Interannual variability in the trophic niche of young-of-year fish belonging to four piscivorous species coexisting in a natural lake

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Interannual variability in the trophic niche of young-of-year fish belonging to four piscivorous species coexisting in a natural lake

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Abstract

1. Predatory fish species play a key role in aquatic ecosystems by exerting top-down control on the food web. Also, their intra-guild trophic interactions (i.e. competition) are crucial for the stability of the community. However, most studies focus on adult stages, while juveniles remain poorly studied, although their recruitment is the basis for the maintenance of predator populations.

2. We analysed carbon and nitrogen stable isotopes ratios of the young-of-year of four coexisting widespread predatory fish species (northern pike *Esox lucius*, European perch *Perca fluviatilis*, pikeperch *Sander lucioperca*, and European catfish *Silurus glanis*), sampled over 3 years in a shallow natural lake.

3. We found that the hierarchy in trophic position between species was consistent across years and similar to that known for adults, but with large variations around a general pattern: pike and pikeperch tended to occupy the highest trophic positions while perch occupied the lowest, and catfish had very varying positions.

4. Species partitioned their niches to decrease interspecific competition, but with some occasional overlaps, contributing to preserving their body condition. Depending on density, which was particularly impacted by harsh environmental conditions, niche overlap fluctuated across years, leading to niche enlargement of densely populated species, except for catfish.

5. These mechanisms enabled species coexistence, allowing the co-occurrence of alien and native predators within the same ecosystem.

6. This work advocates for time-integrated studies of trophic webs because they capture the variability of their dynamics better than a static picture. This is particularly true for juveniles whose survival strongly depends on their capacity to cope with competition. Information from trophic mid-term studies of juveniles provides valuable guidance for optimised management of species.

KEYWORDS
Esox lucius, *Perca fluviatilis*, *Sander lucioperca*, *Silurus glanis*, stable isotopes

1 | INTRODUCTION

In aquatic ecosystems, both trophic complexity and consistency have manifold implications for the functioning and stability of trophic webs (Rooney & McCann, 2012). Trophic webs are characterised by the flow of energy reflecting trophic interactions among organisms and ultimately leading to a community structuring (Rooney et al., 2008; Thompson et al., 2012). Within insular systems (such as lakes), resources tend to be limited (Essington & Carpenter, 2000). External and internal stressors can induce fluctuations that lead to shifts in the flow of energy and thus, relocation of biomass and changes in species interactions and trophic positions (TPs) (Sentis et al., 2017; Su et al., 2021). Organism groups such as fish are prone to trophic variability and thus they occupy variable niche space, which in turn may reflect the use of resources or occupied habitats (Haubrock, Balzani, et al., 2021).

Predatory fish species play a crucial role within trophic webs by exerting predatory pressure on lower trophic levels, limiting competition among species within the same guild (top-down control) (e.g. Baum & Worm, 2009; Rosenfeld, 2000). They also compete with each other for prey, resulting in a fragile context-dependent equilibrium, with changes in their abundance having cascading consequences for lower trophic levels (Carpenter et al., 1985; Rooney et al., 2006). In Europe, northern pike *Esox lucius* Linnaeus, 1758, hereafter pike, European perch *Perca fluviatilis* Linnaeus, 1758, hereafter perch, pikeperch *Sander lucioperca* (Linnaeus, 1758), and European catfish *Silurus glanis* Linnaeus, 1758, hereafter catfish, are four widespread predators in lakes, the last two being known alien invasive species in many regions (Copp et al., 2009; Cucherousset et al., 2018; Kottelat & Freyhof, 2007). Although these species can frequent multiple habitat types with seasonal variations (e.g. De Santis & Volta, 2021; Vagnon et al., 2022), they have some habitat preferences. Pike are mainly littoral and prefer vegetated areas (Chapman & Mackay, 1984; Craig, 1996; Jepsen et al., 2001) while pikeperch are nocturnal and mainly frequent the pelagic area (Huuskonen et al., 2019; Vehanen & Lahti, 2003). Perch are in-between pike and pikeperch (Hölker et al., 2007; Schulze et al., 2006; Westrelin et al., 2021) whereas catfish prefer benthic habitats and mainly the lower third of the water column (Copp et al., 2009; Cucherousset et al., 2018; Pohlmann et al., 2001). These differences also seem to exist between juvenile stages (Craig, 2008; Luchiari et al., 2006; Slavík et al., 2007, 2012; Treasurer, 1988), which could favour trophic segregation.

These four species are primarily piscivorous as adults, even if variability in their diet has been reported (Campbell, 1992; Craig, 2008; Dörner et al., 2003; Vejřík et al., 2017). In general, pikeperch is a piscivorous specialist (Huuskonen et al., 2019; Kangur & Kangur, 1998) that occupies the highest position in the trophic web (Pérez-Bote & Roso, 2012), often higher than pike, which is also mainly piscivorous but more plastic (Craig, 2008; Kopp et al., 2009; Pedreschi et al., 2015). By contrast, perch is a generalist species and catfish opportunistic (Dörner et al., 2003; Schulze et al., 2012; Vagnon et al., 2022; Vejřík et al., 2017). These species also undergo some ontogenetic variations in diet.

Pike, pikeperch, and perch feed on zooplankton and other invertebrates when juveniles but then become piscivorous (Jacobson et al., 2019; Matěna, 1998; Mittelbach & Persson, 1998; Vašek et al., 2018; Yazıcıoğlu et al., 2018), while catfish shift from a diverse diet composed of crustaceans, molluscs, and fish as juveniles to a mainly piscivorous diet as adults (Rossi et al., 1991; Syväranta et al., 2010). However, while their function in freshwater ecosystems has often been examined within trophic webs, most studies on trophic interactions between these species concern adults only and, in contrast, the feeding ecology of young-of-year (YOY) remains poorly understood (Nunn et al., 2012).

