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# Resource use of crucian carp along a lake productivity gradient is related to body size, predation risk, and resource competition

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## Abstract

Generalist fish species can feed on a wide resource spectrum and across trophic levels depending on resource availability and trophic interactions. Crucian carp (*Carassius carassius*) represents a good candidate species to investigate variation in the trophic ecology of generalist fish as it can be found in highly variable fish communities and its resource use is well documented. In this study, we explored the trophic ecology of crucian carp at the individual and population levels using stable isotope and gut content analysis. We tested if trophic resource use varied according to lake productivity, predation risk, intra- and interspecific competition, or individual fish size. We found that crucian carp resource preference was highly variable among and within lakes. In predator-free lakes, small crucian carp occurred in high densities, showed increased interindividual specialisation, and relied mainly on pelagic zooplankton. In presence of predators, large crucian carp occurred in low densities and included greater proportions of benthic macroinvertebrates in their diet. This shift in resource use was further favoured in productive, shallow lakes where littoral prey were probably abundant. Resource partitioning was an important factor determining crucian carp niche use, as fish had higher trophic position in absence of other cyprinids. Crucian carp showed highly dynamic resource use and food preferences in response to variable environmental conditions. Overlooking complex diet preferences of generalist fish may lead to an oversimplification of freshwater community dynamics.

KEYWORDS
cyprinid, diet analysis, generalist fish, stable isotopes, trophic ecology

## 1 | INTRODUCTION

Generalist fish species can forage on a wide resource spectrum, regulating the energy flows across trophic levels and between the pelagic and benthic food chains, with profound effects on the food web dynamics of aquatic ecosystems (Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002). Fish with generalist feeding strategies can also be favoured in fluctuating environments as they can respond flexibly to changes in resource availability (Hayden, Harrod, & Kahilainen, 2014; Laske, Rosenberger, Wipfli, & Zimmerman, 2018; Levins, 1968; Persson, Diehl, Johansson, Andersson, & Hamrin, 1991; Pool et al., 2017). Accordingly, generalist fish are expected to vary their resource preferences along productivity gradients (Lesser, James, Stallings, Wilson, & Nelson, 2020). In shallow temperate lakes, an initial increase in the amount of available nutrients intensifies the growth of benthic algae and macrophytes, enhancing invertebrate prey density in the littoral habitat (Moss et al., 2004). As lakes become more eutrophic, nutrient supply often intensifies primary production of the pelagic habitat, with considerable changes in invertebrate and fish community structure (Hayden, Myllykangas, Rolls, & Kahilainen, 2017; Jeppesen, Peder Jensen, Søndergaard, Lauridsen, & Landkildehus, 2000; Olin et al., 2002). Thus, species that can potentially behave as planktivores, benthivores, herbivores, or detritivores could change their trophic ecology in response to resource availability in different systems (Araújo, Bolnick, & Layman, 2011; Vejříková et al., 2017; Werner et al., 1977).

The ability of generalist fish to forage on alternative resources is also strongly dependent on their intra- and interspecific interactions (Bolnick et al., 2010; Nilsson, 1967; Quevedo, Svanbäck, & Eklöv, 2009; Svärdson, 1976). Intraspecific competition can increase population niche variability as conspecifics may adopt different foraging behaviours and use distinct subsets of the population diet breadth (Bolnick et al., 2003). On the other hand, interspecific competition generally constrains niche width by limiting the range of available resources (Schoener, 1974; Van Valen, 1965). The strength of interspecific competition will also depend on fish density and species composition, as closely related species with a similar ecological function are more likely to compete (Nilsson, 1963; Svärdson, 1976; Wootton, 1990). Predation is another important factor determining the trophic niche and population structure of prey (Brabrand & Faafeng, 1993; Brönmark, Skov, Brodersen, Nilsson, & Hansson, 2008; Brooks & Dodson, 1965; Werner & Gilliam, 1984). Predators can increase or decrease the strength of interspecific interactions, and thus resource partitioning, among competing prey (Chase et al., 2002). Interspecific interactions also depend on abiotic characteristics such as habitat heterogeneity. Increased structural complexity of the environment, such as enhanced macrophyte density, usually leads to a decrease of predation pressure, as prey can adopt different antipredator behaviours and seek refuge in alternative habitats (Snickars, Sandström, & Mattila, 2004; Werner, Gilliam, Hall, & Mittelbach, 1983). This change in habitat use is frequently accompanied by a diet shift, leading to decreased growth rates if less favourable food resources are exploited (Werner et al., 1983). Moreover, competing species may occupy the same habitat, e.g., a refuge from predators, or select sub-optimal habitats as the preferred one is already occupied (Henseler, Nordström, Törnroos, Snickars, & Bonsdorff, 2020; Mittelbach, 1988). Foraging strategies can differ during ontogeny, as fish with increasing body size have access to larger food items (Scharf, Juanes, & Rountree, 2000). By attaining a larger size, fish can also decrease predation risk by gape-limited predators and use different habitats, with a potential competitive advantage over smaller conspecifics (Byström, Andersson, Persson, & De Roos, 2004; Woodward & Hildrew, 2002). Thus, body size can modify the strength of interspecific interactions in a way that competition or predation can be predominant at certain size classes (Persson, 1988).

Crucian carp (*Carassius carassius*) is a widespread generalist fish belonging to the Cyprinidae family, and can inhabit a variety of habitats, ranging from small ponds to large and often productive lakes. Crucian carp presents a peculiar physiology. In autumn, it builds up a glycogen storage which it uses for anaerobic metabolism in ice-covered anoxic lakes during winter months (Blažka, 1958). Since most other fish are sensitive to oxygen depletion, it is often the only fish species able to survive severe winter conditions (Piironen & Holopainen, 1986). In pond populations, high densities of small crucian carp lead to resource limitation and strong intraspecific competition (Holopainen, Tonn, & Paszkowski, 1997; Pettersson & Brönmark, 1997). In contrast, in more complex fish communities, crucian carp occurs at low densities and individuals usually attain larger sizes. This fish displays an elusive behaviour in lakes with piscivores (e.g. Vinterstare, Hulthén, Nilsson, Sköld, & Brönmark, 2020) and is well-known for developing a deep-bodied morphology in response to gape-size-limited predators (Brönmark & Pettersson, 1994; de Meo et al., 2021). Although the effect of predation risk on crucian carp resource use is well documented (Andersson, Johansson, & Söderlund, 2006; Paszkowski, Penttinen, Holopainen, & Tonn, 1996; Pettersson & Brönmark, 1993), the potential role of interspecific competition has often been overlooked. This species shows a wide diet spectrum, including zooplankton, benthic insect larvae, macrophytes, and detrital material (e.g. Penttinen & Holopainen, 1992). In warm, shallow, eutrophic lakes, its diet can vary greatly and consists mainly of plant material and zooplankton or detritus (Gao, Zhong, Ning, Liu, & Jeppesen, 2017). Benthic foraging of crucian carp can also cause resuspension of sediment and increase nutrient concentrations, with potential effects on the lake's trophic state and water quality (He et al., 2019).

