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Littoral resources, food chain length and top predator size - Are these connected with lake size?

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ABSTRACT

The size of a lake ecosystem sets many direct and indirect physical limits for habitats available for different food web compartments as well as the taxa inhabiting these. We tested the hypotheses that 1) reliance of fish on littoral resources increase in lakes with shoreline development, and 2) food chain length and 3) top predator size increase with lake size. We analyzed food web trophic structure, based on stable isotope analyses (SIA) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), in six boreal lakes in southern and eastern Finland (area 0.13–567 km²). We also applied data from gillnet monitoring of two common predatory fish, perch (*Perca fluviatilis*) and pike (*Esox lucius*), in >100 lakes as well as data from national large pike (weight > 10 kg) competition. Our results based on SIA did not support the first two hypotheses. Mixing-model results indicated great contribution of littoral resources for many fish, however, showing considerable within-taxa variation for some species. Fish reliance on littoral resources was not directly related to lake shoreline development. The lakes had four trophic levels and large predators coupled both littoral and pelagic habitats. The very rare freshwater pinniped, Saimaa ringed seal (*Pusa hispida saimensis*), shared the same trophic position with piscivorous fish. However, we found some support for the third hypothesis. The maximum size of perch was positively correlated with lake size, and the majority (88 %) of very large pikes (>10 kg) were caught from lakes with the area > 1 km², indicating habitat size importance for large predators.

1. Introduction

Ecosystem size and primary productivity have crucial impacts on energy flow, trophic structure, diversity and biotic interactions in aquatic food webs. The early food-web theories by Elton (1927) and Lindeman (1942) focused mainly on productivity, energy flow and trophic transfer efficiency in ecosystems. Although all consumers are dependent on primary producers for energy and essential nutrients, later analyses have shown that productivity alone seems not to be a major factor influencing trophic structure and food-chain length in aquatic ecosystems (e.g. Pimm, 1982; Hairston and Hairston, 1993; Post et al., 2000; Vander Zanden and Fetzer, 2007). In many aquatic food web analyses, ecosystem size (especially volume) has been found as a good predictor for the food-chain length and success of top-predator populations (Post et al., 2000; Post, 2007; Takimoto and Post, 2012;

Griffiths, 2013). However, food-chain length hypotheses also including productivity with habitat heterogeneity (Persson et al., 1992; Thompson and Townsend, 2005; Tunney et al., 2012) or space i.e. 'productive space hypothesis' (Schoener, 1989; Vander Zanden et al., 1999; Doi et al., 2009), fish species richness (Rasmussen and Vander Zanden et al., 1999, Eloranta et al., 2015), and the role of disturbance (Takimoto and Post, 2012; Terui and Nishijima, 2019) are widely tested and debated in the literature (see also Ward and McCann, 2017 with more references).

Current understanding on aquatic food web structure and energy flow largely bases on results of stable isotope analyses (SIA) (e.g. Fry, 2006; Layman et al., 2012; Gilbert et al., 2019), applied in mixing models (e.g. Phillips and Gregg, 2001; Parnell et al., 2010; Phillips et al., 2014). Stable carbon isotope ratios ($\delta^{13}\text{C}$) are widely used for estimating diet origin in consumers, e.g. contribution of littoral vs. pelagic (France, 1995; Hecky and Hesslein, 1995; Post, 2002; Parnell et al., 2010),

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autochthonous vs. allochthonous (Grey et al., 2001; Rautio et al., 2011) and methane-based vs. pelagic carbon origin (Kiyashko et al., 2001; Jones and Grey, 2011). However, overlapping values, more than two diet sources and possible lipid correction for $\delta^{13}\text{C}$ values in the calculations can yield equivocal mixing model results (Fry, 2013; Brett, 2014; Arostegui et al., 2019). The knowledge of the heavier ^{15}N isotope enrichment in the food chain ($\delta^{15}\text{N}$) is successfully applied in estimating biomagnification of contaminants (Cabana and Rasmussen, 1994; Borgå et al., 2012), food web length and trophic position of an organisms in the food web (e.g. Peterson and Fry, 1987; Post et al., 2000; Vander Zanden and Rasmussen, 2001; Post, 2002). The $\delta^{15}\text{N}$ values of primary producers, i.e. food-web baseline, is strongly influenced by the utilized nitrogen sources, which is crucial for estimating a consumer position and the food web length in an ecosystem (Post, 2002; Kendall et al., 2007; Guiry et al., 2020). In addition, nitrogen concentration in water, omnivory, starvation and variation in ^{15}N enrichment at different food-chain levels also cause challenges for the estimates (Hansson et al., 1997; Perga and Gerdeaux, 2005; Bunn et al., 2013; Gilbert et al., 2019; Trochine et al., 2019). Therefore, the trophic position and food chain length estimates need to be baseline-corrected for each lake (Post, 2002).

Predators at the top of the trophic pyramid usually have greater demands for habitat and home range size, and large-bodied predators forage on larger spatial areas than consumers at lower trophic levels (Woolnough et al., 2009; McMeans et al., 2016). In a dataset collected from 387 North American lakes, Griffiths (2012, 2013) found support for the hypothesis that the mean and maximum size of fish as well as their trophic level will increase along with lake size, and the shape of body size distribution will change from unimodality towards bimodality because of greater relative importance of large predatory species in large lakes. However, he concluded that also postglacial recolonisation and evolutionary change are important determinants of body size distributions at regional or larger scales (Griffiths, 2012, 2013). A significant relationship between trophic position and animal body size in aquatic ecosystems was also found by Potapov et al. (2019), who analyzed available $\delta^{15}\text{N}$ data and phylogeny of marine, freshwater and terrestrial food webs (1093 taxa with baseline-calibrated $\Delta^{15}\text{N}$ values and average body mass). In marine systems, main primary producers are unicellular eukaryotic algae and small pelagic primary consumers can effectively graze whole algae (Kjørboe, 2011). Accordingly, the consumer body size and trophic position are strongly correlated in marine food chains, which are based on unicellular algae. For freshwater ecosystems, the authors found a significant but a weaker correlation than in marine systems, but in terrestrial ecosystems, based on primary producers of various body size and type, no such correlation was found (Potapov et al., 2019). Vertebrates commonly occupy higher trophic positions than invertebrates both in aquatic and terrestrial systems (Riede et al., 2011). However, large mammals are typical primary consumers in terrestrial ecosystems (Price and Hopkins, 2015), and also appear as secondary consumers, like krill-feeding blue whales (*Balaenoptera musculus*), in the oceans (Miller et al., 2019).

Although many mammals like Eurasian river otter (*Lutra lutra*), American mink (*Neovision vision*), bears (*Ursus* spp.), exploit freshwater resources, large mammals living solely in freshwater environments are few. Among over 30 species of marine pinnipeds, only two species, ringed seal (*Pusa hispida*) and harbor seal (*Phoca vitulina*), occupy freshwater or brackish habitats. In total five seal stocks live more or less permanently in freshwater lakes or rivers (Sipilä et al., 1996; Smith et al., 2006; Hauser et al., 2008; Losey et al., 2023). One of those is the population of Saimaa ringed seal (*P. h. saimensis*), living in the large basins of Lake Saimaa system, eastern Finland (Kunnasranta et al., 2020). The rare and endangered seal population was isolated after land uplift since last glaciation in the shallow lake system, characterized by very long shoreline with a mosaic of islands and bays (Nyman et al., 2014).

Lakes of a wide size variation (<0.1 to >100 km²) are typical ecosystems in the boreal landscape (Downing et al., 2006; Verpoorter et al.,

2014) and the number of lakes decreases with lake size. For example, in Finland, the number of lakes with an area 0.0005–0.1 km² is ca. 170,000, those in the size classes 0.1–10 and 10–100 km² are 13,114, and 2283, respectively, and there are 47 lakes with an area > 100 km² (Raatikainen and Kuusisto, 1988). Large lakes are typically deeper than small ones, have more variable habitats and overall higher number of species (Barbour and Brown, 1974). The relative importance of littoral area of the whole lake area varies according to lake size, depth profile and shoreline length and development (Wetzel, 1990; Vadeboncoeur et al., 2008; Dolson et al., 2009; Alahuhta et al., 2012). As a continuum from terrestrial to aquatic environment and maintaining primary producers of many life forms, the heterogeneous littoral areas are very important habitats for diverse invertebrate and vertebrate consumers and their predators, especially at the juvenile stage (Tolonen et al., 2003; Winfield, 2004; Strayer and Findlay, 2010).

We analyzed food web structure, littoral vs. pelagic carbon contribution and food chain length in boreal lakes, based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of different food web compartments collected from pelagial, littoral and profundal zones of six lakes within a size gradient ranging from 0.1 to 567 km². The trophic status of the lakes varied between oligotrophy and mesotrophy. Saimaa ringed seal inhabits the two largest lake basins of this study. Large European perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) are the two most typical piscivorous fish in the boreal lakes (Tammi et al., 2003). Thus, we combined food-web SIA information from the six lakes with wider national monitoring data available for the abundance and size of perch and pike in more than 100 lakes within the same size range, located similar latitudes in southern and eastern Finland, and having similar total phosphorus concentration (<50 $\mu\text{g L}^{-1}$) and water color (<90 mg Pt L⁻¹). In addition, we apply data of very large (>10 kg) pikes caught by recreational anglers during the years 2002–2020 from lakes in Finland.

Our study questions and hypotheses were:

- 1) How littoral contribution in fish diets vary with lake size and littoral habitat availability? We hypothesize that the proportion of littoral resources in the diets will increase with shoreline development of the lakes.
- 2) Does food chain length increase with lake size? We test the hypothesis by Post et al. (2000) by using lake area and shoreline development as proxies.
- 3) Will larger lake area maintain larger piscivores? Lake size and habitat diversity are crucial factors for the survival and growing of top predator populations. We hypothesize that larger lakes support bigger top predators.

2. Material and methods

2.1. Study lakes

Food web compartments were sampled and analyzed from six lakes in southern and eastern Finland, varying in area (0.1–567 km²) and depth (max. 5.5–74 m, Table 1). The dataset consists of two oligotrophic clear-water lakes (Kastanjärvi and Säynjälvi), two mesotrophic lakes (Kaukasjärvi and Ormajärvi) and two large oligotrophic basins (Paasivesi and Haukivesi, OECD criteria applied for trophic status). Paasivesi is a sub-basin of Lake Orivesi, which together with Lake Haukivesi belong to hydrologically interconnected Lake Saimaa, having a total area of 4380 km². Data for lake water chemistry are from HERTTA database of Finnish Environment Institute (https://www.syke.fi/en-US/Open_information). All the lakes are dimictic having a clear temperature stratification during summer. Shoreline development index, potentially indicating the importance of littoral communities was estimated according to Seekell et al. (2022). The coverage of forests and agricultural area in the lake drainage area was determined with VALUE tool (<http://paikkatieto.ymparisto.fi/value/>), using CorineLandCover2012_20m database).

Table 1

Location (littoral sampling sites of Paasivesi and Haukivesi within brackets), morphological and chemical properties of the six study lakes and main characteristics of their catchments. Data for lake morphometry and water chemistry are from HERTTA database of Finnish Environment Institute (https://www.syke.fi/en-US/Open_in_formation) and for catchments estimated with VALUE tool (<http://paikkatieto.ymparisto.fi/value/>, using CorineLandCover2012_20m database). ¹⁾ catchment area of the whole Lake Orivesi.

