



Individual variability in ontogenetic dietary shifts and their influence on the trophic interactions of native and non-native freshwater piscivorous fishes

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Received: 5 December 2024 / Revised: 14 April 2025 / Accepted: 19 April 2025 / Published online: 16 May 2025
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Abstract Introduced fishes for enhancing sport angling tend to be large bodied and of high trophic position, raising ecological concerns on their impacts on prey communities and interactions with native fishes in the same functional guild. The piscivorous pikeperch *Sander lucioperca* is invasive in several European countries, including in England where it occupies the same functional guild as native Northern pike *Esox lucius*. Both species undergo ontogenetic dietary shifts from macro-invertebrates to piscivory during their juvenile life stages. The influence of this dietary shift on their trophic positions and niche sizes was assessed across three sites in an invaded lowland river basin in Western England. Stable isotope metrics revealed pikeperch switched to piscivory at smaller body sizes than pike (albeit with high inter-individual

variability); stomach contents analyses revealed pikeperch were piscivorous from 31 mm. Irrespective of ontogeny, there was low overlap in the isotopic niches of the two species, with the niche of pike generally more enriched in $\delta^{13}\text{C}$ but with minimal differences in $\delta^{15}\text{N}$. The prey resources of invasive pikeperch and native pike were thus largely differentiated, suggesting the ecological consequences of pikeperch invasion include increased predation pressure on aspects of prey populations that are usually not depredated upon by pike.

Keywords Pikeperch · Northern pike · Invasive · Stable isotope analysis · Trophic position

Introduction

Recreational angling acts as a major introduction pathway for non-native fishes, with large-bodied species often introduced to diversify sport angling experiences (Britton, 2023; Hickley and Chare, 2004). As these fish are of high trophic position (Eby et al., 2006), their invasions can result in substantial ecological impacts including increased predation pressure on native fish communities (Britton et al., 2023), potentially leading to trophic cascades (Britton et al., 2024). For example, largemouth bass *Micropterus salmoides* (Lacepède, 1802) which have been introduced globally for sport angling, exert strong top-down effects to native prey populations which can result in altered

Handling editor: Michael Power

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10750-025-05888-0>.

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community structure (Long and Seguy, 2024). Indirect ecological impacts can be incurred through both consumptive and non-consumptive effects (Sih et al., 2010). For instance, interactions with functionally analogous native species can result in the species altering their foraging behaviours, and trophic position and niche size, leading to changes to food web structure (Cucherousset and Olden, 2011; Ricciardi et al., 2013).

Understanding intra-guild trophic interactions between native and invasive fishes is important for predicting the ecological consequences of invasions (Guzzo et al., 2013; Britton et al., 2019). Resource partitioning is a key mechanism enabling the co-existence of functionally similar species (Guzzo et al., 2016; Butt et al., 2017; Reinas et al., 2022), with studies suggesting that trophic niche divergence can be important in the structuring of invaded fish communities (Britton 2018; Jackson and Britton, 2014; Comte et al., 2016). This divergence can occur when species minimise inter-specific competition by becoming more specialised in their diets, resulting in reduced population trophic niches that are divergent from competitors (Schulze et al., 2012; Jackson et al., 2016). Alternatively, increased competitive interactions can cause increased intra-specific resource variation and niche expansion through diets becoming more generalised (Svanbäck and Bolnick, 2006).

Ontogenetic dietary switches can influence the extent of intra- and inter-specific resource divergence between co-existing native and non-native fishes that can facilitate their co-existence (Sánchez-Hernández et al., 2018, 2022). In piscivorous fishes, ontogenetic dietary shifts represent the period of development when individuals switch their diet to one primarily comprising of fish, with an early transition to piscivory potentially providing important fitness advantages (Mittelbach and Persson, 1998; Valentine and Whitley, 2024). Ontogenetic dietary shifts can also influence the extent of individual movements and timing of natal departure from nursery areas (Cucherousset et al., 2013; Nyqvist et al., 2018, 2019). Predator–prey interactions in piscivorous fishes are driven by morphological constraints, where maximum prey size is dependent on gape limitations (Mittelbach and Persson, 1998; Lundvall et al., 1999; Schoenebeck et al., 2024). For gape-limited, freshwater piscivores, such as Northern pike *Esox lucius* Linnaeus, 1758 ('pike' hereafter) and

pikeperch *Sander lucioperca* (Linnaeus, 1758) (Nilsson 2001; Bousseba et al., 2024), these ontogenetic dietary switches generally occur in the first year of life, although the size at which this occurs can vary (Mittelbach and Persson, 1998).

The pikeperch is a relatively large-bodied piscivorous fish that has been introduced for angling and aquaculture into countries including France, Spain, Turkey and England (Hickley, 1986; Elvira and Almodóvar 2001; Kopp et al., 2009; Yağcı et al., 2014). In England, where the native pike is the only other large-bodied piscivorous fish present, the first releases of non-native pikeperch for angling enhancement occurred in the 1960s (Hickley and Chare, 2004), with invasive populations then developing in many river catchments in central and southern areas in the 1970s and 1980s (Hickley, 1986). An obligate piscivore (Kopp et al., 2009; Bousseba et al., 2024), ecological concerns on their invasion of English rivers included their predation of native fishes and their potential for adversely affecting native pike populations (Fickling and Lee, 1983). Elsewhere, invasive pikeperch impacts on prey populations has included predator-induced modification of prey behavioural traits and competitive interactions with native piscivores (Hölker and Mehner, 2005). However, their dietary overlap with native fishes is potentially reduced due to inter-specific differences in trophic positions and dietary specialisations that facilitate trophic niche partitioning (Kopp et al., 2009; Alieva et al., 2023). There is, however, considerable uncertainty as to how these ecological interactions and mechanisms develop, especially in relation to ontogeny.

The aim of this study was to quantify the trophic interactions of co-existing native pike and invasive pikeperch populations, and in relation to their diet switch to piscivory. It used the pike and pikeperch populations in three locations across the lower Severn River Basin, Western England, with diet assessments mainly based on stable isotope analysis ($\delta^{15}\text{N}$; $\delta^{13}\text{C}$) (e.g. Cucherousset et al., 2012). Accordingly, the objectives were to: (1) quantify the size ranges at which ontogenetic dietary shifts to piscivory occurs in both species; (2) assess how the ontogenetic dietary switches affect the size and position of their trophic niches; and (3) assess the influence of the switch to piscivory on trophic niche overlaps within and between the species.

Methods

Sampling

The co-existing native pike and invasive pikeperch populations were present in the lower River Severn Basin, Western England, where the native pike and non-native pikeperch populations have co-existed since the early 1980s (Hickley 1986). The River Severn general study areas was located between Diglis Weir (upstream) and Upper Lode Weir (downstream) (Fig. 1a; 52.1819° , -2.2241° to 51.9943° , -2.1735°), with the Warwickshire Avon general study area being close to its confluence with the River Severn but separated from it by two weirs that were considered impassable in both directions to the two species (51.9955° , -2.1579° to 52.1152° , -2.0702° ; Fig. 1).

The primary sampling locations were three sites focused on boat marinas, as these represented the only off-channel habitats in the sampling areas, and these were used as spawning, nursery, foraging and refuge areas by both species (Nolan et al., 2024). One of the marinas was directly connected to the Warwickshire Avon tributary (Site 1; 52.002709° , -2.152218°) (Fig. 1). The other two were directly connected to the lower River Severn, where Site 2 was Upton Marina (52.065292° , -2.212214°) and Site 3 was Tewkesbury Marina (Severn) (51.999995° , -2.154586°) (Fig. 1). Seine netting was used to sample these sites as it was the most efficient sampling method in that habitat. Samples were collected (with supplementary sweep-netting in the littoral zone for macro-invertebrates for stable isotope analysis) was completed every 6 weeks in off-channel areas between December 2016 and December