Since crucian carp can be found along different productivity gradients, it represents a good candidate species to investigate the trophic ecology of generalist fish in small lakes. In this study, we consider how lake characteristics and fish community structure affect the trophic resource use of crucian carp through stable isotopes and gut content analysis. Stable isotope analysis (SIA) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) is a well established method providing integrated information on consumer-trophic ecology. Since isotope ratios of consumers and food sources are closely linked, variation in the environment that affects the isotopic values of food sources at the base of the food chain may also influence the position occupied by consumers in the niche space (Newsome, Martinez del Rio, Bearhop, & Phillips, 2007; Post, 2002). Here, we explored the trophic ecology of crucian carp at the individual and population levels, taking into account the main environmental characteristics potentially underlying variation in isotope ratios of food sources among different lakes. In particular, we wanted to find out if trophic resource use of crucian carp varied according to lake productivity, predation risk, intra- and interspecific competition, or individual fish size. We expected a shift towards more littoral resource use with increasing predator or competitor density, as vegetated littoral habitat provides a refuge and different food sources. At the same time, we predicted this shift to be enhanced by increasing productivity and individual body size, as they influence availability and accessibility of littoral resources. We also expected an increase in IS, and thus an increase in the population-specific niche size in communities where crucian carp was the dominant species, and a narrowing in niche size with higher interspecific competition and predation risk. Thus, investigating resource competition, predation, and body size in lakes with different productivity and fish community structure, we aimed at revealing their relative contribution upon niche use of crucian carp.

## 2 | METHODS

### 2.1 | Study sites and data collection

The selected 12 study lakes and ponds were located in southeastern Norway and were relatively small (0.25–11 ha) and shallow (max depth 1.5–11.3 m; Table 1, Figure S1 in Supplementary Material). Land use of the area surrounding the lakes was different among localities: peat bog-forest of birch or pine (Lakes Posttjernet, Motjennet, and Karussputten), forest with proximity to an urban area (Lakes Øvresetertjern, Svartkulp, Småvanna, Langmyrtjern, and Bjørnmyrdammen), and urban area or farmland (Lakes Bugårdsdammen, Forkerudstjern, Stomperudtjern, and Nusttjennet). Abiotic parameters included lake altitude (m a.s.l.), surface area (ha), maximum depth (m), littoral area (%), specific conductivity (S/cm), Secchi depth (m), total nitrogen (μg/L), phosphorus (μg/L) and organic carbon (mg/L). We estimated lake bathymetry in the field with a portable echosounder, and the littoral area was calculated as the percentage of bottom depth shallower than 3.5 m.

Fish collection was carried out between June and August in 2018 and 2019 during the open-water season to examine the food sources assimilated during the main period of fish growth and activity. We assessed fish density in each lake using Nordic multimesh gillnets consisting of 12 equidistant panels (mesh sizes 5–55 mm) for littoral and pelagic habitats. Moreover, different fishing methods were used to maximise the catch of small crucian carp (see details in de Meo et al., 2021). We calculated CPUE ($n$ fish·net$^{-1}$·h$^{-1}$) for crucian carp (CPUE crucian), invertebrate consumer fish potentially in competition for resources with crucian carp (CPUE comp), and piscivorous fish (CPUE pred; Table 2). Piscivorous fish species in these lakes were brown trout (*Salmo trutta*), European perch (*Perca fluviatilis*), and northern pike (*Esox lucius*). In particular, in lakes at these latitudes, brown trout and perch undergo ontogenetic shifts to piscivory at a size of around 20 cm (Jensen, Kiljunen, & Amundsen, 2012; Jonsson, Næsje, Jonsson, Saksgård, & Sandlund, 1999) and 17 cm (Hjelm, Persson, & Christensen, 2000; Horppila et al., 2000; Svanbäck & Eklöv, 2002), respectively. Consequently, large fish were considered predators. Permission to catch fish was given by the Norwegian Environmental Agency (2018/4155), and fish were sampled after oral approval by the local landowners.

We collected qualitative samples of zooplankton, benthic invertebrates, macrophytes, and sediment to estimate basal resources for SIA. We sampled zooplankton hauling a plankton net through the water column in the pelagic zone of deep lakes or in the non-vegetated area of shallow lakes. Samples were later sieved through a 200-μm mesh. We collected benthic invertebrates from sediments and plants in the littoral habitat using kick nets, and sorted them to the lowest feasible taxonomic level. Samples of sediments and of the most abundant macrophytes (mainly *Potamogeton* spp. and *Nuphar* spp.) were also collected from the littoral zone of each lake. Sediment comprised primarily decaying plant material.

In the laboratory, we measured individual fish total length (±0.1 cm) and wet weight (±0.1 g). A piece of dorsal muscle tissue was dissected from a subsample representative of the length distribution of crucian carp in each lake ($n$ = 30) and frozen at −20°C for later SIA. When possible, we included smaller individuals to avoid under-representation of this size class, especially in a lake with predators. However, young-of-the-year fish were never included in order to remove the influence of this early ontogenetic stage.

**TABLE 1** Environmental characteristics of the study lakes ordered by increasing PC1 score, that is, increasing productivity. Variables include latitude (Lat), longitude (long), lake area (area), maximum depth (MaxD), altitude (alt), Secchi depth (SD), littoral area (lit), specific conductivity (SCond), total nitrogen (TotN), total phosphorus (TotP), total organic carbon (TOC). The first two principal components of the PCA of environmental variables are also included (figure S2)

| Lake | Lat (°N) | Long (°E) | Area (km$^2$) | MaxD (m) | Alt (m a.s.l.) | SD (m) | Lit (%) | SCond (S/cm) | TotN (μg/L) | TotP (μg/L) | TOC (mg/L) | PC1, 55% | PC2, 18% |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Posttjernet | 61.08 | 11.33 | 0.017 | 11 | 270.8 | 2.5 | 26 | 24.3 | 312 | 8 | 9.7 | −3.00 | −1.30 |
| Motjennet | 60.23 | 12.11 | 0.009 | 11.3 | 166.5 | 3.0 | 41 | 11.4 | 688 | 23 | 11.2 | −2.35 | −1.93 |
| Karussputten | 60.02 | 10.66 | 0.003 | 4.6 | 356.0 | 2.0 | 53 | 178.0 | 361 | 9 | 5.4 | −1.97 | 2.01 |
| Øvresetertjern | 59.98 | 10.67 | 0.031 | 3.5 | 478.0 | 1.7 | 84 | 109.1 | 446 | 13 | 6.6 | −1.27 | 1.84 |
| Svartkulp | 59.98 | 10.74 | 0.058 | 10 | 202.0 | 1.2 | 66 | 30.1 | 550 | 13 | 9.9 | −0.97 | −1.19 |
| Småvanna | 59.80 | 10.31 | 0.005 | 3.8 | 222.3 | 1.8 | 70 | 114.6 | 616 | 14 | 10.1 | −0.81 | 0.80 |
| Langmyrtjern | 59.97 | 10.75 | 0.003 | 5 | 206.0 | 1.0 | 70 | 54.3 | 702 | 20 | 14.2 | −0.33 | −0.21 |
| Bjørnmyrdammen | 60.18 | 11.98 | 0.021 | 3.5 | 256.0 | 0.4 | 80 | 24.9 | 672 | 26 | 6.5 | −0.27 | 0.34 |
| Bugårdsdammen | 59.13 | 10.19 | 0.050 | 2 | 42.0 | 1.5 | 100 | 129.4 | 980 | 54 | 9.5 | 1.32 | 0.47 |
| Forkerudstjern | 60.45 | 12.08 | 0.012 | 2.2 | 152.4 | 0.5 | 100 | 82.7 | 1985 | 82 | 23.4 | 2.90 | −0.59 |
| Stomperudtjern | 59.32 | 11.40 | 0.038 | 1.5 | 103.4 | 0.4 | 100 | 186.0 | 1660 | 146 | 18.4 | 3.04 | 0.96 |
| Nusttjennet | 60.28 | 11.66 | 0.110 | 1.5 | 131.0 | 0.4 | 100 | 49.6 | 1090 | 164 | 16.4 | 3.71 | −1.19 |

