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

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**Abstract**  Niche diversification of polymorphic Arctic charr can be altered by multiple anthropogenic stressors. The opossum-shrimp (*Mysis relicta*) was introduced to compensate for reduced food resources for fish following hydropower operations in Lake Limingen, central Norway. Based on habitat use, stomach contents, stable isotopes (δ^{13}C, δ^{15}N) and trophically transmitted parasites, the zooplanktivorous upper water-column dwelling ‘normal’ morph was clearly trophically separated from two sympatric deep-water morphs (the ‘dwarf’ and the ‘grey’) that became more abundant with depth (> 30 m). *Mysis* dominated (50–60%) charr diets in deeper waters (> 30 m), irrespective of morph. *Mysis* and/or zooplankton prey groups caused high dietary overlap (> 54%) between the ‘dwarf’ morph and the two other ‘normal’ and ‘grey’ morphs. After excluding *Mysis*, the dietary overlap dropped to 34% between the two profundal morphs, as the ‘dwarf’ fed largely on deep-water zoobenthos (39%), while the ‘grey’ morph fed on fish (59%). The time-integrated trophic niche tracers (trophically transmitted parasites and stable isotopes) demonstrated only partial dietary segregation between the two deep-water morphs. The high importance of *Mysis* in Arctic charr diets may have reduced the ancestral niche segregation between the deep-water morphs and thereby increased...
their resource competition and potential risk of hybridization.

**Keywords** Salvelinus alpinus · Polymorphism · Ecological divergence · Species introductions · Hydropower effects · Parasite community · Stable isotopes

**Introduction**

Ecologically induced speciation may lead to a continuum of evolutionary differences within and among populations, with some groups being in the process of diversifying and others being reproductively isolated (Schluter, 2000; Hendry et al., 2009). Postglacial lakes are useful systems for studying the impacts of biodiversity changes caused by environmental, ecological and human-induced factors as they are semi-closed ecosystems with relatively well-defined habitats that can host polymorphic populations at different stages of evolutionary divergence (Schluter, 2000; Klemetsen, 2010; Hendry et al., 2017). Human activities may have large impacts on natural environments by rapidly changing the direction of evolutionary development, and in some instances, reverse the evolutionary processes that promote increasing biodiversity (Hendry et al., 2017). Multiple anthropogenic stressors in lake ecosystems, including pollution, commercial fishing and non-native species introductions, have reversed speciation processes (Seehausen et al., 2008; Alexander et al., 2017; Kuparinen & Festa-Bianchet, 2017). For example, reproductive breakdown has been observed in newly differentiated native morph-pairs of whitefish (Coregonus lavaretus) and stickleback (Gasterosteus aculeatus) following the introduction of competitive fish species or invasive crayfish (Taylor et al., 2006; Velema et al., 2012; Bhat et al., 2014).

In postglacial lakes, polymorphic fish populations often diverge along the benthic-pelagic resource axis (e.g. Schluter, 1996, 2000). Charr (Salvelinus spp.) is one of the few genera that is also found to diversify along the shallow vs. deep-water benthic resource axis (Knudsen et al., 2006; Klemetsen, 2010; Muir et al., 2016; Markevich et al., 2018). Knowledge about deep-water (profundal) morphs of Arctic charr (S. alpinus) is still relatively limited, although they seem to occur across the entire Holarctic region (Klemetsen, 2010). The deep-water morphs are typically reproductively isolated from co-occurring littoral and pelagic morphs (Hindar et al., 1986; Westgaard et al., 2004; Simonsen et al., 2017). Moreover, they express heritable specialised physiological, behavioural, and morphological adaptations (Klemetsen et al., 2002, 2006; Knudsen et al., 2015) to effectively exploit (i.e. for foraging and mating) the deep-water niches (Knudsen et al. 2016a). Small-sized deep-water morphs feed mainly on benthic invertebrates, whereas the few known, large-growing deep-water morphs are specialised piscivores (Knudsen et al., 2006, 2016b; Power et al., 2009; Klemetsen, 2010; Mocctei et al., 2019). Although the ecology of the deep-water morph has been studied, little is known about the potential impacts of multiple anthropogenic stressors (e.g. hydropower operations and the introduction of non-native species) on these deep-water morphs.

Lake Limingen, central Norway, has a polymorphic population of Arctic charr, consisting of three morphs: the upper-water ‘normal’ morph, the deep-water ‘dwarf’ morph, and the piscivorous ‘grey’ morph (Nyman et al., 1981; Aass et al., 2004). Following the damming of the lake in 1953 for hydropower production, brown trout (Salmo trutta) and Arctic charr population densities drastically declined (Aass et al., 2004; Gregersen et al., 2006). In 1969, *Mysis relicta* (hereafter *Mysis*) was introduced to compensate for reduced fish food resources and to mitigate the negative impacts of hydropower operations on fish and overall ecosystem productivity (cf. Hirsch et al., 2017). *Mysis* is an opossum shrimp native to Scandinavia, though previously absent from this Limingen region of Norway (Spikkeland et al., 2016). *Mysis* show a pronounced diel vertical migration pattern, with nocturnal foraging on zooplankton in the upper water column potentially resulting in food resource competition with zooplanktivorous Arctic charr (Moen & Langeland, 1989; Næsje et al., 1991; Koksvik et al., 2009). In contrast, deep-water fish (e.g. burbot Lota lota and profundal Arctic charr) may benefit from *Mysis* introductions through increased food availability (Langeland et al., 1991; Næsje, 1995). Whilst introduced *Mysis* populations have become an important prey resource for Arctic charr in Limingen and elsewhere (Garnäs, 1986; Gregersen et al., 2006), detailed studies of their impacts on
trophic differentiation among sympatric Arctic charr morphs have been lacking.

In this study, we investigated the habitat use, diet, parasite infections and stable isotope ratios (δ13C, δ15N) of the three sympatric Arctic charr morphs in Limingen. The aim of the study was to explore the degree of niche overlap between the three sympatric Arctic charr morphs about 50 years after the introduction of *Mysis*. We quantified niche overlap by using data on habitat use and stomach contents (recent niche-use) and by analysing the occurrence of trophically transmitted parasites and stable isotope values that reflect the temporally integrated trophic niches of individual fish (Knudsen et al., 2011). We hypothesised that existing depth-habitat preferences for the sympatric morphs would be maintained. However, due to damming and the introduction of *Mysis*, we also hypothesised that prey resource use would overlap, particularly between the upper-water ‘normal’ and the deep-water morphs.

