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Trophic ecology of piscivorous Arctic charr (*Salvelinus alpinus* (L.)) in subarctic lakes with contrasting food-web structures

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Abstract The trophic ecology of piscivorous Arctic charr (*Salvelinus alpinus* (L.)) in the food webs of large subarctic lakes is not well understood. We assessed charr diets, parasites, growth, maturity, and stable isotope ratios in Fennoscandian subarctic lakes dominated by monomorphic or polymorphic whitefish (*Coregonus lavaretus* (L.)) populations. Charr density was low in all lakes, except in profundal habitats. Charr shifted to piscivory at small size (16–25 cm total length) and consumed a range of prey-fish sizes

(2–25 cm). Cannibalism was observed in a few individuals from one monomorphic whitefish lake. Charr matured at 37–51 cm (5–8 years old), grew to 52–74 cm maximum observed length and 47–83 cm asymptotic length. Charr increased total area of convex hull and core stable isotopic diversity area of the fish community by 51–98% and 44–51% in monomorphic whitefish lakes, but only 8–11% and 7–10% in polymorphic whitefish lakes. The difference was due to increasing food-chain length in monomorphic whitefish lakes, whereas reliance on littoral carbon did not change. Charr were the top piscivores in monomorphic whitefish lakes, but played a less

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important role in polymorphic whitefish lakes, which contained a more diverse predator fauna.

Keywords Diet · Food-chain length · Polymorphism · Predation · Stable isotopes · Whitefish morphs

Introduction

Piscivorous fish play a pivotal role in lake food webs by influencing behavioral decisions of individual prey, size structure of prey populations, and ecosystem-level energy flows (Ferrari et al., 2009; Gallagher et al., 2017). They may exert direct top-down, as well as indirect behavioral control of prey populations, with subsequent cascading effects on lake food webs (Kahilainen et al., 2009; Jensen et al., 2015; Thomas et al., 2017). In addition, the high mobility of top consumers is important for food webs as it allows pelagic and benthic food-web compartments to be linked (Vander Zanden & Vadeboncoeur, 2002; Eloranta et al., 2015a). Large subarctic lakes are fueled by both benthic and pelagic energetic pathways associated with specialist species or morphs, and they could be especially valuable systems for assessing the role of top predators in food webs. The ecology and role of large piscivorous Arctic charr (*Salvelinus alpinus* (L.)) in community and food-web processes in different types of subarctic lakes has remained poorly studied. This likely reflects a limited number of Scandinavian lakes supporting large-bodied piscivorous Arctic charr, as is the case with large piscivorous (ferox) brown trout (*Salmo trutta* L.) (Campbell, 1979). For example, only a few lakes in subarctic Finnish Lapland contain large-bodied Arctic charr populations (Seppovaara, 1969).

Arctic charr is the world's northernmost freshwater fish, being well adapted to cold water, and dominant in freshwater ecosystems with low species diversity throughout the Arctic (Klemetsen, et al., 2003; Elliott & Elliott, 2010). Arctic charr are highly plastic, utilizing contrasting habitats and forming distinct freshwater, river, or anadromous populations, as well as polymorphic populations throughout their core distribution area (Klemetsen, 2013). However, Arctic charr are sensitive to impaired water quality and increased resource competition with other fishes,

making them highly vulnerable to climate warming, increasing productivity, and interactions with invasive species (Lehtonen, 1998; Elliott & Elliott, 2010; Rolls et al., 2017). In this respect, large multispecies subarctic lakes at the edge of the species' core distribution area may provide insights into the current role of Arctic charr in these systems and aid the evaluation of the food-web level consequences of local extinction.

To adequately assess the role of top predators in specific food webs, predator ecology must be considered in the context of the relative abundance of prey and their size distribution (e.g., Jensen et al., 2008). Despite the development of modern stable isotope, fatty acid, and DNA bar-coding methods, stomach content analyses remain crucial for quantifying the diet and ontogenetic diet shifts of the large predatory fish (Nielsen et al., 2018). A combined approach using both stable isotopes and diet allows for quantification of the trophic location of target species in a food-web, as well as the relative abundance of prey-fish in the diet, the number of prey-fish in stomachs, and prey size for estimating the predation window for different prey species (Clark & Levy, 1988; Kahilainen & Lehtonen, 2003; Hrabik et al., 2006). Moreover, such detailed knowledge of prey species consumed is key for understanding food-borne parasite infections in predators (Hammar, 2000; Henriksen et al., 2016; Hammar et al., 2018). Due to the complementary nature of different analyses of resource use, application of multiple methods is the best approach for achieving a deeper understanding of predator–prey interactions, community structure, and energy flows in lake ecosystems.

Combined use of stable carbon and nitrogen isotopes and stomach content analyses have been especially useful in subarctic lakes, where these methods provide good resolution of differentiation between benthic and pelagic energetic pathways (Eloranta et al., 2010, 2015a). Furthermore, stable isotopes can be effectively used to separate invertebrate baselines from all three principal habitats (littoral, pelagic, and profundal) in large and deep subarctic lakes (Harrod et al., 2010). The relatively low number of species in subarctic lakes facilitates the stable isotope assessment of species or morph niches, in addition to community and food-web size (Thomas et al., 2016, 2017). Small subarctic lakes are generally driven by energy derived from benthic algae (e.g.,

Sierszen et al., 2003; Karlsson & Byström, 2005). This is reflected in high littoral reliance of Arctic charr in small lakes, whereas the species increases use of pelagic habitats and prey in larger lakes (Eloranta et al., 2015a). The relatively narrow dietary and isotopic niche of deep-water (profundal) Arctic charr is expected to result from strong interspecific resource competition in multispecies lakes, and is potentially further reinforced by the cold-water preference of Arctic charr (Kahilainen & Lehtonen, 2002; Sandlund et al., 2016; Hammar et al., 2018).

Subarctic Fennoscandian lakes with multiple piscivore and forage fish species provide excellent opportunities to study the role of Arctic charr in food webs. Large lakes (> 10 km² in Finnish Lapland) are deep enough to contain distinct littoral, pelagic, and profundal habitats, each of which is dominated by coregonid fishes providing prey for piscivores such as Arctic charr (Kahilainen & Lehtonen, 2003; Thomas et al., 2017). Whitefish (*Coregonus lavaretus* (L.)) are ubiquitous in the region and they have commonly diverged into benthic and pelagic morphs (Harrod et al., 2010). A few larger lakes have up to four whitefish morphs (Kahilainen et al., 2014; Thomas et al., 2016; Kahilainen et al., 2017). The occurrence of monomorphic and polymorphic whitefish lakes in the same region provides an opportunity to assess the importance of Arctic charr in different kinds of food webs. Besides whitefish, several other putative competitor fish species from both the invertebrate-feeding and piscivorous foraging guilds coexist with Arctic charr (Thomas et al., 2017).