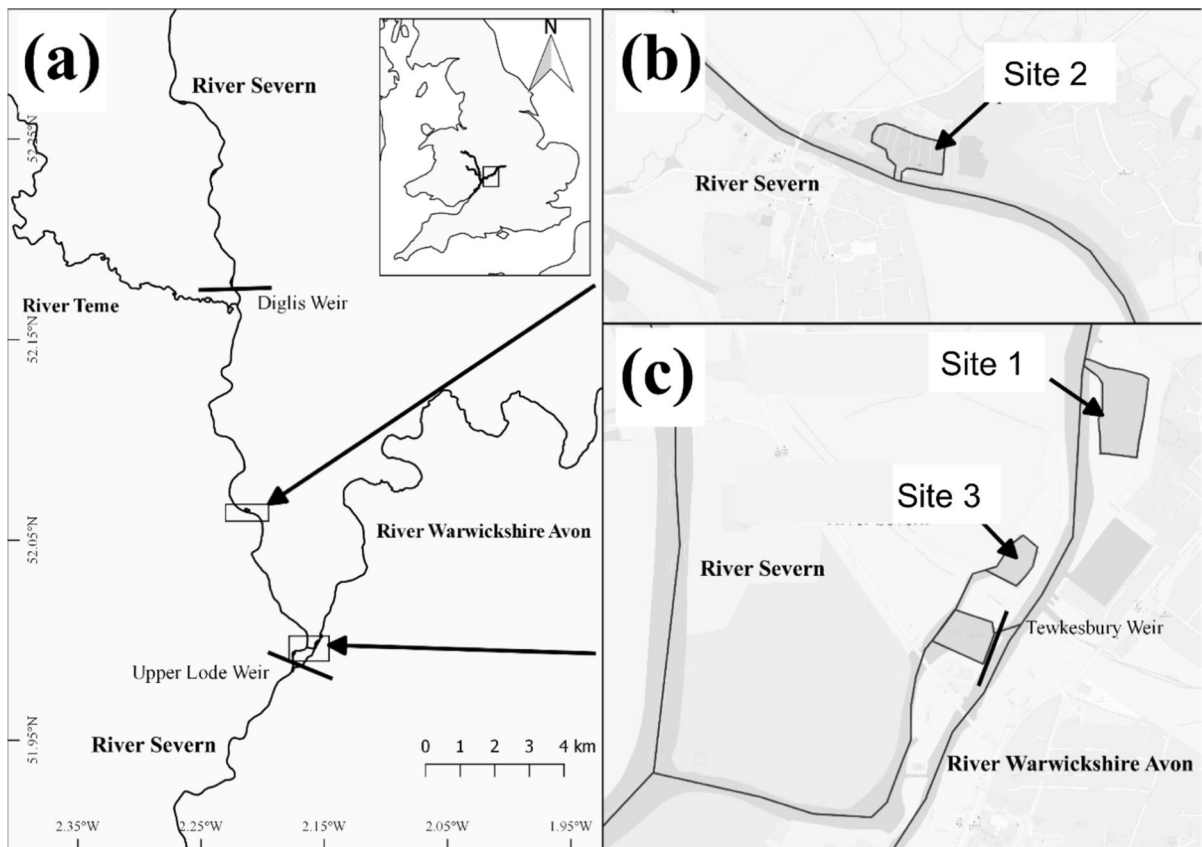


Fig. 1 a Sampling locations on the Rivers Severn and Warwickshire Avon within the lower reaches of the River Severn basin in Western England (inset) and the position of off-channel sampling areas including. b Site 2 (Upton Marina, River

Severn) and c Tewkesbury marinas, one with connection to the River Severn (Site 3) and one with connection to the River Warwickshire Avon (Site 1). Weirs are shown as solid lines

2018. During this sampling, captured fish were identified to species, measured (nearest mm), and scale samples taken (3–5 scales per fish, collected from the body area between the dorsal fin and lateral line). The non-native pikeperch were then euthanised (overdose of anaesthetic, MS-222), and transported on ice to the laboratory for processing for stable isotope and stomach contents analysis. All of the captured pike were returned alive due to their importance as the only native piscivore in the recreational fisheries of the rivers.

To supplement the samples from the boat marinas, fish samples from the connected main river channels were also collected. In these areas, both rivers had widths averaging 20 m with depths to at least 4 m, meaning that the application of traditional fish sampling techniques (e.g. electric fishing, seine netting, fyke netting) was largely inefficient. However, these river sections are popular sport fishing locations for both species (all catch-and-release) practised between mid-June and mid-March (Nolan et al., 2019a). Accordingly, sampling of pike and pikeperch in the main river channels was primarily through catch-and-release angling conducted by specialist anglers between June 2014 and December 2018 (except between mid-March and mid-June of each year due to a closed season). This sampling was coordinated by the Environment Agency (the inland fishery regulatory body of England), who provided training in the collection of fish scales (from the body area between the dorsal fin and lateral line) and the recording of associated fish length information and capture details (general location and river, date). Although the primary purpose of the scale sample collection was for fish age determination for management purposes, the scales also provided material suitable for stable isotope analysis (SIA) (Nolan et al., 2019b). At each site, angler captured fish were only used when they had been caught within the same river section as where boat marina was located.

Stable isotope analysis

Fish scales are used regularly in stable isotope studies as a non-destructive sampling alternative in place of tissues such as muscle, with this particularly important for use in fisheries that operate on catch-and-release (Bašić and Britton, 2015). Scales tend to have a longer stable isotope half-life than muscle and fin tissue (Heady and Moore, 2013; Busst and Britton, 2017), with predictable relationships for both

pike and pikeperch between their scale stable isotope data and those derived from dorsal white muscle and fin tissue (Nolan and Britton, 2018b; Winter et al., 2019). Processing of scale for isotope analysis was as per Trueman and Moore (2007), with scales cleaned with distilled water and the outer portion of the scale, which represents the most recent growth (generally the last full year), removed for analysis. Scale decalcification was not performed prior to analyses since the removal of inorganic carbonates has no significant effect on scale $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Ventura and Jeppesen 2010). One to three scales per individual fish were used for SIA (dependent on quantity of material). For macro-invertebrates, one to three individuals of the same family were used for analysis (dependent on body sizes); family groups were Asellidae [*Asellus aquaticus* (Linnaeus, 1758)], Chironomidae (non-biting midge larvae) and Gammaridae. For pikeperch < 100 mm, the small size of their scales prevented their effective use within SIA and so a portion of white dorsal muscle was used as an alternative tissue. All SIA samples were cleaned with distilled water and dried to constant mass at 60 °C prior to their analysis at the Cornell Isotope Laboratory, New York, USA. The samples were then ground to powder, weighed to ~1000 µg and analysed on a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, USA) interfaced to a NC2500 elemental analyser (CE Elantach Inc., USA). Verification of accuracy was against internationally known reference material and was tested every 10 runs. No lipid correction was performed as C:N ratios indicated low lipid content across all taxa (< 3.5; Post et al., 2007).

Stomach content analysis

The pikeperch sampled from the boat marinas were analysed for their stomach contents to complement the SIA. This was not completed for pike as these were all returned alive following their capture and processing. Following estimation of total stomach fullness (% volume), the prey items present in stomachs were identified to their lowest possible taxonomic level and their contribution to overall stomach fullness assessed. To quantify dietary shifts with body length, the prey items in stomachs were then categorised as either ‘macro-invertebrates’ or ‘fish’, and their contributions to diet expressed as percentages in terms of frequency of occurrence and prey-specific

abundance. Frequency of occurrence (% F_i) of a given prey type was defined as the number of stomachs in which that prey occurred, expressed as a frequency of the total number of stomachs in which prey were present (Costello, 1990). For prey-specific abundance, prey type contribution was first estimated in proportion to overall stomach fullness (in volume). The proportional fullness contribution of each diet category was then expressed as percentage prey-specific abundance (% P_i) (Eq. 1):

$$\%P_i = \left(\frac{\sum F_i}{\sum F_t} \right) \times 100$$

where P_i was the prey-specific abundance of prey i , F_i was the stomach content fullness for diet category i and F_t was the total stomach fullness in only those predators with prey i in their stomach (Amundsen et al., 1996).

Analyses of stable isotope data

Prior to analysing the stable isotope data, it was necessary to convert pikeperch muscle isotope values to their equivalent scale values using pikeperch specific conversions due to inherent inter-tissue differences in their stable isotope values (Nolan and Britton 2018b). There was then a need to determine whether stable isotope data for pike, pikeperch and macro-invertebrates could be combined across sampling areas and years for the River Warwickshire Avon and the River Severn respectively (Supplementary material, Table S1). For pike and pikeperch, this was completed using analysis of covariance (ANCOVA), testing for the independent and interactive effects on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of sampling area and year sampled (main effects), and fish length (covariate) (Table S1). For macro-invertebrates, analysis of variance (ANOVA) tested for the independent and interactive effects on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of sampling area and year sampled (Table S1). Temporal differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were non-significant (Supplementary material, Table S2), but there were consistent, significant spatial differences for pikeperch $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between the River Severn and Tewkesbury marina (River Severn side) (Supplementary material, Table S2). Consequently, all subsequent analyses were completed for three distinct areas (sites) in the study area: Site 1: the Warwickshire Avon, incorporating the River Warwickshire Avon and

Tewkesbury marina (River Warwickshire Avon side); Site 2: the Severn, incorporating the River Severn and Upton marina; and Site 3: Tewkesbury marina (River Severn side) (Table 1, Fig. 1).