Materials and methods

Study lake

Lake Limingen (64°50’N, 13°13’E) is a large (surface area = 95.7 km²), deep (Zmax = 192 m, Zmean = 87 m), dimictic, oligotrophic and relatively clear (Secchi depth = 9–12.7 m) lake situated at 418 m a.s.l. in the north boreal vegetation zone of central Norway. Originally, the lake drained to the Ånger-månävlen watercourse in northern Sweden, but after hydropower development in 1953 most of the water was diverted to the Namsen watershed in Trøndelag County, Norway (Sandlund et al., 2017). Today, the lake is regulated with a maximum annual water level amplitude of 8.7 m. Spruce forests with some birch dominate the riparian vegetation, and there are only a few low-intensity farms around the lake. In addition to the polymorphic Arctic charr, the lake has a small population of brown trout, a littoral population of minnow (*Phoxinus phoxinus*; introduced in 1980s) and a very sparse population of three-spined stickleback (introduction date unknown) (Aass et al., 2004; Gregersen et al., 2006).

Fish material

Arctic charr were sampled in August 2016 with Nordic multi-mesh gill-nets consisting of 2.5 m panels with 12 different knot-to-knot mesh sizes from 5 to 55 mm (Appelberg et al., 1995). The nets were set in the littoral (1.5 m high benthic nets; 0–15 m depth), pelagic (6 m high offshore gill-nets set from the surface; above 30 m depth), and profundal (1.5 m high benthic nets; at 20–50 m depth) zones. Additional sampling with a pelagic pair trawl caught 63 ‘normal’ morph Arctic charr (see details in Sandlund et al., 2017). Fish were weighed (closest 0.1 g) and measured (closest 1 mm, fork length, Lf). Otoliths were removed for age determination.

Individual Arctic charr were classified to one of three possible morphs based on head and body morphology, maturation, and colouration following guidelines produced from earlier studies of similar polymorphic populations (Skoglund et al., 2015; Simonsen et al., 2017). In total, we sampled 178 Arctic charr from Limingen, with stomachs analysed from 171 individuals. The catch per unit of effort (CPUE) was estimated as the number of fish caught per 100 m² gillnet per night. A subsample of mature individuals from all three morphs was assessed for parasite assemblages and sampled for stable isotope ratios (δ13C and δ15N). The number of each morph included in the parasite and stable isotope sampling were: ‘normal’ morph (n = 39; mean ± SD: Lf = 310.6 ± 83.7 mm; age = 6.7 ± 2.5 years), ‘dwarf’ morph (n = 27; Lf = 173.9 ± 31.7; age = 6.4 ± 2.6), and ‘grey’ morph (n = 14; Lf = 297.1 ± 59.3; age = 9.5 ± 3.4).

Growth differences among morphs were described by mean length-at-age using a modified von Bertalanffy growth model (Roff, 1984): 

\[
L_T = L_\infty \ast (1 - \exp(-k \ast A_T)),
\]

whereLT is fish body length at time T, L_\infty is the asymptotic fish length, k is the growth coefficient, and A_T is the age at time T. This simplified model has been shown to work well with inland polymorphic salmonids (Jonsson et al., 1988).

Diet

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

Parasites

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

Stable isotopes

Stable isotopes of carbon (δ¹³C) and nitrogen (δ¹⁵N) are commonly used to estimate the dietary sources (littoral vs. pelagic carbon) and trophic position of organisms in lake food webs, as well as the intra- and inter-specific niche segregation of fish populations (e.g. Boecklen et al., 2011; Layman et al., 2012). Here, a small piece of dorsal muscle tissue, obtained posterior to the dorsal fin, was dissected from a subsample of fish and frozen at –20°C. Tissue samples were dried at 60°C for 48 h and homogenised using a pestle and mortar. Approximately 0.3 ± 0.05 mg of dried tissue was weighed and placed in tin capsules for analyses completed at the University of Waterloo, Canada, on a Delta plus continuous flow stable isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyser (CHNS-O EA1108, Carlo Erba, Milan, Italy). The machine analytical precision of ± 0.2‰ (δ¹³C) and ± 0.3‰ (δ¹⁵N) was determined through the repeat analysis of internal laboratory standards calibrated against International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen.

Statistical analyses

All statistical analyses were computed using R (version 3.4.2, R Core Team, 2017). Differences in the number of parasite taxa among morphs were compared using a general linear model fitted with a Gaussian distribution family. Differences in total parasite abundance and the abundance of each parasite taxon among charr morphs were examined using a series of generalized linear models, with the exception of five rare taxa (*C. truncatus*, *E. salvelini*, *S. edwardsii*, Acanthocephalan sp., unidentified nematode), which were excluded from further analysis. Generalized linear models were fitted with a quasipoisson distribution and log-link function due to the over-dispersion of abundance data. Fish age (years) was included as a continuous fixed factor in all general and generalized linear models to account for the influence of varying host age on parasite abundance and richness. Potential outliers were identified by graphically examining the raw data and by running models with and without outliers to assess their influence on model outcomes. Analysis of variance was used to assess whether the interaction term...
Results

Fish community, habitat preference and Arctic charr growth

Arctic charr was the dominant species \( (n = 168) \) in the benthic habitats (i.e. littoral and profundal), whereas only nine ‘normal’ Arctic charr were caught in the pelagic zone \((0.6 \text{ charr per 100 m}^2 \text{ gillnet area})\). Additionally, 34 brown trout, 68 minnows and one three-spined stickleback were caught from the littoral zone. The CPUE of Arctic charr (overall mean: 3.8 fish per 100 m\(^2\) benthic gillnet per night) increased with depth from about 1.8 at 0–10 m, 2.2 at 10–20 m, 5.2 at 20–30 m to \( > 8 \) at \( > 30 \text{ m} \) depth. The ‘normal’ morph was most abundant in the upper water-column layers (Fig. 1a), down to 30 m depth (CPUE-range 2–4.5). The ‘dwarf’ morph was most abundant at depths \( > 20 \text{ m} \) (CPUE: \( > 4 \)), and the ‘grey’ morph was most abundant within the 30–50 m depth zone (CPUE: \( > 2 \)).

Length-at-age differed among the morphs, with significant differences in mean length \( (t \text{ tests}, P < 0.05) \) observed between ‘normal’ and profundal ‘dwarf’ morphs for each age-class between 4 and 9 years (Fig. 1b). Estimated von Bertalanfly growth models indicated greater asymptotic lengths for the ‘normal’ and ‘grey’ morphs as compared with the ‘dwarf’ morph, with non-overlapping confidence intervals indicating significantly different maximal sizes for all morphs. Growth rate \( (k) \) similarly differed between the morphs as indicated by non-overlapping confidence intervals, being lower in the ‘normal’ and ‘grey’ morphs and highest in ‘dwarf’ morph (Table 1). It should be noted that the precision of parameter estimates for the ‘grey’ morph was possibly affected by the smaller number of fish available for estimating model parameters.