Here, we used a large dataset from three pairs of subarctic lakes in northern Fennoscandia hosting contrasting multispecies fish communities. Two lakes have Arctic charr and monomorphic whitefish, two lakes have Arctic charr and polymorphic whitefish, and two lakes have non-Arctic charr piscivores with mono- and polymorphic whitefish (Thomas et al., 2017). Here, we addressed two broad objectives: the first was to evaluate the general role of Arctic charr in different types of whitefish dominated lake food webs (based on habitat, diet, prey size, parasites, growth, and maturation), and the second was to compare stable isotope food-web metrics in lakes with and without Arctic charr. Specifically, we tested two predictions: (1) the diet, life-history traits and parasite load of Arctic charr will reflect their position as apex predators in subarctic lake food webs and (2) as Arctic

charr are located at the top of the food chain; their presence will increase the overall size of the food-web as estimated with stable isotope analyses.

Methods

Study lakes

All six oligotrophic, clear-water, subarctic study lakes are located in Finnish Lapland (Fig. 1; Table 1). Arctic charr (hereafter charr) inhabit Lakes Kilpisjärvi, Rahajärvi, Muddusjärvi and Inarijärvi, but not Lakes Vuontisjärvi and Paadarjärvi (hereafter shortened without “lake” or “järvi”, the Finnish word for lake), which were used as controls for food-web analyses. Charr naturally reproduce in four studied charr lakes, but are currently supplemented by stocking in Inari, and have been stocked historically in Muddus and Raha. In the latter two lakes, stocked charr were relatively easy to exclude from analyses based on their large size, deteriorated fins and adipose fin-clipping. In Inari, charr are stocked mainly in their first year of life (0 + ; circa 5–8 cm of total length) and cannot be as easily identified as adults. Thus our data may contain stocked individuals. All six lakes are multispecies systems dominated by coregonid fishes (Kahilainen et al., 2017; Thomas et al., 2017). Kilpis, Raha and Vuontis have only a single whitefish morph, whereas Muddus, Inari, and Paadar contain four sympatric morphs (Thomas et al., 2017). Monomorphic lakes only support populations of the large sparsely rakered (LSR) whitefish that use all principal habitat types, including littoral, pelagic and profundal zones (Harrod et al., 2010). In lakes with polymorphic whitefish, LSR whitefish use littoral habitat, small sparsely rakered (SSR) whitefish use the profundal zone, whereas the densely rakered (DR) and large densely rakered (LDR) whitefish use the pelagic zone as their main foraging habitat (Kahilainen et al., 2014, Thomas et al., 2016; Kahilainen et al., 2017). The non-native pelagic planktivorous coregonid, vendace (*Coregonus albula* L.) has been stocked in Inari and Raha, where it currently forms a part of the pelagic fish community (Kahilainen et al., 2011; Thomas et al., 2016). In Inari, piscivorous lake trout (*Salvelinus namaycush* Mitchell) and land-locked salmon (*Salmo salar* m. sebago L.) have been introduced and currently make a relatively limited contribution to

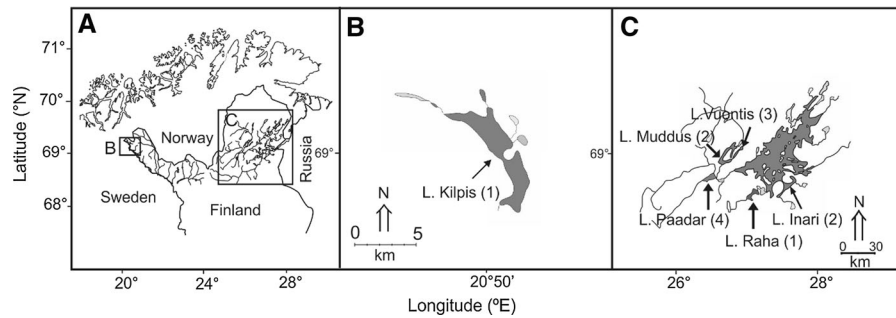


Fig. 1 Map of northern Fennoscandia (A) showing the location of study lakes in western (B) and eastern (C) Finnish Lapland. The number in the parentheses after lake name refers to type of fish population: 1 = charr and monomorphic whitefish

the fish community (Eloranta et al., 2015b). In all study lakes, whitefish are an important prey for piscivorous fish (Thomas et al., 2017).

Sampling of fish and invertebrates

Due to the low abundance of charr in most study lakes, we combined data from open water season sampling over several years and used multiple gears to increase sample sizes (see Tables 1 and 2 for details of sampling gear, years and efforts). Sampling of the entire fish community was conducted with gill-net series comprised of eight 30 m long and 1.8 m high nets with knot-to-knot mesh sizes of 12, 15, 20, 25, 30, 35, 45, and 60 mm (Table 1). This method generally captures fish with total length range of 9–65 cm. Predatory fish samples were supplemented by large-mesh gill-net series composed of five 5 m high and 60 m long nets with knot-to-knot mesh sizes of 35, 40, 45, 50, and 55 mm (Kahilainen & Lehtonen, 2002; Table 2). Gill-nets were set in littoral, pelagic, and profundal habitats in the evening and lifted the following morning with total soak times of ~ 12 h. Fish were immediately killed after removal from the gill-net with a sharp blow to the head that caused immediate unconsciousness followed by death. The gill-net catch was held on ice and later processed in the laboratory.

Benthic invertebrates were sampled with an Ekman grab (area 272 cm²) along a transect from lake shore areas (1 m depth) towards the deepest areas. Profundal sampling was limited to 40 m depth, except in Vuontis, where the deepest point of the lake was 31 m (Table 1). Each sampling depth (1, 2, 3, 5, 10,

populations, 2 = charr and polymorphic whitefish populations, 3 = no charr and monomorphic whitefish populations and 4 = no charr and polymorphic whitefish populations

15, 20, 30, and 40 m) included three replicates located around 10 m apart. Samples were immediately sieved through a 500 µm mesh and remaining animals and sediment were stored in a plastic bucket filled with water. In the field laboratory, benthic animals were sorted to the lowest feasible taxonomic level (varying from species to genus). Sorted samples were stored frozen (− 20°C) in 2 ml plastic tubes. Zooplankton were sampled by vertical hauls through the uppermost 20 m of the water column using a plankton net (diameter = 25 cm, mesh size = 50 µm). This sampling station was located near the deepest sampling point of the benthic transect so as to collect pelagic plankton at their main distribution depths. Zooplankton samples were first stored in a 1-L bucket and then transported to the laboratory for further sieving through a 50 µm mesh to remove extra lake water. Remaining samples consisting of both cladocerans and copepods were stored in 2 ml plastic tubes and frozen at − 20°C.

