Author(s): Eloranta, Antti P.; Finstad, Anders G.; Sandlund, Odd Terje; Knudsen, Rune; Kuparinen, Anna; Amundsen, Per-Arne

Title: Species interactions, environmental gradients and body size shape population niche width

Year: 2022

Version: Published version

Please cite the original version:

RESEARCH ARTICLE

Species interactions, environmental gradients and body size shape population niche width

Antti P. Eloranta[1,2] 🆔 | **Anders G. Finstad**[3] 🆔 | **Odd Terje Sandlund**[2] 🆔 |
Rune Knudsen[4] 🆔 | **Anna Kuparinen**[1] 🆔 | **Per-Arne Amundsen**[4] 🆔

[1]Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

[2]Department of Aquatic Biodiversity, Norwegian Institute for Nature Research (NINA), Trondheim, Norway

[3]Department of Natural History, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway

[4]Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway

Correspondence
Antti P. Eloranta
Email: antti.p.eloranta@jyu.fi

Funding information
Norges Forskningsråd, Grant/Award Number: 186320 and 243910; Academy of Finland, Grant/Award Number: 317495 and 340901

Handling Editor: Carola Gómez-Rodríguez

Abstract

1. Competition for shared resources is commonly assumed to restrict population-level niche width of coexisting species. However, the identity and abundance of coexisting species, the prevailing environmental conditions, and the individual body size may shape the effects of interspecific interactions on species' niche width.

2. Here we study the effects of interspecific and intraspecific interactions, lake area and altitude, and fish body size on the trophic niche width and resource use of a generalist predator, the littoral-dwelling large, sparsely rakered morph of European whitefish (*Coregonus lavaretus*; hereafter LSR whitefish). We use stable isotope, diet and survey fishing data from 14 subarctic lakes along an environmental gradient in northern Norway.

3. The isotopic niche width of LSR whitefish showed a humped-shaped relationship with increasing relative abundance of sympatric competitors, suggesting widest population niche at intermediate intensity of interspecific interactions. The isotopic niche width of LSR whitefish tended to decrease with increasing altitude, suggesting reduced niche in colder, less productive lakes.

4. LSR whitefish typically shifted to a higher trophic position and increased reliance on littoral food resources with increasing body size, although between-lake differences in ontogenetic niche shifts were evident. In most lakes, LSR whitefish relied less on littoral food resources than coexisting fishes and the niche overlap between sympatric competitors was most evident among relatively large individuals (>250 mm). Individual niche variation was highest among >200 mm long LSR whitefish, which likely have escaped the predation window of sympatric predators.

5. We demonstrate that intermediate intensity of interspecific interactions may broaden species' niche width, whereas strong competition for limited resources and high predation risk may suppress niche width in less productive environments. Acknowledging potential humped-shaped relationships between population niche width and interspecific interactions can help us understand species' responses to

environmental disturbance (e.g. climate change and species invasions) as well as the driving forces of niche specialization.

KEYWORDS

diet selection, high-latitude lakes, individual specialization, niche expansion, ontogeny, resource competition, salmonid, trophic niche

1 | INTRODUCTION

Ecologists have long studied the role of abiotic and biotic factors in determining species' diversity and population niche width. A wide population niche width is commonly assumed to result from ecological release from interspecific competition and/or intense intraspecific competition forcing individuals to utilize a wider spectre of contrasting, specialized niches (Roughgarden, 1972; Van Valen, 1965). However, some empirical studies provide contrasting evidence for the diversifying and constraining effects of intraspecific and interspecific competition, respectively (Bolnick et al., 2010; Parent et al., 2014). Recent studies have quantified how the extent of among-individual variation is influenced by ecological interactions and how it varies among populations or contexts (Araújo et al., 2011; Jesmer et al., 2019). The synthesis by Jones and Post (2016) demonstrates that intraspecific competition can have either a restricting or a diversifying effect on population niche width and the degree of individual specialization. Consequently, they question the common competitive diversification hypothesis that within-population variation increases with increasing intraspecific competition, and they propose an alternative intermediate competitive diversification hypothesis (IDH) that predicts a hump-shaped relationship between intraspecific competition and population niche width (Jones & Post, 2016).

Compared to biotic interactions, the importance of abiotic environmental characteristics, such as ecosystem size and climate, for population niche width and among-individual diet variation, has remained less studied. The recent study by Bolnick and Ballare (2020) demonstrates a hump-shaped response of among-individual diet variation within stickleback *Gasterosteus aculeatus* populations to increasing lake size due to high resource diversity in intermediate-sized lakes. Similar hump-shaped relationships seem ubiquitous when looking at, for example, species richness and abundance across environmental gradients (e.g. Allouche et al., 2012; Dodson et al., 2000; Finstad et al., 2014), but they are rarely considered in studies of niche variation (but see Bolnick & Ballare, 2020; Jones & Post, 2016; Svanbäck et al., 2015). In essence, and to the best of our knowledge, no previous studies have considered the potential diversifying effect of varying interspecific interactions on the population niche width of generalist species.

Recent studies of generalist fishes demonstrate how individual niche variation can also vary through ontogeny and be shaped by the community composition as well as diversity of available prey resources (Sánchez-Hernández et al., 2016, 2020; Svanbäck et al., 2015). The ubiquitous ontogenetic niche shifts by generalist species are typically related to size-dependent changes in predation risk, foraging efficiency and competitive dominance (Sánchez-Hernández et al., 2019; Werner & Gilliam, 1984; Woodward et al., 2005). Hence, besides prevailing abiotic and biotic environmental conditions, the body size of individuals is likely a factor determining among-individual niche variation and population-level niche width of generalist species (Häkli et al., 2018; Svanbäck et al., 2015). However, no empirical studies have simultaneously tested for potential linear or nonlinear effects of competitor abundance, environmental conditions and individual body size on population niche width and degree of among-individual variation.

We used a unique dataset collected from 14 subarctic lakes in the Finnmark region, northern Norway, to study how the population niche width and the degree of among-individual diet variation of a generalist salmonid, the littoral-dwelling large, sparsely rakered (LSR) morph of European whitefish (*Coregonus lavaretus*; hereafter LSR whitefish), are affected by the intensity of interspecific and intraspecific interactions, individual body size and lake abiotic characteristics. Lakes are highly variable, largely closed ecosystems with well-defined boundaries, which makes them ideal for studying the effects of biotic and abiotic factors on population niche width and individuals' resource use. Lake abiotic characteristics (e.g. surface area and altitude) are fundamental factors determining species diversity, abundance and size structure as well as food-web dynamics in high-latitude lakes. Generalist fishes tend to shift from littoral to pelagic resources with increasing lake area (Eloranta et al., 2015) and productivity (Hayden et al., 2019). The present study lakes are situated along an altitude (and thus climatic and productivity) gradient and they host fish communities dominated by one or more of the following species: European whitefish, European perch (*Perca fluviatilis*; hereafter perch), Arctic charr (*Salvelinus alpinus*; hereafter charr) and European grayling (*Thymallus thymallus*; hereafter grayling), as well as scarce populations of some other fish species (see *Data collection* for details). Based on previous research in northern Europe, these percid and salmonid fishes generally prefer littoral habitat and food resources (Eloranta et al., 2013; Eloranta et al., 2015; Berezina et al., 2018) and thus compete for shared resources with LSR whitefish (Eloranta et al., 2011; Hayden et al., 2013). Some lakes host polymorphic whitefish populations consisting of up to three ecologically and phenotypically divergent morphs, including a small pelagic, densely rakered (DR) and a small profundal, sparsely rakered (SSR) whitefish that coexist with the large and generalist, sparsely rakered LSR whitefish (Häkli et al., 2018; Siwertsson et al., 2013). Besides interspecific interactions with coexisting fishes, intraspecific resource competition among whitefish morphs may also influence the diet and habitat

use of the generalist LSR whitefish (Harrod et al., 2010; Siwertsson et al., 2013). In northern Europe, percids are typically the most abundant and competitively dominant fishes in relatively warm and productive mesotrophic lakes, whereas salmonids dominate in the most oligotrophic and cold high-altitude lakes (Hayden et al., 2014, 2017). This is also the case in the Finnmark region, where perch is most abundant at lower altitudes and salmonids like whitefish, charr and grayling dominate at higher altitudes (Supporting Information A Table S1). These relatively pristine lakes provide a suitable scenario to study how the identity and intensity of interspecific and intraspecific interactions shape niche width and resource use of generalist salmonid populations under natural conditions.

We used stable isotope data (δ^{13}C and δ^{15}N) to estimate population niche width and trophic diversity among individuals, and stomach contents data to estimate the degree of among-individual diet variation in each LSR whitefish population. Thereafter, we tested how these niche parameters were affected by the intensity of interspecific and intraspecific interactions, as well as by the lake area and altitude (a proxy for temperature conditions and lake productivity). Data from multi-mesh survey gillnet catches (number and biomass of fish) were used to estimate the intensity of interspecific and intraspecific interactions in each study lake. Hence, our data provide the opportunity to use continuous measures of interspecific and intraspecific interactions and test their effects on the population niche width and degree of among-individual diet variation. We expected LSR whitefish population niche width and degree of among-individual diet variation (a) to decrease with increasing intensity of interspecific interactions and (b) to increase with increasing intraspecific competition. Moreover, we expected LSR whitefish (c) to undergo ontogenetic dietary shifts and increase niche variation with increasing size due to reduced predation risk and increased competitive dominance. We further expected LSR whitefish (d) to utilize more pelagic food resources than the coexisting percid or salmonid fishes that are strong competitors for littoral resources, as well as potential predators of small whitefish (Amundsen et al., 2003, 2010; Eloranta et al., 2011; Hayden et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Data collection

The 14 study lakes are relatively small (0.19–23.7 km^2), dimictic and meso- or oligotrophic lakes situated along an altitude gradient (275–540 m a.s.l.) in the Finnmark region. Meteorological data obtained from years 2005–2009 (https://seklima.met.no/observations/) indicate clear differences in mean summer (June–August period: 11.6 vs. 9.5°C) and winter (December–February period: −12.5 vs. −7.4°C) air temperatures and in snow depth (19.9 vs. 31.4 cm) at two monitoring stations located at 307 m (Kautokeino) and 381 m a.s.l. (Suolovuopmi – Lulit). Hence, even larger differences in climatic conditions are expected for the 14 study lakes covering an altitude gradient of 265 m. The study area has very limited human activity and the catchment

areas consist mainly of mountain birch forest and bogs (Figure 1; Table 1). No major fishery or any stocking activity occur in the study lakes. Most lakes belong to the Kautokeino watercourse draining to Altaelva river, except Iddjajavri and Vuoddasjavri that drain to Tanaelva (Tenojoki) river. Besides whitefish, perch, grayling and charr, some lakes have relatively scarce populations of burbot *Lota lota*, brown trout *Salmo trutta*, pike *Esox lucius*, European minnow *Phoxinus phoxinus* and/or nine-spined stickleback *Pungitius pungitius*. LSR whitefish is present in all study lakes, whereas six of the lakes host polymorphic whitefish populations having the additional presence of a small pelagic, densely rakered (DR) and/or a small profundal, sparsely rakered (SSR) whitefish morph (Table 1; Table S1; Häkli et al., 2018; Siwertsson et al., 2013).

