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RESEARCH

Trophic organisation of a large lake fish community: comparing alternative models and evaluating resource use based on stable isotope ratios

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Abstract Understanding trophic relationships is fundamental for investigating ecosystem processes and their role in community dynamics. Several theories on trophic organisation of biotic communities have explored how resource use, niche breadth, and trophic position vary among organisms. Traditional approaches typically assume invariant trophic traits within species, whereas alternative theories emphasize size-structured relationships, where trophic attributes scale with body size across taxonomic groups – often leading to controversial interpretations. In this study, we examined the relative roles of species identity and body size in the trophic organisation of a large shallow lake fish community using stable isotope analysis based on $\delta^{13}C$ and $\delta^{15}N$. By comparing the explanatory power of alternative trophic models, we found that models incorporating both species identity and body size overperformed simpler models that included only one of these factors. Models incorporating full factorial effects of species and body size performed the best, suggesting that ontogenetic changes in resource use are species-specific, while the pure body size model provided only marginal or no explanatory power in the community level analysis. Our analysis revealed that fish in Lake Balaton rely primarily on the open-water basal carbon and nitrogen sources and most species exhibit substantial among-individual variation in both trophic position and isotopic food niche breadth. We conclude that stable isotope analysis, has the potential to provide a detailed understanding of the trophic organisation of lake fish assemblages. Based on our results, we recommend that trophic modelling of fish communities should consider both among species and size-related within species variability.

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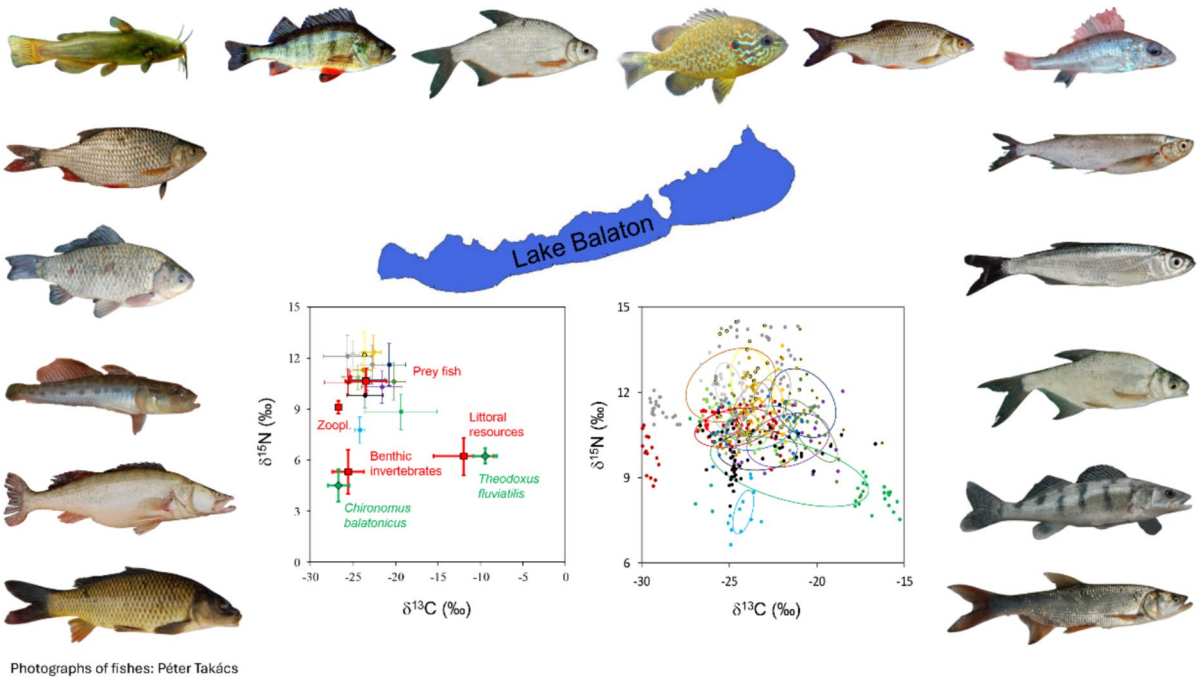
Graphic abstract



Keywords Ontogenetic diet shift · Niche breadth · Resource partitioning Size-structured · Stable isotopes Trophic level

Introduction

Trophic relationships are major components of community organisation and ecosystem functioning as well as key factors influencing system-level productivity and biotic diversity (Garvey and Whiles 2016). Information on trophic position, niche breadth and food resource partitioning of organisms is used, for example, to help evaluate structuring processes and stability of the food web (Potapov et al. 2019; Funes et al. 2022), evaluate and predict the community effect of environmental changes (McMeans et al. 2016; Britton et al. 2022; Lacerot et al. 2022), assess the invasive potential and impacts of non-native species (Wainright et al. 2021; Quintana et al. 2023; Czeglédi et al. 2024; Šmejkal et al. 2024), and support conservation planning (Decker et al. 2017; Eero et al. 2021).

There are several alternative theories on the trophic organisation of communities, specifically on how resource use, food niche breadth and trophic position (trophic level) vary among organisms. The traditional approach is to characterise trophic attributes and relationships at the species level (Root 1967; McCann 2011). Community ecology is therefore traditionally species-based, implicitly assuming that trophic traits are invariant among individuals of the same species (Nakazawa 2015). Other approaches emphasize the general relevance of size-structured relationships and assume that trophic attributes and functions scale with body size of organisms both within and across taxonomic groups (Cohen et al. 1993, 2003). The underlying rationale of this concept is that because consumers are often gape-limited and constrained to feed on prey smaller than their own size, consumer size should also be positively associated with trophic

position (Cohen et al. 1993; Woodward et al. 2005; Brose et al. 2006). Several studies have tested the size-structured trophic theory and revealed highly variable results. For example, while size-based theory proved to be highly relevant in marine consumers (Al-Habsi et al. 2008; Potapov et al. 2019; Maitland et al. 2024), the strength of the relationship between the trophic position and body size varied notably among freshwater ecosystems (Ou et al. 2017; Potapov et al. 2019; Lacerot et al. 2022) and seemed to have little or no relevance in terrestrial consumers (Potapov et al. 2019). In contrast, integrated approaches are based on the principle that trophic characters may change with ontogeny in most species, and thus species identity and body size should be considered together in trophic models (Werner and Gilliam 1984; de Roos and Persson 2013; Nakazawa 2015; Sánchez-Hernández et al. 2019). Ontogenetic changes may either be scaled with body size monotonically or may be manifested in definite shifts resulting in stage-specific trophic traits (Werner and Gilliam 1984; Mittelbach and Persson 1998; Scharf et al. 2000; Specziár and Rezsu 2009; Nakazawa 2015). However, we have rather limited information on how these models actually perform relative to each other in real communities.

Stable isotope analysis (SIA) based on $\delta^{13}C$ and $\delta^{15}N$ is a widely applied tool to study resource use, trophic niche size and trophic position of organisms as well as organisation of community food webs (Layman et al. 2007, 2012; Boecklen et al. 2011; Shipley and Matich 2020). Major advantages of SIA compared to traditional diet analysis methods (e.g. gut content and faeces analyses) are that it provides information on the average assimilated diet of organisms over a certain time period (typically from few weeks to few months) and quantitative indication on the tropic status as well. In addition, because SIA infers individual trophic traits based on the isotope level of common trace elements, standardized resource use data may be obtained even for all trophic groups (e.g. species, size groups) of a community, which largely facilitates the comparison of alternative community models (Stock et al. 2018).

In the present study, we compare the explanatory power of the alternative trophic models outlined above, fitted to SIA inferred resource use data of a large lake (Lake Balaton, Hungary) fish community, and then we evaluate the trophic structure of the community with special emphasis on the patterns in trophic position, trophic niche breadth and resource use. Fish are a species-rich and functionally diverse group with representation at all consumption levels from primary consumers (herbivores) to top predators, and they occur in wide size-ranges with the majority of the species showing ontogenetic changes in their resource use (Gerking 1994). Therefore, fish are ideal model organisms for studying principles of community organisation and testing the performance of alternative trophic models. In addition, all the pure species (e.g., Parzanini et al. 2017; Kaymak et al. 2018; Cicala et al. 2020; Park et al. 2020), the pure body size (Al-Habsi et al. 2008; Romanuk et al. 2011; Ou et al. 2017; Lacerot et al. 2022) and the species and body size (Livingston 1982; Deudero et al. 2004; Specziár and Rezsu, 2009; Czeglédi et al. 2024) trophic models have been applied widely for fish communities. However, their fits to real data have not yet been explicitly compared. We predict that models including information on both species identity and ontogeny, represented by body size, will outperform simpler models in assessing trophic attributes of fish. We also predict that the pure body size-based model will be the least informative as it does not account for species-specific traits.

