

**Trophic niche segregation among native whitefish and invasive vendace in a north  
Norwegian lake system**

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## **Abstract**

Introductions and invasions of non-native species alter nutrient cycling and trophic dynamics resulting in significant ecological disturbance. Stable isotope data were used to test for evidence of invader-induced trophic niche differences in a north Norwegian lake system differentially dominated by native European whitefish (*Coregonus lavaretus*) morphotypes and invasive vendace (*Coregonus albula*). Aspects of both realized trophic niche position and trophic niche width were affected by the invader, with the effects varying by whitefish morphotype. Densely rakered pelagic whitefish demonstrated a relatively lower reliance on pelagic resources in the presence of the invader and the isotopic niche size was relatively larger in conjunction with the broadening of the prey base. Within the benthic-dwelling sparsely rakered whitefish morphotype, the trophic impacts of invading vendace were size-dependent, with larger individuals experiencing niche compression. Smaller sparsely-rakered whitefish increased, contrary to our hypothesis, reliance on pelagic-based energy in the face of invasion. Our findings demonstrate that the trophic ecology of invaded systems can differ in multiple and subtle ways that have consequences for community- and ecosystem-level energy flows, which if persisting over time are likely to have implications for the recruitment, growth and reproductive rate of the native fishes.

## **Introduction**

Introductions and invasions of non-native species can cause significant ecological disturbance and constitute a threat to the structure and dynamics of native ecological communities (Shea & Chesson, 2002). In any biological invasion, the success of the invader is never guaranteed, with the invader having to overcome both biotic and environmental resistance before a process of integration into the invaded ecosystem can begin (Moyle & Light, 1996). As a result the success of invaders can be surprisingly low (Williamson & Fritter, 1996), although when successful, invasions commonly yield ecosystem impacts, albeit not necessarily large or obvious ones (Simberloff, 2011). The success and impacts of an invader often depend on how it interacts with native species and resources (Mack et al., 2000; Shea & Chesson, 2002). One of the more important impacts relates to the alteration of trophic pathways and energy flows (Vitousek, 1990). Hence, the trophic position and linkages established by an invader are thought to hold significant implications for the community- and ecosystem-level impacts of their success (e.g., Elton, 1958; Moyle & Light, 1996; Ehrenfeld, 2010). As such, trophic hypotheses have come to dominate views regarding the potential ecological impacts of invaders, either through predator impacts on community structure or via competition and niche-based mechanisms, e.g., niche replacement, compression, and/or divergence (Riccardi, Hoopes, Marchetti & Lockwood, 2013; Tran, Jackson, Sheath, Verreycken & Britton, 2015), with dietary interactions between native and invading species often determining the eventual success of an invader (Jackson et al., 2012; Kakareko et al., 2013).

Fish, in particular, are a commonly introduced taxon in freshwater ecosystems, with introductions often being mediated by human activities, whether intentional or accidental (Copp et al., 2005). The most commonly reported impacts associated with fish introductions are

changes in either the distribution or relative abundance of the affected or introduced species, whereas descriptions of changes in energy pathways or food-web interactions tend to be rarer (Simon & Townsend, 2003). Stable isotope analyses (SIA), however, offer the opportunity to document the ecological impacts of introductions and determine underlying mechanisms because of their ability to temporally integrate ecological (i.e. trophic) signals (Cucherousset, Bouletreau, Martino, Roussel & Santoul, 2012). SIA have been used to describe the impacts of a freshwater fish introduction on food web structure and trophic niche overlap (Özdilek, Partal & Jones 2019) and experimentally to determine the role of trophic niche divergence in facilitating the integration and coexistence of invading fish species into various freshwater communities (Tran, Jackson, Sheath, Verreycken & Britton, 2015; Britton, Ruiz-Navarro, Verreychen & Amat-Trigo, 2018; Britton, Gutmann Roberts, Amat Trigo, Nolan & De Santis, 2019).

