

Lake morphometry and resource polymorphism determine niche segregation between cool- and cold-water-adapted fish

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Abstract. Climate change is increasing ambient temperatures in Arctic and subarctic regions, facilitating latitudinal range expansions of freshwater fishes adapted to warmer water temperatures. The relative roles of resource availability and interspecific interactions between resident and invading species in determining the outcomes of such expansions has not been adequately evaluated.

Ecological interactions between a cool-water adapted fish, the perch (*Perca fluviatilis*), and the cold-water adapted European whitefish (*Coregonus lavaretus*), were studied in both shallow and deep lakes with fish communities dominated by (1) monomorphic whitefish, (2) monomorphic whitefish and perch, and (3) polymorphic whitefish and perch. A combination of stomach content, stable-isotope, and invertebrate prey availability data were used to identify resource use and niche overlap among perch, the trophic generalist large sparsely rakered (LSR) whitefish morph, and the pelagic specialist densely rakered (DR) whitefish morph in 10 subarctic lakes at the contemporary distribution limit of perch in northern Scandinavia.

Perch utilized its putative preferred littoral niche in all lakes. LSR whitefish utilized both littoral and pelagic resources in monomorphic whitefish-dominated lakes. When found in sympatry with perch, LSR whitefish exclusively utilized pelagic prey in deep lakes, but displayed niche overlap with perch in shallow littoral lakes. DR whitefish was a specialist zooplanktivore, relegating LSR whitefish from pelagic habitats, leading to an increase in niche overlap between LSR whitefish and perch in deep lakes.

Our results highlight how resource availability (lake depth and fish community) governs ecological interactions between native and invading species, leading to different outcomes even at the same latitudes. These findings suggest that lake morphometry and fish community structure data should be included in bioclimate envelope-based models of species distribution shifts following predicted climate change.

Key words: biological invasion; climate change; *Coregonus lavaretus*; Finnish Lapland; intraspecific morphs; lake depth; *Perca fluviatilis*; resource competition; species distribution; stable isotopes; thermal guild; trophic niche.

INTRODUCTION

Climate change continues to drive shifts in species distribution patterns across the globe (Parmesan 2006, Moritz et al. 2008, Graham and Harrod 2009). There is convincing evidence that many species have extended their range toward higher latitudes and/or elevations in accordance with changing temperature regimes (Parmesan and Yohe 2003, Tingley et al. 2009). Altitudinal and latitudinal distribution shifts are especially evident in terrestrial and marine species; however, far less is known about such patterns in freshwater fauna (Parmesan 1996, 2006). The outcomes of such climate driven migrations has been a source of considerable discussion

in the ecological literature (Graham and Harrod 2009, Pereira et al. 2010). Key to determining these outcomes is an understanding of the importance of resource availability in receiving ecosystem and how this affects the trophic interactions between native and invading species (Helland et al. 2011).

Temperature is of fundamental importance across all levels of biological organization (Brown et al. 2004). Many attempts to predict the range migrations of plants and animals have utilized bioclimatic envelope models to predict the range of species following changes in temperature (Araújo and Peterson 2012). In fish, temperature has been considered as an ecological resource to which species are differently adapted. Consequently, fish species can be classified into thermal “guilds” depending on their adaptation to different water temperatures (Magnuson et al. 1979). Further-

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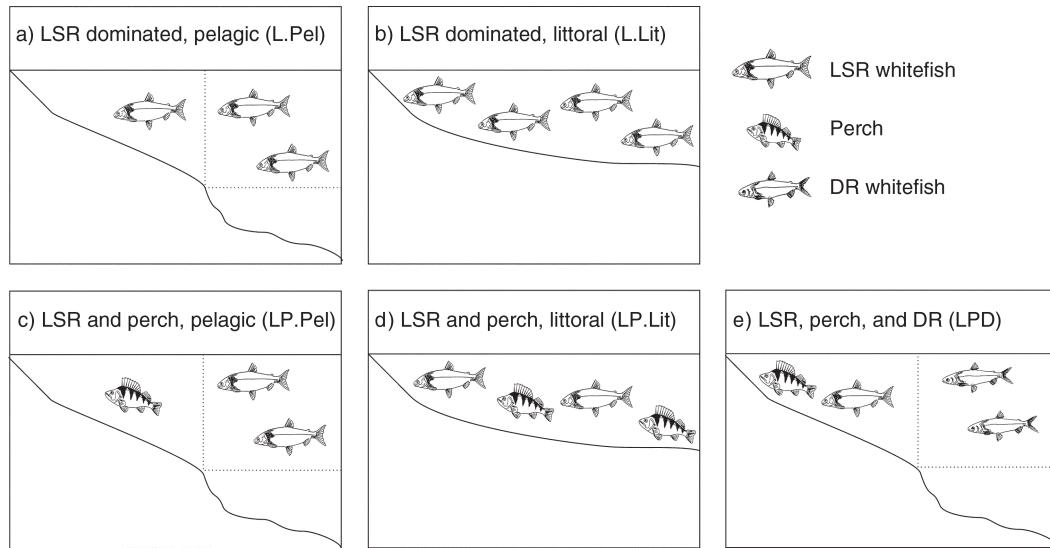


FIG. 1. Schematic overview of resource use by European whitefish, *Coregonus lavaretus* (the large sparsely rakered [LSR] whitefish morph and the densely rakered [DR] whitefish morph), and perch (*Perca fluviatilis*) in the study lakes in northern Scandinavia. LSR whitefish act as trophic generalists in (a) deep (Pel, pelagic) and (b) shallow (Lit, littoral) lakes dominated by LSR (prefix “L.”). (c) LSR whitefish and perch segregate along a benthic–pelagic axis when a pelagic resource is available, but (d) in fully littoral systems, both species feed on benthic resources (the prefix “LP.” indicates both LSR and perch). (e) The presence of planktivorous DR whitefish excludes generalist LSR whitefish and perch from pelagic feeding, driving increased niche overlap on littoral benthic resources (lakes with both of the whitefish morphs and perch are designated LPD). The solid lines represent the lake bed, and dotted lines indicate littoral–profundal–pelagic habitat boundaries.

more, species actively search and compete for their optimal thermal habitats, i.e., areas in which their metabolic and behavioral performance is at the highest level (Fry 1971). Therefore, under a bioclimatic envelope modeling perspective, fish species would be expected to segregate their distribution based on their temperature preferences.

However, these models have received much criticism, as they rarely account for interspecific interactions, which also play a key role in determining species range (Pearson and Dawson 2003, Araújo and Peterson 2012). It is more likely that species range is determined by complex interactions of climate, biotic interactions, and dispersal barriers (Araújo and Luoto 2007, Hein et al. 2011). As freshwater fishes are confined to river and lake catchments, their potential for thermal segregation is restricted, and interspecific interactions are likely to play a crucial role in determining the distribution range of each species (Parmesan 2006). Furthermore, the outcomes of these interactions may be affected by the abiotic and biotic properties of the habitat in which they occur (Fig. 1).

The Fennoscandian (continental part of Scandinavia) landscape north of the Arctic Circle is scattered with shallow and deep lakes, which form highly connected, large watercourses. These watercourses represent pronounced climatic and fish community gradients and encompass the distribution limits of numerous European freshwater fishes (Rask et al. 2000, Tammi et al. 2003). Recent climate change in Fennoscandian subarctic lakes has been manifested by longer summers and

shorter periods of winter ice cover (Lei et al. 2012), resulting in changes to primary producer communities from benthic toward pelagic species (Sorvari et al. 2002) and facilitating the invasion of cool-water-adapted fish species (Byström et al. 2007). As such, northern Fennoscandian lakes provide an excellent natural setting to examine the relative importance of resource availability and ecological interactions in the range expansions of nonnative species and their impacts on the trophic ecology of resident biota. Compared to temperate and boreal systems, these oligotrophic and cold-water subarctic lakes have relatively simple food webs. Most of these holomictic, clear-water lakes are fully littoral i.e., shallow enough to support benthic primary production across the entire lake bed (Sorvari et al. 2002). Larger and deeper lakes are thermally stratified and contain distinct littoral, pelagic, and profundal habitats (Kahilainen et al. 2004). Increasing lake size is positively correlated with fish species diversity and food chain length (Barbour and Brown 1974), and with levels of trophic polymorphism within some fish taxa, e.g., *Coregonus* spp (Siwertsson et al. 2010). Furthermore, shallow and deep lakes are likely to display different responses to increasing temperatures, as deep lakes are more likely to retain cold thermal habitats, e.g., in a profundal zone (Lehtonen 1996, Jeppesen et al. 2010). In such a variable scenario, the impacts of climate-mediated range expansion of species from the northern boreal zone may vary considerably across different lakes. In lakes with a less diverse array of potential resources, species that are expanding their range may