The linear relationships of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ versus body length were then tested for pike and pikeperch at each site using linear regression. The trophic positions (TP) of pike and pikeperch at distinct size classes within each population were then calculated through Bayesian estimation completed within the package 'tRophicPosition' in R (Quezada-Romegialli et al., 2017). Analyses were performed using the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the consumers pike and pikeperch and the baselines (macro-invertebrates) for each site. As such, a one baseline, two-trophic discrimination Bayesian model was run for each site with 5 parallel chains and 10,000 adaptive iterations which assumed a baseline trophic position of 2. The trophic discrimination factors used were $3.35 \pm 0.5\text{‰}$ for $\delta^{15}\text{N}$ and $3.49 \pm 0.5\text{‰}$ for $\delta^{13}\text{C}$, values which are suitable for piscivorous fish stable isotope data from scales (Nolan et al., 2019b). As ontogenetic dietary switches in pike and pikeperch are often apparent at lengths below 100 mm (Mittelbach and Persson 1998), this was tested in each species by estimating their posterior trophic positions at each 10 mm length increment for fish below 100 mm. For fish above this length, the grouping length increments were increased to 100 mm. Model outputs were reported as the means of all feasible solutions and the 5th-95th credible intervals of the distribution range. To then identify these dietary switches at the individual level, for pikeperch < 150 mm and pike < 300 mm, their $\delta^{15}\text{N}$ data were converted to trophic position (TP) according to Olsson et al. (2009): $\text{TP} = (\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{prey}} / 3.4) + 2$ (Eq. 2), where TP and $\delta^{15}\text{N}_{\text{fish}}$ are the trophic positions and the nitrogen ratios of each pike or pikeperch, $\delta^{15}\text{N}_{\text{prey}}$ is the mean nitrogen ratio of the macro-invertebrate sample at that sampling location and year (Table S1) and 2 is their trophic position (as primary consumers), and 3.4 was the fractionation factor used between adjacent trophic levels (Post, 2002).

The trophic niche of pike and pikeperch was calculated as the isotopic niche and was estimated at each site (population level) and before and after the dietary shift to piscivory, where this shift was informed by the posterior trophic positions by size class. The isotopic niches were estimated using metrics based on stable isotope standard ellipse areas and completed within

Table 1 Mean ($\pm$ SD) carbon and nitrogen stable isotope ratios for pike and pikeperch from scale tissues and macro-invertebrates by site, including the number of samples and their length range (mm)

Species	Site	N	Length range (mm)	Mean length (mm)	Range $\delta^{13}\text{C}$ (‰)	Mean $\delta^{13}\text{C}$ (‰)	Range $\delta^{15}\text{N}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)
Pikeperch	Site 1	54	40–870	206 $\pm$ 227	–32.99 to –25.19	–28.99 $\pm$ 1.93	13.19–21.72	18.30 $\pm$ 1.77
	Site 2	42	48–838	500 $\pm$ 234	–28.90 to –19.73	–24.94 $\pm$ 1.78	12.61–17.38	15.98 $\pm$ 0.85
	Site 3	67	29–331	76 $\pm$ 57.8	–32.79 to –27.43	–30.38 $\pm$ 1.43	13.20–20.82	17.65 $\pm$ 1.65
Pike	Site 1	35	101–1020	352 $\pm$ 283	–30.03 to –16.05	–26.46 $\pm$ 2.66	15.44–21.24	18.47 $\pm$ 1.33
	Site 2	78	114–1060	572 $\pm$ 295	–28.22 to –16.34	–23.54 $\pm$ 2.77	12.08–17.32	15.86 $\pm$ 1.00
Invertebrate	Site 1	25	NA	NA	–35.32 to –27.93	–30.16 $\pm$ 1.75	11.78–18.09	15.48 $\pm$ 1.79
	Site 2	17	NA	NA	–32.31 to –26.22	–29.46 $\pm$ 1.53	11.11–15.27	13.44 $\pm$ 1.23
	Site 3	18	NA	NA	–34.91 to –28.88	–32.15 $\pm$ 1.63	14.52–18.35	16.29 $\pm$ 1.04

Site 1: Warwickshire Avon, Site 2: River Severn, and Site 3: Tewkesbury marina, River Severn. NA: not applicable

the package ‘Stable Isotope Bayesian Ellipses in R’ (SIBER; Jackson et al., 2011), with isotope niche metrics only calculated for sample sizes ≥ 5 (Table 3). Metrics included standard ellipse areas (SEA), this is a bivariate measure of the distribution of individuals in isotopic space and represents the typical resource use of a population (Jackson et al., 2011, 2012). Additional calculations were the total area of the convex hull encompassing the data points (TA), the correction applied to SEA to account for small sample sizes (SEA_C), and the Bayesian estimated standard ellipse area (SEA_B) and their 95% credible intervals. Significant differences in the size of isotopic niches were identified when $\geq 95\%$ of posterior draws from SEA_B for one area were smaller than the other. The area of niche overlap between ellipses was also calculated representing the area, in units of per mil squared, contained by the shape that lies within the overlapping ellipses. This was calculated both as the total proportional area of overlap and the proportional area of overlap for each ellipse.

Here error is expressed around the mean, and it represents $\pm 95\%$ confidence limits unless otherwise stated. All statistical analysis and graphical outputs were performed using R (version 3.5.3; (R Development Core Team 2018)).

Results

Stable isotope-length relationships

For pike, there were significant increases in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with increasing length at all sites, except for $\delta^{15}\text{N}$ at site 1 (Fig. 2, Table 2). Pike posterior trophic positions (TP) by size class ranged from 2.07 to 2.96, with a general pattern of TP increasing as body size increased and with the smallest size class (100 to 199 mm) having the lowest trophic position (Fig. 3a). This increasing TP with length was also seen at the individual level, where at lengths between 101 and 300 mm, there was a significant increase in TP by approximately one trophic level ($R^2=0.80$; $F_{1,36}=109.4$, $P<0.001$; Fig. 3b).

For pikeperch, regression analyses revealed significantly higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with increasing body length at all sites (Fig. 2; Table 2). Pikeperch posterior TP by size class ranged from 2.02 to 3.21, with

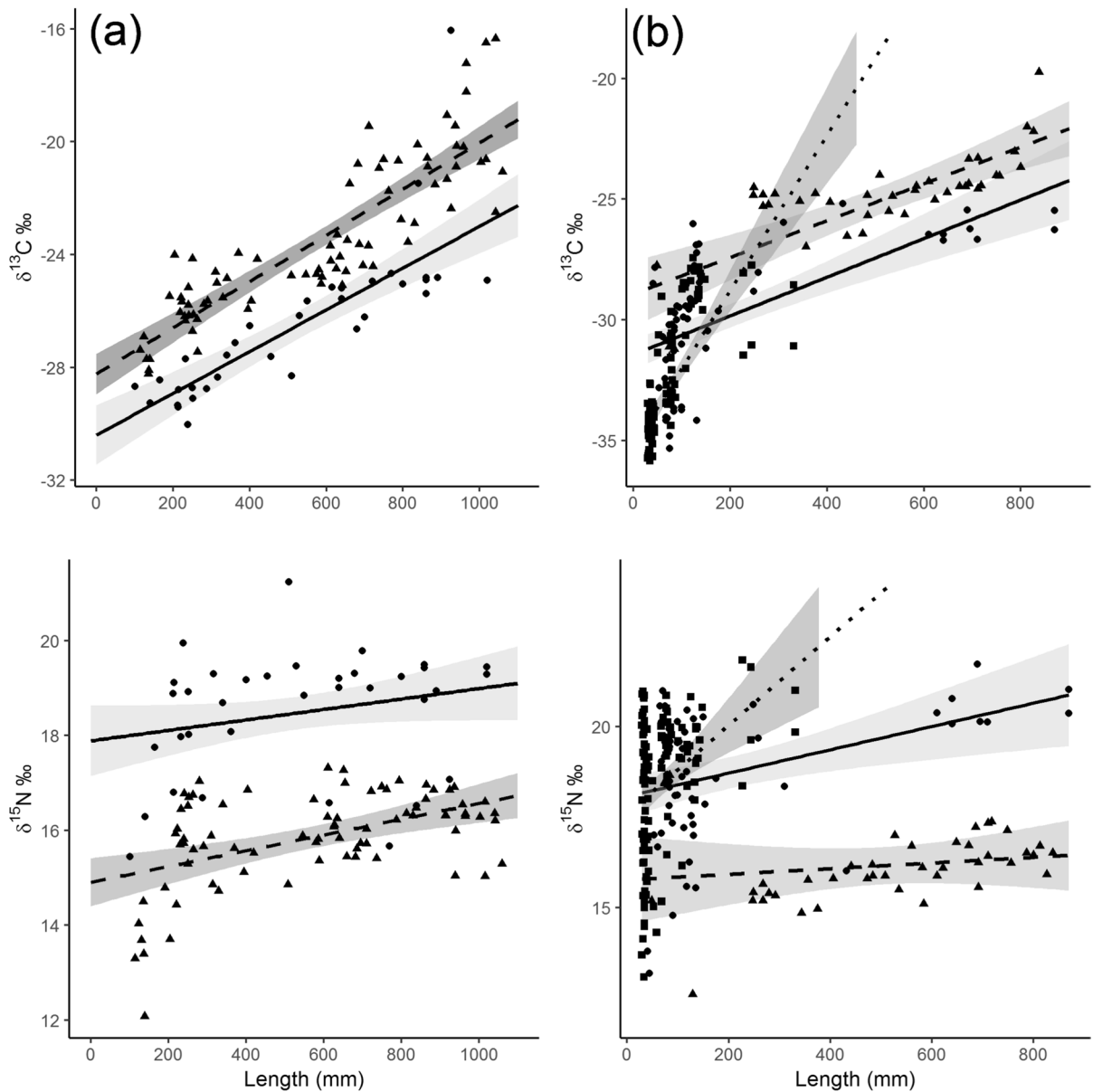


Fig. 2 Linear relationships between pike (a) and pikeperch (b) length with $\delta^{13}\text{C}$ (top) and $\delta^{15}\text{N}$ (bottom) for site 1 (circle, solid line), site 2 (triangle, dashed line) and site 3 (square, dotted line) with 95% confidence intervals around the fitted values

