



Contrasting patterns in trophic niche evolution of polymorphic Arctic charr populations in two subarctic Norwegian lakes

Paolo Moccetti · Anna Siwertsson · Runar Kjær · Per-Arne Amundsen · Kim Præbel · Ana-Maria Peris Tamayo · Michael Power · Rune Knudsen

Received: 31 August 2018 / Revised: 31 March 2019 / Accepted: 7 May 2019 / Published online: 15 May 2019
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Abstract Parallelism in trophic niches of polymorphic populations of Arctic charr was investigated in two similar subarctic lakes, Tårnvatn and Skøvatn, in northern Norway. Analysis of eleven microsatellite loci confirmed, respectively, the existence of three and two genetically differentiated morphs. Three methods were used to describe their trophic niches: habitat choice and stomach contents for the recent feeding behaviour, and trophically transmitted parasites and stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) as proxies for the

longer term trophic niche differences. The results showed a distinct segregation in trophic resource utilization of the different morphs. Tårnvatn has three morphs: a littoral omnivorous (LO), a small-sized profundal benthivorous (PB), and a large-sized profundal piscivorous (PP). In contrast, a novel Arctic charr morph was discovered in Skøvatn: a small-sized profundal zooplanktivorous-morph (PZ), which when compared to the sympatric LO-morph, had distinct stable isotope values and a contrasting parasite community. A parallelism in habitat choice and external morphology was found among the small-sized, deep-water morphs and between the upper-water, omnivorous LO-morphs in both lakes. There was a no parallel pattern in diet choice between the PB- and the PZ-morphs. These findings show how evolution can produce diverse outcomes, even among

Guest editors: C. E. Adams, C. R. Bronte, M. J. Hansen, R. Knudsen & M. Power / Charr Biology, Ecology and Management

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10750-019-3969-9>) contains supplementary material, which is available to authorized users.

P. Moccetti (✉) · A. Siwertsson · R. Kjær · P.-A. Amundsen · R. Knudsen
Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Langnes, P.O. Box 6050, 9037 Tromsø, Norway
e-mail: moccetti.paolo@gmail.com

K. Præbel · A.-M. P. Tamayo
Norwegian College of Fishery Science, UiT The Arctic University of Norway, Langnes, P.O. Box 6050, 9037 Tromsø, Norway

A.-M. P. Tamayo
Faculty of Applied Ecology, Agricultural sciences and Biotechnology, Inland Norway University of Applied Sciences, Campus Evenstad, 2418 Elverum, Norway

M. Power
Department of Biology, University of Waterloo, Waterloo, ON N2L 3G1, Canada

systems with apparently similar environmental and ecological conditions.

Keywords *Salvelinus alpinus* · Polymorphism · Genetic differences · Trophic niche divergence · Stomach contents · Stable isotope analyses · Trophically transmitted parasites

Introduction

A resource polymorphism is defined as the occurrence of distinct morphs specialized in different resource use within a single species (Skúlason & Smith, 1995). Polymorphic populations of several fish species have repeatedly been found in postglacial lakes, especially within the genera *Salvelinus*, *Gasterosteus*, and *Coregonus* (Skúlason & Smith, 1995; Skúlason et al., 1999; Amundsen et al., 2008; Klemetsen, 2013). Since polymorphisms are considered to be an important step in an ecologically induced speciation process (Wimberger, 1994; Gíslason et al., 1999; Snorrason & Skúlason, 2004; Amundsen et al., 2008; Siwertsson et al., 2013a), freshwater systems of recent origin are viewed as hotspots for investigating the function and role of ecological components in divergent evolution (Schluter, 1996; Snorrason & Skúlason, 2004; Klemetsen, 2010). Similar ecological niches and environments in many isolated postglacial lakes have resulted in parallel adaptations in the morphology, behaviour, physiology, and life-history traits of several fish species (Endler, 1986; Schluter, 2000), including Arctic charr, *Salvelinus alpinus* (L.) (Skúlason & Smith, 1995; Klemetsen, 2010), which is the target species of the present study.

The initial step in the evolutionary divergence of northern fishes has been suggested to be competition for discrete habitats and food resources, which allow fish to specialize and segregate in distinctive niches (Wimberger, 1994; Skúlason & Smith, 1995; Jonsson & Jonsson, 2001; Adams et al., 2003; Garduño-Paz & Adams, 2010). A repeatedly found pattern of trophic niche segregation in postglacial lakes occurs along the benthic-pelagic resource axis, with benthivorous morphs exploiting the littoral area, and planktivorous and/or piscivorous morphs residing in the pelagic zone (Wimberger, 1994; Skúlason & Smith, 1995; Schluter, 1996; Sigursteinsdóttir & Kristjánsson, 2005). The

degree of divergence within lakes varies considerably, with containing completely reproductively isolated morphs (populations) and other showing variable levels of reproductive isolation within a common species (Gíslason et al., 1999; Skúlason et al., 1999; Hendry et al., 2009; Klemetsen, 2010). The frequent incidents of parallel evolution observed in several fish taxa, such as e.g. Arctic charr and three-spined stickleback (*Gasterosteus aculeatus* L.), are considered strong evidence of ecologically induced divergence, as they are unlikely to arise solely by genetic drift or other nonecological mechanisms (Schluter & Nagel, 1995; Schluter, 1996, 2001; Nosil & Rundle, 2009; Kaeuffer et al., 2012; Saltykova et al., 2017).

Arctic charr is considered to be a highly variable and plastic species, showing a myriad of differences in coloration, morphology, ecology, and life history traits (Johnson, 1980; Skúlason et al., 1999; Alexander & Adams, 2000; Jonsson & Jonsson, 2001; Klemetsen, 2010). Polymorphic Arctic charr may represent two (e.g. Fjellfrøsvatn; Klemetsen et al., 1997), three (e.g. Loch Rannoch; Adams et al., 1998), and even four (e.g. Thingvallavatn; Sandlund et al., 1992) distinct morphs within a single lake (Smith & Skúlason, 1996; Jonsson & Jonsson, 2001; Klemetsen, 2010; Jacobs et al., 2018). The evolution of phenotypic and ecological divergence in Arctic charr has mediated the accumulation of genetic differences among the morphs both when occurring as allopatric and polymorphic sympatric morphs (e.g. Gomez-Uchida et al., 2008; Power et al., 2009; Præbel et al., 2016; Jacobs et al., 2018; O'Malley et al., 2019). Most Arctic charr morphs are segregated along the littoral-pelagic axis, but deep-water living Arctic charr morphs adapted to the profundal habitat have also been described in a few lakes (Klemetsen, 2010; Markevich & Esin, 2018). The present study addresses the trophic niche utilization of polymorphic Arctic charr populations in two subarctic lakes, with special emphasis on the trophic ecology of profundal-dwelling morphs.

Two well-studied examples of profundal Arctic charr morphs are those in lakes Fjellfrøsvatn and Skogsfjordvatn, northern Norway (Klemetsen et al., 1997; Knudsen et al., 2006, 2016a, b; Amundsen et al., 2008; Smalås et al., 2013). In both lakes, there are two distinct, replicated morphs: a littoral spawning omnivorous 'LO-morph' feeding on littoral macrobenthos and zooplankton, and a small-sized profundal spawning benthivorous 'PB-morph' that forages on soft-

bottom benthic invertebrates (Klemetsen et al., 1997; Smalås et al., 2013). Additionally, Skogsfjordvatn hosts a rare profundal spawning piscivorous ‘PP-morph’ that feeds mostly on conspecific Arctic charr and, to a lesser extent, on three-spined stickleback (Smalås et al., 2013; Knudsen et al., 2016b). Within each lake the different morphs are clearly segregated in habitat and diet, as reflected by their stable isotope values and parasite loads (e.g. Knudsen et al., 2016a, Siwertsson et al., 2016), and in life history strategies and morphology (e.g. Smalås et al., 2013; Skoglund et al., 2015). The different morphs were first classified on the basis of external morphological functional traits including: body and head shape, eye and mouth size, and coloration (Knudsen et al., 2007; Skoglund et al., 2015; Saltykova et al., 2017; Simonsen et al., 2017), and have subsequently been shown to be reproductively isolated (Klemetsen et al., 1997; Smalås et al., 2017) and genetically distinct based on microsatellite loci (Præbel et al., 2016; Simonsen et al., 2017).