Dietary niches

Generally, the abundance (%) of Mysis in charr stomach contents increased with depth, independent of the morph considered (Fig. 2a), being about 10% in the upper water column \((0–10 \text{ m})\) and \( > 60\% \) in deep waters \((> 50 \text{ m})\). In contrast, the diet of all Arctic charr captured in the uppermost water column \((< 30 \text{ m} \text{ depth})\) was dominated by zooplankton \((> 53\% \)) and surface insects \((> 20\% \)). Mysis constituted 18% of the diet of the ‘normal’ morph, 35\% of the ‘grey’ morph diet and 39\% of the ‘dwarf’ morph diet (Fig. 2b). The ‘dwarf’ morph consumed zooplankton \((29\% \)) and benthos \((23\% \)) in addition to Mysis. The ‘dwarf’ morph ate much less Daphnia and Bythotrephes, but approximately equal amounts of Bosmina and Holopedium when compared with the ‘normal’ morph. The ‘grey’ morph relied more heavily on fish \((38\% \)) than the other morphs, which had less
than 1.5% fish in their stomachs. Common consumption of Mysis and/or zooplankton prey groups caused a relatively high dietary overlap (54–56%) between the ‘dwarf’ morph and the two other morphs when considering all prey groups (23 taxa). Dietary overlap was lower (41%) between the ‘normal’ and the ‘grey’ morph. After removing Mysis as a prey group, the dietary overlap dropped to 34% between the two deep-water morphs, as the ‘dwarf’ morph fed mainly on zooplankton (49%) and deep-water zoobenthos (39%), while the ‘grey’ morph fed mainly on fish (59%).

Parasite community composition

A total of 11 parasite taxa were found, including eight trophically transmitted parasites, one directly transmitted parasite (S. edwardsii) and two trematode taxa

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

| Charr morph | # fish | Asymptotic length, $L_\infty$ | SE | 95% CI (lower and upper bound) | Growth coefficient, $k$ | SE | 95% CI (lower and upper bound) |
|-------------|--------|-----------------------------|----|-------------------------------|------------------------|----|-------------------------------|
| ‘Normal’    | 132    | 496.2                       | 36.2| 424.5–567.7                  | 0.14                   | 0.02| 0.11–0.18                     |
| ‘Dwarf’     | 81     | 196.2                       | 6.2 | 183.8–208.5                  | 0.39                   | 0.03| 0.32–0.45                     |
| ‘Grey’      | 18     | 360.3                       | 38.7| 278.3–442.4                  | 0.20                   | 0.05| 0.08–0.31                     |
transmitted from snail intermediate hosts. Taxon richness increased with host age for both ‘normal’ and ‘dwarf’ morphs, whereas age did not influence parasite taxon richness in the piscivorous ‘grey’ morph (GLMmorph:age: $F_{2,67} = 5.16, P = 0.008$; Tables 2 and S1). Total parasite abundance was significantly higher in the ‘normal’ morph compared to the ‘dwarf’ morph, while the piscivorous ‘grey’ morph had intermediate infection levels (GLMmorph: $F_{2,70} = 4.70, P = 0.012$; Tables 2 and S1).

Parasite community composition in individual Arctic charr appeared to be more similar in the two profundal morphs compared to the ‘normal’ morph (Fig. 3). Of the three parasite taxa non-trophically transmitted to charr, Diplostomum sp. and Apatemon sp. were the most prevalent among morphs (~ 40–65%), whereas S. edwardsii tended to occur in the ‘normal’ charr morph (20%). The abundance of non-trophically transmitted parasites was consistently low (< 3 individual parasites per fish) and did not differ among morphs, although there was a positive relationship between Diplostomum sp. abundance and charr age (Tables 3, S2). Of the trophically transmitted parasites, the upper water-column ‘normal’ morph had the highest prevalence for five of eight parasite taxa, and the remaining three parasite taxa were most prevalent in the piscivorous ‘grey’ morph. Two Gammarus transmitted taxa, C. truncatus and Acanthocepha sp., were restricted to ‘normal’ charr morphs only. Dibothriocephalus spp. cestode larvae were the most prevalent trophically transmitted parasite and occurred in similar abundances in all morphs (Tables 3, S2). The copepod-transmitted taxa, i.e. Proteocephalus sp. and Eubothrium sp., were more prevalent in the ‘normal’ morph than in the deep-water charr morphs. Proteocephalus sp. abundance was greater in the ‘normal’ morph than in the ‘dwarf’ morph, with the abundance of this parasite declining with charr age (Tables 3, S2). The swim bladder nematode C. farionis was found most often in the piscivorous ‘grey’ morph, although it was in consistently low abundance in all charr morphs (Table 3).

The community composition of trophically transmitted parasites in individual charr was significantly explained, albeit moderately, by the diet composition of the individual (Canonical Correlation $R_{adj}^2 = 0.30, P < 0.001$; Fig. 4). Thus, when visualizing both the most recent diet (stomach contents) and the temporally integrated characterization of resource use as measured by trophically transmitted parasites, all morphs appeared to have different trophic niches (Fig. 4).
| Parasite taxa | Stage | Site | Interm. host | Trophic transm. | Normal | Dwarf | Grey | Contrasts<sup>b,c</sup> |
|--------------|-------|------|--------------|----------------|--------|-------|------|---------------------|
|              |       | Prev | Abund |       |        |       |       |                     |
|              |       | Prev | Abund |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| Trematoda    |       |      |       |       |        |       |       |                     |
| *Apatemon* sp.<sup>a</sup> | L    | e    | Snails, fish | No   |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| *Crepidostomum* spp. | A  | i    | Insect larvae | Yes  |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| *Diplostomum* sp.<sup>a</sup> | L    | e    | Snails, fish | No   |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| Cestoda      |       |      |       |       |        |       |       |                     |
| *Cyathoecephalus truncatus* | A  | i    | Amphipods | Yes  |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| *Dibothriocephalus* spp. | L  | v    | Copepods, fish | Yes  |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| *Eubothrium salvelini* | A  | i    | Copepods, fish | Yes  |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| *Proteocephalus* sp. | A  | v    | Copepods, fish | Yes  |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| Nematoda     |       |      |       |       |        |       |       |                     |
| *Cystidicola farionis* | A  | sb   | Amphipods | Yes  |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| Unidentified nematode | A  | i    | Unknown | Yes  |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| Acanthocephala |       |      |       |       |        |       |       |                     |
| Acanthocephalan sp. | A  | i    | Amphipods | Yes  |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
| Copepoda     |       |      |       |       |        |       |       |                     |
| *Salmincola edwardsii* | A  | fg   | None | No   |       |       |       |                     |
|              |       |      |       |       |        |       |       |                     |
|              |       |      |       |       |        |       |       |                     |

*Prev* prevalence %, *Abund* mean abundance ± SE, stage (*L* larval, *A* adult), infection site (*v* viscera, *i* intestine, *k* kidney, *sb* swim bladder, *fg* fins/gills)

NS not significant

<sup>a</sup>Prevalence and abundance estimated from single eye

<sup>b</sup>Summary of inter-morph contrast analyses

<sup>c</sup>See Supplementary Table S2 for details. *P* < 0.05
two deep-water morphs were located closest to each other, indicating they have more similar trophic niches. The ‘normal’ morph was more separated (Fig. 4) and associated with higher infections of *Proteocephalus* sp. and *Crepidostomum* spp. as a result of feeding on a different assemblage of zooplankton species and insect larvae than the ‘dwarf’ or ‘grey’ morphs. The ‘grey’ and ‘dwarf’ morphs were mainly associated with infections of *Dibothriocephalus* spp. and *C. farionis*, linked to feeding on *Mysis*, mussels, chironomid larvae, and fish.