The effects of species invasions can be evident at multiple ecological levels (Mack et al., 2000) and dependent on the degree of complexity existing within the invaded ecosystem (Simberloff, 2011). One such example is the case of the specialist zooplanktivore vendace *Coregonus albula* (L.) that has invaded a hydropower-altered, subarctic watercourse along the Norwegian-Russian border previously dominated by the closely related European whitefish *Coregonus lavaretus* (L.). The whitefish in the watercourse is polymorphic, primarily dominated by a pelagic densely rakered (DR) morphotype that typically uses zooplankton as a food resource, and a larger benthic-dwelling sparsely rakered (LSR) morphotype known to forage mainly on benthic invertebrates (Amundsen et al., 1999; Amundsen, Bøhn, & Vågå, 2004). The morphs have been differentiated by genotype, morphology, ecology and thermal habitat use (Amundsen, Bøhn, & Vågå, 2004; Østbye et al., 2006; Præbel et al., 2013; Kelly, Amundsen & Power, 2015). Vendace invaded the watercourse in the early 1990's following an upstream

introduction, and the invader spread rapidly, establishing populations throughout the watercourse (Amundsen et al., 1999, 2012). However, the greatest invasion success is evident from lakes and reservoirs in the upstream part of the watercourse where vendace has become the dominant species in the pelagic habitat following a competitive exclusion of the DR whitefish morph (Bøhn & Amundsen, 2001; Bøhn, Amundsen, & Sparrow, 2008). As a result, the DR whitefish have been relegated to benthic habitats, increasing the potential for competitive interactions between the DR and LSR morphs (Bøhn, Amundsen & Sparrow, 2008; Sandlund, Gjelland, Bøhn, Knudsen & Amundsen, 2013). The effects of the vendace invasion have been less severe in the downstream part of the watercourse. There, a large part of the DR whitefish population has been able to remain and coexist in the pelagic habitat with a less abundant vendace population, partly facilitated through the use of different microhabitats available within the deeper pelagic zone (Gjelland, Bøhn, & Amundsen, 2007). Hence, a contrasting interaction scenario has been established following the vendace invasion, with potentially stronger competitive interactions between vendace and whitefish and among the whitefish morphs in the upstream relative to the downstream parts of the watercourse.

Stable isotopes were used to explore hypotheses regarding trophic niche separation and width among the native whitefish morphs and the invading vendace, comparing two lakes, differentially dominated by the invader. First, we hypothesized (H1) that native DR whitefish will obtain a lower proportion of their diet from the pelagic zone in the upstream lake where invasive vendace have become numerically dominant. Secondly, (H2), we hypothesized that the DR whitefish morph would broaden their prey base, with the result that DR whitefish would have a larger isotopic niche in the highly invader-impacted upstream lake compared to the less invader-impacted downstream lake. Finally, we hypothesized (H3) that the littoral-adapted LSR

morph would undergo niche compression showing a narrower prey base and a smaller isotopic niche in the upstream lake as a result of increased littoral resource utilization by the relegated DR whitefish.

## **Methods**

### ***Sampling***

The Pasvik watercourse serves as the border between northern Norway and Russia, originating in Lake Inarijärvi and draining into the Barents Sea (Fig. 1). The watercourse is impacted by seven dams which have removed natural rapids and increased the lacustrine habitat within the system (Bøhn & Amundsen, 2001; Gjelland, Bøhn, & Amundsen, 2007). The fish community consists mainly of whitefish, vendace and perch (*Perca fluviatilis*). There are also populations of pike (*Esox lucius*), burbot (*Lota lota*), grayling (*Thymallus thymallus*) and nine-spined stickleback (*Pungitius pungitius*) as well as a small population of brown trout (*Salmo trutta* L.), which is supplemented by annual stocking. Yearly sampling is undertaken by researchers at UiT The Arctic University of Norway as part of a long-term ecological research program (Amundsen et al., 2019). Within this program, two sites in the Pasvik watercourse were sampled from the 12<sup>th</sup> to the 16<sup>th</sup> of September 2013: one site in an upstream lake where vendace are numerically dominant (Lake Tjærebukta), and one site in a downstream lake where the vendace population is less abundant (Lake Skrukkebukta). Both sites are affected by water regulations for hydropower production, with regulation amplitudes that are similar and moderate and within the natural fluctuation levels (<80 cm).