Recent fish management surveys of additional northern Norwegian lakes have suggested that lakes Tårnvatn and Skøvatn, similarly harbour polymorphic Arctic charr (three and two putative morphs, respectively), with the varieties morphologically resembling those described from Skogsfjordvatn and Fjellfrøsvatn. These preliminary observations suggest that both Tårnvatn and Skøvatn harbour a normal growing LO-morph and potentially a small-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 putative PP-morph in Tårnvatn would exhibit a distinctive piscivorous feeding strategy, preying upon small-sized charr (i.e. cannibalism) in the profundal habitat.

Materials and methods

Study area description and field sampling

Tårnvatn and Skøvatn are subarctic lakes situated at 107 and 180 m, respectively, above sea level at 69°N in northern Norway. They have surface areas of 3.2 and 6.2 km² and maximum depths of 53 and 119 m, respectively. Both lakes are dimictic, oligotrophic, and are usually icebound from December to May. The linear distance between the two water bodies is about 33 km. Tårnvatn has a very simple fish community, consisting entirely of land-locked Arctic charr and brown trout (*Salmo trutta* L.). Skøvatn is an open system directly connected to sea with a 14-km-long unobstructed river and hosts mostly resident Arctic charr and brown trout, but also small stocks of

anadromous Arctic charr, brown trout, and Atlantic salmon (*Salmo salar*). The Secchi disk transparency was measured to be approximately 8 and 10 m in Tårnvatn and Skøvatn, respectively. The euphotic depth (< 1% of surface light) was estimated as two times the Secchi disk-depths and was standardized to 15 m in both lakes.

Fishing was conducted during the lake turnover period in late October 2016 in the littoral (1.5 m high benthic nets, 0–10 m depth), profundal (1.5 m high benthic nets, 15–35 m depth), and pelagic habitats (6 m high floating nets set offshore above 35 m depth) using multi-mesh gillnets 40 m long with mesh sizes from 10 to 45 mm (knot to knot) set overnight (see details in Smalås et al., 2013). The number of multi-mesh benthic nets used to survey the littoral and profundal habitats was, respectively, four and six in Tårnvatn, and six and four in Skøvatn. Two multi-mesh floating nets were set out in the pelagic zone in Tårnvatn, whereas, 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 m² 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

To establish the extent of genetic divergence among the morphs in Tårnvatn and Skøvatn, a small sample of gill-lamella was cut out from each fish and stored in 96% ethanol. DNA was extracted using an E-Z96 Tissue DNA Kit (OMEGA Bio-tek®) following manufacturer instructions. A total of 133 individuals were included in the genetic analysis (Table 1). Eleven microsatellite loci were amplified in two multiplex polymerase chain reactions (PCR) using forward labelled primers (Appendix Table 1). The PCRs consisted of 1.25 µL QIAGEN® Multiplex PCR Master Mix, 0.25 µL primer mix (multiplex panel Sal_Mp1 or 2), 0.5 µL water, and 5–10 ng template DNA. The general PCR profile for all multiplex reactions was: 95°C for 15 min followed by 25 cycles of 94°C for 30 s, Ta for 3 min, and 72°C for 1 min, with a final 60°C extension for 30 min, where Ta was 60°C and 55°C for Sal_Mp1 and 2, respectively. The analysis included 3% blank and 3% replicate samples,

Table 1 Samples of Arctic charr included in the genetic analysis

Lake	Morph	Code	<i>n</i>	<i>H_e</i>	<i>F_{IS}</i>
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

Number of morphs and individuals (*n*) and their code (Morph) in the genetic analysis are given. Expected heterozygosity (*H_e*) and *F_{IS}* is also given per morph. None of the *F_{IS}* values displayed significant deviations from Hardy–Weinberg expectations

which were blank or matched to the original samples, respectively. The PCR products were separated on an ABI 3130XL Automated Genetic Analyzer (Applied Biosystems) using LIZ500 as an internal standard, and the alleles were scored using the GeneMapper 3.7 software (Applied Biosystems). Each genotype was automatically binned in predefined allelic bins by the GeneMapper software and verified by visual inspection.

Departures from Hardy–Weinberg equilibrium (HWE) among loci within populations and among populations, and linkage disequilibrium (LD) among loci within populations were estimated using GENEPOP 4.0 (Rousset, 2007). All pair-wise estimates were corrected using Bonferroni corrections (Rice, 1989). The locus Sco204 was removed from the subsequent analysis as it was consistently linked with Sco218 across all populations, and with Sco220 in TvPP and SvLO, and with SMM22 in SvLO. Hence, all subsequent estimates were based on variation at 10 microsatellite loci. Summary statistics for each locus per population were estimated in GenAlEx 6.5 (Peakall & Smouse, 2006) (Appendix Table 2).

The genetic divergence between morphs within lakes was estimated by F_{ST} (Weir & Cockerham, 1984) and tested for statistical significance using 10,000 bootstraps in ARLEQUIN 3.5.1.2 (Excoffier & Lischer, 2010). Divergence among morphs within lakes was inferred using Bayesian clustering as implemented in STRUCTURE 2.3.4 (Pritchard et al., 2000; Hubisz et al., 2009). The most likely number of populations (K) and their admixture (q) within each lake was estimated using a model assuming admixture and correlated allele frequencies. The LOCPRIOR option was used to assist the clustering as recommended by the software documentation in situations with weak genetic divergence among populations in the dataset. The model was tested with 50,000–150,000 burn-ins and Markov chain Monte Carlo (MCMC) replicates from 100,000 to 300,000. The optimal condition considering computational time versus model convergence was found to be 100,000 burn-ins and 200,000 MCMCs. The analysis was repeated 10 times for each K, and the most likely K per lake was estimated by assessing the mean $\text{LnP}(K)$ and ΔK as implemented in STRUCTURE HARVESTER (Earl & vonHoldt, 2012).

Diet composition

Stomachs were removed and stored in 70% ethanol. The number of empty stomachs was low in both lakes (19.1% and 6.6% in Tårnvatn and Skøvatn, respectively). Prey items were identified and sorted to the lowest practical taxonomic groups, and their contribution to the total stomach fullness was evaluated (0–100%) following Amundsen (1995). A total of 12 different prey types were identified in the 180 stomachs analysed for both lakes (see Appendix Table 4 for details). Rarefaction curves indicated that sample sizes in this study produced a good approximation of the diet diversity for the different morphs (Appendix Fig. 3). The different prey types were divided into five categories: zooplankton (limnetic cladocerans and copepods), littoral benthos (gastropods, larvae of stoneflies, caddisflies, and fish eggs), *Gammarus lacustris* (littoral amphipod), profundal benthos (chironomid larvae, *Pisidium* sp. mussels and *Acanthocyclops* sp. benthic copepods), and fish (Arctic charr). The proportion of each prey type in the diet was estimated as percent prey abundance following Amundsen et al. (1996). Dietary niche overlap between the different Arctic charr morphs was quantified using Schoener's (1970) similarity index. To visualize the diet of individual Arctic charr in the two lakes, a non-metric multidimensional scaling analysis (NMDS) based on the Bray–Curtis index of similarity was computed using relative prey abundance. The analysis was executed using the vegan package (Oksanen et al., 2013) in R version 3.3.1. (R Core Team, 2016). For the NMDS analysis, the LO- and PP-morph individuals were divided in two size groups to explore possible ontogenetic diet shifts. In the LO-morph, the division of small (< 16 cm) and large (> 16 cm) individuals was based on the onset of maturation sizes for the LO-morph observed, 17 cm and 16 cm, respectively, for Tårnvatn and Skøvatn (Kjær, 2018). The size-group division was also compared with that reported for earlier studies of polymorphic Arctic charr populations in the same region (Amundsen et al., 2008; Knudsen et al., 2016a) that contrasted the trophic niche of adult small-sized profundal morphs with juveniles of the upper-water (LO) morph. The threshold size for the PP-morph in Tårnvatn was set at 20 cm based on the piscivorous diet shift size reported for the PP-morph in Skogsfjordvatn (Knudsen et al., 2016b).