Resource partitioning is one of the most important mechanisms allowing species coexistence (Chase & Leibold, 2003; Chesson, 2000; Schoener, 1986). The competitive exclusion principle (niche theory) states that sympatric species can not have completely overlapping niches (Gause, 1934; Hardin, 1960). Equally, the theory of limiting similarity states that there is some maximum level of similarity possible (Abrams, 1983). Niche differences are stabilising mechanisms that permit species coexistence in niche theory as well as in the more recent coexistence theory, and the intraspecific variability that affects intraspecific competition is also a crucial process (Chesson, 2000; Chu et al., 2017). As an outcome of high intra- and/or interspecific competition and limited resource availability, lower body condition is expected (De Santis et al., 2022; Gaygusuz et al., 2013; Kamimura et al., 2021; Verdiell-Cubedo et al., 2006).

The introduction of invasive fish species directly impacts recipient ecosystems by restructuring trophic webs (Bissattini et al., 2021; Haubrock et al., 2019) and increasing interspecific variability. This can lead to negative interactions with native species (Champneys et al., 2021; Haubrock et al., 2018; Martin et al., 2010), for example in cases when invasive and native species have overlapping niches (Haubrock, Pilotto, et al., 2021). The analysis of carbon and nitrogen stable isotopes is a powerful tool to obtain long-term and time-mediated information on the trophic structure of communities (Layman et al., 2012; Post, 2002) and can give useful insights into how species coexist and how alien species integrate into the native food web (Gutmann Roberts & Britton, 2018; Stellati et al., 2019). Although stable isotope analysis (SIA) is now widely applied, comparatively few studies investigate temporal variations within the same ecosystem (Haubrock, Balzani, et al., 2021). Indeed, most such studies focused on seasonal variation in trophic niches within 1 year (Fitzgerald et al., 2017; Neves et al., 2021), and little is known about interannual and same-season variations occurring within one ecosystem.

In the present work, we sampled the YOY community of four predatory fish species over 3 years in a shallow natural lake in southeastern France. We aimed to evaluate the interspecific trophic interactions and the degree of trophic niche partitioning (as opposed to niche overlap) occurring between these coexisting cohorts. By investigating variations in trophic interactions across years, we hypothesised that: (1) predatory YOY coexisted by partitioning their trophic niches; (2) trophic interactions (niche segregation vs niche

overlap) among species were stable across time; and (3) the rising abundance of the YOY of alien invasive fish species would enhance competitive pressure on YOY of native species.

2 | MATERIAL AND METHODS

2.1 | Study site

Etang des Aulnes is a shallow lake (mean depth 3.8 m, maximum depth 6 m, area 104 ha), located in south-eastern France in a protected natural area. Previous sampling revealed that the fish assemblage consists of pikeperch, catfish, pike, and 13 other species, the most abundant being bream (*Abramis brama*, relative abundance 65%), perch (13%), and pumpkinseed (*Lepomis gibbosus*, 8%) (Westrelin et al., 2022). The Etang des Aulnes is eutrophic (see Appendix S1 and Table S1).

2.2 | Sample collection and measurements

The fish community of Etang des Aulnes was sampled in autumn over 3 years (October 2018, 2019 and 2020). October was chosen as the sampling period because SIA of fin tissues (detailed below) is integrative of the three previous months (Busst & Britton, 2018; Willis et al., 2013), corresponding to the summer period. The feeding intensity is usually very high in summer (Balik et al., 2006; Copp et al., 2009; Dominguez & Pena, 2000; Yazıcıoğlu et al., 2016), which encompasses the important growth period of YOY in northern temperate lakes before winter (Kubečka, 1994; Nunn et al., 2002). Fish were caught using fyke nets set equally in the pelagic and littoral zones, and using fish traps and electrofishing in the littoral zone. The YOY of pike, perch, pikeperch, and catfish were collected on each sampling occasion. Based on informations on the growth of these species at our site or neighbouring ecosystems and in the literature (Beeck et al., 2002; Dubois et al., 2008; Goubier, 1975; Poulet, 2004; Schlumberger & Proteau, 2001), we used the following upper limits for YOY, as total length: 400, 140, 280 and 350 mm, respectively for pike, perch, pikeperch and catfish. Due to the very high number of fish, we could not handle all individuals and therefore visually estimated size class for most of them. Catch per unit effort (CPUE, number of caught fish per net per day) was calculated accordingly (Figure 1).

For SIA, specimens of each species were randomly selected (Table 1). For catfish, however, all specimens were analysed for the needs of another project focusing on this species, except in 2019 when the YOY cohort was very important and thousands of individuals were caught. They were stocked for a few hours in aerated basins, then anesthetised in a tank containing a solution of benzocaine (80 mg/L) before being weighed (accuracy 1 g) and measured (total length, accuracy 1 mm). For SIA, a non-lethal and non-invasive
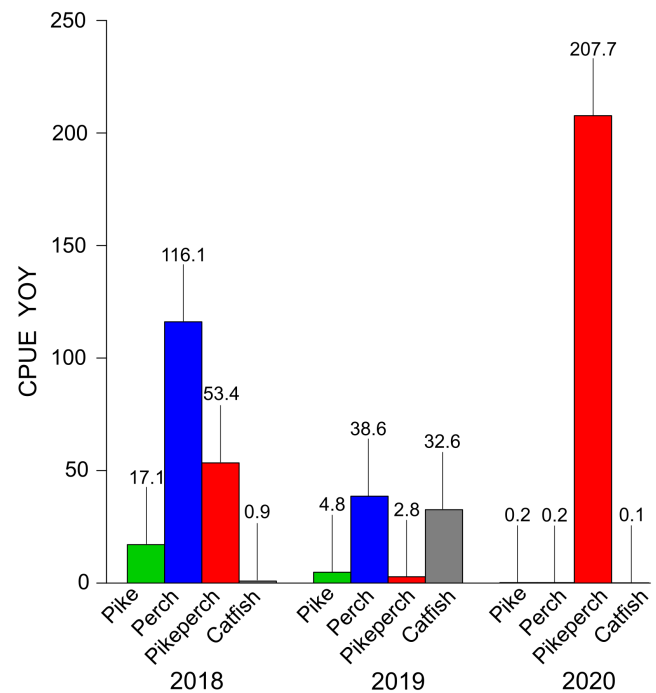

FIGURE 1 Catch per unit effort of young-of-year (YOY) per species per year. The unit is the number of fish per net in a day. Catch per unit effort (CPUE) values are given at the top of the graph. Barplots for pike, perch, pikeperch, and catfish are respectively coloured in green, blue, red and grey.

tissue sampling technique was used (Hayden et al., 2015; Jardine & Cunjak, 2005; Kelly et al., 2006) by extracting 0.25 cm^2 of the pelvic fin tips. Fish then spent 3–6 hr in recovery basins before being released. To evaluate the body condition of each individual, the relative weights were also calculated as the ratio of the observed weight over the expected weight calculated from the linear regression $log(Weight) = a * log(Total\_length) + b$ where a and b are the regression coefficients (Blackwell et al., 2000; Kraus et al., 2020).

