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Variable diet plasticity in Eurasian perch (*Perca fluviatilis*): Current versus seasonal food uptake

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Abstract

Diet plasticity is often studied in Eurasian perch (*Perca fluviatilis*), a species commonly described as having generalist populations composed of specialised individuals. Perch diet was examined using gut content analysis (GCA) and stable isotope analysis (SIA), and individual specialisation was calculated in two study lakes within 2 years. Mostly only one diet category was present in the perch stomach, with more variation in the diet in the Most lake compared to the Milada lake between 2013 and 2014. The calculated degree of individual specialisation indicated higher specialisation in the Most lake. Interestingly, despite the different or almost uniform diet composition between the years, the total niche width (based on SIA) of the population remained similar in both lakes. This suggests that the overall variation in the sources utilised by the entire population remained consistent between the years. GCA mostly indicated zooplankton as the prevailing food source, whereas SIA indicated significant utilisation of YOY fish earlier that year, an information that was completely missed by the GCA of fish caught in September. The differences between GCA and SIA results could be attributed to the different time intervals reflected by the methods, but possibly to the conversion of the diet into the body tissues that is reflected by SIA and may depend on the diet's nutritional values rather than the proportion of different prey consumed.

KEYWORDS
gut content analysis, individual specialisation, stable isotope analysis, total niche width

1 | INTRODUCTION

Many generalist populations are composed of specialised individuals, whose niches are small subsets of the population niche (Araújo et al., 2011). Individual diet variation depends on the level of intra and interspecific competition, ecological opportunity, and predation (Araújo et al., 2011), and individual specialisation is common in natural populations (Bolnick et al., 2003). Intra-population niche differences are related to sexual dimorphism (Meiri et al., 2005; Schoener, 1986), ontogenetic variability, or discrete polymorphism (Svanbäck & Persson, 2004). The specialisation is induced gradually through the expansion of population niche width and species adaptation to novel food sources (Dieckmann & Doebeli, 1999; Smith & Skúlason, 1996). Individual specialisation was described in about 200 species (Araújo et al., 2011; Bolnick et al., 2003), mostly among predators (Araújo et al., 2011; Matthews et al., 2010). It has been studied the most in fish so far, as the most diverse taxonomic group within vertebrates, followed by birds (Araújo et al., 2011). However, many case studies report only seasonal or temporal specialisation unconfirmed for longer time periods

(Bolnick et al., 2003). Strict long-term specialisation can even lead to the formation of new species (speciation), such as among cichlids (Cichlidae) in Lake Tanganyika (Kohda, 1994; Sturmbauer et al., 1992). It has been currently observed in three-spined stickleback (*Gasterosteus aculeatus*) where individuals specialising in pelagic prey show a higher trophic position than benthic individuals and, at the same time, they undergo noticeable morphological changes. The pelagic individuals with higher trophic levels have a greater gill raker length (Matthews et al., 2010). A similar morphological example can also be found in the Arctic charr (*Salvelinus alpinus*) in the Thingvallavatn lake, Iceland. Four coexisting morphs can be identified by their head morphology, which appears to be related to feeding habits, either benthivorous or planktivorous-piscivorous (Skúlason et al., 1989). Interesting morphological differences described in Eurasian perch (*Perca fluviatilis*) are deeper versus shallower body morphs deriving from the use of benthic versus pelagic habitats (Scharnweber et al., 2016; Svanbäck & Eklöv, 2003), as observed in Swedish lakes and also induced in laboratory experiments (Svanbäck & Eklöv, 2006). In general, a single species can express regional phenotypic variations that could represent local adaptation and is not or may not be determined on a genetic basis (Schluter, 2000; Skúlason et al., 2019). Several studies have shown how different developmental trajectories of fish can be shaped by interactions with the environment (Skúlason et al., 2019 and related studies).