Parasite communities

Past diet was inferred from trophically transmitted parasites in a subset of Arctic charr from each morph. Trophically transmitted parasites reside in specific prey types and are ingested together with the prey. These parasites can live in the Arctic charr host for months or years (depending of the parasite life expectancy, Table 4) and act as tracers of long-term feeding patterns (Knudsen et al., 1996, 2008). For the purposes of this study, particularly relevant parasites were transmitted to Arctic charr by the amphipod *G. lacustris* (the cestode *Cyathocephalus truncatus*), insect larvae (the trematodes *Crepidostomum* spp. and *Phyllodistomum umblae*), and different species of pelagic copepods (the cestodes *Eubothrium salvelini*, *Proteocephalus* sp., and *Dibothriocephalus* spp.) (Knudsen, 1995; Knudsen et al., 1997, 2007, 2014; Jonsson & Jonsson, 2001; Siwertsson et al., 2016). All parasite species are in the adult stage in the Arctic charr except for larval *Dibothriocephalus* spp. (former *Diphyllobothrium* spp., see Waeschenbach et al., 2017). Prevalence (i.e. proportion of individuals infected in a host morph) and abundance (i.e. average number of parasites in host fish from a given morph) were calculated for each parasite species following Bush et al. (1997). Rarefaction curves indicated that sample sizes in this study produced a good approximation of the parasite diversity for the different morphs (Appendix Fig. 4). Individual species richness of trophically transmitted parasites is related to the diet niche width, since utilization of a larger range of different prey types is associated with higher infection risks from a multitude of food transmitted parasites. Thus, differences in individual parasite species richness between morphs were tested using non-parametric Mann–Whitney *U* tests to account for non-normality. Differences between morphs in the abundance of single parasite species were tested using generalized linear models (GLMs), specifying Poisson distributions typically used for count data. Whenever pairwise tests were performed, a Bonferroni correction was applied (Rice, 1989) such that for all tests when comparing morphs within the two lakes (four pairwise comparisons) a *P* value < 0.0125 was considered statistically significant.

Stable isotope analysis

For stable isotope analyses, a muscle tissue sample from each fish was cut from the dorsal area posterior to the dorsal fin and above the lateral line and immediately frozen. Littoral zoobenthos (*G. lacustris*, insect larvae, and snails) and pelagic zooplankton samples from both lakes were collected and used to explore baseline differences in stable isotope values between the major lake habitats (Fig. 6). Zooplankton sampling from the whole water column was carried out using a plankton net (diameter 26 cm, mesh size 90 μm) hauled three times vertically from a depth of 15 m to the surface. Benthic littoral macroinvertebrates were sampled using a benthos hand square net. Both zooplankton and littoral benthos samples were immediately frozen. Littoral benthos samples were sorted into *G. lacustris*, Megaloptera, Ephemeroptera, Trichoptera, Plecoptera, Chironomidae, and molluscs. Only the soft body tissue of molluscs was prepared for analyses. Samples were dried at 60°C for 24 h, homogenised using mortar and pestle, and weighed (0.3 ± 0.05 mg) into tin capsules. The analyses were performed 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 analyser (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an analytical precision of $\pm 0.2\text{‰}$ ($\delta^{13}\text{C}$) and $\pm 0.3\text{‰}$ ($\delta^{15}\text{N}$). Analytical accuracy was established through the repeat analysis of internal laboratory standards calibrated against International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen. Analytical precision was established by the repeat analysis of one in ten samples. All results were reported in conventional delta notation (δ) relative to international standard Vienna Pee Dee Belemnite, VPBD, for $\delta^{13}\text{C}$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (Mariotti, 1983). As tissue samples had C:N values < 4, lipids were neither extracted nor corrected for using mathematical models (Jardine et al., 2013). Due to the non-normality of stable isotope values, Kruskal–Wallis and pair-wise Mann–Whitney *U* tests were used to statistically test for differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among the morphs within the two lakes. Whenever pairwise tests were performed, a Bonferroni correction was applied (Rice, 1989).

Results

Genetic analyses

The five samples of morphs were all in HWE (Table 1), and none of the loci displayed deviation from HWE after Bonferroni corrections. Ten of 225 pairwise comparisons showed significant LD, but only one (OMM1105 vs SMM22 in SvLO) of 225 remained significant after Bonferroni corrections. The number of alleles per morph varied from one (Sco215 in SvLO, TvLO, TvPP, and TvPB) to 19 in SvLO (Sco218) (Appendix Table 2). The genetic variation (expected heterozygosity, H_e) of the Arctic charr morphs was higher in Skøvatn ($H_e = 0.729–0.739$) than in Tårnvatn ($H_e = 0.593–0.693$), and none of the morph samples displayed significant inbreeding signatures (Table 1).

In Tårnvatn, the LO-morph displayed F_{ST} s of 0.134 ($P < 0.001$) and 0.121 ($P < 0.001$) compared to the PB and PP-morphs, respectively (Table 2). The genetic divergence between the PP- and PB-morphs was lower ($F_{ST} = 0.042$), but significant ($P < 0.001$). The STRUCTURE analysis identified $K = 2$ or $K = 3$ clusters in Tårnvatn (Fig. 1A, B). In both cases, the LO-morph formed its own cluster, where PB- and PP-morphs grouped together for $K = 2$ (Fig. 1A). The groupings revealed by STRUCTURE followed the visual phenotypic classification of individuals completed in the field. The two morphs in Skøvatn showed a significant genetic divergence with an F_{ST} value of 0.041 (Table 2). The result was supported by the STRUCTURE analysis, which clustered the morphs in

Table 2 Genetic divergence among morphs within and across lakes as inferred by F_{ST} (below diagonal) and the associated P values (above diagonal)

	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	–

Sv Skøvatn, Tv Tårnvatn

*** $P < 0.001$

two separate clusters according to their phenotype (Fig. 1C).