	Kaukasenjärvi	Kastanajärvi	Säynäjärvi	Ormajärvi	Paasivesi	Haukivesi
Latitude (°N)	61°10.11'	61°13.42'	61°16.01'	61°05.94'	62°08.38' (62°07.23')	61°57.90' (61°59.30')
Longitude (°E)	24°54.19'	24°46.25'	24°52.01'	24°46.25'	29°20.15' (29°20.59')	28°43.80' (28°46.23')
Area (km ²)	0.128	0.333	0.429	6.57	124	567
Mean depth (m)	3.9	3.5	5.5	9.6	21	9.1
Max. depth (m)	5.5	6	20	29	74	55
Shoreline length (km)	1.4	3.3	3.9	16.2	185.8	2398.0
Shoreline development index	1.5	1.9	1.9	1.4	2.4	11.7
Volume (10 ⁹ m ³)	0.5	1.2	2.3	63	2604	5114
Catchment area (km ²)	6.6	3.0	2.2	75	27599 ¹⁾	50,149
Agricultural land% of the catchment	20	0	1	26	4	6
Forests% of the catchment	57	70	68	47	62	61
O ₂ saturation% at the bottom	9	56 ± 10.1	28 ± 12	16 ± 13	80 ± 9	78 ± 13
Tot P (µg L ⁻¹)	30	6 ± 1	7 ± 3	22 ± 3	7 ± 1	8 ± 2
TotN (µg L ⁻¹)	950	355 ± 13	340 ± 17	950 ± 168	401 ± 40	420 ± 40
pH	6.7	6.7 ± 0.2	6.7 ± 0.1	7.3 ± 0.4	7.0 ± 0.2	7.0 ± 0.2
Color (mg Pt L ⁻¹)	80	19 ± 3	17 ± 7	35 ± 18	50 ± 13	40 ± 9

2.2. Sampling protocol

Food web compartments were sampled once during the growing season. Lakes Kaukasenjärvi and Kastanajärvi were sampled in August–September 2004, whereas Säynäjärvi and Ormajärvi were sampled in July–August 2005. The two largest lake basins, Haukivesi and Paasivesi, were sampled in early September 2008. For these two lake basins, additional fish and Saimaa ringed seal data were obtained from the previous study (Auttila et al., 2015).

In the four smallest lakes, pelagic and profundal samples (seston <50 µm, zooplankton, profundal benthos, sediment) were taken from the middle of the lake and in two largest lakes in the deeper part of the lake. The littoral compartments (macrophytes, periphyton, sediment, zooplankton, macroinvertebrates) were collected at least from three sites around the lake. In the two largest lakes, respective samples were taken from one pelagic site and from three sites on a shore area typical for the lake basin (see Table 1 for coordinates).

2.2.1. Seston <50 µm

Seston samples were taken with Limnos water sampler from the euphotic zone (0–2 m) and filtered through a 50 µm net into 3–5 replicate buckets, which were transported to laboratory for concentrating for stable isotope analyses. For the four smallest lakes, particles <50 µm were collected on 10 µm net from which the biomass was scraped on to aluminum foil cups for drying. For the two largest lakes 3–5 L water was filtered on pre-ignited Whatman GF/D glass-fiber filters (nominal pore size ca. 2.7 µm), and the filtrate was re-filtered on GF/F (nominal pore size 0.7 µm). Biomass in aluminum cups (four smallest lakes) and filters (two largest lakes) were dried at +60 °C for 24 h and the dried material was scraped into small tin cups. Dry matter for the three smallest lakes proved to be too low for replicate analyses and, thus, these were pooled for one sample per lake. No result for the seston of Ormajärvi was obtained.

2.2.2. Zooplankton

Zooplankton from littoral areas and from the pelagic area of the two smallest lakes were taken as 3–5 horizontal hauls (ca. 3–10 m) of net with a mesh size of 100 µm. In the other lakes pelagic zooplankton samples were collected as 3–5 vertical hauls from ca. 2 m above the bottom to surface. The samples were stored as frozen (–18 °C). After storage the samples were carefully defrosted on ice and major taxonomical groups (Cyclopoida, Calanoida, filter-feeding Cladocera and occasional predatory cladocerans *Polyphemus pediculus* and *Leptodora*

kindtii) were separated under a microscope using tweezers and picked into small pre-weighed tin cups for drying. The analyzed dry mass per sample varied between 0.2 and 0.8 mg.

2.2.3. Littoral macrophytes and periphyton

At least three shoots of predominant emergent and submersed plant taxa were cut above the littoral sediment surface of each lake. In the laboratory, periphyton on the plant surface was washed away and the plants were dried at +60 °C at least 24 h.

In the four smallest lakes periphyton samples were taken by cutting submerged parts of at least three shoots of the predominant plant taxa. The shoot pieces were put into jars with a mixture of 0.5 L filtered (0.2 µm) lake water and MQ-water and transported to the laboratory. The shoot surfaces were gently brushed into the water in the jars and large particles and animals were removed by filtering the water through a 500 µm net. Periphyton was filtered on 10 µm filters, from which the biomass was scraped into aluminum foil cups for drying at +60 °C for 24 h. In the two largest lakes, periphyton samples were taken from small stones located at ca. 0.5–1 m depth. The stone surface was gently brushed into MQ-water and the samples were frozen (–18 °C) in aluminum foil cups.

2.2.4. Macroinvertebrates

In the littoral zone macroinvertebrates were collected from 3 to 4 sites by kick netting and from oxic profundal zone with Ekman sampler. The samples were sieved through a 0.5 mm net and different taxonomical groups and/or functional types were separated into jars with filtered water for 4–6 h for gut evacuation and then frozen at –18 °C. In the deepest Lake Paasivesi pelagic macroinvertebrate (*Mysis relicta* and *Gammaracanthus lacustris*) samples were also taken as horizontal hauls with a Hydrobios MultiPlankton Sampler from the depth of 45 m (see Salonen et al., 2019).

2.2.5. Sediment

Sediment samples were taken with a Kajak gravity corer from the profundal zone (3–5 replicates, deepest point of the lake) of each lake and with an acrylic plastic tube from the littoral of the two largest lakes. Only the oxic surface layers were taken for δ¹⁵N and δ¹³C analyses, i.e. the uppermost 0.5 cm of the four smallest lakes and 0–1 cm layer of the two largest lakes.

2.2.6. Fish

To get fish samples for SIA in the four smallest lakes, fish were caught with Nordic standard gillnets (6–8 nets/lake, overnight fishing with

approximately 12 h soaking time) for catching predominant species (Olin et al., 2013), i.e. perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), bleak (*Alburnus alburnus*; only in Lake Ormajärvi) to cover the size distribution of population. Few individuals of pike (*Esox lucius*) caught in the nets were also taken for analyses. In the two largest lakes, benthic fish samples for SIA were caught with a net series of mesh sizes of 16, 30, 35, 45 and 55 mm and for catching pelagic species, vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*), a net series with mesh sizes 8, 10, 12, 14, 16, 18 and 22 mm were used in epilimnion. Nets were set overnight (ca. 12 h) and captured fish were immediately euthanized with sharp blow on head. The actual fishing licenses were obtained from lake owners and from Regional Centre of Economic Development, Transport and Environment, and all treatments were done according to Finnish fishery legislation. All captured fish were identified, measured for total length (1 mm accuracy) and weight (0.1 g) and samples of dorsal muscle were dissected and stored at -18°C in aluminum foil.

2.3. Stable carbon and nitrogen isotope analyses

All fresh and/or frozen material was dried at $+60^{\circ}\text{C}$ (24 or 48 h) and homogenized if necessary, using a plant mill (macrophytes) or mortar and pestle (macrophytes, periphyton, macroinvertebrates, fish muscle). Small amounts of homogenized samples (plants ca. 1.5 mg, animals 0.5–1 mg, sediment 5–6 mg) were weighted and encapsulated into small tin cups (2–3 replicates), which were stored in a desiccator before isotope analyses.

Stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses of major ecosystem compartments for the four smallest lakes were done with an elemental analyzer Flash EA 1112 (Italy) coupled with isotope ratio mass spectrometer Thermo Finnigan Advantage IRMS (Germany) at the Department of Environmental and Biological Sciences in Kuopio (University of Eastern Finland) and for the two largest lakes with the similar instruments at the Department of Biological and Environmental Sciences (University of Jyväskylä). Internal laboratory working standards consisted of dried and homogenized potato leaves (for plants) and fish muscle tissue (for fish and invertebrates). The results are expressed as ‰ relative to the international IAEA standards Pee Dee belemnite for C and atmospheric nitrogen for N (precision 0.2 ‰ and 0.3 ‰, respectively). In addition, for obtaining more comprehensive picture of the food webs of Lakes Haukivesi and Paasivesi, we also apply data on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of Saimaa ringed seal and fish analyzed with the same instrument at the Department of Biological and Environmental Science (University of Jyväskylä), originally sampled during the years 2010–2011 for supporting Saimaa ringed seal diet analyses (see Auttila et al., 2015).

2.4. Perch and pike abundance and size

Because perch and pike appear abundantly in boreal lakes and large perch individuals (≥ 15 cm perch) and all pikes are usually piscivorous (Mittelbach and Persson, 1998; Horppila et al., 2000; Haakana et al., 2007), we used available standard fish monitoring data for testing the hypothesis 3 whether top-predator individual size increase with lake area. The relative abundance and size structure of pike and piscivorous perch were obtained from standard test fishing (CEN, 2005) conducted in the SIA study lakes in 1998 (Kastanjärvi and Ormajärvi; number of gillnet nights = 18 and 52), 1999 (Kaukasenjärvi, $n = 18$), 2005 (Säynäjärvi, $n = 15$) (see also Olin et al., 2002), and 2008 (Orivesi and Haukivesi, $n = 66$ in both cases). Perch catch in each gillnet was counted and weighed (nearest g), and every individual or random sample of 30 individuals was measured for length (total length, 1 cm size class). The index of piscivorous (≥ 15 cm) perch abundance was calculated as CPUE (catch per unit effort, n gillnet night $^{-1}$). The mean length of ten largest individuals represented the maximum size of perch in the lakes.

To test the assumed relationships between lake size and piscivorous perch and pike maximum size and abundance, a larger lake set was

selected from national standard gillnet database. The 156 waterbodies for perch and 136 for pike were chosen to have similar total phosphorus concentration ($< 50 \mu\text{g l}^{-1}$), water color ($\leq 90 \text{ mg Pt l}^{-1}$) and climate conditions ($^{\circ}\text{N}$ latitude limited to $< 63^{\circ} 4' 53,648''$) following the food web SIA study lakes. As most of the lakes had several sampling years, the year closest to the sampling year-range of the original study lakes and with at least 50 perch individuals was included. Piscivorous perch abundance and maximum size were estimated as described before. Because pike is a sedentary species and not easily caught by standard gillnet monitoring during late summer (Olin et al., 2016), data collection for large pike differed from that for perch. We included only the lakes with at least three pike individuals in the catches, and for reducing variability, data of all sampling years were pooled assuming that the populations were quite stable having only minor yearly fluctuation. The largest observed individual was used as the maximum size of pike in the lakes, and CPUE of > 66 cm (total length) pike (represented 90th percentile of the total pike length data) as the index of large pike abundance. In addition, we used data available for caught, and well-documented with body size and photograph, very large pikes (> 10 kg) announced for a journal of recreational anglers (Finnish journal Metsästys ja Kalastus; <https://metsastysjakalastus.fi/kymppikerho>) reporting during the years 2002–2020 (total $n = 605$ pikes from 265 lakes). Subsequently, the lake area data for those 265 lakes was retrieved from HERTTA database of Finnish Environment Institute (https://www.syke.fi/en-US/Open_information). Unfortunately, there is no SIA data available for piscivorous fish and lake food web baselines of these CPUE or very large pike datasets.