The variation in foraging behaviour of Eurasian perch is commonly associated with size, often described as switching between three stages: zooplanktivorous, benthivorous and piscivorous (Hargeby et al., 2005; Mittelbach & Persson, 1998). In fact, niche widens with morphological improvements associated with growth rather than the species strictly switching from one prey to another (Araújo et al., 2011; Nosil & Reimchen, 2005; Persson & Greenberg, 1990). The spectrum of potential food sources expands as the gape limitation decreases (Christensen, 1996). The diet composition depends on the prey availability (Haakana et al., 2007; Mills et al., 1986; Persson et al., 2000) as well as perch population fluctuation and age composition (Svanbäck & Persson, 2004). Young-of-the-year (YOY) perch is also an important food source for older perch and cannibalism is a common occurrence (Persson et al., 2000, 2003). The lower the adult perch density, the higher the YOY perch density, and vice versa (Svanbäck & Persson, 2004). Persson et al. (2004) also pointed out that during low adult perch density years, the population of benthic invertebrates was large, whereas zooplankton density was low due to high predation pressure from abundant YOY perch. In contrast, higher adult perch density resulted in lower benthos and higher zooplankton density, which lead to zooplanktivory in some adult perch. Due to its crucial role that may trigger a trophic cascade, perch is considered a key species in many water bodies (Craig, 2000; Vejřík et al., 2016). The mentioned fluctuating population dynamics typical for Eurasian perch may be a possible explanation for why not all polymorphic populations lead to speciation; instead, the dynamics may favour the evolution of phenotypic plasticity (Svanbäck & Persson, 2009). The degree of specialisation increases with the increasing adult perch population (Haakana et al., 2007; Horppila et al., 2000). It also depends on the trophic level of individuals, when the highest among-individual diet variation of Eurasian perch was observed at the intermediate trophic levels (Svanbäck et al., 2015).

The diet variability can be revealed by two different approaches, gut content analysis (GCA) and stable isotope analysis (SIA). GCA often indicates strict specialisation, as only one type of diet is mostly found in the perch stomach (Amundsen & Sánchez-Hernández, 2019). However, GCA reflects only the current state (foraging effort of last 24 h or even less depending on water temperature and gastric evacuation rate) whereas SIA reveals the diet over a more extended period of time. SIA is commonly used to analyse the food web structure of aquatic ecosystems (Hansson et al., 1997).

This study aims to determine (i) the short-term diet of Eurasian perch and the degree of IS based on the GCA, and (ii) the long-term diet of Eurasian perch based on the SIA. Finally, (iii) the differences between SIA and CGA results are discussed with focus on potential factors influencing the variability.

2 | METHODS

2.1 | Study area

The study was conducted in two lakes created after aquatic restorations of mining pits, the Milada and Most lakes, Czech Republic. The oligo- to mesotrophic Milada lake has an area of 250 ha, volume of 36×10^6 m^3 and max. depth of 25 m, and the oligotrophic Most lake has an area of 310 ha, volume of 70×10^6 m^3 and maximum depth of 75 m (Figure 1). Aquatic restoration in the Milada and Most lakes continued for 10 years (2001–2011) and 6 years (2008–2014), respectively. The fish community is similar in both lakes, the occurring species being Eurasian perch, rudd (*Scardinius erythrophthalmus*), roach (*Rutilus rutilus*), ruffe (*Gymnocephalus cernua*) and tench (*Tinca tinca*) in both lakes and rarely asp (*Leuciscus aspius*) and pikeperch (*Sander lucioperca*) in the Milada lake. European catfish (*Silurus glanis*) and Northern pike (*Esox lucius*) were stocked to both lakes and whitefish (*Coregonus* sp.) to the Most lake (for more information, see Vejříková et al., 2016).