**Stable isotopes**

The three Arctic charr morphs showed significant differences in δ13C (Kruskal–Wallis: χ² = 10.69, df = 2, P = 0.005) and δ15N (χ² = 42.93, df = 2, P < 0.001) values. The ‘normal’ morph had significantly lower (i.e. more pelagic) δ13C values than the ‘grey’ morph (Mann–Whitney pairwise comparison: P = 0.002), whereas the other between-morph differences in δ13C were non-significant (P = 0.07–0.09). The ‘normal’ morph showed variable but significantly lower δ15N values than either the ‘dwarf’ or ‘grey’ morphs (Mann–Whitney pairwise comparisons; P < 0.001; Fig. 5a) and was separated from both by approximately one trophic level (i.e. ~3%). In contrast, the ‘dwarf’ and ‘grey’ morphs did not differ in δ15N (Mann–Whitney pairwise comparisons; P = 0.268), although ‘grey’ morph individuals tended to have higher δ15N values consistent with piscivorous feeding. Isotopic niche overlap analyses showed that the ‘dwarf’ and ‘grey’ morphs had high probabilities of sharing the same niche region (70% and 76%), while they had lower probabilities of overlapping with the ‘normal’ morph (32% and 25%) (Table 4; Fig. 5b). The ‘normal’ morph had the lowest probabilities of overlapping with either of the profundal morphs (14% and 10%) (Table 4).

**Discussion**

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

A corresponding trophic segregation between the ‘normal’ morph and the sympatric profundal morphs occurs in some other polymorphic lakes (Knudsen et al., 2006, 2016a; Amundsen et al., 2008; Moccetti et al., 2019). In Arctic charr, a zooplanktivorous diet is generally found in southern Scandinavian lakes (e.g. L’Abée-Lund et al., 1993; Sandlund et al., 2016;
Fig. 5  a Boxplots and b a biplot showing differences in δ¹³C and δ¹⁵N values for the three Arctic charr morphs: ‘normal’, ‘dwarf’ and ‘grey’ found in Limingen. The letters in a) indicate significant differences (P < 0.05) in pairwise comparisons, based on Mann–Whitney U tests. The δ¹³C values reflect littoral (low δ¹³C) versus pelagic (high δ¹³C) resource use by fish, whereas δ¹⁵N values reflect trophic position of fish in the lake food web. Niche regions in (b) are illustrated by ellipses containing approximately 95% of the data points for each morph (Jackson et al., 2011)

Table 4  Probabilistic niche overlap calculated from nicheRover using the 95% niche regions between each pair of Arctic charr morphs from Limingen (Swanson et al., 2015)

|       | Normal | Dwarf  | Grey   |
|-------|--------|--------|--------|
| Normal| –      | 14.5 [5–27] | 10.1 [2–28] |
| Dwarf | 31.7 [9–59] | –      | 69.9 [46–91] |
| Grey  | 25.5 [2–65] | 76.1 [51–95] | –      |

Mean [range 95% credibility interval] probability (%) of finding an individual of the morph in the row within the niche region of the morph in the column

Jensen et al., 2017; Paterson et al., 2019), in lakes regulated for hydropower production (e.g. Hirsch et al., 2017), and in northern lakes with benthivorous competitors (e.g. Skoglund et al., 2013; Eloranta et al., 2013). In northern lakes with deep-water morphs, the upper water-column ‘normal’ Arctic charr morph may also include littoral resources in the diet (Knudsen et al., 2010, 2016a; Eloranta et al., 2013; Moccetti et al., 2019). In Limingen, however, the benthic resources in shallow littoral areas are restricted due to water level fluctuations that reduce littoral zone productivity (e.g. Hirsch et al., 2017) and the occupancy of available shallow areas by abundant minnows and a few brown trout (Aass et al., 2004; Gregersen et al., 2006). Low presence of littoral benthos in the diet of the ‘normal’ morph is supported by low infection by the few parasite species transmitted from benthic prey (i.e. Crepidostomum sp.), as also observed in other studies in this geographic region (Paterson et al., 2018, 2019).

The small-sized deep-water ‘dwarf’ morph included both zooplankton and Mysis in the diet, resulting in a relatively high dietary overlap with the ‘normal’ and ‘grey’ morphs. Small-sized deep-water Arctic charr morphs typically specialize on soft-bottom benthos (Hindar & Jonsson, 1982; Knudsen et al., 2006, 2016a, b; Hooker et al., 2016; Moccetti et al., 2019), as do profundal whitefish morphs (Harrod et al., 2010; Præbel et al., 2013; Siwertsson et al., 2013) and brown trout (Piggott et al., 2018). In Limingen, excluding Mysis consumption reduced the apparent dietary overlap between the two profundal
morphs, with consumption of prey resources other than Mysis pointing to a more distinct benthivorous dietary niche for the ‘dwarf’ morph. Although separation into morph groupings was not reported, zoobenthos were noticeably more common in the diet of Arctic charr prior to the Mysis introduction (Gregersen et al., 2006). The introduction of Mysis may have induced a dietary shift by the ‘dwarf’ morph towards a more pelagic diet as a result of the diel vertical migration of Mysis within the water column. The ‘dwarf’ morph also had significantly higher δ15N values and less diverse parasite fauna when compared to the ‘normal’ morph in Limmingen and nearby lakes (Paterson et al., 2018, 2019), as has been reported for other polymorphic Arctic charr lakes (Knudsen et al., 1997, 2016a; Siwertsson et al., 2016). Despite the apparently large dietary overlap, the above suggests that the ‘dwarf’ morph has a less unique benthivorous diet in Limmingen than in other lakes (see also Moccetti et al., 2019).