2.5. Data analyses

2.5.1. Carbon source and food web structure

Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of different compartments were used for viewing food web structure of the studied six lakes. Because seston was sampled differently in the two largest lakes than in the four smaller ones and presumably consisted of a mixture of bacteria, phytoplankton, small zooplankton and detritus, no further analyses based on their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was done.

Contribution of littoral and pelagic sources in fish diets was estimated by using IsoError 1.04 model (Phillips and Gregg, 2001) for one isotope ($\delta^{13}\text{C}$), dual sources (littoral and pelagic). Two isotope, three-source model, including terrestrial sources and/or methane could not be applied because there were no realistic estimates for $\delta^{15}\text{N}$ values for those to be applied for each catchment and lake. Moreover, terrestrial $\delta^{13}\text{C}$ values of boreal C3-plants are typically between littoral and pelagic values (around -27 ‰) and, thus, cannot be reliably separated from those. Based on water color values ($17\text{--}50 \text{ mg Pt l}^{-1}$), the impact of terrestrial organic matter seemed not have been very prominent in the lakes with the exception of the smallest lake (Kaukasenjärvi, color 80 mg Pt l^{-1}). Because > 90 % of terrestrial C in boreal freshwaters is in dissolved form (Mattsson et al., 2005), we assumed that terrestrial impact via microbial food chain did not differ between littoral and pelagic zones.

Littoral diet sources were estimated by using 1) average $\delta^{13}\text{C}$ value ($\pm\text{SD}$) of littoral benthic invertebrates and 2) average $\delta^{13}\text{C}$ value ($\pm\text{SD}$) of littoral macrophytes and periphyton. Pelagic diet source was estimated as average $\delta^{13}\text{C}$ value ($\pm\text{SD}$) of pelagic zooplankton (see e.g. Marty and Planas, 2008; Taipale et al., 2016). The $\delta^{13}\text{C}$ values of zooplankton and benthos were arithmetically corrected for their lipid content according to Syväranta and Rautio (2010) and those of fish according to Kiljunen et al. (2006). We assumed 0.5 ‰ enrichment $\delta^{13}\text{C}$ by each trophic level (Vander Zanden and Rasmussen, 2001). Lipid-corrected values are only used in the fish diet source estimation, the other $\delta^{13}\text{C}$ results below and in the Suppl. Table 1 are shown without lipid correction.

2.5.2. Trophic position and food chain length

Trophic position (TP) of different fish species and Saimaa ringed seal as well as the food web length was estimated with the equation of Vander Zanden and Fetzer (2007):

$$TP = (\delta^{15}N_{\text{fish or seal}} - \delta^{15}N_{\text{baseline indicator}}) / 3.4 + \lambda$$

The average lake-specific $\delta^{15}N$ value of primary consumers (filter-feeding cladocerans, *Asellus aquaticus*, Ephemeroptera, Trichoptera and littoral Chironomidae), i.e. having the trophic position 2 ($\lambda = 2$), were

used as $\delta^{15}N$ baseline indicators (Suppl. Table 2). However, for two profundal habitat using fish species in the two largest lake basins, ruffe (*Gymnocephalus cernua*) and burbot (*Lota lota*), the average $\delta^{15}N$ values of macroinvertebrates ($\lambda = 3$) living in the deep profundal zone (chaoborids in both lake basins, *Mysis relicta* in Paasivesi and gammarids in Haukivesi), were used as baseline indicators.

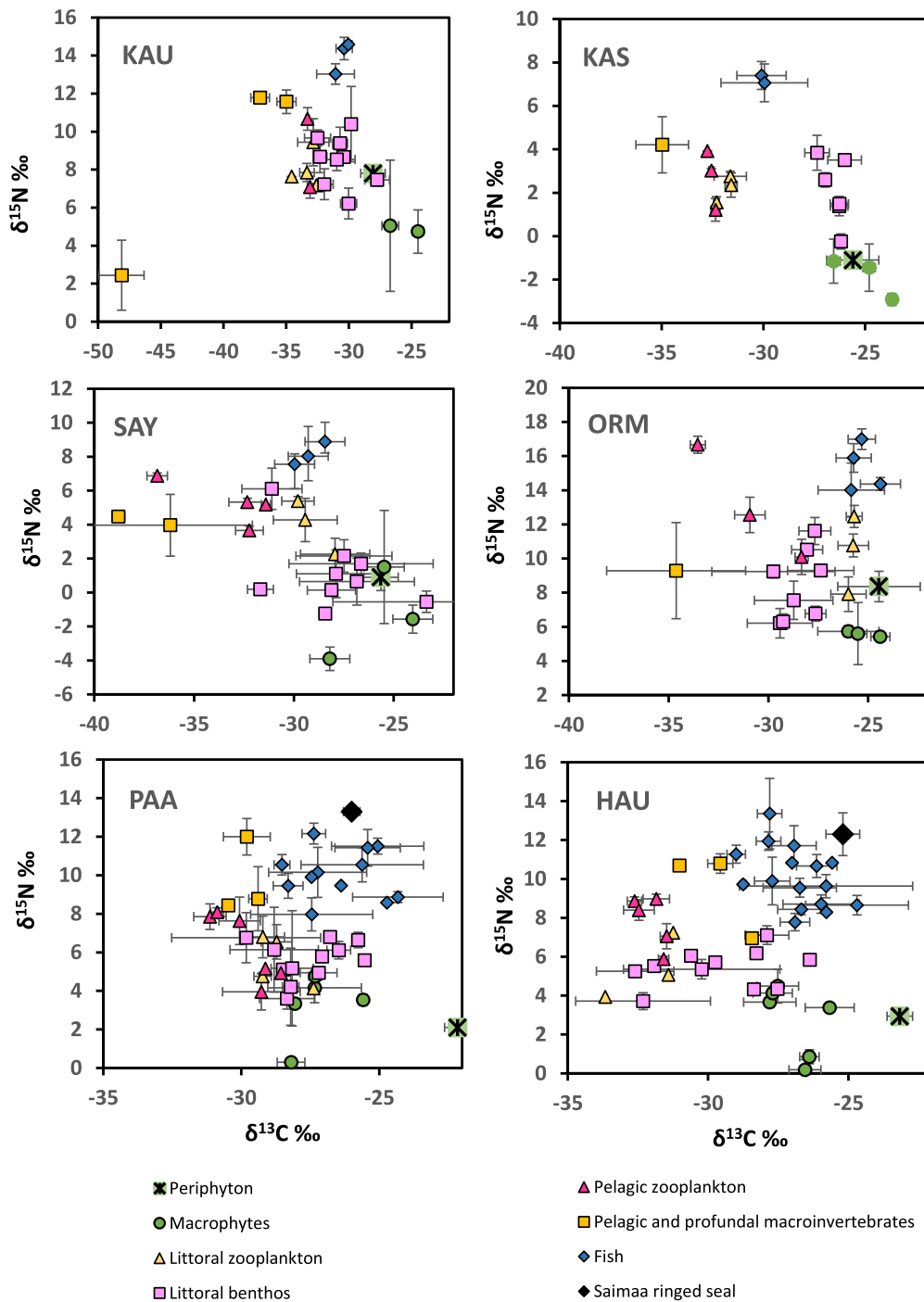


Fig. 1. Food web biplots of the six lakes, KAU = Kaukasenjärvi, KAS = Kastanajärvi, SAY = Säynäjärvi, ORM = Ormajärvi, PAA = Paasivesi, HAU = Haukivesi. The data for Saimaa ringed seal is from Auttila et al. (2015). Please note different scales of x- and y-axis.

3. Results

3.1. Primary producers and invertebrates

Biplot SIA figures (Fig. 1) of the six lakes revealed typical phenomena in lake food webs; more enriched $\delta^{13}\text{C}$ values in the littoral compared with pelagic communities, and a clear enrichment of $\delta^{15}\text{N}$ values towards higher trophic levels. Average $\delta^{13}\text{C}$ values of littoral periphyton varied between -22.2 and -28.1 ‰, which were positively correlated with lake size (Suppl. Fig. 1A). The $\delta^{13}\text{C}$ values of littoral macroinvertebrates (6–12 taxa analyzed for each lake) varied between -20.2 and -33.8 ‰. In each lake these were, in average, significantly more ^{13}C enriched (1.5–6.0 ‰) than pelagic crustacean zooplankton (t -test, $p < 0.001$ – 0.012 , for n see Suppl. Table 1). In most lakes, the $\delta^{13}\text{C}$ values of littoral and pelagic cladocerans and copepods were close to those in the pelagic zone. For some littoral macroinvertebrate taxa the $\delta^{13}\text{C}$ values overlapped with those of pelagic zooplankton. The greatest differences between pelagic zooplankton and littoral invertebrates were observed in the two oligotrophic clear-water lakes (Kastana and Säynäjärvi, 6.0 and 5.8 ‰), where the $\delta^{13}\text{C}$ values of the latter group were close to those of littoral primary producers (Fig. 1). The difference between average $\delta^{13}\text{C}$ values between littoral macroinvertebrates and periphyton increased with lake size (Suppl. Fig. 1B).

In the whole dataset, the $\delta^{15}\text{N}$ values of macrophytes, periphyton, profundal sediment and primary consumers, used as baseline indicators, were strongly correlated with each other and the proportion of agricultural area in the catchment as well as with totN and totP concentration (Table 1, Suppl. Table 3). The highest $\delta^{15}\text{N}$ baseline indicator values were obtained for the mesotrophic lakes Kaukasenjärvi and Ormajärvi (7.4 and 8.0 ‰, respectively). The $\delta^{15}\text{N}$ values of copepods were ca. 2–3.5 ‰ higher than those of filter-feeding cladocerans. Predatory invertebrates in the littoral zone, including Acari, Odonata larvae, chaoborids and hirudineans, had ca. 2–3 ‰ higher $\delta^{15}\text{N}$ values compared with taxa classified as primary consumers.

Only 1–3 taxa of pelagic and profundal macroinvertebrates were analyzed per lake. The $\delta^{13}\text{C}$ values of profundal chironomid larvae were lowest (-48.1 ± 1.8 ‰) in the smallest, mesoeutrophic lake Kaukasenjärvi, where also benthic chaoborids and ceratopogonids also had slightly lower (2–3.8 ‰) $\delta^{13}\text{C}$ values than pelagic zooplankton. In the clear-water Säynäjärvi, also the amphipod *Monoporeia affinis* had low $\delta^{13}\text{C}$ values (-38.8 ± 0.3 ‰). In the two largest lake basins the $\delta^{13}\text{C}$ values of *Mysis relicta*, *Gammaracanthus lacustris* (only in Paasivesi), gammarids (Haukivesi) and chaborids (both basins) were close to those of pelagic zooplankton.

With the exception of chironomids in Kaukasenjärvi, the $\delta^{15}\text{N}$ values in profundal chironomids and chaoborids as well as in pelagic macrocrustaceans were slightly higher (1–2 ‰) than those in littoral macroinvertebrates. However, the ^{15}N enrichment in *G. lacustris*, a glacial relict amphipod inhabiting deep zones (below 20 m) of Paasivesi, was on the same level ($\delta^{15}\text{N}$ 12.0 ± 0.8) with those of fish.

