).

469   The parallelisms in habitat choice and trophic tracers between the LO-morphs from the

470   two study lakes were similar to patterns observed in earlier studies of morphs from the same

471   geographic region (Knudsen et al., 2016a; Siwertsson et al., 2016). The LO-morphs in

472   Tårnvatn and Skøvatn had a generalist trophic niche, with a mixed diet obtained from the

473   littoral-pelagic habitat, a rich parasite community, and a relative broad isotopic range, similar

to the niches described earlier for polymorphic populations in Fjellfrøsvatn and
Skogsfjordvatn (Knudsen et al., 2011, 2016a; Amundsen et. al, 2008; Siwertsson et al., 2016).
Such a broad dietary niche typically occurs also in monomorphic Arctic charr populations in
the sub-Arctic region (Johnson, 1980; Amundsen, 1995; Klemetsen et al., 2003). In addition,
the LO-morphs in Tårnvatn and Skøvatn share similar life history traits, particularly fast
growth, similar maximal lengths (29-34 cm) and maturation at between 19-22 cm (Kjær,
2018). Thus, it seems reasonable to consider the LO-morph in both lakes to be analogous.

The adult PP-morph, in Tårnvatn only, displayed partly piscivorous foraging behaviour
as hypothesised. A noticeable proportion (32.3 %, Appendix Table 5) of individuals with
empty stomachs was observed in the PP-morph as is commonly reported for piscivorous fish
(Arrington et al., 2002; Vinson & Angradi, 2011; Amundsen, 2016). The PP-morph had a clear
ontogenetic shift in foraging habits moving from a dominance of profundal benthic prey in the
small young individuals to a diet composed by fish and *G. lacustris* in the large older fish, with
$\delta^{15}N$ values in the 12-14 ‰ (Fig. 6a) consistent with heavy reliance on fish as prey (Guiguer
et al., 2002). Similar to the PP-morph in Skogsfjordvatn, the piscivorous diet shift occurred at
an approximate length of 20 cm coincident with when individuals reached a size sufficient to
prey on other fish (Knudsen et al., 2016b). As with other piscivorous Arctic charr morphs and
in contrast to the sympatric LO- and PB-morph, the PP-morph had high accumulation of
Dibothriocephalus spp. and *E. salvelini* (Frandsen et al., 1989; Siwertsson et al., 2016). These
parasite species have the capacity to re-establish in piscivorous hosts (Curtis, 1984; Frandsen
et al., 1989; Henriksen et al., 2016) and typically accumulate with age in the infected fish
(Svenning, 1993; Knudsen & Klemetsen, 1994; Hammar, 2000; Knudsen et al., 2004). The PP-
morph also had high infections of littoral-prey-transmitted *Crepidostomum* spp., reflective of
the feeding on *G. lacustris* (Knudsen et al., 2008, 2014). Stable isotope values of the PP-morph
further supported the contention of a mixed piscivorous-littoral benthivorous niche.

499   Individuals with high δ15N and low δ13C values likely fed on conspecifics in the profundal zone

500   (Jardine et al. 2003; Knudsen et al. 2016 a,b), whereas individuals with low δ15N and high δ13C

501   had values typical of littoral dwelling fish (Vander Zanden & Rasmussen, 1999; Jardine et al.

502   2003). Analogous to Skogsfjordvatn (Smalås et al., 2013), Kjær (2018) has shown that the PB-

503   and PP-morphs have contrasting life history strategies, with the PB-morph having a

504   significantly slower growth rate and earlier sexual maturation (approximately 5 years) than

505   the PP-morph (approximately 7 years). Arctic charr is the only suitable fish prey that is

506   available for the PP-morph in Tårnvatn, as only Arctic charr and brown trout are present.

507   Juvenile brown trout do not commonly reside in the profundal zone, preferring to occupy

508   streams or lacustrine littoral areas (L'Abée-Lund et al., 1992; Amundsen & Knudsen, 2009;

509   Eloranta et al., 2013). Thus, the piscivorous PP-morph can only feed on small conspecifics. In

510   contrast the PP-morph in Skogsfjordvatn is able to feed on both Arctic charr and three-spined

511   sticklebacks (Knudsen et al., 2016b). Cannibalism in Arctic charr has been widely reported

512   both as an outcome of ontogenetic niche shifts in large fish and as an occurrence of

513   specialized piscivorous morphs (Amundsen, 1994, 2016; Svenning & Borgstrøm, 1995;

514   Klemetsen et al., 2003; Knudsen et al., 2016b). Nevertheless, piscivorous charr morphs

515   generally reside in shallow-water habitats (Sandlund et al., 1992; Adams et al., 1998).

516   Skogsfjordvatn is one of the few described cases with a piscivorous morph residing entirely in

517   the profundal zone (Smalås et al., 2013; Skoglund et al., 2015; Knudsen et al., 2016b) (but see

518   Power et al., 2009). The presence of abundant and suitable prey fishes, i.e. the PB-morph and

519   juvenile LO-morph in deep-waters, is probably a key factor in the local evolution of the PP-

520   morph in Tårnvatn, as in Skogsfjordvatn, where a process of niche expansion in response to

521   ecological opportunity has been suggested (Skoglund et al., 2015; Knudsen et al., 2016b).

522   In contrast to the LO-morphs, the PB-morphs from the two lakes showed both parallel

523   and non-parallel patterns in trophic niche utilisation. As predicted, the PB-morph in Tårnvatn

524   evidenced dietary specialization based on its stomach contents, preying profundal soft-

525   bottom benthic invertebrates as has been reported for the PB-morphs in Fjellfrøsvatn and

526   Skogsfjordvatn (Knudsen et al., 2006, 2016a). Specialization was also supported by the low

527   species richness and infection rates (prevalence and abundance) of all examined parasites

528   typical of the small-sized profundal morphs (Knudsen et al., 1997; Siwertsson et al., 2016).

529   Stable isotope values, on the other hand, suggested utilisation of a wide spectrum of prey

530   resources along the littoral-pelagic-profundal habitat axis (Vander Zanden & Rasmussen,

531   1999). Thus, while dietary specialization as reflected in stomach contents and parasites is

532   occurring, prey sourcing appears to occur from both littoral and profundal habitats. Deep-

533   water morphs with a similar benthic feeding strategy have also been reported from Siberia

534   (Alekseev & Pichugin, 1998), Canada (O'Connell et al., 2005), central Europe (Brenner, 1980),

535   and Scandinavia (Hindar & Jonsson, 1982) (reviewed by Klemetsen, 2010), and with similar

536   dichotomous use of deeper and shallower littoral habitats having been observed in the

537   generally deep-water morph found in Gander Lake, Newfoundland (O'Connell et al., 2005;

538   Power et al., 2012).

539   When compared to the benthivorous PB-morph in Tårnvatn and other lakes, the deep-

540   water morph in Skøvatn used a different trophic niche despite identical life-history patterns,

541   e.g. reduced growth and early maturation (Klemetsen et al., 1997; Smalås et al., 2013; Kjær,

542   2018). The zooplankton dominated diet of the Skøvatn deep-water morph was reflected by

543   high infections of copepods-transmitted *Dibothriocephalus* spp.. However, the lower $\delta^{13}C$ and

544   higher $\delta^{15}N$ values when compared to the sympatric LO-morph, also suggested a greater

545   reliance on profundal benthic resources (Hayden et al., 2014; Knudsen et al., 2016 a,b). Since

546   stable isotopes reflect diet over an approximate 3-4 month period before capture (Post, 2002;

547   Buchheister & Latour, 2010; Knudsen et al., 2014), the Skøvatn deep-water morph likely

548   consumed profundal prey during the early ice-free season when a high density of chironomid

549 pupae emerge from the bottom substrate and zooplankton biomass is low (Klemetsen et al.,

550 1992; Dahl-Hansen et al., 1994; Primicerio & Klemetsen, 1999; Amundsen et al., 2008;

551 Mousavi & Amundsen, 2012; Kahilainen et al., 2016). The parasite community composition

552 supported these findings as the small-sized profundal morph had low species richness and

553 very low abundance for most parasites (except for *Dibothriocephalus* spp.), as typical of other

554 deep-water morphs (Siwertsson et al., 2016). Since the Skøvatn profundal morph deviates

555 clearly in its diet (zooplanktivory) from the benthivore PB-morph in Tårnvatn and elsewhere

556 (Klemetsen, 2010; Knudsen et al., 2016a), and potentially spawns in deep-waters (Kjær,

557 2018), it is probably best denoted as a distinct small-sized deep-water planktivorous morph

558 and is hereinafter referred using the acronym PZ ("Profundal spawning Zooplanktivore").

