Contrasting patterns in trophic niche evolution of polymorphic Arctic charr *Salvelinus alpinus* L. populations in two subarctic lakes, northern Norway

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Acknowledgements

When my laptop decided to break few days before the deadline for the master's thesis, I was about to jump into the fjord with a stone around my neck. Then, I thought that Runar would have won our competition and I changed my mind. So, I managed to deliver in time.

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"Look at where Jesus went to pick people. He didn't go to the colleges; he got guys off the fishing docks."

- Jeff Foxworthy

"*Ul pess gross al mangia ul pess pinín*"[1]

(Swiss-Italian dialect proverb)

A nonno Leo

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[1] "*Big fish eat small fish*"

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Abstract

The trophic niche (recent and time-integrated niche estimates) of polymorphic populations of Arctic charr was investigated in two lakes in Northern Norway. The lakes, Tårnvatn and Skøvatn, have three and two morphs, respectively. Since the two systems are very similar in environmental conditions and fish communities, comparable niches between similar trophic morphs across lakes were expected caused by parallel local evolutionary process. Three methods were used to describe the niches: habitat choice and stomach content to estimate the recent feeding behaviour, and time integrated methods like trophically-transmitted parasite communities and stable isotopes (δ^{13}C and δ^{15}N) as proxies for the long-term trophic niches. The combined data from habitat distribution, stomach contents, parasites, and stable isotopes analyses showed a distinct segregation in stable trophic resource utilization of the different Arctic charr morphs in Skøvatn and Tårnvatn. The trimorphic Tårnvatn has one littoral omnivorous (LO), one small-sized profundal benthivorous (PB), and a large-sized profundal piscivorous (PP) morph foraging on conspecifics (cannibalistic), only reported once in the same region in Norway. In contrast, a novel charr variety was discovered in Skøvatn: a small-sized profundal zooplanktivorous-morph (PZ). Compared to the sympatric LO-morph, the PZ-morph has different stable isotope values and also contrasting parasite communities, including heavy infection by copepod-transmitted *Diphyllobothrium*-parasites. A rather clear parallelism in habitat choice and external morphology was found between the small-sized deep-water morphs and the upper-water omnivore LO-morphs in the two lakes. This suggested a common parallel evolutionary process along the depth gradient across lakes. However, contrary to the hypotheses, there was an evident non-parallel pattern in diet between the small-sized profundal benthivorous PB-morph and the zooplanktivorous PZ-morph indicating partially different evolutionary histories. These findings show how evolutionary forces can create diverse outcomes, even among systems with apparently similar environmental and ecological conditions.

Introduction

Postglacial lakes of the northern hemisphere are evolutionary young systems that originated approximately 10 000 - 15 000 years ago, at the end of the Wisconsin-Weichsel glaciation period (Schluter 1996). Polymorphic populations of several fish species have repeatedly been found in these lakes, especially within the genera *Salvelinus*, *Gasterosteus*, and *Coregonus* (Skùlason & Smith 1995; Skúlason et al. 1999; Amundsen et al. 2008; Klemetsen 2013). These polymorphic stocks are generally considered having a sympatric origin, i.e. the morphs have arisen locally (Skúlason *et al.* 1999; Jonsson & Jonsson 2001; Snorrason & Skúlason 2004; Klemetsen 2010). However, in some cases, the intralacustrine variation may also be the result of repeated colonisations of different fish lineages, as suggested by molecular genetic analyses (Bernantchez & Dodson 1990; Schluter & Rambaut 1996; Klemetsen 2010; Verspoor et al. 2010; Præbel et al. 2013).

Resource polymorphism, defined as the occurrence of distinct morphs specialized in different resource use within a single species (Skùlason & Smith 1995), is considered to be an important step in an ecological induced speciation process (Wimberger 1994; Gíslason et al. 1999; Snorrason & Skúlason 2004; Amundsen et al. 2008; Siwertsson et al. 2013a). Thus, freshwater systems of recent origin are viewed as hotspots to investigate the function and role of ecological components in divergent evolution (Schluter 1996; Snorrason & Skúlason 2004; Klemetsen 2010). Ecological speciation theory predicts the manifestation of ecologically based divergent (including disruptive) selection which favours alternative phenotypes within and/or between populations and eventually may cause speciation through the formation of complete reproductive barriers between the resulting ecotypes (Schluter 2001, 2009; Nosil and Rundle 2009).

In northern lakes, one source of divergent selection is proposed to be a discrete availability of resources (habitat and food), that allows fish to specialize and segregate in distinct niche use as a main outcome of resource competition (Wimberger 1994; Skúlason & Smith 1995; Jonsson & Jonsson 2001; Adams et al. 2003; Garduño-Paz & Adams 2010). The resulting trophic polymorphism is often believed to be the starting point of divergent evolution since it offers stable alternative foraging strategies upon which natural selection can act, ultimately causing reproductive isolation (Gíslason et al. 1999; Skúlason et al. 1999; Adams &

Huntingford 2004; Amundsen et al. 2008). A common pattern of trophic niche segregation found repeatedly in postglacial lakes is along the benthic-limnetic (pelagic) resource axis, with benthivorous morphs exploiting the littoral area, and planktivorous and/or piscivorous morphs residing in the epipelagic zone (Wimberger 1994; Skùlason & Smith 1995; Schluter 1996; Sigursteinsdóttir & Kristjánsson 2005). The stage of divergence between these ecotypes varies considerably, with some populations consisting of completely reproductively isolated forms, whereas other systems may show from low to high levels of interbreeding between the fish varieties (Skúlason et al. 1999, Gíslason et al. 1999; Hendry et al. 2009; Klemetsen 2010). These frequent incidents of parallel evolution from several fish taxa are considered as a strong evidence of ecological induced evolutionary process. The repeated and independent evolution of the same pattern of diversification in distinct systems is unlikely to arise only by genetic drift or other nonecological mechanisms (Schluter & Nagel 1995; Schluter 2001; Nosil and Rundle 2009; Kaeuffer et al. 2011 Saltykova et al. 2017). Hence, parallel evolution predicts that natural selection under similar environmental and ecological conditions promotes the development of analogous adaptations (Schluter & Nagel 1995; Schluter 1996, 2001; Sigursteinsdóttir & Kristjánsson 2005; Siwertsson et al. 2013b; Saltykova et al. 2017). Nevertheless, despite these numerous examples documented in the literature, the ecological mechanisms initiating and driving the speciation process are in general still poorly understood.

In the present study, the trophic niche utilization within polymorphic populations of Arctic charr (*Salvelinus alpinus* L.) was investigated in two subarctic lakes in Northern Norway. The Arctic charr is a cold-water species with a circumpolar distribution and it is the northernmost of all diadromous and freshwater fishes (Johnson 1980; Klemetsen et al. 2003a; Klemetsen 2010). It is considered to be one of the most variable vertebrate on earth (Klemetsen 2010; Klemetsen 2013), since it shows a myriad of differences in coloration, morphology, ecology and life history occurring both among allopatric populations and in sympatry within the same lake system (Johnson 1980; Skùlason et al. 1999; Alexander & Adams 2000; Jonsson & Jonsson 2001; Klemetsen 2010). Over the years, sympatric morphs have been described in several localities, and 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 charr morphs have been detected living within a single lake (Smith & Skúlason 1996; Jonsson & Jonsson 2001; Klemetsen 2010). Most charr varieties are apparently segregated between the littoral-pelagic areas, but deep-water living charr morphs adapted to the profundal habitat have also been described in a few lakes (Klemetsen 2010).

Two well-studied examples of profundal morphs are from the lakes Fjellfrøsvatn and Skogsfjordvatn (the suffix "vatn" means "lake" in Norwegian) in Troms county, Northern Norway (e.g. Klemetsen et al. 1997; Knudsen et al. 2006, 2016 a,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" foraging on profundal benthic invertebrates (Klemetsen et al. 1997; Smalås et al. 2013). Additionally, Skogsfjordvatn hosts a rare profundal spawning piscivore "PP-morph" feeding mostly on young charr and, to a less extent, on three-spined sticklebacks (Smalås et al. 2013; Knudsen et al. 2016b). These different ecotypes were first classified on the basis of the external morphological traits, which are recognized as having an important functional role (Snorrason et al. 1994; Jonsson & Jonsson 2001; Knudsen et al. 2007; Skoglund et al. 2015; Saltykova et al. 2017; Simonsen et al. 2017). Several studies have shown that all these Arctic charr morphotypes are reproductively isolated from each other (Klemetsen et al. 1997; Smalås et al. 2017). Furthermore, they are also clearly and stably segregated in resource use (habitat and diet) within each lake, as shown by time-integrated trophic tracers (food borne parasite communities and stable isotopes ratios) (Knudsen et al. 2016a, Siwertsson et al. 2016). Further investigations revealed also a strong relationship between the phenotypic differences and the genetic structure of the morphs in the two lakes (Præbel et al. 2016; Simonsen et al. 2017). Thus, the morphological classification may be considered as a sound and valid approach to identify Arctic charr morphs with distinctly different ecology, life history, and genetic make-up.

Recently, two new lakes from this same region, Tårnvatn and Skøvatn, were found with polymorphic populations (three and two putative morphs respectively). The morphology and the capture habitat of the morphs in these lakes strongly resemble the charr varieties described in Fjellfrøsvatn and Skogsfjordvatn, with both lakes having a normal growing LO-morph and a potential small-sized PB-morph. In addition, Tårnvatn may host a large profundal morph similar to the PP-morph in Skogsfjordvatn. The two lakes are both deep, dimictic and oligotrophic, and experience an analogous subarctic climate similarly to Fjellfrøsvatn and Skogsfjordvatn. Moreover, they host similar fish communities and likely have the same variety and distribution of prey resources (i.e. zooplankton and benthic invertebrates) for fish. Hence, although little is known about their ecology and life history, the same nomenclatures (i.e. LO, PB, PP) have been used to name the potentially different morphs.

In this study, the trophic ecology of polymorphic Arctic charr populations (morphs) in Tårnvatn and Skøvatn is explored by using several different methods like stomach contents examination, food-transmitted parasites identification and stable isotopes analysis (SIA). The first hypothesis of this investigation was that the sympatric charr morphs had a clear trophic niche divergence within each of the two study lakes (habitat and diet preferences) that was stable in time (parasite community and SIA as long-term ecological tracers). Secondly, since two of the morphs had similar phenotypes in both lakes, it was hypothesized that charr populations have undergone parallel evolutionary processes in respect of the LO- and PB- morphs, similarly as described for Fjellfrøsvatn and Skogsfjordvatn. In particular, it was predicted that the LO-morphs had a generalist foraging behaviour, feeding on pelagic zooplankton and littoral benthos, in contrast to the small-sized deep-water morphs being specialized in eating profundal soft-bottom macro invertebrates. Finally, it was hypothesized that the potential PP-morph in Tårnvatn had a piscivorous feeding strategy, preying upon small-sized charr (i.e. cannibalistic) in the profundal habitat, as in Skogsfjordvatn.

Material and methods

Study site description

In this study, two postglacial lakes were sampled: Tårnvatn and Skøvatn. Both lakes are located in the subarctic region, in Troms county, northern Norway. At this latitude, there are approximately two months of midnight sun during summer (May-July) and two months of polar night in winter (November-January). Both lakes are oligotrophic and dimictic, and they are usually icebound six-seven months a year (December to May/June). The distance between the two water bodies is about 33 km as the crow flies (Google-maps).
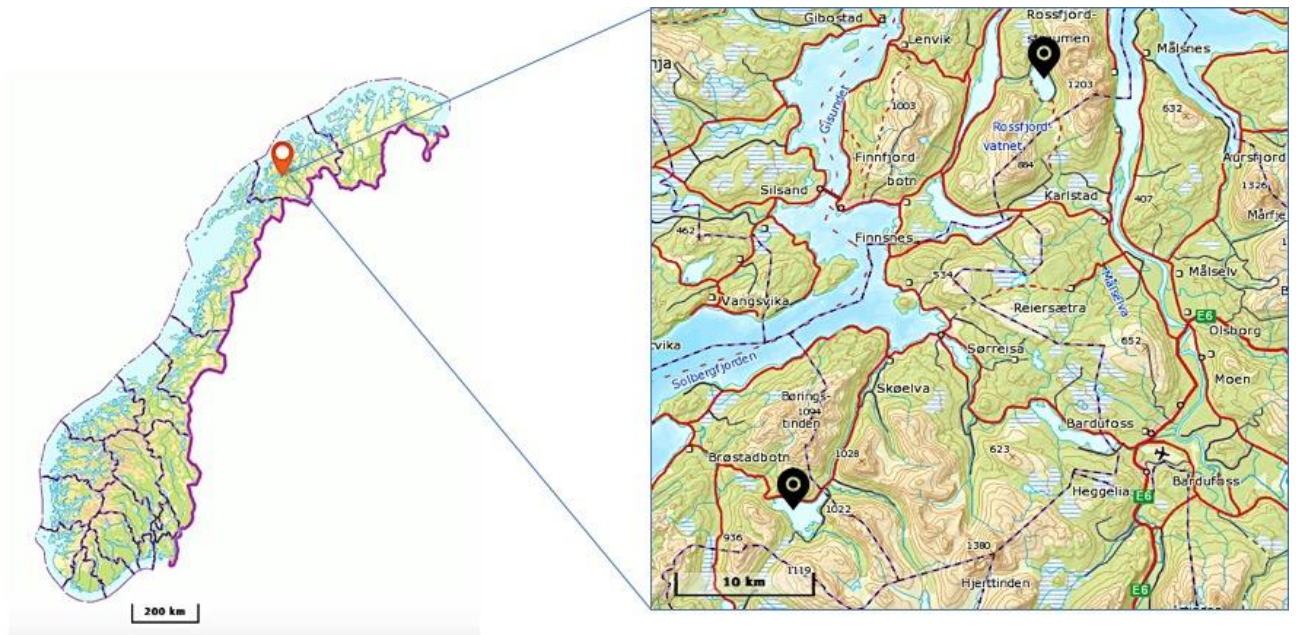
Figure 1. The map of Norway with the location of the two lakes (from norgeskart.com).