Survey fishing was conducted between 8th August and 17th September in 2005–2009 using the same multi-mesh gillnets set overnight in the littoral, profundal and pelagic habitats of each study lake. All study lakes were sampled in a single year between 2007 and 2009, except Stuorajavri with main fish sampling in 2005 supplemented by profundal sampling in 2008 (Table 1), following the same sampling protocols and mostly by the same personnel. Therefore, the obtained survey fishing and SIA data are expected to be sufficient to estimate fish community compositions and niche width and resource use of LSR whitefish in our relatively remote study lakes, which are not subject to direct human impacts, such as inter-annual variation in fish stocking, fishing pressure or land-use activities. Multi-mesh survey gillnets is a well-established and generally used method to characterize lacustrine fish communities (e.g. Alexander et al., 2015), and are expected to yield more representative data than alternative methods such as hydroacoustics (Malinen et al., 2013), especially for the shallow littoral areas that is the predominant fish habitat in small subarctic lakes. No ethical permission is required from the Norwegian Animal Research Authority for collection with gill nets and the associated sacrifice of fish (FOR 1996-01-15 nr 23, the Norwegian Ministry of Agriculture and Food). However, a fishing permission is required from the fishing right owner, and this was obtained from the County Governor of Finnmark with legal authority through LOV 1992-05-15 nr 47, §13.

The used multi-mesh gillnets were 40 m long and composed of eight randomly distributed 5 m panels of 10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm bar mesh sizes (knot to knot). In the littoral (0–8 m depth) and profundal (>12 m depth) habitats, 1.5 m deep bottom nets were used, whereas 6 m deep floating nets were used in the pelagic zone in each lake. Supplementary material for stable isotope (hereafter SIA) and stomach contents (hereafter SCA) analyses were sampled using 30 m long and 1.5 m deep single-mesh (20, 22, 26, 32, 35 mm) gillnets. However, the supplementary samples were excluded from catch statistics as described below. Unfortunately, we failed to catch sufficient samples of LSR whitefish for SIA ($n = 14$) and SCA ($n = 12$) from the high-altitude lake Gæsjavri with a fish community dominated by charr (Table 1).

The survey gillnet catch data were used to estimate the intensity of interspecific interactions (*Inter*) and intraspecific resource competition (*Intra*) in each study lake, which were used as covariates in
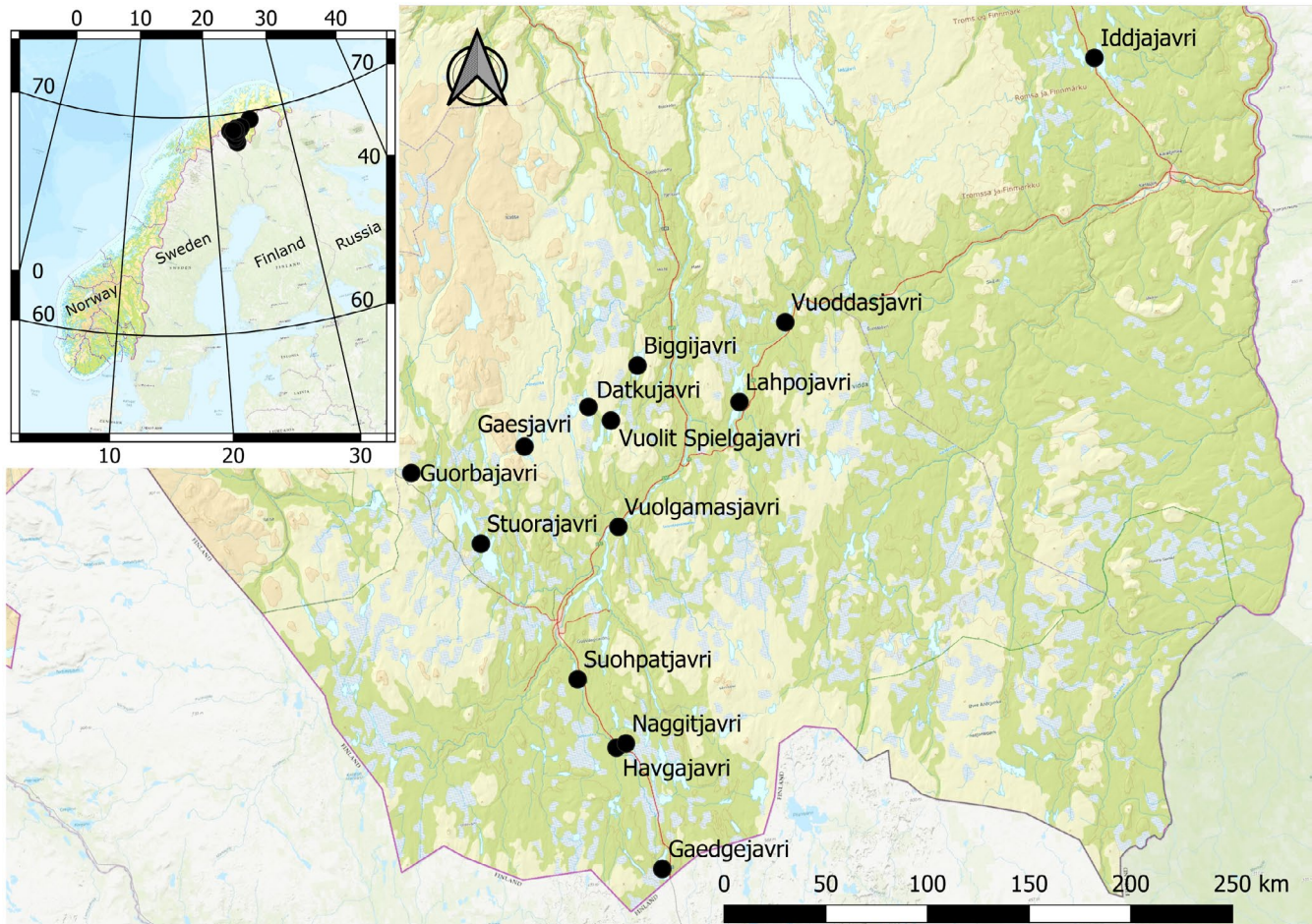
FIGURE 1 Location of 14 study lakes in the Finnmark region, northern Norway

the subsequent analyses. The proxy variable *Inter* was measured as the proportion of fish species other than whitefish in the total multi-mesh survey gillnet catches (i.e. total fish biomass in grams including fish from all habitats) in each lake. The reason for using relative proportion in total fish biomass instead of number of sympatric fish species as a proxy for intensity of interspecific interactions is that this relative measurement is less sensitive to among lake variability in sampling effort (see Supporting Information A Table S1) and fish catchability. Moreover, predatory fishes, such as pike, charr and brown trout, can be relatively scarce (see Table S1) but attain a large body size and therefore strongly affect the abundance (via direct predation) and niche use (indirectly via predation risk) of whitefish in subarctic lakes (Kahilainen & Lehtonen, 2003; Kahilainen et al., 2009; Öhlund et al., 2020). Thus, their potential impacts on LSR whitefish populations would likely be underestimated if *Inter* was based on numbers instead of fish biomass.

In contrast, the proxy variable *Intra* was standardized for different sampling efforts in each study lake (Table S1) by calculating total catch per unit of effort (CPUE; measured as the number of whitefish individuals caught per 100 m^2 gillnet area per night), including all present whitefish morphs in each lake. As intraspecific competition is particularly strong in polymorphic populations hosting small-sized DR and SSR whitefish morphs, the number of conspecifics is likely

more relevant ecological driver for LSR whitefish than the total population biomass. Hence, *Intra* provides a proxy for density-dependent processes that commonly influence whitefish growth and population dynamics (Mayr, 2001). However, we want to emphasize that we did not measure or manipulate competitive pressures in any way, but instead we used the available fish population, SIA and SCA data to test for patterns in population niche width and resource use of LSR whitefish along gradients in biotic and abiotic environmental factors.

Most fish caught were subsequently prepared for stomach content and stable isotope analyses, reflecting the recently ingested and long-term assimilated diets of fish, respectively, thereby allowing individual- and population-level analyses of LSR whitefish niche use (Amundsen & Sánchez-Hernández, 2019; Layman et al., 2012). After removal from the gillnets, fish were killed by a sharp blow on the head, kept cool and brought to the field laboratory, where they were identified, measured (fork length, mm) and weighed (g). From a subsample of fish, a small piece of dorsal muscle tissue was dissected and stored at −20°C until subsequent preparation for SIA. The stomachs were removed, preserved in 96% ethanol and later opened to visually estimate the total fullness on a percentage scale ranging from empty (0%) to full (100%; Amundsen & Sánchez-Hernández, 2019). The prey items were identified to species, genus or family level and their relative contribution to the

TABLE 1 Basic characteristics and sampling period of each study lake. *Inter* (% of total catch) and *Intra* (*n* fish 100 m^{-2} net night^{-1}) refer to intensity of interspecific interactions and intraspecific resource competition based on survey gillnet catches

Lake name	Sampling year	Sampling month	Surface area (km^2)	Altitude (m a.s.l.)	Maximum depth (m)	*Inter*	*Intra*	Fish species
Guorbajavri	2008	Aug	0.65	454	12	0.002	5.10	**WF**, BU, AC, MI
Naggitjavri	2007	Sept	0.78	369	17	0.163	12.55	**WF**, PI, AC
Gædgejavri	2007	Sept	4.25	387	20	0.069	9.38	**WF**, PE, PI, BU, AC
Havgajavri	2007	Aug	0.19	359	16	0.045	12.55	**WF**, BU, AC, MI
Iddjajavri	2009	Aug	6.40	275	30	0.495	8.97	**WF**[a], **PE**, **GR**, PI, SB, BT
Lahpojavri	2007	Sept	8.12	327	36	0.187	16.72	**WF**[a], **PE**, PI, BU, BT
Suohpatjavri	2007	Aug	2.00	325	25	0.421	10.63	**WF**[a], **PE**, PI, BU, AC, MI
Stuorajavri	2005 and 2008	Aug	23.70	374	30	0.431	15.06	**WF**[a], **PE**, PI, AC, BU, BT, MI
Vuoddasjavri	2008	Aug	2.90	334	32	0.379	24.78	**WF**[a], **PE**, PI, GR, BU, BT
Vuolgamasjavri	2008	Aug-Sept	2.76	301	30	0.295	5.36	**WF**[a], **PE**, PI, BT, AC, BU, MI
Biggijavri	2008	Sept	5.35	381	52	0.481	4.96	**WF**, **AC**, **GR**, BT, BU, MI, PI
Vuolit Spielgajavri	2008	Sept	3.30	436	12	0.656	7.70	**WF**, **AC**, **GR**, BT, BU
Datkujavri	2009	Sept	4.20	474	17	0.650	8.39	**WF**, **AC**, **GR**, BT, BU, MI
Gæsjavri	2009	Sept	4.83	540	—	0.908	1.13	**WF**, **AC**, BU, MI

Abbreviations: AC, Arctic charr; BT, brown trout; BU, burbot; GR, grayling; MI, minnow; PE, perch; PI, pike; SB, nine-spined stickleback; WF, whitefish. The most abundant fish species are highlighted in bold.