559   The PZ-morph in Skøvatn is the first documented case of a potential profundal

560 planktivorous Arctic charr morph in northern Norway. Similar partly zooplanktivorous small-

561 sized deep-water morphs have been described e.g. in southern Norway (Telnes & Sægrov,

562 2004), in central Europe (Brenner, 1980), and in Transbaikalia (Alekseyev et al., 2002;

563 Samusenok et al., 2006). Compared to zooplanktivory, one of the main advantages of a deep-

564 water benthic diet may be lower parasite infections (Siwertsson et al., 2016) and associated

565 higher fitness. A second advantage may be the year-round availability of prey items. The

566 observed deviation from the more common deep-water benthivorous diet may be related to

567 low productivity in the profundal zone, with the scarcity of deep-water benthic biomass

568 inducing a shift to zooplanktivory. Overall, zooplankton is a generally more abundant

569 resource in the late summer and autumn than profundal benthic invertebrates in many

570 northern lakes (Primicerio & Klemetsen, 1999; Mousavi, 2002; Hayden et al., 2014; Kahilainen

571 et al., 2016). As described for some monomorphic Arctic charr populations (e.g. Eloranta et al.,

572 2010; Hayden et al., 2014; Kahilainen et al., 2016), the PZ-morph may alternate between

573   benthivorous behaviour in winter and spring and zooplanktivory in autumn when

574   zooplankton preys are abundant.

575   　　　While parallelism in trophic ecology was evident in the LO-morphs from the two study

576   lakes, the two small-sized profundal morphs differed substantially in their diets. The PB-

577   morph in Tårnvatn along with the PB-morphs in Fjellfrøsvatn and Skogsfjordvatn are well-

578   documented cases of parallel evolution in Arctic charr, given their similarity in habitat

579   preferences, diet, parasite fauna, morphology and life history (Knudsen et al., 2016a;

580   Siwertsson et al., 2016; Saltykova et al., 2017). Parallel patterns are usually considered as

581   evidence of similar selection pressures favouring the development of similar adaptive traits

582   among fishes in postglacial lakes (Schluter, 2001; Sigursteinsdóttir & Kristjánsson, 2005;

583   Kaeuffer et al., 2012; Præbel et al., 2013; Siwertsson et al., 2016; Saltykova et al., 2017; Häkli

584   et al., 2018). Thus, the discrepancy in the dietary niche of the PB- and PZ-morphs in Tårnvatn

585   and Skøvatn, respectively, is of great interest to improve the knowledge of evolutionary

586   mechanisms driving adaptations.

587   　　　The observed divergent patterns in local trophic adaptations (i.e. non-parallelism) of

588   the PB- and the PZ-morphs of Arctic charr might have been promoted by differences in

589   ecological and environmental factors occurring between the two lake systems (Kaeuffer et al.,

590   2012; Kristjánsson et al., 2012; Siwertsson et al., 2013b; Saltykova et al., 2017). Such

591   dissimilarities could be e.g. in bathymetric conditions, productivity, and fish community, as

592   Skøvatn (unlike Tårnvatn) hosts anadromous fish including Arctic charr, brown trout, and

593   Atlantic salmon (Smalås & Henriksen, 2016). Alternatively, different adaptive responses may

594   have been induced by the standing genetic variation of the colonizing ancestral populations

595   (West-Eberhard, 1989) or as an outcome of genetic drift (Sigursteinsdóttir & Kristjánsson,

596   2005; Kaeuffer et al., 2012; Saltykova et al., 2017).

597   To conclude, the combined data describing habitat use, stomach contents, parasites,

598   and tissue stable isotopes indicated clear trophic resource segregation between the

599   genetically differentiated polymorphic Arctic charr morphs in Tårnvatn and Skøvatn. Results

600   as described here are consistent with the occurrence of an ongoing process of trophic

601   divergence, the consequences of which are reflected in a concomitant separation among the

602   morphs in life history traits such as growth and maturation (Kjær, 2018). Furthermore, there

603   were clear patterns of genetic divergence among the morph-pairs within these two lakes.

604   Within the study lakes a clear parallelism in habitat choice, external morphology, and life

605   history was found for the upper-water omnivore LO-morphs and the small-sized deep-water

606   morphs, suggesting the effect of parallel evolutionary processes along the depth gradient

607   across lakes. Contrary to our hypotheses, there was an evident difference in dietary niches

608   between the small-sized profundal benthivorous PB-morph and the zooplanktivorous PZ-

609   morph indicating partially different evolutionary histories. Finally, the data describe for the

610   first time in northern Norway the occurrence of the PZ-morph and the exclusively

611   cannibalistic PP-morph from the deep-water environment. This study demonstrates how

612   evolution can produce diverse outcomes, even among systems with apparently similar

613   environmental and ecological conditions.

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FIGURE LEGENDS

Fig. 1. Genetic structuring of Arctic charr morphs from Tårnvatn (A, B) and Skøvatn (C) as

inferred by STRUCTURE. In the STRUCTURE analysis, black lines separate individuals from

different morphs (as determined in the field) and each individual is represented by a thin

vertical line, which is partitioned into K-coloured segments representing the individual's

estimated membership fractions in K clusters. For each lake, the mean values of lnP(K) and ΔK

are given in Appendix Table 3.

Fig. 2. Percent abundances of the major prey groups found in the stomach contents of the

different Arctic charr morphs from Tårnvatn and Skøvatn (October 2016). For a more detailed

diet description, see Appendix Table 4.

Fig. 3. Diet composition of individual Arctic charr of the various morphs in Tårnvatn and

Skøvatn depicted by non-metrical multidimensional scaling (NMDS; stress = 0.12). LOts =

small LO-morph (< 16 cm) in Tårnvatn (n=15), LOtl = large LO-morph (> 16 cm) in Tårnvatn

(n=33), PBt = PB-morph in Tårnvatn (n=24), PPts = small PP-morph (< 20 cm) in Tårnvatn

(n=10), PPtl = large PP-morph (> 20 cm) in Tårnvatn (n=11), LOss = small LO-morph (< 16

cm) in Skøvatn (n=19), LOsl = large LO-morph in Skøvatn (> 16 cm) (n=37), PBs = PB-morph

in Skøvatn (n=35). The acronyms indicate average values for each morph in the two lakes.

Fig. 4. Distribution (%) of the number of parasite species per host in the different morphs of

Arctic charr in Tårnvatn (*left*) and Skøvatn (*right*).

1045   **Fig. 5.** Mean abundance (± S.E) of the six parasites genera found in the different Arctic charr

1046   morphs from Tårnvatn and Skøvatn (October 2016). The first three parasite species are

1047   associated with littoral feeding, the last three with pelagic.