2.2 | Sampling

Animals were treated in accordance with the guidelines and under permission from the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic (Ref. No. 4253/2019-MZE-17214). The field study did not involve endangered or protected species. Eurasian perch for GCA and SIA were sampled in September 2013 and 2014. Benthic (height 1.5 m, length 30 m) and pelagic (height 3 m, length 30 m) multi-mesh gillnets (12 mesh sizes ranging from 5 to 55 mm knot-to-knot,

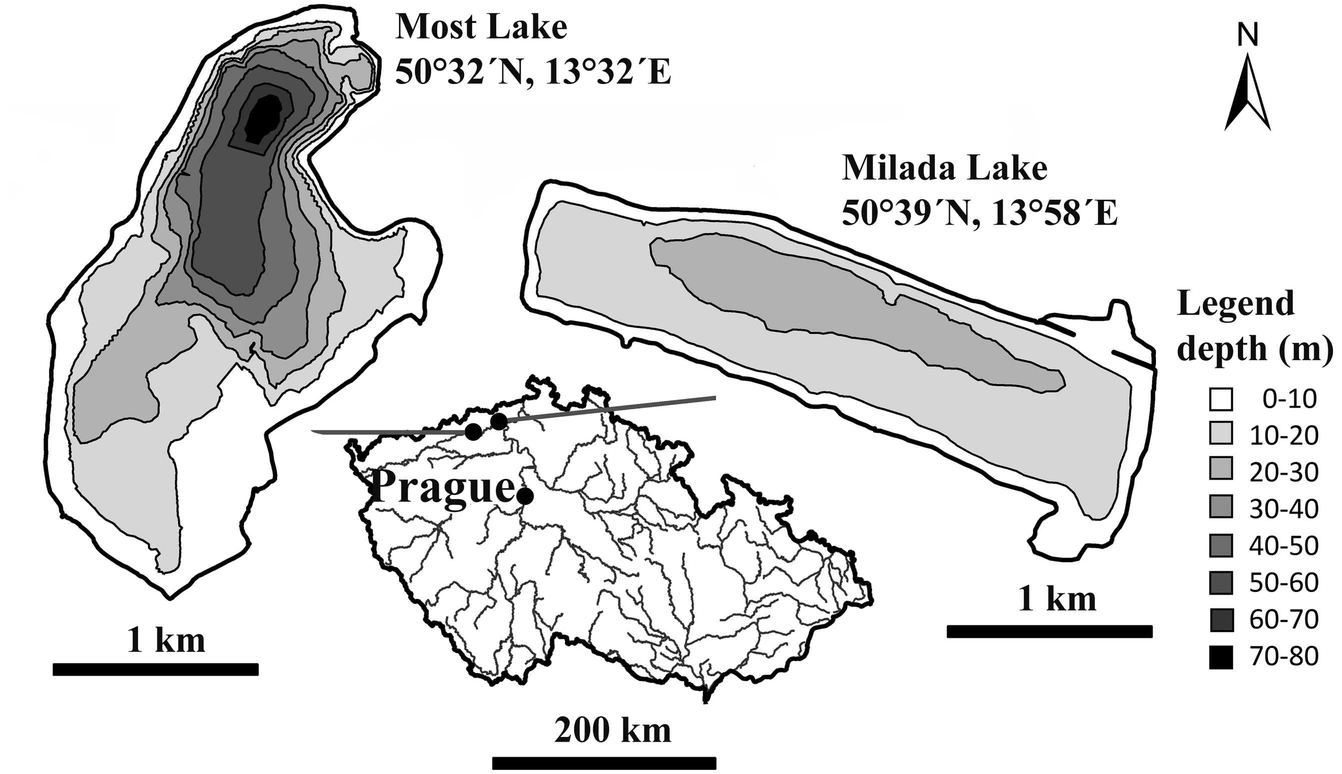

FIGURE 1 Bathymetric maps of the two study lakes created after aquatic restorations of mining pits and their location in the Czech Republic.