**TABLE 2** Mean (±SD) total length (TL) of crucian carp used in stable isotope analysis, mean (±SD) catch per unit effort (CPUE) of crucian carp, predator, and competitor fish and number of fish species present in the study lakes

| Lake | TL (cm) | Crucian CPUE ($n \cdot net^{-1} \cdot h^{-1}$) | Predator CPUE ($n \cdot net^{-1} \cdot h^{-1}$) | Competitor CPUE ($n \cdot net^{-1} \cdot h^{-1}$) | *n*. Fish species |
|---|---|---|---|---|---|
| Posttjernet | 19.3 (3.6) | 0.19 (0.19) | 0.01 (0.02) | 0.76 (0.90) | 3 |
| Motjennet | 11.9 (3.0) | 7.8 (5.08) | – | – | 1 |
| Karussputten | 14.5 (3.4) | 0.99 (0.27) | 0.01 (0.03) | 0.14 (0.19) | 2 |
| Øvresetertjern | 28.8 (3.6) | 0.42 (0.61) | 0.23 (0.30) | 1.55 (2.21) | 3 |
| Svartkulp | 19.8 (4.7) | 0.30 (0.41) | 0.16 (0.30) | 0.64 (1.09) | 4 |
| Småvanna | 15.4 (2.2) | 1.03 (1.39) | 0.03 (0.05) | 0.32 (0.43) | 3 |
| Langmyrtjern | 10.7 (2.8) | 2.07 (2.15) | – | 0.62 (1.08) | 2 |
| Bjørnmyrdammen | 18.0 (1.7) | 2.11 (2.39) | 0.02 (0.03) | 0.20 (0.28) | 3 |
| Bugårdsdammen | 31.5 (6.8) | 0.10 (0.06) | 0.17 (0.12) | 1.23 (0.59) | 3 |
| Forkerudstjern | 11.4 (1.9) | 10.63 (6.5) | – | – | 1 |
| Stomperudtjern | 19.1 (9.5) | 0.42 (0.34) | 0.03 (0.03) | 1.72 (2.51) | 6 |
| Nusttjennet | 33.1 (1.6) | 0.45 (0.26) | 0.11 (0.12) | 2.13 (3.19) | 5 |

## 2.2 | Stable isotope analysis and rescaling

Fish muscle, invertebrate, plant, and sediment samples were freeze-dried at −50°C for 48 h, ground to a homogeneous fine powder, weighed, and encapsulated into tin cups. We analysed stable carbon and nitrogen isotope ratios using a Costech 4010 elemental analyser (Costech, California, USA) coupled to a Delta Plus continuous flow mass spectrometer (Thermo Finnigan, Bremen, Germany). Precision of internal standards was better than 0.1‰ for $\delta^{13}C$ and 0.2 ‰ for $\delta^{15}N$. Elemental C:N ratios were low in all fish samples (3.3 ± 0.1) indicating low lipid concentrations and $\delta^{13}C$ values were arithmetically lipid-corrected prior to analyses (Kiljunen et al., 2006).

Since basal food isotope ratios varied greatly across lakes, it was necessary to take into account this variation when comparing changes in isotopic niche of crucian carp. In order to remove this variation not associated with trophic changes and make fish isotopic values directly comparable, we used a method based on modified Z-scores (Fry & Davis, 2015). This method was adapted by Lejeune et al. (2021) to compare isotopic values of newts from different communities. Isotope values of consumers were standardised by rescaling raw isotope data into modified Z-scores using the mean and standard deviation of their prey community at each location. In this study, the mean of pelagic zooplankton, pooled benthic macroinvertebrates collected from the littoral area, and pooled plant and sediment were used as sources for calculation of the parameters (Table S1). Rescaled stable isotope values are expressed using a Δ notation instead of δ notation and conserve the original measurement unit (‰ deviation from international standards).

## 2.3 | Diet analysis

We examined the gut contents of all the fish which were used in SIA. When feasible, we included more individuals to increase sample size, since fish with empty gut were excluded from the analysis. We estimated the proportion occupied by each prey category observed in the anterior third of crucian carp gut under a stereomicroscope using percentage scale. Pelagic prey included (I) pelagic cladocerans (mainly *Bosmina* sp., *Daphnia* sp.), (II) copepods (Calanoida and Cyclopoida), (III) other rare pelagic prey items (chironomid pupae, water mites, Chaoborid larvae); benthic prey comprised (IV) chironomid larvae, (V) gastropods, (VI) benthic cladocerans (mainly *Chydorus* spp.), and (VII) other benthic invertebrates (Odonata nymphs, Trichoptera, Ephemeroptera, and Coleoptera larvae, *Asellus aquaticus*, ostracods). We also observed (VIII) plant (mainly filamentous algae and macrophytes) and (IX) sediment, largely composed of decaying organic material.

Diet breadth was quantified using the Levins' index standardised for resource richness (Krebs, 1999). The index ranges between 0 and 1 and is used to show the relative level of diet specialisation at the population level. Low index values characterise a population diet dominated by few prey items, while high values are indicative of a more generalist diet. In addition, we assessed the relative degree of IS measuring the proportion of the total niche width explained by within-individual variation (Bolnick, Yang, Fordyce, Davis, & Svanbäck, 2002; Roughgarden, 1974). Values approaching 1 indicate that all individuals utilise the full range of the population's niche, while values near 0 indicate high IS. We calculated Levins' index and IS using the R package “RInSp” (Zaccarelli, Bolnick, & Mancinelli, 2013).

## 2.4 | Statistical analysis

### 2.4.1 | Environmental structure

We used the abiotic variables measured at each lake to explore potential environmental drivers of variation in the raw stable isotope values of basal sources ($\delta^{13}C$ and $\delta^{15}N$ of littoral invertebrates, zooplankton, and plants and sediments), and crucian carp among the different systems. Abiotic variables included lake morphometry and physical–chemical factors (Table 1). We identified main environmental gradients reducing the set of our abiotic variables using principle component analysis (PCA). Then, we explored the association between the first two PC axes and basal resource values through correlation analysis (i.e. Pearson correlation coefficient).