Habitat and diet

In Tårnvatn, the LO-morph (mean length \pm S.D.: 20.6 \pm 5.6 cm) was caught in all three habitats, but at highest densities in littoral and pelagic areas (CPUE: 16.7 and 31.7, respectively; Table 3). The diet of the LO-morph in Tårnvatn included chiefly zooplankton (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 \pm S.D.: 14.0 \pm 5.6 cm) largely exploited profundal benthic prey groups, mostly chironomid larvae (Fig. 2, Appendix Table 4). The PP-morph (mean length \pm S.D.: 26.0 \pm 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 \pm S.D.: 18.5 \pm 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 \pm S.D.: 9.5 \pm 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

Fig. 1 Genetic structuring of Arctic charr morphs from Tårnavatn (**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 $\ln P(K)$ and ΔK are given in Appendix Table 3

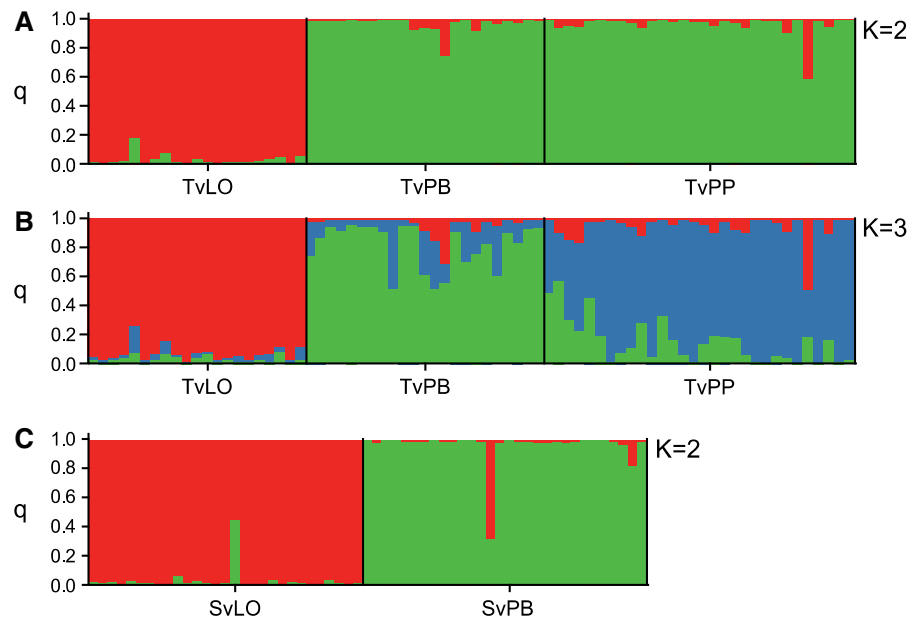


Table 3 Catch per unit effort (CPUE = number of fish caught per 100 m² multi-mesh gill-nets per night) of the Arctic charr morphs in the different habitats in Tårnavatn and Skøvatn

Habitat	Tårnavatn			Skøvatn	
	LO	PB	PP	LO	PB
Littoral	16.7 (<i>n</i> = 40)	0.0	0.0	24.0 (<i>n</i> = 43)	1.0 (<i>n</i> = 2)
Profundal	9.4 (<i>n</i> = 18)	10.0 (<i>n</i> = 13)	7.8 (<i>n</i> = 18)	0.0	3.0 (<i>n</i> = 8)
Pelagic	31.7 (<i>n</i> = 39)	0.0	0.0	–	–

The number (*n*) of fish caught in the different habitat is also provided

individuals (Fig. 3). The two small-sized deep-water PB-morphs, on the other hand, revealed contrasting feeding strategies in the two lakes with low dietary similarity (29%) (Figs. 2, 3, Appendix Table 4). The PB-morph in Skøvatn had the highest dietary similarity with the small LO-morphs from both lakes, feeding mainly on cladocerans (Fig. 3). The two PB-morphs showed no signs of ontogenetic dietary changes. The Tårnavatn PP-morph diet was distinctly different between small and large size-classes (Fig. 3). The small PP-morph (< 20 cm) almost exclusively consumed profundal benthos and had diet similar to the PB-morph in Tårnavatn (Fig. 3). The larger individuals (> 20 cm) relied predominantly on *G. lacustris* and fish, having the most distinctive diet of all the studied morphs (Fig. 3).

Parasite communities

In total, six different food-borne parasite genera were recorded in Arctic charr in both lakes, including four cestodes (pelagically transmitted *Dibothriocephalus* spp., *E. salvelini*, and *Proteocephalus* sp., and littoral *C. truncatus*) and two littoral benthic-transmitted trematodes (*Crepidostomum* spp. and *P. umblae*). No nematodes were found in any fish. All morphs in the two lakes harboured all six trophically transmitted parasites taxa.

In Tårnavatn, the PB-morph had the lowest parasite richness (mean number \pm S.E.: 2.0 ± 0.2 ; Mann–Whitney *U* test: $P < 0.001$) (Fig. 4), whereas there was no significant difference in the number of parasite species between the LO- (3.7 ± 0.2) and PP- (3.4 ± 0.2) morphs (Mann–Whitney *U* test:

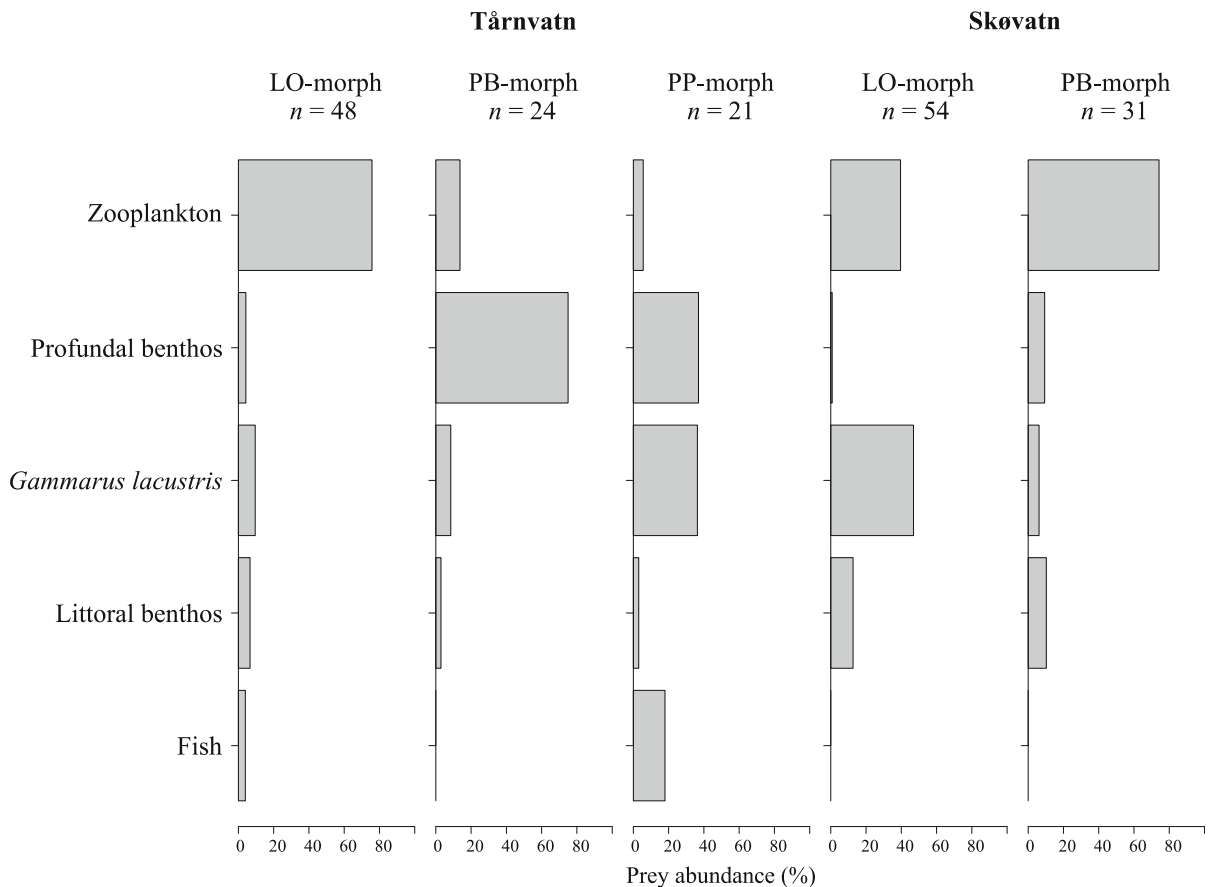


Fig. 2 Percent abundances of the major prey groups found in the stomach contents of the different Arctic charr morphs from Tårnvatn and Skøvavn (October 2016). For a more detailed diet description, see Appendix Table 4