[a]WF indicates polymorphic whitefish populations.

total fullness was estimated (Amundsen et al., 1996; Amundsen & Sánchez-Hernández, 2019). For graphical visualization of LSR whitefish diets (Supporting Information A Figure S1), the prey taxa were subsequently grouped into (a) cladoceran zooplankton (*Bosmina* sp., *Daphnia* sp., *Holopedium gibberum*, *Bythotrephes longimanus*, *Polyphemus* sp.); (b) copepod zooplankton (Cyclopoida and Calanoida); (c) pleuston (adult stages of terrestrial insects, pupal stages of Chironomidae and Trichoptera); (d) semi-benthic crustaceans (*Gammarus lacustris*, *Asellus aquaticus*, *Eurycercus lamellatus*, *Sida crystallina*, Ostracoda); (e) insect larvae (Chironomidae, Trichoptera, Megaloptera, Ephemeroptera, Plecoptera, Tipulidae, Coleoptera); (f) mollusks (*Lymnaea* sp., *Valvata* sp., Planorbidae); and (g) fish. However, all 26 prey taxa were included in the calculation of proportional diet similarity index (PS_i) for each individual fish, as well as the degree of among-individual diet variation ($V = 1 - \text{mean } PS_i$) in each whitefish population following the equations described in Bolnick et al. (2002) and Svanbäck et al. (2015). The PS_i index compares each individual's diet to that of the entire population, with values ranging between 0 and 1. In populations where individuals specialize on different kinds of prey, the PS_i values tend to be low and the resulting population-level V values tend to be high, that is, approaching 1 (Bolnick et al., 2002; Svanbäck et al., 2015). Only fish with stomach fullness exceeding 10% were included in SCA analyses to avoid potential confounding effect of incidental feeding on an atypical prey item or upscaling the importance of indigestible remains of certain prey types (Amundsen & Sánchez-Hernández, 2019).

Besides fish muscle tissue, qualitative samples of putative littoral and pelagic food resources were collected for SIA from each lake in August/September 2007–2009 to study the overall food-web structures (Figure 2) and particularly to estimate the relative littoral reliance (*LR*), trophic position (*TP*) and isotopic population niche width (cf. Petta et al., 2020) of LSR whitefish in the study lakes. The raw $\delta^{13}C$ and $\delta^{15}N$ values of fish were transformed to *LR* and *TP* estimates that account for between-lake differences in baseline variation and thus allow comparison of resource use and niche width of LSR whitefish across the study lakes (Layman et al., 2012). The *LR* (Equation 1) and *TP* (Equation 2) estimates were calculated using the linear isotopic mixing models described in Post (2002):

$$LR = \left(\delta^{13}C_{fish} - \delta^{13}C_{pel}\right) / \left(\delta^{13}C_{lit} - \delta^{13}C_{pel}\right), \tag{1}$$

$$TP = \lambda + \left(\delta^{15}N_{fish} - \left[\delta^{15}N_{lit} \times LR + \delta^{15}N_{pel} \times (1 - LR)\right]\right) / \Delta_n, \tag{2}$$

where $\delta^{13}C_{fish}$ and $\delta^{15}N_{fish}$ refer to isotope values of individual fish; $\delta^{13}C_{lit}$, $\delta^{15}N_{lit}$, $\delta^{13}C_{pel}$ and $\delta^{15}N_{pel}$ refer to the lake-specific $\delta^{13}C$ and $\delta^{15}N$ values for the littoral and pelagic isotopic end-members; λ is the trophic position of the organisms used to estimate $\delta^{15}N_{lit}$ and $\delta^{15}N_{pel}$ (here $\lambda = 2$ for primary consumers); and Δ_n is the mean trophic fractionation of muscle tissue $\delta^{15}N$ (i.e. 2.9‰; McCutchan et al., 2003). For *LR* calculation, $\delta^{13}C_{fish}$ were corrected for trophic fractionation by subtracting 1.3‰ from the original $\delta^{13}C$ value (McCutchan et al., 2003). The littoral and pelagic isotopic end-members were defined as the mean isotope values of algae-grazing
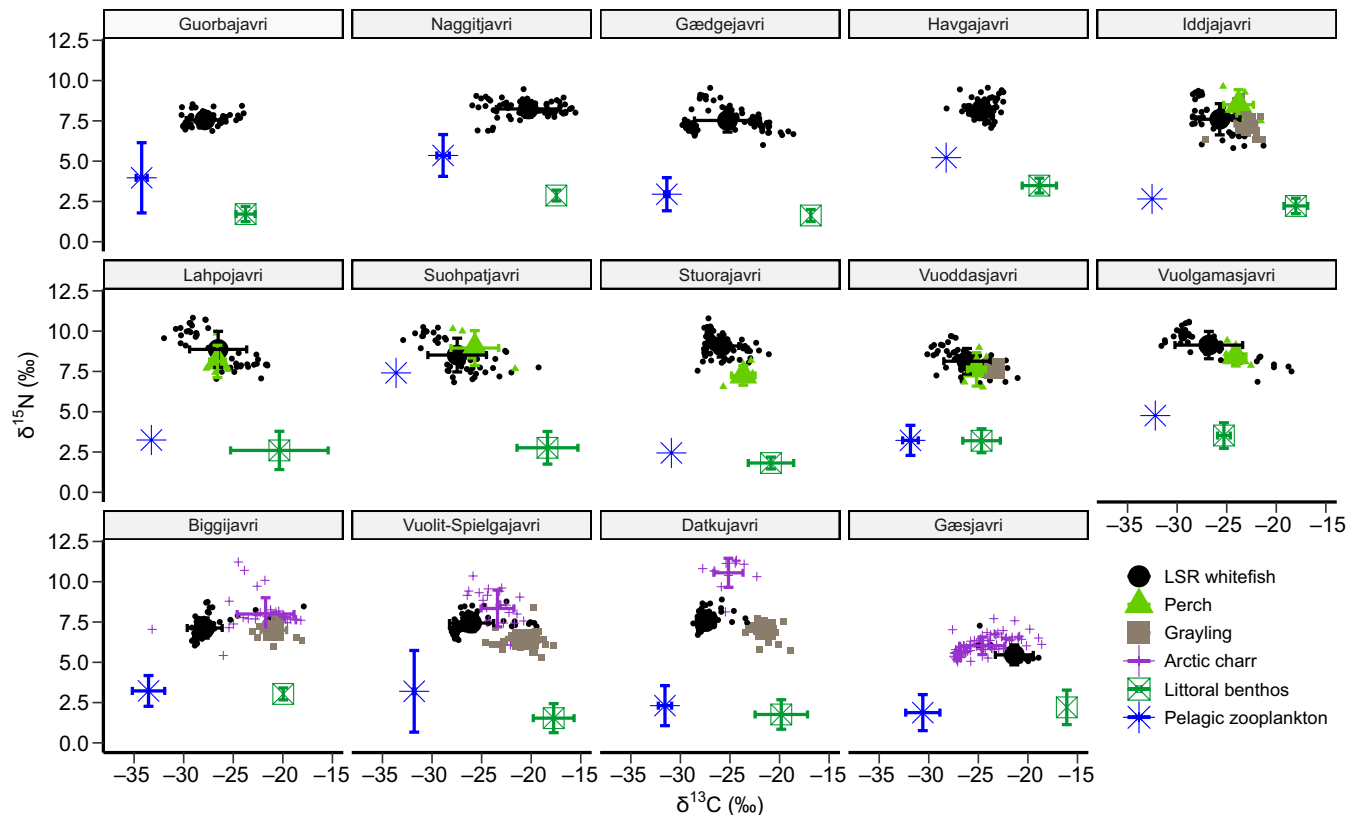
FIGURE 2 Stable isotope biplots showing the mean ± SD δ^{13}C and δ^{15}N values of littoral and pelagic isotopic end-members, as well as the individual and mean isotope values of coexisting LSR whitefish, perch, grayling and charr

littoral benthic invertebrates (i.e. snails, *Gammarus lacustris* amphipods and chironomid larvae; δ^{13}C ≥ −25‰) and pelagic zooplankton (δ^{13}C ≤ −28‰), respectively. In 3% of the cases (22 out of 810 LSR whitefish), the *LR* estimate of individual fish exceeded 1 (equalling to 100% reliance on littoral resources), most likely due to specialized foraging on littoral benthic prey taxa (e.g. algae-grazing snails) with exceptionally high δ^{13}C values. In such cases, we decided not to set the estimate to 1 but instead used the original estimate to avoid artificial bias and non-normality of the variable distribution. The SIA samples were analysed either at the Department of Biological and Environmental Science, University of Jyväskylä, Finland, or at the NERC Life Sciences Mass Spectrometry Facility, East Kilbridge, Scotland. For full details of the collection, processing and analysis of SIA samples, see Eloranta et al. (2011) presenting SIA and SCA data from three of the 14 present study lakes.

The *LR* and *TP* estimates were finally used in calculation of population niche width, measured as the total convex hull area (*TA*; see Jackson et al., 2011 for details) encompassing the *LR* and *TP* values of all whitefish individuals in each lake. This measure of 'isotopic niche width' may be sensitive to variation in sample size and therefore it has become more common to use standard ellipse area (*SEA*; Jackson et al., 2011) as a population niche width metric. However, as stated by Syväranta et al. (2013), 'use of a metric value that does not include all individuals in a population risks ignoring important information on intraspecific variation that should

be considered when describing the niche of a population'. Although all individuals are used in calculation of *TA* and *SEA*, the latter may thus fail in considering individuals that deviate isotopically from the core population. Moreover, our SIA data of LSR whitefish indicated high correlation between the *TA* and sample-size corrected *SEA$_c$* (Jackson et al., 2011) estimates (Pearson correlation: $r = 0.95$, $p < 0.001$), but *TA* showed lower correlation with sample size ($r = −0.06$, $p = 0.827$) than *SEA$_c$* did ($r = −0.21$, $p = 0.481$). Therefore, we decided to use *TA* as a measure of LSR whitefish population niche width in our subsequent analyses. Although Bayesian approaches are commonly preferred for measuring isotopic niche areas and resource use of consumers (Jackson et al., 2011; Layman et al., 2012), the present Bayesian models for isotopic niche areas cannot incorporate additional covariates like some recently developed Bayesian isotopic mixing models do (e.g. MixSIAR; Stock et al., 2018). Because we were thus not able to use a Bayesian approach to study the effects of biotic and abiotic factors on population niche width of LSR whitefish, we used original Layman's metrics (Layman et al., 2007) as predicted variables in the subsequent analyses. However, to validate the robustness of our results, we also present the sample-size corrected *SEA$_c$* and the Bayesian *SEA$_b$* estimates along with the *TA* estimates. Finally, we also calculated the mean nearest neighbour distances (*MNND*), based on Euclidean distances between individual data points in the *LR* – *TP* space, to measure trophic diversity among LSR whitefish individuals (Jackson et al., 2011).