### 2.4.2 | Crucian carp resource use and niche width

In order to estimate the predominant trophic resource use of crucian carp at the population level, we used Bayesian isotope-mixing models from the R package 'simmr' (Parnell, Inger, Bearhop, & Jackson, 2010). Mean and standard deviation of pelagic zooplankton (PEL), pooled benthic invertebrates (LIT) and combined plant and sediment (SED) were used as baseline values. Trophic fractionation values of 3.4 ± 1.0‰ for $\delta^{15}N$ and 0.4 ± 1.3‰ for $\delta^{13}C$ were used in the model (Post, 2002). Difference in trophic resource use of crucian carp among lakes was compared by looking at the overlap of the 95% credibility limits of each source. Moreover, we performed generalised linear mixed-effects models to test for the effects of size (TL), productivity (PC1), and density of crucian carp (CPUEcrucian), competitor fish (CPUEcomp), and predators (CPUEpred) on individual $\Delta^{13}C$ and $\Delta^{15}N$ values, as calculated from the modified Z-scores. We also included interactions of crucian carp size with predator and competitor fish density and considered "Lake" as random effect. The full model equation was: $\Delta^{13}C/\Delta^{15}N \sim PC1 + CPUEcrucian + TL^{*}CPUEcomp + TL^{*}CPUEpred$. Variance inflation factor (VIF) was used to detect potential multicollinearity. As values indicated low correlation ($VIF < 2.3$), all predictor variables were included in the full model. Selection of the best models was performed by backward elimination of nonsignificant fixed-effect terms. We investigated diet shifts related to body size measuring Pearson correlation coefficient between the mean total length of crucian carp from each lake and the relative proportion of littoral prey, pelagic prey, and pooled plant and sediment in gut contents. Finally, we calculated the isotopic niche width of crucian carp in each lake as the standard ellipse area corrected for small sample sizes (SEAc) using 'Stable Isotope Bayesian Ellipses in R' (SIBER; Jackson, Inger, Parnell, & Bearhop, 2011). The isotopic niche space consisted of the individual $\Delta^{13}C$ and $\Delta^{15}N$ values. We interpreted differences in niche areas examining the overlap of the 95% credible intervals.

## 3 | RESULTS

### 3.1 | Environmental characteristics

Stable isotope values of basal sources (littoral invertebrates, zooplankton, plants, and sediments), and crucian carp varied greatly among the different lakes (Figure 1). At the population level, we observed the lowest $\delta^{15}N$ ratios for crucian carp in Karussputten (3.6 ± 0.4‰) and the highest in Stomperudtjernet (13.6 ± 1.2‰). The lowest $\delta^{13}C$ ratios were measured in Småvanna (−36.5 ± 1.4‰) and the highest in Øvresetertjern (−28.1 ± 0.5‰). The first two axes of the PCA accounted for 74% of the variation in the predictor variables (Figure S2). The first axis explained 56% of the variance and was loaded positively by all nutrient values and littoral area and negatively by maximum depth and transparency. Specifically, lakes were increasingly shallow, turbid, and productive along PC1 axis. Thus, we interpreted this axis as a gradient in lake productivity. The second axis explained 18% of the variance and was positively loaded to specific conductivity and altitude and negatively to maximum depth and total organic carbon. We found positive correlations between productivity gradient and nitrogen values of fish and all baselines (Figure S3), as PC1 axis was positively correlated with $\delta^{15}N$ of crucian carp ($r = 0.82$, $p < .001$), zooplankton ($r = 0.88$, $p < .001$), littoral invertebrates ($r = 0.72$, $p < .001$), plants ($r = 0.73$, $p < .001$) and sediments ($r = 0.54$, $p = .006$). The correlation between productivity gradient and $\delta^{13}C$ was statistically significant only for crucian carp ($r = 0.29$, $p < .001$). We also found positive correlation between PC2 axis and sediment nitrogen values ($r = 0.51$, $p = .009$) and zooplankton carbon values ($r = 0.39$, $p = .024$). However, variation along this axis seems mainly driven by a few relatively deeper lakes, and correlations should be interpreted carefully.

### 3.2 | Fish community

A total of 10 fish species was recorded from the study lakes. Crucian carp density and fish community composition showed different patterns (Figure S4). Small lakes were inhabited mainly by high densities of crucian carp (Motjennet and Forkerudstjern), or by crucian carp and minnow (*Phoxinus phoxinus;* Langmyrtjern). Crucian carp coexisted with brown trout (Posttjernet, Karussputten, and Småvanna) or brown trout and perch (Svartkulp and Øvresetertjern) in mesotrophic lakes. Minnow also occurred in some of these lakes (Posttjernet, Småvanna, and Svartkulp). In Bjørnmyrdammen only perch was present together with a very low density of tench (*Tinca tinca*). In large and productive lakes (Bugårdsdammen, Stomperudtjern, and Nusttjennet), perch and pike were the main predator fish species present. In particular, lakes Stomperudtjern and Nusttjennet presented the richest number of species, including high densities of roach (*Rutilus rutilus*), bream (*Abramis brama*), and rudd (*Scardinius erythrophthalmus*), while perch and pike occurred at low densities.

### 3.3 | Crucian carp trophic resource use

Fish community structure, productivity, and individual body size were all important determinants of crucian carp trophic resource use. Results of model selection show that variation in $\Delta^{13}C$ values was mainly explained by fish body size, productivity, predator density, and the interaction of fish size with predator density. In