3.2. Littoral and pelagic resource utilization by fish

In fish, the $\delta^{13}\text{C}$ values varied between -24.4 and -30.4 ‰. Because we had data only for roach and perch from all six lakes, these results are given with more details below. The $\delta^{15}\text{N}$ values of roach did not increase with fish size (Suppl. Fig. 2), thus, no size-group separation was done for the data. In perch, $\delta^{15}\text{N}$ values increased significantly with fish length in each lake (Suppl. Fig. 2). Thus, perch data were grouped for those <15 cm and the larger ones, known to have a piscivorous feeding mode. In the clear-water Lakes Kastana and Säynäjärvi, the use of both average littoral macroinvertebrate and vegetation $\delta^{13}\text{C}$ values yielded very close estimates in mixing model calculations of the proportions of littoral and pelagic resources in the diets of roach and perch (Suppl. Table 4). In the other lakes, the use of littoral invertebrate $\delta^{13}\text{C}$ values yielded variable and even unrealistic >100 % proportion of littoral

resources in fish diets, presumably due to overlapping values of littoral macroinvertebrates and pelagic zooplankton. Thus, we regard $\delta^{13}\text{C}$ values based on littoral vegetation more reliable for the estimates and report these results below (Fig. 2).

In three smallest lakes, the proportion of pelagic resources was estimated to be greater than littoral resources in the diets of roach, small (<15 cm) and large perch (>15 cm), (80–90 %, 90–100 % and 56–100 %, respectively), as well as in pike (samples only from Kaukasenjärvi and Säynäjärvi, 80 and 67 %, respectively). In Lake Ormajärvi, roach was estimated to rely solely (100 %) on littoral resources and also the bulk of the diets of bleak, pike and perch originated from littoral sources (80, 63, 62 %, respectively).

In the two largest lakes, 71–97 % of the diets of small perch, pike-perch, vendace and smelt were estimated to consist of pelagic resources. For many fish species (white bream, bream, pike, ruffe, burbot, large perch, roach) the mixing model estimates showed high (>50 %) proportions of littoral origin diets or equal with those from pelagic sources. However, the confidence limits are wide and overlapping. Only in nine-spined stickleback, sampled from Lake Haukivesi, the proportion littoral diets was estimated ca. 100 % and the confidence limits did not overlap with those for pelagic resources. Littoral contribution in the diets of both perch (size classes <15 and >15 cm) and roach, the only species for which we had data for all six lakes, were not significantly correlated with lake shoreline development index ($p > 0.05$ for both species).

3.3. Trophic position of fish and Saimaa ringed seal

In the four smallest lakes, roach had slightly lower $\delta^{15}\text{N}$ values than small perch (<15 cm), thus, indicating lower trophic position (mean TP 3.7–3.9 and 3.8–4.2, respectively, Table 2). For piscivorous large perch (>15 cm) and pike, the estimates indicated TP 4.0–4.6 in these lakes. In the two large lakes, roach seemed to have a lower TP (3.0–3.2) than those in the small lakes. Bleak, rudd, and nine-spined stickleback were also approximately on the same trophic level as roach. In the two large lakes, the TP of small perch, white bream, bream (samples only from Haukivesi) varied between 3.0 and 3.6. Pelagic smelt seemed to have a slightly higher TP than vendace.

In the two large lakes, the median TP of piscivorous fish (large perch, pike, pikeperch, burbot) varied between 4.0 and 4.2, thus, being at the similar level of those in the four smaller lakes (Fig. 3). Saimaa ringed seal shared the same trophic position with piscivorous fish (TP adults 4.2 ± 0.8). The $\delta^{15}\text{N}$ value of seal pups, supported by their mothers' milk, was on average 1.2 ‰ higher than that of adult seals (see Auttila et al., 2015).

3.4. Top predator size

The maximum size of the piscivorous perch increased with lake area (Fig. 4A, linear regression, $df = 5$, $r^2 = 0.798$, $F = 15.755$, $p = 0.017$) in the six study lakes. Similar results were also obtained from the larger dataset (156 lakes) despite wide between-lake variation (Fig. 4B, linear regression, $df = 155$, $r^2 = 0.175$, $F = 32.745$, $p < 0.001$). However, the catch per unit effort (CPUE), i.e. relative fish abundance, of piscivorous perch was not related to lake area in the datasets (Suppl. Fig. 3).

In the fish monitoring data from 136 lakes, the maximum size and the CPUE of large pike (>66 cm) were not related to lake size (Suppl. Fig. 4). In the other long-term dataset collected for very large (>10 kg) pike caught by recreational anglers from a total of 265 lakes in Finland, the pike weight was not related to lake area (Suppl. Fig. 5). However, the majority (88 %) of large pikes were captured from lakes with an area >1 km² and none of them was caught in the smallest lake category (area <0.01 km²) (Fig. 5). All the largest lakes (area >100 km²) and 28 % of the lakes in the category 10–100 km² were represented in the dataset, whereas in the smaller size classes large pikes were caught in <5 % of the lakes in the respective size category (Suppl. Table 5). The smallest lakes (0.01–0.1 km², $n = 5$) from which very large pike were caught are

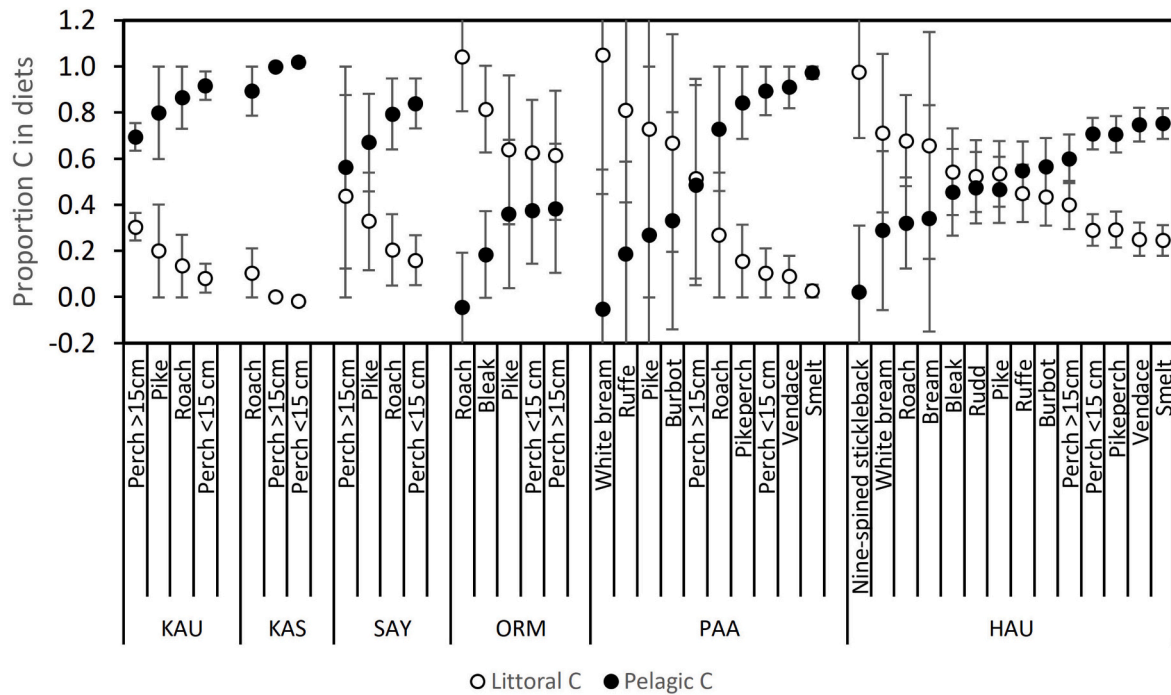


Fig. 2. Estimated (IsoError 1.04 model) average proportions of littoral and pelagic carbon in the diets of fish in the study lakes ranked from left to right according to lake size. The bars denote 95 % confidence limits. For lake name abbreviation see the Fig. 1 captions.

Table 2

Mean (±SD) trophic position (TP) of the studied fish species a) in the four smallest and b) in the two largest lakes as well as TP of Saimaa ringed seal in the whole Lake Saimaa.

a)												
Lake	Kaukasenjärvi			Kastanjärvi			Säynäjärvi			Ormajärvi		
	mean TP	SD	n	mean TP	SD	n	mean TP	SD	n	mean TP	SD	n
<i>Alburnus alburnus</i> (common bleak)												
<i>Esox lucius</i> (pike)	4.1	± 0.0	2				4.2	± 0.3	3	3.8	± 0.5	15
<i>Perca fluviatilis</i> (perch) <15 cm	3.9	± 0.1	9	3.8	± 0.2	13	3.8	± 0.1	11	4.2	± 0.2	11
<i>P. fluviatilis</i> > 15 cm	4.2	± 0.0	6	4.0	± 0.1	2	4.4	± 0.9	4	4.2	± 0.3	4
<i>Rutilus rutilus</i> (roach)	3.7	± 0.2	15	3.7	± 0.3	15	3.8	± 0.2	16	3.9	± 0.1	15

b)						
Lake	Paasivesi			Haukivesi		
	mean TP	SD	n	mean TP	SD	n
<i>Abramis brama</i> (bream)	3.6		1	3.4	± 0.2	6
<i>Blicca bjoerkna</i> (white bream)	3.3	± 0.1	4	3.4	± 0.1	5
<i>Alburnus alburnus</i> (common bleak)				2.9	± 0.1	11
<i>Coregonus albula</i> (vendace)	3.4	± 0.2	23	3.5	± 0.0	4
<i>C. lavaretus</i> (whitefish)	3.4		1	3.8		1
<i>E. lucius</i> (pike)	4.0	± 0.1	3	3.8	± 0.2	5
<i>Gymnocephalus cernua</i> (ruffe)	3.6	± 0.3	10	4.3	± 0.5	7
<i>Leuciscus idus</i> (ide)				3.1		1
<i>Lota lota</i> (burbot) <30 cm	3.8	± 0.3	4	3.7	± 0.2	11
<i>L. lota</i> > 30 cm				4.5	± 0.0	2
<i>Osmerus eperlanus</i> (smelt)	3.7	± 0.2	17	3.9	± 0.1	15
<i>Perca fluviatilis</i> (perch) <15 cm	3.5	± 0.3	10	3.3	± 0.1	10
<i>P. fluviatilis</i> > 15 cm	4.1	± 0.2	4	3.9	± 0.3	7
<i>Pungitius pungitius</i> (nine-spined stickleback)				3.2	± 0.1	10
<i>Rutilus rutilus</i> (roach)	3.0	± 0.3	12	3.2	± 0.1	14
<i>Salmo trutta</i> (brown trout)				3.8		1
<i>Sander lucioperca</i> (pikeperch) <40 cm	4.2	± 0.1	2	4.1	± 0.1	13
<i>S. lucioperca</i> > 40 cm	4.3	± 0.2	3	4.2	± 0.1	3
<i>Scardinius erythrophthalmus</i> (common rudd)	3.2		1	3.1	± 0.1	5
<i>Pusa hispida saimensis</i> Saimaa ringed seal pups				4.5	± 0.8	30
<i>P. hispida saimensis</i> Saimaa ringed seal adults				4.2	± 0.8	23

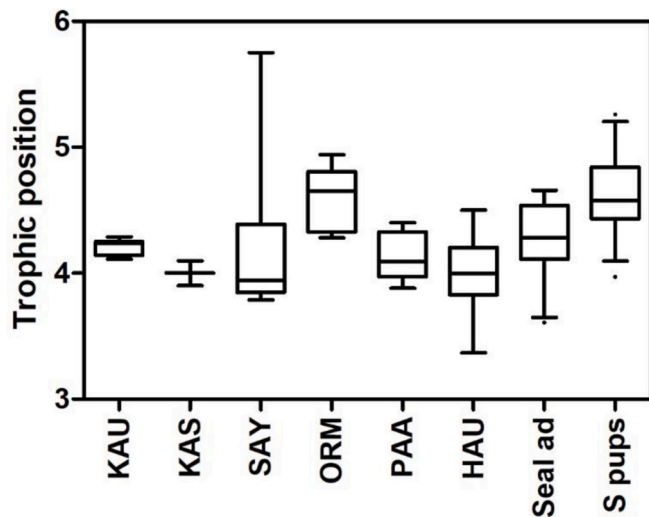


Fig. 3. Boxplots and median trophic position (TP with 5–95 % percentiles) of piscivorous fish; perch (>15 cm) and pike in the six study lakes, and also including pikeperch (> 40 cm) and burbot (> 30 cm) in the two largest lake basins. The lakes are ranked from left to right according to lake size. TP calculated also for Saimaa ringed seal adults and pups in the whole Lake Saimaa (data from [Auttila et al., 2015](#)). For lake name abbreviations see [Fig. 1](#) captions.