Lake Tårnvatn (69°18'N 18°21'E) is situated in the mucipality of Lenvik at 107 m above sea level. It has a surface area of 3.21 km^2 and a maximum depth of 53 m (Schartau et al. 2017; Norges vassdrag- og energidirektorat, 2018). The catchment area of the lake is 34,1 km^2, consisting of mountains with alpine landscape and woodland dominate by birch (*Betula pubescens*). The lake has three affluent rivers (Svartbekken, Fiskebekken and Mellælva) and a 2 km long emissary, Tårnelva river, that drains into Rossfjordvatnet, a meromictic lake directly connected to Malangen fjord, which harbours several fish species including anadromous

salmonids. Despite this connection, in Tårnvatn there is no anadromous fish, since the migration upstream from the fjord is prevented by the steep river's conformation. The anthropic impact on the lake in terms of nutrient loadings is low, as only few cottages and no farmlands are located around the basin. The total phosphorus and nitrogen levels are 2.0 and 121 µg/l, respectively (Schartau et al. 2017). The Secchi depths measured during sampling in late October was at 10 meters. The lake is hardly accessible in winter, when the only existent road is closed and, thus, it is impossible to reach Tårnvatn by car. The lake has a very simple fish community, consisting entirely of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*).
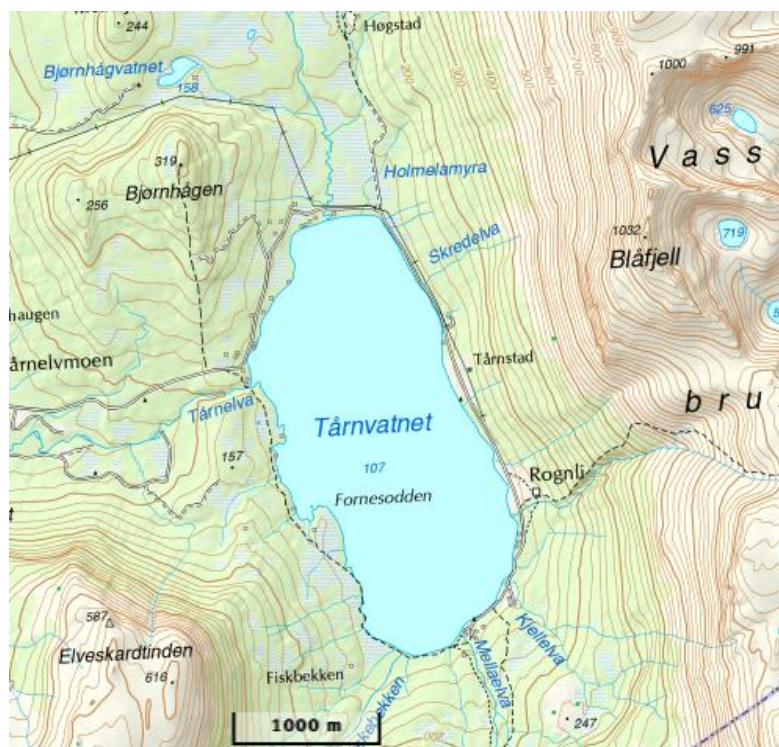
Figure 2. Map of Lake Tårnvatn (norgeskart.com).

Lake Skøvatn (69°01'N 17°52'E) is located in between the municipalities of Sørreisa and Dyrøy at 180 m above sea level and has an area of 6.2 km^2. The mean and the maximum depths of the lake are 41m and 119 m, respectively. The drainage basin is 51.6 km^2 in area and consists of relatively low mountains, birch forests interrupted by marshes and some farm lands which may provide the lake with some humic influxes (Norges vassdrag- og energidirektorat, 2018). The Secchi depth in October was registered to be 8 m. The lake is easily accessible by means of a paved road along the north side and some minor roads allowing to reach numerous cabins. The lake has two tributaries (Mølnelva and Sæterelva) and one outflowing river (Skøelva),

which links Skøvatn to Finnfjord. The lake contains mostly resident Arctic charr and brown trout, but occasionally also anadromous individuals, including Atlantic salmon (*Salmo salar*), that can exploit the unhindered Skøelva river to migrate upstream from the sea (Smalås & Henriksen 2016). In the late 1980's the landowner's association concluded that the Arctic charr population in the lake was stunted. Since 1989 until recently a massive removal of small-sized charr (more than 650 000 individuals removed) has been operated by local landowners (Smalås & Henriksen 2016).

Figure 3. Map of Lake Skøvatn (norgeskart.com).

Data collection

Fish sampling

Fishing was conducted in late October 2016. In order to get a representative overview of the habitat distribution and size composition of the fish populations present in the lake, three different types of monofilament gillnets of various mesh sizes were used: two multi-mesh sized nets called BGO and FGO and a standard size single mesh gillnet (SG). The BGO gillnet (from Norwegian "Benthic Gillnet Overview") is 40 m long and 1.5 m deep and was used to survey

the benthic areas in littoral (1-15 m depth) and profundal (>15 m depth) habitats. The FGO net (from Norwegian "Floating Gillnet Overview") is 40 m long and 6 m deep and was used to sample the (epi)pelagic zone (offshore, 0-6 m depth). These two types of gillnets have eight randomly distributed panels, each 5 m long with bar mesh size 10, 12.5, 15, 18, 22, 26, 35 and 45 mm. The SG (from Norwegian "Standard Gillnet") is a bottom net measuring 30 m long and 1,5 m deep which has only a single meshing size throughout the whole net. Also this gillnet was used both in the littoral and the profundal zone. The gillnets were set out in the evening, left overnight for approximately 12 hours, and taken out the following morning.

Tårnvatn

Fish were collected in Lake Tårnvatn for two nights from 24th to 26th of October 2016. In the littoral zone, a BGO gillnet was put out at three different sites from the shoreline down to the deep (0.5-10 m). In the pelagic area, one link made up of two FGO nets was set out, anchored to a depth of 25 m. In the profundal zone, three links consisting of a BGO and a SG net (bar mesh size 6, 8, 10, 12, 20, 25, 30 and 40 mm) were put out at distinct localities at different depths (14-20, 22-27 and 27-36 m).

Skøvatn

Fieldwork in Skøvatn was carried out during the night of 26 to 27 October 2016. Three BGO gillnets were set on the littoral area at separate sites (1-15 m depth). In the profundal habitat three links were placed at different spots, at 12, 25 and 35 m depth. Each link was made up of BGO and SG nets, with a range of mesh size from 8 to 40 mm (knot to knot). The survey did not include the pelagic habitat.

After capture, all the fish (both Arctic charr and brown trout) were recorded and frozen before further laboratory analyses. Since the current study is focused only on Arctic charr, all the procedures described hereafter concern only this species. Before freezing, all the charr individuals were classified into different morph groups according to their external morphology (head and body shape and colour). The morphological characterization of the different morphs was based on previous studies on polymorphic charr populations in northern Norway (Skoglund et al. 2015; Saltykova et al. 2017). In Tårnvatn, fish were sorted into three distinct morphs: littoral spawning omnivore morph (LO), profundal spawning benthivore morph (PB) and profundal spawning piscivore morph (PP). The LO-morph adult fish has typical charr breeding coloration with red-orange abdomen and paired fins edged in white, while the basic

body colour is silver. The head and associated characters (mouth and eyes) are relatively smaller compared to the body size. Juvenile fish generally have parr marks along their body sides. The PB-morph mature fish has a pale yellow-brown coloration with a brass hue. Usually it does not have (or very pale) parr marks. The body is small and deep, and the head is relative large, blunt and rounded with big eyes compared to the short body length. The PP-morph has a slender elongated body shape, a robust, large, pointed head with sharp teeth on the palate and the tongue. The head, the caudal fin and the back are very dark, with shades of grey and black, while the abdomen and the flanks have an opaque orange colour with white bordered paired fins, similarly to LO-morph. In Skøvatn, charr were separated in two morph groups: LO-morph and PB-morph. The LO-morph has the same appearance as the LO in Tårnvatn, whereas the PB-morph resembles the PB-morph of Tårnvatn but has clearer and more silvery body colour with evident parr marks.

In the laboratory, fork length (mm) and weight (g) were measured for each charr. The abdomen was opened and cysts plerocercoids of *Diphyllobothrium* spp. occurring on the stomach wall, visceral organs and flesh were enumerated. Stomachs were removed and conserved for diet analysis, while intestine, kidney and swim bladder were separated for parasites examination. A sample of muscle tissue for stable isotope analysis was cut out and stored at - 20°C.

Zooplankton and zoobenthos sampling

In both lakes, pelagic zooplankton and littoral zoobenthos were collected for stable isotope analysis. 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. The specimens were frozen and conserved at -20 °C. Benthic littoral macroinvertebrates were sampled using a benthos hand square net.

Stomach content analyses

Laboratory analyses

The stomachs were opened, and the fullness was estimated by using a percentage scale from 0% (empty) to 100% (full). The prey items were identified and sorted to taxonomic groups, and their contribution to the total stomach fullness was evaluated (0-100%) (Amundsen 1995). The different prey types were divided into five categories: zooplankton (cladocerans and copepods), littoral benthos (gastropods, larvae of mayflies, stoneflies, caddisflies, and fish eggs), *Gammarus lacustris*, profundal benthos (Chironomid larvae, *Pisidium* sp. Mussels and *Acanthocyclops* sp. benthic copepods), and fish. In Tårnvatn, 13.8 % of the LO-morph, only few PB-morph (4.3 %), and almost half of the PP-morph (44.4 %) individuals had empty stomachs. While there were only 3.6 % of the LO-morph and 11.4 % of the PB-morph with empty stomachs in Skøvatn. Stomach content analysis allowed to describe the short-term diet of fish (approximately until 1-2 days before the capture) (Hayden et al. 2014; Knudsen *et al.* 2014).

Data and statistical analyses

Diet composition

The proportion of each prey type to the diet was estimated as percent prey abundance (A_i):

$$A_i = (\Sigma\ S_i\ /\ \Sigma\ S_t) * 100,$$

where S_i is the total stomach fullness of prey category i and S_t is the total stomach fullness of all the fish individuals in a group or population (Amundsen et al. 1996).

Diet width

The diet niche width of the different morphs and size classes of Arctic charr was assessed from stomach contents using the Levins' B index (Levins 1968):

$$B = 1/\Sigma p_i^2,$$

where p_i is the proportion of prey i in the diet of a length group or population. It this study B could have values between 1 (only one prey category is present) and 12 (equal percent abundance of all prey types).

Diet overlap

Dietary similarity between the different charr morphs and size groups within and between the lakes was determined using Schoener's index (D) (Schoener 1970):

$$D = 100 * (1 - 0.5 \Sigma \, |p_{ix} - p_{iy}|),$$

where D is the percent food item overlap, p_{ix} is the fraction of resource i in the diet of fish x, and, p_{iy} is the proportion of prey type i eaten by fish y. A value of 0 % expresses no diet overlap and 100 % full overlap. The diet similarity is commonly interpreted as biologically significant at values > 60 % (Wallace 1981).

NMDS

To visualize the diet of the charr morphs in the two lake systems a non-metric multidimensional scaling analysis (NMDS) based on Bray-Curtis index of similarity was used (Kruskal & Wish 1978). This was executed using the vegan package in R (Oksanen et al. 2013). The Bray-Curtis similarity matrix was generated from the relative abundances of 13 prey items for each fish individual of all the charr morphs in both lakes (Knudsen et al. 2016a). Fish individuals with a stomach   fullness < 1 % were not included in the analysis. The stress criterion was used to establish if the two-dimensional representation was an accurate illustration of the multivariate data. A stress value < 0.2 is considered as an indication of good fit (Kruskal & Wish 1978).

All the analyses were conducted in R, version 3.3.1 (R Core Team, 2016), and Microsoft excel (2016).

Parasites identification

Most fish parasites are trophically transmitted, i.e. the fish hosts are infected by particular parasites through the food consumption of specific organisms (Curtis 1995). In the case of Arctic charr, particularly relevant parasites are transmitted by the amphipod *Gammarus lacustris* (*Cyathocephalus truncatus*, *Cystidicola farionis* parasites), insect larvae (*Crepidostomum* and *Phyllodistomum umblae*) and different species of pelagic copepods (*Eubothrium salvelini*, *Proteocephalus* sp., *Diphyllobothrium* spp., *Philonema oncorhynchi*) (Knudsen 1995; Knudsen et al. 1997, 2007, 2014; Jonsson & Jonsson 2001; Siwertsson et al. 2016). Thus, by means of the parasites in fishes it is possible to trace the long-term diet (months

or years, depending of the parasite life expectancy) and the habitat utilization of the fish (Knudsen et al. 1996; Knudsen et al. 2014). For this reason, all the parasites were identified and enumerated. Since generally parasites colonize specific parts of the host, a particular emphasis was placed on the body cavity (for *Diphyllobothrium* spp. and *P. oncorhynchi*), intestine (trematodes and cestodes), swim bladder (*C. farionis*) and kidney (P. umblae).

Table 1. Latin names, class, intermediate hosts and habitat of the most relevant trophically transmitted Arctic charr parasites.

Parasite species	Class	Intermediate host	Fish host habitat
Diphyllobothrium spp.	Cestodes	Copepods	Viscera
Cyathocephalus truncatus	Cestodes	*Gammarus lacustris*	Intestine
Eubothrium salvelini	Cestodes	Copepods	Intestine
Proteocephalus sp.	Cestodes	Copepods	Intestine
Cystidicola farionis	Nematodes	*Gammarus lacustris*	Swim-bladder
Philonema oncorhynchi	Nematodes	Copepods	Viscera
Crepidostomum spp.	Trematodes	Insect larvae	Intestine
Phyllodistomum umblae	Trematodes	Insect larvae	Kidney

Laboratory analyses

All the fish body cavities were controlled for P. *oncorhynchi and* cysts of *Diphyllobothrium* spp.. Swim bladders and kidneys were examined, and all the detected parasites enumerated. The intestines and pyloric caeca were cut out and the content was shaken in a glass containing water and filtered (with a 180 µm filter) in order to separate intestinal parasites and food items from the mucus. Subsequently, all the parasites were identified, and their number registered.