TP most variable at lengths below 100 mm and with the lowest TP in the 40–49 mm size class (Fig. 3a). This high variability in TP in pikeperch < 100 mm was also seen at the individual level, where there were differences in individual TP of almost one trophic position in fish of 29–50 mm. The relationship between individual pikeperch length and TP was significant $R^2 = 0.26$; $F_{1,96} = 30.1$, $P < 0.001$; Fig. 3b).

This variability in TP in smaller pikeperch was supported by their stomach contents analyses (Table 3). Although piscivory was evident in individuals as small as 31 mm, macro-invertebrates were important prey for individuals up to 153 mm at site 1. At site 2, all analysed pikeperch were piscivorous, although sample size was low ($n = 7$; Table 3).

Table 2 Relationships between pike and pikeperch length with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each site according to linear regression

Species	Site	Relationship	Statistics (<i>a</i> slope and <i>b</i> intercept.)
Pike	Site 1	$\delta^{13}\text{C}$	$R^2=0.61$, $F_{1,33}=54.38$, $P<0.001$, $a=0.01$, $b=-30.40$
		$\delta^{15}\text{N}$	$R^2=0.03$, $F_{1,33}=1.94$, $P=0.17$, $a=0.01$, $b=17.89$
	Site 2	$\delta^{13}\text{C}$	$R^2=0.76$, $F_{1,76}=243.2$, $P<0.001$, $a=0.01$, $b=-28.23$
		$\delta^{15}\text{N}$	$R^2=0.23$, $F_{1,76}=24.03$, $P<0.001$, $a=0.01$, $b=14.91$
Pikeperch	Site 1	$\delta^{13}\text{C}$	$R^2=0.50$, $F_{1,52}=54.98$, $P<0.001$, $a=0.01$, $b=-30.24$
		$\delta^{15}\text{N}$	$R^2=0.29$, $F_{1,52}=22.42$, $P<0.001$, $a=0.01$, $b=17.42$
	Site 2	$\delta^{13}\text{C}$	$R^2=0.65$, $F_{1,40}=76.83$, $P<0.001$, $a=0.01$, $b=-28.02$
		$\delta^{15}\text{N}$	$R^2=0.35$, $F_{1,40}=22.97$, $P<0.001$, $a=0.01$, $b=14.89$
	Site 3	$\delta^{13}\text{C}$	$R^2=0.60$, $F_{1,65}=99.26$, $P<0.001$, $a=0.02$, $b=-31.84$
		$\delta^{15}\text{N}$	$R^2=0.32$, $F_{1,65}=32.22$, $P<0.001$, $a=0.02$, $b=16.41$

Site 1: the Warwickshire Avon, Site 2: the Severn and Site 3: Tewkesbury marina, River Severn

Isotopic niche sizes and overlaps

The largest isotopic niches of pike and pikeperch were in Site 1 (Fig. 4a; Table 4), where inter-specific differences were not significant in niche size and niche overlap (pikeperch shared 34%, while pike shared 33%). The isotopic niches of pike and pikeperch were smallest at Site 2 (Fig. 4b, Table 4), where pike had a significantly larger niche and shared less niche space than pikeperch (42% versus 75%). The isotopic niche size of pikeperch at Site 3 was lower than at the other two sites (Fig. 4c, Table 4).

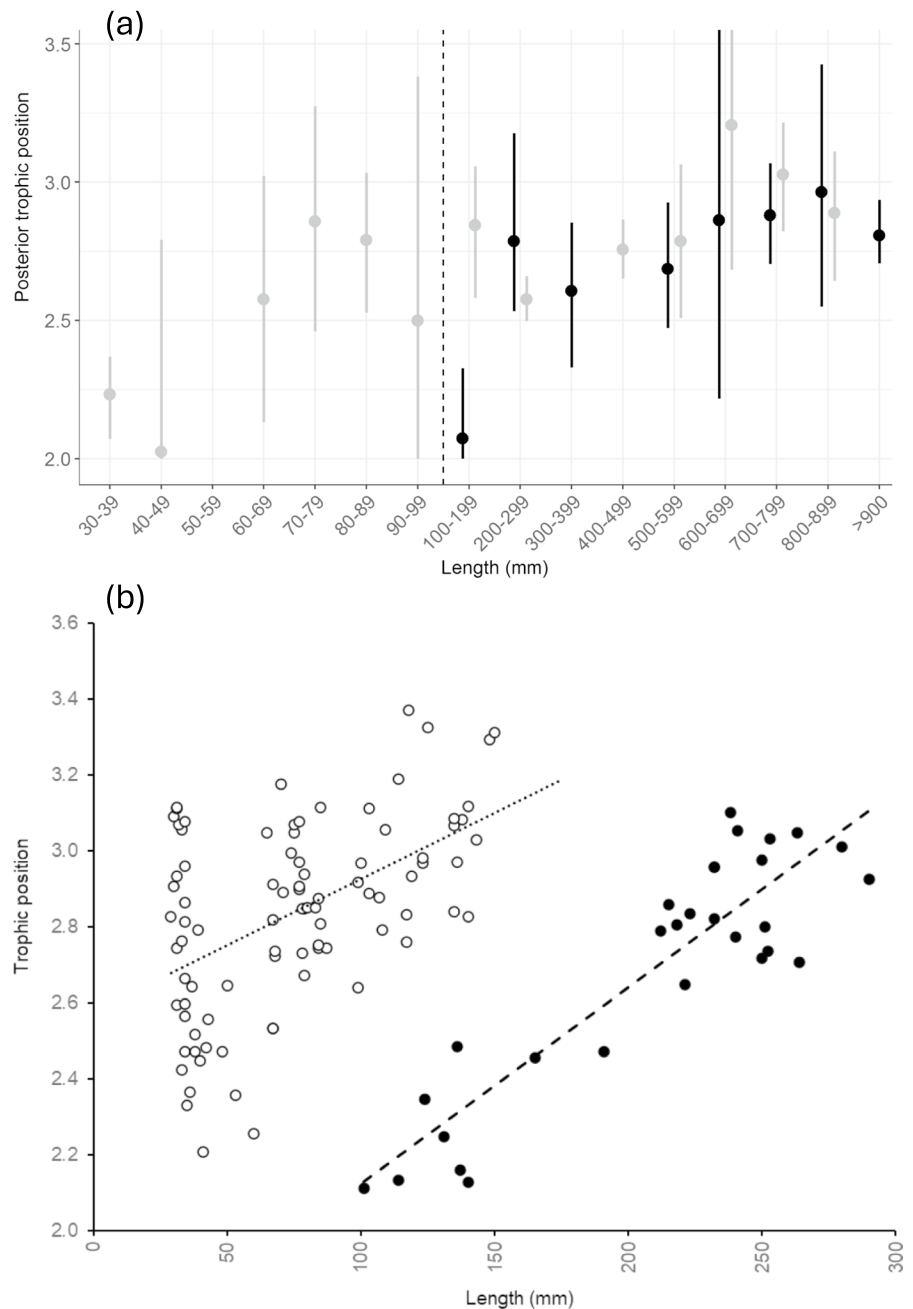
Isotopic niche size could only be estimated pre- and post-ontogenetic dietary switch to piscivory for pike at Sites 1 and 2 (approximate maximum size at piscivory: 200 mm; Fig. 3), and pikeperch at Site 1 (approximate maximum size at piscivory: 100 mm; Fig. 3). There was significant niche expansion after switching to piscivory for pike but not for pikeperch, with minimal niche overlap before and after the switch to piscivory within both species (Fig. 4, Table 4). Only at Site 1 could inter-specific differences be tested in isotopic niche overlap before and after the switch to full piscivory. Prior to full piscivory, pike had a significantly smaller niche than pikeperch and shared 14% of their isotopic niche space (Fig. 4). Following the switches to piscivory in both species, there was no significant difference in their isotopic niche sizes and their niche overlap increased (total overlap 10%, shared overlap 19% each).