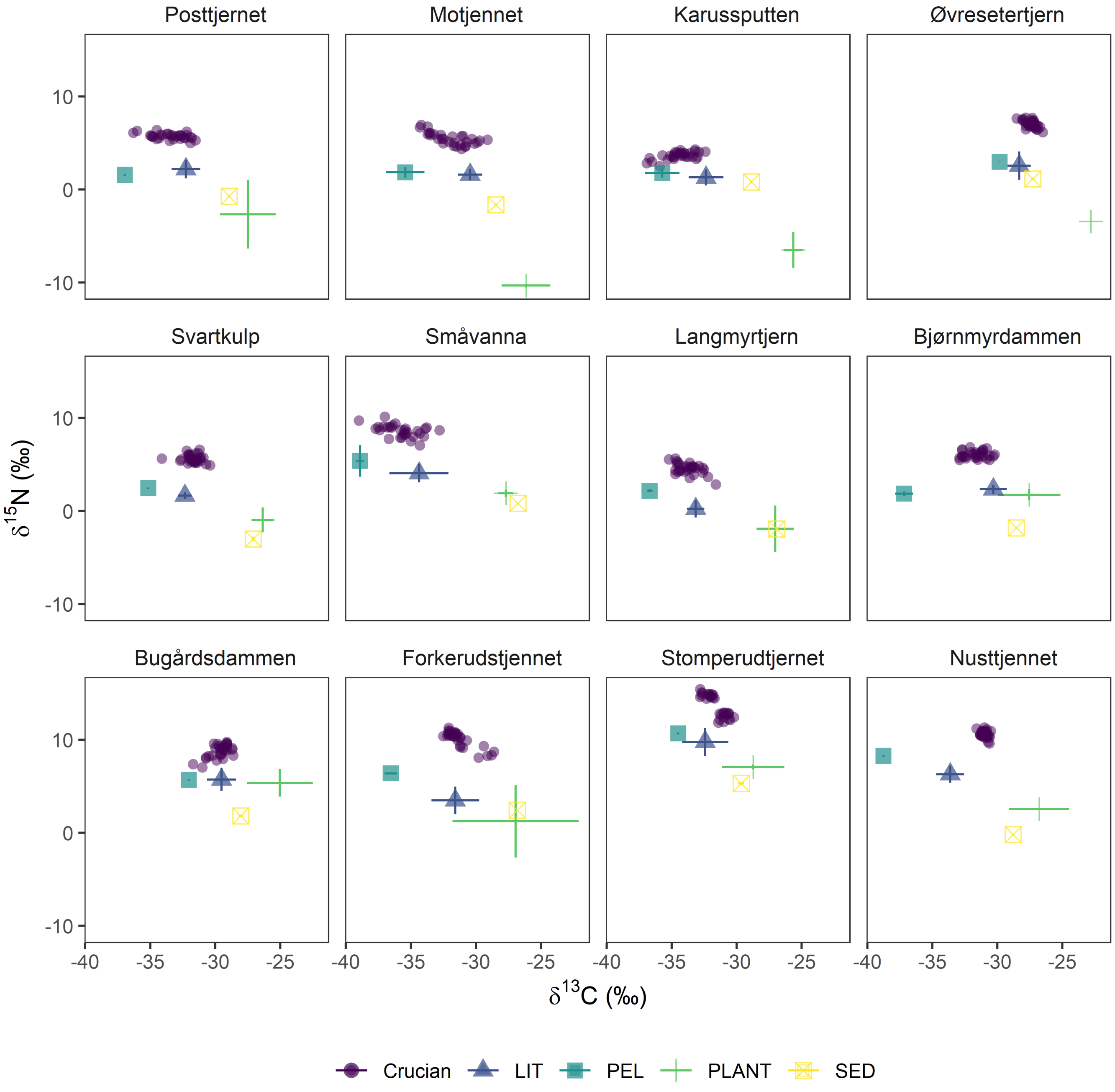

**FIGURE 1** Stable isotope biplots of $\delta^{15}$N and $\delta^{13}$C of crucian carp and basal food sources (means ± SD) from 12 lakes ordered by increasing PC1 score, as per Table 1

particular, $\Delta^{13}$C values showed a strong positive association with productivity (Table 3; Figure 2a). Fish body size and its interaction with predator density had also a significant effect on $\Delta^{13}$C values. In general, small individuals showed great variation in $\Delta^{13}$C values, while larger fish from lakes with high predator density were more $^{13}$C enriched (Figure 2b). Results of model selection show that variation in $\Delta^{15}$N values was explained mainly by fish body size, competitor density, and their interaction. Fish body size and its interaction with competitor density had a significant effect on $\Delta^{15}$N values (Table 3). In particular, $\Delta^{15}$N values of large crucian carp above ~15 cm in size varied greatly in comparison with small individuals (Figure 2c).

Bayesian mixing models revealed great variation in crucian carp trophic resource use. Reliance on plants and sediment increased in productive lakes (Figure 3), which could contribute to explain the higher $^{13}$C values observed from generalised mixed models. Reliance on pelagic and littoral resources did not show a clear pattern. In general, crucian carp from populations with small average body size seemed to rely more on pelagic rather than littoral invertebrates. Mottjennet represented an exception to this pattern, although gut content analysis revealed that pelagic prey, and particularly cladocerans, made up the largest proportion of the diet (Table 4). On the contrary, with increasing average body size, fish seemed to rely mostly on littoral invertebrates or on littoral and pelagic resources in similar proportions. Gut content analysis confirms this pattern, as average body size was positively correlated with the proportion of littoral prey ($r = 0.85$, $p < .001$; Figure S5) and negatively correlated with the proportion of pelagic prey ($r = -0.82$, $p = .001$). However, body size was not correlated with the proportion of pooled plants and sediments ($r = -0.45$, $p = .14$).

### 3.4 | Crucian carp niche size

Standard ellipse area of $\Delta^{13}$C and $\Delta^{15}$N isotope ratios of crucian carp varied among lakes. Populations from predator-free lakes with small fish (Motjennet, Langmyrtjern, and Forkerudstjern), and lakes with low productivity (Posttjernet, Karussputten, Øvresetertjern, and Svartkulp), had smaller isotopic niches compared to populations from more productive lakes (Figures 4 and Figure S6). Fish from these lakes had also a very similar diet breadth index (Table 4). Bugårdsdammen had the largest isotopic niche area, although diet breadth and inter-individual variation appeared to be low. In this lake, however, benthic invertebrates made up 60.2% of the diet and were grouped in a single category even if they constituted a very heterogeneous group, including coleopterans and *Asellus aquaticus*, possibly underestimating diet breadth and inter-individual variation. As to the opposite, Nusttjernet, a productive lake with large fish, presented a remarkably low isotopic niche area. Fish from this lake had also the lowest interindividual variation in diet and very similar sizes. In particular, fish showed specialisation on benthic cladocerans, mainly small bottom-dwelling chydorids, which accounted for more than 50% of the diet (Table 4). Chydorids were also the main diet item of crucian carp from Stomperudtjern, which had very similar environmental characteristics to Nusttjernet. Crucian carp from Stomperudtjernet, however, grouped clearly in large and small individuals in isotopic space, resulting in a wider niche area (Figure 4).

TABLE 3 Results of the best linear mixed models explaining the relation between rescaled $\Delta^{13}$C and $\Delta^{15}$N values of crucian carp and environmental variables

| | Estimate (±SE) | *t*-value | *P*-value |
|---|---|---|---|
| Selected model: $\Delta^{13}$C ~ Size + Predators CPUE + Size: Predators CPUE + Productivity | | | |
| (Intercept) | −0.26 (±0.31) | −0.83 | .415 |
| Size | −0.03 (±0.01) | −3.36 | .001* |
| Predators CPUE | 0.15 (±0.32) | 0.47 | .642 |
| Productivity (PC1) | 0.96 (±0.24) | 3.91 | .003* |
| Size: Predators CPUE | 0.03 (±0.01) | 2.96 | .003* |
| Selected model: $\Delta^{15}$N ~ Size + Competitor CPUE + Size:Competitor CPUE | | | |
| (Intercept) | 4.01 (±0.65) | 6.17 | .000* |
| Size | 0.08 (±0.01) | 8.84 | .000* |
| Competitor CPUE | −1.11 (±0.63) | −1.76 | .11 |
| Size: Competitor CPUE | 0.01 (±0.01) | 2.45 | .015* |

* denote statistically significant value ($P < .05$).

## 4 | DISCUSSION

Crucian carp showed great variation in trophic resource use. Productivity, individual body size, and interspecific interactions were all important underlying factors of niche use. Low densities of large fish were found in shallow lakes in association with different sympatric fish species, including top predators such as pike. In general, in these macrophyte-dominated lakes, crucian carp used more littoral prey sources. In contrast, small crucian carp were typical in lakes where other species were absent or present in very low densities. Here, constituted an important part of their diet.