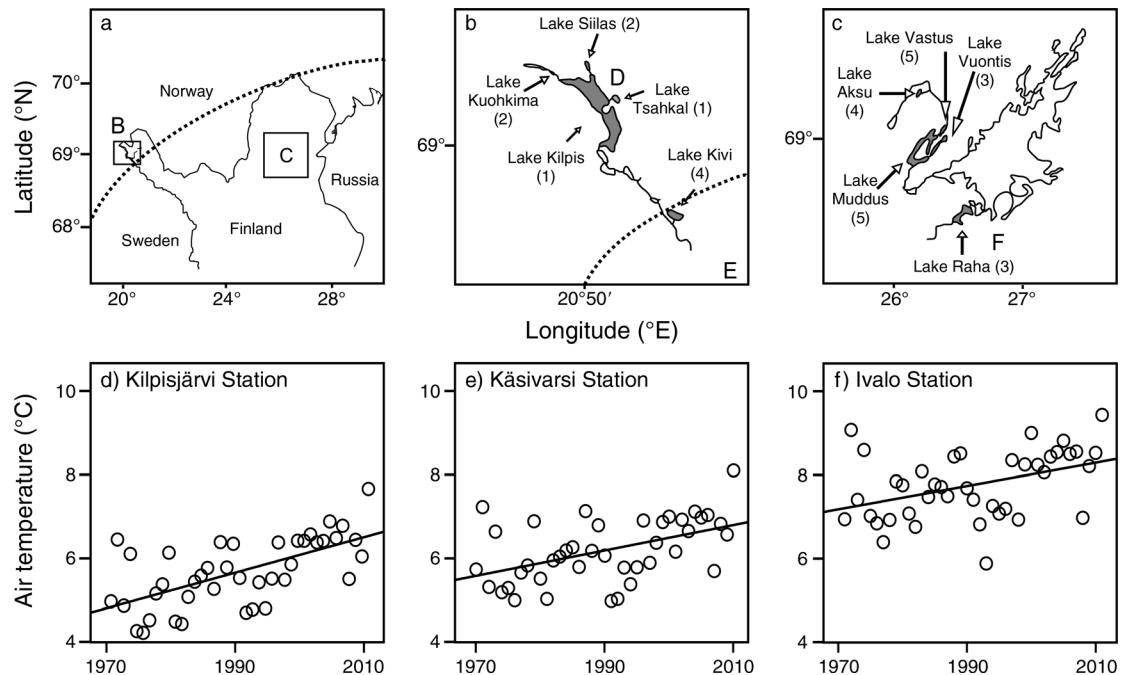


FIG. 2. (a) Location of study lakes (shown in gray) in northern Fennoscandia; boxes labeled B and C correspond to enlarged maps in panels (b) and (c). (b) The LSR-dominated lakes [L.Pel (1) and L.Lit (2)] are located in northwestern Lapland. (b, c) LSR and perch lakes [LP.Pel (3) and LP.Lit (4)] and polymorphic whitefish and perch lakes (5) are located in northeastern Lapland. The northern limit of perch distribution is highlighted by a broken line in panels (a) and (b). The labels D, E, and F in panels (b) and (c) show the location of the corresponding meteorological stations in panels (d)–(f), which show the mean open-water season (May–October) air temperature during 1971–2011 at meteorological stations (d) above, (e) at, and (f) below the current distribution limit of perch.

dominate a niche to which they are ecomorphologically specialized, relegating resident taxa to alternative niches (Bøhn and Amundsen 2001, Bøhn et al. 2008). Conversely, in systems with more abundant resources, novel species may be accommodated into the food web with less impact on resident biota (Sax et al. 2007).

Here, we focus on ecological interactions between two of the most abundant fish species in the region, the cold-water-adapted European whitefish, *Coregonus lavaretus* (L.), and the cool-water-adapted Eurasian perch, *Perca fluviatilis* (L.). The whitefish is a cold-water stenothermic species, with optimum growing temperature of 18°C (Siikavuopio et al. 2013). It is the most abundant freshwater fish in the subarctic lakes of northern Fennoscandia (Siwertsson et al. 2010). Perch is a cool-water eurythermal species, with an optimum growing temperature of 23°C (Fiogbe and Kestemont 2003). Whitefish and perch are typically associated with a generalist feeding strategy, utilizing both pelagic and benthic habitats during an ontogenetic trophic shift from zooplankton to benthic macroinvertebrates. In contrast to whitefish, perch frequently display an ontogenetic shift to piscivory both in temperate and subarctic lakes (Persson 1983, Amundsen et al. 2003).

The study area represents the current northern distribution limit of perch (Fig. 2). In Finnish Lapland, whitefish dominate subarctic lakes, but a shift to perch

domination is apparent in adjacent boreal lakes (Tammi et al. 2003). Recent studies from subarctic lakes have found evidence of the cool-water fishes northern pike (*Esox lucius* L.), ruffe (*Gymnocephalus cernuus* L.), and perch above their historical latitudinal distribution, indicating that the species may be becoming more established at these latitudes as water temperatures increase (Byström et al. 2007, Hayden et al. 2013b). An assessment of the trophic ecology of whitefish above and below the current distribution limit of perch provides an opportunity to determine the potential effects of a range expansion by perch on resident biota and also examine how these are influenced by variation in habitat and resource availability.

Polymorphic whitefish populations are present in a subset of lakes within the study region (Østbye et al. 2006, Siwertsson et al. 2010). The most common polymorphism pattern is a split along the littoral–pelagic resource axis, which has occurred in large and deep lakes with extensive pelagic areas (Siwertsson et al. 2010). In the most complex scenario, trimorphic populations with specialized pelagic, littoral, and profundal morphs have evolved from a generalist phenotype to utilize vacant niche space (Harrod et al. 2010). Whitefish morphs are typically distinguished by their gill raker morphology, which is strongly linked to prey selection (Kahilainen and Østbye 2006). The

ubiquitous large sparsely rakered (LSR) whitefish has a maximum length of >50 cm, a subterminal mouth and intermediate number (20–30) of widely spaced gill rakers reflecting a generalist diet including both benthic macroinvertebrates and pelagic zooplankton (Kahilainen et al. 2007). The profundal, small sparsely rakered (SSR) morph, is typically of a smaller size (<25 cm) with a comparatively large head size, large eyes, pronounced subterminal mouth, and low number (12–20) of widely spaced, short gill rakers. SSR whitefish has been found only in five lakes within the study region and, where found, they constitute a relatively small proportion of the fish fauna (Harrod et al. 2010). The densely rakered (DR) whitefish is smaller (maximum length <20 cm) with a slender body shape, pointed snout, and numerous (30–40), long and tightly spaced gill rakers, making it an efficient pelagic zooplankton specialist (Kahilainen et al. 2011). Where present, DR whitefish is typically the most abundant of morphs, although it only occurs in lakes with LSR whitefish (Kahilainen et al. 2004, Harrod et al. 2010, Siwertsson et al. 2010). In polymorphic lakes (i.e., lakes that contain both LSR and DR whitefish), the morphologically specialized DR whitefish dominates the pelagic zooplankton resource and restricts the generalist LSR whitefish to benthic prey (Kahilainen et al. 2007, Harrod et al. 2010). In this study, we focus only on the pelagic and littoral resource axes, which are the most productive in these lakes and where resource polymorphism is most common (Kahilainen et al. 2003, 2005, Harrod et al. 2010). This littoral–pelagic resource segregation between whitefish morphs is common across lakes, but little is known about the strength of intraspecific segregation between morphs in relation to interspecific niche segregation in the presence of sympatric competitors.