To capture and account for spatial and temporal variations at the base of the food web, snails and zooplankton were collected during the same field campaigns as fish to be used as baselines (i.e. representing primary consumers) (Post, 2002). Aquatic gastropods (*Radix* sp. and *Physa* sp., $n = 7$, 8, and 12 in 2018, 2019 and 2020 respectively) were collected along the lake littoral; only their feet were used for SIA. Bulk zooplankton ($n = 9$, 10, and 15 in 2018, 2019, and 2020 respectively) were collected from the pelagic zone by taking diagonal hauls from 1 m above the lake bottom to the surface along a 10-m boat track. It was immediately sieved with a 250-µm mesh. Samples were screened under a microscope to limit debris contamination. These organisms represent the littoral and pelagic baselines, respectively, to account for these two distinct carbon pathways commonly found in lake webs (France, 1995; Post, 2002). All fish and invertebrates samples were rinsed thoroughly with distilled water, stored individually without any chemical and preserved at −20°C for a few days before being dried in an oven at 60°C for 60 h.

	Pike	Perch	Pikeperch	Catfish
n				
2018	16	16	13	36
2019	13	38	14	111
2020	14	4	34	9
Total length				
2018	311 (230–382)	97 (76–130)	161 (138–248)	291 (179–342)
2019	299 (239–380)	122 (102–140)	254 (181–280)	271 (159–350)
2020	310 (239–393)	139 (136–140)	210 (174–273)	309 (279–350)

TABLE 1 Characteristics of young-of-year sampled each year for stable isotope analysis.

Note: Their number and mean (range) total length (in mm) are given.

2.3 | Stable isotope analysis

Carbon ratios relate to the major energy sources, while nitrogen ratios relate to the TP of a consumer within a food web (Fry, 2006; Layman et al., 2012). SIA is based on predictable changes occurring in the isotopic ratios from prey to consumer, being enriched by 1‰ for carbon and by 2.5‰–5‰ for nitrogen for each trophic level (Post, 2002; Vanderklift & Ponsard, 2003). Dried samples were sent to the Cornell University Isotope Laboratory, New York for SIA. They were ground into a fine and homogenised powder with a Spex CertiPrep 6,750 Mill and packed into tin capsules for isotopic analyses (approximately 1 mg of material per sample). Samples were analysed with a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyser. Isotope compositions were expressed as ‰ with the δ notation, based on $\delta^{13}C$ or $\delta^{15}N = \left[\left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000\right]$ where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios. Results were referred to Vienna Pee Dee Belemnite for carbon and to atmospheric N_2 for nitrogen, with laboratory standards routinely calibrated against reference materials provided by the International Atomic Energy Association.

After analysis, $\delta^{13}C$ was corrected for lipid content according to Post et al. (2007) when the C:N ratio was greater than 3.5. Out of 318 values, 200 were corrected and corrections ranged in [0.15; 0.94]. Mean bulk stable isotope ratios for fish species and baselines of Etang des Aulnes are given in Table S2.

We used the TP and the littoral reliance (LR) of fish to correct for differences in basal resources for nitrogen and carbon. For a two-source food web, the TP of a fish is calculated as follows (Post, 2002):

$$TP_{fish} = 2 + \frac{\left(\delta^{15}N_{fish} - \left[\delta^{15}N_{gastropod} \times LR_{fish} + \delta^{15}N_{zooplankton} \times \left(1 - LR_{fish}\right)\right]\right)}{3.4}$$

where 2 is the TP of the baseline (i.e. primary consumer), 3.4 is the enrichment in $\delta^{15}N$ per trophic level and LR_{fish} is the proportion of nitrogen in the fish ultimately derived from the base of littoral food web (Post, 2002), also called LR as it quantifies the percentage contribution of littoral pathway, and calculated as follows (Vander Zanden & Vadeboncoeur, 2002):

$$LR_{fish} = \frac{\delta^{13}C_{fish} - \delta^{13}C_{zooplankton}}{\delta^{13}C_{gastropod} - \delta^{13}C_{zooplankton}}$$

LR_{fish} greater than 1 means that the ^{13}C enrichment of the fish is higher than the littoral baseline one (Gastropods). TP_{fish} and LR_{fish} are unitless numbers.

Because life history traits (optimum spawning temperature Souchon & Tissot, 2012, growth rates, size) of the four species differ, we used multiple linear regressions to test if species, year of sampling and size of species could explain TP and LR. To smooth these differences already comprised within the *species* factor, for each species, the size was divided by the maximum size of YOY over the 3 years. The model could be written as follows:

$$\overline{\text{Trophic metric}} = \alpha + \text{SPECIES} \times \text{YEAR} \times \text{NormalisedSIZE} + \varepsilon$$

where $\overline{\text{Trophic metric}}$ is the expected mean TP or LR, NormalisedSIZE is the size normalised by the maximum size of YOY of the considered species over the study period, α is the overall intercept and ε is the error term following a normal distribution with zero mean.

When significant, interactions were further analysed by Tukey comparisons of pairwise estimated marginal means of the different factor levels of predictors at the 5% significance level (emmeans R package; Lenth, 2016).

2.4 | Isotopic niche analysis and overlap

For each species of YOY and year, the isotopic niche size was estimated in the LR–TP space with standard ellipse areas (SEAs): considering 40% of data points, SEA40% were plotted to visualise the isotopic niche, and their Bayesian distribution (SEAb 40%) used for statistical comparisons (95% credible intervals based on 200 iterative draws) (SIBER R package; Jackson et al., 2011). Additionally, Layman metrics (Layman et al., 2007) were calculated for each YOY species and year as well as for the whole YOY community. TP and LR ranges (TP_range and LR_range) as well as TA are measurements of the extent of the LR–TP bi-plot, reflecting the species/community niche width. TA is the total area of the convex hull encompassing all the individuals (at the species level) or the centroids of each species' trophic niche (at the community level). The mean distance to the centroid (CD) provides a measure of the trophic diversity among individuals when calculated on species and between species when calculated on the whole community. The mean nearest neighbour

distance (MNND) and its standard deviation relate to the distance of individuals/species and indicate the degree of trophic redundancy.