Fish processing

Each fish was identified to species: whitefish were identified to morph based on differences in body, head, and gill raker characteristics (see next paragraph). Total length (± 1 mm) and blotted wet mass (± 0.1 g) were recorded. From subsamples of fish (target sample size of 30 individuals per species), a piece of white muscle tissue posterior to the dorsal fin was dissected, stored in a 2 ml plastic tube and frozen at − 20°C for stable isotope analysis (SIA). The body cavity of charr was opened to determine sex and maturity (0 = immature, 1 = mature). Sagittal otoliths

Table 1 Lake type (*mono-WF* monomorphic whitefish, *poly-WF* polymorphic whitefish), location, morphological properties, water chemistry and numerical proportion of different fish species present in the study lakes, based on multi-mesh (12–60 mm) gill-net catches (height 1.8 m) in the three major habitats in each lake

Parameter	Kilpis	Raha	Muddus	Inari	Vuontis	Paadar
Lake type	Charr and mono-WF	Charr and mono-WF	Charr and poly-WF	Charr and poly-WF	No charr, mono-WF	No charr, poly-WF
Location	69°00'N, 20°49'E	68°45'N, 27°17'E	69°00'N, 26°50'E	68°58'N, 27°40'E	69°01'N, 27°04'E	68°52'N, 26°35'E
Area (km ²)	37	23	48	32*	11	21
Altitude (m a.s.l.)	473	132	146	118	151	144
Max depth (m)	57	46	73	40*	31	56
Mean depth (m)	19.4	14.1	8.5	14.5	6.5	11.7
Tot P (µg L ⁻¹)*	3	4	4	5	5	7
Tot N (µg L ⁻¹)*	100	100	160	150	180	160
Compensation depth (m)	10	9	7	8	12	5
Percentage profundal (%)	71	57	41	40	20	62
Fishing effort (1.8 m net series)	69	18	30	14	14	42
Fishing effort (5 m net series)	47	18	329	27	23	10
Arctic charr (%)	4.3	3.3	0.1	7.6	–	–
LSR whitefish (%)	88.8	57.7	15.3	10.5	90.4	22.7
DR whitefish (%)	–	–	49.8	13.1	–	43.7
SSR whitefish (%)	–	–	15.6	30.4	–	22.0
LDR whitefish (%)	–	–	2.5	1.8	–	2.0
Vendace (%)	–	9.6	–	24.3	–	–
Perch (%)	–	26.8	14.2	10.9	8.7	5.6
Brown trout (%)	1.4	0.5	1.1	1.0	0.2	1.4
Burbot (%)	3.4	1.4	0.6	0.2	0.2	1.8
Pike (%)	0.1	0.6	0.7	0.1	0.4	0.1
Grayling (%)	0.9	0.2	0.1	+	0.1	0.5
Minnow (%)	0.8	+	+	+	+	0.1
Alpine bullhead (%)	0.3	–	–	–	–	–
Nine-spined stickleback (%)	–	+	+	+	+	+
Threespined stickleback (%)	–	+	+	+	+	+
Lake trout (%)	–	–	–	+	–	–
Land-locked salmon (%)	–	–	–	+	–	–

Fishing effort refers to the number of sampling occasions with two gill-net series (1.8 m high and 5 m high). Compensation depth refers to the water column depth, where 1% of surface light was maintained, denoting the border between the littoral and profundal zones. Percentage of profundal is the proportion of this habitat to the total lake surface area. The abbreviations for whitefish morphs are: *LSR* large sparsely rakered whitefish, *DR* densely rakered whitefish, *LDR* large densely rakered whitefish, and *SSR* small sparsely rakered whitefish. Minus sign (–) refers to absence and plus sign (+) presence of species in the lake, based on all used fishing methods and stomach content analyses. Note that Vuontis and Paadar are not inhabited by charr

*Area and max depth of sampled site are from Nanguvuono bay

Table 2 Biological metrics of charr (mean \pm 95% CL)

Parameter	Kilpis	Raha	Muddus	Inari
Lake type	Charr and mono-WF	Charr and mono-WF	Charr and poly-WF	Charr and poly-WF
Sampling years	2002, 2005–2006, 2009–2012	2005	1999–2002, 2004–2007, 2011	2009–2010
Number of charr	159	66	164	108
Mean total length (cm)	42.6 \pm 2.5	33.3 \pm 2.5	39.1 \pm 1.1	29.9 \pm 3.1
Total length range (cm)	13–74.3	13.6–51.5	15–59.3	11.2–70
Mean weight (g)	1163.3 \pm 187.4	401.3 \pm 74.5	576.5 \pm 49.6	545.9 \pm 139.6
Weight range (g)	14.2–5525	16.3–1296.6	23–2368.4	9.7–4234
Mean age (years)	6.8 \pm 0.3	7.5 \pm 0.7	6.7 \pm 0.2	4.1 \pm 0.5
Age range (years)	1–12	2–13	3–9	1–9
Profundal (%)	84.9	98.3	54.5	100
Littoral (%)	12.6	1.7	45.5	0
Pelagic (%)	2.5	0	0	0
Growth rate (k; vonBertalanffy)	0.14 \pm 0.01	0.22 \pm 0.01	0.46 \pm 0.02	0.11 \pm 0.01
Asymptotic length (L_{∞})	83.4 \pm 1.7	46.8 \pm 0.9	48.8 \pm 0.5	79.4 \pm 3.4
t_0	1.32	0.9	3.0	– 0.54
Age at sexual maturity (50%)	8.3 \pm 0.9	8.6 \pm 1.6	5.9 \pm 0.3	6.7 \pm 1
Length at sexual maturity (50%)	50.8 \pm 2.5	37.2 \pm 4.8	36.6 \pm 1.1	43.9 \pm 4.7
Shift to piscivory length (50%)	15.9 \pm 5.6	24.8 \pm 3.6	17.6 \pm 6.1	16.5 \pm 5.8
Length range of charr with fish prey in their stomachs (cm)	15.0–70.4	19.7–51.5	16.2–51.0	11.2–54
Mean prey length (cm)	9.4 \pm 0.9	9.6 \pm 1.4	12.4 \pm 0.6	7.6 \pm 1.6
Range of prey size (cm)	1.9–25.2	2.5–18.1	5.5–24	1.9–17.2
Mean number of fish in stomach	2.8 \pm 0.9	2.5 \pm 0.6	2.1 \pm 0.4	2.2 \pm 1.0
Number of fish in stomach range	0–21	0–9	0–8	0–21
<i>Coregonus</i> sp. (mean \pm 95%CL;range)	–	11.1 \pm 3.1;6.5–17;	12.5 \pm 1.2;5.5–21;	13.5 \pm 1.8; 7–17.2
LSR whitefish	12.1 \pm 1.1;5.6–25.2	12.7 \pm 1.4;6.5–19	13.9 \pm 3.6;7–24	–
DR whitefish	–	–	12.2 \pm 0.6;4–15.1	10.5
Vendace	–	10.7 \pm 4.3;8–15	–	7.8 \pm 1.3;6.2–14.5
Nine-spined stickleback	–	3.2 \pm 0.3;2.5–4.7	–	2.8 \pm 0.3;1.9–4.5
Alpine bullhead	5.0 \pm 0.3;1.9–7	–	–	–
Arctic charr	12.9 \pm 1.9;11.3–15.2	–	–	–
Burbot	18.1	–	5.5	–
Perch	–	–	11	–

Lake type (*mono-WF* monomorphic whitefish, *poly-WF* polymorphic whitefish), sample size, proportion of females, size and condition, capture habitat of charr samples, von Bertalanffy growth modeling results, sexual maturation, total length at shift to piscivory, range of prey total length and mean total lengths

were removed from charr for age estimation done by examining whole otoliths submerged in distilled water under a microscope. Stomach contents of charr were quantified using a modified points method (Swynerton & Worthington, 1940), where stomach fullness was first visually classified from 0 (empty) to 10

(maximum full). Prey items were then identified to the lowest feasible taxonomic level and their relative contribution to total fullness was visually estimated. For undeteriorated prey-fish, total length was estimated (\pm 1 mm).