2.2 | Data analysis

We decided to exclude lake Gæsjavri from the main analyses due to the insufficient data of LSR whitefish for niche and diet analyses (n_{SIA} = 14, n_{SCA} = 12). The modelling results based on available data from all 14 study lakes are presented in Supporting Information C (Tables S4–S7).

Linear models (one per population metric) were used to test how the population niche width (*TA* and SEA_c), trophic diversity among individuals (*MNND*) and degree of among-individual diet variation (*V*) in LSR whitefish were affected by the intensity of interspecific (*Inter*) and intraspecific (*Intra*) interactions and by the lake environmental properties, namely the lake surface area (*Area*, in km^2) and elevation (*Altitude*, in m a.s.l.). Based on initial exploration of variable relationships (Supporting Information A Figure S2), both linear and quadratic terms for the measure of interspecific interactions were included in the full models. Prior to modelling, right-skewed *Area* was ln-transformed and all explanatory variables were standardized to have a mean of zero and a standard deviation of one, allowing subsequent comparison of effect sizes.

In addition to population-level analyses, we ran linear mixed-effects models using individual data to test if the estimated whitefish littoral reliance (*LR*), trophic position (*TP*) and proportional diet similarity (PS_i) were affected by the intensity of interspecific (*Inter*) and intraspecific (*Intra*) interactions, lake abiotic characteristics (*Area* and *Altitude*), and individual body size (fork length). The linear mixed-effects models were ran using lmer function in the LME4 v.1.1-26 package (Bates et al., 2015). For consistency with the population-level analyses, both a linear and a quadratic term for *Inter* were included in the initial full mixed-effects models. Because we did not aim to quantify among lake differences in ontogenetic niche shifts of LSR whitefish, we added fish size (*Length*) as a random slope nested within each lake (1 + *Length*|*Lake*). The continuous explanatory variables were transformed and standardized as explained above. The explanatory variables included in the full models showed no multicollinearity (for data excluding Gæsjavri: VIF ≤ 4.1, pairwise Pearson r ≤ ±0.40; see correlation plots for full dataset in Supporting Information A Figures S2 and S3).

Model selections (Supporting Information B Tables S3–S3) were performed using the dredge function in the MuMIn v. 1.43.17 package (Barton, 2020) in R (R Core Team, 2020). Models with ∆AIC < 2 were considered to have equal support (Burnham & Anderson, 2002). As several top candidate models with ∆AIC ≤ 2 were often supported, we used the model.avg function in the MuMIn package to calculate conditional averages of parameter estimates and their 95% confidence intervals, as well as importance function to calculate relative variable importance. The model residual analyses indicated no violation of linear model assumptions. All statistical analyses were performed using R computing program v. 4.0.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Population niche width and among-individual diet variation

A total of 1,525 LSR whitefish (2,332 whitefish including all morphs), 693 perch, 372 grayling, 134 charr, 50 burbot, 24 pike, 26 minnow and 17 brown trout were captured from the 14 study lakes (Supporting Information A Table S1). After excluding insufficient data from Gæsjavri, a total of 796 (*n* = 46–84 per lake) and 1,000 (*n* = 40–123 per lake) LSR whitefish were used in statistical analyses based on SIA and SCA data, respectively (Table 1).

We found strong support for a humped-shaped relationship between LSR whitefish population niche width (*TA*, SEA_c and SEA_b) and increasing intensity of interspecific interactions (Table 2; Figure 3), with all models in the top set of candidate models (∆AIC ≤ 2) including the quadratic term of *Inter* (Supporting Information Table S2). The models predict the widest population niche width of LSR whitefish at intermediate relative abundance of sympatric fish species (*c.* 20%–40% of the total survey net catch), and a more compressed niche width with decreasing as well as increasing intensity of interspecific interactions. The most compressed niche width (based on *TA*) was found in the excluded Gæsjavri situated above the treeline and with charr dominating the fish community (91% of the total survey net catch biomass; Table S1; see Supporting Information C for statistical analyses of the full dataset). We also found some, although non-significant, support for a humped-shaped effect of *Inter* and for a positive effect of *Intra* on trophic diversity among LSR whitefish individuals (*MNND*; Table 2; Table S2; Figure S2).

In contrast, when using SCA data, we found no support for effects of the intensity of interspecific interactions and intraspecific resource competition or lake abiotic characteristics on among-individual diet variation of LSR whitefish (Table 2; Supporting Information Table S3). Notwithstanding, SCA indicate only minor between-lake differences in diet specialization among LSR whitefish (*V* = 0.39–0.53).

3.2 | Whitefish resource use and niche partitioning

The mean littoral reliance (*LR*) and trophic position (*TP*) estimates of whitefish varied between 0.24–0.64 and 2.9–4.4, respectively (Table 3), suggesting a diet consisting of invertebrates, with variable contributions of littoral benthos and pelagic zooplankton (Supporting Information A Figure S1). We found support for a positive effect of LSR whitefish body size on *LR* and *TP* estimates (Table 4, Supporting Information Table S5), suggesting an ontogenetic shift to a more littoral diet (Figure 4) and to a higher trophic position (Figure 5) with increasing fork length. However, ontogenetic niche shifts of LSR whitefish were not evident in all lakes, and in Gæsjavri LSR whitefish shifted from littoral to a more pelagic diet with increasing size (Figures 3 and 4). The largest variation in *LR* and *TP* estimates was

Model	Estimate	SE	RVI	2.5% CI	97.5% CI
(a) Population niche width (TA)					
Intercept	0.674	0.076	—	**0.506**	**0.842**
Inter	−0.044	0.047	0.20	−0.150	0.061
Inter^2	−0.191	0.066	1.00	**−0.337**	**−0.046**
Intra	0.010	0.054	0.12	−0.111	0.131
Altitude	−0.028	0.084	0.12	−0.215	0.159
Area	−0.057	0.050	0.25	−0.169	0.055
(b) Population niche width (SEA$_c$)					
Intercept	0.180	0.027	—	**0.123**	**0.238**
Inter	−0.016	0.014	0.37	−0.047	0.015
Inter^2	−0.053	0.021	0.91	**−0.099**	**−0.007**
Intra	0.008	0.016	0.19	−0.027	0.043
Altitude	−0.024	0.026	0.29	−0.080	0.032
Area	−0.009	0.015	0.10	−0.043	0.025
(c) Trophic diversity among individuals (MNND)					
Intercept	0.031	0.004	—	**0.022**	**0.040**
Inter	−0.001	0.002	0.13	−0.006	0.004
Inter^2	−0.007	0.004	1.00	−0.015	0.001
Intra	0.004	0.002	0.86	−0.001	0.009
Altitude	0.003	0.004	0.27	−0.006	0.011
Area	−0.002	0.002	0.32	−0.007	0.003
(d) Among-individual diet variation (V)					
Intercept	0.476	0.022	—	**0.431**	**0.522**
Inter	−0.009	0.012	0.18	−0.037	0.020
Inter^2	−0.031	0.019	0.57	−0.072	0.009
Intra	−0.013	0.011	0.50	−0.038	0.011
Altitude	−0.024	0.013	0.65	−0.054	0.005
Area	0.017	0.012	0.73	−0.009	0.044

TABLE 2 Generalized linear models (conditional averages of top candidate models with ΔAIC ≤ 2) for the effects of interspecific (*Inter*) and intraspecific (*Intra*) interactions and lake abiotic characteristics (surface area and altitude) on whitefish population isotopic niche width measured as (a) total convex hull area (*TA*) and sample-size corrected standard ellipse area (*SEA$_c$*), as well as on (c) trophic diversity among individuals measured as mean nearest neighbour distance (*MNND*) in *LR*–*TP* space, and (d) among-individual diet variation based on SCA data (Equation 1). Here Gæsjavri with insufficient data of LSR whitefish (*n* = 14) was excluded from the analyses. Parameter estimates (on standardized scale) are interpretable as effect size because they describe changes in units of standard deviation of the original variable. Standard error (*SE*), relative variable importance (*RVI*) and 95% confidence intervals (*CI*) for each parameter are shown, with significant parameters (*p* < 0.05) highlighted in bold. The parameter estimates in the top candidate models (ΔAIC ≤ 2) are given in Supporting Information B Table S2. The modelling results based on full dataset (*n* = 14 lakes) are presented in Supporting Information C Tables S4–S5

often observed among individuals exceeding 200 mm fork length (Figures 3 and 4). Although some top models included only fork length or intercept (Table 4; Supporting Information C Tables S6–S7), we found some support for a humped-shaped relationship between LSR whitefish littoral reliance and intensity of interspecific interactions (Table 4; Supporting Information A Figure S3). In addition, lake area had a positive effect on trophic position, whereas the quadratic term of *Inter* and *Altitude* had positive effects on proportional diet similarity (*PS$_i$*) of LSR whitefish (Table 4; Figure S3). However, when Gæsjavri was included in the analyses, none of the explanatory variables except *Length* were included in the top candidate models for *LR* and *PS$_i$* estimates, whereas *Area* still had a positive effect on *TP* estimates (Supporting Information C Tables S6–S7).

Whitefish was generally the most pelagic species and showed at least partial niche segregation with the main coexisting competitor species, particularly in lakes hosting abundant populations of both charr and grayling (Figure 4). In these lakes, charr generally occupied a higher trophic position than LSR whitefish, suggesting piscivorous foraging on small whitefish and other prey fishes (Figure 5). In lakes

hosting abundant whitefish and perch, no consistent between-species differences in *TP* were found as LSR whitefish occupied either on average lower or higher *TP* as compared to perch. The highest niche overlap between coexisting fishes was typically found among relatively large-sized individuals (>250 mm).