$P = 0.378$) (Fig. 4). The prevalence in the LO- and PP- morphs was high for most of the parasite species, especially for *Dibothriocephalus* spp., *Crepidostomum* spp. and *E. salvelini* (Table 4). In contrast, the PB-morph had a low prevalence for all parasites, except for *Crepidostomum* spp., which infected a high proportion of individuals (Table 4). In Tårnvatn, the PP-morph had the highest total parasite abundance (mean number \pm S.E.: 129.1 ± 37.7), followed by the LO-morph (67.9 ± 16.2), whereas the PB-morph had the lowest (35.3 ± 16.2). The LO-morph had the highest abundance of *P. umblae* and *Proteocephalus* sp. (GLMs: $P < 0.001$), whereas the PP-morph had the highest infection of *C. truncatus*, *Crepidostomum* spp., *E. salvelini*, and *Dibothriocephalus* spp. (GLMs: $P < 0.001$) (Fig. 5). In contrast, the PB-morph had low abundance for most of the parasites, with the lowest infections of *Proteocephalus* sp., *E. salvelini*,

and *Dibothriocephalus* spp. (GLMs: $P < 0.001$) (Fig. 5).

The LO-morph in Skøvavn had the highest parasite richness, harbouring up to six different parasite genera in one individual (mean number \pm S.E.: 3.3 ± 0.3 S.E.) (Mann–Whitney U test: $P < 0.001$) (Fig. 4). In contrast, a lower parasite richness (1.5 ± 0.2) with a maximum of four parasite taxa was recorded in the PB-morph (Fig. 4). In Skøvavn, the LO-morph in general had a high parasite prevalence, with the greatest occurrence of *Dibothriocephalus* spp. and *Crepidostomum* spp. (Table 4). In contrast, the PB-morph showed a lower prevalence than the LO-morph for all parasites except for *Dibothriocephalus* spp., which was more frequently present in the PB-morph (Table 4). The LO-morph had a higher parasite abundance (mean number \pm S.E.: 118.7 ± 33.6) compared to the PB-morph (67.9 ± 17.4). In Skøvavn, the highest mean

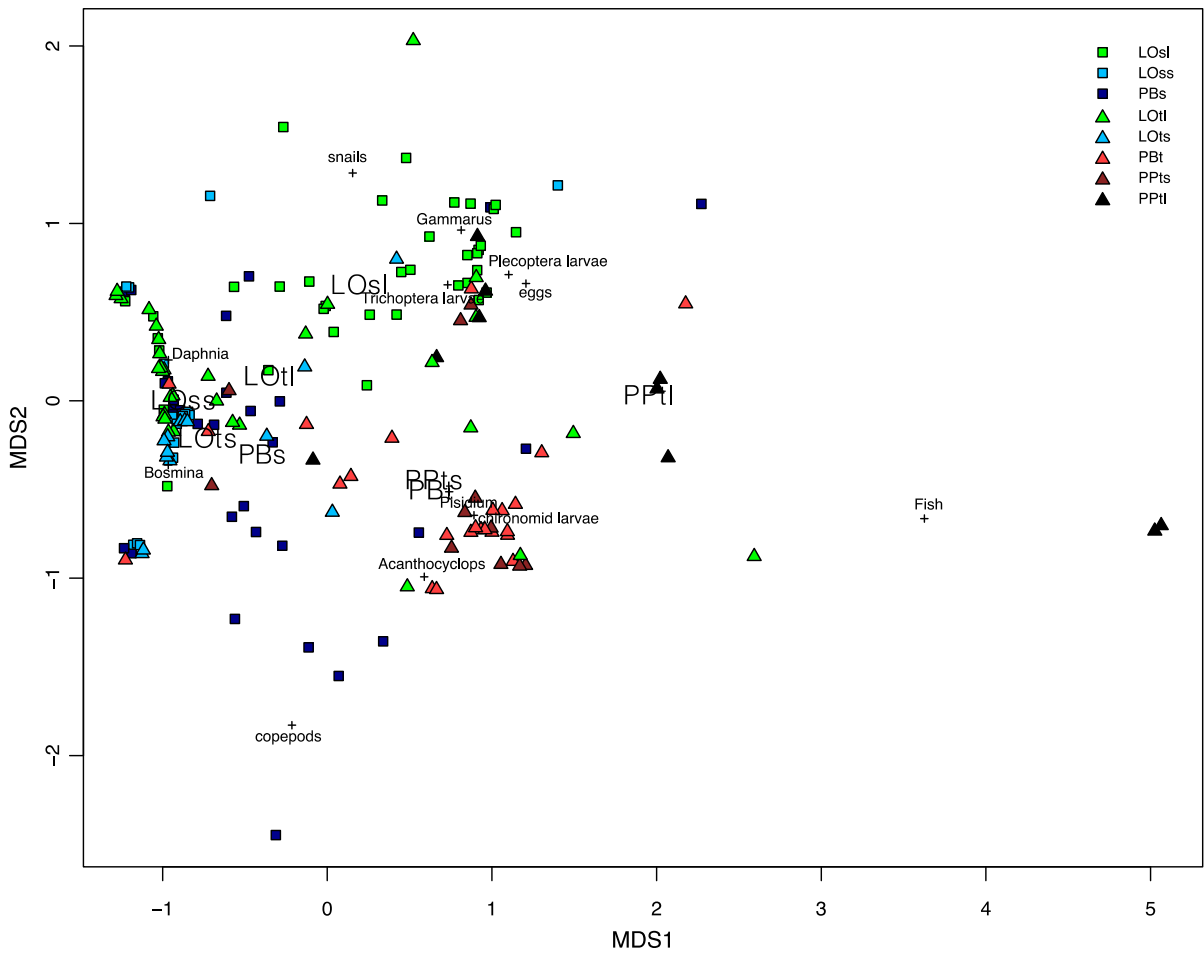


Fig. 3 Diet composition of individual Arctic char of the various morphs in Tårnvatn and Skøvatn depicted by non-metrical multidimensional scaling (NMDS; stress = 0.12). LOTs = small LO-morph (< 16 cm) in Tårnvatn (*n* = 15), LOTl = large LO-morph (> 16 cm) in Tårnvatn (*n* = 33), PBt = PB-morph in Tårnvatn (*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

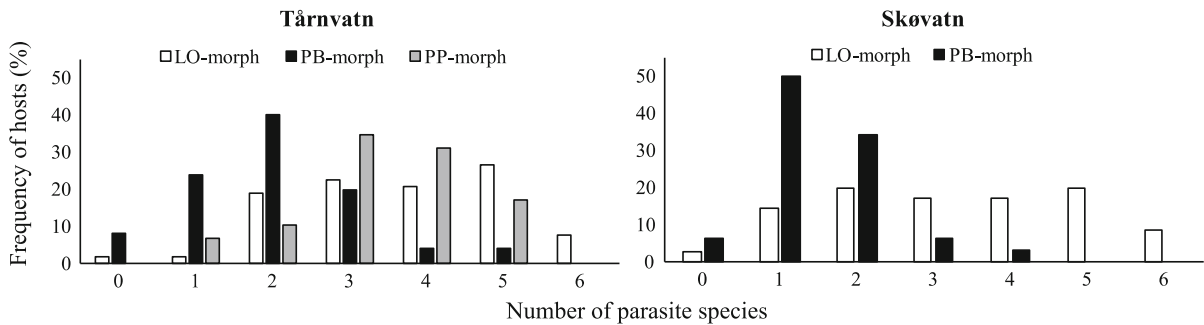


Fig. 4 Distribution (%) of the number of parasite species per host in the different morphs of Arctic char in Tårnvatn (left) and Skøvatn (right)