Data and statistical analyses

Prevalence, mean abundance, and mean intensity were calculated for each parasite in both lakes according to the terminology by Bush et al. (1997).

Prevalence is the proportion (%) of individuals in a host population infected with one or more specimens of a particular parasite species (number of hosts infected / total number of hosts examined x 100).

Mean abundance is the average number of individuals of a given parasite species in a host population (number of parasites / total number of hosts examined).

Mean intensity is the average number of individuals of a given parasite species among the infected members of a host population (number of parasites / total number of infected hosts).

Similarity

The Renkonen index of similarity (P) (Krebs 1989) was used to quantify similarities in parasite community between size groups and morphs within and across the lakes:

$$P = 100 * (1 - 0.5 \, \Sigma \, |p_{ix} - p_{iy}|),$$

where P is the percentage parasite similarity between sample x and y, p_{ix} is the fraction of parasite species *i* in the fish sample *x*, and, p_{iy} is the proportion of parasite *i* in the fish population *y*. A value of 0 % expresses no similarity and 100 % complete equivalence. The Renkonen index is equivalent to Schoener's index used for the diet. However, the former is generally used for community comparisons, the latter for diet overlap calculations.

Diversity

To assess the diversity in parasite community among the charr morphs the frequency distribution (%) of the number of parasite species per host and the avearge parasite species richness (mean number of different parasite species per individual) were calculated (Poulin 1995).

Statistical tests

Parasites data hardly fit normal distribution, since macro parasites tend to be accumulated over their host population, with most host individuals having low numbers of parasites, and few hosts suffering high infections (Shaw & Dobson 1995; Wilson & Grenfell 1997). Thus, differences in parasite species richness among the morphs were evaluated mainly using the non-parametric Mann-Whitney U test. The parametric Student's t test was used only for a single comparison after a log-transformation (ln + 1) to fit parametric assumptions. Differences in abundance of parasite species within and across lakes were tested using a generalized linear models (GLMs) assuming a Poisson distribution. The GLMs are considered as an effective tool for testing the typical negative binomial distribution of parasite counts (Wilson & Grenfell

1997). For pairwise tests, a Bonferroni correction was applied in order to limit the increased error rate correlated with multiple testing (Rice 1989). A P-value < 0.0125 was considered as significant.

NMDS

A non-metric multidimensional scaling analysis (NMDS) based on Bray-Curtis index of similarity was used to visualize differences in parasite assemblages among charr morphs in the two lake systems (Kruskal & Wish 1978). This was conducted using the vegan package in R (Oksanen et al. 2013). The Bray-Curtis similarity matrix was generated from the abundance of 6 parasite species for each fish individual of all the morphs in both lakes.

Stable isotope analyses (SIA)

With stable isotope analysis, it is possible to assess the trophic habitat and the food web position of predators (Zanden & Rasmussen 1999, 2001; Post 2002; Buchheister & Latour 2010; Knudsen et al. 2014). In a lacustrine ecosystem, each organism has a specific composition of carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotopes, and the ratio values of lighter (^{12}C and ^{14}N) and heavier (^{13}C and ^{15}N) isotopes of a consumer depend on the isotopic composition of its feeding source (Zanden & Rasmussen 1999; Jardine et al. 2003; Eloranta 2007). The δ^{13}C ratio varies nearly insignificantly between prey and predator (enrichment of 0.4 ‰ in average) (Zanden & Rasmussen 1999) and, thus, it can be used as dietary tracer to infer the foraging habit of consumers (Zanden & Rasmussen 2001; Post 2002; Fry 2006). On the other side, the δ^{15}N value changes markedly from a trophic level to another, with an enrichment of ^{15}N of approximately 3-4 ‰ and, therefore, it provides a tool to estimate the trophic position of a predator in a food web (Zanden & Rasmussen 1999).

Laboratory analyses

To perform the SIA, a flesh sample from each fish was cut out, because the muscle tissue has a long isotopic turnover rate and permits to evaluate the long-term diet (last 3-4 months before capture) (Post 2002; Buchheister & Latour 2010; Knudsen et al. 2014). These specimens, along with zoobenthos and plankton samples (used as base-line isotopes indicators) (Zanden & Rasmussen 1999; Post 2002), were dried at 60°C for 24 hours, powdered using a pestle and

mortar, and weighed (1 ± 0.1 mg) (see e.g. Guiguer et al. 2002; Power et al. 2009; Hayden et al. 2014 for detailed method description). The analyses were performed at the University of Waterloo, Canada. The dried tissue samples were analysed for $\delta^{13}C$ and $\delta^{15}N$ through combustion conversion of sample material to gas through a 4010 Elemental Analyzer (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer (CFIRMS). The stable isotope ratios were calculated by the equation:

$\delta X = [(Rsample/Rstandard) - 1] * 1000$

where X is either 13C or 15N, R is the ratio of the heavy isotope to the light isotope for the element X. International standard ratios were used for carbon (Vienna PeeDee Belemnite) and nitrogen (atmospheric nitrogen) (Fry 2008).

Data and statistical analyses

Mean stable isotope values

Pair-wise Mann-Whitney U tests were used to test differences in $\delta^{13}C$ and $\delta^{15}N$ values among the morphs within the two lakes. A Kruskal-Wallis test was performed for comparing more than two morphs (Tårnvatn). The P-values were adjusted using a Bonferroni correction. For all tests a P-value < 0.0125 was considered statistically significant.

Comparison of SI values between lakes were not implemented as $\delta^{13}C$ and $\delta^{15}N$ can be considerably diverse among different aquatic ecosystems (Jardine et al. 2003; Post 2002).

Isotopic niche width and overlap

To estimate the isotopic niche width of each morph, mixing models were used in the SIBER package in R (Jackson et al. 2011). The standard ellipse area corrected for sample size (SEA$_C$; Jackson et al. 2011) was calculated to measure the niche width of each morph. A Bayesian estimation of SEA$_c$ was further calculated to overcome differences in sample size among morphs (SEA$_B$; Jackson et al. 2011).

To quantify the niche overlap between morphs the core isotopic niche overlap of SEA$_C$ (CIO) was calculated (Van Dorst 2015).

Correlation diet – parasites – stable isotopes

The correlation between stomach contents, trophically transmitted parasites, and stable isotopes values was performed by Mantel permutation tests (Mantel 1967) with the Vegan package in R (Oksanen et al. 2013). To run Mantel tests, similarity matrices between morphs were implemented. Bray-Curtis distances were used for diet and parasites matrices, while Euclidean dissimilarities were used for stable isotopes.

Results

Habitat distribution

In Skøvatn, the small-sized PB-morph was caught nearly exclusively in deep-water (15 and 25 m deep), whereas most of the LO-morph individuals were caught in upper-water layers (Tab. 2).

Table 2. Habitat choice of the different Arctic charr morphs in Skøvatn (October 2016).

Skøvatn		Habitat choice (%)		
Morph	**n**	**Littoral**	**Pelagic**	**Profundal**
LO	56	70	-	30
PB	35	3	-	97

The LO-morph in Tårnvatn was caught in all the habitats, but predominantly in shallow waters (65%) (Tab. 3). In contrast, all the PB- and PP- morphs showed a strong preference for the profundal zone and were only caught at depths > 35 m (Tab. 3).

Table 3. Habitat choice of the different Arctic charr morphs in Tårnvatn (October 2016).

Tårnvatn		Habitat choice (%)		
Morph	**n**	**Littoral**	**Pelagic**	**Profundal**
LO	65	34	31	35
PB	23	0	0	100
PP	27	0	0	100

Recent diet

Within-lake variation

A total of 14 different prey types were identified in the 180 stomachs analysed for both lakes (Appendix Tab. 1 for details).

The diet of the LO-morph in Skøvatn was relatively broad (niche width index: 3.27, Appendix Tab. 3), including zooplankton (exclusively cladocerans; percent abundance: 39.6 %), and littoral benthos, with *Gammarus lacustris* as main benthic prey (46.9 % abundance) (Fig. 4, Appendix Tab. 1). In Skøvatn, the small-sized profundal morph fed mainly on zooplankton (abundance: 74.2 %), particularly on the cladocerans *Bosmina* and *Daphnia* spp. (Fig. 4, Appendix Tab. 1) and had a niche breadth of 3.63 (Appendix Tab. 3). In Skøvatn, therefore, the two morphs revealed two distinct feeding strategies with a diet overlap of 49 % (Schoener's similarity index; Appendix Tab. 2).

In Tårnvatn, the LO-morph had also a wide diet (3.69 niche breadth; Appendix Tab. 3), inclusive of zooplankton (cladocerans; 60.4 %), and littoral benthos, with *Gammarus* as an important benthic prey (25.6 %) (Fig. 4, Appendix Tab. 1). The PB-morph had mainly eaten potential profundal benthic prey groups (79.6 %), mostly chironomid larvae (Fig. 4, Appendix Tab. 1), and thus had a narrow diet breadth (2.46; Appendix Tab. 3). The PP-morph in Tårnvatn exhibited two principal food categories: profundal benthos (60.1 %) and fish (juvenile charr; 31.8%) (Fig. 4, Appendix Tab. 1). Due to the high consumption of profundal benthic food, the PP-morph had a significant dietary similarity with PB-morph in the same lake (65%; Appendix Tab. 2) and an equal diet width index (2.46; Appendix Tab. 3). In contrast, the diet overlap of LO- and PP-, and LO- and PB- morphs in Tårnvatn appeared well distinct (15% and 26% diet overlap, respectively; Appendix Tab. 2).

Between-lake variation

The LO-morph showed similar stomach contents across the two lakes with a significant niche overlap of 69 % (Appendix Tab. 2) and clustered together (Fig. 5). However, there were also differences. The LO-morph in Skøvatn seemed to rely more on littoral resources than the LO-morph in Tårnvatn (59.6% vs. 31.2%), which had, on the opposite, a higher abundance of zooplankton (60.5 % vs. 39.6%) (Figs. 4, 5). The composition of the littoral preys (other than *Gammarus*) also varied between the lakes, with snails (*Radix* sp. and *Planorbidae*) as the main

food type in Skøvatn (5.7 %) and trichopteran larvae in Tårnvatn (3.8 %) (Fig. 5, Appendix Tab. 1).

The two small-sized deep-water morphs, on the other hand, revealed contrasting feeding strategies in the two lakes with a low diet overlap of 28% (Appendix Tab. 2). Conversely to the zooplanktivorous PB-morph in Skøvatn, the diet of the PB-morph in Tårnvatn was dominated by profundal benthic macroinvertebrates (Figs. 4, 5, Appendix Tab. 1). High feeding on cladocerans, caused the PB-morph in Skøvatn to cluster relatively close to the LO-morphs from both lakes (Fig. 5).

The PP-morph had the most distant diet to all morphs, mainly associated to fish consumption (Fig. 5).
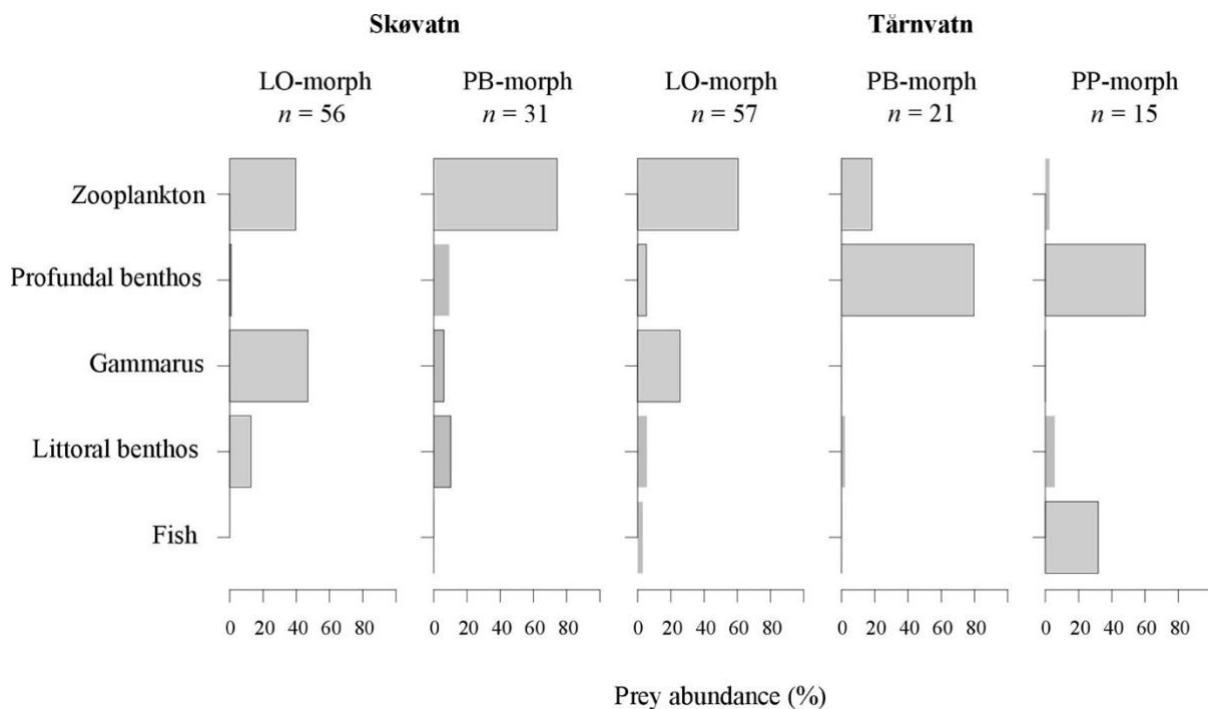
Figure 4. Percent abundances of major prey groups found in the stomach contents of the different morphs of Arctic charr in samples from Skøvatn and Tårnvatn (October 2016).
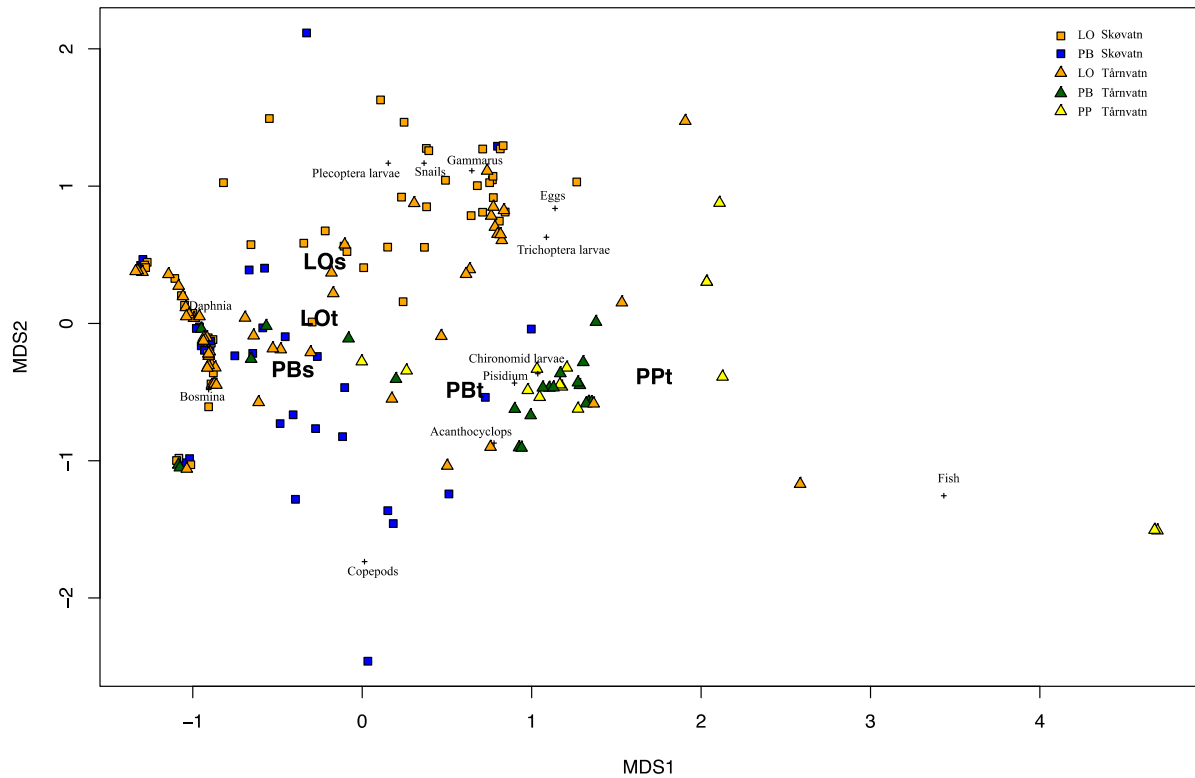
Figure 5. Diet composition of individual Arctic charr of the various morphs in Skøvatn and Tårnvatn depicted by non-metrical multidimensional scaling (NMDS; stress = 0.12). LOs = LO-morph in Skøvatn, PBs = PB-morph in Skøvatn, LOt = LO-morph in Tårnvatn, PBt = PB-morph in Tårnvatn, PPt = PP-morph in Tårnvatn. The acronyms indicate average values for each morph in the two lakes.