In this study, we compared niche utilization of perch and LSR whitefish in shallow and deep lakes in three types of multispecies lake ecosystems: (1) lakes with monomorphic LSR whitefish populations, (2) lakes with monomorphic LSR whitefish and perch populations, and (3) lakes with polymorphic whitefish and perch populations (Fig. 1). To examine how trophic interactions between fish species belonging to distinct thermal guilds are affected by resource polymorphism, the study was based on three principal hypotheses. Although zooplanktivory by perch is observed in mesotrophic systems (Svanbäck and Eklöv 2002), they predominantly feed as benthivores in subarctic lakes (Amundsen et al. 2003, Hayden et al. 2013b). Therefore, we hypothesized that (1) where present, perch populations will predominantly feed on littoral prey resulting in increased pelagic feeding by LSR whitefish in lakes containing perch, but no other whitefish morphs. (2) Resource availability will determine the degree of niche overlap between LSR whitefish and perch. In deep lakes, LSR whitefish will utilize the pelagic niche to avoid resource competition with perch; however, both species will feed on littoral benthic prey in shallow lakes, which by definition do not

support high densities of pelagic zooplankton. (3) In lakes with polymorphic whitefish, DR whitefish will dominate pelagic resources (Kahilainen et al. 2007), relegating generalist LSR whitefish from pelagic to littoral habitats, increasing resource competition with perch.

METHODS

Field study

The study was conducted in 10 oligotrophic subarctic lakes in Finnish Lapland (Table 1, Fig. 2; see Plate 1). All study lakes contained 4–12 fish species/morphs with a clear dominance by whitefish and perch (combined numerical percentage = 74–97% of fish fauna; Table 1). Monthly mean air temperature data (May–October, 1971–2011) were obtained from Finnish Meteorological Institute weather stations above (Kilpisjärvi), at (Käsi-*varsi*), and below (Ivalo) the current latitudinal distribution limit of perch (Fig. 2; Klein Tank et al. 2002). Prior to sampling, bathymetric maps were created using hydroacoustics and light compensation depths (depth at which light equals 1% of surface light) were measured (Lampert and Sommer 2007). Littoral (benthic areas situated in waters shallower than the compensation depth), profundal (benthic area below the compensation depth), and pelagic (open water above the profundal) zones were identified and quantified in each lake prior to sampling.

The study sites included four LSR whitefish-dominated (prefix L.) lakes: two deep lakes with a defined pelagic zone (L.Pel lakes) and two shallow littoral lakes (L.Lit lakes); four LSR whitefish and perch lakes (prefix LP.), including two pelagic (LP.Pel lakes), and two littoral (LP.Lit lakes) systems; and two polymorphic lakes with LSR whitefish, perch, and DR whitefish (LPD lakes), both of which contained a pelagic zone (Fig. 1). No shallow littoral lakes supporting polymorphic whitefish populations have been reported from this region (Siwertsson et al. 2010). Fish and invertebrate samples were collected from each lake during a single sampling event in August or September between 2001 and 2011 (Table 1).

Benthic macroinvertebrates were collected using an Ekman grab (sampling area of 272 cm²) along a depth transect following Kahilainen et al. (2003). Three replicates at each depth were taken along a depth contour (1, 2, 3, 5, 10, 15, 20, 30, and 40 m) representing a continuum from littoral through to profundal habitats. Samples were sieved through a 0.5-mm mesh, individuals were identified to family level and density (number/m²) of each functional group was calculated. As a profundal zone was not present in all lakes, comparisons of between-lake variation in benthic macroinvertebrate community abundance were limited to littoral samples. Zooplankton samples were collected at 1 m depth intervals through the pelagic zone using a Limnos tube (7.1 L) in Lakes Kilpis, Raha, Vuontis, Aksu, Vastus, and Muddus. In Lakes Tsahkal, Kuohki-

TABLE 1. Biotic and abiotic background data from the study lakes.

Parameter	Lake									
	Kilpis	Tsahkal	Siilas	Kuohkima	Raha	Vuontis	Kivi	Aksu	Muddus	Vastus
Lake class	L.Pel	L.Pel	L.Lit	L. Lit	LP.Pel	LP.Pel	LP.Lit	LP.Lit	LPD	LPD
Survey year	2005	2011	2007	2010	2005	2004	2011	2007	2001	2005
Latitude (° N)	69°00'	69°01'	69°04'	69°03'	68°45'	69°00'	68°49'	69°13'	69°00'	69°03'
Longitude (° E)	20°49'	20°50'	20°45'	20°33'	27°17'	27°04'	21°15'	26°53'	26°50'	27°07'
Surface area (km ²)	37.3	1.1	1.0	0.3	22.9	10.9	3.5	3.8	48	4.3
Mean depth (m)	19.4	9.0	5.2	2.6	14.1	6.5	2.8	3.5	8.5	2.7
Max. depth (m)	57	30	15	10	46	31	10	10	73	15
Percentage pelagic	71	41	0	1	57	20	16	19	41	31
pH	7.1	6.6	6.9	...	7.2	7.2	7.2	7
Total P (µg/L)	4	5	4	3	4	7	5	7
Total N (µg/L)	120	140	74	200	100	170	210	...	160	240
Compensation depth (m)	10	7	15	8	9	12	5	4	7	3
Species	b,e,f,g, k,l,m,n	b,e,m,l	b,f,g,k, l,m,n	b,f,g, k,l,n	b,d,e,f, g,h,i,j, k,l,m	b,f,g,h, i,j,k,l,m	b,f,j,k,l, m,n,o	b,f,g,h, i,j,k,l,m	a,b,c,e, f,g,h,i,j, k,l,m	a,b,f, g,h,i,j, k,l,m
LSR whitefish (%)	97	89	86	89	53	81	40	82	16	48
Perch (%)					26	15	42	15	15	24
DR whitefish (%)									43	25

Notes: See Fig. 1 for clarification of lake class. Species composition is designated as follows: a, densely rakered whitefish morph (DR; *Coregonus lavaretus*); b, large sparsely rakered whitefish morph (LSR); c, small sparsely rakered whitefish morph (SSR); d, vendace (*Coregonus albula* L.); e, Arctic charr (*Salvelinus alpinus* L.); f, grayling (*Thymallus thymallus* L.); g, minnow (*Phoxinus phoxinus* L.); h, three-spined stickleback (*Gasterosteus aculeatus* L.); i, nine-spined stickleback (*Pungitius pungitius* L.); j, perch (*Perca fluviatilis*); k, pike (*Esox lucius* L.); l, burbot (*Lota lota* L.); m, brown trout (*Salmo trutta* L.); n, alpine bullhead (*Cottus poecilopus* Heck.); and o, ruffe (*Gymnocephalus cernuus* L.). Water chemistry data was provided by Lapland Centre for Economic Development, Transport and the Environment (Rovaniemi, Finland) and courtesy of S. Taipale. Ellipses indicate that no data were available.

ma, Kivi, and Siilas, zooplankton were sampled using a zooplankton net (25 cm diameter, 50-µm mesh size), hauled vertically through the whole water column at the deepest point of each lake. The use of alternate sampling methods precluded a robust comparison of zooplankton density between lakes. Individuals were identified to family level, and body length (0.01 mm) was measured from a random subsample ($n = 30$, when available) of individuals of each family in each lake using an Olympus CK30-F200 microscope (Olympus Optical, Hamburg, Germany).

Fish were sampled using gill nets. Each net series consisted of eight, 30×1.8 m nets with knot-to-knot mesh sizes of 12, 15, 20, 25, 30, 35, 45, and 60 mm (Kahilainen et al. 2004). Benthic nets were set overnight in littoral and profundal zones of each lake. The pelagic zone was sampled using similar floating nets in Lakes Kilpis, Tsahkal, Kivi, Siilas, Aksu, and Muddus and a pelagic trawl (4×8 m, cod end mesh size 3 mm) in Lakes Raha, Vuontis, and Vastus (Kahilainen et al. 2011). Consequently, fish density analysis was limited to data collected from benthic set gills nets, which were comparable across all systems. The total sampling effort was determined by the size of the lake; however, within each lake, at least three replicates were conducted in each habitat type (littoral, profundal, and pelagic).

All fish captured were identified to species level, and whitefish were further identified to morph level according to gill raker number, and head and body shape (Kahilainen and Østbye 2006). After identification, total

length (± 1 mm) and wet mass (± 0.1 g) were recorded for each individual, and a representative subsample of fish were frozen (-20°C) for subsequent analysis of diet, growth, and carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable-isotope ratios.