4 | DISCUSSION

We expected LSR whitefish population niche width and degree of among-individual diet variation to decrease with increasing intensity of interspecific interactions and to increase with increasing intraspecific competition. Our results did not fully support these predictions as the isotopic niche width of LSR whitefish showed a hump-shaped relationship with increasing intensity of interspecific interactions. Intraspecific competition had no significant effect on any of the isotopic niche metrics, and among-individual diet variation (based on SCA) was not affected by any of the lake biotic and abiotic variables. Despite marked between-lake differences in expected ontogenetic niche shifts, LSR

Intensity of interspecific interactions
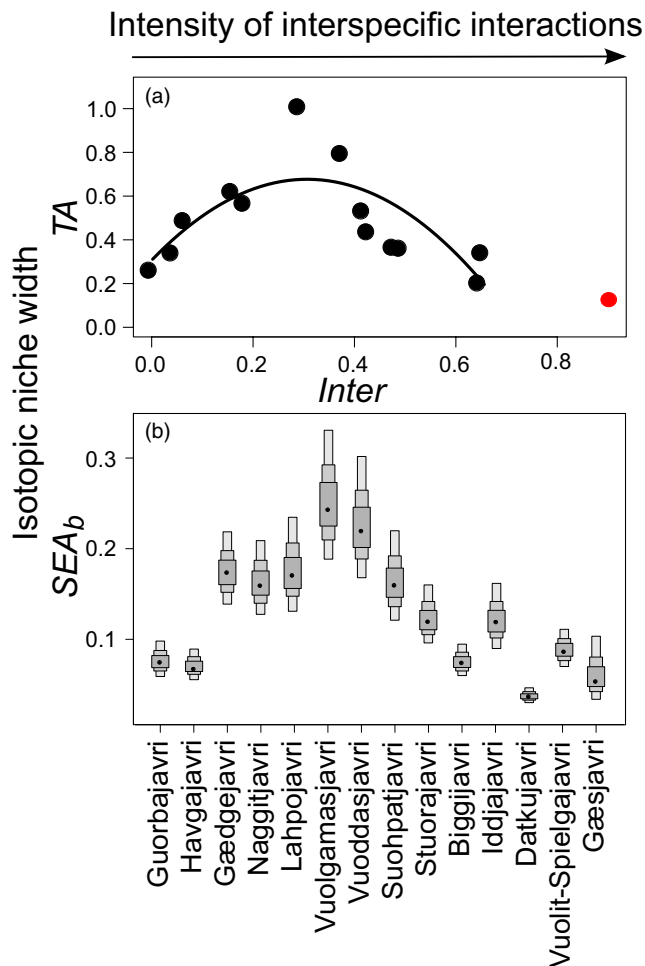
FIGURE 3 Isotopic niche width of LSR whitefish measured as (a) total convex hull area (*TA*) regressed against intensity of interspecific interactions (*Inter*) and as (b) Bayesian estimates of Standard Ellipse Area (*SEA_b*), with black dots depicting modes and boxes depicting the 95%, 75% and 50% credibility intervals. The 14 study lakes are arranged by increasing *Inter* measured as the relative proportion of fish species other than whitefish in the total survey gillnet catches (total biomass of captured fish) in each lake. The estimates for Gæsjavri (red dot) were excluded from the linear models due to insufficient data of LSR whitefish (*n* = 14)

whitefish typically shifted to a more littoral diet (*LR*) and to a higher trophic position (*TP*) with increasing body length and showed highest niche variation at relatively large body sizes. As expected, LSR whitefish often included more pelagic food resources and thereby likely reduced niche overlap with more littoral-oriented percid and salmonid fishes.

4.1 | Effects of interspecific and intraspecific interactions on population niche width

The large-growing, generalist LSR whitefish showed increased isotopic niche in lakes where coexisting fish species (mainly perch) were roughly equally abundant. The narrowest isotopic niches were found in lakes where coexisting fishes were either scarce or dominating in

the fish community. These findings partly deviate from the common view of a negative impact of interspecific competition on population niche width (e.g. Araújo et al., 2011 and references therein). At low to moderate abundance of sympatric fishes, interspecific interactions are relaxed and most LSR whitefish individuals may consume the most beneficial benthic prey, which reduces both among-individual diet variation and population niche width. The wide population niche of LSR whitefish in low-altitude perch lakes is suggested to result from the combined effect of higher resource availability and diversifying effect of moderate interspecific but strong intraspecific interactions with the other whitefish morphs (Supporting Information Table S1). In relatively unproductive high-altitude lakes, interspecific interactions with other salmonid fishes (i.e. charr and grayling) and the scarcity of alternative food resources evidently suppress individual specialization and thus population niche width of LSR whitefish. Our study provides further empirical evidence for context-dependent species interactions that can act as either broadening or suppressing forces on species' population niche width depending both on the relative abundance and on the identity of coexisting species (cf. Bolnick et al., 2010; Costa et al., 2008).

Our results suggest that the presence of perch and sympatric whitefish morphs may facilitate population-level niche expansion of LSR whitefish. The reason why abundant perch did not suppress LSR whitefish niche width in the same way as abundant salmonids might be related to the species' relatedness. Closely related species are ecologically more similar and thus stronger resource competitors, which may, in turn, reduce the potential for individual specialization (cf. Costa et al., 2008). However, perch can be an efficient resource competitor and potential predator of small whitefish in subarctic lakes (e.g. Amundsen et al., 2003; Hayden et al., 2013). Hence, the littoral-oriented perch may force some LSR whitefish to use suboptimal sublittoral, profundal and pelagic food and habitat resources (Sandlund et al., 2010) that in our perch lakes are dominated by the specialized DR and SSR whitefish morphs. This implies that the outcomes of interspecific interactions between littoral-dwelling perch and LSR whitefish likely are modified by strong intraspecific interactions between sympatric whitefish morphs. The observed positive, although non-significant, diversifying effect of increasing intraspecific competition on isotopic niche width of LSR whitefish (Supporting Information A Figure S2) supports this notion and corresponds with previous research of population density effects on niche width of generalist perch (Svanbäck & Persson, 2004).

In addition to interspecific and intraspecific interactions, the wide population niche of LSR whitefish may be partly related to higher resource availability in low-altitude lakes hosting perch and polymorphic whitefish. Fish communities in subarctic lakes generally utilize more pelagic-derived carbon in warm and more productive lakes than in cold, less-productive lakes (Hayden et al., 2019). Low-altitude perch lakes are warmer and more productive than oligotrophic, clear-water high-altitude lakes where littoral basal and secondary production prevail and salmonid species dominate (Eloranta et al., 2015; Hayden et al., 2017; Karlsson & Byström, 2005). Hence, the low-altitude perch lakes likely provide more zooplankton

TABLE 3 Number of LSR whitefish samples (*n*) in stable isotope (SIA) and stomach contents (SCA) analyses, population-level isotopic niche width estimates (i.e. total convex hull area *TA* and sample-size corrected standard ellipse area *SEA_c*), as well as mean, standard deviation (*SD*), minimum and maximum values for fork length (mm; given here for individuals analysed in SIA), littoral reliance (*LR*) and trophic position (*TP*) estimates, and proportional diet similarity index (*PS_i*) of LSR whitefish in each study lake

Lake	n SIA	n SCA	Niche width TA	Niche width SEA_c	Fork length (mm) Mean	SD	Min	Max	Littoral reliance LR Mean	SD	Min	Max	Trophic position TP Mean	SD	Min	Max	Diet similarity PS_i Mean	SD	Min	Max
Guorbajavri	59	81	0.272	0.076	219	66	115	320	0.48	0.18	0.26	0.86	3.61	0.23	3.26	4.19	0.58	0.15	0.09	0.78
Naggitjavri	63	40	0.633	0.162	217	33	141	361	0.64	0.28	0.14	1.27	3.54	0.30	2.70	4.05	0.55	0.10	0.22	0.66
Gædgejavri	76	123	0.499	0.177	193	47	97	295	0.33	0.23	0.02	0.79	3.73	0.25	3.30	4.37	0.55	0.07	0.22	0.67
Havgajavri	71	64	0.351	0.072	231	41	178	342	0.24	0.12	−0.13	0.48	3.18	0.21	2.84	3.72	0.60	0.10	0.31	0.75
Iddjajavri	47	72	0.373	0.123	228	72	112	407	0.38	0.14	0.19	0.69	3.76	0.32	3.16	4.35	0.50	0.13	0.15	0.70
Lahpojavri	46	70	0.579	0.176	218	27	133	265	0.42	0.22	0.00	0.81	4.03	0.35	3.40	4.67	0.50	0.14	0.19	0.76
Suohpatjavri	46	81	0.543	0.168	240	49	158	350	0.32	0.19	−0.04	0.86	2.89	0.28	2.28	3.49	0.50	0.13	0.15	0.74
Stuorajavri	60	74	0.448	0.126	232	46	140	303	0.37	0.17	0.13	0.85	4.37	0.23	3.79	4.93	0.50	0.11	0.26	0.68
Vuoddasjavri	49	64	0.806	0.230	204	35	102	333	0.61	0.33	0.06	1.33	3.70	0.27	3.23	4.23	0.57	0.12	0.14	0.78
Vuolgamasjavri	51	83	1.020	0.257	216	41	142	309	0.59	0.49	−0.10	1.80	3.76	0.17	3.28	4.14	0.46	0.13	0.13	0.69
Biggijavri	72	68	0.378	0.076	225	49	96	347	0.32	0.13	0.23	1.06	3.37	0.22	2.99	3.93	0.57	0.10	0.27	0.75
Vuolit Spielgajavri	72	74	0.352	0.090	254	49	123	352	0.32	0.16	0.17	0.78	3.64	0.22	3.23	4.25	0.61	0.11	0.17	0.80
Datkujavri	84	106	0.213	0.038	246	37	177	330	0.24	0.08	0.13	0.60	3.85	0.16	3.55	4.34	0.54	0.15	0.12	0.78
Gæsjavri	14	12	0.139	0.059	155	69	83	366	0.55	0.13	0.30	0.71	3.17	0.22	3.00	3.83	0.51	0.09	0.30	0.65

TABLE 4 Mixed-effects models (conditional averages of top candidate models with ΔAIC ≤ 2) predicting whitefish (a) littoral reliance, (b) trophic position and (c) proportional diet similarity as a function of whitefish body size (i.e. fork length), interspecific and intraspecific interactions and lake abiotic characteristics (Equation 2). Here Gæsjavri with insufficient samples of LSR whitefish (n = 12–14) was excluded from the analyses. Parameter estimates (on standardized scale) are interpretable as effect size because they describe changes in units of standard deviation of the original variable. Standard error (*SE*), relative variable importance (RVI) and 95% confidence intervals (CI) for each parameter are shown, with CIs of significant parameters highlighted in bold. The parameter estimates in the top candidate models (ΔAIC ≤ 2) are given in Supporting Information B Table S3. The modelling results based on full dataset (n = 14 lakes) are presented in Supporting Information C Tables S6–S7