Material and methods

Study area

With its 596 km^2 surface area, Lake Balaton is the largest shallow lake in Central Europe. Its mean depth is 3.3 m. The lake is meso-eutrophic (Istvánovics et al. 2007). A significant part of the lake shore was stabilized with stones and concrete structures, while ca. 45% of the shore is still vegetated and covered mainly by reed grass *Phragmites australis* stands. Although a predominant part of the biotic diversity concentrates in the vegetated littoral zone (Árva et al. 2015; Karádi-Kovács et al. 2023), open water planktonic and benthic organisms dominate the food web (Istvánovics et al. 2007; Bernát et al. 2020). Twenty-six native and ten non-native species comprise the fish fauna, with *Alburnus alburnus*, *Abramis brama* and *Pelecus cultratus* being the most abundant ones, and common carp *Cyprinus carpio* being the most preferred and intensively stocked game fish (Specziár and Erős 2020). The main food resources for the fish include zooplankton, benthic chironomids, dreissenid mussels and littoral crustaceans. Some fishes (e.g.,

Table 1 Fish species sampled, their standard length (SL; mean, SD and range), sample size (*n*), carbon to nitrogen ratio (C:N; mean and SD) and stable isotope values ($\delta^{13}C$ and $\delta^{15}N$; mean and SD)

Species	SL (mm)	SD	Range	*n*	C:N	SD	$\delta^{13}C$ (‰)	SD	$\delta^{15}N$ (‰)	SD
Abramis brama	104.8	73.3	14–230	55[a]	3.20	0.15	−25.60	2.74	10.59	0.75
Alburnus alburnus	97.1	7.5	85–110	19	3.32	0.09	−25.32	1.04	10.89	0.36
Ameiurus melas	111.0	57.0	29–200	28	3.26	0.10	−22.59	0.89	11.39	0.94
Blicca bjoerkna	148.0	51.3	77–250	31	3.22	0.05	−24.44	1.57	10.89	0.73
Carassius gibelio	96.2	106.5	33–340	30	3.29	0.12	−19.34	4.23	8.83	1.06
Cyprinus carpio	442.4	27.6	395–474	12	3.37	0.29	−24.19	0.62	7.78	0.76
Gymnocephalus cernua	67.2	16.6	49–105	19	3.20	0.04	−23.37	2.13	10.74	0.68
Lepomis gibbosus	93.9	45.0	39–157	16	3.27	0.05	−20.75	1.88	11.62	1.22
Leuciscus aspius	205.4	145.9	80–500	25	3.20	0.04	−23.70	1.20	12.20	1.33
Neogobius fluviatilis	64.0	12.4	48–87	17	3.17	0.05	−21.63	2.38	10.31	0.95
Pelecus cultratus	245.0	43.9	121–310	23	3.40	0.23	−25.04	0.80	12.24	0.76
Perca fluviatilis	110.0	62,3	57–221	30	3.22	0.07	−22.78	1.25	11.60	1.15
Rutilus rutilus	92.3	72.5	12–240	55[a]	3.27	0.20	−23.60	2.14	9.81	0.74
Sander lucioperca	149.6	175.2	11–570	56[a]	3.27	0.19	−25.68	2.85	12.12	1.19
Sander volgensis	118.3	90.6	43–285	30	3.23	0.04	−23.84	1.13	11.32	1.02
Scardinius erythrophthalmus	141.5	80.3	68–320	21	3.23	0.15	−20.24	1.52	10.62	1.09
Total: 16 species			11–570	467						

[a]Each sample of the SL ≤ 20 mm fish size groups contained multiple individuals to ensure enough sample quantity for stable isotope analysis

Rutilus rutilus and *Scardinius erythrophthalmus*) also utilize plant-based resources, such as filamentous algae, macrophytes and detritus (Specziár and Rezsu 2009).

Fish and food resource sampling

We collected samples of 16 fish species representing wide size ranges for majority of the species (Table 1) by using multiple sampling techniques – multi-mesh gillnetting (5 to 80 mm mesh sizes), battery powered electrofishing (1 and 6 mm anode ring mesh sizes), benthic sledging (2 mm mesh size; towed at speed of 5.4–5.8 km h^{-1}) and dip netting (1 mm mesh size) – and fishing in various habitat types (offshore benthic and water column, littoral vegetated and riprap) (for details of fish sampling methodology see Specziár and Erős 2020). Most samplings were performed in August and September 2022, but to cover life-span diet ontogeny, the earliest life stages of some characteristic fish species (standard length, SL ≤ 50 mm) collected few weeks after the spawning of fish, in May and June 2023, were also included to samples. Collected individuals were immediately transported in a cooling box into the Balaton Limnological Research Institute where they were stored frozen (− 20 °C) until the laboratory processing (within 1–2 weeks).

Parallel to fish samplings we also collected samples of the potential food resources proved to be used by fishes in Lake Balaton (Specziár and Rezsu 2009). We collected crustacean zooplankton (mixed) using a plankton net (mesh size: 60 µm) and separated from the seston under a stereomicroscope. We collected benthic chironomid larvae *Chironomus balatonicus* using an Ekman grab sampler and separated from the sediment by washing the samples through a 0.25 mm mesh sieve, and benthic mussel *Dreissena* spp. (*D. bugensis* and *D. polymorpha*) by hand. From the littoral zone, we collected filamentous algae *Cladophora glomerata*, a mixture of submerged aquatic macrophytes (*Ceratophyllum demersum*, *Myriophyllum spicatum*, *Najas marina* and *Potamogeton perfoliatus*), snail *Theodoxus fluviatilis* and amphipod *Dikerogammarus* spp. by hand. Further, to represent prey fishes as food resource we included samples of *A. alburnus*, *Gymnocephalus cernua* and *Neogobius fluviatilis* being the most abundant fishes in the diet of piscivorous fishes in Lake Balaton (Specziár 2011).

Each sample of the smallest fish size groups (SL ≤ 20 mm), as well as zooplankton, chironomid

Table 2 Main resource categories, their sampled components, sample sizes (n) and stable isotope values ($\delta^{13}C$ and $\delta^{15}N$; mean and SD). Resource component used also as baselines for trophic position assessment are indicated along with their assumed trophic position values (λ). Each sample, except preyfish, contained multipe individuals to ensure enough sample quantity for stable isotope analysis

Main food resources	Specific components	Baseline (λ)	n	$\delta^{13}C$ (‰)	SD	$\delta^{15}N$ (‰)	SD
Zooplankton	Mixed, excl. adult *Leptodora kindtii*	–	24	−26.73	0.27	9.12	0.40
Benthic invertebrates				−25.61	1.83	5.32	1.32
	Mussels (*Dreissena* spp.)	–	15	−23.84	0.99	6.60	0.58
	Chironomid larvae (*Chironomus balatonicus*)	offshore baseline ($\lambda = 2$)	24	−26.72	1.28	4.52	0.97
Littoral resources				−12.18	3.63	6.26	1.13
	Algae (*Cladophora glomerata*)	–	7	−15.73	1.39	4.78	0.81
	Submerged macrophytes (mixed)	–	17	−11.85	1.77	5.77	1.16
	Snails (*Theodoxus fluviatilis*)	littoral baseline ($\lambda = 2$)	33	−9.47	1.38	6.25	0.43
	Macroinvertebrates (*Dikerogammarus* spp.)	–	12	−18.30	0.92	7.85	0.76
Preyfish	*Alburnus alburnus*, *Gymnocephalus cernua*, *Neogobius fluviatilis*	–	55	−23.51	2.41	10.66	0.73

larvae, mussels, snails and amphipods comprised multiple individuals to have sufficient biomass for SIA (Table 1, Table 2).

All procedures involving the handling and treatment of animals were in accordance with Hungarian law and the permit for the delivery and use of aquatic animals for scientific purposes (permit reg. no.: VE-I-001/01890-3/2013, valid between 22 August 2013 and 21 August 2023, issued by the Food-Security and Animal Health Directorate, Governmental Office of Veszprém County, Hungary). Moreover, to minimize the environmental impact of the study, fish samples were mainly collected as part of the prescribed fish monitoring survey under the EU Water Framework Directive by selecting the injured specimens, and only minimal additional sampling was carried out.

Sample processing and stable isotope analysis

Fish were measured for SL to the nearest 1 mm and dorso-lateral muscle tissue samples were dissected for SIA. Food resource samples were kept in whole, except for mussels and snails, in which organism we used their soft tissues only (shells being indigestible for fish were removed). All samples were dried at 50 °C to a constant mass and then ground to a fine powder with a mortar and pestle. Ground samples were stored in Eppendorf tubes at − 35 °C for further processing. Three parallel subsamples of each fish (except some small individuals with limited sample quantity, which were not subsampled) and food resource samples weighting 362–2208 µg were encapsulated in tin capsules (pressed standard weight, 8 × 15 mm; Sercon Limited, UK) for SIA.