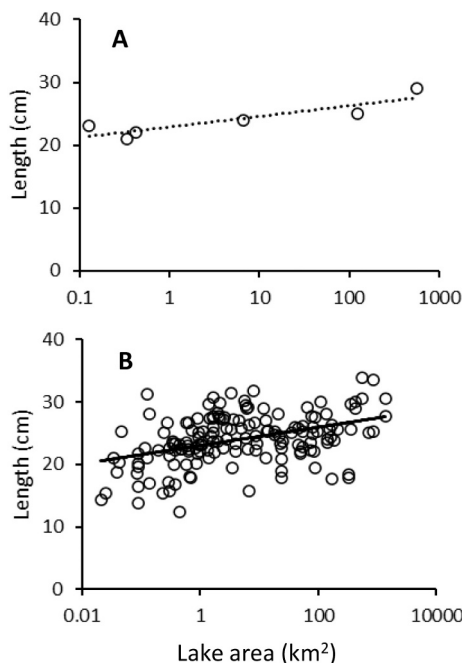


Fig. 4. Maximum total length (A) of perch in relation to lake surface area of the six SIA study lakes, and respective values (B) in the larger gill-net monitoring dataset of 156 lakes.

connected by brooks and/or ditches to larger lakes. For example, the smallest lake in this size group, Enanlampi, (area 0.05 km²) is located on an island of a large lake (Puruvesi, area 420 km²).

4. Discussion

We estimated that littoral resources play an important role for many fish species in shallow boreal lakes. We found that piscivorous fish size increased towards larger lakes especially with large perch and potentially with very large pikes. However, within this boreal lake dataset

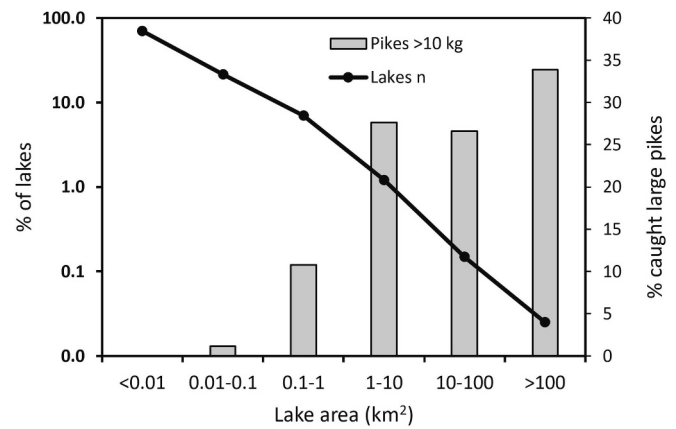


Fig. 5. Proportion (%) of very large pikes (>10 kg, $n = 605$) caught from lakes of different size classes during the years 2002–2020 (grey bars). Percentage of lakes in different size classes (black line) in Finland are from [Raatikainen and Kuusisto \(1988, see also Suppl. Table 5\)](#).

including the population of an endemic Saimaa ringed seal, there was no evidence that large lakes have longer food chains than the small ones. All lakes supported four trophic levels. Lack of a clear relationship between food chain length and lake size potentially reflects the relatively shallow nature of study lakes that increases littoral and pelagic coupling of top predators. Larger lakes had bigger top predators likely reflecting wider prey and habitat availability for top predators.

4.1. Littoral, pelagic and profundal carbon

In optimal cases, stable carbon analyses of food web compartments can distinctly separate littoral, pelagic and profundal resources available for consumers in the lake food webs (e.g. [Vander Zanden and Rasmussen, 1999](#); [Harrod et al., 2010](#)). As expected, littoral macroinvertebrate $\delta^{13}\text{C}$ values were significantly higher than those in pelagic zooplankton, and thus, the difference could be used for tracing carbon source in the study lakes. The greatest littoral-pelagic difference (ca. 6 ‰) was found in the small clear-water lakes (Kastana and Säynäjärvi), where the littoral invertebrate $\delta^{13}\text{C}$ values were very close to those of periphyton, indicating their main diet source. In the small mesotrophic brown-water lake Kaukasenjärvi, the distinction between littoral and pelagic invertebrate communities was less clear, which may be due to contribution of allochthonous carbon ($\delta^{13}\text{C}$ of C3 plants ca. 27 ‰) in both zones. In the studied six lakes, littoral periphyton $\delta^{13}\text{C}$ values were positively correlated with lake size (0.1– > 500 km²). This is in accordance with the positive relationship found by [Post \(2002\)](#) for both littoral and pelagic carbon baselines (mussels and snails) in 25 north temperate lakes in USA within an area range ca. 0.1–10,000 km². Although we do not have data on $\delta^{13}\text{C}$ values of dissolved inorganic carbon (DIC) source available for primary producers in the lakes, it is likely that in small lakes, a larger proportion of ^{13}C -depleted DIC originated from community respiration ([Karlsson et al., 2007](#)), whereas in large lakes DIC may had been more in balance with atmospheric DIC and/or originated from rock weathering as assumed by [Post \(2002\)](#). Increasing difference between $\delta^{13}\text{C}$ values of periphyton and littoral benthic invertebrates along with lake size suggests that advective mixing may have transported pelagic resources available also for littoral invertebrates. In an extensive study of a large (area 270 km²) shallow temperate eutrophic lake, Vörtsjärv, [Cremona et al. \(2014\)](#) concluded that in the whole lake area the benthic food web was mostly sustained by carbon of phytoplankton origin. This is also supported by findings from subarctic lakes in Finnish Lapland, where benthic food webs are fuelled by pelagic phytoplankton energy along with increasing total phosphorus concentration ([Hayden et al., 2019](#)).

In most lakes the small differences of $\delta^{13}\text{C}$ values between littoral and pelagic cladocerans, as well as between copepods in these zones,

suggest similar diet sources and differing from that of benthic invertebrates. In general, pelagic copepods had ca. 1–4 ‰ lower $\delta^{13}\text{C}$ values than cladocerans, which is presumably due to greater accumulation of isotopically-light lipids in the copepods (Siväranta and Rautio, 2010). Very low values of $\delta^{13}\text{C}$ (–48 to –35 ‰) in profundal chironomids, chaoborids and the amphipod *M. affinis* sampled from the three smallest lakes indicate contribution of methane-derived carbon in their diets (Jones and Grey, 2011).

4.2. Littoral/pelagial diet sources of fish

Mixing-model estimates of littoral and pelagic sources in the diets of roach and perch, based on $\delta^{13}\text{C}$ values of the potential macroinvertebrate prey taxa, seemed to be reliable only in the two small clear-water lakes (Kastana and Säynäjärvi), having ca. 6 ‰ difference between the sources and distinct for detecting carbon origin in the food webs (e.g. France, 1995; Fry, 2006). In the other lakes, the $\delta^{13}\text{C}$ values between littoral macroinvertebrates and pelagic zooplankton overlapped and the mixing model calculations showed unreliable estimates when littoral invertebrate $\delta^{13}\text{C}$ values were used in the calculations. By using littoral vegetation and pelagic zooplankton as baseline $\delta^{13}\text{C}$ values, the mixing model estimates were more realistic, showing ca. 70–100 % pelagic carbon origin for the fish species known to appear solely in the pelagic zone and feeding on zooplankton, i.e. vendace and smelt in these lakes (Karjalainen et al., 1997; Northcote and Hammar 2006). More distinct baseline invertebrate values for mixing models could have been obtained from species with a longer life cycle such as large snails and clams, which maintain isotope ratio for a long time (Post, 2002; Hayden et al., 2019). Unfortunately, such data was not available for all study lakes. On the other hand, increasing pelagic production along eutrophication and browning may promote the importance of pelagic carbon also in littoral food webs and, thus, shift even long-lived baseline invertebrate $\delta^{13}\text{C}$ values closer to each other (Hayden et al., 2019). In the current study, we observed such signs in Lake Haukivesi, where the pond snail (*Lymnaea* sp.) in the littoral zone had identical $\delta^{13}\text{C}$ values with pelagic zooplankton.

Despite above-mentioned uncertainties in the mixing model estimates, our study, however, supports the findings of Vander Zanden et al. (2011) on the importance of littoral resources for fish in the lakes. Based on a dataset consisting of 546 fish populations from 75 lakes worldwide, they estimated in average 57 % littoral reliance of fish, independent from morphological and limnological attributes of lakes. In our study, the contribution of littoral resources was also estimated to be large (>50 %) for many fish species in the three largest lakes. Our results indicate that littoral contribution in fish is not directly related to lake littoral area, estimated as lake shoreline development index, as we hypothesized. This was seen as a poor correlation between the index and littoral resources in perch and roach. Moreover, wide and overlapping confidence limits between littoral and pelagic diet sources in the analyzed fish in the three largest lakes support this conclusion. Roach, perch and white bream are generalist species using a range of littoral and pelagic habitats that could be observed also here with variable stable isotope values among the study lakes. Small perch typically feeds on zooplankton before shifting to littoral benthic invertebrates, and later on fish (e.g. Horppila et al., 2000). With the exception of Ormajärvi, this was seen in our estimates indicating >50 % pelagic carbon contribution in their diets. Roach populations are more variable, and some populations can rely heavily on pelagic resources (e.g. Horppila et al., 2000) as seen in our estimates. We had reliable results for smelt and vendace as the most pelagic, and nine-spined stickleback as the most littoral species as found in large subarctic lakes (Kahilainen et al., 2019). Feeding in profundal sites was not possible to estimate separately in this study. Ruffe, pikeperch and burbot are well known to use profundal resources and they often have elevated $\delta^{15}\text{N}$ values in boreal and subarctic lakes (Ravinet et al., 2010; Hayden et al., 2013; Huuskonen et al., 2019).

4.3. Nitrogen baseline, trophic position and food chain length

The strong correlation of baseline $\delta^{15}\text{N}$ values with lake totN and totP concentration and the proportion of agricultural area in the catchments indicates differences in N loading sources and cycling processes in the study lakes, which points out the need for reliable estimates of baseline $\delta^{15}\text{N}$ values for food web studies (c.f. Kendall et al., 2007, Curt et al., 2004, Diebel and Vander Zanden, 2009).