CEN, 2015) were used in both lakes. The gillnets were set overnight (2h before sunset and lifted 2h after sunrise; Prchalová et al., 2010) at depths of 0–3, 3–6, 6–9 and 9–12m at one pelagic and two benthic localities in three repetitions for both types of gillnets in both lakes and years. All captured fish were immediately anaesthetized by a lethal dose of tricainemethanesulfonate (MS-222, Sigma Aldrich Co.). The perch individuals (98 and 90 individuals in Milada lake, 105 and 120 individuals in Most lake in 2013 and 2014, respectively) were measured to the nearest 0.5cm, weighed to the nearest gram and their stomachs were dissected for GCA. A small part of dorsal muscle was collected for SIA from individuals randomly chosen from the entire size range of the catch, i.e., all perch subjected to SIA were also subjected to GCA. Specifically, it was 65 individuals (size range 100–340mm SL; mean 160 ± 51 SD) and 64 individuals (size range 100–280mm SL; mean 151 ± 41 SD) in the Milada lake in 2013 and 2014, respectively. In the Most it was 67 individuals (size range 115–360mm SL; mean 204 ± 71 SD) and 62 individuals (size range 105–375mm SL; mean 208 ± 79 SD) in 2013 and 2014, respectively.

The potential food sources for SIA were collected as follows: zooplankton was sampled by performing three vertical tows from a depth of 30m to the surface four times per year using a net (mesh size 170μm), benthic organisms (*Asellus aquaticus*, *Chironomus*, *Diptera*, *Ephemeroptera*, *Odonata* and *Trichoptera*) were collected directly from the bottom with the help of tweezers and placed in a 100mL plastic test tube by SCUBA divers during summer, and YOY fish (perch, roach and rudd) were collected by gillnet sampling described above. All SIA samples were stored frozen at −20°C prior to final preparation for SIA in the laboratory.

2.3 | Gut content analysis

The percent composition of the diet categories by volume was determined in the field by a visual analysis of the content of the perch stomach using the Stereoscopic microscope STM 701 24 BT. The current stomach content is influenced by the time the fish was entangled in gillnets (sunset/sunrise), whether the fish was entangled at the beginning, middle or at the end of the hunting period, and by the time of gillnet handling and fish dissection. The determined categories were: *Asellus*, *Chironomus*, crayfish, *Daphnia*, *Diptera*, *Ephemeroptera*, *Leptodora*, *Odonata*, *Trichoptera*, YOY perch, YOY roach and YOY ruffe. The YOY fish were specified based on the determination elements like scales, otholits or diagnostic bones (Čech et al., 2008). The diet was categorised by volume since the diet offered in these newly created lakes is relatively simple and except of fish and Odonata larvae the other prey items were present in hundreds (*Asellus* and *Chironomus*) or even thousands of individuals (*Daphnia*) in each stomach. The percentage of each category was calculated as a proportion of all dietary items combined (Vejříková et al., 2016). The number of individuals with empty stomachs were 17 and 23 in Milada lake, and 35 and 42 in Most lake in 2013 and 2014, respectively.

2.4 | Stable isotope analysis of fish and potential food sources

All frozen SIA samples, the fish samples and potential food sources, were dried at 60°C for 48 h and ground into a homogenous powder using a ball-mill Retsch MM 200 (Retsch GmbH, Haan, Germany). Small subsamples (0.520–0.770 mg) were weighed into tin cups for the analysis of δ^{15}N and δ^{13}C. All SIA runs were conducted using a FlashEA 1112 elemental analyser coupled to a Finnigan DELTA^{plus} Advantage mass spectrometer (Thermo Fisher Scientific Corporation, Waltham, MA, U.S.A.) at the University of Jyväskylä, Finland. Stable nitrogen and carbon ratios are expressed as delta values (δ^{15}N and δ^{13}C, respectively) relative to the international standards for nitrogen (atmospheric nitrogen) and carbon (Vienna PeeDeeBelemnite). Analytical precision was always better than 0.20‰ for both isotopes and was based on standard deviation of repeated analysis of working standards (pike white muscle tissue and birch leaves) inserted in each run after every five samples. As C:N ratios were consistently lower than 3.5 (in 96% of cases), obtained stable isotope values of the fish were not lipid corrected (Post et al., 2007).