Ontogenetic changes

The diet of the LO-morphs exhibited different ontogenetic diet patterns between the two lakes (Fig. 6a). In Skøvatn, there was a clear shift from a zooplanktivorous feeding behaviour in the small individuals (< 150 mm) (93.7 %; niche breadth: 2.26, Appendix Tab. 3) towards a diet based entirely on benthic prey (100 %; niche breadth: 1.60, Appendix Tab. 3) in the largest individuals (> 250 mm) (Fig. 6a). The intermediate size class (150 – 250 mm) had a mixed diet composed by benthic preys (73.8 %) and to a lesser extent by zooplankton (26.2 %) (niche breadth: 2.47, Appendix Tab. 3) (Fig. 6a). The niche overlap was low between the small individuals and intermediate sized fish (32 %), and small and large individuals (5 %) (Appendix Tab. 2). On the opposite, there was high similarity between the intermediate and

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large size groups, with an overlap of 64 % (Appendix Tab. 2). Similarly, the LO-morph in Tårnvatn had high abundance of zooplankton in the smallest size class (87.2 %, Fig. 6a; niche width: 2.02, Appendix Tab. 3). Nevertheless, in this lake, pelagic zooplankton remained the prevalent food source even in the intermediate sized-charr (44.6 %; niche width: 4.42) and in the largest individuals (70.8 %; niche width: 1.91) (Fig. 6a, Appendix Tab. 3). There was a moderate diet overlap between small and intermediate sized charr (46 %), and between small and large individuals (35 %). In contrast, the similarity between medium- and large-sized fish was high (66%) (Appendix Tab. 2).
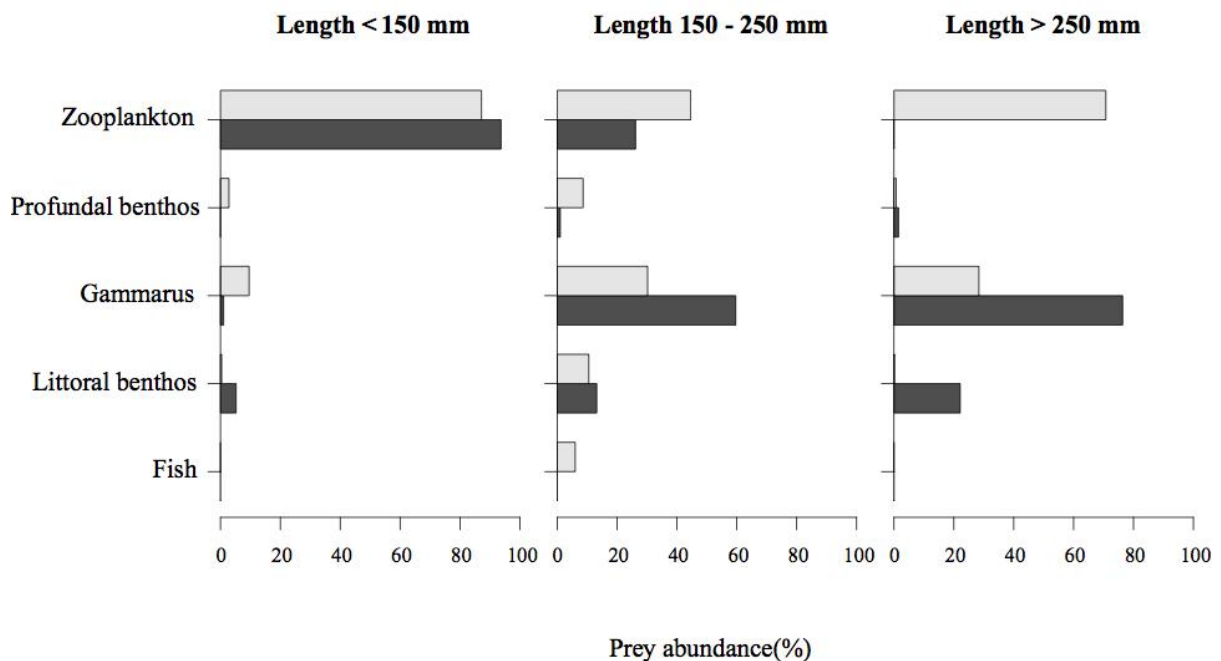
Figure 6a. Prey abundance of different size groups of LO-morph from October sampling. Skøvatn (black bars) has 17, 30, and 7 individuals for the three size-classes respectively, Tårnvatn (grey bars) has 12, 30, 14 individuals.

In the PP-morph (Tårnvatn), the diet was distinctly different between the two size-classes (21 % overlap; Appendix Tab. 2). The PP-morph < 200 mm consumed nearly exclusively profundal benthos (92.5 %, Fig. 6b; niche width: 1.37). The larger individuals (> 200 mm) relied predominantly on fish as prey (72.5 %; niche width: 1.79) and to a little extent on benthic

food (18.7%) (Fig. 6b). The two small-sized PB-morphs did not change diet by increasing size (not shown).

Length < 200   **Length > 200**
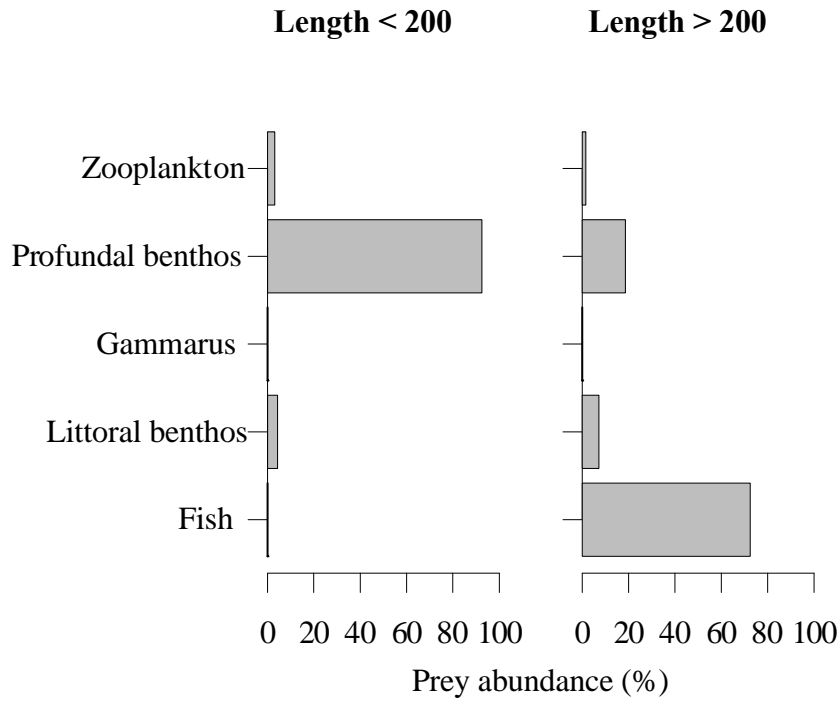
Figure 6b. Prey abundance of small (< 200 mm, n = 7) and large (> 200 mm, n = 8) PP-morph individuals from Tårnvatn (October 2016).

Parasites analyses

Parasite community composition

In total, six different food borne parasite genera were recorded in Arctic charr in both lakes, including four cestodes (*Diphyllobothrium* spp., *Eubothrium salvelini*, *Proteocephalus* sp., and *Cyathocephalus truncatus*) and two trematodes (*Crepidostomum* spp. and *Phyllodistomum umblae*). No nematodes (*Cystidicola farionis* and *Philonema oncorhynchi*) were found in any fish. The parasite communities were dominated by the copepods-transmitted *Diphyllobothrium* spp. and the insect larvae-transmitted *Crepidostomum* spp., which accounted for 49% and 29% of the total number of parasite individuals recorded in Skøvatn and 41% and 28% in Tårnvatn. All the morphs in the two lakes harboured all six parasites taxa.

Parasite species richness and total abundance

The LO-morph in Skøvatn had the highest parasite richness, harbouring up to six different parasites genera in one individual (mean: 3.3 ± 1.7 SD) (Mann-Whitney U test: P < 0.001; Appendix Tab. 4) (Fig. 7 and Tab. 4). In contrast, a low parasite richness (1.5 ± 0.8 SD) with a maximum of four parasite taxa was recorded in one PB-morph individual (Fig. 7 and Tab. 4). The LO-morph had also the highest parasite abundance (118.7 ± 33.6 SE) compared with the PB-morph (67.9 ± 17.4 SE) (Tab. 4).

In Tårnvatn there was no significant difference in parasite specie richness between the LO- (3.7 ± 1.3 SD) and PB- (1.8 ± 0.9) morphs (Mann-Whitney U test: P = 0.215; Appendix Tab. 4) (Fig. 7 and Tab. 4). On the other hand, the PB-morph had the lowest number of parasites (1.8 ± 0.9 SD; Mann-Whitney U and Student's t tests P < 0.001; Appendix Tab. 4) (Fig. 7 and Tab. 4). The PP-morph had the highest total parasite abundance (134.7 ± 36.9 SE), followed by the LO-morph (81.2 ± 20.3 SE), whereas the PB-morph had the lowest (7.5 ± 3.2 SE) (Tab. 4).

The parasite species richness was similar between the two LO- morphs (P = 0.185) and PB-morphs (P = 0.094) from Skøvatn and Tårnvatn (Fig. 7, Tab. 4, Appendix Tab. 4). However, the LO- and PB- morphs in Skøvatn had a higher total parasite abundance than the corresponding morphs in Tårnvatn (Tab. 4).
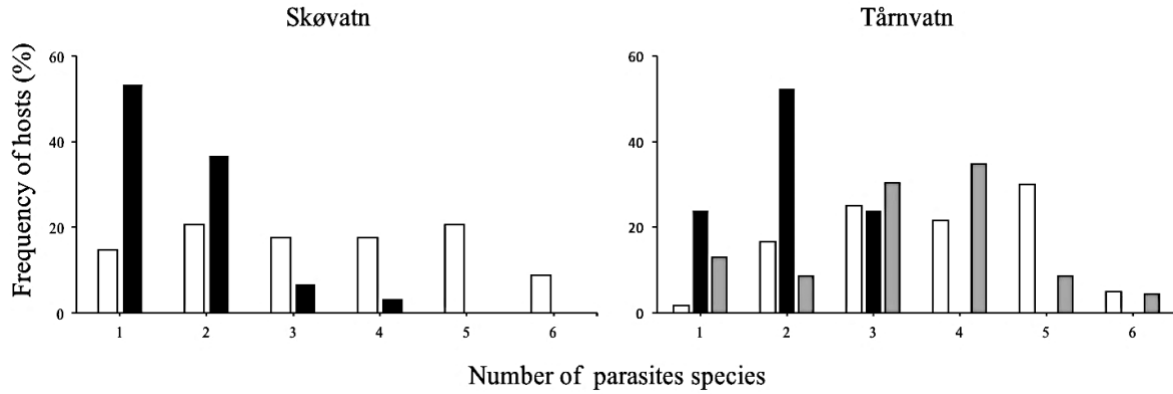
Figure 7. Distribution (%) of the number of parasite species per host in the different morphs of Arctic charr in Skøvatn (*left*) and Tårnvatn (*right*). *Black bars* represent the PB-morph, *open bars* the LO-morph, and *grey bars* the PP-morph.