Laboratory analysis

Stomach fullness was estimated on a scale of 0–10 (with 0 being empty and 10 being extended, full stomach), and stomach contents were identified to family level. The relative proportion of each prey group to total stomach fullness was calculated using the points method (Hynes 1950), whereby each prey group was given a points value from 0 (absent) to 10 (the only prey category in a fully extended stomach). Stomach contents were subsequently classified as either benthic (insect larvae [Chironomidae, Trichoptera, Megaloptera, Hydracarina, Ephemeroptera, Dytiscidae, Plecoptera, Odonata], Crustacea [*Eurycerus lamellatus* and *Megacyclops* sp., *Gammarus lacustris*, and *Asellus aquaticus*], and Mollusca [*Pisidium* sp., *Valvata* sp., and *Lymnaea* sp.]), or pelagic prey (chironomid pupae, terrestrial adult insects and zooplankton [*Daphnia* sp., *Bosmina* sp., Cyclopoida, Calanoida, *Holopedium gibberum*, and *Alona* sp.]). For the purpose of stomach content analysis, chironomid pupae were characterized as a pelagic prey item rather than benthic, as the abundance of chironomid pupae in the diet is consistently higher in pelagic DR whitefish diet, whereas other benthic whitefish morphs only frequently consume them during

the single peak hatching period in June (Kahilainen et al. 2004, Kahilainen et al. 2009, Harrod et al. 2010).

As we were investigating interactions between perch and whitefish utilizing similar resources, we classified piscivorous perch as a distinct group, and removed them from further comparative analyses. Of the 236 perch sampled that had consumed fish, only 35 had also consumed non-fish prey: Of these, fish was the dominant item in the stomach in >90 % of cases. Where fish prey could be identified, whitefish were the most frequently consumed prey item (mean abundance $61\% \pm 49\%$ [mean \pm SD]; mean whitefish prey length 68 mm, range 22–150 mm).

A piece of dorsal muscle tissue was dissected from of a subsample of both whitefish morphs and perch (where possible, 50 individuals per species/morph were sampled from the observed length distribution) and used for stable-isotope analysis (SIA). Muscle tissue was dried for 24 h at 60°C, ground to a fine powder, weighed (0.5–0.6 mg), and encapsulated in an aluminum foil cup. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\pm 0.1\%$) were recorded using a FlashEA 1112 elemental analyzer (Thermo Fisher Scientific, Delt, The Netherlands), coupled to Thermo Finnigan DELTAPLUS Advantage mass spectrometer (Thermo Finnegan MAT, Brehmen, Germany) (Harrod et al. 2005). Fish $\delta^{13}\text{C}$ values were arithmetically lipid normalized to remove the influence of variable lipid concentrations (Kiljunen et al. 2006).

To provide an isotopic baseline for subsequent analysis, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were also recorded from a subsample of each benthic macroinvertebrate family and zooplankton collected from each lake. As such baseline data were not available for Lake Aksu, values from the nearby Lake Vastus were used during subsequent analysis. Zooplankton isotope data for Lake Siilas were collected in September 2012; all other invertebrate sampling was contemporaneous with fish sampling.

Data analysis

Variation in fish and invertebrate community structure, and stomach contents of fish was examined using PERMANOVA (PRIMER 6.1.13; PRIMER-E 2009), a nonparametric permutation-based analogue of analysis of variance between two or more groups based on a distance measure (Anderson 2001, McArdle and Anderson 2001). In each case, a Bray-Curtis similarity matrix was created from non-transformed abundance data. Two-factor PERMANOVAs were performed on the fish and macroinvertebrate community structure similarity matrices to test the effect of “lake” (10 levels, random) and “lake classification: littoral/pelagic” (two levels, fixed), with “lake” nested within “lake classification,” on variation within the data set.

Individual fish were aged using burned and cracked otoliths (Bagenal and Tesch 1978). Asymptotic length (L_{∞}) and the rate at which L_{∞} is reached, i.e., growth rate (k), were derived from the Von Bertalanffy nonlinear

growth equation and calculated using the program SIMPLY GROWTH (Pisces Conservation 1998). Variation in growth (L_{∞} and k) between lake types was determined using on a two-factor PERMANOVA (“lake classification,” “species”) of a Bray-Curtis similarity matrix created from the growth characteristics of each population.

The three hypotheses relating to trophic interactions between whitefish and perch (H1–H3) were tested using a combination of stomach contents and stable-isotope data. An additional factor, “species” (three levels, fixed), was added to the existing PERMANOVA design to test for variation in stomach contents of LSR whitefish and perch between lakes (H1). In lakes containing LSR whitefish, perch, and DR whitefish, levels of dietary overlap were calculated using pairwise PERMANOVA (H2 and H3). In instances where significant variation ($P < 0.05$) was observed between groups, percentage similarity analysis (SIMPER) was used to determine which prey items contributed most to the difference (Clarke 1993). Dietary niche width of each species was calculated using a standardized Levins’ index (Levins 1968). As the value of Levins’ index increases with sample size, niche width was calculated based on the diet of a randomly selected subsample of individuals ($n = 30$).

Consumer stable-isotope ratios largely reflect that of their prey, which can vary both spatially and temporally (Syyväranta et al. 2006). As such, we did not conduct direct between-lake analyses, but used the outputs of stable-isotope mixing models to compare relative resource use (Parnell et al. 2010). Isotope values of benthic macroinvertebrate families collected from the littoral and profundal zones in each lake were pooled to provide a representative baseline value for each habitat. Zooplankton constituted the pelagic baseline value in each lake. The relative importance of each prey source to either species was subsequently estimated using the Bayesian mixing model “SIAR” (Parnell et al. 2010). Standard trophic fractionation values for muscle tissue ($\Delta^{13}\text{C} = 1.3\text{‰} \pm 0.3\text{‰}$, $\Delta^{15}\text{N} = 2.9\text{‰} \pm 0.3\text{‰}$) were used in all cases (McCutchan et al. 2003). Comparison of resource use between species and systems was conducted by comparing the 95% credibility limits of each prey source, i.e., if credibility limits did not overlap species were deemed to be utilizing the resource at significantly different levels (H1). Levels of overlap between species stable-isotope ratios within each lake was determined using pairwise PERMANOVA analysis of $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$ centroids, of a Euclidean distance matrix created from the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of LSR whitefish, perch, and DR whitefish (H2 and H3). To determine whether pelagic resource availability accounted for the observed resource use, Spearman rank correlation was employed to test for a relationship between the level of pelagic resource use of LSR whitefish and lake size, a proxy for pelagic resource availability, in all monomorphic lakes.

The isotopic niche width of each species was calculated based on the standardized ellipse of $\delta^{13}\text{C}$ –

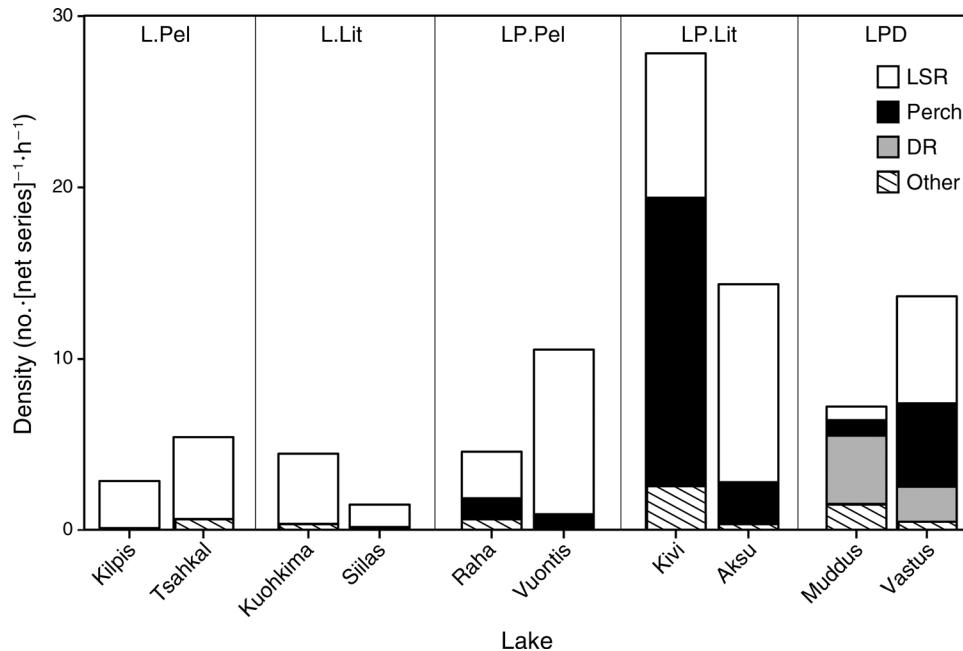


FIG. 3. Mean density of LSR whitefish, perch, DR whitefish, and combined other species (see Table 1) recorded in each lake. For abbreviations see Fig. 1.