2.5 | Data processing and statistical analysis

A paired *t*-test was used to compare the proportions of the diet categories revealed by GCA between years 2013 and 2014, The chi-square Goodness of fit was used to test the categorical variability in a distribution of the diet categories revealed by GCA for both lakes and both years separately. It revealed whether the food sources were represented equally. Due to the skewness of data distribution, the nonparametric Mann–Whitney *U* test was used to compare the differences of the stable isotope ratios of perch between 2013 and 2014 in both study sites, and also to test whether the stable isotope ratios of the three diet categories changed significantly between 2013 and 2014 in both study sites.

The degree of individual specialisation (IS) was calculated as dietary variation within individuals (Bolnick et al., 2003). The degree of IS comprises values from 0 to 1. A high value means that all individuals utilise the entire niche of the population, whereas low values signify low intraspecific overlap and thus greater IS (Matich et al., 2011). The degree of IS from GCA was processed in IndSpec, a program developed to calculate the diet specialisation described by Bolnick et al. (2002), and the following equations were used:

$$\mathrm{PS}_i = 1 - 0.5\Sigma_j \mid p_{ij} - q_j \mid$$

where p_{ij} is the proportion of category *j* in the individual i's diet, and q_j is the proportion of category *j* in the population as a whole. The prevalence of individual specialisation in the population is then measured by the average of individuals' PS values:

$$\mathrm{IS} = \Sigma_i \left(\mathrm{PS}_i\right) / N$$

The SIBER package (Stable Isotope Bayesian Ellipses in R; version 2.1.6.; Jackson et al., 2011) was used to estimate sample-size corrected standard ellipse areas (SEAc), total convex hull areas (TA), and proportional overlap of the SEAc areas based of δ^{13}C and δ^{15}N of muscle tissue from 2013 and 2014.

The proportions of different resources in the diet of the perch population over time were estimated using Bayesian stable isotope mixing models, as implemented in the package MixSIAR (Stock et al., 2018). Prey items were grouped into zooplankton, zoobenthos and YOY fish. All statistical analyses were conducted using R software version 4.1.1 (R Core Team, 2021).

To compare the diet percentage representation revealed by GCA and SIA (MixSIAR mixing model), GCA categories were grouped into the three main categories: zooplankton (*Daphnia* and *Leptodora*), zoobenthos (*Asellus*, *Chironomus*, crayfish, *Diptera*, *Ephemeroptera*, *Odonata* and *Trichoptera*) and YOY fish (YOY perch, YOY roach and YOY ruffe).

3 | RESULTS

3.1 | Gut content analysis

The distribution of the diet categories significantly differed in both lakes and both years (Milada 2013: $\chi^2 = 142$, df = 9, $p < 2.2\text{e-}16$; Milada 2014: $\chi^2 = 217$, df = 10, $p < 2.2\text{e-}16$; Most 2013: $\chi^2 = 71.2$, df = 10, $p = 2.599\text{e-}11$; Most 2014: $\chi^2 = 34.7$, df = 9, $p = 6.821\text{e-}05$). Based on the paired *t*-test of the diet categories, the perch diet did not differ significantly between 2013 and 2014 in the Milada lake ($t = 4.1298\text{e-}10$, df = 14, $p = 1$). The paired t-test of all diet categories in the Most lake was not significant either (0.07, df = 14, $p = .8$), however, the most consumed diet category varied between the 2 years. In the Milada Lake, *Daphnia* prevailed in both years (67% and 60%), whereas in the Most lake, YOY perch (37%) dominated the diet in 2013, and *Daphnia* (45%) dominated in 2014. The perch diet as observed in the stomach consisted of only one diet category in most cases. The combination of two categories was present only at 9% and 5% in the Milada lake in 2013 and 2014, respectively, whereas it was present at 14% and 15% in the Most lake in 2013 and 2014, respectively. The most common combination of two diet categories in the stomach was *Daphnia* with *Chironomus* (3% and 2% in the Milada lake, and 11% and 4% in the Most lake in 2013 and 2014, respectively). The combination of three diet categories was extremely rare, observed only once in the Milada lake in 2013 (*Chironomus*+*Ephemeroptera*+*Odonata*). The proportions of all diet categories revealed by GCA are summarised in the Supporting Information (Table S1).