Samples were analysed using a SERCON Integra 2 Elemental Analyzer and Isotope Ratio Mass Spectrometer (Sercon Limited, UK) to determine their percent C and N content as well as stable C ($\delta^{13}C$) and N ($\delta^{15}N$) isotope signals. Stable isotope ratios are expressed in ‰ with a standard delta (δ) notation, standardized in relation to reference material, as follows: $\delta X\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N and R is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio. We used Tuna Protein standard certified for both ^{13}C and ^{15}N (Sercon Limited, UK). Measurement precision, based on the replicate runs of the reference material was better than ± 0.03 ‰ for $\delta^{13}C$ and ± 0.1 ‰ for $\delta^{15}N$. Since the vast majority of fish muscle samples had a C:N ratio below or close to 3.5 indicating a low lipid content (Table 1), we did not correct $\delta^{13}C$ values for lipids (Post et al. 2007).

Statistical analysis

Isotopic measurements obtained for parallel subsamples (up to three per individual) were averaged for each fish specimen and these average values were used in the further analyses.

All data analyses were performed in the R environment (R Core Team 2024). We used general linear modelling (GLM) to test the relative role of species identity and body size in structuring the isotopic signals, and consequently, the inferred trophic organisation and resource use of the fish community. For this purpose, we compared the explanatory power of six alternative models with different covariate structures, separately for $\delta^{13}C$ and $\delta^{15}N$ data: 1) model Intercept-only, with no explanatory variable included; 2) model Length, with SL included as fixed continuous effect; 3) model Species, with species identity included as categorical fixed effect; 4) model Species + Length, with main effects included only; 5) model Species: Length, with interaction effect included only; and 6) model Species × Length, with both main and interaction effects included. The best model was selected by using the Akaike information criterion corrected for sample size (AIC_c) and the corresponding AIC_c weights, which can be interpreted as conditional probabilities for each model (Wagenmakers and Farrel 2004). In order to evaluate species-specific effect of body size on stable isotope signals, we used linear regression analysis and tested the relationship between SL, and $\delta^{13}C$ and $\delta^{15}N$ data in each fish species.

We estimated the trophic position of fish by using the R package *tRophicPosition* 0.8.0. (Quezada-Romegialli et al. 2018) and the two-baseline full model Bayesian procedure (both $\delta^{13}C$ and $\delta^{15}N$ data are considered). According to Post (2002), we chose snail *Thedoxus fluviatilis* grazing on algae growing on the surface of rocks and macrophytes (Skoog 1978) as littoral primary consumer baseline, and chironomid larvae *Chironomus balatonicus* collecting and filtrating live and dead pelagic and benthic algae (Specziár and Vörös 2001) as offshore benthic primary consumer baseline. We set the trophic level of the two baselines to $\lambda = 2$ and applied the trophic discrimination factor of 1.30 ± 0.30 (mean ± SD) for $\delta^{13}C$ and 2.90 ± 0.32 for $\delta^{15}N$ as suggested by McCutchan et al. (2003) for consumer muscle tissue samples. For the Bayesian simulation of trophic position, we applied five parallel chains of 100 000 burn-in, 100 000 adaptive and 100 000 actual iterations, at which parameters the Gelman and Rubin (1992) diagnostics (at ≤ 1.05) indicated the convergence of results in our data (see also Quezada-Romegialli et al. 2018). We estimated the probability of overlap in trophic position between each species using the function *pairwiseComparisons* in the package *tRophicPosition.*

We analysed the isotopic niche structure of the fish community using the R package *SIBER* 2.1.7. (Jackson and Parnell 2023). We estimated the Bayesian standard ellipse areas corrected for small sample size (SEA_c) to indicate and compare core isotopic niche widths and core isotopic niche overlaps across species within the fish community. SEA_c contains approximately 40% of the data. Compared to the convex hull area and the 95% ellipse, SEA_c is unbiased with respect to sample size; therefore, it provides a robust estimate and comparison of core isotopic niche width (Jackson et al. 2011). For the assessment of SEA_c we ran the Bayesian simulation in five chains of 100 000 iterations of which 10 000 was used as burn-in. We assessed the degree of SEA_c overlap between fish species using the likelihood test in the SIBER package and used it to indicate pairwise similarity in food resource use (Jackson et al. 2011).

To evaluate within fish community diet partitioning, we used the MixSIAR Bayesian tracer mixing model (package *MixSIAR*; Stock et al. 2018, 2022) and tested the relative performance of four isotope mixing models with different covariate structures: 1) model Intercept-only, with no explanatory variable included; 2) model Length, with SL included as fixed continuous effect; 3) model Species, with species identity included as categorical fixed effect; and 4) model Species + SL, with species included as fixed categorical and SL included as fixed continuous effect. Note that MixSIAR provides less option for model formulation compared to traditional linear model tests and particularly, it does not support the inclusion of interaction effects. Since performance of the two stable isotopes mixing model is highly dependent on the number of resource categories considered (Brett 2014), we combined all potential food resources into four main resource categories: zooplankton, benthic invertebrates (chironomids and mussels), littoral resources (filamentous algae, macrophytes, snails and amphipods)

and prey fish (Table 2). *Leptodora kindtii* was excluded from the zooplankton because its isotopic signal range heavily overlaps with the signal range of prey fish and is consumed only by very limited group of fish in Lake Balaton. Fractionation factors between resources and the fish were assumed to be 1.30 ± 0.30 (mean ± SD) for $\delta^{13}C$ and 2.90 ± 0.32 for $\delta^{15}N$ (McCutchan et al. 2003). For the model evaluation, we used the uninformative prior – where all values between 0 and 1 are equally likely for each resource category –, chose the full model option considering both residual and process type of error, and run the Bayesian simulation in three chains of 300,000 iterations of which 200,000 was used as burn-in. Convergence of the mixing models was checked using the Gelman and Rubin (1992) diagnostics (at ≤ 1.05). The best-fitting of the four alternative mixing models was selected using the approximate leave-one-out cross-validation information criterion (LOOic) approach (Vehtari et al. 2017; Stock et al. 2018). Finally, to evaluate size dependent patterns in resource use of each fish species, we also used the MixSIAR mixing model with SL included as fixed continuous effect, and run it separately for each species with the same simulation parameters as in the community level data.

Results

Patterns of stable isotope ratios

We collected 467 muscle tissue samples of 16 fish species within the size range of SL = 11–570 mm (Table 1) as well as 187 samples of potential food resources grouped into four main categories (Table 2).

The Species × Length full model received 100% AIC_c weight of being the best model and provided noticeably the best explanatory power ($r^2_{adj.} = 0.570$) to describe within fish community patterns of the $\delta^{13}C$ data (Table 3). Other, less complex models including species identity provided substantially less explanatory power ($r^2_{adj.} = 0.121$–0.412), whereas the pure Length model had zero explanatory power.

Again, the Species × Length full model received 100% AIC_c weight of being the best model to describe within fish community patterns of the $\delta^{15}N$ data ($r^2_{adj.} = 0.810$; Table 3), but the Species + Length

Table 3 Fit statistics and results of the Akaike information criterion (AIC) analysis for six competing general linear models considering the influence of fish standard length and species identity on stable isotope $\delta^{13}C$ and $\delta^{15}N$ values. Models are listed in decreasing order of their performance

Model	Model fit		Best model selection						
	r^2_{adj}	df	F	p	K	log(L)	AIC_c	ΔAIC_c	AIC_c weight
$\delta^{13}C$									
Species × Length, full factorial design	0.570	31, 435	20.9	< 0.001	33	− 936.6	1944.5	0	1.000
Species + Length, main effects only	0.418	16, 450	21.9	< 0.001	18	− 1015.3	2068.1	123.6	0.000
Species	0.412	15, 451	22.8	< 0.001	17	− 1018.0	2071.3	126.8	0.000
Species:Length, interaction only	0.121	16, 450	5.0	< 0.001	18	− 1111.4	2260.3	315.8	0.000
Intercept-only	0.000	0, 466	–	–	2	− 1149.7	2303.4	358.9	0.000
Length	0.000	1, 465	0.3	0.558	3	− 1149.5	2305.0	360.5	0.000
$\delta^{15}N$									
Species × Length, full factorial design	0.810	31, 435	65.1	< 0.001	33	− 421.3	913.7	0	1.000
Species + Length, main effects only	0.759	16, 450	92.5	< 0.001	18	− 485.1	1007.7	94.0	0.000
Species:Length, interaction only	0.656	16, 450	56.5	< 0.001	18	− 567.8	1173.2	259.5	0.000
Species	0.545	15, 451	38.3	< 0.001	17	− 633.3	1302.0	388.3	0.000
Length	0.133	1, 465	72.8	< 0.001	3	− 791.1	1588.3	674.6	0.000
Intercept-only	0.000	0, 466	–	–	2	− 825.1	1654.2	740.5	0.000