Discussion

Ontogenetic dietary shifts to piscivory are an important feature of the ecology of freshwater piscivorous fishes with body size determining the extent of predator–prey interactions. Here, stable isotopes revealed an ontogenetic dietary switch at smaller lengths for pikeperch compared to pike according to fish length/ $\delta^{15}\text{N}$ relationships and trophic position (by size class using Bayesian estimates and at the individual level). Trophic position changes were reflective of an ontogenetic dietary shift towards piscivory in both species, with trophic position estimates revealing an increase in trophic position at 30–70 mm for pikeperch and from 100 to 200 mm for pike. For both species, these diet switches to piscivory were occurring during the first year of life (Nolan and Britton, 2018a). The influence of these ontogenetic dietary shifts on the isotopic niches of the species was intra-specific isotopic niche segregation pre- and post-diet switching in both species, with some inter-specific niche partitioning evident that occurred irrespective of the dietary switch to piscivory.

For pikeperch, a dietary switch to piscivory occurred at relatively small sizes when compared to pike, with this evident in both the stable isotope data and stomach contents analysis, where there was consistency in the size at which fish were the dominant prey item in pikeperch stomachs across the sites. In a review of the dietary ontogeny of freshwater piscivorous fishes, pikeperch switched to piscivory at lengths of 35–100 mm, which is usually within their first summer of life (Mittelbach and Persson, 1998). This pattern was also well supported in other studies of pikeperch ontogenetic dietary switches (e.g.

Fig. 3 Relationships of trophic position with fish length. **a** Posterior trophic position estimates (bars show 95% credible interval of each posterior trophic position) for pike (black) and pikeperch (grey) by size class within the Severn River Basin catchment, Western England, as calculated in the R package ‘tRophicPosition’. **b** Trophic position (Eq. 2) versus fish length for individual pikeperch (clear circle) and pike (filled circle), where the dashed lines represent the significant relationships according to linear regression



Persson and Brönmark, 2002). For pike, the size at which their diet switches to piscivory was consistent across the analytical methods and sites. These sizes were larger than reported for pike by Mittelbach and Persson (1998), where ontogenetic dietary switches to piscivory were from 45 to 100 mm, although there can be considerable variation between individuals (Nygqvist et al., 2018) and high levels of dietary

overlap between different ontogenetic stages in pike (Amundsen et al., 2003).

An early ontogenetic dietary shift towards piscivory has been associated with a faster growth rate in the early life stages of piscivorous fishes, with benefits including increased energy returns and growth which increase the long-term survival and fecundity of individuals (Mittelbach and Persson, 1998;

Table 3 Frequency of occurrence (% F_i) and prey-specific abundance (% P_i) of diet by prey types ‘macro-invertebrates’ and ‘fish’ for pikeperch from the River Severn basin Western

England, by site, including the number of samples, number of empty stomachs and their length ranges (mm)

Site	n	Empty stomachs (n)	Length range (mm)	Invertivorous length range (mm)	Piscivorous length range (mm)	% F (macro-invertebrates)	% F (fish)	% P_i (macro-invertebrates)	% P_i (fish)
Site 1	46	13	19–222	19–153	48–222	36.36	63.64	25.89	74.11
Site 2	7	3	48–490	–	77–100	0	100	0	100
Site 3	73	22	14–148	14–31	31–148	5.88	94.12	2.57	97.43

Site 1: the Warwickshire Avon, Site 2: the Severn and Site 3: Tewkesbury marina, River Severn

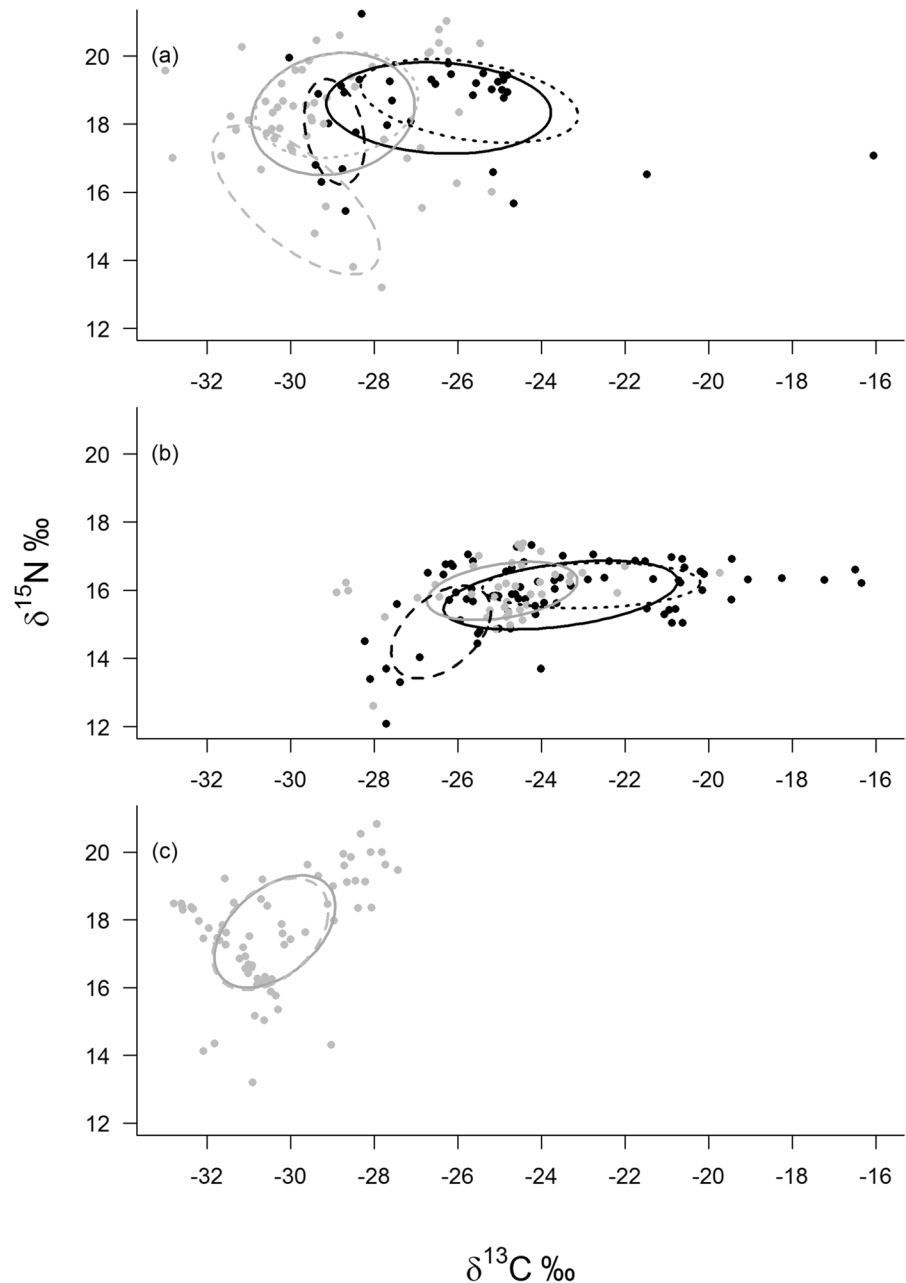
Sánchez-Hernández et al., 2018). Although it is common for pike and pikeperch to switch to piscivory in their first growth season (Mittelbach and Persson, 1998), this switch can be delayed in the absence of suitable prey species (Ginter et al., 2011). Indeed, synchronisation of ontogenetic diet shifts with fluctuations in resource availability, such as new cohorts of prey, has been observed (Persson and Brönmark, 2002), and individual variability in the timing of dietary switch can result in intra-cohort variation in the size of juveniles where there are both fast-growing piscivorous and slow-growing macro-invertebrate feeding individuals (Nyqvist et al., 2018, 2019). Despite the differences in size at ontogenetic dietary switch found here, they do represent a switch to piscivory in their first year of life, where the average size of pike and pikeperch at age 1 from the sampled population was 281 and 188 mm respectively (E. Nolan, unpublished data).

Inter- and intra-specific trophic interactions of pike and pikeperch were assessed at both the population and group level. When the isotopic niches pre- and post-diet switching were estimated, pike and pikeperch were largely diverged, with the between-species piscivorous life stages displaying more convergence in isotopic niche space and being of similar sizes. Niche sizes pre- and post-diet switching also showed some intra-specific niche divergence and constriction. A moderate niche compression of pike in response to the introduction of pikeperch was observed in a whole lake experiment in Germany (Schulze et al., 2012), where the extent of pike niche modification was reduced and the overlap between niches was asymmetrical towards pike due to a less specialised diet composition. Pike populations were also resilient to adverse effects from invasive pikeperch in rivers in southwest France due to differences in their trophic

positions that suggested some key dietary differences (pike: 3.7, pikeperch: 4.2) (Kopp et al., 2009). Here, the estimates of trophic positions (TP) for both pike and pikeperch were lower in the River Severn catchment than found for these sympatric populations in southwest France, with intra-specific differences in trophic position generally more apparent than inter-specific differences. Categorical size classes are often used to examine shifts in diet and trophic position, but the use of size groupings should be biologically relevant and made alongside assessments of continuous predictors if possible (Hammerschlag-Peyer et al., 2011).