Model	Estimate	*SE*	RVI	2.5% CI	97.5% CI
(a) Littoral reliance (*LR*)					
Intercept	0.436	0.059	—	**0.321**	**0.551**
Length	0.087	0.020	1.00	**0.048**	**0.127**
Inter^2	−0.092	0.041	0.27	**−0.172**	**−0.012**
(b) Trophic position (*TP*)					
Intercept	3.644	0.100	—	**3.449**	**3.840**
Length	0.096	0.024	1.00	**0.049**	**0.142**
Area	0.199	0.083	0.33	**0.036**	**0.361**
(c) Proportional diet similarity (*PS$_i$*)					
Intercept	0.531	0.031	—	**0.470**	**0.593**
Inter^2	0.059	0.012	0.61	**0.036**	**0.083**
Altitude	0.050	0.010	0.39	**0.029**	**0.070**
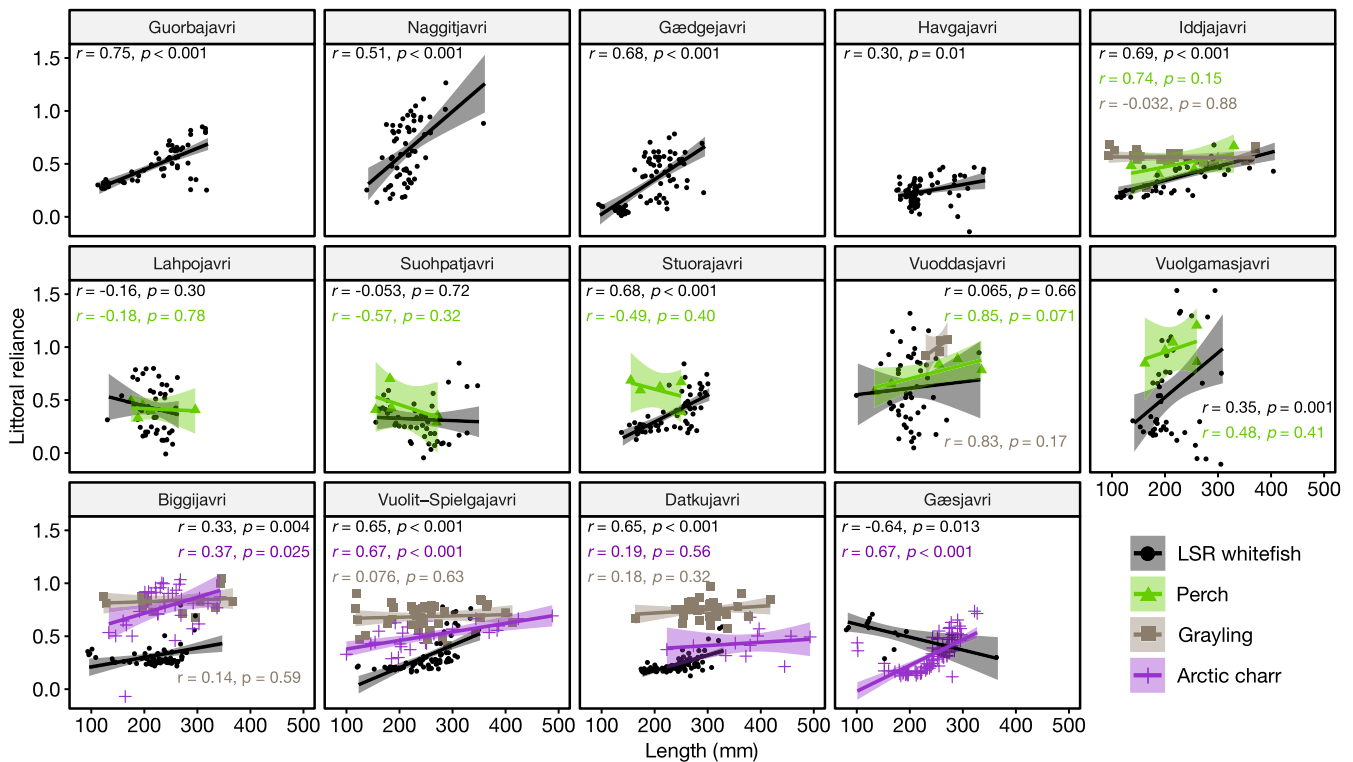
FIGURE 4 Littoral reliance (*LR*) of LSR whitefish and coexisting perch, grayling and charr in each lake regressed against fork length (mm). Littoral reliance estimates (Post, 2002) exceeding 1 result from high δ^{13}C of fish that exceed the δ^{13}C value of littoral isotopic end-member (Figure 2). The predicted regression lines with standard error bounds are drawn for each fish species using geom_smooth function with lm method in GGPLOT2 R package (Wickham, 2016). Pearson correlation coefficients (r) and p-values for the *LR–Length* relationships are reported for each species

resources for whitefish. Lakes situated below the treeline are also supplied with allochthonous resources, including terrestrial insects that are important prey for fish in some high-latitude lakes (Hayden et al., 2013; Milardi et al., 2016). This high availability and diversity of food resources, together with the broadening effect of perch presence through interference competition, are the likely
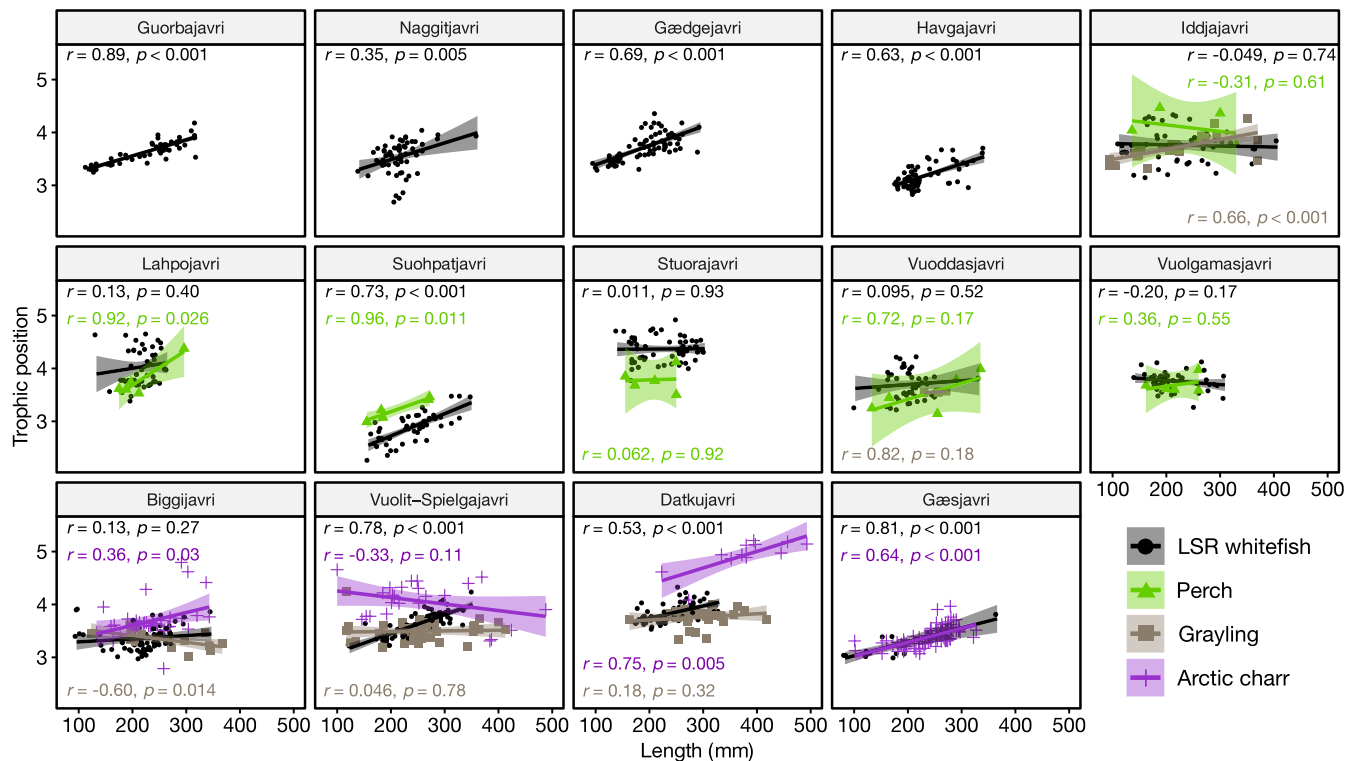
FIGURE 5 Trophic position (*TP*) of LSR whitefish and coexisting perch, grayling and charr in each lake regressed against fork length (mm). The predicted regression lines with standard error bounds are drawn for each fish species using geom_smooth function with lm method in GGPLOT2 R package (Wickham, 2016). Pearson correlation coefficients (*r*) and *p*-values for the *TP–Length* relationships are reported for each species

mechanisms facilitating a wide population niche and increased trophic diversity among whitefish individuals in lower-altitude lakes. For the whitefish-dominated lakes, it should be noted that they were among the smallest study lakes and thus likely provide more restricted pelagic and profundal food and habitat resources to support niche divergence among whitefish individuals. Hence, in these lakes, the narrow population niche likely results from individuals' shared utilization of similar benthic resources (Supporting Information A Figure S1). This notion is supported by Bolnick and Ballare (2020) showing that stickleback consume predominantly benthic and pelagic invertebrates in small and large lakes, respectively, whereas a greater among-individual diet variation is found in intermediate-sized lakes with high resource diversity.

4.2 | Effect of body size on niche variation

The numerous studies reviewed by Araújo et al. (2011) demonstrate that the intensity of interspecific and intraspecific competition, predation and ecological opportunity—commonly defined as 'the availability of ecologically accessible resources that may be evolutionarily exploited' (cf. Stroud & Losos, 2016)—largely determine among-individual diet variation and thus the species' population niche width. While ecosystem size and productivity may determine resource availability and competition (Bolnick & Ballare, 2020; Eloranta et al., 2015, 2016; Hayden et al., 2019), predation risk may influence among-individual

diet variation and population-level niche width by restricting habitat choice in prey (Eklöv & Svanbäck, 2006). Compared to small-sized perch, charr can grow relatively large and predate on a wider range of prey sizes (Amundsen, 1994; Kahilainen & Lehtonen, 2003). Hence, the observed niche suppression of LSR whitefish in lakes hosting abundant charr and grayling populations may result from the combined effects of strong competition for littoral resources with both charr and grayling as well as predatory impacts of large piscivorous charr (Amundsen, 1994; Amundsen et al., 2010; Eloranta et al., 2011). In these lakes, the presence of predatory charr may explain the apparent late ontogenetic shift of a few large (>250 mm) LSR whitefish to a littoral diet, except in the high-altitude Gæsjavri where small (<250 mm) LSR whitefish and the more abundant charr segregated into littoral and pelagic niches, respectively. The presence of large piscivorous charr in high-altitude lakes may also partly explain the lack of whitefish polymorphism. Contrary to the generalist charr, grayling is a specialized littoral benthivore whose high abundance likely contributes to the observed niche suppression associated with partial exclusion of LSR whitefish from the littoral niche (Amundsen et al., 2010; Eloranta et al., 2011). These results correspond with previous experimental studies (Bolnick et al., 2010) indicating that both the relative abundance and the identity of sympatric competitors can influence species' population niche width within restricted habitats, such as in subarctic lakes. Moreover, our results demonstrate increased among-individual variation and between-species overlap of isotopic niches (i.e. long-term diets) with increasing LSR whitefish body size. These findings

likely reflect the reduced predation risk and competitive dominance of large LSR whitefish individuals, allowing more adaptive niche use as compared to smaller conspecifics or other co-occurring fish species (Saksgård et al., 2002; Sandlund et al., 1995).