K: The number of parameters in the model (note that baseline is $K = 2$); L: likelihood, the value describing how likely the model is, given the data; AIC_c: Akaike information criterion score corrected for sample size; ΔAIC_c: the difference in AIC_c between each model and the model with lowest AIC_c; AIC_c weight: best model probability

Table 4 Results of the linear regression analysis testing the relationship between the standard length and $\delta^{13}C$ and $\delta^{15}N$ values in fish. Significant *p*-values are highlighted by bolding

	$\delta^{13}C$						$\delta^{15}N$					
	Slope		Model fit				Slope		Model fit			
	b	SE	r^2_{adj}	*F*	df	*p*	*b*	SE	r^2_{adj}	*F*	df	*p*
Abramis brama	0.0233	0.0040	0.376	33.6	1, 53	**< 0.001**	0.0067	0.0011	0.418	39.8	1, 53	**< 0.001**
Alburnus alburnus	0.0082	0.0334	0.000	0.1	1, 17	0.810	0.0211	0.0106	0.142	4.0	1, 17	0.062
Ameiurus melas	−0.0080	0.0026	0.230	9.0	1, 26	**0.006**	0.0109	0.0024	0.423	20.8	1, 26	**< 0.001**
Blicca bjoerkna	−0.0051	0.0055	0.000	0.8	1, 29	0.369	0.0054	0.0024	0.118	5.0	1, 29	**0.033**
Carassius gibelio	−0.0290	0.0050	0.536	34.4	1, 28	**< 0.001**	0.0090	0.0008	0.815	129.1	1, 28	**< 0.001**
Cyprinus carpio	−0.0154	0.0052	0.414	8.8	1, 10	**0.014**	−0.0089	0.0083	0.013	1.1	1, 10	0.310
Gymnocephalus cernua	−0.0725	0.0257	0.278	7.9	1, 17	**0.012**	−0.0138	0.0094	0.061	2.2	1, 17	0.160
Lepomis gibbosus	−0.0160	0.0103	0.086	2.4	1, 14	0.142	0.0244	0.0031	0.799	60.5	1, 14	**< 0.001**
Leuciscus aspius	−0.0030	0.0016	0.104	3.8	1, 23	0.064	0.0078	0.0010	0.721	62.9	1, 23	**< 0.001**
Neogobius fluviatilus	−0.0379	0.0483	0.000	0.6	1, 15	0.447	0.0285	0.0184	0.080	2.4	1, 15	0.143
Pelecus cultratus	−0.0061	0.0037	0.067	2.6	1, 21	0.122	0.0147	0.0020	0.711	55.0	1, 21	**< 0.001**
Perca fluviatilis	0.0128	0.0029	0.385	19.2	1, 28	**< 0.001**	0.0169	0.0014	0.832	145.1	1, 28	**< 0.001**
Rutilus rutilus	0.0028	0.0040	0.000	0.5	1, 53	0.486	0.0061	0.0011	0.347	29.7	1, 53	**< 0.001**
Sander lucioperca	0.0080	0.0019	0.229	17.4	1, 54	**< 0.001**	0.0061	0.0004	0.814	242.4	1, 54	**< 0.001**
Sander volgensis	0.0027	0.0220	0.015	1.5	1, 28	0.237	0.0094	0.0012	0.686	64.4	1, 28	**< 0.001**
Scardinius erythrophthalmus	0.0015	0.0043	0.000	0.1	1, 19	0.734	−0.0047	0.0029	0.075	2.6	1, 19	0.121

model, including the main effects only, performed also very well in terms of the explanatory power ($r^2_{adj.} = 0.759$). Other models including species identity provided less, but still useful explanatory power ($r^2_{adj.} = 0.545$–0.656), whereas the pure Length model had very low explanatory power ($r^2_{adj.} = 0.133$).

We found weak to moderate relationship ($r^2_{adj.} = 0.229$–0.536 at $p < 0.05$) between fish SL and $\delta^{13}C$ values in seven of the 16 fish species, and a weak to strong relationship ($r^2_{adj.} = 0.118$–0.832 at $p < 0.05$) between fish SL and $\delta^{15}N$ values in 11 of the 16 fish species (Table 4, Online Resource (1). The species showing significant ontogenetic changes in both $\delta^{13}C$ and $\delta^{15}N$ signals were the *A. brama*, the *Ameiurus melas*, the *Carassius gibelio*, the *Perca fluviatilis* and the *Sander lucioperca*. *C. carpio* and *G. cernua* showed ontogenetic changes in $\delta^{13}C$ values only, whereas *Leuciscus aspius*, *Lepomis gibbosus*, *P. cultratus* and *Sander volgensis* showed ontogenetic changes in $\delta^{15}N$ values only.

Trophic position

Littoral (snails) and offshore benthic (chironomid larvae) baselines had significantly different $\delta^{13}C$ signals (mean ± SD: -9.46 ± 1.38 ‰ and −26.7 ± 1.28 ‰, respectively; *t*-test, df = 55, $t = 47.9$, $p < 0.001$) and provided a good representation of littoral and pelagic carbon sources within the food web.

Mean trophic position of fish species ranged between 3.0 and 4.5 (Fig. 1a). *C. carpio* and *C. gibelio* occupied the lowest, whereas *L. aspius*, *P. cultratus* and *S. lucioperca* occupied the highest trophic ranges within the fish community. In most species, 95% credibility intervals covered more than an entire trophic level indicating a high individual variability in trophic position. *C. carpio* occupied a significantly (probability test, $p < 0.05$) lower trophic position than all the other fish species except the *C. gibelio* (Online Resource (2). Trophic position of *C. gibelio* was also significantly lower than that of 10 of the 15 other fish species. However, trophic positions of most fish species overlapped substantially with each other. The complete matrix of overlapping probabilities between trophic position values of fish species is shown in Online Resource (2).

Posterior α values indicate that most fish species predominantly utilize offshore (pelagic) basal resources (Fig. 1b). Fishes that are most likely to

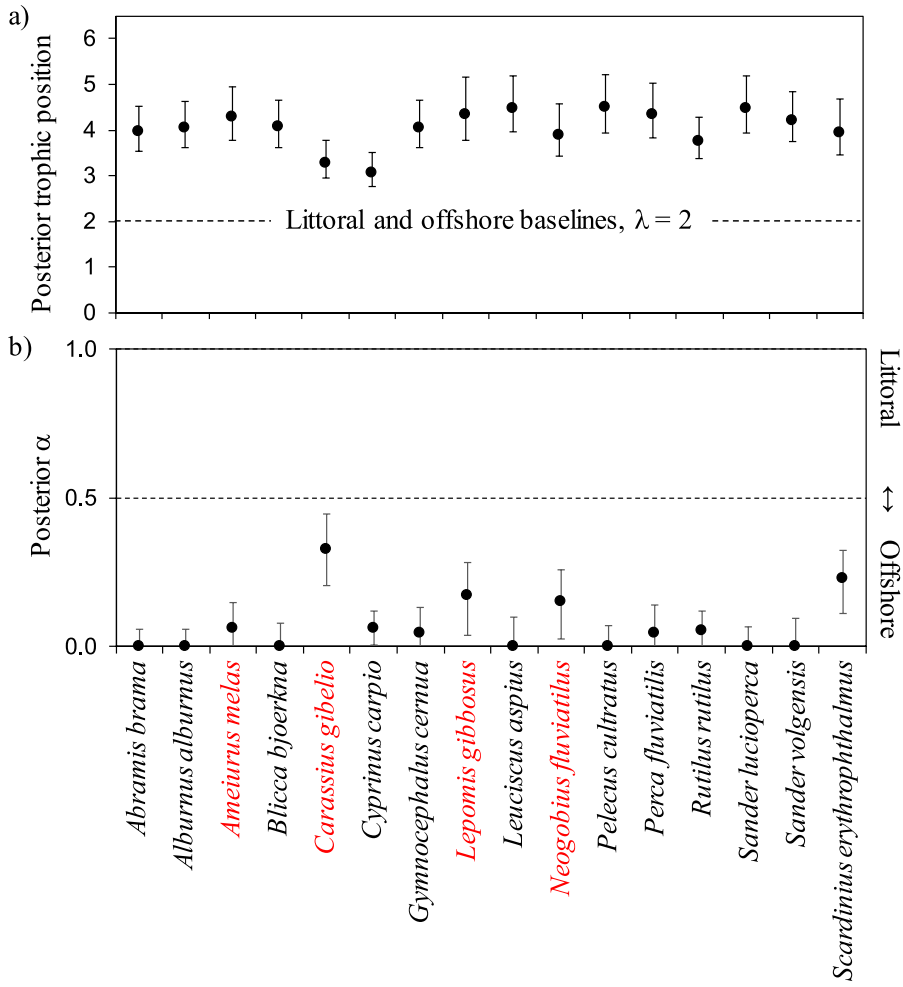


Fig. 1 Estimated posterior trophic position (**a**) and posterior α indicating the relative contribution of littoral and offshore (pelagic) carbon and nitrogen sources to the diet (**b**) of 16 fish species in Lake Balaton, Hungary. Mean values and 95% credibility intervals are indicated. Non-native species are highlighted in red. Pairwise comparison of trophic position values is presented in Online Resource 2

utilize littoral basal resources as well (with 95% credibility intervals not including the $\alpha = 0$ value) were the *C. gibelio*, the *L. gibbosus*, the *N. fluviatilis* and the *S. erythrophthalmus*.