1048

1049   **Fig. 6.** Stable isotope biplots displaying the $\delta^{13}C$ and $\delta^{15}N$ values of dorsal muscle tissue

1050   samples of Arctic charr caught in Tårnvatn and Skøvatn in October 2016. The LO-morphs are

1051   represented by *white dots* (n = 34, 29, respectively), the PB-morphs (*n* = 25, 25, respectively)

1052   by *grey triangles*, and the PP-morphs in Tårnvatn (*n* = 32) by *black diamonds*. Mean values (±

1053   SD) of pelagic (*black squares*) and littoral (*white squares*) prey sampled in June 2017 are also

1054   given.

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1056

1057   Fig. 1.
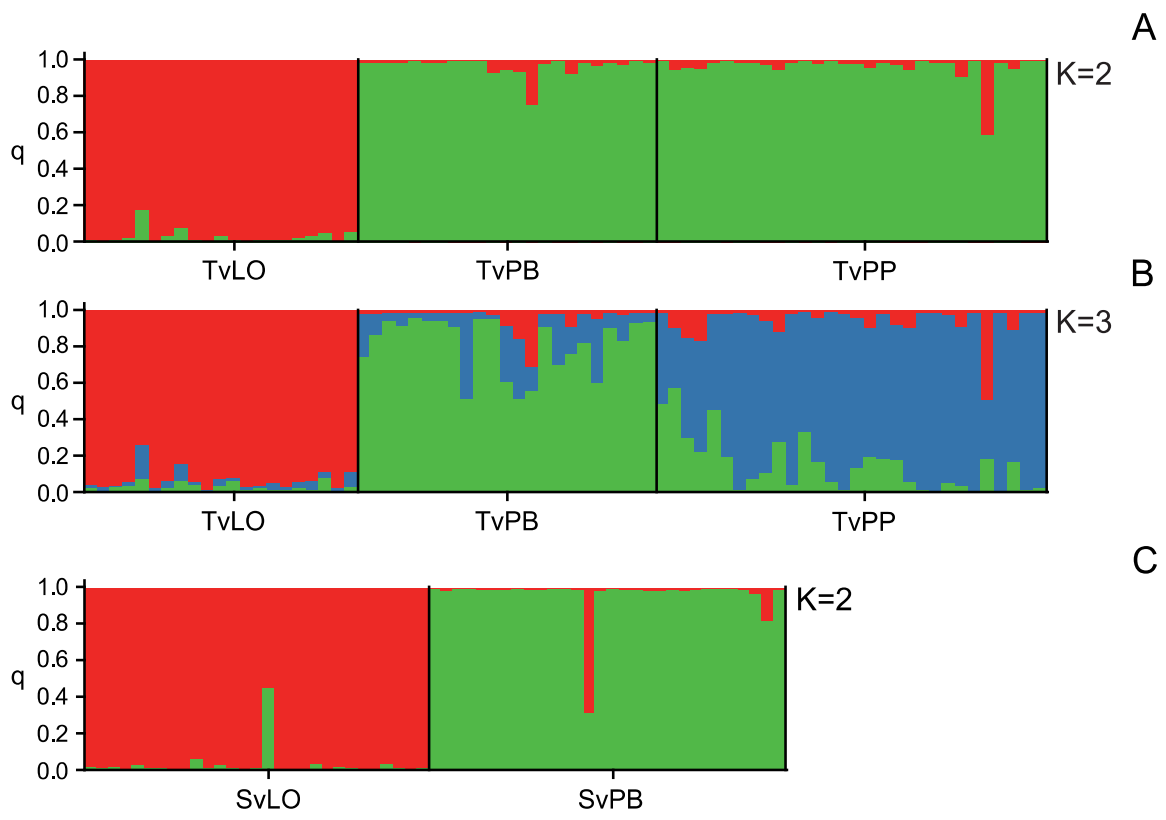
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1059

1060 Fig. 2.

Prey abundance (%)
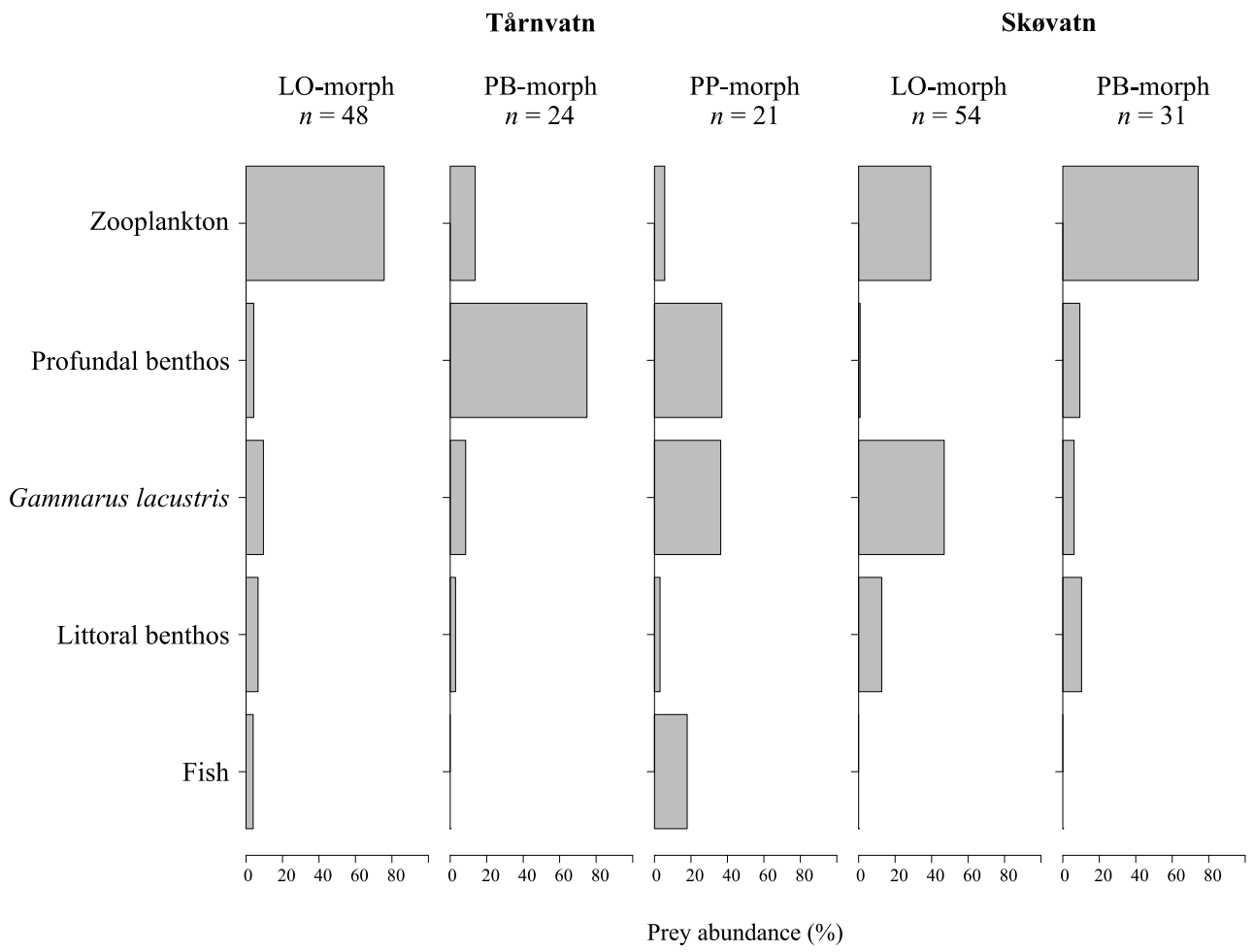
1061

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1063   Fig. 3.