The degree of IS (0 = highest IS; 1 = lowest IS) according to GCA was 0.52 and 0.41 in the Milada lake and 0.25 and 0.27 in the Most lake in 2013 and 2014, respectively.

3.2 | Stable isotope analysis

The isotopic signals of all three diet categories did not differ significantly between 2013 and 2014 for both the Milada and Most lakes, so the isotopic signals were merged for each category (Figure 2; for detailed summary of mean ± SD and Mann–Whitney *U* test results for both δ^{13}C and δ^{15}N of all three diet categories in both lakes, see Table S2). The isotopic signals of the adult perch in the Milada lake differed significantly between 2013 and 2014, both in the values of δ^{13}C (Mann–Whitney *U* Test: $W = 1643$; $p = .02$) and δ^{15}N (Mann–Whitney *U* test: $W = 276$; $p < .001$), meaning that the perch diet differed significantly between the 2 years (Figure 2a). In contrast, the isotopic signals of the adult perch in the Most lake did not show a statistical difference between years in either δ^{13}C (Mann–Whitney *U* Test, $W = 1248$; $p = .55$), or δ^{15}N (Mann–Whitney *U* test: $W = 1510$; $p = .28$), indicating a uniform diet over the years in the Most lake (Figure 2b). The total niche width (TNW) of the adult perch population represented by the corrected standard ellipse area (SEAc) in the Milada lake reached 3.50 and 3.40 in 2013 and 2014, respectively. In the Most lake, the SEAc reached 4.06 and 4.28 in 2013 and 2014, respectively. Distribution of the isotopic signal of individual perch in the population was even and no segregated subgroups that would indicate specialisation for a certain diet were observed in both lakes and both years. (Figure 2).