Crucian carp and all basal resources had increasingly higher nitrogen-stable isotope values ($\delta^{15}$N) along the productivity axis. Nutrient inputs from agriculture or sewage usually elevate $\delta^{15}$N ratio at the base of the food chain (Kendall, Elliott, & Wankel, 2007),

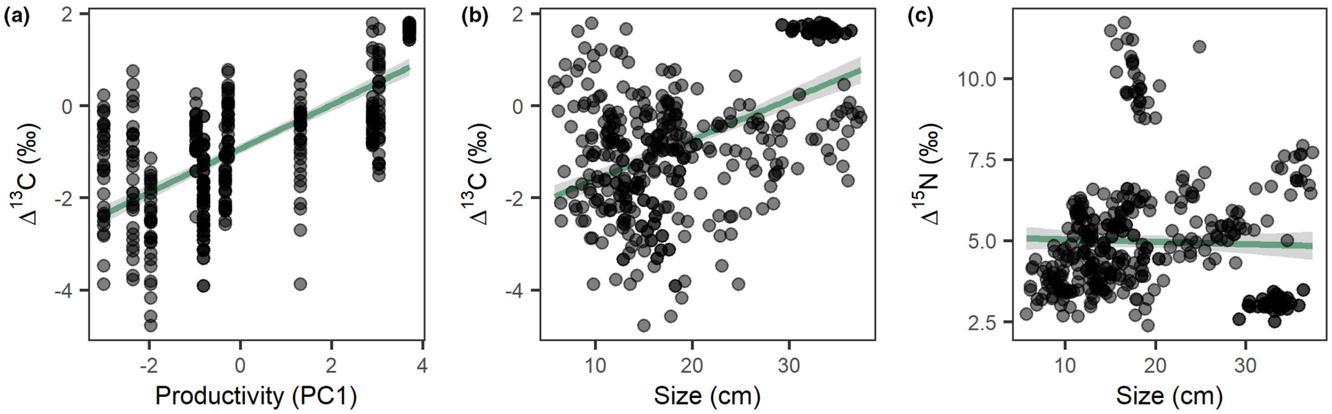

FIGURE 2 Relationship between rescaled $\Delta^{13}$C values of crucian carp and (a) productivity (PC1) and (b) individual body size (cm), and between (c) rescaled $\Delta^{15}$N values of crucian carp and individual body size (cm). The 95% confidence level interval for predictions from a linear model is shown for each plot

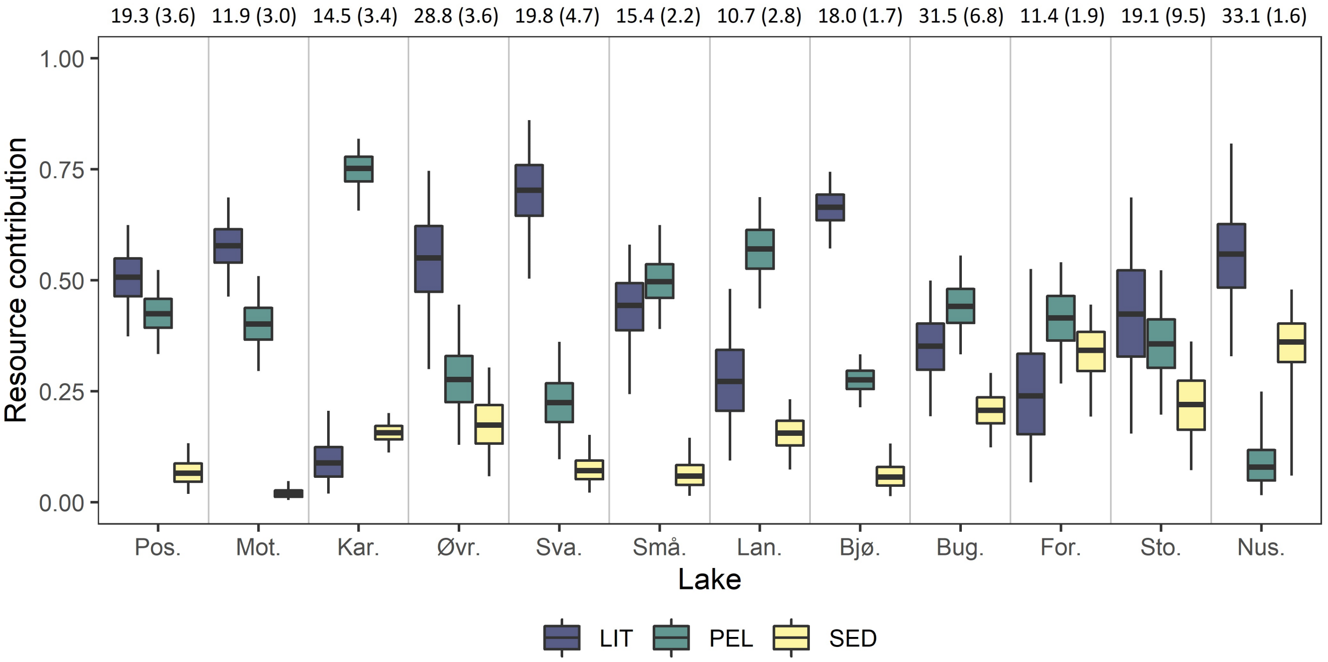

**FIGURE 3** Littoral (LIT), pelagic (PEL), and pooled plant and sediment (SED) resource use of crucian carp for each lake according to the Bayesian isotope mixing models. The box is drawn around the 25th and 75th quartiles, representing 50% credible intervals, while whiskers represent 95% credible intervals. Numbers show mean (±SD) total length of crucian carp. Lakes are arranged in order of their PC1 score, as per Table 1

**TABLE 4** Diet composition of crucian carp in the study lakes. Standardised Levins' index indicating population diet breadth, individual specialisation (IS, where 0 = complete individual specialisation, 1 = no individual specialisation), number of full stomachs analysed (*n*), and standard ellipse area (SEA$_c$) of crucian carp niche in rescaled isotopic space ($\Delta^{13}$C, $\Delta^{15}$N) are also shown

| Prey items (%) and diet metrics | Lake | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pos. | Mot. | Kar. | Øvr. | Sva. | Små. | Lan. | Bjø. | Bug. | For. | Sto. | Nus. |
| (I) Pelagic cladocerans | 38.1 | 55.9 | 27.4 | 13.6 | 15.1 | 33.6 | 57.8 | 61.8 | 12.3 | 43.1 | 30.8 | 13.2 |
| (II) Copepods | 0 | 16.9 | 0 | 3.2 | 2.0 | 3.2 | 0 | 0.5 | 0.3 | 4.9 | 2.4 | 2.9 |
| (III) Pelagic invertebrates | 1.4 | 0 | 9 | 0 | 12.8 | 0 | 0.4 | 1.4 | 2.3 | 0.9 | 0 | 0.1 |
| (IV) Chironomid larvae | 2.3 | 7.5 | 46.1 | 9.2 | 17.7 | 5.4 | 2.2 | 10.4 | 7.2 | 5.0 | 2.2 | 17.0 |
| (V) Gastropods | 1.7 | 0 | 0 | 3.2 | 0 | 0 | 0 | 0.4 | 5.7 | 0 | 0 | 1.0 |
| (VI) Benthic cladocerans | 6.7 | 6.9 | 7.9 | 6.0 | 6.0 | 5.3 | 1.7 | 8.9 | 4.3 | 0 | 57.8 | 50.5 |
| (VII) Benthic invertebrates | 44.2 | 11.1 | 7.7 | 59.6 | 28.2 | 14.8 | 8.1 | 12.9 | 60.7 | 8.9 | 5.9 | 11.5 |
| (VIII) Plant | 0 | 0 | 0.6 | 1.2 | 0 | 3.2 | 1.5 | 1.2 | 4.8 | 35.6 | 0.2 | 1.5 |
| (IX) Sediment | 5.9 | 1.7 | 1.1 | 4.0 | 18.2 | 34.5 | 28.3 | 2.5 | 2.3 | 1.6 | 0.7 | 2.3 |
| Pelagic prey | 39.5 | 72.8 | 36.4 | 16.8 | 29.9 | 36.8 | 58.1 | 63.7 | 15.0 | 48.9 | 33.2 | 16.2 |
| Benthic prey | 53.2 | 25.4 | 61.8 | 74.8 | 51.9 | 25.5 | 12.0 | 32.1 | 72.2 | 13.9 | 66.0 | 79.0 |
| Sediment | 5.9 | 1.7 | 1.8 | 5.2 | 18.2 | 37.7 | 29.8 | 3.8 | 7.4 | 37.2 | 0.8 | 3.8 |
| Standardised Levins' index | 0.41 | 0.55 | 0.54 | 0.35 | 0.89 | 0.64 | 0.40 | 0.30 | 0.31 | 0.51 | 0.38 | 0.36 |
| IS | 0.61 | 0.68 | 0.57 | 0.75 | 0.65 | 0.64 | 0.30 | 0.59 | 0.82 | 0.56 | 0.78 | 0.89 |
| *n* | 22 | 38 | 31 | 25 | 25 | 33 | 27 | 28 | 30 | 47 | 53 | 46 |
| SEA$_c$ | 1.14 | 1.18 | 0.97 | 1.19 | 0.59 | 1.58 | 0.80 | 1.43 | 2.82 | 0.94 | 1.79 | 0.05 |