Whitefish and vendace were collected in the two sites using gill nets (mesh size 6–45 mm knot to knot) set overnight in pelagic, littoral and profundal habitats, as defined in Bøhn, Amundsen, & Sparrow (2008), where the pelagic zone was considered to be surface waters to a

depth of 6 m at the deepest part of the lake, the littoral zone was considered to be shoreline areas to a depth of 5 m, and the profundal zone was defined as the bottom 2 m in the deepest part of the lake. Permission for the gill net fishing in the two lakes was obtained from the County Governor of Finnmark, which is the official fishing right owner on Government land in Finnmark County. No ethical permission is required from the Norwegian Animal Research Authority for collection with gill nets and the associated sacrifice of fish. The sampling was performed in strict accordance with Norwegian legislation and fish were euthanized by means of cerebral concussion prior to sample collection. Fish were measured (fork length, mm) and weighed (g) and dissected on site. Whitefish morphs were identified by gill raker numbers and morphology as DR (densely rakered, pelagic specialized morph) and LSR (large sparsely rakered, littoral specialized morph) following Siwertsson et al. (2010). Dorsal fish muscle tissue was removed and frozen on site, and subsequently dried in the lab at 60 °C for 24 hours for SIA. The C:N ratio of the fish muscle tissue was <4 and therefore lipid extraction prior to analysis was not conducted (e.g. Fagan, Koops, Arts, & Power, 2011).

Prey samples, including zooplankton (pelagic) and chironomids (littoral), were collected and frozen on site, then dried and analysed to establish the isotope baseline at the two sites. Zooplankton were collected with a zooplankton net (125 µm mesh size) at 1 m below the surface by a 10 minute horizontal tow and subsampled in triplicate for analysis. This approach enabled the collection of a spatially homogenized sample for each site. Chironomids were collected manually from three locations in the littoral zone of each site at a depth of 30 cm. Multiple chironomids at each of the three sampling locations were pooled for stable isotope analysis to ensure a sufficient amount of material was available for analysis. Samples to establish the baseline were frozen on site, and subsequently dried in the lab at 60 °C for 24 hours for SIA.

### *Stable isotope analysis*

All isotope samples were analysed at the University of Waterloo Environmental Isotope Laboratory (UWEIL) and are reported in standard  $\delta$  notation:

$$\delta = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000 (\text{‰}).$$

Samples were analysed with a 4010 Elemental Analyser (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) having a precision of 0.2‰ (UWEIL).  $\delta^{13}\text{C}$  was measured relative to Vienna Pee Dee Belemnite (VPDB) and  $\delta^{15}\text{N}$  was measured relative to atmospheric nitrogen.

### *Statistical Analysis*

All analyses were performed in R version 3.6.1 (R Core Team, 2013). A Shapiro-Wilk test (Royston, 1982) and a normal quantile-quantile plot were used to assess the normality of the data.

Fish can undergo ontogenetic shifts in dietary and habitat resource use as they grow. To avoid the confounding factor of changes in diet and habitat, correlation analyses of the relationship between fish length  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were conducted. Where there was a significant correlation, fish species/morphs were separated into ‘small’ and ‘large’ size classes where a suitable break in the length distribution occurred suggesting different age classes (DR and vendace), or where a distinct ontogenetic dietary niche shift has been shown to occur (LSR) (van Dorst 2015; P-A Amundsen, unpublished data). The small and large size classes were then analysed separately within the statistical analysis.

To assess H1, that native whitefish will obtain a lower proportion of their diet from the pelagic zone in the upstream lake where vendace have become numerically dominant, a two source mixing model was used to determine percent pelagic resource use by DR, LSR and



vendace (Sherwood & Rose, 2005; Dixon, Power, Dempson, Sheehan, & Chaput, 2012). More sophisticated models for assessing individual prey contributions to fish predator diets are now commonly used to investigate fish diet in detail (e.g. MixSIAR). However, for the narrow question of the pelagic contribution to fish diet, a simple two source mixing model is more appropriate. The mixing model used was:

$$\% \text{ pelagic resource use} = (\delta^{13}\text{C}_{\text{consumer}} - \delta^{13}\text{C}_{\text{L}} - \text{TF} / \delta^{13}\text{C}_{\text{P}} - \delta^{13}\text{C}_{\text{L}}) * 100$$