Table 4 Prevalence (%) of the different parasite taxa found in the Arctic charr morphs in Tårnvatn and Skøvatn

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
<i>C. truncatus</i>	Months	L	22.6	16.0	37.9	54.3	12.5
<i>P. umblae</i>	1–2 years	L	54.7	8.0	17.2	42.9	3.1
<i>Crepidostomum</i> spp.	1–2 years	L	73.6	76.0	89.7	77.1	31.3
<i>Proteocephalus</i> sp.	1–2 years	P	69.8	40.0	41.4	25.7	9.4
<i>E. salvelini</i>	1–2 years	P	67.9	20.0	75.9	48.6	9.4
<i>Dibothriocephalus</i> spp.	many years	P	79.2	40.0	79.3	77.1	84.4

The life expectancy in the host and the intermediate host's habitat (L = Littoral and P = Pelagic) are also signed

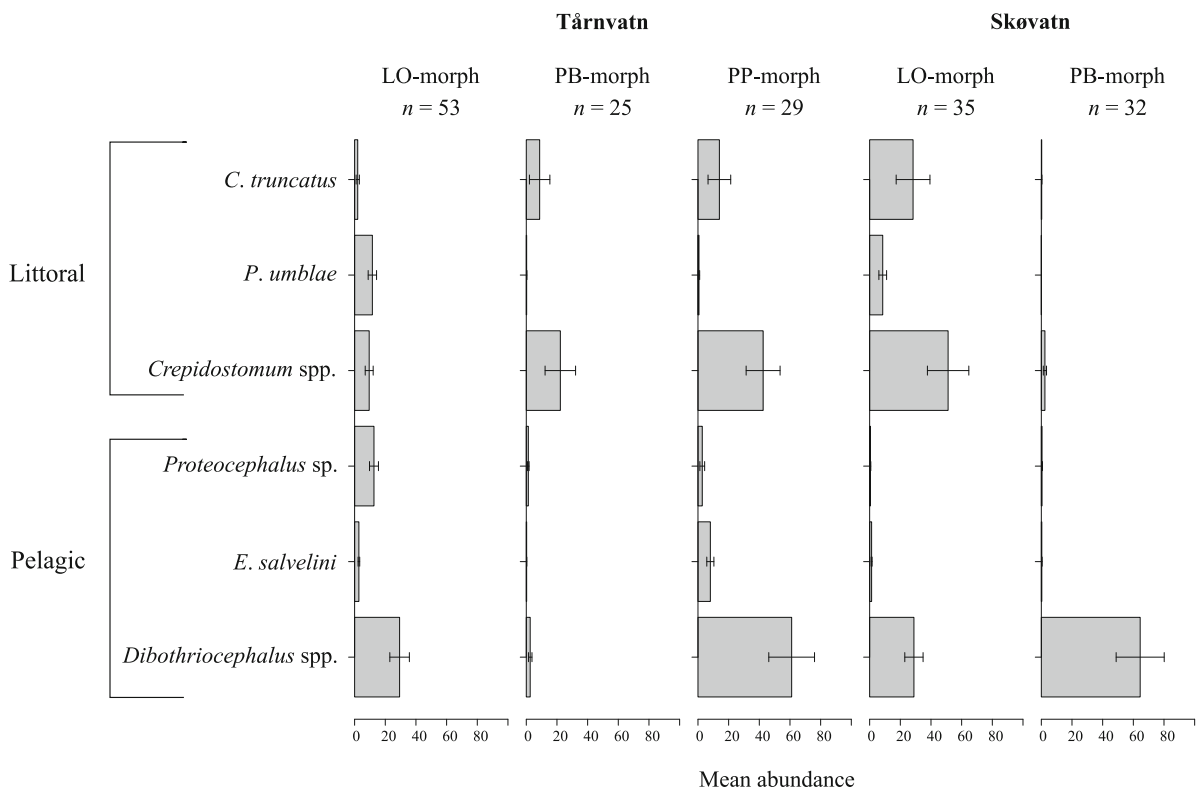


Fig. 5 Mean abundance (\pm S.E) of the six parasites genera found in the different Arctic charr morphs from Tårnvatn and Skøvatn (October 2016). The first three parasite species are associated with littoral feeding, the last three with pelagic

abundance in the LO-morph was found for *Crepidostomum* spp., followed by *Dibothriocephalus* spp., *C. truncatus*, and *P. umblae*, whereas the infection rate was very low for *E. salvelini* and *Proteocephalus* sp. (Fig. 5). On the other hand, the PB-morph generally had low infection levels, with significantly lower

abundance for all parasites species (GLM: $P < 0.001$), except *Proteocephalus* sp. (GLM: $P = 0.791$) and *Dibothriocephalus* spp. (Fig. 5). The abundance of *Dibothriocephalus* spp. was higher in the PB-morph than in the LO-morph (GLM: $P < 0.001$) (Fig. 5).

Parasite species richness was similar across lakes between the two LO- morphs (Mann–Whitney U test: $P = 0.231$) and PB-morphs (Mann–Whitney U test: $P = 0.061$) (Fig. 4). Nevertheless, the LO- and PB-morphs in Tårnvatn had a lower total parasite abundance than the corresponding morphs in Skøvatn. A similar pattern of prevalence for the LO-morphs was observed in the two lakes, with the majority of fish infected by *Dibothriocephalus* spp. and *Crepidostomum* spp. However, the LO-morph in Tårnvatn showed a greater occurrence of pelagically transmitted parasites, but a lower prevalence of the *G. lacustris*-transmitted *C. truncatus* (Table 4). The PB-morph in Tårnvatn had a higher prevalence than the PB-morph in Skøvatn for all parasites, except for *Dibothriocephalus* spp., which was more prevalent in Skøvatn (Table 4). The two LO-morphs had significant differences in the abundance of all parasites species (GLM: $P < 0.001$) except for *Dibothriocephalus* spp. (GLM: $P = 0.700$) (Fig. 5). The PB-morph in Skøvatn had a higher abundance of *Dibothriocephalus* spp. than the PB-morph in Tårnvatn (GLM: $P < 0.001$), but lower abundances of *C. truncatus*, *Crepidostomum* spp. and *Proteocephalus* sp. (GLM: $P < 0.001$) (Fig. 5). The abundances of the other parasite species were not significantly different (GLMs: $P > 0.060$) (Fig. 5).

Stable isotope analysis

There were significant differences in the stable isotope values among the morphs in Tårnvatn (Kruskal–Wallis tests: $P < 0.001$). The PB- and PP-morphs had similar $\delta^{13}\text{C}$ mean values (Mann–Whitney U test: $P = 0.015$), but higher compared to the sympatric LO-morph (Mann–Whitney U tests: $P \leq 0.0125$) (Fig. 6A; Appendix Table 4). The LO-morph had the lowest $\delta^{15}\text{N}$ values (Mann–Whitney U test: $P < 0.001$) in comparison with the other morphs, which were similar (Mann–Whitney U test: $P = 0.339$) (Fig. 6A; Appendix Table 4).