*Note:* Pelagic prey (%) was calculated as the sum of I, II, and III, Benthic prey (%) as the sum of IV, V, VI, and VII and Sediment (%) as the sum of VIII and IX.

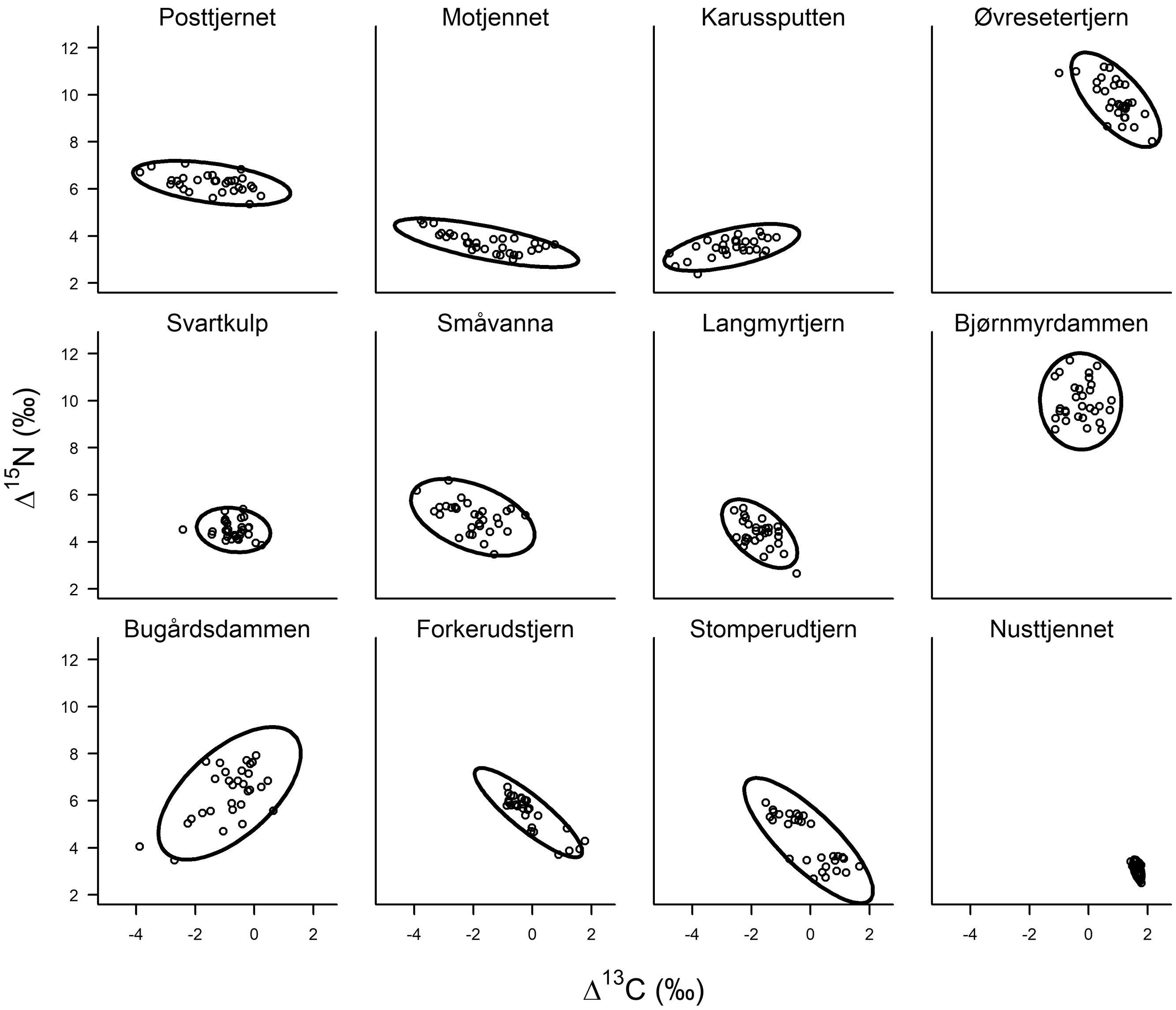

**FIGURE 4** Standard ellipse areas ($SEA_c$) representing the core isotopic niche space of crucian carp as determined through SIBER models. Lakes are arranged in order of their PC1 score, as per Table 1. Please note that *x*- and *y*-axis values are the rescaled isotope values

and thus increase $\delta^{15}N$ ratio of all consumers (Botrel, Gregory-Eaves, & Maranger, 2014; Harrington, Kennedy, Chamberlain, Blum, & Folt, 1998). This large variation in isotopic ratios is common in many other eutrophic lakes (e.g. Vuorio, Meili, & Sarvala, 2006). Raw carbon stable isotope values of crucian carp showed also a weak positive correlation with productivity. Yet, even after accounting for this variation in the baselines, productivity represented one of the main drivers of fish trophic resource use. Reliance on $^{13}C$-enriched resources increased along the productivity gradient, and fish included higher proportions of sediments and plants in the most eutrophic lakes. Fish community structure was also shifting from a dominance of brown trout to perch and finally to high densities of cyprinids along the productivity gradient, as previously observed on broader spatial scales (Hayden et al., 2017). In turn, fish species composition, and in particular progressively efficient gape-size-limited predators, can determine an increase in body height and size of crucian carp (de Meo et al., 2021). Thus, trying to tell apart the main drivers explaining crucian carp resource use can be hampered by the fact that productivity and community structure were highly interconnected, although explanatory variables were not directly correlated in our study.