Within a year, the degree of isotopic niche overlap between pairwise species was estimated by using the equation of Stasko et al. (2015) which gives the proportion of total ellipse space occupied in overlap:

$$\% \, Overlap = \frac{(\text{area of overlap between } SEA1 \text{ and } SEA2) \times 2}{SEA1 + SEA2} \times 100$$

where $SEA1$ and $SEA2$ are the ellipse areas calculated from species 1 and species 2 samples, respectively. This metric stands as a quantitative measure for diet similarity among different species (Jackson et al., 2012). %Overlap was calculated for each posterior draw of the Bayesian estimates of overlap and SEAb (*SIBER* R package) to get its distribution (95% credible intervals based on 200 iterative draws).

Additionally, to test the degree of partitioning among species' niches in each year, we also used a PERMANOVA (Euclidian distance, permutations = 999) on LR and TP followed by multiple comparisons with Pillai–Bartlett statistic (Hand & Taylor, 1987) using false discovery rate adjusted *p*-values (Jafari & Ansari-Pour, 2019). PERMANOVA was performed with the *vegan* R package (Oksanen et al., 2020) and multiple comparisons with *RVAideMemoire* R package (Hervé, 2021).

All statistical analyses were made with R version 3.6.3 (R Core Team, 2020).

3 | RESULTS

3.1 | Morphometrics and CPUE

We found significant differences in morphometric measures within each species across the sampled years as well as among species within the same year (Table 1; Table S3). The greatest CPUEs were observed in perch and pikeperch, while pike and catfish had the lowest, albeit large variations between years (Figure 1). Pikeperch in 2019 and catfish in 2020 both had very low CPUE values, which were not associated with higher body condition (Table S3). Conversely, high CPUEs, in 2020 for pikeperch and in 2019 for catfish, were associated with lower body condition (Table S3). In contrast, for pike and perch in 2018, when their CPUE was highest, their body condition was higher than in both other years.

3.2 | Trophic dynamics

Both TP and LR varied among species differently across different years and sizes (Table 2a,b). TP and LR showed significant interannual variations within species (Figure 2a,b). In 2018, TP and LR of each species were higher than in 2019 and 2020 (Table 2a,b, Figure 2a,b). TP and LR also showed significant interannual variations among species. Each year, the TP hierarchy between species changed, except for perch which always had the lowest TP (Figure 2a). Perch LR was, however, as high as those of pike and/or pikeperch (Figure 2b). Perch in 2018 and pikeperch in 2020 showed a particularly wide range for LR (Table 3), when their CPUE was the highest (Figure 1). Pike and pikeperch often had among the highest TP, but lower than catfish in 2020 (Figure 2a). Catfish considerably shifted its TP, having the highest in 2020, the lowest—with perch—in 2019, and an intermediate one in 2018. Catfish LR followed the same variations as TP across years (Figure 2a,b); catfish had the highest correlation between TP and LR (Pearson coefficient $r_{154} = 0.84$, $p < 0.001$; $r_{56} = 0.39$ for perch, $p = 0.002$; $r_{59} = 0.68$ for pikeperch, $p < 0.001$ and $r_{41} = 0.61$ for pike, $p < 0.001$). The largest variability in TP, of about one TP, was found for pike in 2018 and catfish in 2019 (Table 3). LR was significantly correlated to TP (Pearson coefficient $r_{316} = 0.66$, $p < 0.001$), yet to different degrees depending on species as shown above. All YOY had a LR > 1 in 2018, all < 1 in 2019 and only a few individuals (six pike, two pikeperch, and one catfish) > 1 in 2020. In 2018, catfish had a lower LR than pike and perch; in 2019, it had a lower LR than all three other species, while in 2020 pike and catfish both had a higher LR than perch and pikeperch.

3.3 | Trophic niche space

The graphical representation of the trophic niches in the LR–TP space illustrates the variations of species niche size and trophic interactions among species across years (Figure 3). As for TP and LR, no consistent pattern of niche size was visible across years (Figure 4). In 2018, perch occupied a larger niche than pikeperch and catfish, which had occupied comparable niche sizes (0.986, 0.301 and 0.269, respectively), while pike showed an intermediate niche size (0.663). In 2019, niche sizes appeared very similar among species and overall narrow compared to other years; this was typically the case for the numerous catfishes sampled (*n* = 111; Table 1), although their niche was comparably small. In 2020, pikeperch had the largest niche, when their resource range was very large (Table 3) and their CPUE the highest (Figure 1), while perch had the smallest one (Figure 4). Within species, catfish showed the most stable niche size across years while perch niche significantly differed from 1 year to another. Pike niche showed varying size across years, albeit to a lesser degree, with the largest niche observed in 2018 when their range of TP was very large (Table 3) and their CPUE the highest (Figure 1). Pikeperch had a comparable niche size in 2018 and 2019 but occupied a much larger niche in 2020 (Figure 4).

The trophic diversity of catfish, quantified by CD, was noticeably stable across years and often the lowest compared to other species. The CD of the three other species varied by a factor of two between years (Table 3), but in 2018 and 2019 perch had the largest CD among species (in 2020 the sample size was low). Catfish had the lowest MNND in 2018 and 2019, meaning that, on average, individuals had a higher trophic redundancy than other species. The three other species showed comparable trophic redundancy. In 2020, catfish trophic redundancy was comparable to other species (Table 3).

TABLE 2 Numeric results from the multiple linear regressions that tested the fixed effects of species, year and normalised size and their interactions on young-of-year trophic position (panel a) and littoral reliance (panel b).