Where  $\delta^{13}\text{C}_{\text{Consumer}}$  is the mean  $\delta^{13}\text{C}$  value of the consumer,  $\delta^{13}\text{C}_{\text{L}}$  is the mean  $\delta^{13}\text{C}$  value of the littoral baseline (mean littoral chironomid  $\delta^{13}\text{C}$ ), TF is the trophic fractionation from the base of the food web to the consumer, and  $\delta^{13}\text{C}_{\text{P}}$  is the  $\delta^{13}\text{C}$  value of the pelagic baseline (mean pelagic zooplankton  $\delta^{13}\text{C}$ ). The median trophic fractionation factor (0.8) reported for freshwater fish species in the meta-analysis of McCutchan, Lewis, Kendall and McGrath (2003) was used for TF. A t-test was used to compare the percentage of pelagic resource use by DR and LSR morphs between the two sites. The trophic fractionation factor cited here is widely used throughout the literature (e.g., Sherwood & Rose, 2005), but not specific to the species in this study. Therefore, we ran the analysis with two additional trophic fractionation factors (0.3 and 1.3) to test the sensitivity of the results to the chosen fractionation parameter. While the resulting per cent reliance on pelagic resources did change with a change in TF, the change was not large and the overall patterns in resource use and the outcome of the statistical tests remained the same.

To assess H2, that DR whitefish morph would broaden their prey base in the upstream site, and H3, that LSR whitefish would narrow their prey base in the upstream site, the maximum likelihood Bayesian ellipse areas ( $\text{SEA}_{\text{B}}$ ) and 95% credibility intervals were calculated in R with the SIBER package (Jackson, Inger, Parnell, & Bearhop, 2011) for each species/morph. The  $\text{SEA}_{\text{C}}$ , which is a calculation of ellipse area corrected for small sample size, is also reported.

## Results

Correlation analyses of the relationship between fish length and  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicated ontogenetic shifts in diet in some but not all whitefish morphs and vendace (Table 1). The DR morph in the upstream site showed a significant positive correlation between fish length and  $\delta^{15}\text{N}$  ( $p = 0.002$ ,  $r^2 = 0.51$ ) but not  $\delta^{13}\text{C}$ . Therefore, the DR morph data from the upstream site was separated into two size classes to evaluate H2: ‘small’ (< 225 mm) and ‘large’ (> 225 mm), in accordance with a break in the length data signifying different age classes. No significant correlation was found for either isotope with length for DR in the downstream site, therefore separation into distinct size classes was unnecessary.

Significant correlations were found between the length of the LSR morph and both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the upstream site ( $\delta^{13}\text{C}$ ,  $p < 0.001$ ,  $r^2 = 0.33$ ;  $\delta^{15}\text{N}$ ,  $p < 0.001$ ,  $r^2 = 0.28$ ) and the downstream site ( $\delta^{13}\text{C}$ ,  $p < 0.001$ ,  $r^2 = 0.24$ ;  $\delta^{15}\text{N}$ ,  $p = 0.02$ ,  $r^2 = 0.11$ ). Therefore, to test H3, the LSR morphs at both sites were separated into ‘small’ (< 250 mm) and ‘large’ (> 250 mm) size classes based on the known ontogenetic shift in diet found at 250 mm (van Dorst 2015, P.-A. Amundsen, unpublished data).

Significant correlations were found between the length of vendace and  $\delta^{13}\text{C}$  ( $p < 0.001$ ,  $r^2 = 0.65$ ) and  $\delta^{15}\text{N}$  ( $p < 0.001$ ,  $r^2 = 0.58$ ) in the downstream site but not the upstream site. Therefore, data for vendace from the downstream site is presented in two size classes: ‘small’ (< 110 mm) and ‘large’ (> 110 mm) in accordance with a break in the length data at 110 mm indicating distinct age classes.

As hypothesized, the two-member mixing model showed that DR whitefish obtain a lower percentage of their diet from the pelagic zone in the upstream site (64.5 %) where vendace are numerically dominant. Compared to the downstream site (72.0 %), however, the difference

was not significant ( $t_{16.9} = 1.72$ ,  $p=0.10$ ) (Table 2). Also as hypothesized, vendace used a higher percentage of pelagic based food in the upstream site (90.6 %) compared with vendace in the downstream site (72.0 and 83.0 % for small and large vendace, respectively). For LSR, the percentage of pelagic sourced food was higher in the upstream site, but the difference was only significant for small LSR (small:  $t_{11.8} = 4.6$ ,  $p<0.001$ ; large:  $t_{8.2} = 0.6$ ,  $p=0.59$ ). Small LSR had a higher pelagic percentage in their diet regardless of site.

The ellipse sizes ( $SEA_B$ ) of small and large DR were more than double the size in the upstream site, where vendace is numerically dominant, relative to the  $SEA_B$  of DR in the downstream site (Fig. 2a, Table 3), with the differences in ellipse size indicating a broader prey base in the upstream site as hypothesized. Comparisons of ellipse areas between sites for the LSR morph yielded different results depending on size class. Large LSR had a smaller ellipse area in the upstream site, as hypothesized, however the opposite was true for small LSR (Fig. 2b, Table 3).