1064

1065

1066   Fig. 4.

1067   Number of parasite species

1068

1069   Fig. 5.

Tårnvatn   **Skøvatn**

LO-morph   PB-morph   PP-morph   LO-morph   PB-morph
 n = 53   n = 25   n = 29   n = 35   n = 32

Littoral
  C. truncatus
  P. umblae
  Crepidostomum spp.

Pelagic
  Proteocephalus sp.
  E. salvelini
  Diphyllobothrium spp.

0 20 40 60 80   0 20 40 60 80   0 20 40 60 80   0 20 40 60 80   0 20 40 60 80

Mean abundance

1070

1071

Fig.6.

a) **Tårnvatn**

b) **Skøvatn**

$\delta^{13}C$ (‰)

1073
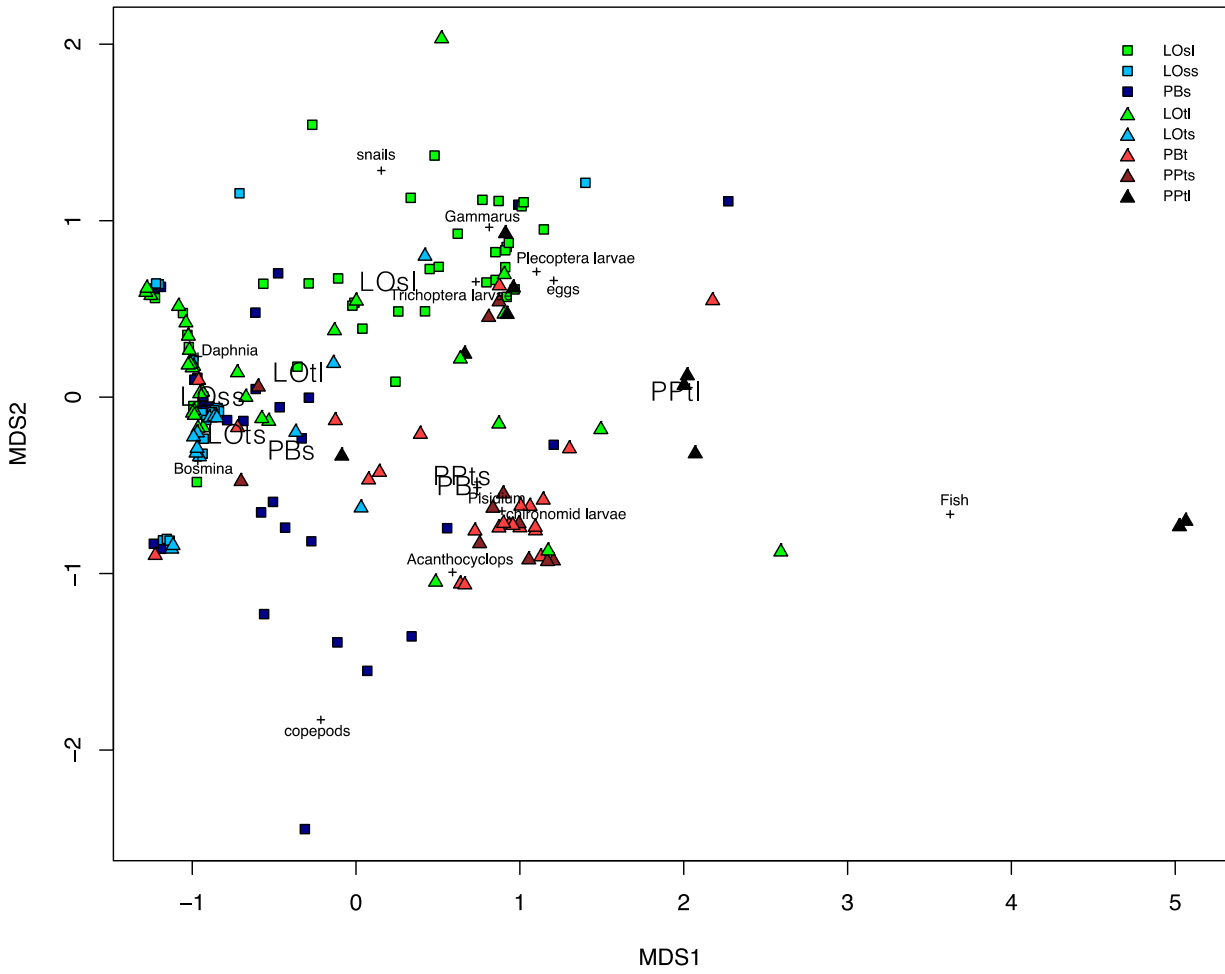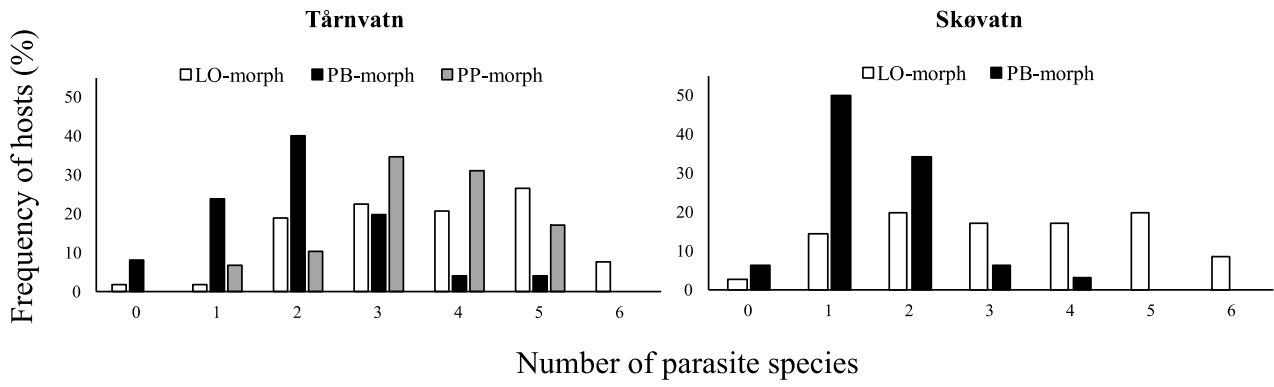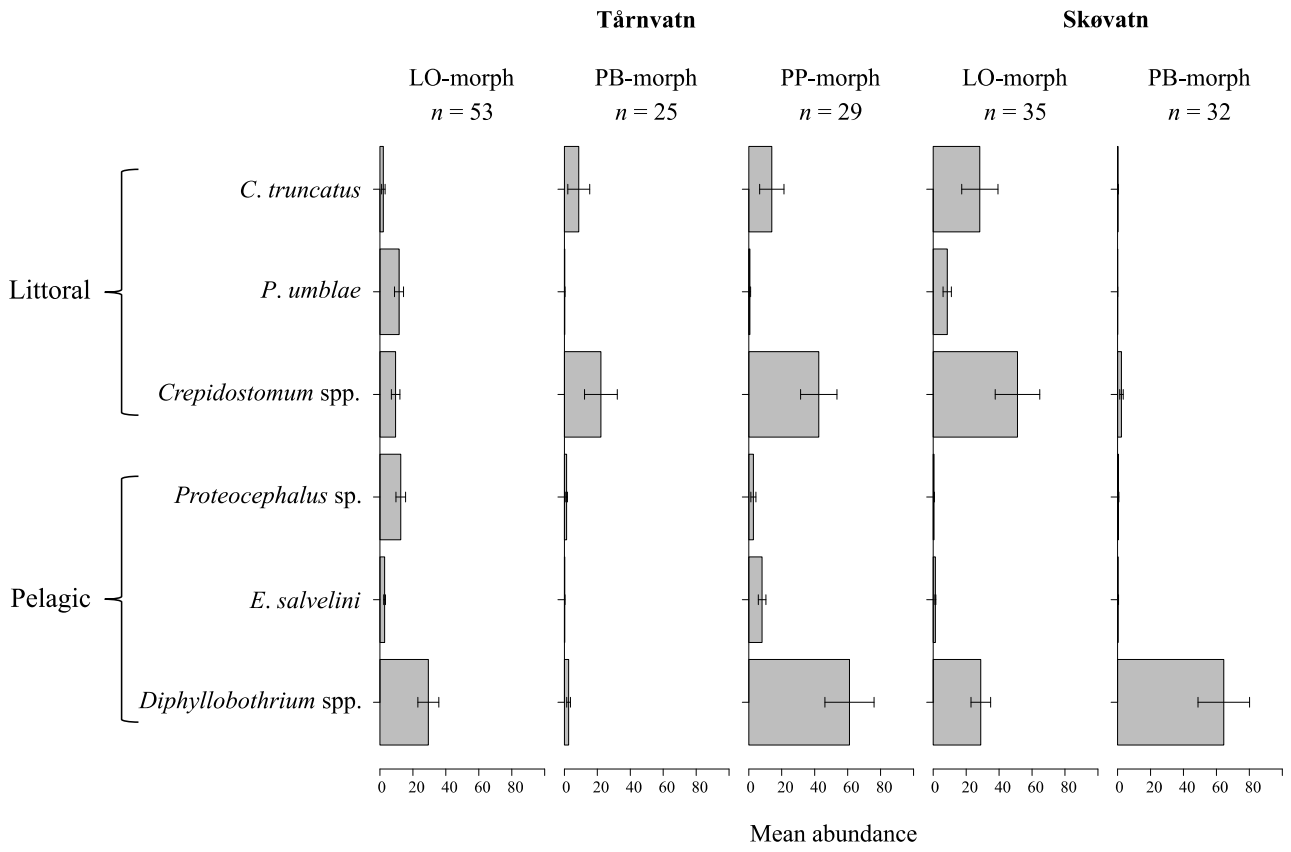
1074 Table 1. Samples of Arctic charr included in the genetic analysis. Number of morphs and