The ^{15}N enrichment in herbivores has been generally observed to be lower (2–3 ‰) than in carnivores, especially in vertebrates (3–4 ‰) (Vander Zanden and Rasmussen, 2001, Vanderklift and Ponsard, 2003, Matthews and Mazumder, 2008; Bunn et al., 2013; Perkins et al., 2014;). In our study lakes the littoral invertebrate taxa known to have a predatory feeding mode, were ca. 2–3 ‰ more ^{15}N enriched than primary consumers, and copepods were also ca. 1–3 ‰ more ^{15}N enriched than filter-feeding cladocerans, which suggest omnivorous feeding mode of many taxa. We assume that average 3.4 ‰ trophic enrichment (c.f. Post, 2002, Vander Zanden and Fetzer, 2007) can be generalized up to vertebrates in study lakes, although different fractionation values are proposed (Vanderklift and Ponsard, 2003; Bunn et al., 2013), and metabolic rate and ontogenic stage may influence isotopic fractionation in fish tissues (Scharnweber et al., 2021). In Lake Paasivesi, the $\delta^{15}\text{N}$ values of the cold-stenothermic amphipod *Gammaracanthus lacustris* suggests its high trophic position, on the same level as predatory fish. The species is long-lived (3–4 years) and typically feed on other crustaceans including *Mysis relicta* and *Pallaseopsis quadrispinosa* (Hill et al., 1990; Salonen et al., 2019). The high $\delta^{15}\text{N}$ values of fish feeding in the profundal zone are typical for many lakes; ruffe feeds on previously mentioned crustaceans whereas burbot and pikeperch may feed on ruffe (Hayden et al., 2013; Thomas et al., 2016; Huuskonen et al., 2019). Pike and perch instead are more littoral oriented fish in large lakes and typically have slightly lower trophic position than profundal fish (4.1–4.5).

Our analysis of stable carbon and nitrogen isotope data from six lakes, varying in area from 0.1 to >500 km² and volume from 5×10^5 to 5×10^9 m³, did not support the hypothesis presented by Post et al. (2000) that food chain length increase with ecosystem size. They found a significant positive correlation between food chain length and lake volume (range from 3.8×10^5 to 1.7×10^{12} m³) in a dataset of 25 temperate North American lakes having lake trout (*Salvelinus namaycush*) at the highest trophic position in the largest lakes. Wide lake volume range seems to be essential to reveal positive relationship between lake volume and trophic position, but such a clear relationship was not found in smaller lakes (Ward and McCann, 2017). Tunney et al. (2012) modelled the role of pelagial – littoral habitat coupling and food chain length in lakes with empirical data from 40 lakes having lake trout as a top predator. They estimated that the food chain length increases from ca. 4.2 to ca. 4.5–4.6 with increasing littoral contribution but balances at a level of ca. 4.5 in the lakes with an area > 10 km². However, the data of lake trout trophic position is very scattered especially among the lake size range 1–10 km² (Tunney et al., 2012), thus, it is uncertain whether the relationship is valid for lakes in general. In our study lakes the access to diverse littoral resources did not impact food-chain length, as we hypothesized. Top predator fish consist of several species (perch, pike, pikeperch, burbot) and their estimated trophic position fits within the range of 4.0–4.6 (see Table 2). Our SIA dataset was limited to a small number of shallow boreal oligotrophic and mesotrophic lakes, inhabiting both planktivorous, omnivorous and piscivorous fish, and excluding very small lakes and fishless ponds, which may have influenced the results. However, similar results were found in a larger dataset of 17 subarctic lakes (area 0.5–1084 km²), in which the trophic position of the top predator, Arctic charr (*Salvelinus alpinus*), was positively related only to fish species richness, but lake area, depth and productivity were not selected for the model explaining food chain length (Eloranta et al., 2015).

Top predatory fish, perch (>15 cm) and pike in small lakes, and perch (>15 cm), pike, pikeperch and Saimaa ringed seal in the large

lakes share the same trophic position (4.2–4.6). Saimaa ringed seal inhabits interconnected basins of Lake Saimaa (total area 4380 km²), including the two largest lake basins of our study. The main prey items of seals are smelt, roach, ruffe, perch and vendace, of an average size of 8.6 ± 3.4 cm, based on stomach content analyses of dead animals (Kunnasranta et al., 1999; Auttila et al., 2015). Corresponding whole food web SIA results reveal that Saimaa ringed seal has the same trophic position of (4.2 ± 0.8) as ringed seal (*Phoca hispida*), in the North Water Polynya in the Arctic, 4.5 (Hobson et al., 2002) and Lake Baikal seal (*Phoca sibirica*), 4.0 (Yoshii et al., 1999), whereas *P. hispida* in the northernmost basin of Baltic Sea (Bothnian Bay) have a slightly higher trophic position, 4.8 ± 0.2 (Kiljunen et al., 2020).

4.4. Top-predator size

Perch and pike are the most common species in Finnish lakes (Tammi et al., 2003), which shift to piscivory and are able to reach a large size. For piscivorous perch, sampled from the SIA study lakes and from fish monitoring of 156 boreal lakes, we found some support for the hypothesis that top predator size increases with lake size. Individual perch are able to reach a large size in very small lakes via cannibalism (e.g. Persson et al., 2003), whereas in large lakes piscivorous perch have access to more abundant stands of available key prey fish, such as smelt, vendace, sticklebacks, bullhead, whitefish and bleak (Haakana et al., 2007; Thomas et al., 2016). Large lakes also provide more habitats for large perch, such as deep-water pelagic areas for foraging and overwintering. However, the relative abundance of large perch was not related to lake size. This may be, at least partly, due to foraging behaviour of large perch hunting in shoals (Eklöv, 1992), which may increase the variability in gillnet catches and hide the pattern in fish abundance.

In the gill net monitoring data for pike, neither size nor relative abundance were related to lake size. However, pike catchability in standard gill netting is low (Olin et al., 2016). The dataset of long-term records of very large pike (weight > 10 kg), caught by recreational anglers, illustrates the range of maximum ranges of pike size, which very seldomly exceed 15 kg (Milardi et al., 2014). Majority (88 %) of these large pikes were caught from lakes with an area > 1 km² and none of them from the lakes <0.01 km². These results suggest that pike need larger space to find enough prey resources as well as colder water for summer habitats (Skov and Nilsson, 2018). Similarly to perch, pike will also benefit from a greater habitat and prey resource availability provided by large lakes. Larger individuals have lower temperature optimum than small ones, which often means habitat segregation; the small individuals remain in shallow littoral areas and larger ones use deeper benthic and pelagic areas for foraging on small fish such as burbot and ruffe (Kahilainen and Lehtonen, 2003; Skov and Nilsson, 2018). In small lakes with low prey fish diversity, pike may rely mainly on perch and cannibalism which often provide fluctuating foraging resource and, thus, limits growing to the largest size categories (Skov and Nilsson, 2018). As shown by the available data, large pike could be occasionally captured from smaller water bodies. This is often related to spawning period in smaller lakes connected with larger ones or alternatively to provision of artificial prey resources such as stocked rainbow trout (*Oncorhynchus mykiss*).

Saimaa ringed seal is the largest top predator (asymptotic body length 132 cm, mass 59 kg, Auttila et al., 2016) in Lake Saimaa, including the two largest SIA study lake basins. Thus, together with the results on piscivorous perch and pike, our hypothesis on the importance of lake size and habitat heterogeneity on top predator size is supported. The few freshwater lakes also maintaining pinniped populations are of the same size category or even larger than Lake Saimaa; harbor seals in Lacs des Loups Marins, Quebec, Canada, (Smith et al., 2006) and Iliamna Lake in Alaska, USA (Hauser et al., 2008), ringed seals in Lake Ladoga, Russia (Sipilä et al., 1996) and Baikal seals in Lake Baikal, Russia (Losey et al., 2023). Along with lake size, many other factors together with

available habitat and home range size influence how these very rare seal populations thrive in these lakes. Although Saimaa ringed seal population is adapted to live in the shallow Lake Saimaa, characterized by a very long shoreline, climatic factors, especially ice and snow cover, as well as human activities influence how this endangered seal population can thrive in this lake system (Niemi et al., 2019; Kunnasranta et al., 2020).

4.5. Conclusions

Our results from six shallow boreal lakes (area 0.1–567 km²) did not support the hypothesis that food chain length increases with lake size. All studied lakes maintain four trophic levels. Littoral energy sources had a high importance in large lakes and piscivores efficiently coupled littoral and pelagic habitats. Data on perch collected from more than 100 lakes suggest that the size of top predatory fish increase towards larger lakes with diverse fish fauna and greater habitat availability. Future work should involve a wide range of lake size, morphometry, stratification, productivity, and terrestrial organic matter contribution to test if our results from the current study are general features of boreal lake food webs.

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CRedit authorship contribution statement

Paula Kankaala: Writing – original draft, Methodology, Investigation, Data curation, Conceptualization. **Kimmo K. Kahilainen:** Writing – original draft, Investigation, Data curation, Conceptualization. **Mikko Olin:** Writing – original draft, Investigation, Data curation. **Antti J. Rissanen:** Writing – original draft, Investigation, Data curation.

Declaration of competing interest

None.

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Appendix A. Supplementary data