	Trophic position		
a	**df**	**F**	**p-value**
Species	3	20.067	<0.001
Year	2	317.515	<0.001
Normalised size	1	47.864	<0.001
Species: Year	6	12.575	<0.001
Species: Normalised size	3	3.403	0.018
Year: Normalised size	2	0.172	0.842
Species: Year: Normalised size	6	9.239	<0.001
Residuals	294		
	Multiple R^2	Adjusted R^2	
	0.751	0.731	
	$F = 38.46$, (23, 294 df), $p < 0.001$		
	Littoral reliance		
b	**df**	**F**	**p-value**
Species	3	133.384	<0.001
Year	2	1,526.759	<0.001
Normalised size	1	6.978	0.009
Species: Year	6	21.250	<0.001
Species: Normalised size	3	19.596	<0.001
Year: Normalised size	2	11.671	<0.001
Species: Year: Normalised size	6	4.384	<0.001
Residuals	294		
	Multiple R^2	Adjusted R^2	
	0.926	0.921	
	$F = 160.7$, (23, 294 df), $p < 0.001$		

Note: At the bottom of each table is shown the *F*-test of overall significance that tests whether or not the linear regression model provides a better fit to the dataset than a model with no predictor variables. *p* is the associated *p*-value.

Variations around this pattern were high as the standard deviation of the nearest neighbour distance was of the same order of magnitude as MNND (Table 3).

At the community level, in 2018 and 2019, Layman metrics were quite similar (Table 4). In 2020, these metrics all increased, indicating a higher trophic diversity within the food web and a greater trophic diversity between species (as indicated by the higher CD and MNND, Table 4). As a result of the distance between species niches, the community TA considerably varied across years, being especially high in 2020 when the niches of the four species were more segregated compared to other years (Table 4, Figure 3).

Overlapping niches showed very large confidence intervals (Figure 5). Nevertheless, if we exclude perch in 2020 ($n = 4$), the mean SEAb 40% overlap laid in 0%–9% (Figure 5). PERMANOVA results showed significant differences among the species niches in all 3 years (2018: pseudo-$F_{3,79} = 8.853$, $p = 0.001$; 2019: pseudo-$F_{3,173} = 22.389$, $p = 0.001$; 2020: pseudo-$F_{3,57} = 18.156$, $p = 0.001$). In particular, the species niches were all segregated

($p < 0.01$ for all pairwise comparisons in all 3 years), except for perch and pikeperch in 2018 ($p = 0.151$), pike and perch in 2019 ($p = 0.086$) and pike and pikeperch in 2019 ($p = 0.168$).

4 | DISCUSSION

Trophic webs are complex and fragile, especially when encompassing YOY of predatory fish species. These stages are indeed less resilient because they need to maximise growth (Miller et al., 1988) during the months after hatching to rapidly exceed predator gape limitations, make ontogenetic shifts, and increase survival by reaching a sufficient size to escape harsh environmental conditions (Cowan et al., 2000; Logez et al., 2021). We found that YOY had segregated trophic niches and identified some general patterns, especially in the trophic positioning, with perch always in a lower position than pike and pikeperch. By contrast, we found pikeperch and especially catfish to have variable trophic positioning. All species presented high
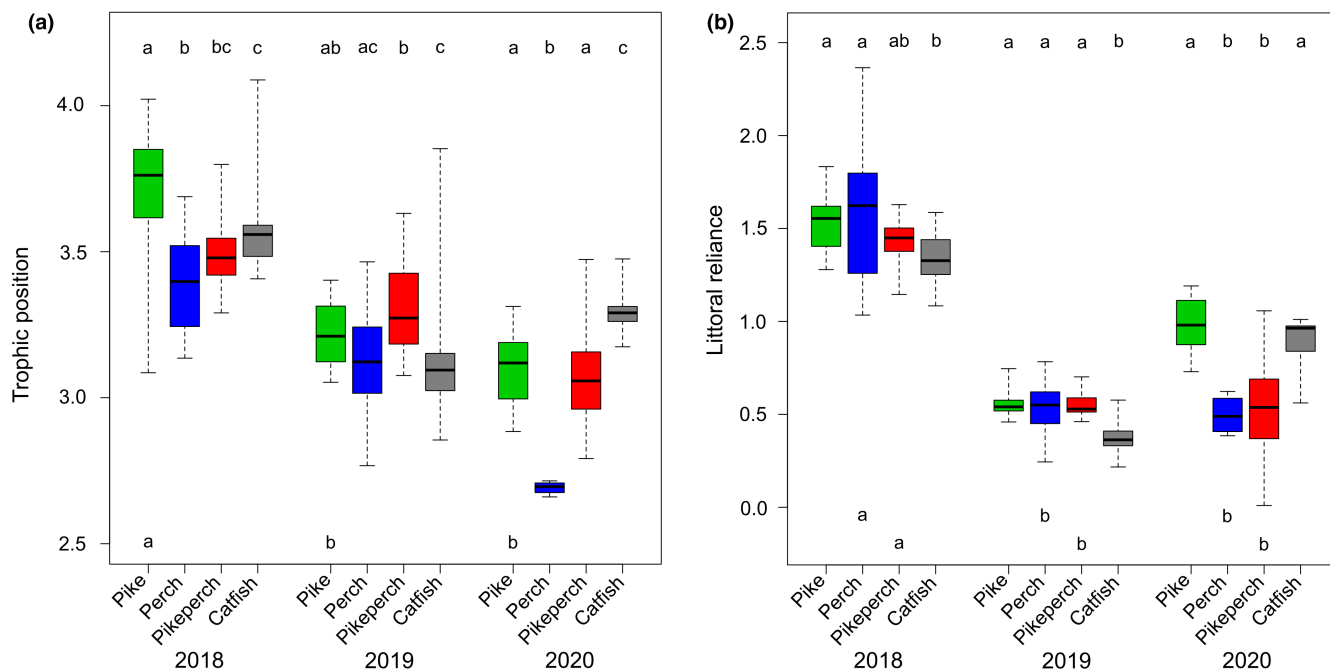
FIGURE 2 Distribution of trophic position (a) and littoral reliance (b) of young-of-year by species and year. Boxplots for pike, perch, pikeperch, and catfish are respectively coloured in green, blue, red, and grey. Above the boxplots, within a year, distributions for species that share a same letter are not different (5% significance level). Below the boxplots, within a species, distributions for years that share a same letter are not different (5% significance level); for better readability, no letter is present for species for which the distributions of the 3 years are different.

temporal variability in their TP and LR, reflected in their respective niche size and interspecific relationships.