Table 4. Parasite species richness (mean ± S.D) and total mean parasite abundance (mean ± S.E) of different Arctic charr morphs in Skøvatn and Tårnvatn.

	Skøvatn		Tårnvatn		
	LO-morph	PB-morph	LO-morph	PB-morph	PP-morph
Species richness	3.3 ± 1.7	1.5 ± 0.8	3.7 ± 1.3	1.8 ± 0.9	3.3 ± 1.3
Mean abundance	118.7 ± 33.6	67.9 ± 17.4	81.2 ± 20.3	7.5 ± 3.2	134.7 ± 36.9

Prevalence

In Skøvatn, the parasites with highest prevalence in the LO-morph were *Diphyllobothrium* spp. and *Crepidostomum* spp. (equal prevalence of 77.1 %), followed by *C. truncatus* (54.3 %), *E. salvelini* (48.6 %), *Phyllodistomum umblae* (42.9 %), and the copepods-transmitted *Proteocephalus* sp. with the lowest occurrence (25.7) (Tab. 5). In contrast, the PB-morph showed a general low prevalence for all the parasites (3.1 – 31.3 %) except for *Diphyllobothrium* spp., which infected 84.4 % of the fish (Tab. 5).

In Tårnvatn, a similar pattern was observed in the LO-morph as in Skøvatn, with *Diphyllobothrium* spp. and *Crepidostomum* spp. having the highest prevalence (80.3 % and 77.0 %, respectively) (Tab. 5). However, the LO-morph in Tårnvatn showed a greater occurrence of pelagic-transmitted parasites (*E. salvelini* 65.6 %, *Proteocephalus* sp. 62.3 %),

but lower of *Gammarus*-transmitted *C. truncatus* (32.8 %) (Tab. 5). In Tårnvatn, the prevalence of the PB-morph was lower than in LO-morph for all the parasites species (Tab. 5). On the other hand, the PB-morph in Tårnvatn had a higher prevalence than the PB-morph in Skøvatn for the two trematode species, *E. salvelini*, and *Proteocephalus* sp., but lower for *C. truncatus* and *Diphyllobothrium* spp. (Tab. 5). All the individuals of the PP-morph were infected with *Crepidostomum* spp., while *Diphyllobothrium* spp. and *E. salvelini* were present in most of the fish (78.3 and 73.9 %, respectively). The trematode *P. umblae* had the lowest prevalence in the PP-morph, with 13% of fish parasitized (Tab. 5).

**Table 5.** Prevalence (%) of the different parasites taxa found in the charr morphs in Skøvatn and Tårnvatn.

Parasite species	Skøvatn		Tårnvatn		
	LO	PB	LO	PB	PP
	n=35	n=32	n=61	n=23	n=23
C. truncatus	54.3	12.5	32.8	8.7	21.7
P. umblae	42.9	3.1	52.5	4.3	13.0
Crepidostomum spp.	77.1	31.3	77.0	60.9	100
Proteocephalus sp.	25.7	9.4	62.3	47.8	43.5
E. salvelini	48.6	9.4	65.6	26.1	73.9
Diphyllobothrium spp.	77.1	84.4	80.3	34.8	78.3

Mean abundance

In Skøvatn, the highest mean abundance in the LO-morph was found for *Crepidostomum* spp. (51.2), followed by *Diphyllobothrium* spp. (28.9), *C. truncatus* (28.3) and *P. umblae* (8.5), whereas the infection rate was very low for *E. salvelini* (1.3) and *Proteocephalus* sp. (0.5) (Fig. 8, Appendix Tabs. 5, 6). On the other side, the PB-morph had generally very low infection levels, with significantly lower abundance for most of the parasites species (GLM: $P < 0.001$), except for *Proteocephalus* sp. (0.5 abundance; GLM: $P = 0.791$) and *Diphyllobothrium* spp.. The abundance of *Diphyllobothrium* spp. was surprisingly higher in the PB-morph (64.5) than in the LO-morph (GLM: $P < 0.001$) (Fig. 8, Appendix Tabs. 5, 6).

In Tårnvatn, the LO-morph had the highest abundance of *C. truncatus* (11.6), *P. umblae* (10.3), and *Proteocephalus* sp. (10.8) (GLMs: P < 0.001), whereas the PP-morph had the highest infection of *Crepidostomum* spp. (47.8), *E. salvelini* (10.0), and *Diphyllobothrium* spp. (72.2) (GLMs: P < 0.001) (Fig. 8, Appendix Tabs. 5, 6). In contrast, the PB-morph had the lowest mean abundance for all the parasites (0.1 – 2.9; GLMs: P < 0.005), aside from *P. umblae*, that infected the PB- and PP-morphs in similar number (GLM: P = 0.740) (Fig. 8, Appendix Tabs. 5, 6).

The two LO-morphs had significant differences in the abundance for all the parasites species (GLM: P < 0.01) excluding for *Diphyllobothrium* spp. infections which were similar (GLM: P = 0.231) (Fig. 8, Appendix Tabs. 5, 6). On the opposite, the PB-morph in Skøvatn had a much higher abundance of *Diphyllobothrium* spp. than the PB-morph in Tårnvatn (64.5 vs. 2.2, respectively; GLM: P < 0.001), but lower number of *Proteocephalus* sp. (0.5 vs. 1.8; GLM: P < 0.001). The abundances of the other parasite species were not significantly different (GLMs: P > 0.125) (Fig. 8, Appendix Tabs. 5, 6).
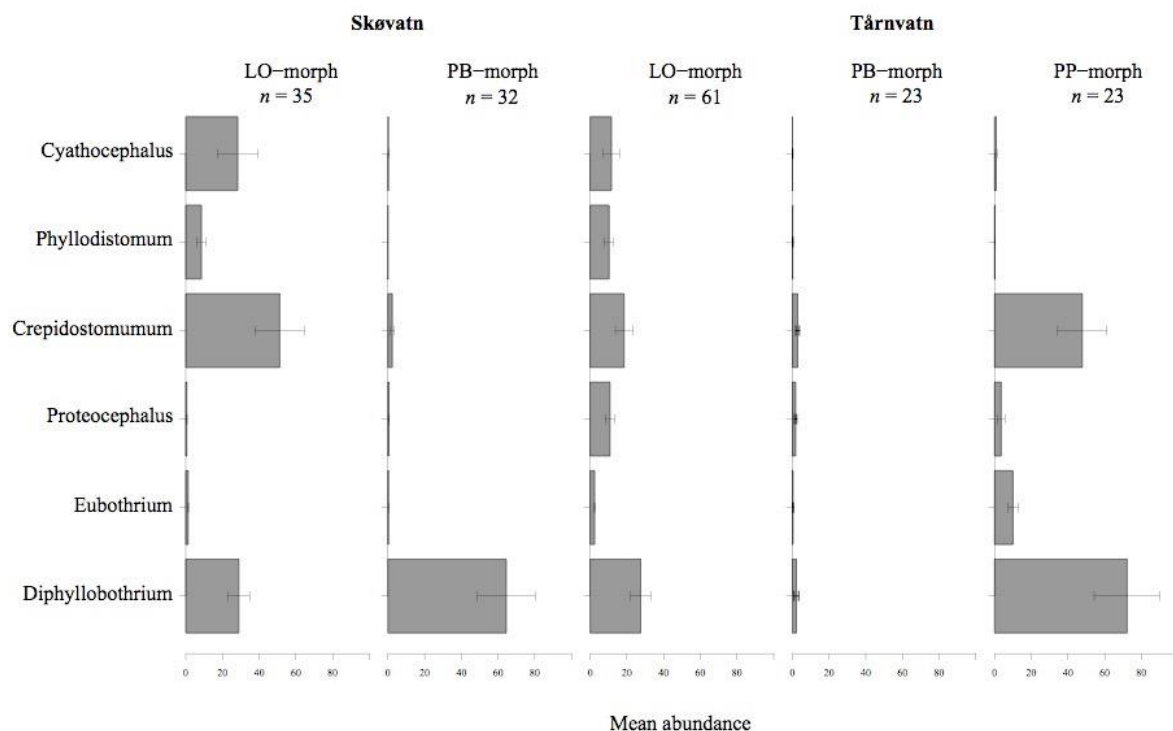
Figure 8. Mean abundance (± S.E) of the six parasites genera found in the different morphs of Arctic charr in samples from Skøvatn and Tårnvatn (October 2016).

Percent similarity and NMDS

Overall, the lowest similarity in parasite community composition (Renkonen index) was found between the LO- and PB-morph in Skøvatn (29%; Fig. 9 and Appendix Table 7). In Tårnvatn in contrast, there was a high similarity among all the morphs with index values > 60%. A comparison between the lakes revealed a high similarity in parasite community between the LO-morphs (70%) and relatively low similarity between the two small-sized profundal morphs (34%).
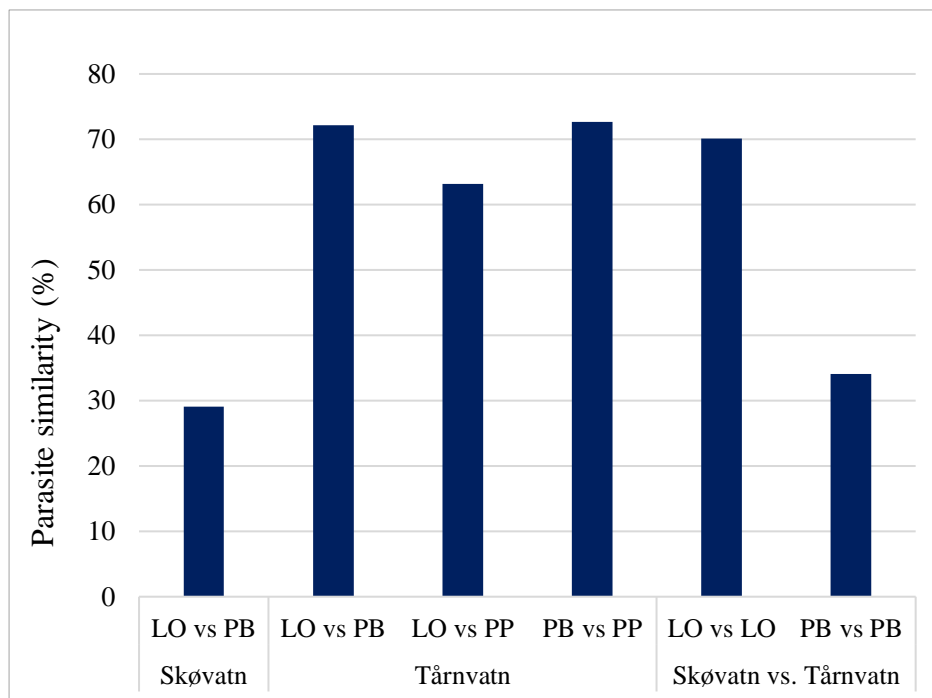
Figure 9. Parasite similarity (Renkonen index) among the different morphs in Skøvatn and Tårnvatn (October 2016 sampling).

There was a clear separation among morphs within each lake, except for the LO- and the PB-morphs in Tårnvatn, which were relatively close to each other (non-metrical multidimensional scaling NMDS; Fig. 10). The PP-morph in Tårnvatn was clearly separated from its co-occurring LO- and PB- morphs but clustered together with the LO-morph in Skøvatn. The PB-morph in Skøvatn was distinctly separate from all other morphs, and strongly associated to *Diphyllobothrium* spp. infection (Fig. 10).

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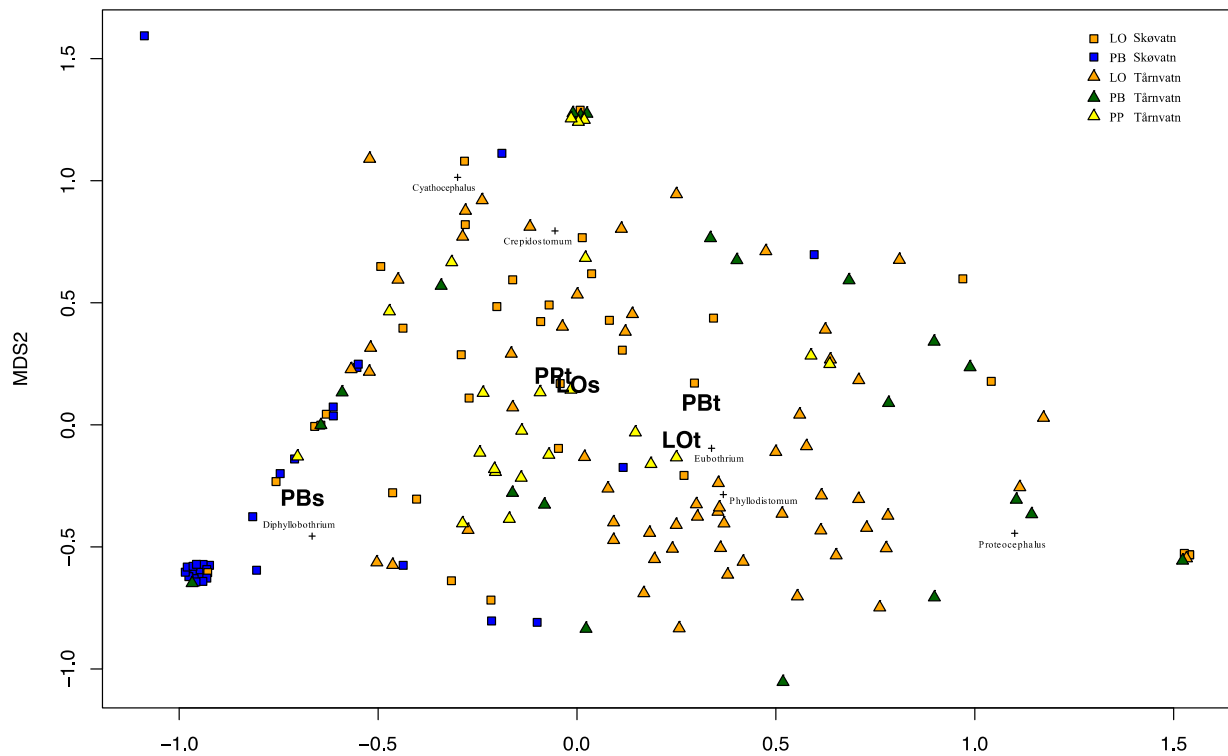
Figure 10. Parasite community of individual Arctic charr in Skøvatn and Tårnvatn (NMDS, stress = 0.17). The acronyms indicate average values of each morph in the two lakes (see Fig. 5).