## **Discussion**

Stable isotope data collected for native whitefish morphotypes in the Pasvik reservoir system indicated differences in the realized trophic niche and niche width of the whitefish morphotypes in the presence of invading vendace. As hypothesized, DR whitefish displayed a lower reliance on pelagic resources in the upstream lake where invasive vendace were numerically dominant, suggesting that vendace have been able to outcompete DR whitefish. Similarly, as hypothesized, the isotopic niche of the large DR whitefish was larger in the upstream lake relative to the downstream lake suggesting a broadening of their prey base. Size-dependent niche compression was evident in the littoral-adapted LSR morphotype for large LSR but not small LSR whitefish. While large LSR whitefish decreased pelagic reliance in the face of

invasion, smaller LSR fish increased their reliance on pelagic-based energy. On the basis of the comparison between the highly invaded and marginally invaded lake ecosystems, it is evident that the trophic ecology of an invader can have significant implications for community- and ecosystem-level energy flows as a result of the differences in observed niches among the resident morphotypes of native whitefish in the Pasvik lakes.

There are several effects of the vendace invasion that have resulted in changes to the energy flow of the system, including an alteration of the zooplankton community composition towards smaller species and smaller individuals (Bøhn & Amundsen, 1998; Amundsen, Siwertsson, Primicerio, & Bøhn, 2009), a major change in prey size of piscivorous predators (Jensen, Bøhn, Amundsen, & Aspholm, 2004; Jensen et al., 2008), large inter-annual variations in the density of zooplankton predators, in particular vendace (Sandlund, Gjelland, Bøhn, Knudsen, & Amundsen, 2013; Amundsen et al., 2019), new and unanticipated feeding links (Liso, Gjelland, Reshetnikov, & Amundsen, 2011), and an increased utilization of pelagic prey by benthic piscivores like pike and burbot (Amundsen et al., 2019). The results in this study provide further evidence of the differences in energy flows in this system where vendace have invaded.

The effects of species invasions are often manifested in diet shifts in native species, with such shifts having the potential to significantly alter ecosystem processes such as nutrient cycling (Ehrenfeld, 2010) and trophic structure (Vitousek, 1990). In that context the relatively lower reliance on pelagic resources in the invaded lake by DR whitefish was not unexpected as the native whitefish may have shifted diets to reduce competitive interactions with invading vendace, particularly as the extent of species' niche overlap and divergence have been suggested as an effective indicator of inter-specific competition (e.g., MacArthur & Levins 1967; Abrams,

1983). In Canadian lakes the reduction in the diversity and abundance of littoral prey fish by invasive smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) forced native lake trout (*Salvelinus namaycush*) toward an increased reliance on pelagic zooplankton as prey (Vander Zanden, Casselman, & Rasmussen, 1999). In stream-dwelling fish, differential shifts in foraging mode between species across varying resource gradients have been suggested as one mechanism facilitating resource partitioning that allows coexistence (Nakano, Fausch, & Kitano, 1999), which is likely to operate when closely related species encounter each other in the context of habitat invasions. Similarly, experimental studies of invasion impacts have suggested that some form of niche divergence and/or reduction response by native fishes may facilitate coexistence with the invader (Tran, Jackson, Sheath, Verreycken, & Britton, 2015). More generally, an early ecological response to an ecosystem invasion may be manifested in the trophic re-organisation of the food web to minimise the interactions between competing species (Britton, Ruiz Navarro, Verreychen, & Amat Trigo, 2018).

There has been a marked increase in our understanding of the importance of the ecological effects of individual variation within species (Des Roches et al., 2018), with variation in traits such as body size also known to affect the structure and dynamics of food webs (Woodward et al., 2005). For instance, the trophic ecology of invasive crayfish (*Procambarus clarkii*) has been found to vary with individual body size (Jackson et al., 2017), as have the trophic interactions of species with overlapping ranges (brook trout *Salvelinus fontinalis* and yellow perch *Perca flavescens*) when examined in allopatry and sympatry (Browne & Rasmussen, 2009). As predators and prey often scale with each other (Dörner, Hülsmann, Hölker, Skov, & Wagner, 2007), the effects of an invader on the native species it competes with should similarly scale with body size. For example, studies of mixed communities of native and