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References

- Alahuhta, J., Kanninen, A., Vuori, K., 2012. Response of macrophyte communities and status metrics to natural gradients and land use in boreal lakes. *Aquat. Bot.* 103, 106–114.
- Arostegui, M.C., Schindler, D.E., Holtgrieve, G.W., 2019. Does lipid-correction introduce biases into isotopic mixing models? Implications for diet reconstruction studies. *Oecologia* 191, 745–755.
- Auttilla, M., Sinisalo, T., Valtonen, M., Niemi, M., Viljanen, M., Kurkilahti, M., Kunnasranta, M., 2015. Diet composition and seasonal feeding patterns of a freshwater ringed seal (*Pusa hispida saimensis*). *Mar. Mamm. Sci.* 31, 45–65.
- Auttilla, M., Kurkilahti, M., Niemi, M., Levänen, R., Sipilä, T., Isomursu, M., Koskela, J., Kunnasranta, M., 2016. Morphometrics, body condition, and growth of the ringed seal (*Pusa hispida saimensis*) in Lake Saimaa: implications for conservation. *Mar. Mamm. Sci.* 32, 252–267. <https://doi.org/10.1111/mms.12256>.
- Barbour, C.D., Brown, J.H., 1974. Fish species diversity in lakes. *Am. Nat.* 108, 473–489.
- Borgå, K., Kidd, K.A., Muir, C.G., Berglund, O., Conder, J.M., Gobas, F.A.P.C., Kucklick, J., Malm, O., Powell, D.E., 2012. Trophic magnification factors: considerations of ecology, ecosystems, and study design. *Integr. Environ. Assess. Manag.* 8, 64–84. <https://doi.org/10.1002/ieam.244>.
- Brett, M., 2014. Resource polygon geometry predicts Bayesian stable isotope mixing model bias. *Mar. Ecol. Prog. Ser.* 514, 1–12.
- Bunn, S.E., Leigh, C., Jardine, T.D., 2013. Diet-tissue fractionation of $\delta^{15}\text{N}$ by consumers from streams and rivers. *Limnol. Oceanogr.* 58, 765–773.
- Cabana, G., Rasmussen, J.B., 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372, 255–257.
- CEN, 2005. Water Quality Sampling of Fish with Multimesh Gillnets. European Committee for Standardization, Brussels (EN 14757).
- Cremona, F., Timm, H., Agasild, H., Tonno, I., Feldmann, T., Jones, R.I., Noges, T., 2014. Benthic foodweb structure in a large shallow lake studied by stable isotope analysis. *Freshw. Sci.* 33, 885–894.
- Curt, M.D., Aguado, P., Sánchez, G., Bigeriego, M., Fernández, J., 2004. Nitrogen isotope ratios of synthetic and organic sources of nitrate water contamination in Spain. *Water Air Soil Pollut.* 151, 135–142.
- Diebel, M.W., Vander Zanden, M.J., 2009. Nitrogen stable isotopes in streams: effects of agricultural sources and transformations. *Ecol. Appl.* 19, 1127–1134.
- Doi, H., Chang, K.-H., Ando, T., Ninomiya, I., Imai, H., Nakano, S.-I., 2009. Resource availability and ecosystem size predict food-chain length in pond ecosystems. *Oikos* 118, 138–144.
- Dolson, R., McCann, K., Rooney, N., Ridgway, M., 2009. Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos* 118, 1230–1238. <https://doi.org/10.1111/j.1600-0706.2009.17351.x>.
- Downing, J.A., Prairie, Y.T., Cole, J.J., Duarte, C.M., Tranvik, L.J., Striegl, R.G., McDowell, W.H., Kortelainen, P., Caraco, N.F., Melack, J.M., Middelburg, J., 2006. The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol. Oceanogr.* 51, 2388–2397.
- Eklöv, P., 1992. Group foraging versus solitary foraging efficiency in piscivorous predators: the perch, *Perca fluviatilis*, and pike, *Esox lucius*, patterns. *Anim. Behav.* 44, 313–326.
- Eloranta, A.P., Kahilainen, K.K., Amundsen, P.-A., Knudsen, R., Harrod, C., Jones, R.I., 2015. Lake size and fish diversity determine resource use and trophic position of a top predator in high-latitude lakes. *Ecol. Evol.* 5, 1664–1675. <https://doi.org/10.1002/ece3.1464>.
- Elton, C., 1927. *Animal Ecology*. The Macmillan Company, New York, 207 p.
- France, R.L., 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol. Oceanogr.* 40, 1310–1313.
- Fry, B., 2006. *Stable Isotope Ecology*. Springer, New York, 308 p.
- Fry, B., 2013. Alternative approaches for solving underdetermined isotope mixing problems. *Mar. Ecol. Prog. Ser.* 472, 1–13.
- Gilbert, P.M., Middelburg, J.J., McClelland, J., Vander Zanden, M.J., 2019. Stable isotope tracers: enriching our perspectives and questions on sources, fates, rates, and pathways of major elements in aquatic systems. *Limnol. Oceanogr.* 64, 950–981.
- Grey, J., Jones, R.I., Sleep, D., 2001. Seasonal changes in the importance of the source of organic matter to the diet of zooplankton in Loch Ness, as indicated by stable isotope analysis. *Limnol. Oceanogr.* 46, 505–513.
- Griffiths, D., 2012. Body size distributions in north American freshwater fish: large-scale factors. *Glob. Ecol. Biogeogr.* 21, 383–392.
- Griffiths, D., 2013. Body size distributions in north American freshwater fish: small-scale factors and synthesis. *Ecol. Freshw. Fish* 22, 257–267.
- Guiry, E.J., Buckley, M., Orchard, T.J., Hawkins, A.L., Needs-Howarth, S., Holm, E., Szpak, P., 2020. Deforestation caused abrupt shift in Great Lakes nitrogen cycle. *Limnol. Oceanogr.* 65, 1921–1935.
- Haakana, H., Huuskonen, H., Karjalainen, J., 2007. Predation of perch on vendace larvae: diet composition in an oligotrophic lake and digestion time of the larvae. *J. Fish Biol.* 70, 1171–1184. <https://doi.org/10.1111/j.1095-8649.2007.01383.x>.
- Hairston, N.G., Hairston, N.G., 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am. Nat.* 142, 379–411.
- Hansson, S., Hobbie, J.E., Elmgren, R., Larsson, U., Fry, B., Johansson, S., 1997. The stable nitrogen isotope ratio as a marker of food-web interactions and fish migration. *Ecology* 78, 2249–2257.
- Harrod, C., Mallela, J., Kahilainen, K.K., 2010. Phenotype-environment correlations in a putative whitefish adaptive radiation. *J. Anim. Ecol.* 79, 1057–1068. <https://doi.org/10.1111/j.1365-2656.2010.01702.x>.
- Hauser, D.D.W., Allen, C.S., Rich Jr., H.B., Quinn, T.P., 2008. Resident harbor seals (*Phoca vitulina*) in Iliamna Lake, Alaska: summer diet and partial consumption of adult sockeye salmon (*Oncorhynchus nerka*). *Aquat. Mamm.* 34, 303–309. <https://doi.org/10.1578/AM.34.3.2008.303>.
- Hayden, B., Holopainen, T., Amundsen, P.-A., Eloranta, A.P., Knudsen, R., Præbel, K., Kahilainen, K.K., 2013. Interactions between invading benthivores and native whitefish in subarctic lakes. *Freshw. Biol.* 58, 1234–1250.
- Hayden, B., Harrod, C., Thomas, S.M., Eloranta, A.P., Myllykangas, J.-P., Siwertsson, A., Præbel, K., Knudsen, R., Amundsen, P.A., Kahilainen, K.K., 2019. From clear lakes to murky waters – tracing the functional response of high-latitude lake communities to concurrent ‘greening’ and ‘browning’. *Ecol. Lett.* 22, 807–816. <https://doi.org/10.1111/ele.13238>.
- Hecky, R.E., Hesslein, R.H., 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. *J. N. Am. Benthol. Soc.* 14, 631–653.
- Hill, C., Fürst, M., Hammar, J., 1990. Introduction of the amphipods *Pallasa quadrispinosa* and *Gammaracanthus lacustris* into lakes in northern Sweden. *Ann. Zool. Fenn.* 27, 241–244.
- Hobson, K.A., Fisk, A., Karnovsky, N., Holst, M., Gagnon, J., Fortier, M., 2002. A stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) model for the north water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep-sea Res. Part II Topic. Stud. Oceanogr.* 49, 5131–5150.
- Horppila, J., Ruuhijärvi, J., Rask, M., Karppinen, C., Nyberg, K., Olin, M., 2000. Seasonal changes in the diets and relative abundances of perch and roach in the littoral and pelagic zones of a large lake. *J. Fish Biol.* 56, 51–72.
- Huuskonen, H., Piironen, J., Syyväranta, J., Eronen, R., Biasi, C., Kiiskinen, P., Kortet, R., Vainikka, A., 2019. Diet and movements of pikeperch (*Sander lucioperca*) in a large oligotrophic lake with an exceptionally high pikeperch yield. *Ecol. Freshw. Fish* 28, 533–543.
- Jones, R.I., Grey, J., 2011. Biogenic methane in freshwater food webs. *Freshw. Biol.* 56, 213–229.
- Kahilainen, K.K., Lehtonen, H., 2003. Piscivory and prey selection of four predator species in a whitefish dominated subarctic lake. *J. Fish Biol.* 63, 659–672. <https://doi.org/10.1046/j.1095-8649.2003.00179.x>.
- Kahilainen, K.K., Thomas, S.M., Harrod, C., Hayden, B., Eloranta, A.P., 2019. Trophic ecology of piscivorous Arctic charr (*Salvelinus alpinus* (L.)) in subarctic lakes with contrasting food-web structures. *Hydrobiologia* 840, 227–243.
- Karjalainen, J., Turunen, T., Helminen, H., Sarvala, J., Huuskonen, H., 1997. Food selection and consumption of 0+ smelt (*Osmerus eperlanus* (L.)) and vendace (*Coregonus albula* (L.)) in pelagial zone of Finnish lakes. – Archiv für Hydrobiologie. *Spec. Issues Adv. Limnol.* 49, 37–49.
- Karlsson, J., Jansson, M., Jonsson, A., 2007. Respiration of allochthonous organic carbon in unproductive forest lakes determined by the Keeling plot method. *Limnol. Oceanogr.* 52, 603–608.
- Kendall, C., Elliott, E.M., Wankel, S.D., 2007. Tracing anthropogenic inputs of nitrogen to ecosystems. In: Michener, R., Lajtha, K. (Eds.), *Stable Isotopes in Ecology and Environmental Science*. Wiley, pp. 375–449. <https://doi.org/10.1002/9780470691854>.
- Kiljunen, M., Grey, J., Sinisalo, T., Harrod, C., Immonen, H., Jones, R.I., 2006. A revised model for lipid-normalizing $\delta^{13}\text{C}$ values from aquatic organisms, with implications for isotope mixing models. *J. Appl. Ecol.* 43, 1213–1222.
- Kiljunen, M., Peltonen, H., Lehtiniemi, M., Uusitalo, L., Sinisalo, T., Norikko, J., Kunnasranta, M., Torniainen, J., Rissanen, A.J., Karjalainen, J., 2020. Benthic-pelagic coupling and trophic relationships in northern Baltic Sea food webs. *Limnol. Oceanogr.* 65, 1706–1722.
- Kjørboe, T., 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biol. Rev. Camb. Philos. Soc.* 86, 311–339.
- Kiyashko, S., Narita, T., Wada, E., 2001. Contribution of methanotrophs to freshwater macroinvertebrates: evidence from stable isotope ratios. *Aquat. Microbial Ecol. Int. J.* 24, 203–207.
- Kunnasranta, M., Hyvärinen, H., Sipilä, T., Koskela, J.T., 1999. The diet of the Saimaa ringed seal *Phoca hispida saimensis*. *Acta Theriol.* 44, 443–450.
- Kunnasranta, M., Niemi, M., Auttila, M., Valtonen, M., Kammonen, J., Nyman, T., 2020. Sealed in a lake - biology and conservation of the endangered Saimaa ringed seal: a review. *Biol. Conserv.* 253, 108908. <https://doi.org/10.1016/j.biocon.2020.108908>.
- Layman, C.A., Araujo, M.S., Bouček, M., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z. R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S., 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol. Rev.* 87, 545–562.
- Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23, 399–417.
- Losey, R.J., Nomokonova, T., Pastukhov, M.V., Hunter, A., Novikov, A.G., Goriunova, O. I., Weber, A.W., 2023. A body size approach to understanding Holocene seal hunting at Lake Baikal in Siberia. *Archaeol. Anthropol. Sci.* 15, 49. <https://doi.org/10.1007/s12520-023-01753-0>.
- Marty, J., Planas, D., 2008. Comparison of methods to determine algal $\delta^{13}\text{C}$ in freshwater. *Limnol. Oceanogr. Methods* 6, 51–63.
- Matthews, B., Mazumder, A., 2008. Detecting trophic-level variation in consumer assemblages. *Freshw. Biol.* 53, 1942–1953.
- Mattsson, T., Kortelainen, P., Räike, A., 2005. Export of DOM from boreal catchments: impacts of land use cover and climate. *Biogeochemistry* 76, 373–394.
- McMeans, B.C., McCann, K.S., Tunney, T.D., Fisk, A.T., Muir, A.M., Lester, N., Shuter, B., Rooney, N., 2016. The adaptive capacity of lake food webs: from individuals to ecosystems. *Ecol. Monogr.* 86, 4–19. <https://doi.org/10.1890/15-0288.1>.
- Milardi, M., Lappalainen, J., Juntunen, T., 2014. Variation in length, girth and weight of large northern pikes (*Esox lucius*) in Finland. *Ann. Zool. Fenn.* 51, 335–339. <https://doi.org/10.5735/086.051.0305>.