The relative importance of Mysis in the diet of the ‘grey’ morph is not typical for large-growing Arctic charr (but see Eloranta et al., 2015), although lake charr (S. namaycush) predate substantially on Mysis (e.g. Chavarie et al., 2016) particularly when introduced to oligotrophic lakes (e.g. Ellis et al., 2011). In Limmingen, fish was an important prey for the ‘grey’ morph, but not for the sympatric ‘normal’ and ‘dwarf’ morphs, indicating the position of ‘grey’ Arctic charr as specialized piscivores (Adams et al., 1998; Power et al., 2005; Knudsen et al., 2016a; Moccetti et al., 2019). The inclusion of a specialized piscivore among lake-resident morphs is also found in other polymorphic Salvelinus spp. populations (Muir et al., 2016; Markevich et al., 2018). Although the relatively high δ15N values of the ‘grey’ morph partly reflected their piscivorous diet, the morph was less clearly separated from the ‘dwarf’ morph than has been evident in studies of other profundal morph-pairs (Knudsen et al., 2016a; Moccetti et al., 2019). The ‘grey’ morph had a higher diversity of trophically transmitted parasites than ‘dwarf’ morph, likely passed on via prey fish as has been noted elsewhere (Siwertsson et al., 2016; Moccetti et al., 2019). The ‘grey’ morph also had aggregated high Dibothriocephalus spp. infections (a cestode able to re-establish in predatory fish; e.g. Curtis, 1984), as is often seen in other piscivorous Salvelinus spp. morphs (Frandsen et al., 1989; Butorina et al., 2008; Siwertsson et al., 2016; Moccetti et al., 2019). However, the parasite data also suggest abundant ingestion of Mysis by the ‘grey’ morph, as C. farionis (a swim-bladder nematode potentially transmitted by mysids; Black & Lankester, 1980) were most frequent in the ‘grey’ morph. Overall, the parasite results (i.e. community structure and/or abundance) described here support previous conclusions that piscivorous predators are exposed to a portfolio of parasite species that differ from those found in sympatric invertebrate feeding morphs (Smiertsøn et al., 2016; Moccetti et al., 2019).

The profundal ‘grey’ and ‘dwarf’ morphs in Limmingen also showed greater similarity in diets and growth rates than the sympatric deep-water benthi-vorous and piscivorous charr morphs found elsewhere (Smaalås et al., 2013; Knudsen et al., 2016a, b; Moccetti et al., 2019), likely as a result of Mysis consumption as has been noted for lake charr feeding on introduced Mysis in Flathead Lake, Montana (Ellis et al., 2011). The introduced Mysis is also one of the main reasons for the high dietary overlap, which was similarly reflected in the overlap in isotopic niches and parasite fauna between the deep-water Arctic charr morphs. When present, Mysis may dominate the diet of benthic and pelagic Arctic charr in Scandinavian lakes in all seasons, but especially during winter when zooplankton are scarce (Garnås, 1986; Næsje, 1995; Hammar, 2014). Introduction of Mysis in polymorphic Arctic charr lakes may therefore diminish the ecological segregation between sympatric morph pairs and alter the local selection regimes. Whilst there is no information regarding reproductive isolation (e.g. time and place of spawning) for Limmingen Arctic charr, the morphs are thought to be genetically different (Nyman et al., 1981). In several other postglacial lakes, upper water-column morphs of Arctic charr and whitefish are genetically different from their sympatric benthivorous deep-water morphs, as well as from resident piscivorous morphs (Verspoor et al., 2010; Prebel et al., 2013, 2016; Siwertsson et al., 2013; Simonsen et al., 2017; Moccetti et al., 2019). The ‘normal’ morph in Limmingen differs from the other two sympatric morphs in terms of habitat depth, whereas the two deep-water morphs segregate in terms of piscivory; yet, all three morphs prey on the introduced Mysis. Thus, reliance on Mysis clearly reduces the niche segregation between the morphs and has also likely affected energy flow pathways through the lake food web.
(e.g. Ellis et al., 2011). Ecological convergence (e.g. similarity in diet) as observed in the present ‘dwarf’ and ‘grey’ morphs, may even promote hybridization. The ‘reverse speciation’ process (increased hybridization) among native fish morphs has been reported from other lakes where the introduction of non-native competitors or potential prey has impaired ecological segregation (e.g. Taylor et al., 2006; Vonlanthen et al., 2012; Bhat et al., 2014).

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

For management of the scattered and unique deep-water morphs of Arctic charr, it is important to obtain an overview of the occurrence of intra-lake divergence within populations, describe their biological characteristics and determine the environmental prerequisites for their occurrence. Based on recent ecological and genetic studies, deep-water morphs of Arctic charr and whitefish are replicated in several locations and appear to originate locally (Knudsen et al., 2006; Østbye et al., 2006; Klemetsen, 2010; Præbel et al., 2013, 2016). Profundal morphs of Arctic charr have evidently inherited traits selected for surviving in cold, dark and nutrient-poor deep-water environments, including specific adaptations in trophic morphology, behaviour and growth (Klemetsen et al., 2002, 2006; Knudsen et al., 2015). Other traits seem to a lesser degree to be under strong natural selection, such as temperature preference and vision capabilities (Siikavuopio et al., 2014; Kahlilainen et al., 2016). Without appropriate knowledge of the occurrences of traits within and among populations of Arctic charr, and of northern lake resident fish in general, a full understanding of the functional biodiversity within these lakes will remain unknown. Functional diversity is an important component of biodiversity in northern lakes (Sandlund & Hesthagen, 2011) and its categorization is particularly important given the rapid anthropogenic induced environmental changes that are altering ecosystems and biodiversity faster than the diversity can be inventoried (Reist et al., 2013).

A second concern and challenge for management is to identify potential threats to these deep-water morphs that may reduce their abundance or even cause local extinction. There seems to be no population-specific, cold-water adaptations in deep-water Arctic charr morphs as they have the same estimated temperature preferences as those from Svalbard and most of Scandinavia (Larsson et al., 2005; Siikavuopio et al., 2014). Profundal morphs, however, tend to spawn later than sympatric upper water-column morphs, during the winter when lakes are normally ice-covered (Klemetsen et al., 1997; Smalås et al., 2017). The profundal zones in deep oligotrophic postglacial lakes are relatively stable environments, experiencing less variability in food supply and temperature regimes (e.g. Mousavi & Amundsen, 2012). Thus, populations inhabiting these lakes may be less affected by moderate global warming (Poesch et al., 2016), as they can thermally buffer in cold deep waters isolated from summer temperature stratification. Arctic charr populations that spawn in shallow areas may actively avoid the warm upper water-column layers during summer stratification (Murdoch & Power, 2012) but may alter spawning timing or habitat (e.g. Winfield et al., 2010; Jeppesen et al., 2012). Thus, upper water-column morphs may be more severely affected by an accumulation of anthropogenic-induced stressors, e.g. climate change and hydropower-induced water level fluctuations. Furthermore, if whole lake ecosystems are significantly modified, there may be cascading ecological consequences even for deep-water morphs, as has been
suggested by the data from Limingen. This may include an increased risk of hybridization between morph-pairs that will eventually reduce the intraspecific biodiversity apparent in many Scandinavian lakes.