introduced salmonid fishes in Utah reservoirs have suggested more predominant trophic niche effects on smaller native benthivorous rainbow trout (*Oncorhynchus mykiss*) than larger conspecifics that have switched to piscivory. Studies of zooplankton size spectra in the Pasvik River system have shown a similar significant shift toward smaller-bodied zooplankton in the upper lakes and a reduction in larger-bodied zooplankton (Bøhn & Amundsen, 1998; Amundsen, Siwertsson, Primicerio, & Bøhn, 2009). The reduction in larger zooplankton densities in the upper lake is consistent with the trophic effects observed in the upstream site for larger DR whitefish. Thus, one effect of invading vendace appears to have been a disruption of the normal ontogenetic dietary shift of whitefish from reliance on small cyclops to predation on cladocerans (e.g., Sandlund, Næsje, & Jonsson, 1992; Anneville, Laine, Benker, Ponticelli, & Gerdeaux, 2007) as body size increases.

In cases where species overlap sufficiently in food and habitat use for competition to occur, prey density can be reduced by competition from the invading species with the result that resident species are expected to undergo spatial "compression", equated with showing a reduction in habitat use and an expansion in diet (MacArthur & Levins, 1967). Such a prediction would be consistent with the pattern of DR whitefish relegation from the pelagic zone (Amundsen et al., 1999, 2019; Bøhn, Amundsen, & Sparrow, 2008; Sandlund, Gjelland, Bøhn, Knudsen, & Amundsen, 2013), the restricted use of profundal microhabitats (Gjelland, Bøhn, & Amundsen, 2007) and an associated broadening of the prey base as reflected in the measured shifts in  $\delta^{13}\text{C}$  noted here. Similarly, data from habitat use studies of introduced darter (*Etheostomids*) species have shown significant compression in habitat use by native darters from allopatry to sympatry (Gray, Kellogg, & Stauffer, 2005). Shifts in patterns of resource use can also occur under natural conditions as a result of the presence/absence of close trophic

competitors. For example, the presence of yellow perch shifted smaller, non-piscivorous-sized brook trout to a lower reliance on littoral resources (Browne & Rasmussen, 2009), with an associated increase in  $\delta^{13}\text{C}$  variation typically thought of as an index for niche diversification at the base of a food web (Layman, Arrington, Montaña, & Post, 2007).

Although successful invading species are generally thought to have broader feeding habits, and thus a wider trophic niche than resident competitors (Lodge, 1993; Moyle & Light, 1996; Moyle & Marchetti, 2006), the reverse was true here. Vendace is a specialist zooplanktivore (Hamrin, 1983; Viljanen, 1983) and through exploitative competition has forced DR whitefish from the pelagic areas by interactive segregation (Bøhn & Amundsen 2001; Bøhn, Amundsen, & Sparrow, 2008). How well an invader performs, however, should be viewed in the wider context of the resource opportunities provided by the invaded community (Shea & Chesson, 2002). When both the resident and the invader are limited by a single resource, as here (i.e., zooplankton), resource acquisition rate determines invasion success and invader resident niche space overlap would be expected (Shea & Chesson, 2002), as would a narrower niche for the invader if successful. Indeed the suggested mechanism for the successful establishment of vendace has been its ability to more effectively exploit smaller zooplankton than DR whitefish (Bøhn & Amundsen, 1998; Amundsen, Siwertsson, Primicerio, & Bøhn, 2009), thereby imposing resource limitations on DR whitefish that have triggered habitat and trophic shifts (Bøhn & Amundsen, 2001; Bøhn, Amundsen, & Sparrow, 2008) and evidenced themselves in reduced abundance of DR whitefish (Bøhn & Amundsen, 2004; Bøhn, Amundsen, & Sparrow, 2008; Sandlund, Gjelland, Bøhn, Knudsen, & Amundsen, 2013; Amundsen et al., 2019).