4.3 | Interspecific niche segregation

LSR whitefish often relied less on littoral food resources than coexisting perch, charr and grayling. This suggests that sympatric competitors and predators may partly exclude LSR whitefish from the diverse and often highly abundant littoral resources (Amundsen et al., 2010; Eloranta et al., 2011; Sandlund et al., 2010). The elevated trophic position of whitefish in some lakes hosting abundant perch might be related to foraging on predatory zooplankton (e.g. *Bythotrephes longimanus*) or on profundal chironomid larvae with elevated δ^{15}N values (Eloranta et al., 2011; Hayden et al., 2013), or more frequent consumption of small prey fish (Supporting Information A Figure S1), which may reflect potential responses to strong competition for littoral benthic resources. At the same time, we found only minor effects of relative competitor abundance and lake abiotic characteristics on littoral reliance (*LR*), trophic position (*TP*) and proportional diet similarity (*PS$_i$*) of LSR whitefish. When excluding the limited data of LSR whitefish in the high-latitude, charr-dominated Gæsjavri from the analyses, we found weak support for a humped-shaped relationship between *LR* estimates of LSR whitefish and increasing intensity of interspecific interactions, as well as for a positive effect of lake area on whitefish *TP* (Supporting Information A Figure S3 and B Table S3). The increased use of diverse littoral food resources likely contributes to the observed population niche expansion under moderate interspecific interactions, whereas the latter supports the notion of longer food chains in larger subarctic lakes (Eloranta et al., 2015). However, it should be noted that our study lakes are all relatively small and located within a restricted geographical area, which likely explains the minor effects of abiotic factors on resource use of LSR whitefish.

5 | CONCLUSIONS

Our results provide novel and unique empirical evidence for a hump-shaped relationship between population niche width and increasing intensity of interspecific interactions in a study system largely free from confounding human impacts. Unlike the study by Jones and Post (2016) compiling data from multiple species and locations, our results indicate that hump-shaped relationships between population niche width and intensity of species interactions can be evident for a single species and within a limited geographical area. However, the fish communities in our study lakes change to a considerable degree along the altitudinal gradient (Supporting Information A Table S1), making it difficult to disentangle the effects of environmental conditions and competitor abundance. Our reanalyses of the full dataset, including high-altitude Gæsjavri with a charr-dominated fish community

(Supporting Information Tables S3–S5), support the notion that competitor abundance and climatic conditions are likely interactive drivers of niche variation among generalist fish species in high-latitude lakes. A larger dataset collected across a wider geographical range and including lakes with both allopatric and sympatric fish communities could allow better separation of the effects of biotic and abiotic factors on species' population niche width and among-individual diet variation.

Traditionally, increasing intraspecific competition is assumed to promote among-individual variation and population niche expansion (Araújo et al., 2011; Jesmer et al., 2019, and references therein). In contrast, a hump-shaped response has been demonstrated for species richness and abundance across environmental gradients such as ecosystem productivity (Dodson et al., 2000) and area (Buckley & Roughgarden, 2006), environmental heterogeneity (Allouche et al., 2012) and allochthonous resource subsidies (Finstad et al., 2014). Such hump-shaped relationships are rarely considered in studies of population niche width (but see Bolnick & Ballare, 2020; Jones & Post, 2016; Svanbäck et al., 2015), and more studies are needed to quantify how among-individual variation and population niche width differ among populations or contexts, depending for instance on prevailing competitive and predatory interactions (Jones & Post, 2016) and ontogenetic niche trajectories (Sánchez-Hernández et al., 2016; Svanbäck et al., 2015). Our results are in line with the intermediate competition diversification (ICD) hypothesis predicting a hump-shaped relationship between population niche width and competition (Jones & Post, 2016). Although our study lacks data on resource availability, the results indicate a narrow population niche in lakes where interspecific competition is either relatively low (allowing the population to concentrate on preferred prey) or high (forcing the population to consume a limited variety of resources). The highest population niche width was typically observed in low-altitude lakes where intermediate intensity of interspecific interactions and higher diversity of benthic, pelagic and terrestrial food resources likely support population niche expansion. Acknowledging humped-shaped relationships between population niche width and interspecific interactions can help us understand the driving forces of niche variation that can increase population stability (Agashe, 2009), facilitate species coexistence (Schreiber et al., 2011) and influence ecosystem properties (Vrede et al., 2011).

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS

DATA AVAILABILITY STATEMENT

ORCID

Antti P. Eloranta https://orcid.org/0000-0002-8893-0135
Anders G. Finstad https://orcid.org/0000-0003-4529-6266
Odd Terje Sandlund https://orcid.org/0000-0001-9528-287X
Rune Knudsen https://orcid.org/0000-0001-8579-4687
Anna Kuparinen https://orcid.org/0000-0002-7807-8946
Per-Arne Amundsen https://orcid.org/0000-0002-2203-8216

REFERENCES

Agashe, D. (2009). The stabilizing effect of intraspecific genetic variation on population dynamics in novel and ancestral habitats. *The American Naturalist*, *174*, 255–267. https://doi.org/10.1086/600085

Alexander, T. J., Vonlanthen, P., Periat, G., Degiorgi, F., Raymond, J.-C., & Seehausen, O. (2015). Evaluating gillnetting protocols to characterize lacustrine fish communities. *Fisheries Research*, *161*, 320–329. https://doi.org/10.1016/j.fishres.2014.08.009

Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M., & Kadmon, R. (2012). Area-heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 17495–17500. https://doi.org/10.1073/pnas.1208652109

Amundsen, P.-A. (1994). Piscivory and cannibalism in Arctic charr. *Journal of Fish Biology*, *45*, 181–189. https://doi.org/10.1111/j.1095-8649.1994.tb01092.x

Amundsen, P.-A., Bøhn, T., Popova, O. A., Staldvik, F. J., Reshetnikov, Y. S., Kashulin, N. A., & Lukin, A. A. (2003). Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. *Hydrobiologia*, *497*, 109–119. https://doi.org/10.1023/A:1025465705717

Amundsen, P.-A., Gabler, H.-M., & Staldvik, F. J. (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. https://doi.org/10.1111/j.1095-8649.1996.tb01455.x

Amundsen, P.-A., Knudsen, R., & Bryhni, H. T. (2010). Niche use and resource partitioning of Arctic charr, European whitefish and grayling in a subarctic lake. *Hydrobiologia*, *650*, 3–14. https://doi.org/10.1007/s10750-009-0054-9

Amundsen, P.-A., & Sánchez-Hernández, J. (2019). Feeding studies take guts – Critical review and recommendations of methods for stomach contents analysis in fish. *Journal of Fish Biology*, *95*, 1364–1373. https://doi.org/10.1111/jfb.14151

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialization. *Ecology Letters*, *14*, 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Barton, K. (2020). *MuMIn: Multi-model inference*. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Berezina, N. A., Strelnikova, A. P., & Maximov, A. A. (2018). The benthos as the basis of vendace, *Coregonus albula*, and perch, *Perca fluviatilis*, diets in an oligotrophic sub-Arctic lake. *Polar Biology*, *41*, 1789–1799. https://doi.org/10.1007/s00300-018-2319-0

Bolnick, D. I., & Ballare, K. M. (2020). Resource diversity promotes among-individual diet variation, but not genomic diversity, in lake stickleback. *Ecology Letters*, *23*, 495–505. https://doi.org/10.1111/ele.13448

Bolnick, D. I., Ingram, T., Stutz, W. E., Snowberg, L. K., Lau, O. L., & Paull, J. S. (2010). Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 1789–1797. https://doi.org/10.1098/rspb.2010.0018

Bolnick, D. I., Yang, L. H., Fordyce, J. A., Davis, J. M., & Svanbäck, R. (2002). Measuring individual-level resource specialization. *Ecology*, *83*, 2936–2941. https://doi.org/10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2

Buckley, L. B., & Roughgarden, J. (2006). A hump-shaped density–area relationship for island lizards. *Oikos*, *113*, 243–250. https://doi.org/10.1111/j.2006.0030-1299.14401.x

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer-Verlag, New York.

Costa, G. C., Mesquita, D. O., Colli, G. R., & Vitt, L. J. (2008). Niche expansion and niche variation hypothesis: Does the degree of individual variation increase in depauperate assemblages? *The American Naturalist*, *172*, 868–877. https://doi.org/10.1086/592998

Dodson, S. I., Arnott, S. E., & Cottingham, K. L. (2000). The relationship in lake communities between primary productivity and species richness. *Ecology*, *81*, 2662–2679. https://doi.org/10.1890/0012-9658(2000)081[2662:TRILCB]2.0.CO;2

Eklöv, P., & Svanbäck, R. (2006). Predation risk influences adaptive morphological variation in fish populations. *The American Naturalist*, *167*, 440–452. https://doi.org/10.1086/499544

Eloranta, A. P., Finstad, A. G., Sandlund, O. T., Knudsen, R., Kuparinen, A., & Amundsen, P.-A. (2021). Data from: Species interactions, environmental gradients and body size shape population niche width. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.gf1vhhmqz

Eloranta, A. P., Helland, I. P., Sandlund, O. T., Hesthagen, T., Ugedal, O., & Finstad, A. G. (2016). Community structure influences species' abundance along environmental gradients. *Journal of Animal Ecology*, *85*, 273–282. https://doi.org/10.1111/1365-2656.12461

Eloranta, A. P., Kahilainen, K. K., Amundsen, P.-A., Knudsen, R., Harrod, C., & Jones, R. I. (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. https://doi.org/10.1002/ece3.1464

Eloranta, A. P., Knudsen, R., & Amundsen, P.-A. (2013). Niche segregation of coexisting Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) constrains food web coupling in subarctic lakes. *Freshwater Biology*, *58*, 207–221. https://doi.org/10.1111/fwb.12052

Eloranta, A. P., Siwertsson, A., Knudsen, R., & Amundsen, P.-A. (2011). Dietary plasticity of Arctic charr (*Salvelinus alpinus*) facilitates coexistence with competitively superior European whitefish (*Coregonus lavaretus*). *Ecology of Freshwater Fish*, *20*, 558–568. https://doi.org/10.1111/j.1600-0633.2011.00504.x