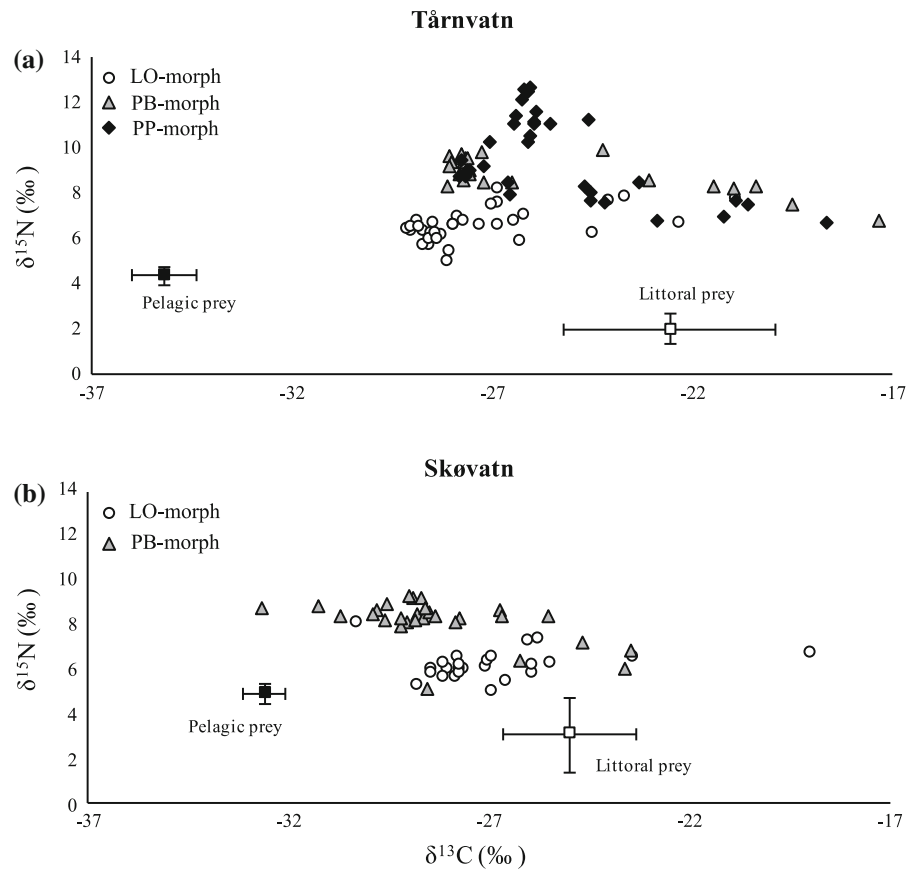
In Skøvatn, the LO-morph had significantly higher $\delta^{13}\text{C}$ values than the sympatric PB-morph (Mann–Whitney U test: $P < 0.005$), but lower $\delta^{15}\text{N}$ (Mann–Whitney U test: $P < 0.001$) (Fig. 6B; Appendix Table 4).

Discussion

As predicted, all the sympatric Arctic charr morphs in the two lakes were genetically differentiated. In both lakes, genetic differences were evident between the LO- and the co-occurring profundal morphs as has been noted in earlier studies of analogous morph-pairs in Fjellfrøsvatn and Skogsfjordvatn (Præbel et al., 2016; Simonsen et al., 2017). The genetic differentiation was weaker, but still highly significant between the PB- and PP-morphs in Tårnvatn. Collectively, the results show that an intra-lacustrine divergence of the Arctic charr morphs is ongoing in both lakes and that all morphs can be genetically discriminated. There was also a clear separation in the trophic niches (habitat and diet) between the upper-water column (LO-morph) and profundal morphs within each lake. Niche segregation among the Arctic charr morphs in both Tårnvatn and Skøvatn was also supported by the differences between the temporally integrated trophic tracers (stable isotopes and parasites) that pointed to the persistence of trophic niche segregation over the ecologically relevant time scales of months (stable isotopes) or years (parasites). The resulting weight of evidence provided by the genetic differences, the clear trophic segregation, and life-history patterns (Kjær, 2018) strongly suggests the existence of two distinct deep-water morphs in Tårnvatn and one in Skøvatn. However, while the LO-morphs appeared to have similar trophic niches in both lakes, the PB-morphs were strikingly different. Although similar in appearance, life histories (Kjær, 2018), and habitat preference, the PB-morph in Skøvatn was feeding mainly on zooplankton while in Tårnvatn they were feeding on profundal benthos like in other lakes in the region (Klemetsen, 2010; Knudsen et al., 2016a).

The parallelisms in habitat choice and trophic tracers between the LO-morphs from the two study lakes were similar to patterns observed in earlier studies of morphs from the same geographic region (Knudsen et al., 2016a; Siwertsson et al., 2016). The LO-morphs in Tårnvatn and Skøvatn had a generalist trophic niche, with a mixed diet obtained from the 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 (Amundsen et al., 2008; Knudsen et al., 2011, 2016a; Siwertsson et al., 2016). Such a broad dietary niche typically occurs also

Fig. 6 Stable isotope biplots displaying the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of dorsal muscle tissue samples of Arctic charr caught in Tårnvatn and Skøvatn in October 2016. The LO-morphs are represented by white dots ($n = 34, 29$, respectively), the PB-morphs ($n = 25, 25$, respectively) by grey triangles, and the PP-morphs in Tårnvatn ($n = 32$) by black diamonds. Mean values (\pm SD) of pelagic (black squares) and littoral (white squares) prey sampled in June 2017 are also given



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 and 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 $\delta^{15}\text{N}$ 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. Individuals with high $\delta^{15}\text{N}$ and low $\delta^{13}\text{C}$ values likely fed on conspecifics in the profundal zone (Jardine et al. 2003; Knudsen et al.

2016a, b), whereas individuals with low $\delta^{15}\text{N}$ and high $\delta^{13}\text{C}$ had values typical of littoral dwelling fish (Vander Zanden & Rasmussen, 1999; Jardine et al. 2003). Analogous to Skogsfjordvatn (Smalås et al., 2013), Kjær (2018) has shown that the PB- and PP-morphs have contrasting life history strategies, with the PB-morph having a significantly slower growth rate and earlier sexual maturation (approximately 5 years) than the PP-morph (approximately 7 years). Arctic charr is the only suitable fish prey that is available for the PP-morph in Tårnvatn, as only Arctic charr and brown trout are present. Juvenile brown trout do not commonly reside in the profundal zone, preferring to occupy streams or lacustrine littoral areas (L'Abée-Lund et al., 1992; Amundsen & Knudsen, 2009; Eloranta et al., 2013). Thus, the piscivorous PP-morph can only feed on small conspecifics. In contrast the PP-morph in Skogsfjordvatn is able to feed on both Arctic charr and three-spined sticklebacks (Knudsen et al., 2016b). Cannibalism in Arctic charr has been widely reported both as an outcome of ontogenetic niche shifts in large fish and as an occurrence of specialized piscivorous morphs (Amundsen, 1994, 2016; Svenning & Borgstrøm, 1995; Klemetsen et al., 2003; Knudsen et al., 2016b). Nevertheless, piscivorous charr morphs generally reside in shallow-water habitats (Sandlund et al., 1992; Adams et al., 1998). Skogsfjordvatn is one of the few described cases with a piscivorous morph residing entirely in the profundal zone (Smalås et al., 2013; Skoglund et al., 2015; Knudsen et al., 2016b) (but see Power et al., 2009). The presence of abundant and suitable prey fishes, i.e. the PB-morph and juvenile LO-morph in deep-waters, is probably a key factor in the local evolution of the PP-morph in Tårnvatn, as in Skogsfjordvatn, where a process of niche expansion in response to ecological opportunity has been suggested (Skoglund et al., 2015; Knudsen et al., 2016b).