The classical ecological template for species invasions suggests successful invaders will out-compete native species by occupying a wider trophic niche (e.g., Elton, 1958; Moyle &

Light, 1996), with recent empirical studies having validated the result in a number of instances including cases involving: the trophic impacts of non-native brown trout, *Salmo trutta*, on native Bonneville cutthroat trout, *Oncorhynchus clarkii*, in Utah (McHugh, Budy, Thiede, & Van Dyke, 2008), invasive crayfish in Sweden (Olsson, Stenroth, Nyström, & Graneli, 2009), dietary overlap between alien and native gastropods in South Africa (Miranda & Perissinotto, 2012), or as in some of the reservoir case studies describing the trophic impacts of invasive white perch, *Morone americana*, on native reservoir fishes in North Carolina (Feiner, Rice, & Aday, 2013). While niche compression was observed among the larger LSR whitefish in the Pasvik system, niche compression was not evident among smaller LSR whitefish. As other studies have shown, niche compression is not an obligatory outcome of a successful invasion, with dietary specialization in the invader and resident species likely to contribute to the narrowing of the trophic niche for both (Tran, Jackson, Sheath, Verreycken, & Britton, 2015; Jackson, Grey, Miller, Britton, & Donohue, 2016). Furthermore, experimental and comparative ecological studies have tended to corroborate theoretical expectations that the species' trophic niches are context dependent, relying on the degree of competition (both intra- and inter-specific), ecological opportunity and predation (Araújo, Bolnick, & Layman, 2011), with the result that under the competitive conditions of invasion, niche widths might be expected to either increase or decrease (Jackson, Grey, Miller, Britton, & Donohue, 2016) or vary with the temporal scale of the analysis (Thomsen, Wernberg, Olden, Griffin, & Silliman, 2011).

While the ecological effects of invasion can include alteration of food webs and trophic dependencies (Simon & Townsend, 2003), resource sharing does not necessarily imply a high degree of potential direct dietary resource competition from the invader, if the invasive fish can find and occupy a distinct portion of isotopic niche space (Hill, Jones, Hill, & Weyl, 2015).



Whitefish, like many species, couple pelagic and benthic energy pathways (Kahilainen, 2003; Nieminen, 2012; Rösch, Lundsgaard-Hansen, Vonlanthen, Taverna, & Seehausen, 2013), with the coupling to some extent buffering individuals against the larger trophic impacts of invasion (e.g., Hecky & Hesslein, 1995). Thus, the ability of whitefish to exploit both pelagic and epibenthic habitats in lakes in which they co-occur with vendace (Næsje, Jonsson, & Sandlund, 1991) may partially buffer them from the full competitive impacts of invasive vendace. Introductions of planktivorous fish in reservoirs have been shown to rapidly eliminate large-bodied zooplankton, shifting the size-spectra distribution to smaller taxa (Ordóñez et al., 2010). The increased predation pressure on large-bodied zooplankton resulting from vendace introductions, therefore, is likely to have had a greater effect on larger LSR whitefish given the known scaling of predator and prey sizes (Bremigan & Stein, 1994), reducing their niche breadth in comparison to smaller LSR whitefish whose ability to exploit smaller zooplankton prey and benthic prey facilitates the maintenance of a broader niche. However, individuals unable to effectively couple benthic–littoral energy pathways may experience decline in body condition, reproduction, and recruitment as has been noted for whitefish (*Coregonus clupeaformis*) in the North American Great Lakes (Mills et al., 2003; Pothoven & Madenjian, 2008; Rennie, Sprules, & Johnson, 2009).

## **Conclusions**

In conclusion, our findings on the trophic impacts of invasive vendace on resident morphotypes of whitefish point to multiple, albeit subtle, effects including differences in the realized trophic niche and niche width of the native whitefish represented by higher reliance on littoral zone resources and size-dependent niche compression. Persisting over time, such impacts could have demonstrable implications for recruitment, potentially leading to lower growth and

reproductive rate of the affected species in ways likely to reduce its relative abundance in the invaded habitats (see also Bøhn, Amundsen, & Sparrow, 2008; Sandlund, Gjelland, Bøhn, Knudsen, & Amundsen, 2013; Amundsen et al. 2019). Future studies designed to collect dietary, stable isotope and condition data from a gradient of affected habitats could clarify the significance of invasion trophic impacts for disrupting energy flows and resident species abundance within lake food webs.

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**Fig 1** Location of the Pasvik watercourse within the northern Fenno-Scandinavian peninsula (a), the Pasvik watercourse (b), Lake Skrukkebukta (c), and Lake Tjærebukta (d)

**Fig 2** Stable isotope values and ellipses drawn to encompass 95% of the data for densely rakered (DR) whitefish *Coregonus lavaretus* (a), sparsely rakered (LSR) whitefish *C. lavaretus* (b) and vendace *C. albula* (c).