Isotopic niche and overlap

Figure 2a shows the positioning of the core isotopic niches of fish species in the isotopic space relative to the signals of the potential food resources and baseline organisms (for the exact positioning of individual fish species see Table 1 and Online Resource (3). Littoral food resources are positioned at the higher end and the three offshore food resources (the zooplankton, the benthic invertebrates and the preyfish) are positioned at the lower end of the $\delta^{13}C$ scale. Fish species are located mainly at the offshore side of the $\delta^{13}C$ gradient close to each other and with many overlaps (Fig. 2a, b). *A. brama*, *A. alburnus*, *P. cultratus* and *S. lucioperca* were the most depleted in $\delta^{13}C$ (most relying on offshore carbon resources), while *C. gibelio*, *L. gibbosus* and *S. erythrophthalmus* were the least depleted in $\delta^{13}C$ (least relying on offshore carbon resources). *C. carpio* and *C. gibelio* were the least enriched in $\delta^{15}N$, whereas *L. aspius*, *P. cultratus* and *S. lucioperca* were the most enriched in $\delta^{15}N$.

The core isotopic niche size, indicated by the SEA_c, varied considerably between fish species ranging between 1.2 ‰^{2} and 11.5 ‰^{2} (Fig. 2b, Fig. 3a). Smallest SEA_c values were found in *A. alburnus*, *C. carpio* and *P. cultratus*. While largest SEA_c values were found in *C. gibelio* and *S. lucioperca.* In addition, analysis of the total convex hull area revealed that some of the species (e.g. *C. gibelio*, *R. rutilus* and *S. lucioperca*) use quite a wide range of food resources covering up to 20–30%

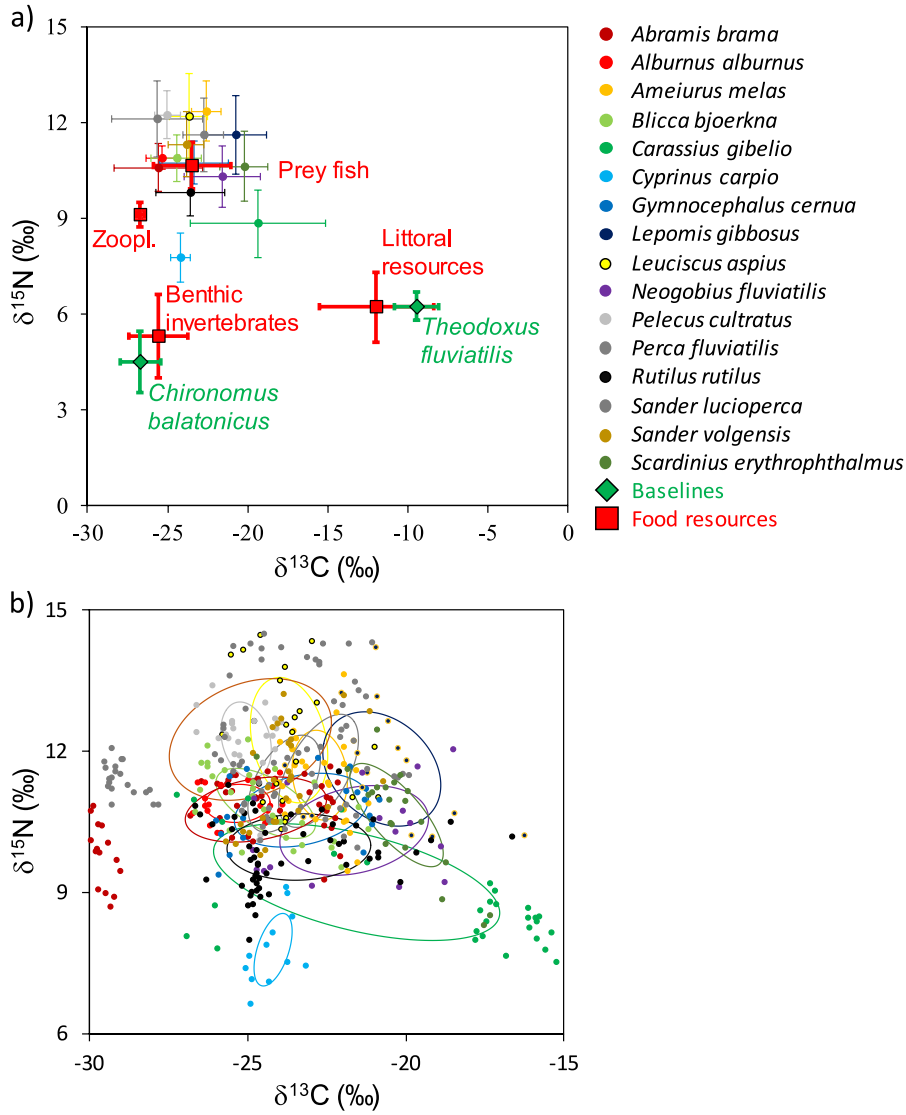


Fig. 2 Isotope values (mean and SD) of 16 fish species, baseline organisms and potential food resources (**a**), and individual samples and isotopic niches indicated by standard ellipses of fish species (**b**) in Lake Balaton, Hungary. Note that baseline organism *Chironomus balatonicus* is also included in the benthic invertebrates resource category and *Theodoxus fluviatilis* is also included in the littoral resources. Positions of standard niche ellipses of each fish species are further clarified in Online Resource 3

of the total resource range of the fish community (Fig. 3b).

Our analyses revealed that simulated core isotopic niches overlapped only narrowly or not at all in majority of species pairs (Fig. 4). Considerable overlap of ≥ 0.6 in core isotopic niches occurred only in 4.9% of all the possible species pair relationships, and these overlaps were highly asymmetrical. For example, the overlap between *P. cultratus* and *S. lucioperca* covered 97% of the core isotopic niche of the former species and only 19% of the latter species (Fig. 4a). Similarly, the overlap between *A. alburnus* and *A. brama* covered 85% of the core isotopic niche of the former species and only 19% of the latter species.