Stable isotopes

Mean stable isotope values and range

In Skøvatn, the LO-morph had significantly higher mean $\delta^{13}C$ values than the PB-morph (-26.9 ‰ ± 2.1 SD vs. -28.3 ‰ ± 2.1 SD; Mann-Whitney U test: P < 0.001), but lower $\delta^{15}N$ (6.2 ‰ ± 0.7 SD vs. 8.1 ‰ ±1.0 SD; Mann-Whitney U test: P < 0.001) (Fig. 11, Appendix Tab. 8). The range of the $\delta^{13}C$ and $\delta^{15}N$ values was wide in both morphs, with the LO-morph having a larger variation in $\delta^{13}C$ (range: -30.3 to -19.1 ‰ vs. -32.7 to -23.48 ‰), and the PB-morph in $\delta^{15}N$ values (range: 5.1 to 9.3 ‰ vs. 5.0 to 8.1 ‰) (Fig. 12a).

There were also significant differences in the stable isotopes values among the morphs in Tårnvatn (Kruskal-Wallis tests: P < 0.001, Appendix Tab. 8). The PP-morph had the highest $\delta^{13}C$ mean value (-25.1‰ ± 2.1 SD; Mann Whitney tests: P ≤ 0.005) compared to its sympatric morphs, but there were no differences between the PB- and LO- morphs (Mann-Whitney U test: P = 0.478) (Fig. 11, Appendix Tab. 8). The PB-morph showed a restricted $\delta^{13}C$ range (from -28.9 to -26.5 ‰) indicative of a specialist trophic behaviour, whereas the LO- and PP-morphs presented a much larger $\delta^{13}C$ range of 11.8 and 7.1 ‰, respectively. The LO-morph had the lowest $\delta^{15}N$ values (6.8 ‰ ± 0.8 SD; Mann-Whitney U test: P < 0.001) in comparison with the other morphs. In contrast, there was no significant difference in $\delta^{15}N$ means between PB- and PP- morphs (Mann-Whitney U test: P = 0.097). Nitrogen range was comparable between the LO- and PB- morphs but was distinctly broader in the PP-morph (from 6.8 to12.6 ‰) (Fig. 12b).
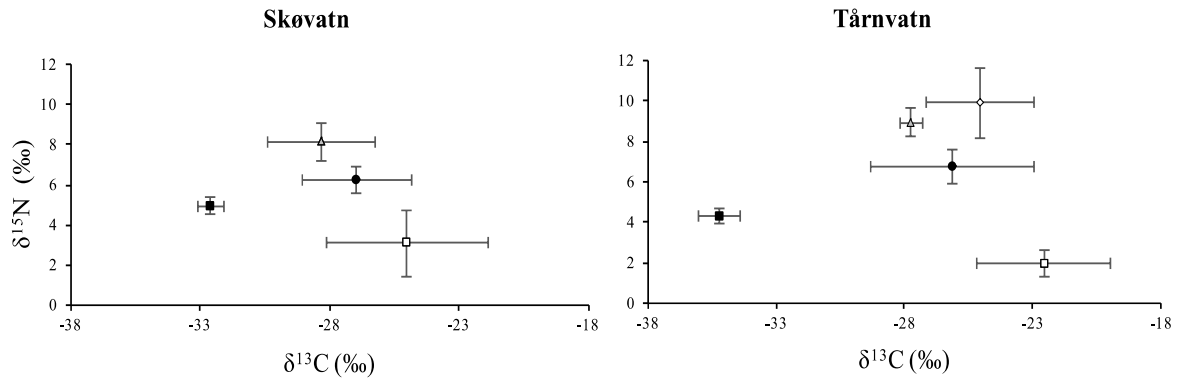
Figure 11. Stable isotope biplots displaying the mean (± SD) $\delta^{13}C$ and $\delta^{15}N$ values of muscle tissue sample of Arctic charr caught in Skøvatn and Tårnvatn in October 2016. The LO-morphs in Skøvatn (n = 29) and in Tårnvatn (n = 42) are represented by *black dots*, the PB-morphs (n = 25, 22, respectively) by *grey triangles*, and PP-morph in Tårnvatn (n = 27) by *white diamonds*. Mean values (± SD) of pelagic (□) and littoral (■) prey sampled in June 2017 are also given.

Isotopic niche width and overlap

In Skøvatn, there was no significant difference in isotopic niche width between the LO- and PB- morphs (Mann-Whitney U test: P = 0.247), which both had a relatively broad niche width (SEA$_B$ 4.61 and 5.56 ‰^{2}, respectively) (Fig. 12a, Tab. 6, Appendix Fig. 1). However, the core isotopic overlap (CIO) was quite small (25.4 %; Fig. 12A, Tab. 6).

The PB-morph had by far the narrowest niche width (Mann-Whitney U test: P < 0.001) in Tårnvatn, with a SEA$_B$ of 0.93 (Figs. 12b, Tab. 6, Appendix Fig. 1), reflecting the modest variation in the $\delta^{13}C$ and $\delta^{15}N$ values. The SEA$_B$ was much broader in the LO- and PP- morphs (7.75 and 9.82, respectively), which did not differ significantly from each other (Mann-Whitney U test: P = 0.171) (Figs. 12b, Tab. 6, Appendix Fig. 1). The core isotopic overlap was low between the PB- and PP- morphs (6.6 %) and the PB- and LO- morphs (3.4 %) and greater (but still low) between the LO- and PP- morphs (21.6 %) (Fig. 12b, Tab. 6, Appendix Fig. 1).
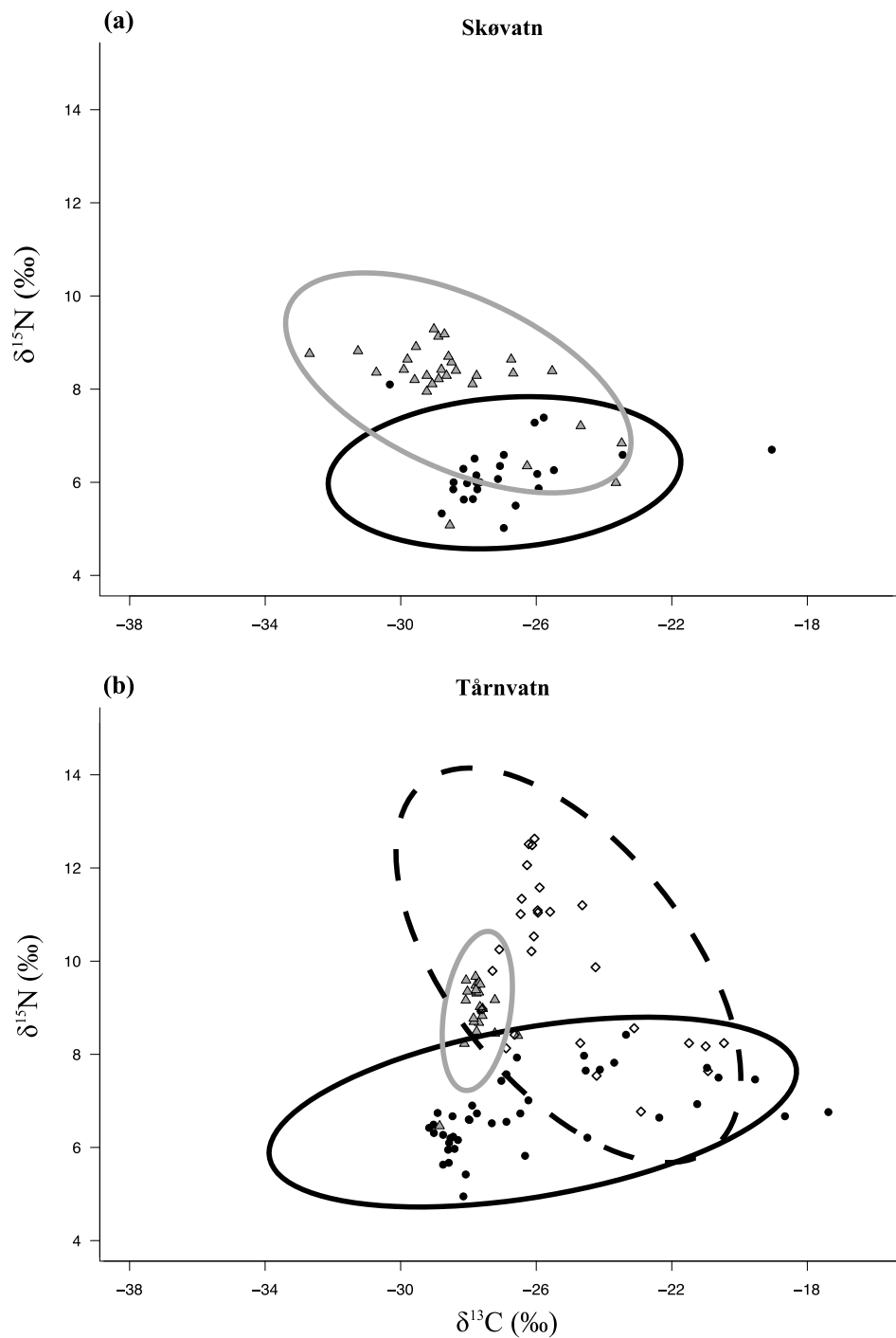
Figure 12. Stable isotopes biplot of $\delta^{13}C$ and $\delta^{15}N$ of Arcitc charr caught in Skøvatn (a) and Tårnvatn (b) in October 2016 with standard ellipse areas (SEA$_c$). The LO-morphs in Skøvatn ($n = 29$) and in Tårnvatn ($n = 42$) are represented by *black dots*, the PB-morphs ($n = 25, 22$, respectively) by *grey triangles*, and PP-morph in Tårnvatn ($n = 27$) by *white diamonds*.

Table 6. Standard ellipse area (SEAc and SEAb; mean and 95% credibility limits of Bayesian estimate) and core isotopic overlap (CIO) of Arctic charr morphs in Skøvatn and Tårnvatn.

Lake	Morph	N	SEA$_c$ (‰^{2})	SEA$_B$ (‰^{2})	CIO (%)
Skøvatn					
	LO	25	4.60	4.61 (2.88 - 6.52)	25.4
	PB	29	5.51	5.56 (3.66 - 7.58)	
Tårnvatn					
	LO	42	7.70	7.75 (5.51 -10.02)	3.4 (LO ∩ PB)
	PB	22	0.93	0.93 (0.55 - 1.36)	6.6 (PB ∩ PP)
	PP	27	9.64	9.82 (6.17- 13.56)	21.6 (LO ∩ PP)

Correlation diet – parasites – stable isotopes

There was a significant association among stomach contents and time-integrated trophic tracers (trophically transmitted parasites and stable isotopes) (significance: 0.001, 999 permutations, for all Mantel tests). The *r* values were 0.1655 (diet vs. parasites), 0.2208 (diet vs. SI), and 0.197 (parasites vs. SI). This indicates that divergences in recent diet, parasites infections, and stable isotope values among morphs most likely reflected dissimilarities of trophic niches among the five morphotypes.

Discussion

There was a clear separation in trophic niches of polymorphic Arctic charr within both lakes. This was stated from the recent niche use with clear habitat segregation and diet differences between the upper-water and profundal morphs within each lake. This niche segregation was also supported by the time-integrated trophic tracers (i.e., parasites and stable isotopes) that revealed a clear long-term trophic niche segregation among the Arctic charr morphs in both Skøvatn and Tårnvatn.

The comparison of the LO- and PB-morphs between Skøvatn and Tårnvatn revealed some unexpected results. As hypothesized, the LO-morphs in both lakes had a generalist and opportunistic trophic niche, similar as described earlier for the polymorphic populations in Fjellfrøsvatn and Skogsfjordvatn (Knudsen et al. 2006; Amundsen et. al 2008; Knudsen et al. 2016a). This broad dietary niche also typically occurs in monomorphic charr populations (Johnson 1980; Amundsen 1995; Klemetsen et al. 2003a). The highly similar littoral-pelagic mixed diets, the rich parasite communities, and the broad isotopic niche widths of the LO-morphs in the two lakes supported this pattern, as also observed in earlier studies in Fjellfrøsvatn and Skogsfjordvatn (Knudsen et al. 2016a; Siwertsson et al. 2016). Additionally, a parallel study investigating the life history of the morphs in Skøvatn and Tårnvatn (Kjær 2018) revealed similar life history traits between the LO-morphs. Hence, since substantial similarities in trophic niche and life history strategies are present, it seems reasonable to consider the LO-morphs in Skøvatn and Tårnvatn to be analogous morphs.

As predicted, the PB-morph in Tårnvatn showed a narrow diet highly specialized on profundal soft-bottom benthic invertebrates, similarly to the PB-morphs in Fjellfrøsvatn and Skogsfjordvatn (Knudsen et al. 2016a). This 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. 2016a), and by the very narrow isotopic niche width (δ^{13}C and δ^{15}N range). Deep-water morphs with a similar benthic feeding strategy have also been reported in Siberia (Alekseev & Pichugin 1998), Canada (O'Connell et al. 2005), central Europe (Brenner 1980), and Scandinavia (Hindar & Jonsson 1982; Klemetsen 2010).