1075 individuals (n) and their code (Morph) in the genetic analysis are given. Expected

1076 heterozygosity (H_e) and F_{IS} is also given per morph. None of the F_{IS} values displayed
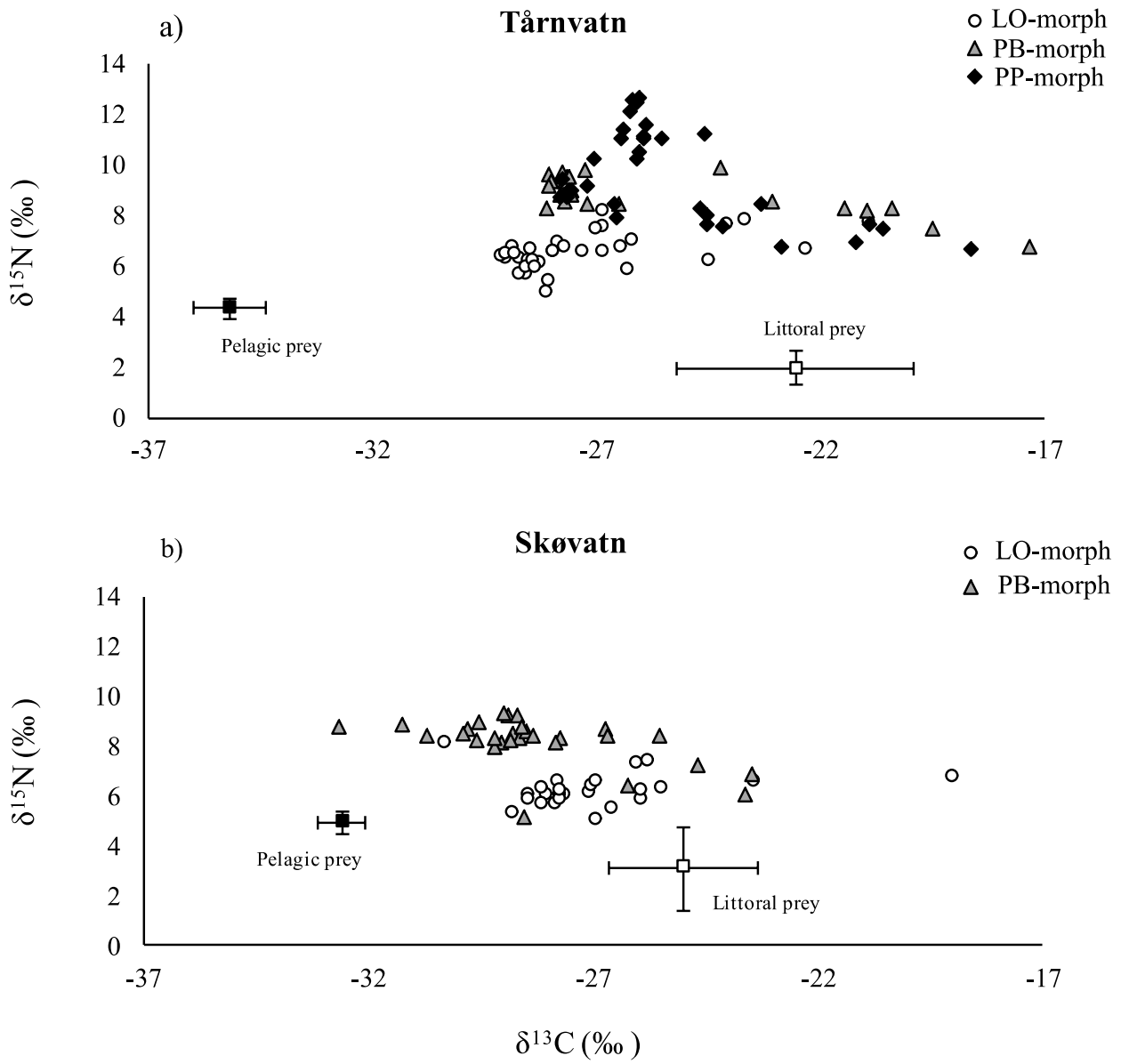
1077 significant deviations from Hardy-Weinberg expectations.

1078

Lake	Morph	Code	n	H_e	F_{IS}
Tårnvatn (Tv)	LO	TvLO	21	0.638	-0.058
	PB	TvPB	23	0.693	-0.030
	PP	TvPP	30	0.593	-0.012
Skøvatn (Sv)	LO	SvLO	29	0.737	0.052
	PB	SvPB	30	0.729	0.021

1079

1080

1081 Table 2. Genetic divergence among morphs within and across lakes as inferred by F_{ST} (below

1082 diagonal) and the associated p-values (above diagonal). *** = p < 0.001. Sv = Skøvatn, Tv =

1083 Tårnvatn.

1084

	SvLO	SvPB	TvLO	TvPB	TvPP
SvLO	-	***	***	***	***
SvPB	0.041	-	***	***	***
TvLO	0.129	0.120	-	***	***
TvPB	0.097	0.088	0.134	-	***
TvPP	0.159	0.133	0.121	0.042	-

1085

Table 3. Catch per unit effort (CPUE = number of fish caught per 100 m² multi-mesh gill-nets per night) of the Artic charr morphs in the different habitats in Tårnvatn and Skøvatn. The number (*n*) of fish caught in the different habitat is also provided.