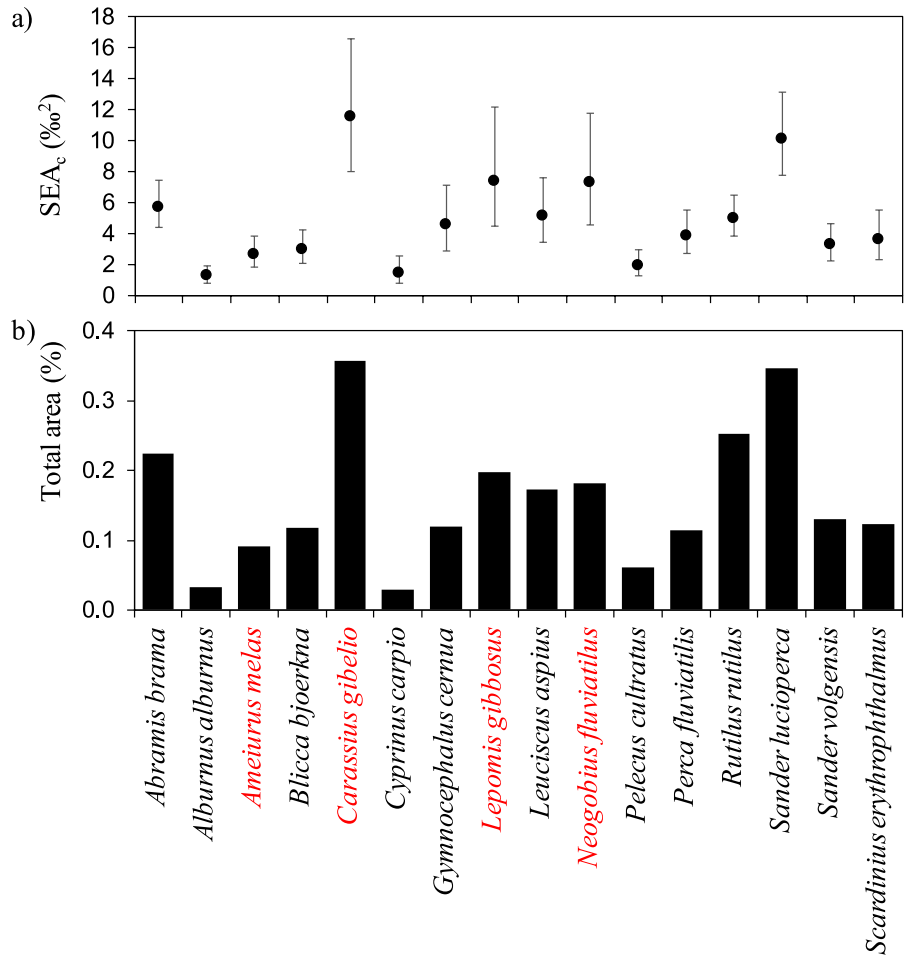


Fig. 3 Core isotopic niche sizes indicated by standard ellipse areas corrected for sample size (SEAc) with posterior 95% credibility interval (**a**) and total convex hull areas relative to the total area covered by the whole fish community (**b**) of 16 fish species in Lake Balaton, Hungary. Non-native species are highlighted in red

Mixing models and resource use

We revealed that food resource mixing model including both species identity as fixed effect and SL as covariate overperformed both the pure species and the pure SL models in predicting the resource use of fish community members based on $\delta^{13}C$ and $\delta^{15}N$ data (Table 5). Size dependent resource use of fish species showed diverse patterns (Fig. 5). The zooplankton were important food resource for most fish species, either during the early ontogeny or in the adult stage. In adult stage, the zooplankton constituted the predominant part of the diet of *A. brama*, *A. alburnus*, *Blicca bjoerkna*, *C. gibelio* and *P. cultratus*. Adult *C. carpio* and *N. fluviatilis* consumed mainly benthic invertebrates as well as certain juvenile stages of some other species did, including e.g., *A. melas*, *C. gibelio*, *R. rutilus* and *S. lucioperca*. Adult *G. cernua* consumed zooplankton and benthic invertebrates in similar proportions. *R. rutilus* proved to be omnivorious, while *S. erythrophthalmus* proved to rely most on littoral food resources. Piscivory increased markedly during the ontogeny in *A. melas*, *L. gibbosus*, *L. aspius*, *P. fluviatilis*, *S. lucioperca*, and *S. volgensis*.

Discussion

Trophic organisation of communities has been modelled using various combination of body size and species identity. In this study, SIA revealed that the pure body size model performed poorly compared to models including species identity based on resource use data of a temperate large lake fish community. The highest predictive powers were obtained with the models that included both species identity and body size. Moreover, the additional

a)

	Abramis brama	*Alburnus alburnus*	***Ameiurus melas***	*Blicca bjoerkna*	***Carassius gibelio***	*Cyprinus carpio*	*Gymnocephalus cernua*	***Lepomis gibbosus***	*Leuciscus aspius*	***Neogobius fluviatilus***	*Pelecus cultratus*	*Perca fluviatilis*	*Rutilus rutilus*	*Sander lucioperca*	*Sander volgensis*	*Scardinius erythrophthalmus*
Abramis brama		0.85	0.09	0.66	0.00	0.00	0.44	0.00	0.10	0.05	0.02	0.20	0.10	0.05	0.46	0.00
Alburnus alburnus	0.19		0.00	0.26	0.00	0.00	0.09	0.00	0.01	0.00	0.02	0.01	0.01	0.04	0.10	0.00
Ameiurus melas	0.04	0.00		0.03	0.00	0.00	0.27	0.11	0.22	0.11	0.00	0.51	0.02	0.02	0.23	0.03
Blicca bjoerkna	0.34	0.60	0.04		0.00	0.00	0.38	0.00	0.08	0.08	0.09	0.15	0.11	0.08	0.42	0.00
Carassius gibelio	0.00	0.00	0.00	0.01		0.01	0.02	0.00	0.00	0.20	0.00	0.00	0.24	0.00	0.00	0.07
Cyprinus carpio	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gymnocephalus cernua	0.35	0.33	0.46	0.57	0.01	0.00		0.08	0.14	0.26	0.01	0.38	0.24	0.01	0.45	0.06
Lepomis gibbosus	0.00	0.00	0.30	0.00	0.00	0.00	0.12		0.06	0.26	0.00	0.33	0.01	0.01	0.04	0.57
Leuciscus aspius	0.09	0.03	0.42	0.14	0.00	0.00	0.17	0.04		0.03	0.33	0.43	0.01	0.28	0.59	0.00
Neogobius fluviatilus	0.06	0.01	0.31	0.19	0.13	0.00	0.43	0.26	0.04		0.00	0.17	0.47	0.00	0.08	0.56
Pelecus cultratus	0.01	0.03	0.00	0.06	0.00	0.00	0.01	0.00	0.12	0.00		0.00	0.00	0.19	0.05	0.00
Perca fluviatilis	0.13	0.01	0.73	0.21	0.00	0.00	0.34	0.17	0.32	0.09	0.00		0.04	0.03	0.44	0.03
Rutilus rutilus	0.09	0.02	0.04	0.19	0.10	0.01	0.26	0.00	0.01	0.32	0.00	0.05		0.00	0.07	0.00
Sander lucioperca	0.10	0.30	0.08	0.26	0.00	0.00	0.02	0.01	0.57	0.00	0.97	0.08	0.00		0.30	0.00
Sander volgensis	0.26	0.26	0.29	0.47	0.00	0.00	0.34	0.01	0.38	0.03	0.08	0.37	0.05	0.10		0.00
Scardinius erythrophthalmus	0.00	0.00	0.04	0.00	0.02	0.00	0.05	0.28	0.00	0.27	0.00	0.03	0.00	0.00	0.00	

b)

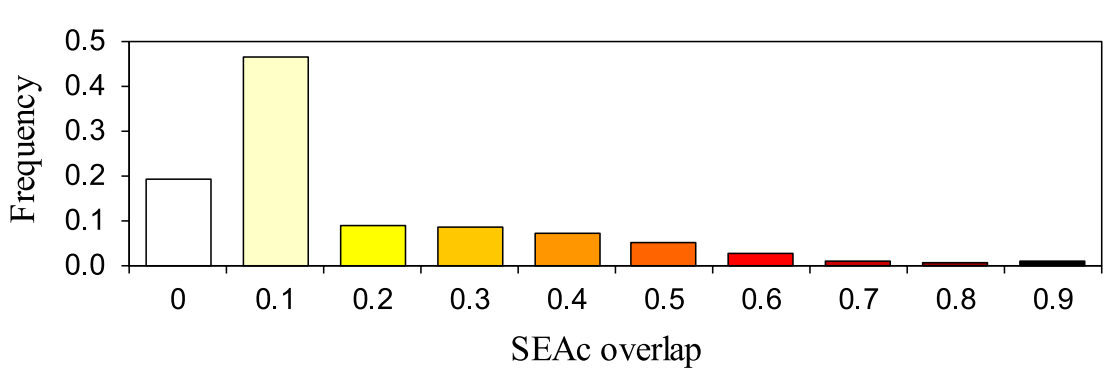


Fig. 4 Pairwise percentage overlap of core isotopic niches between 16 fish species (**a**) and the distribution of pairwise niche overlap values (**b**) in Lake Balaton, Hungary. Note that percentage overlap values are asymmetrical, and the overlapped species are listed in the header row, while the overlapping species are listed in the first column. Non-native species are highlighted in red

gain in the explanatory power related to the inclusion of the species identity × body size interaction effect to the GLM models indicate that ontogenetic changes in resource use are species-specific.