The adult PP-morph seemed to have a piscivorous foraging behaviour as hypothesized. This was inferred from its habitat use, diet, parasite community, and stable isotopes values. The PP-morph had a clear shift in feeding habit from a profundal benthic-based diet to piscivory apparently occurring at an approximate length of 20 cm, i.e. likely when the individuals have reached a sufficient size to prey on small coenspecifics. Comparable results were found in Skogsfjordvatn, where piscivorous charr start to consume fish when they are 15-25 cm long (Knudsen et al. 2016b). This benthic diet in the small young PP-morph individuals caused a significant niche overlap with the PB-morph and likely a competition for resources in their preferred communal profundal habitat. The PP-morph had high accumulation of *Diphyllobothrium* spp. and a moderate abundance of *E. salvelini*, in line with the findings from Skogsfjordvatn (Siwertsson et al. 2016). *Diphyllobothrium* spp. and *E. salvelini* have a documented capacity to re-establish in the piscivores by using smaller prey fish as paratenic hosts (Curtis 1984; Frandsen et al. 1989; Henriksen et al. 2016; Siwertsson et al. 2016) and they typically accumulate with age in the infected fish (Svenning 1993; Knudsen & Klemetsen 1994; Hammar 2000; Knudsen et al. 2004). In contrast, a high infection rate of the littoral-transmitted *Crepidostomum* spp. was unexpected in the PP-morph, since information about its potential ability to re-establish in piscivorous fish is lacking in the scientific literature. Yet, the LO- and PB-morphs, the only two potential prey fish in Tårnvatn, hosted a moderate amount of *Crepidostomum* spp. and it is reasonable to believe that this might be transmitted to the PP-morph after predation. The SI values of the PP-morph did only partly support a piscivorous niche because there was no significant difference in respect to the δ^{15}N between the two deep-water (PP- and PB-) morphs. This contradicts somewhat an expected single cluster of PP-individuals with high δ^{15}N, that is characteristic of piscivores on the top of the food-web (Jardine et al. 2003; Knudsen et al. 2016 a,b). This unanticipated result (relative low δ^{15}N) suggests the PP-morph may prey only partially on the PB-morph (relative high δ^{15}N), also consuming juvenile LO-morph fish. Alternatively, some littoral benthos might also be part of PP-morph's diet, as a moderate SEA niche overlap occurred with the LO-morph fish feeding mainly on littoral benthic preys. Kjær (2018) showed that the PB- and PP-morphs have different life history strategies, with the PB-morph having a significant slower growth rate and an earlier sexual maturation than the PP-morph. Analogous results were also found in Skogsfjordvatn (Smalås et al. 2013). The findings of trophic segregation and life-history differences strongly suggest the existence of two distinct deep-water morphs in Tårnvatn.

In contrast, the deep-water morph in Skøvatn seems to have a different trophic niche compared with the PB-morph in Tårnvatn, although their life-history patterns with reduced growth and early maturation are similar to the PB-morph in Tårnvatn and elsewhere (Smalås et al. 2013; Kjær 2018). The small-sized deep-water morph in Skøvatn had surprisingly a diet composed chiefly by zooplankton and a high abundance of copepods-transmitted *Diphyllobothrium* spp., indicating a strong trophic specialization for zooplankton. The small-sized deep-water morph had also low $\delta^{13}C$ values, indicative of a strong pelagic resource dependence (Jardine et al. 2003; Hayden et al. 2014; Knudsen et al. 2014). At the same time, however, this morph showed a higher $\delta^{15}N$ values then the sympatric LO-morph denotative of a greater reliance on profundal benthic resources (Hayden et al. 2014; Knudsen et al. 2016 a,b). Since the stable isotopes reflect the diet over approximately the last 3-4 months before capture (Post 2002; Buchheister & Latour 2010; Knudsen et al. 2014), it would be expected that this small-sized deep-water morph had partially consumed profundal preys during summer time. This might be related to the high density of chironomid pupae emerging from the bottom substrate and the concomitant low peak of zooplankton biomass and consumption often described in early summer (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 supported these findings with a low species richness and very low prevalence and abundance for most parasites as reported for other small-sized profundal morphs (Siwertsson et al. 2016). Hence, the small-sized deep-water morph in Skøvatn deviates in diet (zooplanktivory) from the more common profundal benthic diet seen in the PB-morph in Tårnvatn and elsewhere (Klemetsen 2010; Knudsen et al. 2016a). Thus, instead of referring to this as a PB ("Profundal spawning Benthivore"), this charr variety will be denoted as a small-sized deep-water planktivorous morph, and hereinafter another more suitable acronym PZ ("Profundal spawning Zooplanktivore") will be used as it potentially may spawn in deep-waters in Skøvatn (Kjær 2018).

The present study questions a parallelism in trophic niche of the profundal morphs in Tårnvatn and Skøvatn. Whilst Tårnvatn strongly resembles Fjellfrøsvatn and Skogsfjordvatn with its PB- and PP-morphs, Skøvatn diverged distinctly from the other lakes due to the main diet (zooplankton) of the PZ-morph, despite clear parallelism in other characteristics such as habitat distribution, external morphology, and several life-history traits (Kjær 2018). Although much less frequently than for the common littoral benthic – pelagic axis segregation, some cases of parallel evolution of upper- versus deep-water adapted morphs have been reported in northern

postglacial fish in recent years. Examples of profundal dwelling fish morphs have been described in *Coregonus* (Kahilainen & Østbye 2006; Præbel et al. 2013; Siwertsson et al. 2013b), *Salmo trutta* (Piggott et al. 2018), *Salvelinus namaycush* (Muir et al. 2016), and more often in Arctic charr (reviewed by Klemetsen 2010). Along with the PB-morph in Tårnvatn, the PB-morphs in Fjellfrøsvatn and Skogsfjordvatn in northern Norway are a well-documented case of parallel evolution in Arctic charr since they were found having similar habitat, diet, parasite fauna, morphology and life history (Knudsen et al. 2016a; Siwertsson et al. 2016a; Saltykova et al. 2017). Parallel evolution occurs when different populations experiencing similar environmental conditions (ecology and habitat) develop analogous adaptations in an independent manner (Schluter & Nagel 1995; Nosil and Rundle 2009; Elmer & Meyer 2011). These convergent patterns are usually considered the result and evidence of similar selection pressures favouring parallel adaptive traits also among fishes in postglacial lakes (Schluter 2001; Sigursteinsdóttir & Kristjánsson 2005; Kaeuffer et al. 2011; Siwertsson et al. 2013b; Siwertsson et al. 2016; Saltykova et al. 2017). These cases of sibling deep-water morphs in Arctic charr and other postglacial fishes seem to support a convergent evolution driven by the conditions specific for the profundal habitat resulting generally also in a benthivorous foraging behaviour (Knudsen et al. 2016a; Saltykova et al. 2017). Thus, the discrepancy in the dietary niche of the PB- and PZ-morphs in Skøvatn and Tårnvatn is of great interest.

This divergence may be caused by several factors. Albeit the lakes apparently have strong similarities, some ecological and environmental differences are certainly present, especially in the fish community. Skøvatn, contrary to Tårnvatn, is an open system with a direct connection to sea, and host anadromous fish including charr, brown trout, and sporadically Atlantic salmon (Smalås & Henriksen 2016). This could result in different ecological interactions between the systems (e.g. competition and predation). Moreover, dissimilarities in lake area, depth, elevation, transparency, and possibly in other physiochemical factors also occur between the two lake systems. This might have promoted the development of divergent local adaptations (i.e. non-parallelism) of the charr populations in response to differences in biotic and abiotic factors (Kaeuffer et al. 2011; Kristjánsson et al. 2012; Siwertsson et al. 2013b; Saltykova et al. 2017). Nevertheless, comparable environmental variations are also present between Fjellfrøsvatn and Skogsfjordvatn without affecting the main characteristics of the PB-morphs, except for minor morphological features (Saltykova et al. 2017). The observed non-parallel dietary traits may be provoked by different responses of the distinct charr populations to almost

identical environmental conditions (Kaeuffer et al. 2011; Siwertsson et al. 2013b). The Arctic charr is recognised having high levels of phenotypic plasticity (Skúlason et al. 1999; Adams & Huntingford 2004; Snorrason & Skúlason 2004; Klemetsen 2010), and different types of plastic responses could arise between separate populations causing variations in the ontogenetic processes (Kaeuffer et al. 2011; Siwertsson et al. 2013b). This divergent adaptive response may be induced by variations in genetic structure among the populations (West-Eberhard 1898), as an outcome of genetic drift or differences in the genetic architecture of the colonizing populations (Sigursteinsdóttir & Kristjánsson 2005; Kaeuffer et al. 2011; Saltykova et al. 2017).

A sympatric origin of co-occurring Arctic charr morphs is often suggested, with a generalist anadromous ancestor that locally diverged into different groups specialized in different resources use (Skúlason et al. 1999; Jonsson & Jonsson 2001; Klemetsen et al. 2003a). However, the observed local variations may also be the result of subsequent invasions of distinct charr lineages evolved allopatrically in separate glacial refugia (Hindar et al. 1986; Verspoor et al. 2010; Præbel et al. 2013). Tårnvatn is at present inaccessible for migrating fish from the ocean due to a steep waterfall, which act as a migration barrier. The presence of the Arctic charr in the lake might be the result of an introduction by man, as suggested for other lakes in the region (Klemetsen et al. 1989, 1997). Nonetheless, the landscape and the sea level could have changed considerably in the region since the end of the last Ice Age until today, and therefore the lake might have been available for direct invasions from the ocean earlier (Klemetsen et al. 1997). In contrast, Skøvatn is still an open system directly connected to the fjord and hosts a small stock of anadromous charr. Hence, a scenario with double invasions of two different monophyletic charr populations is certainly possible.

The profundal habitat in subarctic lakes is considered as a stable but harsh environment to live in, as it is cold and dark, and food resources are scarce (Klemetsen et al. 1992; Klemetsen et al. 2003b; Siwertsson et al. 2013b; Knudsen et al. 2016a). Nevertheless, the deep-water zone can also bring benefits resulting in enhanced individual fitness. The competition for resources is very low or absent as usually no other profundal dwelling fish are present. Furthermore, this habitat is commonly devoid of predators (fish and waterfowl) and is parasite-poor (Klemetsen et al. 1989; Knudsen et al. 1997; Knudsen et al. 2006; Knudsen et al. 2016a; Siwertsson et al. 2016). It was proposed that the deep-water morphs in Fjellfrøsvatn and Skogsfjordvatn originated by a local expansion of the ancestral niche (including littoral and limnetic habitat

use), in response to high intra- and inter-resource competition and predation pressure in the upper-water zone of the lakes (Knudsen et al. 2006; Knudsen et al. 2016 a,b), and parasite-mediated selection (Siwertsson et al. 2016). An equivalent process might have occurred in both Skøvatn and Tårnvatn, with some charr individuals having adopted the vacant profundal habitat as their new niche.

Both the PB- and PZ- morphs seem to have the typical morphological traits and adaptations to the deep-water habitat, with a small body size, relative large head and eyes, pointed snout, and pale coloration (Klemetsen et al. 2002; Siwertsson et al. 2013b; Skoglund et al. 2015; Simonsen et al. 2017). Most of the PB- and PZ-fish were caught in deep water, and Kjær (2018) revealed that several individuals from each of these populations were ripe fish ready to spawn. Thus, it is reasonable to assume that the PB- and PZ-morphs reside stably in the profundal area, also during the spawning time (Kjær 2018). Both the small-sized morphs therefore seem to have adopted a successful strategy in the profundal zone of the respective lakes. Nonetheless, the findings of the present study strongly suggest the occurrence of distinct foraging modes of the PB- and PZ-morphs. The main advantage of a deep-water benthic diet in respect to zooplanktivory may be the lower parasite infections. On the other side, zooplankton seems to be a more abundant resource in the late summer and autumn than the relatively scarce profundal benthic invertebrates for most of the year (Primicerio & Klemetsen 1999; Mousavi 2002; Hayden et al. 2014; Kahilainen et al. 2016). Thus, the PZ-morph might switch from a benthivorous behaviour to zooplanktivory at least in this period of high zooplankton abundance as described for some monomorphic charr populations (e.g. Eloranta et al. 2010; Hayden et al. 2014; Kahilainen et al. 2016). These two alternative strategies were also reflected by differences along the depth gradient, with the PZ-morph caught in shallower water (15-25 m) than the PB-morph (35-45 m). Zooplankton is usually located in upper waters and at a depth of 15-25 m it is presumably considerably more abundant than at higher depths with lower light (Langeland 1974; Helland et al. 2007). Furthermore, a less deep, i.e. more exposed to light habitat may be important for a planktivorous Arctic charr, which is a visual feeder (Amundsen & Knudsen 2009; Elliott 2011; Knudsen et al. 2016a) and, by means of its vision, can spot and pursue the different zooplankton species selectively (Skoglund et al. 2013). In contrast, this visual capacity is likely not essential for foraging on submerged benthic macroinvertebrates in the perpetually dark profundal zone, where Arctic charr could use other senses such as olfaction (Svenning et al. 2007, Elliott 2011).

The PZ-morph in Skøvatn is the first case of a profundal planktivorous Arctic charr morph in northern Norway. However, similar deep-water morphs consuming at least partially zooplankton 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). Whilst planktivory may be a strategy to increase the energy intake and therefore a fitness advantage of the PZ-morph, the high infection of the copepods-transmitted *Diphyllobothrium* spp. might be a costly burden. *Diphyllobothrium* spp. is potentially harmful for Arctic charr (Halvorsen & Andersen 1984; Knudsen & Klemetsen 1994). Considering the small size of the PZ-morph, it is expected that such a high number of plerocercoids as observed in Skøvatn might have a significant negative impact on the state of health of the fishes. The very low condition factor of the PZ-morph reported by Kjær (2018) confirms this suggestion. Infection with *Diphyllobothrium* spp. normally triggers a non-specific inflammatory response in salmonids, consisting in the encapsulation of the plerocercoids (Sharp et al. 1989). In the PB-morph in Skøvatn several larval worms were not encysted (personal observations), suggesting a weak tissue immune response of the fish that might explain the high levels of *Diphyllobothrium* spp. infection. It is also noteworthy that the stomachs were abnormally reduced in several of the fish due to compression by the large mass of parasites. The high accumulation of *Diphyllobothrium* spp. was not fully reflected by the diet of the zooplanktivorous PZ-morph which had eaten only a minor proportion of copepods that are the intermediate host. This was not surprising, as usually the Arctic charr prey selectively on the more visible and less evasive cladocerans rather than copepods (Dahl-Hansen et al. 1994; Eloranta et al. 2013; Skoglund et al. 2013; Kahilainen et al. 2016). The density of cladocerans is usually low in winter time, when most of them have a diapause, with resting eggs (ephippia) deposed on the sediments (Klemetsen et al. 2003b; Larsson & Wathne 2006; Mariash 2012). The PZ-morph might thus forage on copepods in this period. Nevertheless, studies describing the winter diet of LO-morph of Arctic charr seem to support only partially this suggestion (Knudsen & Klemetsen 1994; Klemetsen et al. 2003b; Amundsen & Knudsen 2009). Further investigations, including the diet in the different seasons, could be very helpful to understand the origin of the high *Diphyllobothrium* spp. accumulation in the PZ-morph in Skøvatn.