Habitat	Tårnvatn			Skøvatn	
	LO	PB	PP	LO	PB
Littoral	16.7 (*n* = 40)	0.0	0.0	24.0 (*n* = 43)	1.0 (*n* = 2)
Profundal	9.4 (*n* = 18)	10.0 (*n* = 13)	7.8 (*n* = 18)	0.0	3.0 (*n* = 8)
Pelagic	31.7 (*n* = 39)	0.0	0.0	-	-

Table 4. Prevalence (%) of the different parasite taxa found in the Arctic charr morphs in Tårnvatn and Skøvatn. The life expectancy in the host and the intermediate host's habitat (L = Littoral and P = Pelagic) are also signed.

Parasite species	Life expectancy in the host	Intermediate-host's habitat	Tårnvatn			Skøvatn	
			LO *n*=53	PB *n*=25	PP *n*=29	LO *n*=35	PB *n*=32
C. truncatus	months	L	22.6	16.0	37.9	54.3	12.5
P. umblae	1-2 years	L	54.7	8.0	17.2	42.9	3.1
Crepidostomum spp.	1-2 years	L	73.6	76.0	89.7	77.1	31.3
Proteocephalus sp.	1-2 years	P	69.8	40.0	41.4	25.7	9.4
E. salvelini	1-2 years	P	67.9	20.0	75.9	48.6	9.4
Dibothriocephalus spp.	many years	P	79.2	40.0	79.3	77.1	84.4

1097   Appendix Table 1. Details of the 11 microsatellite loci used to elucidate genetic divergence

1098   between Arctic charr morphs in Tårnvatn and Skøvatn in northern Norway. Details shown are

1099   the locus, the multiplex panel in which the locus was amplified (Panel), the label of the

1100   forward primer for the subsequent discrimination of alleles (Flp), the observed range of allele

1101   sizes (Size), the concentration of each primer pair in the multiplex (Conc), and the reference

1102   to the source of the loci (Ref).

Locus	Panel	Flp	Size	Conc (µM)	Ref
OMM1105	Sal_Mp1	6FAM	120-200	0.20	Rexroad et al., 2002
Sco220	Sal_Mp1	6FAM	323-343	0.10	Dehaan & Ardren, 2005
SalP61SFU	Sal_Mp1	PET	100-160	0.30	McGowan et al., 2004
Sco212	Sal_Mp1	PET	281-317	0.20	Dehaan & Ardren, 2005
SalF56SFU	Sal_Mp1	NED	180-220	0.10	McGowan et al., 2004
Sco218	Sal_Mp1	VIC	165-195	0.10	Dehaan & Ardren, 2005
SMM17	Sal_Mp2	VIC	100-130	0.04	Crane et al., 2004
Sco204	Sal_Mp2	6FAM	121-140	0.15	Dehaan & Ardren, 2005
SalJ81SFU	Sal_Mp2	NED	100-160	0.20	McGowan et al., 2004
Sco215	Sal_MP2	NED	285-293	0.10	Dehaan & Ardren, 2005
SMM22	Sal_Mp2	PET	160-260	0.05	Crane et al., 2004

1103

1104   Appendix Table 2. Summary statistics of the 10 microsatellites used to analyse the Arctic

1105   charr morphs. N = number of individuals analysed per locus. Na = number of alleles per locus

1106   per morph. H_o and H_e = observed and expected heterozygosity. respectively. per locus and

1107   morph. The locus Sco204 was excluded from the analysis as it was consistently linked with

1108   Sco218 across all populations, and with Sco220 in TvPP and SvLO, and with SMM22 in SvLO.

1109

Pop		OMM1105	SalF56SFU	SalP61SFU	Sco212	Sco218	Sco220	SMM17	SMM22	SalJ81SFU	Sco215
SvLO	N	29	29	28	28	29	29	29	29	29	29
	Na	12	5	8	16	19	18	6	12	5	1
	Ho	0.724	0.552	0.714	0.786	0.966	0.931	0.828	0.897	0.621	0.000
	He	0.769	0.559	0.772	0.890	0.920	0.922	0.743	0.884	0.719	0.000
SvPB	N	30	30	30	30	30	30	30	30	30	30
	Na	16	6	8	14	18	20	6	15	8	2
	Ho	0.900	0.567	0.667	0.800	0.900	0.833	0.767	0.867	0.767	0.033
	He	0.883	0.526	0.679	0.871	0.911	0.932	0.723	0.898	0.735	0.033
TvLO	N	21	21	21	20	21	21	21	21	21	21
	Na	6	8	5	9	15	13	3	14	3	1
	Ho	0.762	0.810	0.762	0.950	0.952	0.952	0.333	1.000	0.238	0.000
	He	0.635	0.790	0.702	0.851	0.896	0.904	0.291	0.884	0.291	0.000
	F	-0.200	-0.024	-0.086	-0.116	-0.063	-0.054	-0.144	-0.131	0.183	
TvPP	N	30	30	30	30	30	30	30	30	30	30
	Na	6	6	4	12	10	12	4	9	4	1
	Ho	0.767	0.567	0.533	0.933	0.767	0.767	0.200	0.800	0.667	0.000
	He	0.729	0.569	0.523	0.864	0.778	0.821	0.186	0.746	0.613	0.000
	F	-0.051	0.005	-0.020	-0.080	0.015	0.066	-0.075	-0.073	-0.088	
TvPB	N	23	23	23	23	23	23	23	23	23	23
	Na	9	5	8	14	16	16	5	16	8	1
	Ho	0.913	0.565	0.739	0.870	1.000	0.870	0.522	0.826	0.826	0.000
	He	0.827	0.457	0.647	0.861	0.891	0.922	0.550	0.867	0.757	0.000
	F	-0.104	-0.236	-0.143	-0.010	-0.122	0.056	0.052	0.047	-0.091	

1110

1111

1112   Appendix Table 3. Summary statistics of the STRUCTURE analyses of Arctic charr morphs

1113   from Skøvatn (A) and Tårnvatn (B). The most likely number of clusters, K, was 2 and 2 or 3 in

1114   Skøvatn and Tårnvatn, respectively.

1115

A	# K	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	ΔK
	1	-2397.4300	1.0144	-	-	-
	2	-2312.2333	5.6092	85.196667	225.123333	40.134952
	3	-2452.1600	45.5256	-139.926667	138.906667	3.051175
	4	-2453.1800	27.6125	-1.020000	-	-

B	# K	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	|Ln''(K)|	ΔK
	1	-2593.9300	0.7273	-	-	-
	2	-2432.1100	0.4254	161.820000	163.410000	384.095609
	3	-2433.7000	4.6685	-1.590000	69.670000	14.923386
	4	-2504.9600	10.9355	-71.260000	24.050000	2.199262
	5	-2552.1700	12.1306	-47.210000	-	-

1116

1117

1118 Appendix Table 4. The diet (percent prey abundance ± S.E) and $\delta^{13}C$ and $\delta^{15}N$ isotope values

1119 (mean ± S.D. and range) of the Arctic charr morphs from Tårnvatn and Skøvatn captured in