In general, strong fundamental arguments can typically be presented in support of the relevance of body size-based trophic models – e.g. in many food webs consumers are generally larger than their prey and consequently, a positive correlation could be assumed between consumer size and trophic position –, as well as empirical data have also proved their relevance in many cases (Brose et al. 2006;

Table 5 Comparison of four competing mixing models fit on fish community and food resource $\delta^{13}C$ and $\delta^{15}N$ data to infer food resource partitioning and consider the influence of standard length and species identity using MixSIAR and the leave-one-out cross-validation information criterion (LOOic)

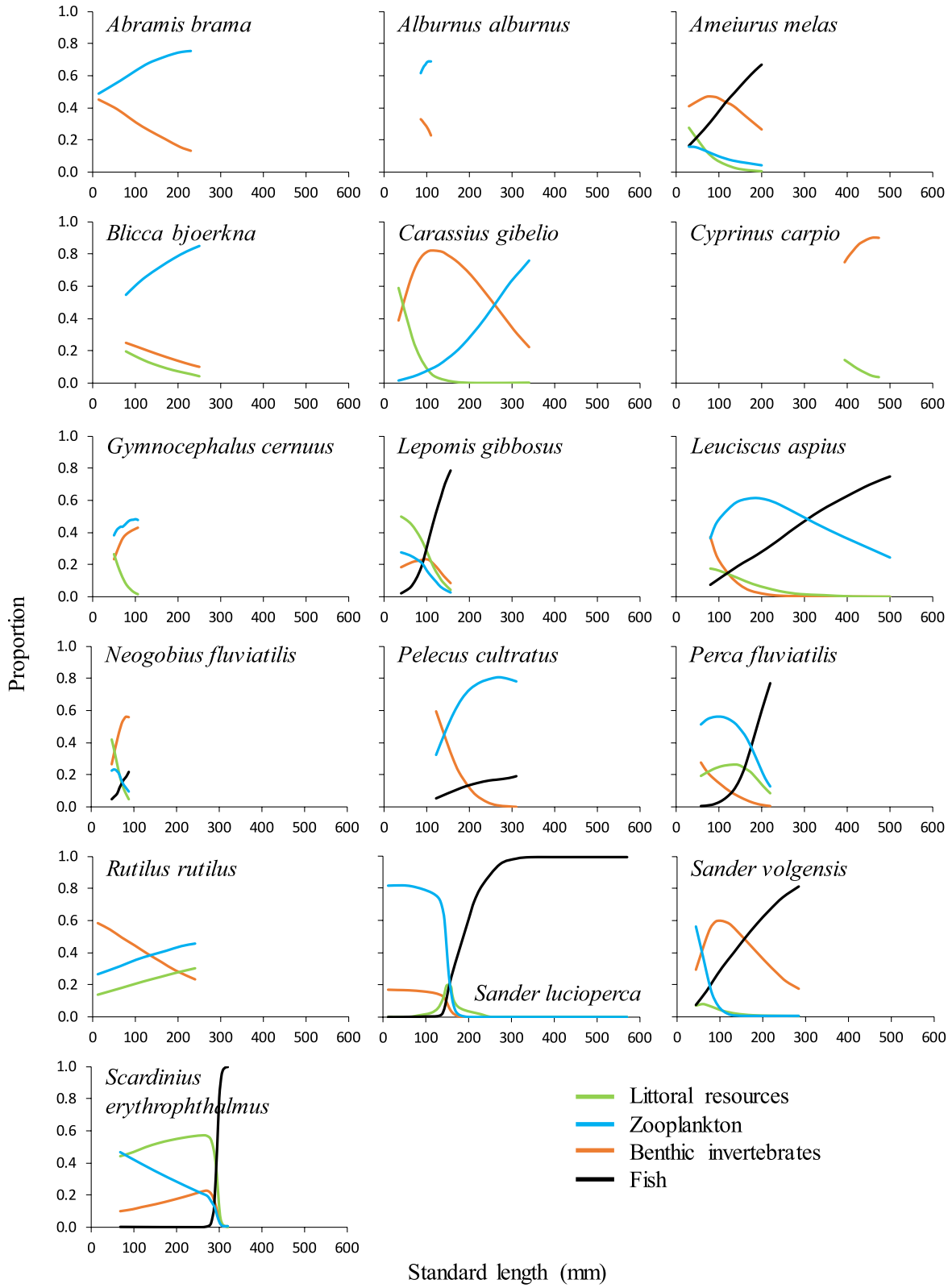
Model	LOOic	SE(LOOic)	ΔLOOic	SE(ΔLOOic)	LOOic weight	$\delta^{13}C$	SD($\delta^{13}C$)	$\delta^{15}N$	SD($\delta^{15}N$)
Species + Length	978.9	56.9	0	–	1.000	1.50	0.48	1.86	0.88
Species	1195.5	48.8	216.6	43.4	0.000	3.83	1.73	3.11	0.41
Length	1538.3	54.0	559.4	51.9	0.000	5.67	1.03	3.30	1.79
Intercept-only	1815.5	50.9	836.6	45.4	0.000	11.66	2.27	8.85	1.40

ΔLOOic: the difference in LOOic between each model and the model with lowest LOOic; LOOic weight: best model probability; $\delta^{13}C$ and $\delta^{15}N$: multiplicative error terms for $\delta^{13}C$ and $\delta^{15}N$, respectively

Riede et al. 2011; Romanuk et al. 2011; Potapov et al 2019). On the contrary, $\delta^{13}C$ and $\delta^{15}N$ data, which infer trophic characteristics and trophic relationships of individual organisms, showed little to no correlation with body size at the fish community level in this study.

Potapov et al. (2019), analysing stable isotope data from 1,093 species, found that the relationship between body size and trophic position tends to be strong in systems where unicellular primary producers dominate within the basal resources, such as pelagic marine communities. However, in systems where higher-order primary producers and decaying organic matter play a significant role within the food web, this relationship tends to be weak or even absent, as is generally the case in terrestrial ecosystems and often in freshwater ecosystems as well. In the freshwater fish community examined in this study, multicellular primary producers and detritus play a non-negligible role in the food web, both in the diet of certain fish species and in the diet of macroinvertebrates that serve as food for the fish (Specziár and Rezsu 2009). This may explain why body size-only model has such weak explanatory power in our case. Studying fish communities in the Mekong River system, Ou et al. (2017) similarly demonstrated that the relationship between body length and trophic position (inferred by $\delta^{15}N$) cannot be considered universal, and its presence varies by habitat and functional group. The relationship was present in piscivorous and omnivorous feeding groups – albeit with only weak explanatory power ($r^2 \leq 0.24$) – while it was absent in detritivorous and insectivorous groups. Furthermore, the relationship between fish body size and trophic position within a community appears to vary with climatic conditions, being more detectable in colder climates and less so in warmer climates (Lacerot et al. 2022). The weakening of this relationship in warmer, tropical climates can be explained by the increased consumption of plants and detritus by omnivorous groups. However, it should also be considered that testing body size-based trophic models is not always independent of taxonomic or species-level information. Specifically, some studies demonstrated the independent role of body size aligns trophic position with the maximum or average body size of species rather than the actual body size of the examined individuals (e.g., Romanuk et al. 2011; Potapov et al. 2019). Such methodological approaches may lead to an overestimation of the independent explanatory power of body size. Our study fills a gap in this regard by examining the principles of trophic organisation across broad size groups of species within a community, both independently of and in relation to species identity.

Since the food resource utilization of individuals of the same size class can vary significantly among different freshwater fish species (Mittelbach and Persson 1998; Specziár and Rezsu 2009; Sánchez-Hernández et al. 2019), it is not surprising that models including species identity performed better in our analysis than purely body size-based models. Romanuk et al. (2011), in an analysis of 8,361 fish species, found that even considering a higher taxonomic level – specifically, order – significantly improved the explanatory power of community-level trophic models compared to purely body size-based model. In their example, the proportion of explained variance in trophic position increased from 19 to 37% in the model included the taxonomic order as well. In our case, the explanatory power of the traditional, purely species-based trophic model was also found to be acceptable ($r^2 = 0.412$ and $r^2 = 0.545$ for $\delta^{13}C$ and $\delta^{15}N$ data, respectively).


Abramis brama
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Cyprinus carpio
Gymnocephalus cernuus
Lepomis gibbosus
Leuciscus aspius
Neogobius fluviatilis
Pelecus cultratus
Perca fluviatilis
Rutilus rutilus
Sander lucioperca
Sander volgensis
Scardinius erythrophthalmus
Proportion
Standard length (mm)
Littoral resources
Zooplankton
Benthic invertebrates
Fish

◂**Fig. 5** Estimated size-dependent contribution of the four main food sources to the diet of 16 fish species in Lake Balaton, Hungary, based on Bayesian tracer mixing model using MixSIAR

However, as expected, the full factorial species identity × body size model (i.e. includes factor interaction as well) that accounted for species-specific ontogenetic (i.e., size-dependent) dietary characteristics performed best. In fish, ontogenetic dietary changes are highly species-specific regarding both their timing and dynamics; changes can be either gradual or occur as definite shifts upon reaching critical body sizes (Werner and Gilliam 1984; Post 2003; Specziár 2011). Moreover, not all the fishes show size-dependent dietary changes, which further justifies the use of models that incorporate species-specific patterns. Similar findings were reported by Deudero et al. (2004) in their study of the coastal fish fauna of the Balearic Islands, where the presence and characteristics of ontogenetic shifts in resource use varied significantly among species. Therefore, based on the results of the GLM analyses and the above outlined consideration, we suggest further development of the stable isotope-based mixing models (e.g., MixSIAR) to include an option for accounting for factor interaction effects as well in analyses of community data.