Finstad, A. G., Helland, I. P., Ugedal, O., Hesthagen, T., & Hessen, D. O. (2014). Unimodal response of fish yield to dissolved organic carbon. *Ecology Letters*, *17*, 36–43. https://doi.org/10.1111/ele.12201

Häkli, K., Østbye, K., Kahilainen, K. K., Amundsen, P.-A., & Præbel, K. (2018). Diversifying selection drives parallel evolution of gill raker number and body size along the speciation continuum of European whitefish. *Ecology and Evolution*, *8*, 2317–2631. https://doi.org/10.1002/ece3.3876

Harrod, C., Mallela, J., & Kahilainen, K. K. (2010). Phenotype-environment correlations in a putative whitefish adaptive radiation. *Journal of Animal Ecology*, *79*, 1057–1068. https://doi.org/10.1111/j.1365-2656.2010.01702.x

Hayden, B., Harrod, C., & Kahilainen, K. K. (2014). Lake morphometry and resource polymorphism determine niche segregation between cool- and cold-water-adapted fish. *Ecology*, *95*, 538–552. https://doi.org/10.1890/13-0264.1

Hayden, B., Holopainen, T., Amundsen, P.-A., Eloranta, A. P., Knudsen, R., Præble, K., & Kahilainen, K. K. (2013). Interactions between invading benthivorous fish and native whitefish in subarctic lakes. *Freshwater Biology*, *58*, 1234–1250. https://doi.org/10.1111/fwb.12123

Hayden, B., Myllykangas, J.-P., Rolls, R. J., & Kahilainen, K. K. (2017). Climate and productivity shape fish and invertebrate community structure in subarctic lakes. *Freshwater Biology*, *62*, 990–1003. https://doi.org/10.1111/fwb.12919

Hayden, B., Thomas, S. M., Kahilainen, K. K., Harrod, C., Amundsen, P.-A., Knudsen, R., Siwertsson, A., Eloranta, A. P., Præbel, K., & Myllykangas, J.-P. (2019). From clear lakes to murky waters – Tracing the functional response of high-latitude lake communities to concurrent 'greening' and 'browning'. *Ecology Letters*, *22*, 807–816. https://doi.org/10.1111/ele.13238

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*, 595–602. https://doi.org/10.1111/j.1365-2656.2011.01806.x

Jesmer, B. R., Kauffman, M. J., Murphy, M. A., & Goheen, J. R. (2019). A test of the Niche Variation Hypothesis in a ruminant herbivore. *Journal of Animal Ecology*, *89*, 2825–2839. https://doi.org/10.1111/1365-2656.13351

Jones, A. W., & Post, D. M. (2016). Does intraspecific competition promote variation? A test via synthesis. *Ecology and Evolution*, *6*, 1646–1655. https://doi.org/10.1002/ece3.1991

Kahilainen, K., & Lehtonen, H. (2003). Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake. *Journal of Fish Biology*, *63*, 659–672. https://doi.org/10.1046/j.1095-8649.2003.00179.x

Kahilainen, K. K., Malinen, T., & Lehtonen, H. (2009). Polar light regime and piscivory govern diel vertical migrations of planktivorous fish and zooplankton in a subarctic lake. *Ecology of Freshwater Fish*, *18*, 481–490. https://doi.org/10.1111/j.1600-0633.2009.00363.x

Karlsson, J., & Byström, P. (2005). Littoral energy mobilization dominates energy supply for top consumers in subarctic lakes. *Limnology and Oceanography*, *50*, 538–543. https://doi.org/10.4319/lo.2005.50.2.0538

Layman, C. A., Araujo, M. S., Boucek, R., Hammerschlag-Peyer, C. M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A. E., Vaudo, J. J., Yeager, L. A., Post, D. M., & Bearhop, S. (2012). Applying stable isotopes to examine food-web structure: An overview of analytical tools. *Biological Reviews*, *87*, 545–562. https://doi.org/10.1111/j.1469-185X.2011.00208.x

Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, *88*, 42–48. https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2

Malinen, T., Tuomaala, A., Lehtonen, H., & Kahilainen, K. K. (2014). Hydroacoustic assessment of mono- and polymorphic *Coregonus* density and biomass in subarctic lakes. *Ecology of Freshwater Fish*, *23*, 424–437. https://doi.org/10.1111/eff.12096

Mayr, C. (2001). The influence of population density on growth of whitefish (*Coregonus lavaretus* L.) in four prealpine lakes. *Limnologica*, *31*, 53–60. https://doi.org/10.1016/S0075-9511(01)80049-9

McCutchan Jr., J. H., Lewis Jr., W. M., Kendall, C., & McGrath, C. C. (2003). Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, *102*, 378–390. https://doi.org/10.1034/j.1600-0706.2003.12098.x

Milardi, M., Käkelä, R., Weckström, J., & Kahilainen, K. K. (2016). Terrestrial prey fuels the fish population of a small, high-latitude lake. *Aquatic Sciences*, *78*, 695–706. https://doi.org/10.1007/s00027-015-0460-1

Öhlund, G., Bodin, M., Nilsson, K. A., Öhlund, S.-O., Mobley, K. B., Hudson, A. G., Peedu, M., Brännström, Å., Bartels, P., Præbel, K., Hein, C. L., Johansson, P., & Englund, G. (2020). Ecological speciation in European whitefish is driven by a large-gaped predator. *Evolution Letters*, *4*, 243–256. https://doi.org/10.1002/evl3.167

Parent, C. E., Agashe, D., & Bolnick, D. I. (2014). Intraspecific competition reduces niche width in experimental populations. *Ecology and Evolution*, *4*, 3978–3990. https://doi.org/10.1002/ece3.1254

Petta, J. C., Shipley, O. N., Wintner, S. P., Cliff, G., Dicken, M. L., & Hussey, N. E. (2020). Are you really what you eat? Analysis and stable isotope ratios do not uniformly estimate dietary niche characteristics in three marine predators. *Oecologia*, *192*, 1111–1126. https://doi.org/10.1007/s00442-020-04628-6

Post, D. M. (2002). Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, *83*, 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Roughgarden, J. (1972). Evolution of niche width. *The American Naturalist*, *106*, 683–718. Retrieved from https://www.jstor.org/stable/2459501

Saksgård, R., Næsje, T. F., Sandlund, O. T., & Ugedal, O. (2002). The effect of potential predators on whitefish (*Coregonus lavaretus*) habitat use in Lake Femund, a deep Norwegian Lake. *Archiv für Hydrobiologie Special Issues Advanced Limnology*, *57*, 537–552.

Sánchez-Hernández, J., Eloranta, A. P., Finstad, A. G., & Amundsen, P.-A. (2016). Community structure affects trophic ontogeny in a predatory fish. *Ecology and Evolution*, *7*, 358–367. https://doi.org/10.1002/ece3.2600

Sánchez-Hernández, J., Finstad, A. G., Arnekleiv, J. V., Kjærstad, G., & Amundsen, P.-A. (2020). Beyond ecological opportunity: Prey diversity rather than abundance shapes predator niche variation. *Freshwater Biology*, *66*, 44–61. https://doi.org/10.1111/fwb.13606

Sánchez-Hernández, J., Nunn, A. D., Adams, C., & Amundsen, P.-A. (2019). Causes and consequences of ontogenetic dietary shifts: A global synthesis using fish models. *Biological Reviews*, *94*, 539–554. https://doi.org/10.1111/brv.12468

Sandlund, O. T., Museth, J., Næsje, T. F., Rognerud, S., Saksgård, R., Hesthagen, T., & Borgstrøm, R. (2010). Habitat use and diet of sympatric Arctic charr (*Salvelinus alpinus*) and whitefish (*Coregonus lavaretus*) in five lakes in southern Norway: Not only interspecific population dominance? *Hydrobiologia*, *650*, 27–41. https://doi.org/10.1007/s10750-009-0075-4

Sandlund, O. T., Næsje, T. F., & Saksgård, R. (1995). Ecological diversity in whitefish *Coregonus lavaretus*: Ontogenetic niche shifts and polymorphism. *Archiv für Hydrobiologie Special Issues Advanced Limnology*, *46*, 49–59.

Schreiber, S., Burger, R., & Bolnick, D. I. (2011). The community effects of phenotypic and genetic variation within a predator population. *Ecology*, *92*, 1582–1593. https://doi.org/10.1890/10-2071.1

Siwertsson, A., Knudsen, R., Præbel, K., Adams, C. E., Newton, J., & Amundsen, P.-A. (2013). Discrete foraging niches promote ecological, phenotypic, and genetic divergence in sympatric whitefish (*Coregonus lavaretus*). *Evolutionary Ecology*, *27*, 547–564. https://doi.org/10.1007/s10682-012-9607-x

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L., & Semmens, B. X. (2018). Analyzing mixing systems using a new

generation of Bayesian tracer mixing models. *PeerJ*, *6*, e5096. https://doi.org/10.7717/peerj.5096

Stroud, J. T., & Losos, J. B. (2016). Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics*, *47*, 507–532. https://doi.org/10.1146/annurev-ecolsys-121415-032254

Svanbäck, R., & Persson, L. (2004). Individual diet specialization, niche width and population dynamics: Implications for trophic polymorphism. *Journal of Animal Ecology*, *73*, 973–982. https://doi.org/10.1111/j.0021-8790.2004.00868.x

Svanbäck, R., Quevedo, M., Olsson, J., & Eklöv, P. (2015). Individuals in food webs: The relationships between trophic position, omnivory and among-individual diet variation. *Oecologia*, *178*, 103–114. https://doi.org/10.1007/s00442-014-3203-4

Syväranta, J., Lensu, A., Marjomäki, T. J., Oksanen, S., & Jones, R. I. (2013). An empirical evaluation of the utility of convex hull and standard ellipse areas for assessing population niche widths from stable isotope data. *PLoS One*, *8*, e56094. https://doi.org/10.1371/journal.pone.0056094

Van Valen, L. (1965). Morphological variation and width of ecological niche. *The American Naturalist*, *99*, 377–390. Retrieved from https://www.jstor.org/stable/2459179

Vrede, T., Drakare, S., Eklöv, P., Hein, A., Liess, A., Olsson, J., Persson, J., Quevedo, M., Stabo, H. R., & Svanbäck, R. (2011). Ecological stoichiometry of Eurasian perch – Intraspecific variation due to size, habitat and diet. *Oikos*, *120*, 886–896. Retrieved from http://www.jstor.org/stable/23014943

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, *15*, 393–425. https://doi.org/10.1146/annurev.es.15.110184.002141

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag. Retrieved from https://ggplot2.tidyverse.org. ISBN 978-3-319-24277-4.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology & Evolution*, *20*, 402–409. https://doi.org/10.1016/j.tree.2005.04.005

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.