1120 October 2016.

Prey groups:	Tårnvatn			Skøvatn	
	LO-morph (*n* = 48)	PB-morph (*n* = 24)	PP-morph (*n* = 21)	LO-morph (*n* = 56)	PB-morph (*n* = 31)
Bosmina	26.1 ± 2.5	4.6 ± 0.9	4.6 ± 2.0	16.8 ± 2.7	32.7 ± 4.0
Daphnia	49.7 ± 3.8	9.1 ± 2.2	1.1 ± 0.3	22.8 ± 2.8	38.5 ± 4.7
Copepods (Cyclopoid and Calanoid)	0	0	0	0	3.0 ± 0.6
Acanthocyclops	0	6.5 ± 1.5	0.6 ± 0.2	0	0.5 ± 0.2
Gammarus lacustris	9.5 ± 1.7	8.4 ± 3.7	36.4 ± 7.2	46.9 ± 5.1	6.2 ± 3.2
Snails (*Radix* and *Planorbidae*)	0.2 ± 0.1	0	0.5 ± 0.2	5.7	0
Pisidium clams	0.1 ± 0.0	11.3 ± 2.0	2.2 ± 0.6	0.2 ± 0.1	6.6 ± 2.5
Chironomid larvae (profundal)	4.1 ± 1.0	57.2 ± 4.8	34.2 ± 5.0	0.6 ± 0.1	2.2 ± 0.6
Trichoptera larvae	4.6 ± 1.8	2.0 ± 0.6	1.7 ± 0.6	0.8 ± 0.5	0
Plecoptera larvae	0	0	0	2.3 ± 0.7	10.3 ± 2.8
Fish eggs	1.7 ± 0.7	0.9 ± 0.4	0.8 ± 0.3	3.9 ± 1.8	0
Fish (Arctic charr)	3.9 ± 1.3	0	18.0 ± 5.6	0	0
$\delta^{13}C$	-27.3 ± 2.0	-25.8 ± 3.3	-25.3 ± 2.3	-26.9 ± 2.1	-28.3 ± 2.1
	(-29.2 to -21.0)	(-28.1 to -17.4)	(-27.8 to -18.7)	(-30.3 to -19.1)	(-32.7 to -23.5)
$\delta^{15}N$	6.5 ± 0.7	8.8 ± 0.8	9.5 ± 1.8	6.2 ± 0.7	8.1 ± 1.0
	(5.0 to 8.1)	(6.8 to 9.9)	(6.7 to 12.6)	(5.0 to 8.1)	(5.1 to 9.3)

1121

1122   Appendix Table 5. For each Arctic charr morph, number of individuals (n), number of empty

1123   stomachs, and proportion of fish with empty stomachs are given.

1124

Lake	Morph	n	Empty stomachs	Proportion
Tårnvatn	LO	58	10	17.2 %
	PB	26	2	7.7 &
	PP	31	10	32.3 %
Skøvatn	LO	56	2	3.6 %
	PB	35	4	11.4 %

1125

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1127   Appendix Figure 1. Photographs of the three morphs in Tårnvatn. Uppermost individual LO-

1128   morph, middle PB-morph, bottom PP-morph.
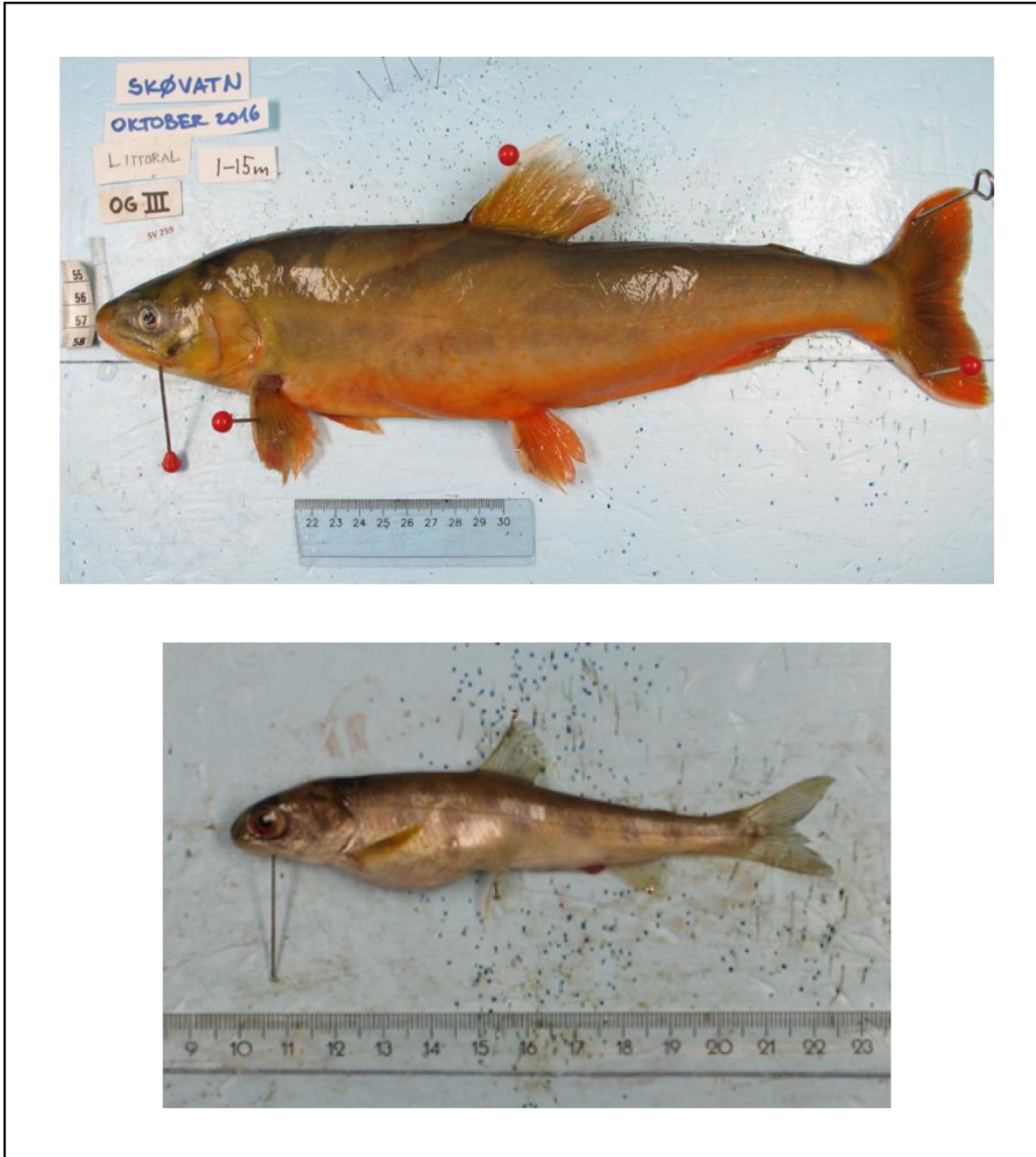
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1132   Appendix Figure 2. Photographs of the two morphs in Skøvatn. Uppermost individual LO-
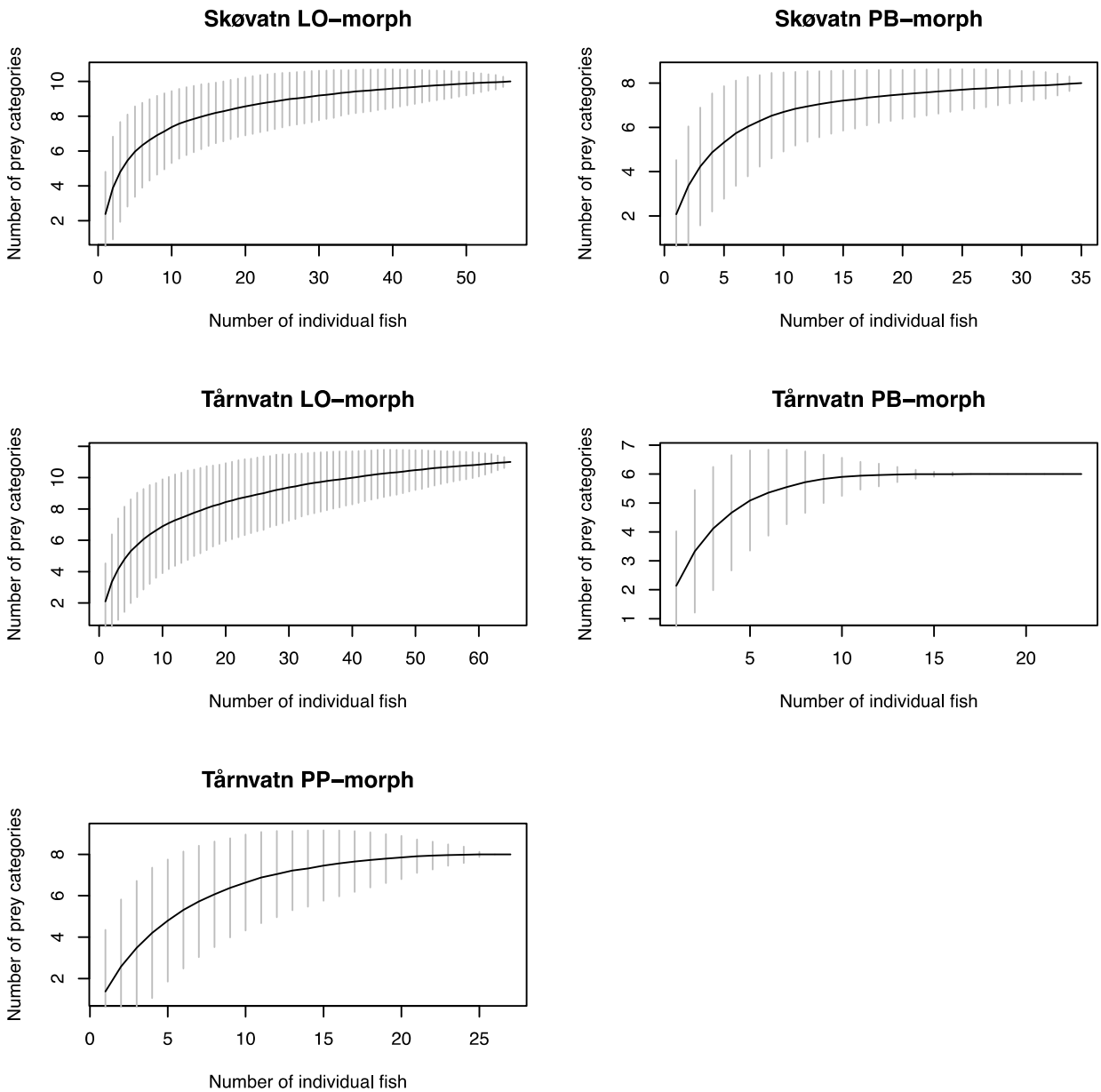
1133   morph, lower PB-morph.