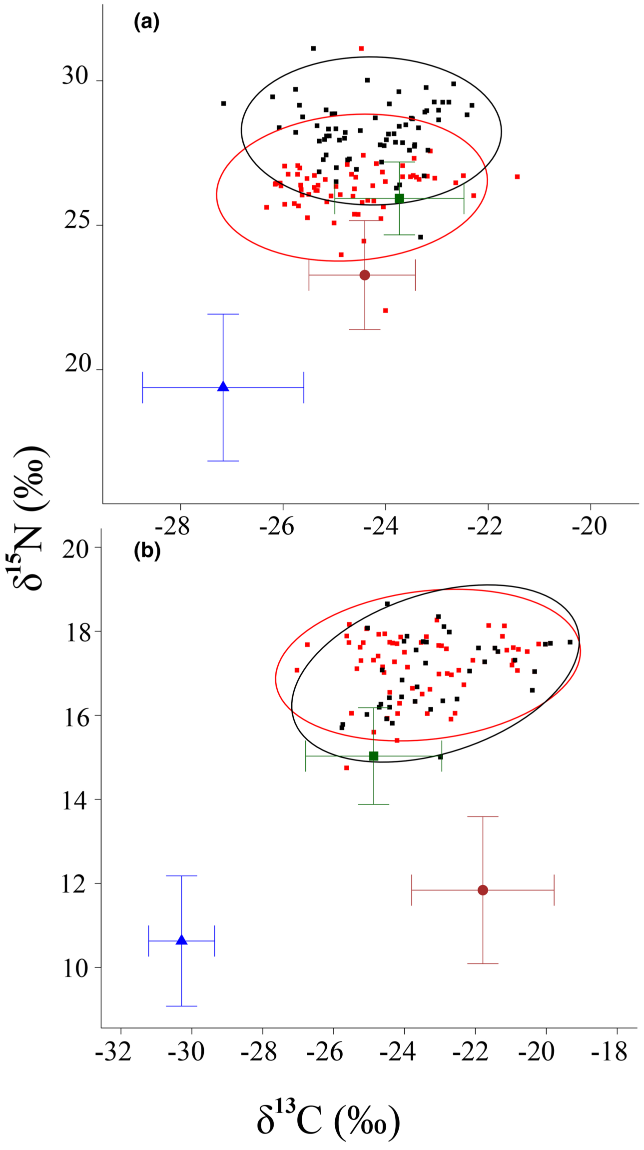

FIGURE 2 The δ^{13}C and δ^{15}N values of individual fish and the estimated isotopic total niche widths of perch population illustrated as sample-size-corrected ellipse areas (SEAc with 95% credibility interval; Jackson et al., 2011) in 2013 (red) and 2014 (black) in (a) Milada, and (b) Most. The mean ± SD δ^{13}C and δ^{15}N values of three basic diet categories (zooplankton (blue), zoobenthos (red), and YOY fish (green)) are shown.

According to the MixSIAR based on SIA, YOY fish was the most consumed prey followed by zoobenthos and zooplankton, except in the Milada lake in 2013. In that case, the representation of diet categories was distributed equally (YOY fish: 33%, zoobenthos: 36%, zooplankton: 31%), however, the uncertainty in the mixing model of Milada 2013 was unfortunately high. In the following year, YOY fish clearly dominated (69%) followed by zoobenthos (16%) and zooplankton (15%). MixSIAR results for the Most lake were more homogenous in the representation of diet categories between the 2 years. YOY fish represented 57% and 50% in 2013 and 2014, respectively, zoobenthos 38% and 45% in 2013 and 2014, respectively, and zooplankton only 5% in both years (Figure 3).

Comparison of the percentage representation of the three main diet categories revealed by GCA and SIA (MixSIAR mixing model) in both lakes in 2013 and 2014 is summarised in Table 1.

4 | DISCUSSION

The relative diet composition of adult perch revealed by GCA was uniform between the 2 years in both lakes based on the test of all diet categories. However, in the Most lake, the most consumed diet category varied between the 2 years, with dominant YOY fish in 2013 and zooplankton in 2014. The fluctuations are typical for diet composition of a perch population dependent on cannibalism (Byström & García-Berthou, 1999; Persson et al., 2003; Wahlström et al., 2000). Cannibalism becomes more prevalent during the years of high YOY perch abundance (Persson et al., 2000). In contrast, zooplankton decreases in the diet of adult perch during these periods, as zooplankton is depressed by the abundant YOY perch. The diet composition of adult perch, as revealed by GCA, reflected this phenomenon in the Most lake where YOY fish prevailed in 2013, a year rich in YOY fish. In contrast, the diet composition in the Milada lake was similar in both years, as the YOY fish richness was also very similar in both 2013 and 2014 (see Table S3). In most cases, only one diet category was present in the perch stomachs (Milada: 91% and 96%; Most: 86% and 85% in 2013 and 2014, respectively). It is in accordance with the Optimal Foraging Theory stating that individuals rank alternative resources according to their energetic value per unit handling time, which depends on resource traits and individual's phenotypic capacity to capture, handle and to digest those resources (Stephens & Krebs, 1986). In particular, foraging for YOY fish requires a learned hunting skill. Once these skills are acquired, the ratio between hunting and searching time is obviously the most profitable (Stephens & Krebs, 1986). The more frequent observation