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References

Aass, P., C. S. Jensen, L. A. Vøllestad & J. H. L’Abée-Lund, 2004. Long-term variation in the population structure of Arctic char, Salvelinus alpinus, and brown trout, Salmo trutta. Fisheries Management and Ecology 11: 125–134.

Adams, C. E., D. Fraser, F. A. Huntingford, R. B. Greer, C. M. Askew & A. F. Walker, 1998. Trophic polymorphism amongst Arctic char from Loch Rannoch, Scotland. Journal of Fish Biology 52: 1259–1271.

Alexander, T. J., P. Vonlanthen & O. Seehausen, 2017. Does eutrophication-driven evolution change aquatic ecosystems? Philosophical Transactions of the Royal Society B 372: 20160041.

Amundsen, P.-A., H. M. Gabler & F. J. Stalvdik, 1996. A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello (1990) method. Journal of Fish Biology 48: 607–614.

Amundsen, P.-A., R. Knudsen & A. Klemtsetn, 2008. Seasonal and ontogenetic variations in resource use of two sympatric Arctic char morphs. Environmental Biology of Fishes 83: 45–56.

Appelberg, M., H. M. Berger, T. Hesthagen, E. Kleiven, M. Kurkilahti, J. Raitaniemi & M. Rask, 1995. Development and intercalibration of methods in nordic freshwater fish monitoring. Water, Air and Soil Pollution 85: 401–406.

Bhat, S., P.-A. Amundsen, R. Knudsen, K. Ø. Gjelland, S. E. Fevolden, L. Bernatchez & K. Præbel, 2014. Speciation reversal in European whitefish (Coregonus lavaretus (L.)) caused by competitor invasion. PLoS ONE 9: e91208.

Black, G. A. & M. W. Lankester, 1980. Migration and development of swim bladder nematodes, Cystidicola spp. (Habronematoidea), in their definitive hosts. Canadian Journal of Zoology 58: 1997–2005.

Boecklen, W. J., C. T. Yarnes, B. A. Cook & A. C. James, 2011. On the use of stable isotopes in trophic ecology. Annual Review of Ecology and Systematics 42: 411–440.

Borgstrøm, R., J. Museth & J. E. Brittain, 2010. The brown trout (Salmo trutta) in the lake, Øvre Heimdalsvatn: long-term changes in population dynamics due to exploitation and the invasive species, European minnow (Phoxinus phoxinus). Hydrobiologia 642: 81–91.

Bush, A. O., K. D. Lafferty, J. M. Lotz & A. W. Shostak, 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83: 575–583.

Butorina, T. E., M. B. Shed’ko & O. Y. Gorovaya, 2008. Specific features of ecology of chars of the Genus Salvelinus (Salmonidae) from the Basin of Lake Kronotskoe (Kamchatka) according to parasitological data. Journal of Ichthyology 48: 622–636.

Chavarie, L., W. J. Harford, K. L. Howland, J. Fitzsimons, A. M. Muir, C. C. Krueger & W. M. Tonn, 2016. Multiple generalist morphs of Lake Trout: avoiding constraints on the evolution of intraspecific divergence? Ecology and Evolution 6: 7727–7741.

Curtis, M.A., 1984. Diphyllobothrium spp. and the Arctic char: parasite acquisition and its effects on a lake-resident population. In Johnson, L. & B. I. Burns (eds), Biology of the Arctic char. Proceedings of the International Symposium on a Arctic char, University of Manitoba Press, Winnipeg: 395–411.

Ellis, B. K., J. A. Stanford, D. Goodman, C. P. Stafford, D. L. Gustafson, D. A. Beauchamp, D. W. Chess, J. A. Craft, M. A. Deleray & B. S. Hansen, 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences 108: 1070–1075.

Eloranta, A. P., R. Knudsen & P.-A. Amundsen, 2013. Niche segregation of coexisting Arctic char (Salvelinus alpinus) and brown trout (Salmo trutta) constrains food web coupling in subarctic lakes. Freshwater Biology 58: 207–221.

Eloranta, A. P., K. K. Kahlilainen, P.-A. Amundsen, R. Knudsen, C. Harrod & R. I. Jones, 2015. Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. Ecology and Evolution 5: 1664–1675.

Frandsen, F., H. J. Malmquist & S. S. Snorrasson, 1989. Ecological parasitology of polymorphic Arctic char, Salvelinus alpinus, in Lake Thingvallavatn, Iceland. Journal of Fish Biology 34: 281–297.

Garnás, E., 1986. Changes in the diet of char Salvelinus alpinus L. after introduction of Mysis relicta Loven in two sub-alpine reservoirs in Norway. Fauna Norvegica Series A 7: 17–22.

Gregersen, F., P. Aass, L. A. Vøllestad & J. H. L’Abée-Lund, 2006. Long-term variation in diet of Arctic char, Salvelinus alpinus, and brown trout, Salmo trutta: effects of changes in fish density and food availability. Fisheries Management and Ecology 13: 243–250.

Hammar, J., 2014. Natural resilience in Arctic char Salvelinus alpinus: life history, spatial and dietary alterations along gradients of interspecific interactions. Journal of Fish Biology 85: 81–118.

Harrod, C., J. Mallela & K. K. Kahlilainen, 2010. Phenotype-environment correlations in a putative whitefish adaptive radiation. Journal of Animal Ecology 79: 1057–1068.
Hendry, A. P., D. I. Bolnick, D. Berner & C. L. Peichel, 2009. Along the speciation continuum in sticklebacks. Journal of Fish Biology 75: 2000–2036.

Hendry, A. P., K. M. Gotanda, M. Kiyoko & E. I. Svensson, 2017. Human influences on evolution, and the ecological and societal consequences. Introduction. Philosophical Transactions of the Royal Society B-Biological Sciences 372: 20160028.

Hindar, K. & B. Jonsson, 1982. Habitat and food segregation of dwarf and normal arctic charr (Salvelinus alpinus) from Vangsvatnet lake, western Norway. Canadian Journal of Fisheries and Aquatic Sciences 39: 1030–1045.

Hindar, K., N. Ryman & G. Ståhl, 1986. Genetic differentiation among local populations and morphotypes of Arctic charr, Salvelinus alpinus. Biological Journal of the Linnean Society 27: 269–285.

Hirsch, P. E., A. P. Eloranta, P.-A. Amundsen, Å. Brabrand, J. Charmasson, P. P. Helland, M. Power, J. Sánchez-Hernandez, O. T. Sandlund, J. F. Sauterleute, S. Skoglund, O. Ugedal & H. Yang, 2017. Effects of water level regulation in alpine hydropower reservoirs: an ecosystem perspective with a special emphasis on fish. Hydrobiologia 794: 287–310.