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1138 Appendix Figure 3. Rarefaction curves for prey types in the LO-, PB, and PP-morph from

1139 Skøvatn and Tårnvatn. Average (black line) and 95% Confidence Interval (grey bars) of the

1140 expected number of prey types for a given number of sampled fish individuals were obtained

1141 from 1000 random permutations of the data (Gotelli & Colwell, 2001).

1142

1143

1144 Appendix Figure 4. Rarefaction curves for parasite species in the LO-, PB, and PP-morph from

1145 Skøvatn and Tårnvatn. Average (black line) and 95% Confidence Interval (grey bars) of the

1146 expected number of parasite species for a given number of sampled fish individuals were

1147 obtained from 1000 random permutations of the data (Gotelli & Colwell, 2001).

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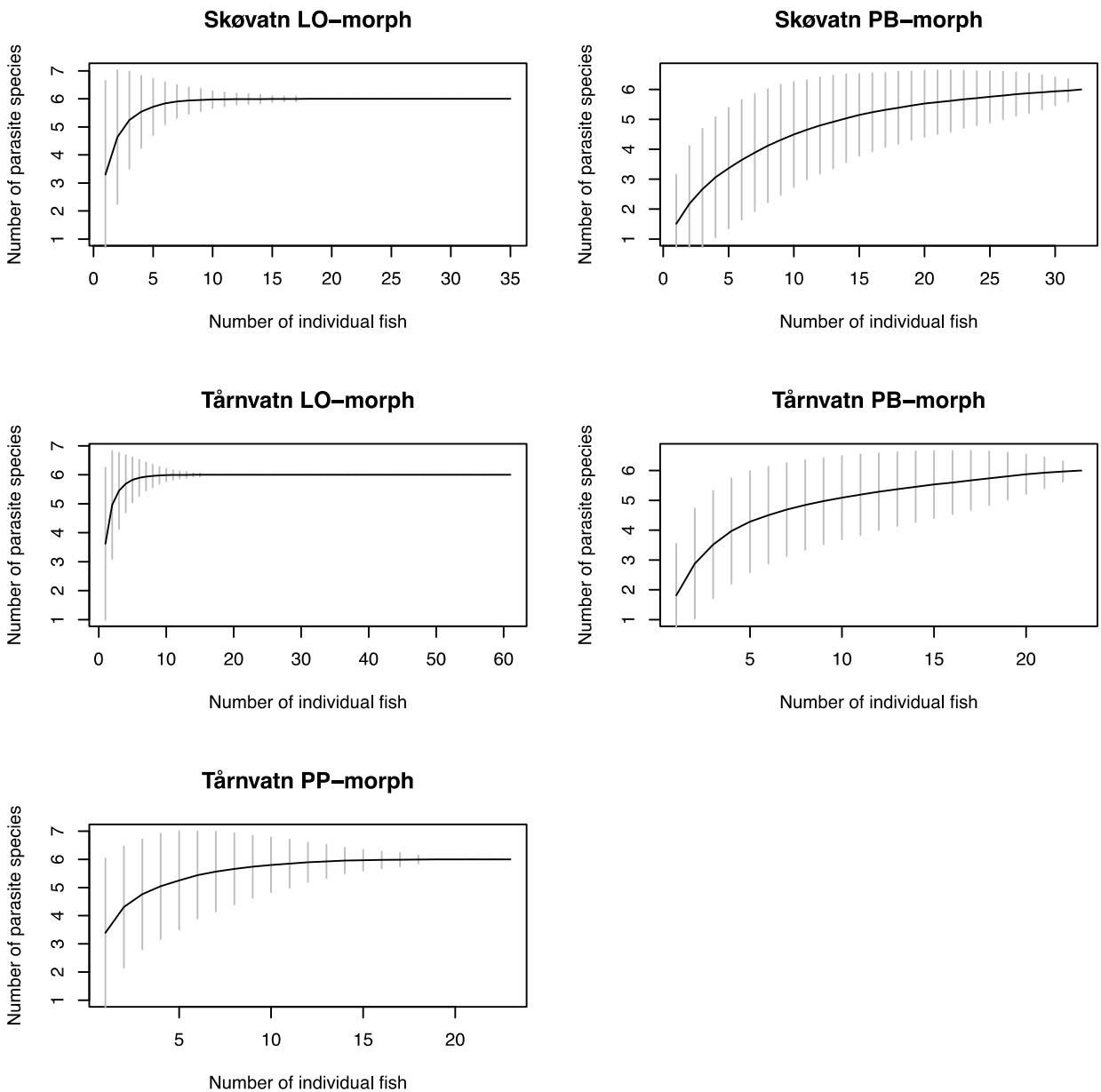
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