The variation of $\delta^{13}C$ and $\delta^{15}N$ values within trophic levels and their enrichment rate along the food web generally differ and represent complementary information about the trophic organisation of communities (Layman et al. 2012). The $\delta^{13}C$ exhibits relatively low enrichment along the food chain and primarily reflects the distinct imprint of basal sources through the consumer levels. In contrast, the $\delta^{15}N$ exhibits stronger enrichment along the food chain, and therefore, it is a reliable indicator of consumers' trophic positions. Our results indicate that the fish community relies primarily on the open-water basal C and N sources and much less on littoral basal resources. This result is in accordance with the characteristics of Lake Balaton, which food web is dominated by the offshore primary producers – the phytoplankton, and to a lesser extent, the offshore phytobenthos –, whereas littoral primary producers contribute much less (Somogyi et al. 2024). In fish species – namely the *C. gibelio*, the *L. gibbosus*, the *N. fluviatilis* and the *S. erythrophthalmus* – where the littoral basal source (i.e., periphyton, macrophytes) also played a detectable supplementary role (either directly as food or indirectly as food of their invertebrate preys), habitat use patterns indicated an association with the shoreline zone, both in Lake Balaton and more generally (Rezsu and Specziár 2006; Specziár and Rezsu 2009; Zapletal et al. 2019; Czeglédi et al. 2024). Based on the observation that more species exhibited size-dependent changes in $\delta^{15}N$ than in $\delta^{13}C$, we can conclude that ontogenetic diet shifts more frequently involve alteration in the trophic level – and always toward higher levels in this study (Table 4) – than adjustments among alternative resources within a given trophic level. Similar findings were reported in other SIA-based studies for fishes (e.g., Deudero et al. 2004; Vašek et al. 2018), but there are also examples when ontogenetic diet shifts occur across multiple basal carbon sources with only little or no change in the trophic position (Davis et al. 2012) as well as toward lower trophic levels (Lemmers et al. 2024). For the two species (i.e. *C. carpio* and *G. cernua*), which exhibited size-dependent changes in $\delta^{13}C$ only, the analysis suggested a further increase in the importance of open-water resources at the expense of the littoral resources with increasing body size (Fig. 5).

Fish community of Lake Balaton covered a trophic range corresponding to approximately two trophic levels, from secondary consumers to apex predators. There were no strictly herbivorous, primary consumer species among the examined fish. The species occupying the lowest trophic position were the *C. carpio*, which primarily feed on zebra mussels (*Dreissena polymorpha*), and the *C. gibelio*, which mainly consume detritus and aquatic invertebrates in Lake Balaton (Specziár and Rezsu 2009). Most fish species occupy the tertiary consumer level and consume various planktonic and benthic macroinvertebrates (see also Specziár and Rezsu 2009). The fish species with the highest trophic position (i.e., the *L. gibbosus*, the *L. aspius*, the *P. cultratus*, the *P. fluviatilis* and the *S. lucioperca*) were those which show high rate of piscivory at least at their older life stages both in Lake Balaton and in general (Specziár and Rezsu 2009; Syväranta et al. 2010; Specziár 2011; Vašek et al. 2018; Kaymak et al. 2018). A crucial consideration is, however, that the trophic position of zooplankton, which serve as primary food source for many fish species, is relatively high in Lake Balaton due to

the considerable proportion of predatory crustaceans (i.e. adults of some copepod species and cladoceran *Leptodora kindtii*; G.-Tóth et al. 2009). Consequently, early life stages of most fish species as well as several small-bodied zooplanktivorous species exhibited higher trophic positions than large-bodied omnivorous *C. carpio*. This observation reinforces why a pure body size-based trophic model lacked explanatory power in the examined fish community. It should be noted, however, that SIA based trophic position values should be handle with caution. The relative trophic positions of individual members of the community are generally well inferred by SIA, as the relationship between the $\delta^{15}N$ and the trophic level is monotonic. However, since consumer discrimination is not constant as assumed in general SIA methodologies but narrows with increasing dietary $\delta^{15}N$, the actual trophic level of consumers close to the top of the trophic pyramid may be underestimated (Hussey et al. 2014). This bias may be particularly significant in apex predators showing cannibalistic behaviour as well, such as in *S. lucioperca* in this study.

Among-individual variation in resource use and trophic position is common in natural populations, and it could be important for trophic organisation of animal communities including fish (Bolnick et al. 2003; Svanbäck et al. 2015). Our analyses also indicated high among-individual variation in both the trophic position covering nearly a full trophic level in most species and the isotopic niche (expressed in SEA_c) reaching a substantial proportion of the total community isotopic niche in several species (Fig. 3). The findings are also consistent with the assumption of Specziár and Erős (2014) who analysed gut content data from 15 fish species, that among-individual variation could be important in the trophic organisation of the fish community in Lake Balaton.

The results of the present study, that majority of fish species show marked size-dependent dietary shifts, support the theory that trophic guilds organise over intraspecific categories and not on species level as assumed originally (Werner and Gilliam 1984; Cohen et al. 1993). Concordant with finding of Specziár and Rezsu (2009) based on gut content analysis, our SIA approved that in several species, different ontogenetic stages (i.e. size-groups) could utilise very different food resources in Lake Balaton. Shifting among food resources during the ontogeny can decrease intraspecific competition, which interaction was reported to be important in population dynamics in several fish population (Byström et al. 1998; Persson and Brönmark 2002; Ward et al. 2006).

In contrast to the snapshot relevance of direct gut content analysis, SIA provides information on the average assimilated diet of organisms over a certain time period. Yet, stable isotopes inferred diet composition assessments of fish species and their size-groups were largely consistent with the findings of Specziár and Rezsu (2009) obtained through gut content analysis. However, some inaccuracies can also be assumed regarding the present diet composition estimates. Unlike direct gut content analysis, which provides higher resolution, the present analyses – due to the limited discriminative power of SIA models regarding the diet components (Brett 2014) – allowed us to distinguish only four aggregated resource categories when describing the diet of fish. Moreover, even among these categories, the isotopic signals of zooplankton and prey fish partially overlapped, which reduced their distinguishability by the model. Another limitation of the SIA that changes in the diet are detectable only with a time delay related to tissue turnover rate, which is however also function of body size (Vander Zanden et al. 2015). In this study, we used muscle tissue samples which isotopic turnover rate typically ranges between few days and few months in fish. Therefore, ontogenetic changes in the resource use, especially during the earliest life stages, will be signalised at overestimated body sizes (Hertz et al. 2016). For example, direct gut content analyses indicated the definite shift of *S. lucioperca* to piscivory between 100 and150 mm SL (Specziár 2011), whereas the SIA signalized this shift between 150 and250 mm SL in this study. Therefore, when it is crucial to estimate the timing of diet shift with a high precision, tissues with higher turnover rate should be preferred. Finally, including the earliest life stages of some characteristic fish species to the analyses benefited with a complete picture of life long trophic processes in fish with different types of feeding strategy (i.e. invertebrivore *A. brama*, omnivore *R. rutilus* and two piscivores *S. lucioperca* and *S. volgensis*). However, inclusion of these earliest, seasonally limited life stages also required a compromise of entering some probable bias in the analyses due to a different sampling time. Although isotopic signals of food resources may vary seasonally (Phillips et al. 2014), this bias does not appear to substantially

affect the present result as the assessed resource use of the earliest life stages of the four species concerned fit perfectly within the life-long diet patterns (Fig. 5) and also match with the results of direct gut content analyses by Specziár and Rezsu (2009).

To conclude, this study demonstrates that food resource use of fish is both species and life-stage specific, and thus, trophic modelling of fish communities should consider both among species and size-related within species variabilities. Although, due to the tissue turnover time, SIA generally detects ontogenetic dietary shifts with some delay, the full factorial species × body size model still could be used effectively for the assessment of the trophic structure of the fish community. SIA combined with species-specific diet ontogeny approach provided a detailed picture about the trophic organisation of a temperate lake fish assemblage covering aspects of trophic position, ontogenetic diet shifts, isotopic niche, food resource partitioning and the trophic guild structure.

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Data availability All of the data supporting the findings of this study are available in the main text and the electronic supplementary material.

Declarations

Conflict of interests The authors have no relevant financial or non-financial interests to disclose.

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