The trophic niche of the PP-morph also requires some further considerations. Cannibalism in Arctic charr has been widely reported both as outcome of ontogenetic niche shift in large fish and as occurrence of specialized piscivorous morphs (Amundsen 1994; Svenning & Borgstrøm

1995; Klemetsen et al. 2003a; Knudsen et al. 2016b). However, piscivorous charr morphs are generally situated in shallow-water habitats (Sandlund et al. 1992; Adams et al. 1998). Skogsfjordvatn is one of the few, if not the only described case with a piscivorous morph residing entirely in the profundal zone (but see Power et al. 2005) (Smalås et al. 2013; Skoglund et al. 2015; Knudsen et al. 2016b). The PP-morph in Tårnvatn appears similar but also distinct from the PP-morph in Skogsfjordvatn, which also feeds on three-spined sticklebacks (*Gasterosteus aculeatus*). In Tårnvatn, the piscivorous PP-morph forages exclusively on small-sized charr. Other cases of potentially specialized cannibalistic Arctic charr are reported from some arctic lakes in Svalbard (Spitzbergen) (Svenning 1993). Nevertheless, to my knowledge, there are no examples of deep-water adapted, purely cannibalistic morphs. Hence, the PP-morph in Tårnvatn might be the first documented case of a profundal piscivorous Arctic charr morph that is entirely cannibalistic. Cannibalism is generally suggested to play a key role in regulating and structuring populations of charr (Amundsen 1994; Svenning & Borgstrøm 1995). It is therefore reasonable to assume that the PP-morph may have a strong impact on all the Arctic charr morphs in Tårnvatn. The presence of abundant and suitable prey fishes, i.e. the PB-morph and juvenile LO-morph at deep-waters, could have been a key factor in a local evolution of the PP-morph in the profundal zone in Tårnvatn, as suggested for Skogsfjordvatn (Skoglund et al. 2015; Knudsen et al. 2016b).

Conclusions

The combined data from habitat distribution, stomach contents, parasites, and stable isotopes analyses indicate a distinct segregation in stable trophic resource utilization of the different Arctic charr morphs in Skøvatn and Tårnvatn. The presented trophic divergence is supported by a concomitant study showing a clear separation in various life history traits among the charr morphs within these two lakes (Kjær 2018).

A rather clear parallelism in several characteristics (habitat choice, external morphology, life history) was found between the small-sized deep-water morphs and the upper-water omnivore LO-morphs in the two lakes. This suggests a common parallel evolutionary process along the depth gradient across lakes. However, contrary to the hypotheses, there was an evident non-parallel pattern in diet between the small-sized profundal benthivorous PB- and the zooplanktivorous PZ- morph indicating partially different evolutionary histories. Detailed genetic analyses may help to shed light on the origin and the degree of reproductive isolation of the different morphs in Tårnvatn and Skøvatn, although differences in time and place of spawning are suggested (Kjær 2018). The novel PZ-morph and the exclusively cannibalistic PP-morph from the deep-water environment are for the first time described in northern Norway. To sum up, this study shows how evolutionary forces can create diverse outcomes, even among systems with apparently similar environmental and ecological conditions.

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Appendix

Table 1. The diet of the Arctic charr morphs (percent prey abundance ± S.E) from Skøvatn and Tårnvatn from October 2016.

| | Skøvatn | | Tårnvatn | | |
| | LO-morph | PB-morph | LO-morph | PB-morph | PP-morph |
Prey groups:	(n = 56)	(n = 31)	(n = 57)	(n = 21)	(n = 15)
Bosmina	16.8 ± 2.7	32.7 ± 4.0	20.8 ± 2.1	8.7 ± 2	1.1 ± 0.3
Daphnia	22.8 ± 2.8	38.5 ± 4.7	39.6 ± 3.4	9.6 ± 2.5	1.4 ± 0.4
Copepods (Cyclopoid and Calanoid)	0	3.0 ± 0.6	0	0	0
Acanthocyclops	0	0.5 ± 0.2	0.1 ± 0.1	7.2 ± 1.7	0.7 ± 0.1
Gammarus lacustris	46.9 ± 5.1	6.2 ± 3.2	25.6 ± 3.4	0	0
Snails (*Radix* and *Planorbidae*)	5.7	0	0.4 ± 0.1	0	0
Pisidium clams	0.2 ± 0.1	6.6 ± 2.5	0.2 ± 0.1	11.6 ± 2.2	4.6 ± 0.9
Chironomid larvae (profundal)	0.6 ± 0.1	2.2 ± 0.6	5.0 ± 0.9	60.9 ± 5.2	54.9 ± 6.6
Trichoptera larvae	0.8 ± 0.5	0	3.8 ± 1.5	2.1 ± 0.7	2.5 ± 0.8
Plecoptera larvae	2.3 ± 0.7	10.3 ± 2.8	0	0	0
Fish eggs	3.9 ± 1.8	0	1.4 ± 0.6	0	3.1 ± 0.7
Fish (Arctic charr)	0	0	3.1 ± 1.1	0	31.8 ± 7.8

Table 2. Schoener's similarity index measuring diet overlap among different morphs and size classes of Arctic charr sampled in Skøvatn and Tårnvatn (October 2016).

Lake	*Morphs*	*Schoener's index (%)*
Skøvatn	LO vs. PB	49
	LO < 150 vs. PB	**75**
	LO < 150 vs. LO 150 - 250	32
	LO < 150 vs. LO > 250	5
	LO 150-250 vs. LO > 250	**64**
Tårnvatn	LO vs. PB	26
	LO vs. PP	15
	PB vs. PP	**65**
	LO <150 vs. PB	22
	LO <150 vs. PP <200	6
	PB vs. PP <200	**74**
	LO >250 vs. PP >200	2
	LO <150 vs. LO 150 -250	46
	LO <150 vs. LO >250	35
	LO 150 -250 vs. LO >250	**66**
	PP <200 vs. PP >200	21
Skøvatn vs. Tårnvatn	LO vs. LO	**69**
	PB vs. PB	28
	LO <150 vs. LO <150	**71**
	LO 150-250 vs. LO 150-250	**62**
	LO >250 vs. LO >250	29

Table 3. Levins diversity index measuring the diet breadth of morphs and size classes of Arctic charr sampled in Skøvatn and Tårnvatn (October 2016).

Lake	Morph	Niche width	Prey richness
Skøvatn	**LO**	**3.27**	**9**
	LO < 150	2.26	
	LO 150 - 250	2.47	
	LO > 250	1.60	
	PB	**3.63**	**8**
Tårnvatn	**LO**	**3.69**	**10**
	LO < 150	2.02	
	LO 150 - 250	4.42	
	LO > 250	1.91	
	PB	**2.46**	**6**
	PP	**2.46**	**8**
	PP <200	1.37	
	PP > 200	1.79	

Table 4. Species richness significancy calculated with Mann-Whitney U and Student's t-tests.

Lake	Morphs	Test	P-value
Skøvatn	LO vs. PB	Mann-Whitney U	**0.000**
Tårnvatn	LO vs. PB	Student's t	**0.000**
	LO vs. PP	Mann-Whitney U	0.215
	PB vs. PP	Mann-Whitney U	**0.000**
Skøvatn vs. Tårnvatn	LO vs. LO	Mann-Whitney U	0.185
Skøvatn vs. Tårnvatn	PB vs. PB	Mann-Whitney U	0.094

Table 5. Mean abundance and intensity of the six parasites genera in Arctic charr morphs in Skøvatn and Tårnvatn (October 2016 sampling).

Parasites species	Skøvatn				Tårnvatn					
	Abundance		Intensity		Abundance			Intensity		
	LO $n = 35$	PB $n = 32$	LO	PB	LO $n = 61$	PB $n = 23$	PP $n = 23$	LO	PB	PP
C. truncatus	28.3	0.3	52.2	2.0	11.6	0.1	0.9	35.4	1.5	4.0
P. umblae	8.5	0.0	19.9	1.0	10.3	0.2	0.2	19.7	4.0	1.7
Crepidostomum spp.	51.2	2.3	66.3	7.5	18.5	2.9	47.8	24.0	4.7	47.8
Proteocephalus sp.	0.5	0.5	2.0	5.0	10.8	1.8	3.6	17.3	3.7	8.3
E. salvelini	1.3	0.3	2.6	3.3	2.4	0.3	10.0	3.7	1.3	13.6
Diphyllobothrium spp.	28.9	64.5	37.4	76.4	27.5	2.2	72.2	34.3	6.3	92.3

Table 6. Differences in parasite infections among charr morphs within and between Skøvatn and Tårnvatn. All the comparisons were done using GLMs. Significant P-values are shown in bold text.

Parasite species	Skøvatn	Tårnvatn			Skøvatn vs. Tårnvatn	
	LO vs. PB	LO vs. PB	LO vs. PP	PB vs. PP	PB vs. PB	LO vs. LO
C. truncatus	**0.000**	**0.000**	**0.000**	**0.002**	0.337	**0.000**
P. umblae	**0.000**	**0.000**	**0.000**	0.740	0.125	**0.007**
Crepidostomum spp.	**0.000**	**0.000**	**0.000**	**0.000**	0.230	**0.000**
Proteocephalus sp.	0.791	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
E. salvelini	**0.000**	**0.000**	**0.000**	**0.000**	0.821	**0.000**
Diphyllobothrium spp.	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.231

Table 7. Renkonen index of similarity comparing the proportional abundances of parasites among the Arctic charr morphs.
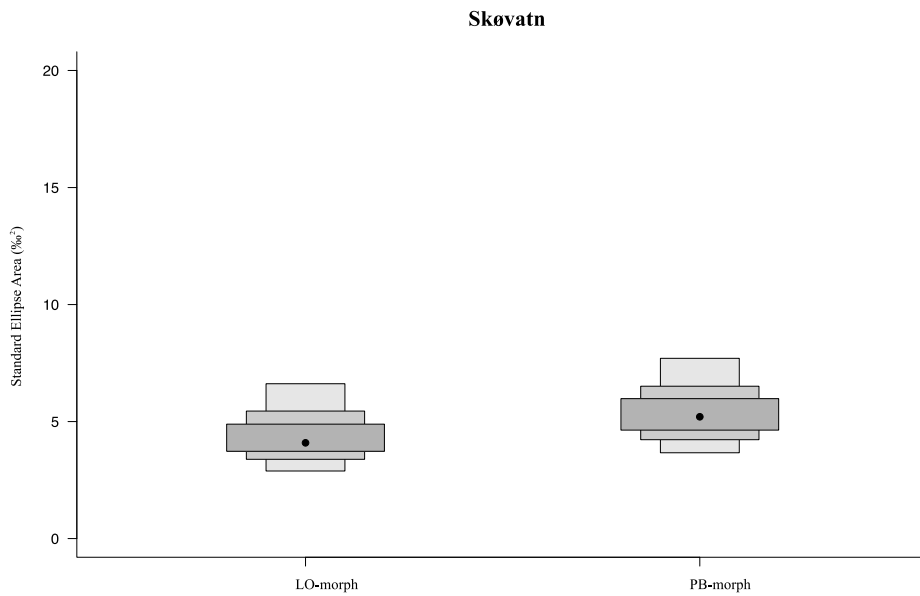
Lake	Morphs	Renkonen index
Skøvatn	LO vs. PB	0,29
	LO < 150 vs. PB	**0,73**
	LO < 150 vs. LO 150-250	0,45
	LO < 150 vs. LO > 250	0,16
	LO 150-250 vs. LO > 250	**0,69**
Tårnvatn	LO vs. PB	**0,72**
	LO vs. PP	**0,63**
	PB vs. PP	**0,73**
	LO < 150 vs. PB	**0,74**
	LO < 150 vs. PP < 200	**0,62**
	PB vs. PP <200	**0,78**
	LO >250 vs. PP >200	0,54
	LO <150 vs. LO 150 -250	0,56
	LO <150 vs. LO >250	0,27
	LO 150 -250 vs. LO >250	**0,71**
	PP <200 vs. PP >200	**0,74**
Skøvatn vs. Tårnvatn	LO vs. LO	**0,70**
	PB vs. PB	0,34
	LO < 150 vs. LO < 150	0,38
	LO 150-250 vs. LO 150-250	**0,84**
	LO > 250 vs. LO > 250	0,42

Table 8. Differences in isotopic composition among the morphs in Skøvatn and Tårnvatn. Kruskal-Wallis and Mann-Whitney U tests were used. Significant P-values are shown in bold text.

Lake	Isotope	P-value	Test
Skøvatn	$\delta^{13}C$	**0.000**	Mann-Whitney U
	$\delta^{15}N$	**0.000**	Mann-Whitney U
Tårnvatn	$\delta^{13}C$	**0.000**	Kruskal-Wallis
	$\delta^{15}N$	**0.000**	Kruskal-Wallis
Tårnvatn (LO-PB)	$\delta^{13}C$	0.480	Mann-Whitney U
Tårnvatn (LO-PP)	$\delta^{13}C$	**0.005**	Mann-Whitney U
Tårnvatn (PB-PP)	$\delta^{13}C$	**0.000**	Mann-Whitney U
Tårnvatn (LO-PB)	$\delta^{15}N$	**0.000**	Mann-Whitney U
Tårnvatn (LO-PP)	$\delta^{15}N$	**0.000**	Mann-Whitney U
Tårnvatn (PB-PP)	$\delta^{15}N$	0.097	Mann-Whitney U

Figure 1. Isotopic niche width of the five morphs of Arctic charr in Skøvatn (a) and Tårnvatn (b). Gradations indicate 50, 75 and 95% credibility intervals of a Bayesian estimate of standard ellipse area (SEA$_b$). *Black dots* denote mean SEA$_b$ values.

a)

b)