Pike generally have broader prey preferences than pikeperch and can ingest larger prey due to their larger gape size (Persson et al., 1996; Dörner et al., 2007). Studies based on stomach contents analysis corroborate the importance of dietary specialisation in the partitioning of prey resources when the two species are in sympatry (Schulze et al., 2012; Didenko and Gurbyk, 2016). Levels of specialisation in pike can vary with prey availability, and although often considered as an obligate piscivore that specialises on fish prey, individual pike have been demonstrated as consuming macro-invertebrates as adults (Chapman et al., 1989; Pedreschi et al., 2015; Cittadino et al., 2024). However, many generalist populations often comprise of subsets of specialised individuals (Araújo et al., 2011) and, although not explored here, pike in the lower River Severn have been identified as being composed of subsets of individual specialists, some of which exploit energy pathways based on large prey items containing marine derived nutrients (MDN), with other individuals only exploiting a freshwater energy pathway (Nolan et al., 2019b). This could provide some explanation for the intra-specific differences in isotope niche size and position

Fig. 4 Stable isotope $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bi-plots for pike (black) and pikeperch (grey). Bayesian standard ellipse areas (40% SEA) are shown for whole population (solid line) and by species before the shift to piscivory as indicated by posterior trophic position (Fig. 3). Plots are shown by location for (a) Site 1, the Warwickshire Avon, (b) Site 2, the Severn and (c) Site 3, Tewkesbury marina, River Severn



for pike at Site 2. Similar patterns in explaining intra-specific variability have been shown in largemouth bass, where ontogenetic dietary shifts result in trophic niche differences, but with individual dietary specialisations (aquatic versus terrestrial resources) being important determinants of within niche variability (Zhao et al., 2014).

Stable isotopes are an important tool when assessing the trophic interactions and ecological effects

of non-native freshwater fish species (Cucherousset et al., 2012; Britton, 2023). In particular, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ enable estimates of trophic positions and energy sources to be made (Fry 2006) and can be used to define isotopic niche space through advanced Bayesian techniques as a reliable proxy for ecological niche (Newsome et al., 2007; Jackson et al., 2011). However, when estimating ontogenetic dietary shifts using stable isotopes, it is also important to account

Table 4 Isotopic niche metrics for pike and pikeperch by site and including groups before (“invertivorous”) and after ontogeny (“piscivorous”), where TA: the total area of the convex hull encompassing the data points, SEA: the Standard Ellipse Area

containing 40% of the data, SEA_C: Correction applied to SEA to account for small sample sizes, and the Bayesian estimate for SEA (SEA_B) with 95% credible intervals

Site	Species	n	Length range (mm)	TA	SEA	SEA _C	SEA _B	SEA _B (95%CI)
1	Pikeperch	54	40–870	44.23	10.65	10.87	10.67	7.91, 13.92
	Pike	35	101–1020	43.71	11.02	11.35	11.16	7.61, 15.30
	Invertivorous pikeperch	5	40–65	9.26	9.91	13.22	7.56	1.85, 17.46
	Invertivorous pike	8	101–238	4.99	3.30	3.85	1.28	0.54, 2.55
	Piscivorous pikeperch	49	67–870	36.09	9.12	9.32	8.59	6.61, 11.68
	Piscivorous pike	27	251–1020	37.17	9.19	9.56	8.89	5.91, 12.56
2	Pikeperch	42	48–838	21.31	4.43	4.54	4.48	3.15, 5.97
	Pike	78	114–1060	23.16	7.96	8.06	8.04	6.27, 9.89
	Invertivorous pike	16	114–241	11.13	4.43	4.74	2.59	1.45, 4.10
	Piscivorous pike	62	250–1060	19.02	5.28	5.37	4.53	3.45, 5.71
3	Pikeperch	67	29–331	25.47	6.57	6.67	6.65	5.11, 8.35
	Invertivorous pikeperch	64	29–148	25.47	6.40	6.50	6.25	4.83, 7.88
	Piscivorous pikeperch	3	227–331	NA	NA	NA	NA	NA

for isotopic turnover (Hertz et al., 2016). Specifically, it should be recognised that there will be a time lag between dietary changes and the stable isotope values of the consumer tissue (Vander Zanden et al., 2015). This is important here, given that growth rates in the early life stages of pike and pikeperch can be extremely high (Rypel 2012; Nolan and Britton, 2018a), and so dietary changes might have occurred at smaller sizes than detected by the stable isotope analyses. However, the combined use of SIA with stomach content analyses for pikeperch here enabled some corroboration on the body size at which the fish switched their diet to piscivory.

The results here were largely based on stable isotope analysis, with stomach contents data limited to the smaller pikeperch and sample sizes of larger fish being limited. The body size bias against larger fish was largely intentional, as ontogenetic shifts to piscivory tend to happen at relatively small sizes and in the first year of life in these species (Mittelbach and Persson, 1998). However, it did prevent further exploration of the extent to which the species are either oligate (eating fish only) or facultative (fish and macro-invertebrates) piscivores (e.g. Pedreschi et al., 2015). It was nevertheless apparent that the prey resources of largely invasive pikeperch and native pike were largely based on fish but with the two populations having divergent niches. This suggests that the ecological consequences of pikeperch invasion include

increased predation pressure on aspects of prey populations that are usually not depredated upon by pike. Although concerns on the ecological impacts of this increased predation pressure on native fish populations in England have persisted (Nolan et al., 2109a), with some basic impact assessment attempted (e.g. Hickley, 1986), there remains a paucity of data on their prey species to enable more precise impact analyses to be completed. This at least in part due to the invaded lowland rivers, such as the Severn and Warwickshire Avon, being sufficiently large to prevent accurate abundance estimates on their prey populations. However, both rivers support large populations of roach *Rutilus rutilus* (Linnaeus, 1758) and common bream *Abramis brama* (Linnaeus, 1758), as well as supporting individual large pike (> 10 kg) (Nolan et al., 2019b; Amat Trigo et al., 2024). Consequently, these populations of native species appear to be at least sustainable and capable of supporting recreational fisheries in pikeperch presence (e.g. Britton and Nolan, 2021), although it remains unknown what the status of these populations would be in pikeperch absence.

The application of stable isotope metrics here thus provided information on the differences on the size at which a native and an invasive fish switched their diet to piscivory, and the influence of this dietary switch on their trophic (isotopic) niches. The results revealed that both before and after switching to piscivory, the

fishes were largely partitioned in their isotopic niches, suggesting some key differences in their exploitation of prey resources, with differences in their gape size and so prey size potentially providing some explanation of this. These results suggest, however, that the influence of invasive pikeperch in these sites was to increase predation pressure across a wider proportion of the prey resources available, rather than increase pressure on those resources already being exploited by pike, although the ecological implications of this require further work.

Acknowledgements The authors would like to thank the anglers of the Severn River basin predator study for their help in collecting scale samples and to Environment Agency staff Brecht Morris and Laura Bullock for their invaluable logistic and practical help and for their contribution in establishing and liaising with the predator angler network.

Author contributions ETN and JRB conceived the study, collected field data, analysed data, wrote the manuscript, and both authors contributed to editing the manuscript. Both authors approve manuscript submission.

Funding ETN was funded by a studentship from Bournemouth University with support from the Environment Agency and the Severn Rivers Trust.

Data availability Any raw data used in the manuscript that are not already provided are available from the corresponding author at reasonable request.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

Ethical approval All aspects of data collection were completed following ethical approval and were licenced under the U.K. Animals (Scientific Procedures) Act (1986) (project licence number: PPL 70/8063).