4.1 | Trophic dynamics

Trophic interactions within predator communities are among the most faceted mechanisms (Schmitz, 2007). In general for adult stages, pike and pikeperch tend to occupy the highest TP throughout the ecosystems they occupy, whereas perch commonly occupies lower TP and catfish—a ubiquitous generalist species—expresses highly adaptive niche occupation. Here, we found similar patterns for the YOY, which is in agreement with our hypothesis that trophic interactions among YOY species would be consistent across time, but with large variations around a general pattern. The observed increase in TP with size (see also Linzmaier et al., 2018; Syväranta et al., 2010; Vašek et al., 2018) could correspond to a shift of the diet towards enhanced piscivory and in this way could reduce intraspecific competition between different ontogenetic stages (Beeck et al., 2002; Ginter et al., 2011; Jacobson et al., 2019; Vašek et al., 2018), but is not necessarily associated with better body conditions. Seemingly, interspecific variations within a year did not affect the body conditions of fish, as all species had comparable body conditions each year. In 2018, the high TP and relatively greater use of littoral resources (e.g. Beaudoin et al., 1999 on pike) were accompanied by better or equal body conditions for all species compared to other years, but neither larger nor heavier individuals (see also

Persic et al., 2004). Having identified LR to be greater than 1 (i.e. an enrichment in ^{13}C greater for fish than for gastropods) might indicate that YOY tend to consume relatively more matter of terrestrial origin (as suggested by Syväranta et al., 2010). Oddly, this phenomenon appeared only in 1 year but occurred in almost all individuals. In 2018, the variability of the isotopic ratios of zooplankton was high, but the mean values remained in agreement with the two other years. Indeed, the observed pattern originated from an unusual enrichment in ^{13}C of fish compared to other years, which was identified in other sampled species such as *Abramis brama*, *Tinca tinca*, *Scardinius erythrophthalmus*, and *Lepomis gibbosus* (and also in *Oligochaeta* sp.), but not in *Pseudorasbora parva* and *Gambusia holbrooki*. This observation remains challenging to explain. One hypothesis could be the role of environmental conditions: in anoxic conditions, the methane pathway is activated and biogenic methane has been shown to be ^{13}C-depleted compared to allochthonous terrestrial plant detritus and autochthonous phytoplankton (Grey, 2016). However, anoxic conditions regularly occur at the lake bottom in summer and the most severe events can even concern the whole water column, especially in shallow lakes (see Westrelin et al., 2022). Depending on environmental conditions, the relative contribution of the different carbon sources to the trophic web could thus change from 1 year to another, and be reflected in the autumnal SIA of individuals that were present in summer. However, in summer 2019, a severe anoxia occurred without any apparent impact on stable isotope ratios. Not only the severity but also the occurrence of anoxic events might probably play a role. In 2018 for example, less severe anoxia events

TABLE 3 Layman metrics of young-of-year species each year.

	Pike	Perch	Pikeperch	Catfish
TP_range				
2018	0.937	0.553	0.508	0.681
2019	0.350	0.698	0.555	0.998
2020	0.429	0.055	0.681	0.301
LR_range				
2018	0.554	1.331	0.484	0.502
2019	0.287	0.539	0.241	0.360
2020	0.461	0.238	1.047	0.449
TA				
2018	0.250	0.402	0.126	0.180
2019	0.054	0.276	0.067	0.266
2020	0.117	0.007	0.382	0.043
CD				
2018	0.232	0.357	0.139	0.134
2019	0.123	0.182	0.155	0.113
2020	0.168	0.092	0.260	0.119
MNND				
2018	0.114	0.137	0.098	0.041
2019	0.053	0.051	0.058	0.023
2020	0.065	0.069	0.063	0.077
SDNND				
2018	0.110	0.082	0.087	0.072
2019	0.032	0.043	0.042	0.042
2020	0.032	0.010	0.041	0.097

Abbreviations: CD, mean distance to centroid; LR_range, range of littoral reliance; MNND, mean nearest neighbour distance; SDNND, standard deviation of the nearest neighbour distance; TA, total area of the data convex hull; TP_range, range of trophic position.

limited to the bottom layer could have occurred frequently, reflected in isotope ratios.

4.2 | Inter- and intraspecific trade-offs

Our results suggest that YOY adapt their trophic niche to minimise both intra- and interspecific competition, with variations between years, as it has been shown in several other ecosystems (Wellard Kelly et al., 2021). Fish species, especially predators, are capable of adapting their feeding strategy to their needs (Beaudoin et al., 1999; Matich et al., 2011; Svanbäck & Persson, 2004), which results in intra- and interspecific trade-offs. The degree of potential competition, as estimated by isotopic niches, fluctuates among years between and within species, depending on their density (Borcherding et al., 2019). Indeed, the observed variability in occupied niches' dimensions seemed to be linked to variations in CPUE. The most evident case in our study is that of pikeperch, that showed huge differences in isotopic niche, with a much wider population niche (SEAb40%) and increased trophic diversity between individuals (CD)

when the CPUE was high. This was also the case for pike and perch. With increased intraspecific competition, pike, perch, and pikeperch would enlarge their niche to decrease competition with conspecifics (Araújo et al., 2011), suggesting that individuals adopt individual strategies rather than a generalist pattern controlling the diet spectrum, although this may also be indicative of resource limitations (Latli et al., 2019). Perch niche size appeared as the most variable between years; as a trophic generalist, perch would adapt its diet according to the concurrent and predatory community (Schulze et al., 2012). Beaudoin et al. (1999) revealed that the TP of pike increases by shifting towards a greater importance of littoral prey, and that individuals could differ by as much as two trophic levels in the same population, lowering intraspecific competition. By contrast, in 2019, the observed niche of catfish did not increase with the larger sample size and much greater CPUE, suggesting that catfish either focus on their niche to decrease interspecific competition, following the classic niche theory (Pianka, 1981), or that resources are not limiting, since the total YOY CPUE (and thus the potential intra- and interspecific competition) in 2019 was much lower than in the two other years. Catfish niche size was, however, the most stable and it was rather narrower than those of piscivorous specialists like pikeperch and pike, as also found in other studies (Haubrock et al., 2019, 2020), which differs from its adult opportunistic generalist trophic behaviour (Vejřík et al., 2017).