$\delta^{15}\text{N}$ data (Jackson et al. 2011). To overcome the disparity in sample sizes, the area of an ellipse corrected for small sample size (SEA_c), calculated using SIBER (Jackson et al. 2011), was used to determine isotopic niche width. Variation in niche width between species was calculated using the likelihood test in SIBER (Jackson et al. 2011). SEA_c of the distribution of invertebrate isotope values were also determined to obtain an estimate of the variation in isotopic baselines between lakes. Both SIAR and SIBER analyses were performed using the SIAR package in R (Parnell et al. 2010, R Development Core Team 2012).

RESULTS

Temperature

Mean monthly air temperatures (May–October) between 1971 and 2011 at Kilpisjärvi ($5.7^\circ \pm 4.5^\circ\text{C}$ [mean \pm SD]), located above the latitudinal distribution limit of perch, were significantly lower than temperatures recorded at the current limit of distribution (at Käsivarsi, $6.2^\circ \pm 5.1^\circ\text{C}$; paired Welch t test, $t = -8.7$, $\text{df} = 245$, $P < 0.001$). Mean monthly air temperature at Ivalo ($7.7^\circ \pm 5.1^\circ\text{C}$), located below the current distribution limit, was higher than at Käsivarsi (paired Welch t test, $t = -37.6$, $\text{df} = 245$, $P < 0.01$). Significant increases in mean annual air temperatures were observed at all three stations between 1971 and 2011 (at Kilpisjärvi, $r^2 = 0.39$, $F_{1,39} = 24.73$, $P < 0.001$; at Käsivarsi, $r^2 = 0.23$, $F_{1,39} = 11.93$, $P = 0.001$; at Ivalo, $r^2 = 0.17$, $F_{1,39} = 7.89$, $P = 0.007$; Fig. 2). A comparison of air and surface water temperatures, recorded daily between May and November 2000–2011 at Lakes

Kilpis and Ivalo meteorological station, which is proximate to Lake Inari ($68^\circ 58' \text{N}$, $27^\circ 40' \text{E}$), reveal a significant relationship between both measures (at Kilpisjärvi, $r^2 = 0.58$, $F_{1,70} = 24.73$, $P < 0.001$; at Lake Inari, $r^2 = 0.93$, $F_{1,69} = 954$, $P < 0.001$; see also Appendix A).

Fish community

The abundance and structure of the fish community, measured as n fish gill net-series $^{-1}\cdot\text{h}^{-1}$ (catch per unit effort, [CPUE]), varied between lakes (pseudo $F_{5,132} = 3.5$, $P < 0.01$) and lake classes (pseudo $F_{4,132} = 15.4$, $P < 0.01$; Table 1, Fig. 3). Whitefish were the most abundant species in all lakes except in Lake Kivi, where perch were dominant (Table 1, Fig. 3). Though variation in growth of perch and LSR whitefish was evident between lakes (Appendix B), no clear variation between lake types was recorded in either species (PERMANOVA, lake classification \times species; pseudo $F_{1,2} = 0.8$, $P = 0.94$).

Resource availability

Potential resource availability varied between sample sites. Lake morphology (area, mean depth, and relative area of littoral, pelagic, or profundal habitats) varied both between lakes and lake types, but broadly supported our original classifications (Table 1). In Lake Kuohkima and Lake Siilas, the entire benthic area was located within the compensation depth, hence, no profundal habitats existed in these lakes. The pelagic zone comprised 15% of the lake area in Lake Kivi and 19% in Lake Aksu. Although the pelagic zone was

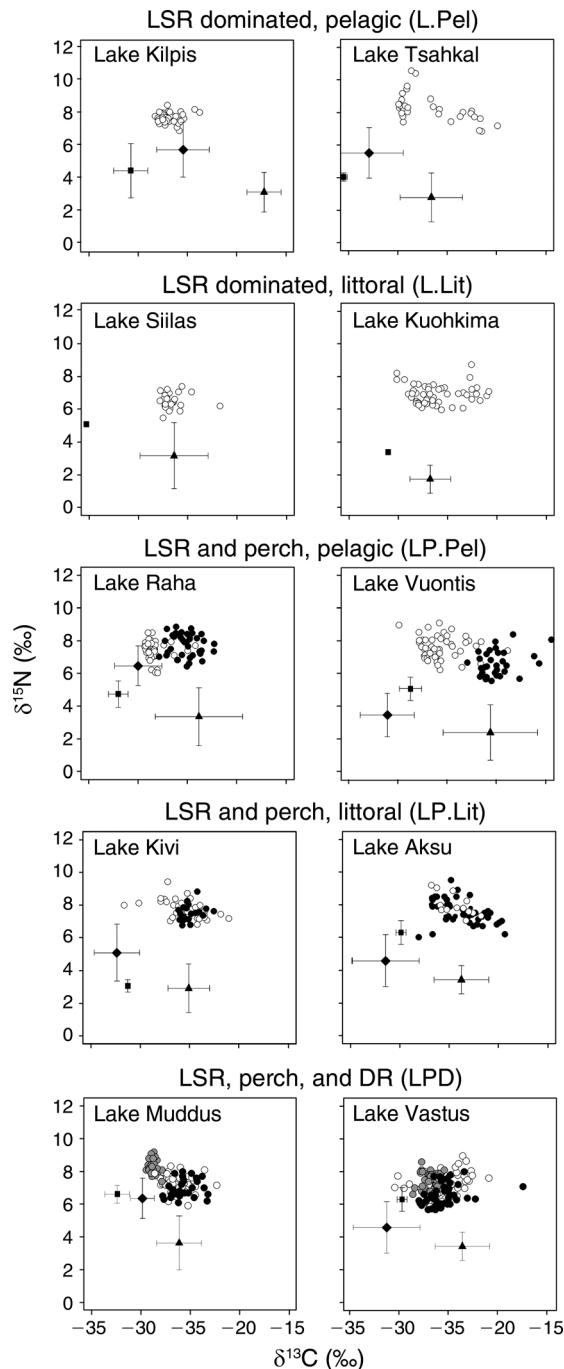


FIG. 4. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of LSR whitefish (white circles), perch (black circles), and DR whitefish (gray circles). Mean (\pm SD) values of pelagic (square), littoral (triangle), and profundal (diamond) baseline samples are included. Isotopic niche width of LSR whitefish, perch, and DR whitefish are presented in Fig. 6.

similarly restricted in Lake Vuontis (20%), the higher mean depth and water clarity of this lake facilitated increased pelagic productivity.

Differences in littoral benthic macroinvertebrate densities (Appendix C) were observed between lakes classes

(pseudo $F_{1,4} = 2.8$, $P = 0.04$), with the lowest densities observed in LP.Lit lakes. Densities of benthic macroinvertebrates did not vary between lakes within each class (interaction “lake” \times “lake class”; pseudo $F_{1,5} = 0.7$, $P = 0.74$), whereas higher densities were recorded in littoral than in profundal samples (pseudo $F_{1,9} = 9.5$, $P < 0.01$).

Copepods were larger in LSR-dominated lakes (mean length = 1 ± 0.15 mm [mean \pm SD]) compared to lakes containing perch (0.77 ± 0.24 mm; Welch t test, $t = 51.1$, $df = 6775.2$, $P < 0.001$) and lakes containing both DR whitefish and perch (0.79 ± 0.24 mm; Welch t test, $t = 38.6$, $df = 4994.4$, $P < 0.001$). Variation in the mean size of cladocerans was also evident, but this was not related to fish community structure (Appendix C).

The range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values of baseline invertebrate organisms varied between lakes: It was the highest in large lakes that contained a defined pelagic zone (Appendix C). Due to this underlying variation, statistical comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were not conducted across different systems. Zooplankton samples were depleted in ^{13}C relative to littoral and profundal macroinvertebrates, whereas profundal invertebrates displayed ^{15}N -enriched values to littoral samples (Fig. 4; Appendix C).

Hypothesis 1: Perch are benthivorous in all systems, whereas LSR whitefish are generalists

Stomach contents of perch were dominated by benthic littoral prey in all lakes (Fig. 5; Appendix D). Perch diet differed between lakes within each class (pseudo $F_{3,332} = 14.3$, $P < 0.01$), but not between lake classes (pseudo $F_{2,332} = 0.5$, $P = 0.92$). Isotope mixing model values also indicated a strong reliance (48–96%) on littoral prey sources in all lakes (Fig. 6; Appendix E). Perch exhibited dietary (paired Welch t test, $t = 0.38$, $df = 5$, $P = 0.72$) and isotopic (Table 2, Fig. 5) niche widths broadly equivalent to LSR whitefish.