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References

- Alieva, A. K., B. M. Nasibulina, S. Bakhshalizadeh, T. F. Kurochkina, N. N. Popov, B. I. Barbol, D. Bănăduc, N. M. Jussupbekova, G. A. Kuanysheva & A. M. Ali, 2023. The low ontogenetic diet diversity and flexibility of the pikeperch, *Sander lucioperca* (Linnaeus, 1758) (Osteichthyes, Percidae): a case study. *Fishes* 8(8): 395. <https://doi.org/10.3390/fishes8080395>.
- Amundsen, P.-A., H.-M. Gabler & F. J. Staldvik, 1996. A new approach to graphical analysis of feeding strategy from stomach contents data—modification of the Costello, 1990. method. *Journal of Fish Biology* 48: 607–614. <https://doi.org/10.1111/j.1095-8649.1996.tb01455.x>.
- Amundsen, P.-A., T. Bøhn, O. A. Popova, et al., 2003. Ontogenetic niche shifts and resource partitioning in a subarctic piscivore fish guild. *Hydrobiologia* 497: 109–119. <https://doi.org/10.1023/A:1025465705717>.
- Araújo, M. S., D. I. Bolnick & C. A. Layman, 2011. The ecological causes of individual specialisation. *Ecology Letters* 14: 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>.
- Bašić, T. & J. R. Britton, 2015. Utility of fish scales from stock assessment surveys in stable isotope analysis for initial assessments of trophic relationships in riverine fish communities. *Journal of Applied Ichthyology* 31: 296–300. <https://doi.org/10.1111/jai.12671>.
- Bousseba, M., S. Ouahb, L. Ferraj, S. Farid, M. Droussi & M. Hasnaoui, 2024. Diet and feeding ecology of the pike perch, *Sander lucioperca*, an invasive fish species: seasonal diet shifts. *Environmental Biology of Fishes* 107: 971–982.
- Britton, J. R., 2018. Empirical predictions of the trophic consequences of non-native freshwater fishes: a synthesis of approaches and invasion impacts. *Turkish Journal of Fisheries and Aquatic Sciences* 19: 529–539.
- Britton, J. R., 2023. Contemporary perspectives on the ecological impacts of invasive freshwater fishes. *Journal of Fish Biology* 103: 752–764.
- Britton, J. R., C. Gutmann Roberts, F. Amat Trigo, et al., 2019. Predicting the ecological impacts of an alien invader: Experimental approaches reveal the trophic consequences of competition. *Journal of Animal Ecology* 88: 1066–1078. <https://doi.org/10.1111/1365-2656.12996>.
- Britton, J. R., A. J. Lynch, H. Bardal, et al., 2023. Preventing and controlling nonnative species invasions to bend the curve of global freshwater biodiversity loss. *Environmental Reviews* 31: 310–326.
- Britton, J. R., D. Andreou, R. Boardman, et al., 2024. The angled-web: Recreational angling as an underappreciated disruptor to the interconnectedness of terrestrial and freshwater food webs. *Freshwater Biology* 69: 1739–1747.
- Busst, G. M. A. & J. R. Britton, 2017. Tissue-specific turnover rates of the nitrogen stable isotope as functions of time and growth in a cyprinid fish. *Hydrobiologia* 805: 49–60. <https://doi.org/10.1007/s10750-017-3276-2>.
- Butt, J. C., R. L. Eberts & C. M. Somers, 2017. Sympatric walleye *Sander vitreus* and sauger *Sander canadensis* in large reservoirs: Variable isotopic niche size and overlap

- across multiple time scales. *Fisheries Management and Ecology* 24: 308–319. <https://doi.org/10.1111/fme.12227>.
- Chapman, L. J., W. C. Mackay & C. W. Wilkinson, 1989. Feeding flexibility in northern pike, *Esox lucius*: fish versus invertebrate prey. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 666–669.
- Cittadino, S., A. S. Tarkan, S. Aksu, R. M. Wright, A. M. Hinder, S. Lane, E. Winter, J. Lyons & J. R. Britton, 2024. Individual variability in the movement ecology of Northern Pike *Esox lucius* in a highly connected wetland system. *Aquatic Science* 86: 105.
- Comte, L., J. Cucherousset, S. Boulêtreau & J. D. Olden, 2016. Resource partitioning and functional diversity of worldwide freshwater fish communities. *Ecosphere* 7: e01356. <https://doi.org/10.1002/ecs2.1356>.
- Cucherousset, J. & J. D. Olden, 2011. Ecological impacts of non-native freshwater fishes. *Fisheries* 36: 215–230. <https://doi.org/10.1080/03632415.2011.574578>.
- Cucherousset, J., S. Bouletreau, A. Martino, et al., 2012. Using stable isotope analyses to determine the ecological effects of non-native fishes. *Fisheries Management and Ecology* 19: 111–119. <https://doi.org/10.1111/j.1365-2400.2011.00824.x>.
- Cucherousset, J., J.-M. Paillisson & J.-M. Roussel, 2013. Natal departure timing from spatially varying environments is dependent of individual ontogenetic status. *Naturwissenschaften* 100: 761–768. <https://doi.org/10.1007/s00114-013-1073-y>.
- Didenko, A. V. & A. B. Gurbyk, 2016. Spring diet and trophic relationships between piscivorous fishes in Kaniv Reservoir Ukraine. *Folia Zoologica*. <https://doi.org/10.25225/fozo.v65.i1.a4.2016>.
- Dörner, H., S. Hülsmann, F. Hölker, et al., 2007. Size-dependent predator-prey relationships between pikeperch and their prey fish. *Ecology of Freshwater Fish* 16: 307–314. <https://doi.org/10.1111/j.1600-0633.2006.00223.x>.
- Eby, L. A., W. J. Roach, L. B. Crowder & J. A. Stanford, 2006. Effects of stocking-up freshwater food webs. *Trends in Ecology & Evolution* 21: 576–584. <https://doi.org/10.1016/j.tree.2006.06.016>.
- Elvira, B. & A. Almodóvar, 2001. Freshwater fish introductions in Spain: facts and figures at the beginning of the 21st century. *Journal of Fish Biology* 59: 323–331. <https://doi.org/10.1111/j.1095-8649.2001.tb01393.x>.
- Fickling, N. J. & R. L. G. Lee, 1983. A Review of the ecological impact of the introduction of the zander, *Stizostedion lucioperca* L. into waters of the Eurasian mainland. *Aquaculture Research* 14: 151–155. <https://doi.org/10.1111/j.1365-2109.1983.tb00065.x>.
- Fry, B., 2006. *Stable Isotope Ecology*, Springer, New York.
- Ginter, K., K. Kangur, A. Kangur, et al., 2011. Diet patterns and ontogenetic diet shift of pikeperch, *Sander lucioperca*, L. fry in lakes Peipsi and Võrtsjärv. *Estonia. Hydrobiologia* 660: 79–91. <https://doi.org/10.1007/s10750-010-0393-6>.
- Guzzo, M. M., G. D. Haffner, N. D. Legler, et al., 2013. Fifty years later: trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie. *Biological Invasions* 15: 1695–1711. <https://doi.org/10.1007/s10530-012-0401-z>.
- Guzzo, M. M., P. J. Blanchfield, A. J. Chapelsky & P. A. Cott, 2016. Resource partitioning among top-level piscivores in a sub-Arctic lake during thermal stratification. *Journal of Great Lakes Research* 42: 276–285. <https://doi.org/10.1016/j.jglr.2015.05.014>.
- Hammerschlag-Peyer, C. M., L. A. Yeager, M. S. Araújo & C. A. Layman, 2011. A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. *PLoS One* 6: e27104. <https://doi.org/10.1371/journal.pone.0027104>.
- Heady, W. N. & J. W. Moore, 2013. Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. *Oecologia* 172: 21–34. <https://doi.org/10.1007/s00442-012-2483-9>.
- Hertz, E., M. Trudel, R. El-Sabaawi, et al., 2016. Hitting the moving target: modelling ontogenetic shifts with stable isotopes reveals the importance of isotopic turnover. *Journal of Animal Ecology* 85: 681–691. <https://doi.org/10.1111/1365-2656.12504>.
- Hickley, P., 1986. Invasion by zander and the management of fish stocks. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 314: 571–582. <https://doi.org/10.1098/rstb.1986.0073>.
- Hickley, P. & S. Chare, 2004. Fisheries for non-native species in England and Wales: angling or the environment? *Fisheries Management and Ecology* 11: 203–212. <https://doi.org/10.1111/j.1365-2400.2004.00395.x>.
- Hölker, F. & T. Mehner, 2005. Simulation of trait-and density-mediated indirect effects induced by piscivorous predators. *Basic and Applied Ecology* 6: 289–300. <https://doi.org/10.1016/j.baae.2004.10.001>.
- Jackson, M. C. & J. R. Britton, 2014. Divergence in the trophic niche of sympatric freshwater invaders. *Biological Invasions* 16: 1095–1103. <https://doi.org/10.1007/s10530-013-0563-3>.
- Jackson, A. L., R. Inger, A. C. Parnell & S. Bearhop, 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R: Bayesian isotopic niche metrics. *Journal of Animal Ecology* 80: 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>.
- Jackson, M. C., I. Donohue, A. L. Jackson, et al., 2012. Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. *PLoS ONE* 7: e31757. <https://doi.org/10.1371/journal.pone.0031757>.
- Jackson, M. C., J. Grey, K. Miller, et al., 2016. Dietary niche constriction when invaders meet natives: evidence from freshwater decapods. *Journal of Animal Ecology* 85: 1098–1107. <https://doi.org/10.1111/1365-2656.12533>.
- Kopp, D., J. Cucherousset, J. Syväranta, et al., 2009. Trophic ecology of the pikeperch, *Sander lucioperca*, in its introduced areas: a stable isotope approach in southwestern France. *Comptes Rendus Biologies* 332: 741–746. <https://doi.org/10.1016/j.crv.2009.04.001>.
- Long, J. M. & L. Seguy, 2024. Global status of non-native Largemouth Bass, *Micropterus salmoides*, Centrarchidae, and Smallmouth Bass, *Micropterus dolomieu*, Centrarchidae.: disparate views as beloved sportfish and feared invader. *Reviews in Fisheries Science & Aquaculture* 32: 81–98.