We identified whitefish morphs whenever possible: intermediate-sized SSR whitefish have a pronounced downward pointing snout and low number of short and bent gill rakers; large-sized LSR whitefish have a downward pointing mouth and intermediate number of short gill rakers; large-sized LDR have a slightly pointed head, longer upper jaw and high number of relatively long gill rakers; and small-sized DR whitefish have a pointed head, equal jaw length and high number of long gill rakers (Kahilainen & Østbye, 2006; Harrod et al., 2010; Kahilainen et al., 2017). Unlike whitefish, vendace have a longer lower jaw and very high number of longer and finer gill rakers (Kahilainen et al., 2011).

The charr shift to piscivory was calculated by excluding data from empty stomachs and coding prey containing stomachs as either 0 (only invertebrates) or 1 (fish or fish and invertebrates). In addition, the normal Levins' B dietary breadth index (Levins, 1968), mean stomach fullness, and number of empty stomachs were reported for each charr population. Finally, *Diphyllobothrium* spp. cysts from the esophagus and stomach wall of charr were counted from Inari, Kilpis and Raha. This copepod-transmitted parasite is capable of being re-established from planktivorous prey-fish to charr, and thus their abundance is correlated with the intensity of piscivory (Hammar, 2000; Henriksen et al., 2016). For parasites, we calculated the mean infection intensity (abundance as cysts/individual) and prevalence of infection (percentage of host individuals infected).

Stable isotope analysis

Frozen fish and invertebrate samples were freeze-dried for 48 h at -50°C or oven dried for 48 h at 60°C . Samples were then ground to a fine powder, weighed (0.5–1.0 mg) and encapsulated in tin cups. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios were measured using an elemental analyzer connected to an isotope flow mass spectrometer at Max Planck Institute for Limnology (Germany), University of Jyväskylä (Finland), University of New Brunswick (SINLAB; Canada), or University of California Davis (SIF; US). All laboratories used their own internal laboratory standards, calibrated with international standards, Vienna PeeDee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$. Analytical precision at all laboratories was $< 0.3\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

based on repeated analyses of internal standards. Charr may have a high lipid content in subarctic lakes (Kahilainen et al., 2016; Thomas et al., 2016), so we arithmetically lipid-corrected carbon values using elemental C:N values (Kiljunen et al., 2006).

Statistical analysis

Prediction 1: The trophic ecology of charr was assessed using biological metrics. A non-linear von Bertalanffy growth model was used to estimate growth rate and asymptotic length (von Bertalanffy, 1938). Probit regression was used to estimate length and age at 50% maturity, and the size at which charr shifted to piscivory. Differences in mean sizes of prey in charr stomachs were tested with ANOVA, followed by pairwise comparisons with Tukey's HSD tests. Statistical significance was set to $P < 0.05$. Analyses were conducted using SYSTAT 11.0 (Systat Software Inc., Chicago, IL, USA).

Prediction 2: The position and role of charr in lake food webs were assessed using stable isotopes. Previously published stable isotope-based food-web data were reanalyzed (Thomas et al., 2017). Inter-lake variation in stable isotope data was removed by transforming $\delta^{13}\text{C}$ values into littoral reliance and $\delta^{15}\text{N}$ values into trophic position estimates using littoral benthic macroinvertebrates and pelagic zooplankton as isotopic end-members and baselines (Karlsson & Byström, 2005). Layman metrics, including littoral reliance (LR) range, trophic position (TP) range, total area of convex hull (TA), mean distance to centroid (CD), mean nearest-neighbor distance (NND), and standard deviation of nearest-neighbor distance (SDNND), and the core stable isotopic diversity area of the fish community (SEAc) were used to assess how community-level isotopic metrics differed between lakes with and without charr (Layman et al., 2007; Jackson et al., 2011; Thomas et al., 2016). Food-web analyses were conducted using the Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al., 2011) package version 3.4.1 (R Development Core Team, 2017).

Results

Prediction 1: population structure and biometrics data

Charr density was relatively low in all study lakes and ranged from 0.1% in Muddus to 7.6% in Inari (Table 1). The profundal zone was the most important feeding habitat for charr (54.5–100%), and charr were absent from the pelagic catches, except in Kilpis, where 2.5% of all charr were captured from pelagic habitats (Table 2). Charr in all lakes attained a large size, with maximum observed total length ranging from 51.5 to 74.3 cm (Table 2). Mean total length and mass of charr were larger in Kilpis (42.6 cm, 1163 g) than in the other charr lakes, whereas the lowest mean age was observed in Inari (Table 2). Asymptotic length ranged 46.8–83.4 cm and growth rate (k) ranged 0.11–0.46, respectively (Table 2). Size at sexual maturity followed the same pattern as asymptotic length: charr in Raha and Muddus reached maturity at a smaller size than conspecifics in Inari and Kilpis (Table 2). Age at sexual maturity was higher in Kilpis and Raha with monomorphic whitefish than in Muddus and Inari with polymorphic whitefish. Charr shifted to piscivory at a length of 15.9–24.8 cm and the smallest individual fish (11.2 cm) with fish prey in its stomach was found in Inari (Table 2). Mean prey length differed among lakes (ANOVA, $F_{3,318} = 15.8$, $P < 0.05$), and was larger in Muddus (12.4 cm) than in the other lakes (Tukey's HSD tests, $P < 0.05$). Prey length ranged 1.9–25.2 cm. The smallest prey were nine-spined stickleback (*Pungitius pungitius* (L.)), whereas the largest were LSR whitefish (Table 2).

Fish prey contributed significantly to diets of charr of all sizes (Table 3), with coregonid fishes being important prey for charr. In monomorphic whitefish lakes, small piscivorous charr initially consumed small-bodied fish, such as alpine bullhead, *Cottus poecilopus* Heckel, (Kilpis) or nine-spined stickleback, (Raha), and later shifted to larger sized LSR whitefish (Tables 2 and 3). Cannibalism was only observed in Kilpis, where four charr had consumed conspecifics. In lakes with polymorphic whitefish populations, piscivorous charr shifted diets from nine-spined sticklebacks to pelagic coregonids, vendace, or DR whitefish (Inari), or as in Muddus fed directly on DR whitefish throughout life (Tables 2 and 3).

Preference for specific fish prey led to relatively low dietary breadth (Levins B) that generally decreased with length, especially in Kilpis and Raha that had monomorphic whitefish where large charr preyed heavily on LSR whitefish (Table 3). Abundance and prevalence of *Diphyllobothrium* spp. cysts in charr increased with size. The trend was more pronounced in Kilpis and Raha with monomorphic whitefish than in Inari with polymorphic whitefish (Table 3).