Except for some occasional (i.e. not constant across years) overlaps, species niches were segregated as hypothesised, indicating that the potential interspecific competition is low. This partitioning probably contributed to preserving body conditions for all species as these were similar within years (Bašić et al., 2019). The observed divergence of niches and their varying interannual degrees of overlap (niche expansion) according to ecological gradients (e.g. environmental variations, community composition) advocate for the *resource diversity hypothesis* prevailing in our lake (Costa-Pereira et al., 2019), which is indeed productive (eutrophic status), with resources appearing as abundant.

4.3 | Importance of environmental factors

Predator assemblages are determined by a combination of local and regional factors—an important one being the environment—acting in synergy (Fernández et al., 2018) whereas their diversity ensures the ecosystem functioning under fluctuating conditions (Yachi & Loreau, 1999). At the end of August 2019, a severe hypoxia in the lake led to the death of numerous fish (see Westrelin et al., 2022 for details on this event). Pikeperch, whose CPUE collapsed, was probably impacted as it has the highest oxygen requirements among the four species (Dolinin, 1974). Perch and catfish were probably the least impacted (see their CPUE) as they are the least demanding in oxygen (Daněk et al., 2014; Jones, 1964; Westrelin et al., 2022). In 2019, the YOY community appeared released from competition, as the total YOY CPUE was the lowest, mainly due to the collapse of the pikeperch stock. Species niches were also narrowed but simultaneously

FIGURE 3 Isotopic niche of young-of-year species over the years 2018 to 2020. Each symbol (triangle, cross, circle and plus for pike, perch, pikeperch, and catfish, respectively) represents the position of an individual in the bidimensional isotopic space (littoral reliance—trophic position). Each species is represented the standard ellipse area 40% (solid line). Pike, perch, pikeperch, and catfish are respectively represented in green, blue, red and black. Panels a, b, and c respectively represent years 2018, 2019, and 2020.
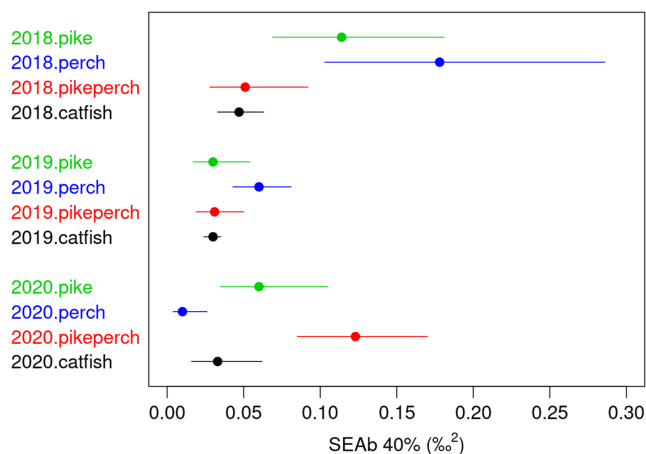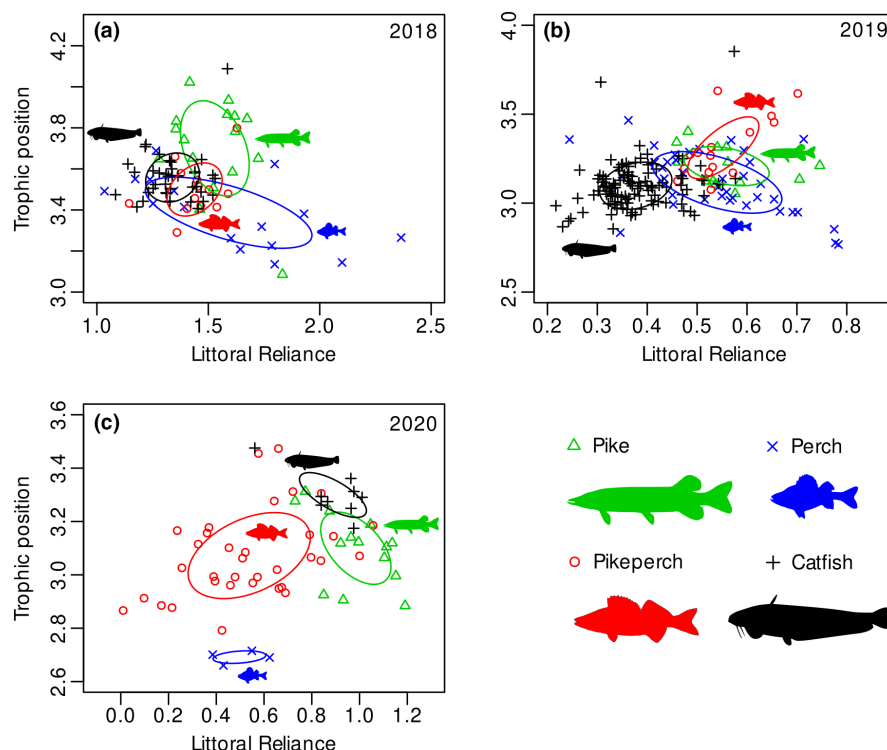

FIGURE 4 Isotopic niche size for each species of young-of-year and year. The Bayesian standard ellipse area (SEAb) 40% is calculated in the littoral reliance–trophic position space; its mean is represented by a dot and its 95% credible interval is represented by a solid line.

less segregated (niches of pike and perch, and pike and pikeperch were not different). The niche variation hypothesis, however, states that the release from competition leads to population niche expansion due to increased interindividual variation and/or increased individual niche widths (Bolnick et al., 2010; Van Valen, 1965). While CPUE provides information on the species abundance in the community at one time, SIA on fin tissue provides time-integrated information on the diet of the three previous months and thus indicative of July–September diet. The juvenile pikeperch cohort is usually abundant in this lake and could also have been abundant in 2019 before the anoxic event at the end of August, approximately 1 month

before our SIA sampling. Thus, it could have happened that inter-specific competition was effectively strong before the anoxia, contributing to narrowed and segregated species niches, and that after the pikeperch collapse, the release from interspecific competition led to less segregation. Our SIA could then be representative of a period over which strong interspecific competition was ongoing for two thirds of the time and competition was released for merely one third. This could explain the mixed pattern we observed on niches. Natural environmental changes have already been shown to affect trophic niches (Persic et al., 2004). This indicates that pikeperch probably shapes the predator community and further strengthens the hypothesis that a species recruitment not only depends on the available resources and its natural enemies but also on its own response to the environment and abilities to adapt to fluctuations (Shea & Chesson, 2002). At the ecosystem level, this underlines the importance of biodiversity, and in this case of predators, which supports ecosystem functioning and resilience against environmental uncertainty (Mori et al., 2013; Thébault & Loreau, 2005).