Hooker, O. E., J. Barry, T. E. Van Leeuwen, A. Lyle, J. Newton, P. Cunningham & C. E. Adams, 2016. Morphological, ecological and behavioural differentiation of sympatric profundal and pelagic Arctic charr (Salvelinus alpinus) in Loch Dhuighall Scotland. Hydrobiologia 783: 209–221.

Jackson, A. L., A. C. Parnell, R. Inger & S. Bearhop, 2011. Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. Journal of Animal Ecology 80: 595–602.

Jensen, H., M. Kiljunen, R. Knudsen & P.-A. Amundsen, 2017. Resource partitioning in food, space and time between Arctic charr (Salvelinus alpinus), brown trout (Salmo trutta) and European whitefish (Coregonus lavaretus) at the southern edge of their continuous coexistence. PloS ONE 12: e0170582.

Jeppesen, E., T. Meiner, J. W. Winfield, K. Kangur, J. Sarvala, D. Gerdeaux, M. Rask, H. J. Malmquist, K. Holmgren, P. Volta, S. Romo, R. Eckmann, A. Sandstrom, S. Blanco, A. Kangur, H. R. Stabo, M. Tarvainen, A. M. Ventela, M. Sondergaard, T. L. Lauridsen & M. Meierhoff, 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. Hydrobiologia 694: 1–39.

Jonsson, B., S. Skulason, S. S. Snorason, O. T. Sandlund, H. J. Malmquist, P. M. Jonasson, R. Gydemo & T. Lindem, 1988. Life history variation of polymorphic Arctic charr (Salvelinus alpinus) in Thingvallavatn, Iceland. Canadian Fisheries and Aquatic Sciences 45: 1537–1547.

Kahlaiinen, K. K., T. Smura, R. Knudsen, P.-A. Amundsen, M. Jokela-Määttä & K. Donner, 2016. Visual pigments of Arctic charr (Salvelinus alpinus (L.)) and whitefish (Coregonus lavaretus (L.)) morphs in subarctic lakes. Hydrobiologia 783: 223–237.

Klemetsen, A., 2010. The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in postglacial lakes. Freshwater Review 3: 49–74.

Klemetsen, A., P.-A. Amundsen, R. Knudsen & B. Hermansen, 1997. A profundal, winter-spawning morph of Arctic charr Salvelinus alpinus (L.) in lake Fjellfrøsvatn, northern Norway. Nordic Journal of Freshwater Research 73: 13–23.

Klemetsen, A., J. M. Elliott, R. Knudsen & P. Sørensen, 2002. Evidence for genetic differences in the offspring of two sympatric morphs of Arctic charr. Journal of Fish Biology 60: 933–950.

Klemetsen, A., R. Knudsen, R. Primicerio & P.-A. Amundsen, 2006. Divergent, genetically based feeding behaviour of two sympatric Arctic charr, Salvelinus alpinus (L.), morphs. Ecology of Freshwater Fish 15: 350–355.

Knudsen, R., R. Kristoffersen & P.-A. Amundsen, 1997. Parasite communities in two sympatric morphs of Arctic charr, Salvelinus alpinus (L.), in northern Norway. Canadian Journal of Zoology 75: 2003–2009.

Knudsen, R., A. Klemetsen, P.-A. Amundsen & B. Hermansen, 2006. Incipient speciation through niche expansion: an example from the Arctic charr in a subarctic lake. Proceedings of the Royal Society of London B 273: 2291–2298.

Knudsen, R., R. Primicerio, P.-A. Amundsen & A. Klemetsen, 2010. Temporal stability of individual feeding specialization may promote speciation. Journal of Animal Ecology 79: 161–168.

Knudsen, R., A. Siwertsson, C. E. Adams, M. Gardunó-Paz, J. Newton & P.-A. Amundsen, 2011. Temporal stability of niche use exposes sympatric Arctic charr to alternative selection pressures. Evolutionary Ecology 25: 589–604.

Knudsen, R., H. Johnsen, B.-S. Sæther & S. I. Siikavuo, 2015. Divergent growth patterns between juveniles of two sympatric Arctic charr morphs with contrasting depth gradient niche preferences. Aquatic Ecology 49: 33–42.

Knudsen, R., P.-A. Amundsen, A. P. Eloranta, B. Hayden, A. Siwertsson & A. Klemetsen, 2016a. Parallel evolution of profundal Arctic charr morphs in two contrasting fish communities. Hydrobiologia 783: 239–248.

Knudsen, R., K. Ø. Gjelland, A. P. Eloranta, B. Hayden, A. Siwertsson, P.-A. Amundsen & A. Klemetsen, 2016b. A specialized cannibalistic Arctic charr morph in the piscivore guild of a subarctic lake. Hydrobiologia 783: 65–78.

Koksvik, J. I., H. Reinertsen & J. Koksvik, 2009. Plankton development in Lake Jonsvatn, Norway, after introduction of Mysis relicta: a long-term study. Aquatic Biology 5: 293–304.

Kuparinne, A. & M. Festa-Bianchet, 2017. Harvest-induced evolution: insights from aquatic and terrestrial systems. Philosophical Transactions of the Royal Society B-Biological Sciences 372: 20160036.

L’Abée-Lund, J. H., A. Langeland, B. Jonsson & O. Ugedahl, 1993. Spatial segregation by age and size in Arctic charr: a trade-off between feeding possibility and risk of predation. Journal of Animal Ecology 62: 160–168.

Langeland, A., J. I. Koksvik & J. Nydal, 1991. Impact of the introduction of Mysis relicta on the zooplankton and fish populations in a Norwegian Lake. American Fisheries Society Symposium 9: 98–114.

Larsson, S., T. Forseth, I. Berglund, A. J. Jensen, I. Näslund, J. M. Elliott & B. Jonsson, 2005. Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. Freshwater Biology 50: 353–368.

Springer
Layman, C. A., M. S. Araujo, R. Boucek, C. M. Hammerschlag-Peyer, E. Harrison, Z. R. Jud, P. Matich, A. E. Rosenblatt, J. J. Vaudo, L. A. Yeager, D. M. Post & S. Bearhop, 2012. Applying stable isotope to examine food-web structure: an overview of analytical tools. Biological Review 87: 545.

Lyssy, M., A. D. Stasko & H. K. Swanson, 2014. nicheROVER: (Niche) (R)egion and Niche (Over)lap Metrics for Multidimensional Ecological Niches. R package version 1.0.

Markevich, G., E. Esin & L. Anisimova, 2018. Basic description and some notes on the evolution of seven sympatric morphs of Dolly Varden Salvelinus malma from the Lake Kronotskoe basin. Ecology and Evolution 8: 2554–2567.

Moccetti, P., A. Siwertsson, R. Kjær, P.-A. Amundsen, A.-M.P. Tamayo, K. Præbel, M. Power & R. Knudsen, 2019. Contrasting patterns in trophic niche evolution of polymorphic Arctic char populations in two subarctic Norwegian lakes. Hydrobiologia. (this issue).