Prediction 2: stable isotopes and food webs

Charr occupied the highest trophic position in all lakes, with $\delta^{15}\text{N}$ values ranging from 10 to 12‰, and with $\delta^{13}\text{C}$ values ranging from -27 to -24 ‰ (Fig. 2; Table 4). In Kilpis and Raha (charr and monomorphic whitefish), charr were clearly the sole top predators, whereas in Inari and Muddus (charr with polymorphic whitefish) other piscivores shared the high trophic position with charr (Fig. 2). In the two control lakes without charr (Vuontis and Paadar), brown trout, pike, and burbot were at the top positions in the food-web, with $\delta^{15}\text{N}$ values varying between 8 and 10‰, and $\delta^{13}\text{C}$ values ranging from -27 to -24 ‰. Mean littoral reliance (LR) of charr ranged from 30 to 60%, while estimated trophic position (TP) ranged from 3.8 to 4.4, but estimates did not differ between mono- or polymorphic whitefish lakes (Fig. 3).

Inclusion of charr increased food-chain length by 17.5–50.5% in monomorphic whitefish lakes and by 2.2–13.9% in polymorphic whitefish lakes, whereas littoral reliance was not affected by charr inclusion in any lake (Fig. 3; Table 5). The total fish community area (TA) increased by 51–97.6% and the core stable isotopic diversity area of fish community (SEA_c) increased by 44.4–50.6% in lakes with monomorphic whitefish, but only 8.1–10.9% and 6.7–9.5% in lakes with polymorphic whitefish, when charr were included in the fish community (Table 5). Inclusion of charr also increased mean distance to centroid (CD) in all lakes, whereas mean nearest-neighbor distance (NND) increased in lakes with monomorphic whitefish and decreased in lakes with polymorphic whitefish populations (Table 5). Lakes without charr (Vuontis and Paadar) had variable TA and SEA_c , but did not have food-chain lengths as long as lakes with charr (Fig. 3; Table 5).

Table 3 The proportion (%) of different prey categories in the diet of different total length categories (cm) of charr in the study lakes

Prey category and diet related calculations	Kilpis			Raha			Muddus			Inari		
	< 20	20–39	≥ 40	< 20	20–39	≥ 40	< 20	20–39	≥ 40	< 20	20–39	≥ 40
Zooplankton	37.3	0	0	53.4	6.4	0	13.3	0	0	15.4	0.9	0
BMI	11.5	3.4	0.6	18.9	9.5	0.6	6.7	3.2	0.4	38.7	4.6	0.2
Vendace	0	0	0	0	6.4	3.9	0	0	0	0	34.7	30.0
Unidentified fish	7.7	11.7	4.6	0	2.1	8.4	0	0.9	0	9.4	22.7	5.4
Perch	0	0	0	0	0	0	0	0	1.1	0	0	0
LSR whitefish	14.5	61.3	69.7	0	46.0	68.8	0	4.5	10.6	0	0	0
<i>Coregonus</i> spp.	0	0	0	0	23.2	18.2	13.3	40.6	26.8	0	34.7	57.9
Nine-spined stickleback	0	0	0	27.7	6.4	0	0	0	0	36.4	2.3	0
DR whitefish	0	0	0	0	0	0	66.7	50.9	60.3	0	0	6.4
Burbot	0	0	4.2	0	0	0	0	0	0.8	0	0	0
Alpine bullhead	29.0	9.2	19.3	0	0	0	0	0	0	0	0	0
Arctic charr	0	14.3	1.5	0	0	0	0	0	0	0	0	0
Proportion of fish (%)	51.3	96.6	99.4	27.7	84.1	99.4	80	96.8	99.6	45.9	94.4	99.8
Levins B	3.8	2.4	1.9	2.5	3.5	1.9	2.1	2.3	2.2	3.2	3.4	2.3
Empty (%)	22.7	25.6	54.2	16.7	5.1	0	0	34.7	37.4	14.9	38.1	60
mean SF	2.8	2.8	2.1	3.9	4.8	5.1	3.8	3.0	3.2	2.8	2.1	1.2
n	22	43	94	12	39	15	4	75	83	47	21	40
<i>Diphyllbothrium</i> cysts	4.2	49	95.8	0.4	23	38.2	–	–	–	0	4.8	15.6
Prevalence (%)	54.6	100	100	41.7	87.2	100	–	–	–	0	42.9	92.5

Please note that in Muddus, *Diphyllbothrium* spp. parasites were not counted. Kilpis and Raha have charr and monomorphic whitefish, whereas Muddus and Inari have charr and polymorphic whitefish

BMI benthic macroinvertebrates, *LSR* large sparsely rakered, *DR* densely rakered, *Levins B* Levins dietary breadth, *empty (%)* proportion of empty stomachs, *SF* stomach fullness (scale 0 = empty, 10 = maximum full), *n* number of studied stomachs, *Diphyllbothrium* cysts mean number of cysts in stomach wall, *prevalence* proportion of individuals infected