Body size was a determining variable in trophic resource use of crucian carp, as fish included more littoral prey in their diet with increasing size. In lakes where no potential predators were present, crucian carp occurred in high densities and small sizes. In these systems, fish relied mainly on pelagic resources. Diet analysis confirmed that PEL (mainly *Bosmina* sp.) represented an important food item in all lakes, while chironomids were always included in the diet in lower proportions. Crucian carp may undergo diet shifts associated with size-specific differences in their ability to ingest prey. Previous studies show that in allopatric lakes the preference for larger prey items increased with fish size, as large insect larvae (e.g. Odonata) were consumed exclusively by fish larger than 13 cm (Penttinen & Holopainen, 1992). Size-related shifts in feeding efficiency of crucian carp have also been demonstrated in the laboratory (Paszkowski, Tonn, & Holopainen, 1989). Our results confirm this pattern as almost all fish from predator-free lakes were below 13 cm and did not include large invertebrates in their diet. However, fish from these lakes also relied on other low-quality resources such as plants and sediments. In particular, in the eutrophic lake Forkerudtjennet, fish included a large proportion of filamentous algae in their diet. Consumption of few prey items such as filter-feeding zooplankton, sediments, or plant material; and exclusion of large predatory benthic copepods or macroinvertebrates from the diet, could also explain the low trophic position and small niche size of crucian carp populations from these lakes. By contrast, with increasing body length, crucian carp seemed not to be limited by a small gape size, as fish were including higher proportions of large macroinvertebrates in their diet.

Higher reliance on pelagic prey could also be associated with an increase in use of the open water zone in absence of predation risk, whereas fish may be confined to the littoral area when a predator was present (Diehl & Eklöv, 1995; Pettersson & Brönmark, 1993). Nevertheless, fish included variable proportions of pelagic resources in their diet even in presence of predators, probably because large fish outside of the predation window would be able to move more freely between open water and shoreline and feed on resources from both lake areas (Werner & Hall, 1988). Moreover, in absence or low density of predators, crucian carp occurred in high densities, and intraspecific competition for food may have determined an increase of among-individual diet variation. By contrast, in productive lakes with predators, crucian carp occurred in low densities and resources were likely very abundant, resulting in low intraspecific competition and IS (Svanbäck & Bolnick, 2007). Predation risk may have also decreased the degree of individual diet variation because of restricted habitat availability and limitation of alternative food sources (Eklöv & Svanbäck, 2006). At the same time, differences in IS might reflect variation in body size compositions among lakes. For example, low IS of crucian carp might indicate a narrow body size range, as it was not possible to include small individuals in all the lakes. This could be the case of Nusttjernet, where there were mainly large crucian carp of similar size.

The presence of competitor species might have also played an important role in crucian carp dietary preferences. In lakes Nusttjernet and Stomperudtjernet, where high densities of different cyprinid species were present, crucian carp included large proportions of small benthic cladocerans in their diet. Previous studies show that omnivorous common carp (*Cyprinus carpio*) and roach are competitor species, where the latter has a higher competitive edge on zooplanktivory (García-Berthou, 2001; Nahon et al., 2020). As to the opposite, bream is a more efficient benthivore than crucian carp and is able to penetrate deep into the sediment and feed on benthic macroinvertebrates of large sizes (Lammens, Geursen, & McGillavry, 1987; Persson & Hansson, 1999). Thus, crucian carp may have been limited to feed on a restricted subset of the total prey spectrum as a result of resource partitioning with other cyprinids. Large proportions of small chydorids in the diet of crucian carp may also explain the low trophic position of fish from these lakes. Competition with minnow might also have influenced crucian carp trophic resource use as they occupy mainly the shallower parts of the littoral zone and can maintain very high population density (Museth, Borgstrøm, Brittain, Herberg, & Naalsund, 2002). Indeed, in Langmyrtjern, crucian carp occurred only with minnow and had the lowest average body size and the highest specialisation among all study lakes, since fish were feeding either on sediments or on zooplankton. This suggests that the combined effect of high intra- and interspecific competition might have constrained crucian carp diet breadth and favoured IS, with negative effects on individual growth. Moreover, these competitive interactions may be intensified in presence of brown trout or perch, as minnow increase their use of shallow waters when occurring with piscivorous species (Eklöv, Greenberg, & Kristiansen, 1994; Museth, Borgstrøm, & Brittain, 2010). In lakes Bjørnmyrdammen, Øvresetetjern, and Bugårdsdammen, where no other cyprinid species was present and small perch represented the main competitor species, crucian carp had distinctly higher nitrogen ratio and included larger proportions of macroinvertebrates in their diet, indicating utilisation of different resources compared to the other lakes. Thus, crucian carp may have been limited to feed on a restricted subset of the total prey spectrum, as a result of resource partitioning with other cyprinids.

Interestingly, crucian carp managed to reach very large body sizes even in lakes with high densities of competitor species and predation risk. These lakes corresponded to the most productive systems and likely presented complex habitat structure and abundant food resources. Here, littoral prey such as benthic cladocerans may be largely available and sustain crucian carp growth even in competitive environments. However, the lack of data on resource abundance prevents us from estimating habitat profitability. Moreover, experimental studies suggest that crucian carp growth is directly or indirectly mediated by predator presence. Better growth conditions seem to be associated with a reduction in activity levels after exposure to predation cues (Holopainen, Aho, Vornanen, & Huuskonen, 1997; Vøllestad, Varreng, & Poleo, 2004). This reduction in activity may save energy, which is then allocated to somatic growth, eventually determining large body sizes (Johansson & Andersson, 2009). Exposure to predators has been also proposed to activate the stress axis and induce the expression of antipredator traits for surviving in risky environments (Vinterstare et al., 2020). Early life stress can have long-term consequences on fish growth, morphology, life-history, and behavioural traits (Jonsson & Jonsson, 2014). Thus, besides resource use, epigenetic effects and energy use may play an important role in crucian carp growth.

Crucian carp changed trophic resource use and food preferences according to variations in specific environmental variables. Fish included more littoral prey sources in their diet with increasing body size, fish community complexity, and lake productivity, all highly interconnected factors. Small fish from allopatric populations, able to use the pelagic habitat in absence of predators, were relying predominantly on zooplankton. Big fish, probably released from gape-limited predators, were able to get larger proportions of benthic macroinvertebrates in their diet. Variation in crucian carp body size composition was a major factor determining changes in resource use among the lakes. However, as for other field studies (Brönmark, Paszkowski, Tonn, & Hargeby, 1995; Vornanen, Asikainen, & Haverinen, 2011), small crucian carp from lakes with predators had very low catchability. These individuals are highly vulnerable to predation and may have very low activity levels. Future studies should include small-sized fish in order to compare resource use of crucian carp of similar size classes among lakes with different environmental characteristics, and remove the effect of body size.

Resource use of cyprinids seems highly context-dependent, and variation in their foraging preferences may have considerable implications for the ecology of freshwater communities (Driver, 2005; Nieoczym & Kloskowski, 2014; Persson & Brönmark, 2002). Crucian carp showed high plasticity in trophic resource use that reflected specific changes in community structure and productivity, suggesting that overlooking the complex diet preferences of generalist fish may lead to an oversimplification of the dynamics of these lake ecosystems.

## AUTHOR CONTRIBUTIONS

**IdM:** Conceptualisation, formal analysis, investigation, methodology, writing – original draft. **KØ:** Conceptualisation, methodology, resources, writing – review & editing. **KKK:** Conceptualisation, formal analysis, methodology, writing – review & editing. **BH:** Conceptualisation, formal analysis, resources, writing – review & editing. **MM:** Conceptualisation, investigation, writing – review & editing. **ABSP:** Conceptualisation, project administration, resources, writing – review & editing.

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## CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in DataverseNO at https://doi.org/10.18710/WQWO24.

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