4.4 | Invasions

The integration of alien species into food webs has shown complex outcomes of competitive interactions within and between species, both alien and resident (Britton et al., 2019). We found no overlap between the catfish isotopic niche and those of native fishes. However, the niche of pikeperch occasionally overlapped with those of pike and perch, which nevertheless maintained abundant populations. Although this does not provide evidence of the detrimental effects of invasive YOY as hypothesised, the introduction of a fish species leads to shared

TABLE 4 Layman metrics of the young-of-year community each year.

	TP_range	LR_range	TA	CD	MNND	SDNND
2018	0.314	0.252	0.034	0.134	0.160	0.053
2019	0.214	0.182	0.017	0.106	0.114	0.034
2020	0.608	0.488	0.130	0.295	0.302	0.093

Abbreviations: CD, mean distance to centroid; LR_range, range of littoral reliance; MNND, mean nearest neighbour distance; SDNND, standard deviation of the nearest neighbour distance; TA, total area of the data convex hull; TP_range, range of trophic position.
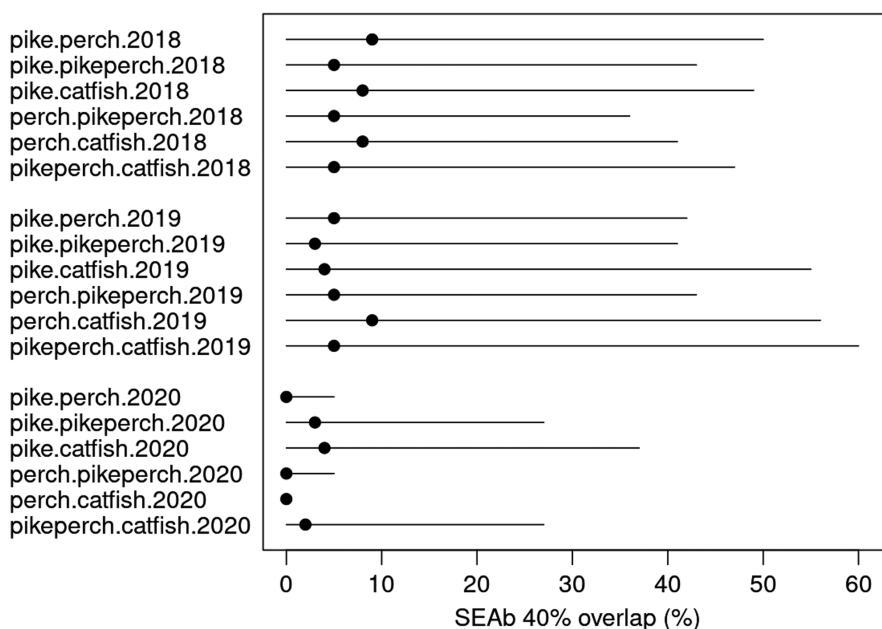

FIGURE 5 Isotopic niche core overlap between young-of-year species each year. The mean Bayesian standard ellipse area (SEAb) 40% overlap is represented by a black dot and its 95% credible interval by a solid line.

resources which can become limiting factors affecting food acquisition, assimilation, growth and survival rates of YOY (Dick et al., 2014, 2017; Gozlan et al., 2010; Gutmann Roberts & Britton, 2018). The successful introduction of alien species is often favoured by their trophic plasticity and generalist diet (Balzani et al., 2021; Cathcart et al., 2019; Comte et al., 2017); this can lead to niche constrictions or shifts of native competing species via trophic specialisation, as a way to preserve growth rates and conditions (Bašić et al., 2019). In our system, however, the niche of these two alien species did not appear larger than those of native species. As discussed above, pikeperch isotopic niche size seemed to be larger when pikeperch density was higher, which could indicate potential intraspecific competition, with pikeperch adapting its trophic niche according to the density of conspecifics. Contrary to expectations, catfish, often labelled as generalist, did not have the largest niche. The abilities of species to partition their niche, along with abundant resources, facilitates the integration of alien species (such as catfish and pikeperch), but with complex interactions between cohorts' strength and intra- and interspecific competition (Britton et al., 2018).

added interesting unexpected features: although a general trophic pattern was found across years for the YOY community, it showed high variability, which was not expected for such a closed system. This variability, however, seemed to be linked to the relative strength of the cohorts, which changed considerably between years and in turn could make the degree of the potential intraspecific competition vary. Environmentally harsh conditions contributed to the interannual variability and underlined the importance of the diversity of predators to maintain their functions in case of the decline of a particular species (Yachi & Loreau, 1999). Indeed, size- and stage-structured predator communities contribute to an efficient transfer of biomass and energy across the web (Gaedke, 2021), thereby increasing the stability of the trophic web (Caskenette & McCann, 2017). Surprisingly, YOY catfish expressed a consistently narrow niche compared to other species. The eutrophic status of this lake, offering rather abundant resources, probably facilitated the coexistence of these four predators. As such, this work demonstrates the importance of viewing trophic webs as dynamic systems and should encourage time-integrated studies to get the most complete and informative picture. Concomitantly, we advocate for more studies of juveniles, as they shape future communities.

5 | CONCLUSION

Apart from certain caveats (see Figure S1), this study highlighted that YOY predators can partition their trophic niche, probably to decrease the potential interspecific competition. The temporal span of the study

AUTHOR CONTRIBUTIONS

Conceptualisation: S.W., F.S. Developing methods: S.W., F.S. Conducting the research: S.W. Data analysis: S.W. Data interpretation: S.W., P.B., P.H. Preparation of figures and tables: S.W. Writing: S.W., P.B., P.H., F.S.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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