The diet of LSR whitefish varied between replicate lakes within each lake classification (pseudo $F_{5,1273} = 17.9$, $P < 0.01$; Appendix D), obscuring any variation attributable to the presence of perch (pseudo $F_{4,1273} = 1.4$, $P = 0.18$; Fig. 5). LSR whitefish consumed more zooplankton in LP.Pel lakes than in any other system (Appendix D), but this zooplankton proportion was not directly related to lake area (Spearman correlation, $n = 10$, $r_S = 0.1$, $P = 0.77$).

Similarly, the resource use of each species, as derived from isotopic mixing models, varied between replicate lakes in each lake classification (Fig. 6). LSR whitefish in Lake Kilpis were closely associated with pelagic feeding, while in Lake Tsahkal, they exhibited a wider niche width reflecting the consumption of benthic resources by some individuals (Fig. 5). LSR whitefish in L.Lit lakes also exhibited a wide niche width including both benthic and pelagic resources (Fig. 6). The existence of such variation in resource use in LSR whitefish within both L.Lit and L.Pel lake classifications confounded our attempts to examine variation in

resource use of LSR whitefish between LSR-dominated lakes and lakes containing perch.

Hypothesis 2: Resource availability determines niche overlap between LSR whitefish and perch

Dietary segregation was evident between species in most cases (Table 2; Appendix D). In both LP.Pel lakes, LSR whitefish utilized more pelagic zooplankton than perch (Fig. 5; Appendix D). Dietary segregation was also observed in LP.Lit lakes. In Lake Kivi, LSR whitefish stomach contents were dominated by small benthic crustaceans (*E. lamellatus* and *Megacyclops* sp.), whereas perch consumed insect larvae (Appendix D). In Lake Aksu, LSR whitefish utilized pelagic zooplankton, whereas the diet of perch was dominated by crustaceans (Appendix D).

Stable-isotope data supported these observations. In both LP.Pel lakes, LSR whitefish and perch could be discriminated along the $\delta^{13}\text{C}$ axis, and LSR whitefish were ^{13}C depleted relative to perch (Fig. 4; Appendix E). The SIAR mixing model revealed a greater reliance on pelagic prey by LSR whitefish than perch in these lakes (Fig. 6). In LP.Lit lakes, LSR whitefish and perch were isotopically indistinguishable (Table 2, Fig. 5) with mixing models, indicating that both species assimilated most of their energy and nutrients from littoral sources (Fig. 6, Appendix E).

Hypothesis 3: DR whitefish dominate pelagic prey increasing niche overlap between perch and LSR whitefish

DR whitefish were pelagic zooplanktivores in both LPD lakes (Fig. 5; Appendix D). They maintained smaller dietary and isotopic niche widths than either LSR whitefish or perch (Table 2). The diet of DR whitefish was dominated by zooplankton and was significantly different from both LSR whitefish and perch, which consumed littoral benthic macroinvertebrates (Fig. 5; Appendix D).

Dietary overlap between LSR whitefish and perch was greater in LPD lakes than in either category of LP lakes. Both species utilized littoral benthic prey (Fig. 5), although variation in diet was evident at a statistically significant level in both lakes (Table 2). Stable-isotope values of both LSR whitefish and perch were strongly associated with littoral resources in LPD lakes (Fig. 6; Appendix E). Although some variation was evident between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ centroids of LSR whitefish and perch in Lake Muddus, they were indistinguishable in Lake Vastus (Table 2).

DISCUSSION

Resource availability and fish community structure governed the outcome of trophic interactions between LSR whitefish and perch. As hypothesized, perch fed exclusively on benthic prey in all systems, whereas LSR whitefish were generalist and used both pelagic and benthic resources in lakes without perch. We found a clear effect of lake morphometry on the interactions

between species: In deep lakes, LSR whitefish shifted to the pelagic, whereas in shallow littoral lakes, both species utilized the same benthic resources. Intraspecific interactions between whitefish morphs outweighed interspecific interactions between LSR whitefish and perch, as LSR whitefish competed with perch for littoral benthic resources rather than for pelagic zooplankton with DR whitefish.

Perch

Perch diet and isotope values were typical of a littoral benthivore in all lakes. In addition, perch displayed dietary and isotopic niche widths equivalent to that of generalist LSR whitefish. These findings are broadly in agreement with previous studies of perch in subarctic lakes (Amundsen et al. 2003, Hayden et al. 2013b) and suggest that planktivory reported in more productive temperate-zone mesotrophic lakes (Persson 1983) may be associated with the greater abundance of zooplankton. Piscivory was detected in all of the perch populations examined, whereas no fish feeding was observed in whitefish. We also showed that whitefish are an important prey for piscivorous perch. In southern Fennoscandia, perch predation can be important part of larval and juvenile coregonid mortality (Heikinheimo 2001), as such increased density of perch may result in additional predation pressure on whitefish. Perch predation on LSR whitefish was limited to whitefish smaller than 15 cm, broadly equivalent to the first two years of life (Kahilainen et al. 2003, Hayden et al. 2013b), indicating that the perch populations currently found in these subarctic lakes may have an adverse effect on whitefish recruitment. This scenario is most likely in shallow lakes, where whitefish juveniles are not able to avoid perch predation by shifting to pelagic habitats.

LSR whitefish

In contrast to perch, the resource use of LSR whitefish varied between lakes and lake types. In the LSR-dominated lakes (L.Pel and L.Lit), the combination of large body sized zooplankton and the relatively high density of benthic macroinvertebrates found in the lake were aligned with a comparatively low density of fish, indicating that, in these systems, prey is not a limiting resource. In these conditions, LSR whitefish were trophic generalists (Fig. 1a, b). In both L.Pel lakes, LSR whitefish diet consisted of equal amounts of benthic and pelagic prey. However, stable isotopes indicated pelagic specialization in Lake Kilpis. In Lake Tsahkal some individuals were littoral benthivores, whereas others were planktivorous, resulting in a large population isotopic niche width. In the presence of benthivorous perch in deep lakes, LSR whitefish shifted to a diet of pelagic prey, as revealed in both short-term (stomach content) and long-term (stable isotope) indicators of diet. In both L.Lit lakes, LSR whitefish predominantly used littoral benthic prey, although results from isotope mixing models indicated pelagic

resource use in Lake Kuohkima. In shallow littoral lakes, perch had a less obvious effect on LSR whitefish, as in these lakes LSR whitefish used a similar proportion of benthic prey to that observed in shallow lakes without perch. Benthic prey also dominated the diet of whitefish in both LPD lakes. Despite both LPD lakes containing a large pelagic zone, zooplankton were rarely consumed by LSR whitefish and stable-isotope values indicated a strong reliance on littoral benthic prey.

DR whitefish

In both LPD lakes (Lakes Muddus and Vastus), DR whitefish fed predominantly on zooplankton and were more closely aligned to pelagic resources than either LSR whitefish or perch. Furthermore, DR whitefish were characterized by a smaller dietary and isotopic niche width than LSR whitefish or perch. This is a likely indication of the ecomorphological specialization of DR whitefish, e.g., gill raker, head, and body shape adaptations for foraging on pelagic prey (Kahilainen et al. 2007). Many other pelagic specialist species also show similar foraging adaptations to exploit a narrow zooplanktivorous niche (Sandlund et al. 1987, Peltonen et al. 2004).

Inter- and intraspecific resource competition

Lake morphometry and resource polymorphism determined the degree of niche overlap between whitefish and perch (Fig. 1). In the first scenario (Fig. 1c), deep lakes with a defined pelagic zone (i.e., LP.Pel lakes: Lakes Raha and Vuontis), LSR whitefish and perch were separated by their respective use of pelagic (LSR whitefish) or benthic (perch) prey. In the second scenario (shallow littoral Lakes Aksu and Kivi; Fig. 1d), both perch and LSR whitefish used littoral benthic prey. Although both species showed complete isotopic overlap, dietary segregation was clear: Stomach content analysis revealed that perch consumed large crustaceans and insect larvae, whereas LSR whitefish fed on small crustaceans, molluscs, and, in Lake Aksu, zooplankton. In the third scenario (Fig. 1e), DR whitefish-dominated pelagic resources, leading to the highest littoral niche overlap between LSR whitefish and perch. Lake Muddus also contained a specialist profundal benthivorous SSR whitefish (Kahilainen et al. 2004), which likely further restricted LSR whitefish and perch to littoral benthic prey.