Moen, V. & A. Langeland, 1989. A diurnal vertical and seasonal horizontal distribution patterns of Mysis relicta in a large norwegian lake. Journal of Plankton Research 11: 729–745.

Mousavi, S. K. & P.-A. Amundsen, 2012. Seasonal variations in the profound Chironomidae (Diptera) assemblage of a subarctic lake. Boreal Environment Research 17: 102–112.

Muir, A. M., M. J. Hansen, C. R. Bronte & C. C. Krueger, 2016. If Arctic char Salvelinus alpinus is ‘the most diverse vertebrate’, what is the lake char Salvelinus namaycush. Fish and Fisheries 17: 1194–1207.

Murdoch, A. & M. Power, 2012. The effect of lake morphometry on thermal habitat use and growth in Arctic char populations: implications for understanding climate-change impacts. Ecology of Freshwater Fish 22: 453–466.

Museth, J., R. Borgstrøm & J. E. Brittain, 2010. Diet overlap between introduced European minnow (Phoxinus phoxinus) and young brown trout (Salmo trutta) in the lake, Øvre Heimdalsvatn: a result of abundant resources or forced niche overlap? Hydrobiologia 642: 93–100.

Næsje, T. F., 1995. Effects of introduced Mysis relicta on habitat utilisation and feeding of Arctic char. Nordic Journal of Freshwater Research 71: 359–371.

Næsje, T. F., A. J. Jensen, V. Moen & R. Saksgard, 1991. Habitat use by zooplankton, Mysis relicta, and Arctic char in Lake Jonsvatn, Norway. American Fisheries Society Symposium 9: 75–87.

Nyman, L., J. Hammar & R. Gydemark, 1981. The systematics and biology of landlocked populations of Arctic char from northern Europe. Report from Institute of Freshwater Research Drottningholm 59: 128–141.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O’Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs & H. Wagner, 2017. vegan: Community Ecology Package. R package version 2.4-4.

Østbye, K., P.-A. Amundsen, L. Bernatchez, A. Klemetsen, R. Knudsen, R. Kristoffersen, T. Næsje & K. Hindar, 2006. Parallel evolution of eco-morphological traits in European whitefish Coregonus lavaretus (L.) during postglacial times. Molecular Ecology 15: 3083–4001.

Paterson, R.A., J. Nefjodova, R.K. Salis & R. Knudsen, 2019. Exploring trophic niches and parasite communities of sympatric Arctic char and brown trout populations of southern Norway. Hydrobiologia. https://doi.org/10.1007/s10750-019-3956-1.

Paterson, R. A., R. Knudsen, I. Blasco-Costa, A. M. Dunn, S. Hyttetrod & H. Hansen, 2018. Determinants of parasite distribution in Arctic char populations: catchment structure versus dispersal potential. Journal of Helminthology. https://doi.org/10.1017/s0022149x18000482.

Piggott, C. V., E. Verspoor, R. Greer, O. Hooker, J. Newton & C. E. Adams, 2018. Phenotypic and resource use partitioning amongst sympatric, lacustrine brown trout, Salmo trutta. Biological Journal of the Linnean Society 124: 200–212.

Poesch, M. S., L. Chavarie, C. Chu, S. N. Pandit & W. Tonn, 2016. Climate change impacts on freshwater fishes: a Canadian perspective. Fisheries 41: 385–391.

Power, M., M. F. O’Connell & J. B. Dempson, 2005. Ecological segregation within and among Arctic char morphotypes in Gander Lake, Newfoundland. Environmental Biology of Fishes 73: 263–274.

Power, M., G. Power, J. D. Reist & R. Bajno, 2009. Ecological and genetic differentiation among the Arctic char of Lake Aigueau, Northern Quebec. Ecology of Freshwater Fish 18: 445–460.

Præbel, K., R. Knudsen, A. Siwertsson, M. Karhunen, K. K. Kahlilainen, O. Ovaskainen, K. Østbye, S. Peruzzi, S.-E. Fevolden & P.-A. Amundsen, 2013. Ecological speciation in postglacial European whitefish: rapid adaptive radiations into the littoral, pelagic and profound lake habitats. Ecology and Evolution 3: 4970–4986.

Præbel, K., M. Couton, R. Knudsen & P.-A. Amundsen, 2016. Genetic consequences of allopatric and sympatric divergence of Arctic char (Salvelinus alpinus (L.)) from Fjellfrøsvatn as inferred by microsatellite markers. Hydrobiologia 783: 257–267.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/.

Reist, J. D., M. Power & B. Dempson, 2013. Arctic char (Salvelinus alpinus): a case study of the importance of understanding biodiversity and taxonomic issues in northern fishes. Biodiversity 14: 45–56.

Roff, D. A., 1984. The evolution of life history parameters in Teleosts. Canadian Journal of Fisheries and Aquatic Sciences 41: 984–1000.

Sandlund, O.T, A. P. Eloranta, R. Borgstrøm, T. Hesthagen, S. Sandlund, O. T. & T. Hesthagen, 2011. Fish diversity in Norwegian lakes. Biodiversity 14: 45–56.

Sjursen & P. Aass, 2017. Fiskebiologiske undersøkelser i Øvre Moaerstaas, Opdal og Sandviharvet i Kråknes og Hovet brakker i Høyfjellssamfunnet og flyttet til Lillefjell. Dansk Fiskebiologi 2017: 29–38.

Solymos, M.H.H. Stevens, E. Szoecs & H. Wagner, 2017. vegan: Community Ecology Package. R package version 2.4-4.

Tamayo, K. Præbel, M. Power & R. Knudsen, 2019. Genetic differences among Arctic char morphotypes in Kronotskoe Basin. Ecology and Evolution 8: 2554–2567.

Vennum, M., W. M. Furgala-Selezniow & A. Wisniewska (eds), 2017. Handbook of Arctic Fishes. Norwegian Marine Research Institute, Tromsø.

Wennergren, M., J. J. Vaudo, L. A. Yeager, D. M. Post & S. Bearhop, 2012. Exploring stable isotope to examine food-web structure: an overview of analytical tools. Biological Review 87: 545.

Wennergren, M., J. J. Vaudo, L. A. Yeager, D. M. Post & S. Bearhop, 2012. Exploring stable isotope to examine food-web structure: an overview of analytical tools. Biological Review 87: 545.

Wennergren, M., J. J. Vaudo, L. A. Yeager, D. M. Post & S. Bearhop, 2012. Exploring stable isotope to examine food-web structure: an overview of analytical tools. Biological Review 87: 545.

Wennergren, M., J. J. Vaudo, L. A. Yeager, D. M. Post & S. Bearhop, 2012. Exploring stable isotope to examine food-web structure: an overview of analytical tools. Biological Review 87: 545.