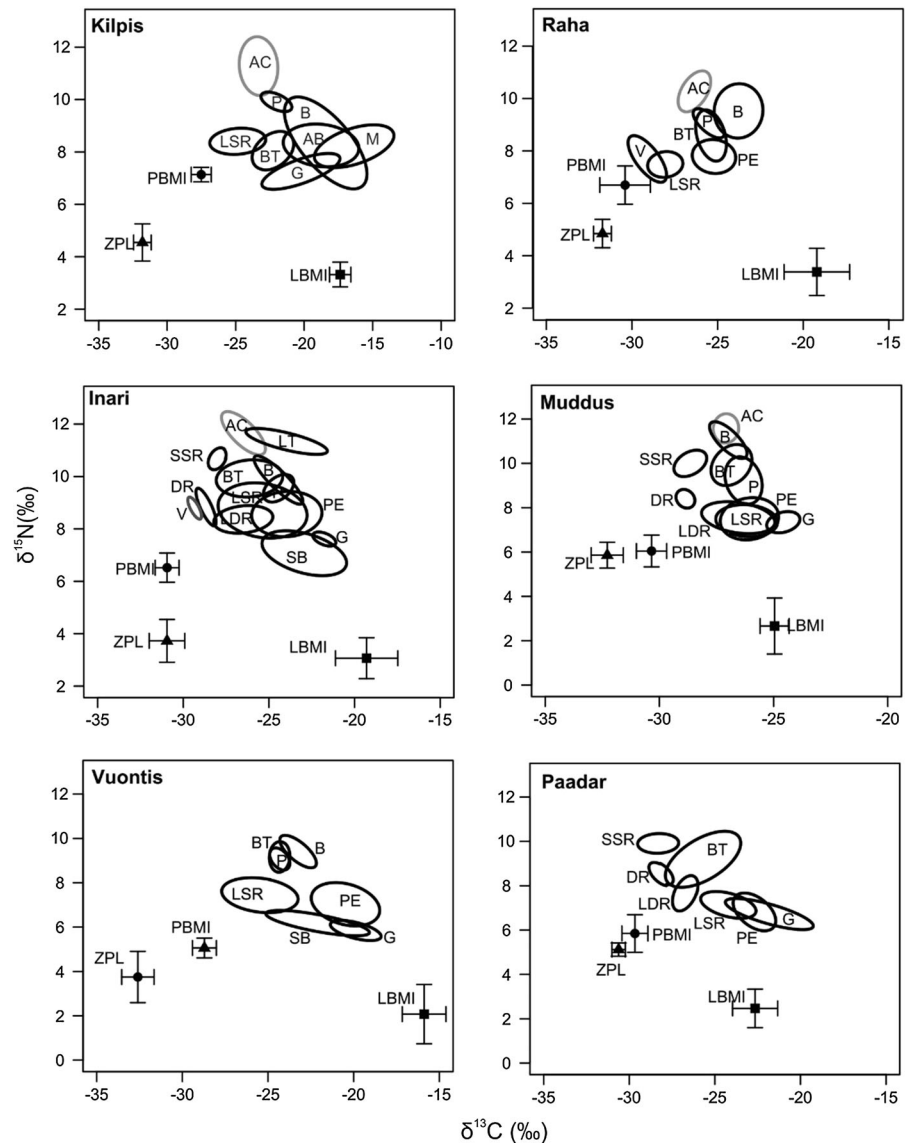
Discussion

Our results showed that charr shifted to piscivory at small size, grew to large asymptotic length, matured late, almost exclusively consumed fish prey, and fed on a wide range of prey sizes. The monomorphic whitefish lakes seemed to have more directed energy flow and based on diet, parasite and stable isotope results had food-chains linking invertebrates to LSR whitefish to charr. Comparisons of the total area of the convex hull and the core stable isotopic diversity area of the fish community demonstrated that charr increased the overall isotopic area of the fish community by increasing food-chain length, especially in monomorphic whitefish lakes where charr was clearly the top consumer. In polymorphic whitefish lakes hosting many piscivores, the food-web structuring effects of charr were less pronounced.

Charr as a part of diverse fish communities

Charr populations studied here had relatively low densities, and mainly inhabited deep profundal habitats. All the fish communities examined here were dominated by coregonid fishes, which contributed more than 60% (numerical abundance) of the fish catch. Whitefish was the most abundant coregonid, which is a well-known resource competitor for charr due to its more efficient zooplanktivory (Svärdson, 1976; Sandlund et al., 2010; Jensen et al., 2017). In Muddus and Inari, whitefish have diverged into morphs spanning across littoral, pelagic, and profundal zones, thereby reducing invertebrate prey resources (Kahilainen et al., 2017). Resource competition of juvenile charr with polymorphic whitefish for both pelagic and benthic invertebrates is likely intense in these lakes, at least during summer months.

Fig. 2 Stable isotope bi-plots showing mean \pm SD values of the littoral benthic macroinvertebrates (LBMI), zooplankton (ZPL) and profundal benthic macroinvertebrates (PBMI). Ellipses show the core isotopic area of different fish species and are presented with abbreviations: *AC* Arctic charr, *LT* lake trout, *P* pike, *B* burbot, *BT* brown trout, *PE* perch, *G* grayling, *SB* nine-spined stickleback, *AB* alpine bullhead, *V* vendace, *M* minnow, *LSR* large sparsely rakered whitefish, *LDR* large densely rakered whitefish, *SSR* small sparsely rakered whitefish, *DR* densely rakered whitefish. Kilpis and Raha have charr and monomorphic whitefish, Muddus and Inari have charr and polymorphic whitefish and control lakes Vuontis (monomorphic whitefish) and Paadar (polymorphic whitefish) do not have charr in the fish community



However, lakes of this size typically support a more diverse range of prey species of varying body sizes, further complicating trophic interactions. This may open an avenue for a small proportion of charr to make a shift to piscivory, ultimately allowing them to prey on their whitefish competitors, further increasing the complexity of interactions between the two species in these systems. In addition, large lakes are generally cold-water environments, where charr may benefit compared to whitefish due to its better growth potential at low temperatures (Siikavuopio et al., 2010). We acknowledge that in small lakes with limited habitat and prey availability, whitefish

introductions can be deleterious to charr populations (Svårdson, 1976). In three of the charr lakes, littoral habitats had abundant populations of Eurasian perch (*Perca fluviatilis* L.) and grayling (*Thymallus thymallus* L.), which are both likely resource competitors for juvenile charr (Eloranta et al., 2011; Sandlund et al., 2010, 2016). Furthermore, pelagic and littoral habitats, especially in polymorphic lakes, contained piscivorous brown trout that are direct competitors for large charr (Kahilainen & Lehtonen, 2002; Thomas et al., 2017). All charr lakes also hosted pike (*Esox lucius* L.) and burbot (*Lota lota* L.) that potentially prey on charr (Svårdson, 1976, Byström et al., 2007;

Table 4 Sample sizes of different fish species used in stable isotope analyses

Species	Kilpis	Raha	Muddus	Inari	Vuontis	Paadar
Lake type	Charr and mono-WF	Charr and mono-WF	Charr and poly-WF	Charr and poly-WF	No charr and mono-WF	No charr and poly-WF
Alpine bullhead	17	–	–	–	–	–
Arctic charr	30	30	14	30	–	–
Brown trout	21	30	30	30	19	30
Burbot	30	13	20	30	21	9
Grayling	26	–	23	27	8	7
Lake trout	–	–	–	30	–	–
Minnow	12	–	–	–	–	–
Nine-spined stickleback	–	–	–	30	5	9
Perch	–	30	30	30	30	30
Pike	30	6	30	25	28	3
DR whitefish	–	–	30	30	–	30
LDR whitefish	–	–	30	30	–	30
LSR whitefish	120	105	30	30	80	30
SSR whitefish	–	–	30	30	–	30
Vendace	–	30	–	30	–	–
Total sample size	286	244	267	382	191	208

Knudsen et al., 2010). Obviously the high resource competition and predation regimes may have contributed to low charr density in the littoral and pelagic zones, and induced a shift by charr to profundal habitats in these lakes.