The degree to which niche overlap corresponds with resource competition is one of the most difficult issues to resolve in ecology. While our data display a relationship between lake depth and niche overlap, the extent of resource competition between LSR whitefish and perch is less easy to quantify. As LSR whitefish utilized both benthic and pelagic resources in LSR whitefish-dominated lakes, it is difficult to ascertain whether increased pelagic feeding in LSR whitefish found in sympatry with perch was a consequence of resource competition for benthic prey, or simply a response to pelagic availability

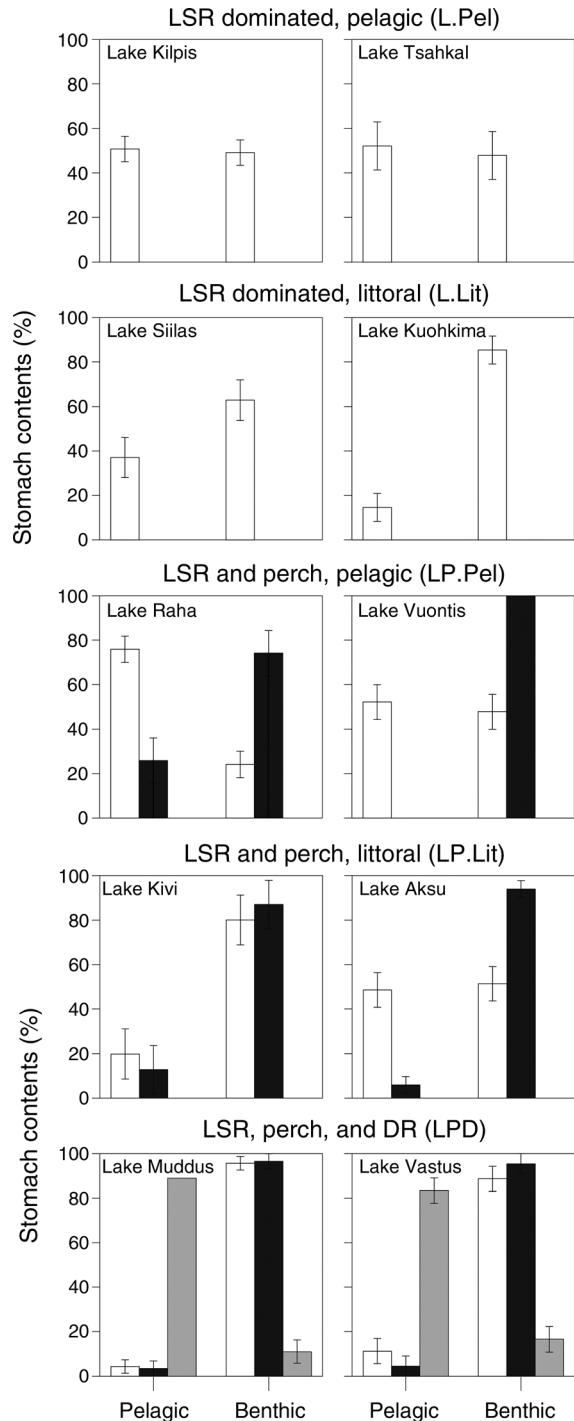


FIG. 5. Relative percentages of pelagic (zooplankton and adult/pupal insects) and benthic (all benthic invertebrates) prey in the stomach contents of LSR whitefish (white bars), perch (black bars), and DR whitefish (gray bars) in each lake. Error bars indicate 95% confidence intervals.

in what is an extremely plastic species. However, the relative availability of benthic resources in both LP.Pel lakes were the lowest recorded in the study, indicating that competitive exclusion for benthic resources may

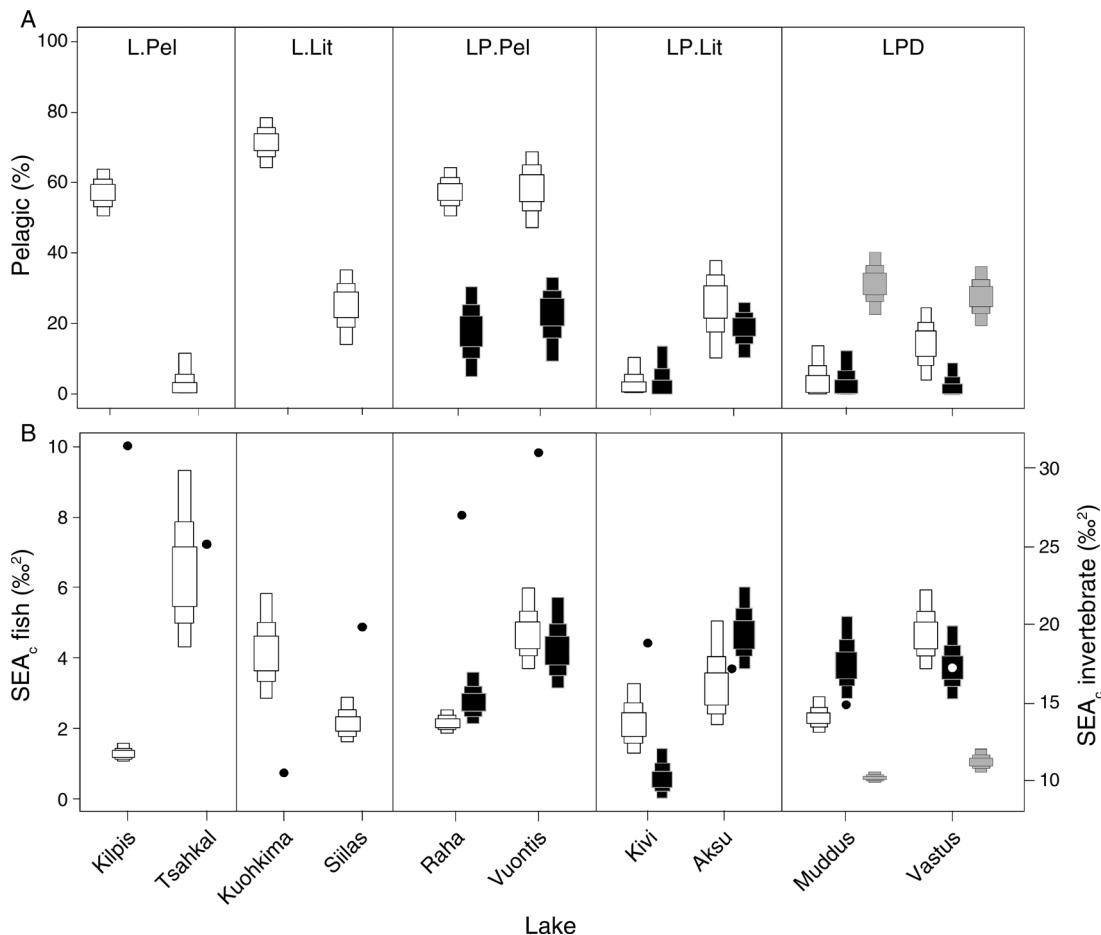


FIG. 6. Comparative plots of (A) percentage of pelagic resources assimilated by LSR whitefish (white boxes), perch (black boxes), and DR whitefish (gray boxes) and (B) isotopic niche size (SEA_c ‰² is the area of a standard ellipse of the $\delta^{13}C$ and $\delta^{15}N$ values of each fish) in 10 study lakes. Gradations represent 50%, 75%, and 95% confidence limits. Mean SEA_c of invertebrate samples (black circles, and white circle for Lake Vastus) are included for comparison with SEA_c of fish. Note that the left and right y-axes in panel (B) have different scales for the fish and invertebrate samples.

have driven the increased utilization of pelagic resources by LSR whitefish. Furthermore, the reduced size of copepods in these lakes relative to LSR-dominated lakes is indicative of an exploited resource (Brooks and Dodson 1965), suggesting that increased planktivory by LSR whitefish is not simply a response to increased zooplankton density. Whitefish outnumbered perch in most lakes. As such, the current smaller population size of perch may have limited influence on the trophic behavior of whitefish, as both species may be able to exploit the same benthic resources without severe resource competition. However, a possible future increase in population size of perch, likely mediated by increased summer temperatures (Lehtonen 1996), would increase the likelihood of both species competing for resources.