- Lundvall, D., R. Svanbäck, L. Persson & P. Byström, 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1285–1292. <https://doi.org/10.1139/f99-058>.
- Mittelbach, G. G. & L. Persson, 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1454–1465. <https://doi.org/10.1139/f98-041>.
- Newsome, S. D., C. M. del Rio, S. Bearhop & D. L. Phillips, 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5: 429–436. <https://doi.org/10.1890/060150.01>.
- Nilsson, P. A., 2001. Predator behaviour and prey density: evaluating density-dependent intraspecific interactions on predator functional responses. *Journal of Animal Ecology* 70: 14–19. <https://doi.org/10.1046/j.1365-2656.2001.00472.x>.
- Nolan, E. T. & J. R. Britton, 2018a. Spatial variability in the somatic growth of pikeperch *Sander lucioperca*, an invasive piscivorous fish. *Ecology of Freshwater Fish* 28: 330–340. <https://doi.org/10.1111/eff.12456>.
- Nolan, E. T. & J. R. Britton, 2018b. Diet of invasive pikeperch *Sander lucioperca*: developing non-destructive tissue sampling for stable isotope analysis with comparisons to stomach contents analysis. *Knowledge & Management of Aquatic Ecosystems* 419: 1–13. <https://doi.org/10.1051/kmae/2018037>.
- Nolan, E. T., S. C. Curtin & J. R. Britton, 2019a. Angler behaviors and motivations for exploiting invasive and native predatory fishes by catch-and-release: a case study on the river severn catchment, Western England. *Human Dimensions of Wildlife* 24: 463–479. <https://doi.org/10.1080/10871209.2019.1628324>.
- Nolan, E. T., C. Gutmann Roberts & J. R. Britton, 2019b. Predicting the contributions of novel marine prey resources from angling and anadromy to the diet of a freshwater apex predator. *Freshwater Biology* 64: 1542–1554. <https://doi.org/10.1111/fwb.13326>.
- Nolan, E. T., A. M. Hindes, J. D. Bolland, P. Davies, C. Gutmann Roberts, A. S. Tarkan & J. R. Britton, 2024. Movements and habitat use of native and invasive piscivorous fishes in a temperate and channelized lowland river. *Hydrobiologia* 852: 2187.
- Nyqvist, M. J., J. Cucherousset, R. E. Gozlan & J. R. Britton, 2018. Relationships between individual movement, trophic position and growth of juvenile pike, *Esox lucius*. *Ecology of Freshwater Fish* 27: 398–407. <https://doi.org/10.1111/eff.12355>.
- Nyqvist, M. J., J. Cucherousset, R. E. Gozlan, et al., 2019. Dispersal strategies of juvenile pike, *Esox lucius* L.: influences and consequences for body size, somatic growth and trophic position. *Ecology of Freshwater Fish* 29: 377.
- Pedreschi, D., S. Mariani, J. Coughlan, et al., 2015. Trophic flexibility and opportunism in pike *Esox lucius*. *Journal of Fish Biology* 87: 876–894. <https://doi.org/10.1111/jfb.12755>.
- Persson, A. & C. Brönmark, 2002. Foraging capacity and resource synchronization in an ontogenetic diet switcher, pikeperch, *Stizostedion lucioperca*. *Ecology* 83: 3014–3022. [https://doi.org/10.1890/0012-9658\(2002\)083\[3014:FCARSI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[3014:FCARSI]2.0.CO;2).
- Persson, L., J. Andersson, E. Wahlstrom & P. Eklov, 1996. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology* 77: 900–911.
- Post, D. M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2).
- Post, D. M., C. A. Layman, D. A. Arrington, et al., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152: 179–189. <https://doi.org/10.1007/s00442-006-0630-x>.
- Quezada-Romegialli, C., A. L. Jackson, B. Hayden, et al., 2017. tRophicPosition, an R package for the Bayesian estimation of trophic position from consumer stable isotope ratios. *Methods in Ecology and Evolution* 9: 1592–1599. <https://doi.org/10.1111/2041-210X.13009>.
- R Development Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reinas, G. C. Z., J. C. Silva & A. Bialecki, 2022. Coexistence patterns between native and exotic juvenile Loricariidae in a Neotropical floodplain: an approach to resource partitioning. *Hydrobiologia* 849: 1713–1726.
- Ricciardi, A., M. F. Hoopes, M. P. Marchetti & J. L. Lockwood, 2013. Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83: 263–282. <https://doi.org/10.1890/13-0183.1>.
- Rypel, A. L., 2012. Meta-analysis of growth rates for a circumpolar fish, the northern pike, *Esox lucius*, with emphasis on effects of continent, climate and latitude. *Ecology of Freshwater Fish* 21: 521–532. <https://doi.org/10.1111/j.1600-0633.2012.00570.x>.
- Sánchez-Hernández, J., A. D. Nunn, C. E. Adams & P.-A. Amundsen, 2018. Causes and consequences of ontogenetic dietary shifts: a global synthesis using fish models. *Biological Reviews* 94: 539–554. <https://doi.org/10.1111/brv.12468>.
- Sánchez-Hernández, J., S. Prati, E. H. Henriksen, A. Smalås, R. Knudsen, A. Klemetsen & P. A. Amundsen, 2022. Exploring temporal patterns in fish feeding ecology: are ontogenetic dietary shifts stable over time? *Reviews in Fish Biology and Fisheries* 32: 1141–1155.
- Schoenebeck, C. W., K. D. Koupal, B. C. Peterson, C. S. Uphoff, Z. Woiak, B. T. Miller, M. R. Wuellner & J. W. Kreitman, 2024. Seasonal prey taxa and size selection and drivers of age-0 walleye ontogenetic diet shifts. *Journal of Freshwater Ecology* 39: 2426555.
- Schulze, T., H. Dörner, U. Baade & F. Hölker, 2012. Dietary niche partitioning in a piscivorous fish guild in response to stocking of an additional competitor—the role of diet specialisation. *Limnologia-Ecology and Management of Inland Waters* 42: 56–64. <https://doi.org/10.1016/j.limno.2011.08.001>.
- Sih, A., D. I. Bolnick, B. Luttbeg, et al., 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* 119: 610–621. <https://doi.org/10.1111/j.1600-0706.2009.18039.x>.

- Svanbäck, R. & D. I. Bolnick, 2006. Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences* 274: 839–844. <https://doi.org/10.1098/rspb.2006.0198>.
- Trueman, C. N. & A. Moore, 2007. Use of the stable isotope composition of fish scales for monitoring aquatic ecosystems. *Terrestrial Ecology* 1: 145–161. [https://doi.org/10.1016/S1936-7961\(07\)01010-X](https://doi.org/10.1016/S1936-7961(07)01010-X).
- Valentine, S. A. & G. W. Whitledge, 2024. Spatial and ontogenetic patterns in the trophic ecology of two predatory fishes in a large river. *Ecology of Freshwater Fish*. <https://doi.org/10.1111/eff.12814>.
- Vander Zanden, M. J., M. K. Clayton, E. K. Moody, et al., 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PloS One* 10: e0116182.
- Ventura, M. & E. Jeppesen, 2010. Evaluating the need for acid treatment prior to $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of freshwater fish scales: effects of varying scale mineral content, lake productivity and CO₂ concentration. *Hydrobiologia* 644: 245–259. <https://doi.org/10.1007/s10750-010-0121-2>.
- Winter, E. R., M. Nyqvist & J. R. Britton, 2019. Non-lethal sampling for stable isotope analysis of pike *Esox lucius*: how mucus, scale and fin tissue compare to muscle. *Journal of Fish Biology* 95: 956–958. <https://doi.org/10.1111/jfb.14059>.
- Yağcı, M. A., A. Alp, A. Yağcı & R. Uysal, 2014. Diet and Prey Selection of Pikeperch, *Sander lucioperca* Linnaeus, 1758. Population in Lake Eğirdir. Turkey. *Archives of Biological Sciences*. 66: 1515–1527. <https://doi.org/10.2298/ABS1404515Y>.
- Zhao, T., S. Villéger, S. Lek & J. Cucherousset, 2014. High intraspecific variability in the functional niche of a predator is associated with ontogenetic shift and individual specialization. *Ecology and Evolution* 4: 4649–4657. <https://doi.org/10.1002/ece3.1260>.

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