- Miller, E.J., Potts, J.M., Cox, M.J., Miller, B.S., Calderan, S., Leaper, R., O'Driscoll, R.L., Double, M.C., 2019. The characteristics of krill swarms in relation to aggregating Antarctic blue whales. *Sci. Rep.* 9, 16487.
- Mittelbach, G.G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences. *Can. J. Fish. Aquat. Sci.* 55, 1454–1465.
- Niemi, M., Liukkonen, L., Koivuniemi, M., Auttila, M., Rautio, A., Kunnasranta, M., 2019. Winter behavior of Saimaa ringed seals: non-overlapping core areas as indicators of avoidance in breeding females. *PLoS One* 14, e0210266.
- Nyman, T., Valtonen, M., Aspi, J., Ruokonen, M., Kunnasranta, M., Palo, J.U., 2014. Demographic histories and genetic diversities of Fennoscandian marine and landlocked ringed seal subspecies. *Ecol. Evol.* 4, 3420–3434.
- Olin, M., Rask, M., Ruuhijärvi, J., Ala-Opas, P., Kurkilahti, M., Ylönen, O., 2002. Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. *J. Fish Biol.* 60, 593–612.
- Olin, M., Rask, M., Ruuhijärvi, J., Tammi, J., 2013. Development and evaluation of the Finnish fish-based lake classification method. *Hydrobiologia* 713, 149–166.
- Olin, M., Tiainen, J., Kurkilahti, M., Rask, M., Lehtonen, H., 2016. An evaluation of gillnet CPUE as an index of perch density in small forest lakes. *Fish. Res.* 173, 20–25. <https://doi.org/10.1016/j.fishres.2015.05.018>.
- Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5, e9672.
- Perga, M.E., Gerdeaux, D., 2005. 'Are fish what they eat' all year round? *Oecologia* 144, 598–606. <https://doi.org/10.1007/s00442-005-0069-5>.
- Perkins, M.J., McDonald, R.A., van Veen, F.J.F., Kelly, S.D., Rees, G., Bearhop, S., 2014. Application of nitrogen and carbon stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to quantify food chain length and trophic structure. *PLoS One* 9, e93281.
- Persson, L., Diehl, S., Johansson, L., Andersson, G.F., Hamrin, S.F., 1992. Trophic interactions in temperate lake ecosystems: a test of food chain theory. *Am. Nat.* 140, 59–84.
- Persson, L., De Roos, A.M., Claessen, D., Westman, E., 2003. Gigantic cannibals driving a whole-lake trophic cascade. *Proc. Natl. Acad. Sci. USA* 100, 4035–4039. <https://doi.org/10.1073/pnas.0636404100>.
- Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18, 293–320.
- Phillips, D.L., Gregg, J.W., 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia* 128, 304.
- Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food-web studies. *Can. J. Zool.* 92, 823–835.
- Pimm, S.L., 1982. *Food Webs*. The University of Chicago Press, Chicago, 219 pp.
- Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83, 703–718.
- Post, D.M., 2007. Testing the productive-space hypothesis: rational and power. *Oecologia* 153, 973–984.
- Post, D.M., Pace, M.L., Hairston, N.G., 2000. Ecosystem size determines food-chain length in lakes. *Nature* 405, 1047–1049.
- Potapov, A., Brose, U., Scheu, S., Tiunov, A., 2019. Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *Am. Nat.* 194, 823–839.
- Price, S.A., Hopkins, S.S.B., 2015. The macroevolutionary relationship between diet and body mass across mammals. *Biol. J. Linn. Soc.* 115, 173–184.
- Raatikainen, M., Kuusisto, E., 1988. Suomen järvien lukumäärä ja pinta-ala (The number and surface area of the lakes in Finland). *Terra* 102, 97–110.
- Rautio, M., Mariash, H., Forsström, L., 2011. Seasonal shifts between autochthonous and allochthonous carbon contributions to zooplankton diets in a subarctic lake. *Limnol. Oceanogr.* 56, 1513–1524.
- Ravinet, M., Syväranta, J., Jones, R.L., Grey, J., 2010. A trophic pathway from biogenic methane supports fish biomass in a temperate lake ecosystem. *Oikos* 119, 409–416.
- Riede, J.O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C.R., Jonsson, T., 2011. Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecol. Lett.* 14, 169–178.
- Salonen, J.K., Hiltunen, M., Figueiredo, K., Paavilainen, P., Sinisalo, T., Strandberg, U., Kankaala, P., Taskinen, J., 2019. Population structure, life cycle, and trophic niche of the glacial relict amphipod, *Gammaracanthus lacustris*, in a large boreal lake. *Freshw. Biol.* 64, 2176–2188.
- Scharnweber, K., Andersson, M.L., Chaguaceda, F., Eklöv, P., 2021. Intraspecific differences in metabolic rates shape carbon stable isotope trophic discrimination factors of muscle tissue in the common teleost Eurasian perch (*Perca fluviatilis*). *Ecol. Evol.* 11, 9804–9814.
- Schoener, T.W., 1989. Food webs from the small to the large. *Ecology* 70, 1559.
- Seekell, D., Cael, B.B., Byström, P., 2022. Problems with the shoreline development index - a widely used metric of lake shape. *Geophys. Res. Lett.* 49, e2022GL098499. <https://doi.org/10.1029/2022GL098499>.
- Sipilä, T., Medvedev, N.V., Hyvärinen, H., 1996. The Ladoga seal (*Phoca hispida ladogensis* Nordq.). *Hydrobiologia* 322, 193–198.
- Skov, C., Nilsson, P.A., 2018. *Biology and Ecology of Pike*. CRC Press, Boca Raton. <https://doi.org/10.1201/9781315119076>.
- Smith, R.J., Cox, T.M., Westgate, A.J., 2006. Movements of harbor seals (*Phoca vitulina mellonae*) in Lacs des loups Marins, Quebec. *Mar. Mamm. Sci.* 22, 480–485. <https://doi.org/10.1111/j.1748-7692.2006.00024.x>.
- Strayer, D.L., Findlay, S.E.G., 2010. Ecology of freshwater shore zones. *Aquat. Sci.* 72, 127–163.
- Syväranta, J., Rautio, M., 2010. Zooplankton, lipids and stable isotopes: importance of seasonal, latitudinal, and taxonomic differences. *Can. J. Fish. Aquat. Sci.* 67, 1721–1729.
- Taipale, S.J., Vuorio, K., Brett, M.T., Peltomaa, E., Hiltunen, M., Kankaala, P., 2016. Lake zooplankton $\delta^{13}\text{C}$ values are strongly correlated with the $\delta^{13}\text{C}$ values of distinct phytoplankton taxa. *Ecosphere* 7, e01392.
- Takimoto, G., Post, D.M., 2012. Environmental determinants of food-chain length: a meta-analysis. *Ecol. Res.* 28, 675–681. <https://doi.org/10.1007/s11284-012-0943-7>.
- Tammi, J., Appelberg, M., Beier, U., Hesthagen, T., Lappalainen, A., Rask, M., 2003. Fish status survey of nordic lakes: effects of acidification, eutrophication and stocking activity on present fish species composition. *Ambio* 32, 98–105. <http://www.ambio.kva.se>.
- Terui, A., Nishijima, S., 2019. Spatial disturbance synchrony alters the association of food chain length and ecosystem size. *Ecol. Res.* 34, 864–871. <https://doi.org/10.1111/1440-1703.12056>.
- Thomas, S.M., Kiljunen, M., Malinen, T., Eloranta, A.P., Amundsen, P.-A., Lodenius, M., Kahilainen, K.K., 2016. Food-web structure and mercury dynamics in a large subarctic lake following multiple species introductions. *Freshw. Biol.* 61, 500–517. <https://doi.org/10.1111/fwb.12723>.
- Thompson, R.M., Townsend, C.R., 2005. Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108, 137–148.
- Tolonen, K.T., Hämäläinen, H., Holopainen, L.J., Mikkonen, K., Karjalainen, J., 2003. Body size and substrate association of littoral insects in relation to vegetation structure. *Hydrobiologia* 499, 179–190.
- Trochine, C., Díaz, Villanueva V., Balseiro, E., Modenutti, B., 2019. Nutritional stress by means of high C:N ratios in the diet and starvation affects nitrogen isotope ratios and trophic fractionation of omnivorous copepods. *Oecologia* 190, 547–557.
- Tunney, T.D., McCann, K.S., Lester, N.P., Shuter, B.J., 2012. Food web expansion and contraction in response to changing environmental conditions. *Nat. Commun.* 3, 1105. <https://doi.org/10.1038/ncomms2098>.
- Vadeboncoeur, Y., Peterson, G.D., Vander Zanden, M.J., Kalff, J., 2008. Benthic algal contributions to primary production across lake size gradients. *Ecology* 89, 2542.
- Vander Zanden, M.J., Fetzner, W.W., 2007. Global patterns of aquatic food chain length. *Oikos* 116, 1378–1388.
- Vander Zanden, M.J., Rasmussen, J.B., 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the trophic position of aquatic consumers. *Ecology* 80, 1395.
- Vander Zanden, M.J., Rasmussen, J.B., 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnol. Oceanogr.* 46, 2061–2066.
- Vander Zanden, M.J., Shuter, B.J., Lester, N., Rasmussen, J.B., 1999. Patterns of food chain length in lakes: a stable isotope study. *Am. Nat.* 154, 406. <https://doi.org/10.1086/303250>.
- Vander Zanden, M.J., Vadeboncoeur, Y., Chandra, S., 2011. Fish reliance on littoral-benthic resources and the distribution of primary production in lakes. *Ecosystems* 14, 894–903.
- Vanderklift, M.A., Ponsard, S., 2003. Sources of variation in consumer-diet $\delta^{15}\text{N}$ enrichment: a meta-analysis. *Oecologia* 136, 169–182.
- Verpoorter, C., Kutser, T., Seekell, D.A., Tranvik, L.J., 2014. A global inventory of lakes based on high-resolution satellite imagery. *Geophys. Res. Lett.* 41, 6396–6402.
- Ward, C.L., McCann, K.S., 2017. A mechanistic theory for aquatic food chain length. *Nat. Commun.* 8, 2028–10.
- Wetzel, R.G., 1990. Land-water interfaces: metabolic and limnological regulators. *Int. Verhandlungen Theor. Angew. Limnol.* 24, 6–24.
- Winfield, I.J., 2004. Fish in the littoral zone: ecology, threats and management. *Limnologica* 34, 124–131.
- Woolnough, D.A., Downing, J.A., Newton, T.J., 2009. Fish movement and habitat use depends on water body size and shape. *Ecol. Freshw. Fish* 18, 83–91. <https://doi.org/10.1111/j.1600-0633.2008.00326.x> 83.
- Yoshii, K., Melnik, N.G., Timoshkin, O.A., Bondarenko, N.A., Anashko, P.N., Yoshika, T., Wada, E., 1999. Stable isotope analyses of the pelagic food web in Lake Baikal. *Limnol. Oceanogr.* 44, 502–511.