Our results indicated that intraspecific competition with DR whitefish outweighed the interspecific effect of perch on LSR whitefish niche selection. Ecomorpho-

logical adaptations of DR whitefish (e.g., the higher number of gill rakers) facilitate foraging on smaller zooplankton prey than LSR whitefish (Kahilainen et al. 2011), effectively relegating generalist LSR whitefish from feeding on pelagic resources. In contrast, the morphological adaptations of the LSR whitefish (i.e., subterminal mouth and lower number of gill rakers) are more beneficial for benthic than pelagic feeding (Kahilainen and Østbye 2006, Harrod et al. 2010). In polymorphic systems, LSR whitefish switch to benthic prey and compete with the more generalist perch. However, the outcomes of invasion by a specialist species may differ from those observed here, involving a generalist. The invasion of a polymorphic whitefish system in Norway by vendace (*Coregonus albula*), a zooplanktivorous specialist, relegated DR whitefish from pelagic to littoral feeding, resulting in direct resource competition with LSR whitefish and potentially also with perch (Bøhn et al. 2008). All this suggests that

TABLE 2. Summary of dietary (stomach content analysis [SCA]) and isotopic (stable-isotope analysis [SIA]) niche overlap between LSR whitefish, perch, and DR whitefish.

Lake class and lake	Species	SCA			SIA				
		<i>n</i>	<i>P</i>	Levins	<i>n</i>	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	<i>P</i>	SEA _c
L.Pel									
Kilpis	LSR	262	...	0.51	50	-26.8 (0.9)	7.6 (0.3)	...	0.85
Tsahkal	LSR	81	...	0.56	36	-27.1 (3.2)	8.3 (0.8)	...	6.9
L.Lit									
Siilas	LSR	96	...	0.25	50	-26.1 (2.5)	6.9 (0.6)	...	4.8
Kuohkima	LSR	110	...	0.37	30	-26.6 (1.2)	6.5 (0.5)	...	1.7
LP.Pel									
Raha	LSR	183	<0.01	0.31	96	-28.4 (1.1)	7.4 (0.6)	<0.01	1.9
	perch	69	...	0.35	45	-25.2 (1.3)	7.8 (0.6)	...	2.6
Vuontis	LSR	151	<0.01	0.18	50	-25.7 (2)	7.6 (0.7)	<0.01	4.4
	perch	30	...	0.21	34	-19.9 (1.8)	6.6 (0.7)	...	4.2
LP.Lit									
Aksu	LSR	133	<0.01	0.37	44	-24.4 (1.9)	7.7 (0.5)	0.22	2.8
	perch	87	...	0.19	25	-25 (0.9)	7.5 (0.5)	...	1.4
Kivi	LSR	47	<0.01	0.25	44	-24.2 (1.6)	7.9 (0.7)	0.46	2.7
	perch	36	...	0.2	50	-23.7 (2.2)	7.6 (0.7)	...	4.6
LPD									
Muddus	LSR	107	<0.01 (L vs. P)	0.22	51	-26.3 (1.2)	7.2 (0.5)	0.02 (L vs. P)	1.9 (L vs. P)
	perch	73	<0.01 (L vs. D)	0.37	29	-25.6 (1.3)	6.9 (0.6)	<0.01 (L vs. D)	3.8 (L vs. D)
	DR	152	<0.01 (D vs. P)	0.08	50	-28.8 (0.3)	8.3 (0.4)	<0.01 (D vs. P)	0.4 (P vs. D)
Vastus	LSR	104	0.02 (L vs. P)	0.22	51	-25.6 (2)	7.3 (0.7)	0.1 (L vs. P)	4.4 (L vs. P)
	perch	38	<0.01 (L vs. D)	0.12	43	-25.7 (1.8)	6.6 (0.7)	<0.01 (L vs. D)	3.6 (L vs. D)
	DR	191	<0.01 (D vs. P)	0.03	50	-26.9 (0.7)	7.5 (0.5)	<0.01 (D vs. P)	1 (P vs. D)

Notes: Lake class is designated by species composition (L, LSR whitefish; P, perch; D, DR whitefish) followed by depth (Pel, pelagic; Lit, littoral). Sample size (*n*) and *P* value of pairwise PERMANOVA are presented for each case. Measures of dietary (calculated using a standardized Levins' index) and isotopic (area of a small-sample size corrected ellipse [SEA_c]) niche width are presented, and pairwise comparisons of isotopic niche width (SIBER likelihood test; values in boldface indicate >95% probability of larger niche width) are also included. Further data are presented in Appendices D and E. Values in parentheses are SDs. Ellipses indicate that no data are possible.

the final outcome of invasion is dependent on an interaction of the efficiency of invading species and the fish community structure and morphometry of the receiving ecosystem.

Although we showed marked shifts in their trophic ecology, LSR whitefish growth did not vary between lake classifications. This indicates that, although whitefish may have a preference for a particular feeding strategy, growth is maintained regardless of the availability of pelagic resources. While this likely relates to density-dependent population and growth regulation mechanisms (Amundsen et al. 2002), it may also help to explain the presence of sympatric LSR and DR whitefish populations in certain lakes, as both populations can maintain themselves effectively while utilizing distinct resources.

Potential sources of error

Any investigation based on field assessments may be subject to certain inadequacies and potential biases. The high degree of variation in lake size between the replicate L.Pel and LPD lakes is one example of this. Similarly, Lakes Aksu and Kivi may have been too large and deep to be deemed true littoral systems. In addition, sampling took place during the late summer in each lake. Lakes at these latitudes are ice-covered for circa six months per

year, resulting in reduced zooplankton density and increased level of benthic feeding by LSR whitefish (Hayden et al. 2013a), which is likely to increase niche overlap with perch. However, in acknowledging these deficiencies, we maintain that the results presented attest to the degree of variation in trophic interactions which can be expected in situations of range expansion.

Conclusions

Species range expansions do not occur through homogenous, uniform landscapes. Rather, they incorporate a variety of habitat types in which the migrating species will have varying levels of success. This is particularly true for freshwater fishes, which cannot bypass inhospitable habitats as easily as terrestrial animals. In the introduction, we referenced an ongoing debate regarding the efficiency of bioclimate envelope models at predicting future species range distributions. Our results highlight how variation in resource availability due to either abiotic factors such as lake morphometry, or biotic factors such as the presence of a resident specialist, can regulate the outcomes of these interactions. We suggest that it is pertinent to include abiotic and biotic characteristics of the invaded systems when modeling climate change-mediated range expansions. Interactions between two closely related and



PLATE 1. Lake Kilpis, a large, deep and oligotrophic lake situated in the northwestern tip of Finnish Lapland. The lake contains a limited fish fauna dominated by LSR whitefish (*Coregonus lavaretus*). Photo credit: Grace Hayden.

ecomorphologically similar species to those studied here from North America, lake whitefish (*Coregonus clupeaformis*) and yellow perch (*Perca flavescens*), are also of particular interest. In both continents, perch are considered as a species likely to benefit from increasing temperatures via higher year class strengths and northward range expansion (Reist et al. 2006, Graham and Harrod 2009), and thus provide an opportunity to test our findings outside of Fennoscandia.

The results of this investigation highlight that the ecology of range expansions and their impact upon resident biota are complex and largely dependent on the biotic and abiotic conditions of the invaded habitat. Even at the limits of their ecological tolerances, a migrating competitor, in this case perch, can dominate their preferred habitat type. However, range expansion may be accommodated into the food web in habitats containing a diversity of niches, as supported by the increased use of pelagic resources by LSR whitefish in deep lakes. As such, we contend that it is not sufficient to predict that species ranges will unilaterally shift in line with warmer temperatures, or that species interactions will govern migration, rather, the interaction between geomorphology, resource availability, and fish community structure plays a key role in determining the outcomes of species establishment.

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SUPPLEMENTAL MATERIAL

Appendix A

Temporal and spatial variation in air temperature within the study region ([Ecological Archives E095-047-A1](#)).

Appendix B

Netting effort and growth data for principal fish species ([Ecological Archives E095-047-A2](#)).

Appendix C

Density and isotopic values of sampled invertebrate taxa ([Ecological Archives E095-047-A3](#)).

Appendix D

Stomach contents of LSR whitefish, perch, and DR whitefish ([Ecological Archives E095-047-A4](#)).

Appendix E

Stable-isotope mixing model values of LSR whitefish, perch, and DR whitefish ([Ecological Archives E095-047-A5](#)).