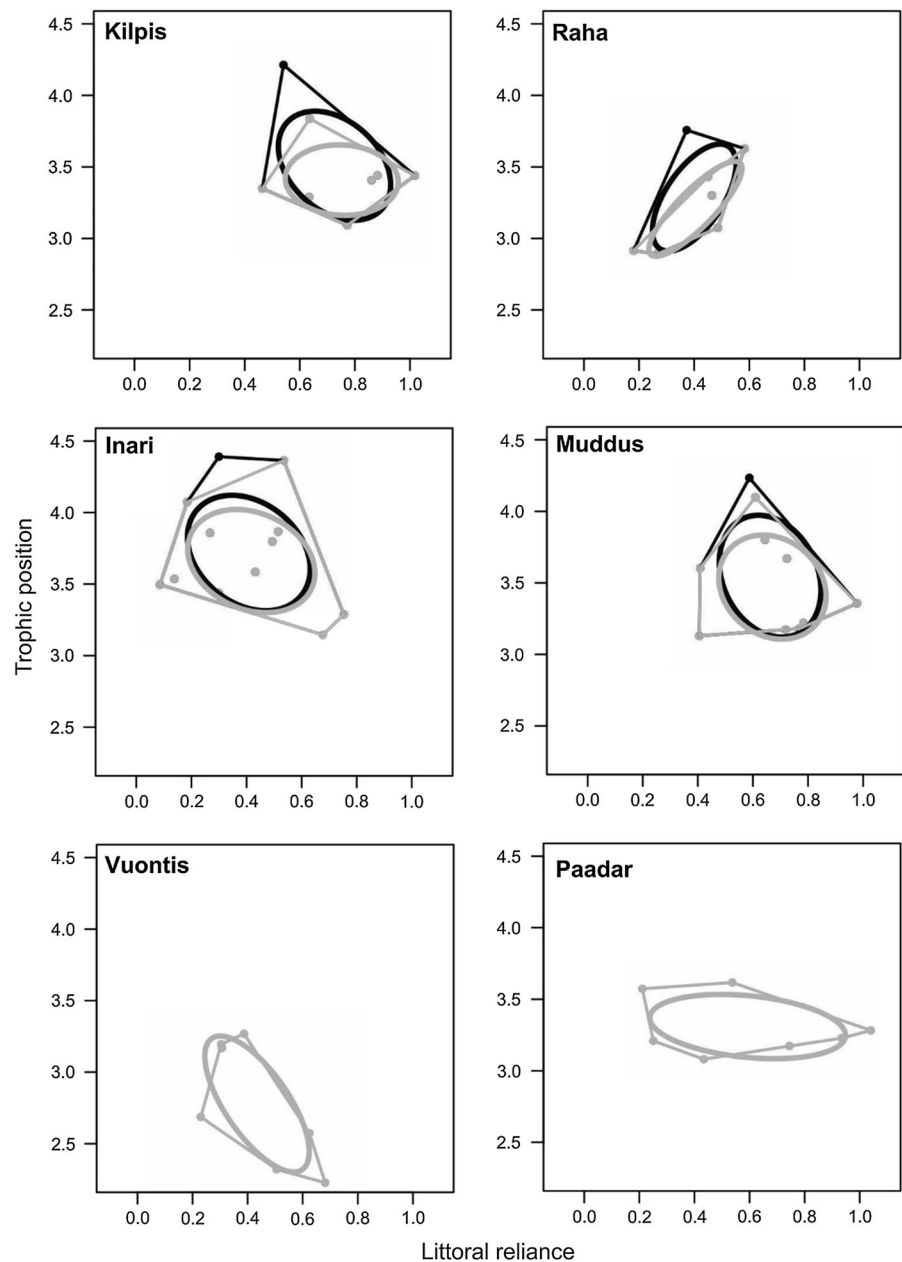
Prediction 1: large-bodied charr as a piscivore in multispecies fish communities

Availability of several small-bodied prey fishes likely facilitated the population-level shift of charr to piscivory at 15–25 cm total length. This length at the shift to piscivory is within the range found in other charr lakes, as well as those found in other piscivorous salmonids (L’Abee-Lund et al., 1992; Amundsen, 1994; Mittelbach & Persson, 1998). The shift to piscivory in all studied charr lakes was associated with fast growth, large maximum size, and late maturation age. In charr lakes, especially in Kilpis, charr growth and maturation size were more similar to the situation found in warmer lakes at lower latitudes, where charr rely on vendace and smelt (*Osmerus eperlanus* L.) as principal prey resources (Hammar, 2014; Hammar et al., 2018). These prey species were not present or native in our subarctic study lakes, in which whitefish

was an important food source for all populations. While the mean prey size was typically < 10 cm, some fish consumed larger prey (up to 25 cm), which were typically whitefish as has been observed in previous studies of charr diet in multispecies lakes (Amundsen, 1994; Hammar, 2014; Hammar et al., 2018).

Small charr preferred small-bodied prey-fish, such as alpine bullhead and nine-spined stickleback. Based on charr diets, these species are potentially abundant in lakes, but their abundance cannot be assessed from gill-net catches due to their small size, slow swimming speed, and low catchability (Malinen et al., 2014). At a larger size, charr used the most available prey-fish, namely coregonid fishes (Eloranta et al., 2015b). The pelagic density of coregonid prey ranged from 80 LSR whitefish per hectare in Kilpis up to 670 DR whitefish per hectare in Muddus (Malinen et al., 2014). In Inari and Raha, pelagic prey-fish density, vendace, whitefish, and their hybrids, reached 390 per hectare in both lakes (Kahilainen et al., 2011; Malinen et al., 2014; Thomas et al., 2016). Prey selection of the most abundant prey in multispecies lakes is typical for charr (Amundsen, 1994; Kahilainen & Lehtonen, 2002; Hammar et al., 2018). However, because charr

Fig. 3 Stable isotopic diversity of the fish communities based on total area (convex hull) and core area (ellipse) with (black line) or without (gray line) including the data for charr. Each point represents the mean value for one fish species. Kilpis and Raha have charr with monomorphic whitefish, but Muddus and Inari have charr with polymorphic whitefish. Please note that Vuontis (monomorphic whitefish) and Paadar (polymorphic whitefish) are not inhabited by charr and presented as control lakes



preferred benthic habitat in all lakes, pelagic prey-fish density may not directly reflect benthic prey availability, especially of benthic LSR whitefish that could be better assessed using gill-net CPUE (Malinen et al., 2014). While cannibalism by charr is common, especially in small lakes with low species diversity, cannibalism was only observed in Kilpis, perhaps because other prey species are generally more abundant and profitable to feed on in multispecies lakes

(Amundsen, 1994; Kahilainen & Lehtonen, 2003; Eloranta et al., 2015a). Strict selection of one or two abundant prey species was also evident based on the generally narrow dietary breadth of charr.

A strong preference for LSR whitefish prey in monomorphic whitefish systems was also indicated by rapidly increasing numbers of *Diphyllbothrium* spp. cysts in the stomach wall of piscivorous charr. This parasite can re-establish infections in salmonid top

Table 5 Food-web metrics derived from stable isotope data (Layman et al., 2007; Jackson et al., 2011) including trophic position (TP) range, littoral reliance (LR) range, total convex hull area (TA), mean distance to centroid (CD), mean nearest-

neighbor distance (NND) and standard deviation of mean nearest-neighbor distance (SDNND) and core stable isotopic diversity area of fish community (SEAc)

Metric	Kilpis			Raha			Inari			Muddus			Vuontis	Paadar
	No charr	Charr	$\Delta\%$	No charr	Charr	$\Delta\%$	No charr	Charr	$\Delta\%$	No charr	Charr	$\Delta\%$	No charr	No charr
TP range	0.75	1.12	50.5	0.74	0.87	17.5	1.22	1.25	2.2	0.97	1.10	13.9	1.04	0.54
LR range	0.55	0.55	0.0	0.40	0.40	0.0	0.67	0.67	0.0	0.57	0.57	0.0	0.45	0.83
TA	0.21	0.32	51.0	0.10	0.19	97.6	0.48	0.52	8.1	0.33	0.36	10.9	0.23	0.27
CD	0.25	0.33	34.9	0.28	0.31	10.9	0.35	0.38	8.6	0.35	0.39	12.0	0.42	0.35
NND	0.18	0.20	8.6	0.15	0.16	9.1	0.18	0.17	- 6.9	0.18	0.16	- 11.5	0.18	0.22
SDNND	0.15	0.14	- 6.9	0.07	0.07	6.6	0.11	0.07	- 35.4	0.12	0.10	- 12.7	0.14	0.09
SEAc	0.16	0.23	44.4	0.09	0.14	50.6	0.25	0.27	6.7	0.22	0.24	9.5	0.20	0.24