In contrast to the LO-morphs, the PB-morphs from the two lakes showed both parallel and non-parallel patterns in trophic niche utilisation. As predicted, the PB-morph in Tårnvatn evidenced dietary specialization based on its stomach contents, preying profundal soft-bottom benthic invertebrates as has been reported for the PB-morphs in Fjellfrøsvatn and Skogsfjordvatn (Knudsen et al., 2006, 2016a). Specialization was also supported by the low species richness and infection rates (prevalence and abundance) of all examined parasites typical of the small-sized profundal morphs

(Knudsen et al., 1997; Siwertsson et al., 2016). Stable isotope values, on the other hand, suggested utilisation of a wide spectrum of prey resources along the littoral-pelagic-profundal habitat axis (Vander Zanden & Rasmussen, 1999). Thus, while dietary specialization as reflected in stomach contents and parasites is occurring, prey sourcing appears to occur from both littoral and profundal habitats. Deep-water morphs with a similar benthic feeding strategy have also been reported from Siberia (Alekseev & Pichugin, 1998), Canada (O'Connell et al., 2005), central Europe (Brenner, 1980), and Scandinavia (Hindar & Jonsson, 1982) (reviewed by Klemetsen, 2010), and with similar dichotomous use of deeper and shallower littoral habitats having been observed in the generally deep-water morph found in Gander Lake, Newfoundland (O'Connell et al., 2005; Power et al., 2012).

When compared to the benthivorous PB-morph in Tårnvatn and other lakes, the deep-water morph in Skøvatn used a different trophic niche despite identical life-history patterns, e.g. reduced growth and early maturation (Klemetsen et al., 1997; Smalås et al., 2013; Kjær, 2018). The zooplankton dominated diet of the Skøvatn deep-water morph was reflected by high infections of copepods-transmitted *Dibothriocephalus* spp. However, the lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ values when compared to the sympatric LO-morph, also suggested a greater reliance on profundal benthic resources (Hayden et al., 2014; Knudsen et al., 2016a, b). Since stable isotopes reflect diet over an approximate 3–4 month period before capture (Post, 2002; Buchheister & Latour, 2010; Knudsen et al., 2014), the Skøvatn deep-water morph likely consumed profundal prey during the early ice-free season when a high density of chironomid pupae emerge from the bottom substrate and zooplankton biomass is low (Klemetsen et al., 1992; Dahl-Hansen et al., 1994; Primicerio & Klemetsen, 1999; Amundsen et al., 2008; Mousavi & Amundsen, 2012; Kahilainen et al., 2016). The parasite community composition supported these findings as the small-sized profundal morph had low species richness and very low abundance for most parasites (except for *Dibothriocephalus* spp.), as typical of other deep-water morphs (Siwertsson et al., 2016). Since the Skøvatn profundal morph deviates clearly in its diet (zooplanktivory) from the benthivore PB-morph in Tårnvatn and elsewhere (Klemetsen, 2010; Knudsen et al., 2016a), and potentially spawns in deep-waters (Kjær,

2018), it is probably best denoted as a distinct small-sized deep-water planktivorous morph and is hereinafter referred using the acronym PZ (“Profundal spawning Zooplanktivore”).

The PZ-morph in Skøvatn is the first documented case of a potential profundal planktivorous Arctic charr morph in northern Norway. Similar partly zooplanktivorous small-sized deep-water morphs have been described, e.g. in southern Norway (Telnes & Sægrov, 2004), in central Europe (Brenner, 1980), and in Transbaikalia (Alekseyev et al., 2002; Samusenok et al., 2006). Compared to zooplanktivory, one of the main advantages of a deep-water benthic diet may be lower parasite infections (Siwertsson et al., 2016) and associated higher fitness. A second advantage may be the year-round availability of prey items. The observed deviation from the more common deep-water benthivorous diet may be related to low productivity in the profundal zone, with the scarcity of deep-water benthic biomass inducing a shift to zooplanktivory. Overall, zooplankton is a generally more abundant resource in the late summer and autumn than profundal benthic invertebrates in many northern lakes (Primicerio & Klemetsen, 1999; Mousavi, 2002; Hayden et al., 2014; Kahilainen et al., 2016). As described for some monomorphic Arctic charr populations (e.g. Eloranta et al., 2010; Hayden et al., 2014; Kahilainen et al., 2016), the PZ-morph may alternate between benthivorous behaviour in winter and spring and zooplanktivory in autumn when zooplankton preys are abundant.

While parallelism in trophic ecology was evident in the LO-morphs from the two study lakes, the two small-sized profundal morphs differed substantially in their diets. The PB-morph in Tårnvatn along with the PB-morphs in Fjellfrøsvatn and Skogsfjordvatn are well-documented cases of parallel evolution in Arctic charr, given their similarity in habitat preferences, diet, parasite fauna, morphology, and life history (Knudsen et al., 2016a; Siwertsson et al., 2016; Saltykova et al., 2017). Parallel patterns are usually considered as evidence of similar selection pressures favouring the development of similar adaptive traits among fishes in postglacial lakes (Schluter, 2001; Sigursteinsdóttir & Kristjánsson, 2005; Kaeuffer et al., 2012; Præbel et al., 2013; Siwertsson et al., 2016; Saltykova et al., 2017; Häkli et al., 2018). Thus, the discrepancy in the dietary niche of the PB- and PZ-morphs in Tårnvatn and Skøvatn, respectively, is of

great interest to improve the knowledge of evolutionary mechanisms driving adaptations.

The observed divergent patterns in local trophic adaptations (i.e. non-parallelism) of the PB- and the PZ-morphs of Arctic charr might have been promoted by differences in ecological and environmental factors occurring between the two lake systems (Kaeuffer et al., 2012; Kristjánsson et al., 2012; Siwertsson et al., 2013b; Saltykova et al., 2017). Such dissimilarities could be, e.g. in bathymetric conditions, productivity, and fish community, as Skøvatn (unlike Tårnvatn) hosts anadromous fish including Arctic charr, brown trout, and Atlantic salmon (Smalås & Henriksen, 2016). Alternatively, different adaptive responses may have been induced by the standing genetic variation of the colonizing ancestral populations (West-Eberhard, 1989) or as an outcome of genetic drift (Sigursteinsdóttir & Kristjánsson, 2005; Kaeuffer et al., 2012; Saltykova et al., 2017).

To conclude, the combined data describing habitat use, stomach contents, parasites, and tissue stable isotopes indicated clear trophic resource segregation between the genetically differentiated polymorphic Arctic charr morphs in Tårnvatn and Skøvatn. Results as described here are consistent with the occurrence of an ongoing process of trophic divergence, the consequences of which are reflected in a concomitant separation among the morphs in life history traits such as growth and maturation (Kjær, 2018). Furthermore, there were clear patterns of genetic divergence among the morph-pairs within these two lakes. Within the study lakes, a clear parallelism in habitat choice, external morphology, and life history was found for the upper-water omnivore LO-morphs and the small-sized deep-water morphs, suggesting the effect of parallel evolutionary processes along the depth gradient across lakes. Contrary to our hypotheses, there was an evident difference in dietary niches between the small-sized profundal benthivorous PB-morph and the zooplanktivorous PZ-morph indicating partially different evolutionary histories. Finally, the data describe for the first time in northern Norway the occurrence of the PZ-morph and the exclusively cannibalistic PP-morph from the deep-water environment. This study demonstrates how evolution can produce diverse outcomes, even among systems with apparently similar environmental and ecological conditions.

Acknowledgements We thank Rachel Patterson and Helge Jakobsen for assistance during the fieldwork, André Frainer for helpful discussion on statistical analyses, and Katja Häkli for handling the DNA fragment analyser. We also thank three anonymous referees for very constructive and helpful reviews.

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