In charr lakes, we included values to represent estimates including (Charr) and discounting charr (No charr) and the resulting proportional difference in values (%). Kilpis and Raha host charr and monomorphic whitefish populations, in contrast to Inari and Muddus which host charr and polymorphic whitefish populations. Vuontis (monomorphic whitefish) and Paadar (polymorphic whitefish) are lakes lacking charr and are presented as control lakes

predators after being ingested in its original coregonid host (Hammar, 2000; Henriksen et al., 2016). Parasite abundance was higher in charr foraging on monomorphic LSR whitefish in Kilpis and Raha (this study, Kahilainen et al., 2011; Hayden et al., 2014), as compared to Inari, where charr fed on a larger variety of prey fishes. This reflects a more direct energy flow from copepods to LSR whitefish, and finally to charr, in monomorphic whitefish systems, as compared to the case in polymorphic whitefish lakes that have more complex prey-fish communities and food-web structures. From a parasite transmission point of view, generalist monomorphic whitefish provide a straight pathway to the next trophic level through charr, whereas in polymorphic systems, several potential intermediate hosts are available, so the probability of parasites encountering a final avian host (gulls and divers) is likely lower. Specialist zooplanktivores in polymorphic whitefish lakes, such as pelagic whitefish morphs and vendace, could also be more resistant to *Diphyllbothrium* spp. infections because their parasite abundance and prevalence was generally much lower than observed for LSR whitefish in monomorphic lakes (Kahilainen et al., 2011; Hayden et al., 2014).

Prediction 2: the role of piscivorous charr in lake food webs

Stable isotopes indicated that charr were the only, or among the main top consumers, in all charr lakes. In lakes with monomorphic whitefish, inclusion of charr clearly increased total area and core isotopic diversity area of the whole fish community relative to Muddus and Inari with polymorphic whitefish populations. The latter lakes had many other predators (e.g., brown trout, burbot, pike, and lake trout) with similar trophic positions to charr, and as a result exclusion of charr did not substantially alter the isotopic niche areas of these fish communities. The difference between lake types was also evident from contrasting patterns of nearest-neighbor distances that were higher in lakes with monomorphic whitefish than in lakes with polymorphic whitefish. This indicates that polymorphic lakes not only have more piscivorous species sharing the top consumer position with charr, but also a wider array of prey-fish (species or ecomorphs). Simpler monomorphic whitefish lakes therefore seem to have more direct food-chains than those in polymorphic whitefish systems. Food-chain length was also generally shorter in lakes without charr. For example, Vuontis (monomorphic whitefish population) has many

predators (pike, burbot, and brown trout) sharing the top consumer position, and thus energy flow is less direct. In contrast, Paadar (polymorphic whitefish) showed less consistent patterns of piscivores, the overall food-web shape was more horizontal than vertical, and there were multiple energy flow pathways.

Our food-web data suggest that the role of large charr as top consumer varies in different lake types. The role as apex predator seems to be most pronounced in Kilpis and Raha, which are both deep lakes with simple prey-fish communities dominated by monomorphic LSR whitefish. These lakes have limited littoral foraging or spawning habitat available for competing piscivores such as pike and brown trout. Top-down regulation by charr is likely strong in both lakes, inducing strong fluctuations of LSR whitefish populations (Kahilainen et al., 2011; Hayden et al., 2014). Piscivory by cold-water adapted charr can be an important source of mortality in late winter and spring when they are more active than their main prey, i.e., LSR whitefish (Siikavuopio et al., 2010). The deep and cold subarctic lakes with monomorphic whitefish have zooplankton communities dominated by copepods, and sheltered soft-sediment habitats harboring abundant benthic macroinvertebrate sources are scarce. Such lake ecosystems reduce the opportunities for morph divergence (Harrod et al., 2010; Hayden et al., 2014). These low diversity conditions have resulted in more direct energy flow in the food-web. They are also prone to population fluctuations across different trophic levels (copepods, LSR whitefish, charr and parasites), making them highly unstable over time as is typical for many Arctic ecosystems (e.g., Hanski et al., 1991; Jepsen et al., 2008). In contrast, higher diversity systems, such as lakes with polymorphic whitefish, have more links and various energy flow pathways to top consumers, making them less prone to fluctuations (MacArthur, 1955; Hutchinson, 1959; Polis & Strong, 1996). Lakes with polymorphic whitefish are associated with a more diverse piscivore fish assemblages within which individuals commonly attain large body-sizes, suggesting that ecological speciation by whitefish has food-web consequences (Thomas et al., 2017). Potentially, the divergence of prey could promote the divergence of predators (Brodersen et al., 2018), but testing this assumption would require considerable research, particularly in large lakes with high habitat availability.

Climate change implications and future of large charr

Climate warming is occurring markedly faster in subarctic and Arctic regions than the global average (Rolls et al., 2017). Climate change is associated with increased nutrient inputs to lakes from surrounding catchments, and invasions by new warm- and turbid-water adapted species have been related to probable local extinction of charr (Hayden et al., 2017). Such invasions are likely important in both high and low diversity systems because the addition of new key species, like vendace, can have considerable ecosystem-level consequences (Bøhn et al., 2008; Kahilainen et al., 2011; Thomas et al., 2016). Increased lake temperature and productivity are also expected to reduce oxygen concentrations in the profundal zone, thereby further squeezing the niche space of charr (Lehtonen, 1996; Guzzo et al., 2017). In addition, polymorphic fish populations are especially susceptible to eutrophication and new species invasions that often lead to local extinction via reverse speciation (Taylor et al., 2006; Vonlanthen et al., 2012; Bhat et al., 2014). All these combined stressors could change the oligotrophic top-down controlled lake ecosystems with long food-chains to bottom-up controlled systems with shorter food-chains where fish communities are exclusively dominated by abundant, small-sized, warm-adapted non-salmonid species (Hayden et al., 2017).

Conclusions

Large piscivorous charr are important apex predators in multispecies subarctic communities. They have an especially important functional role in the species-poor lakes with simple food webs, which are often dominated by monomorphic whitefish. In these lakes, exclusion of charr reduced the stable isotopic area of the fish community by reducing the food-chain length, whereas such effects were less pronounced in systems with more diverse fish fauna (polymorphic whitefish lakes). However, more detailed long-term studies in both lake types are needed for a detailed assessment of the top-down role of charr in whitefish dominated systems. Assessments of how divergence of one species affects other trophic levels, including potential divergence, are also needed. The overall low

abundance of charr in the fish communities studied here suggests that management control of new stressors, such as land-use change, introductions, or the invasions of new species will be needed to maintain the remaining large-bodied charr populations in subarctic Fennoscandia. Moreover, understanding the role of charr in subarctic lakes at present may help to better predict how such systems could change if charr were to become locally extinct as a result of climate change or other anthropogenic factors.

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