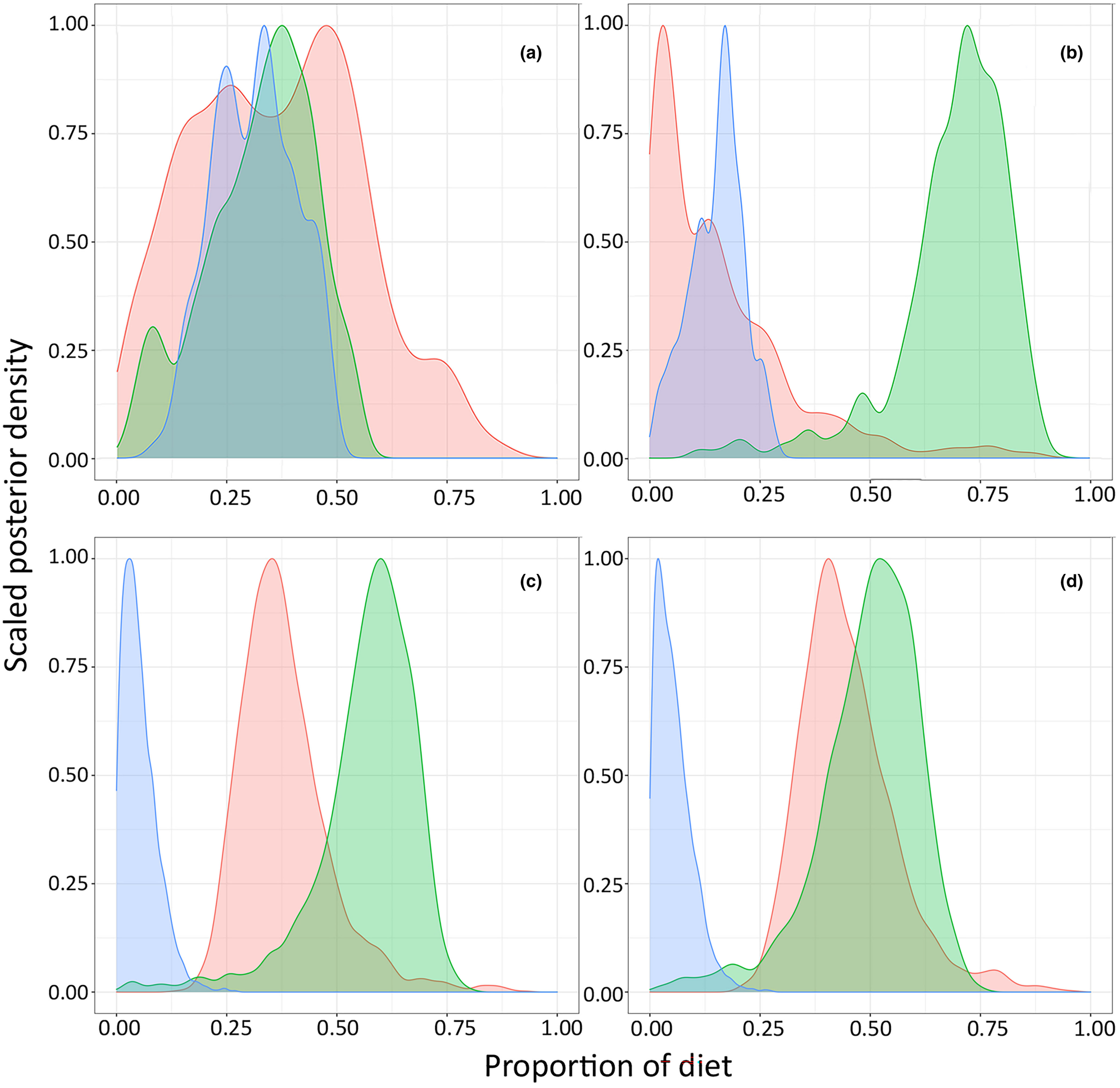

FIGURE 3 MixSIAR (stable isotope mixing model) results showing the scaled posterior probability density of the proportion of the diet categories in perch diet in (a) Milada 2013, (b) Milada 2014, (c) Most 2013, and (d) Most 2014. Blue = zooplankton, red = zoobenthos, and green = YOY fish.

TABLE 1 Comparison of the percentage representation of the three main diet categories revealed by GCA and SIA (MixSIAR mixing model) in both lakes in 2013 and 2014.

Method	GCA/MixSIAR		
Diet category	Zooplankton (%)	Zoobentos (%)	YOY fish (%)
Milada 2013	69/31	11/36	20/33
Milada 2014	60/15	19/16	21/69
Most 2013	19/5	39/38	42/57
Most 2014	54/5	19/45	27/50

of the combination of two categories in Most than in Milada lake could indicate the harder conditions for food search in the oligotrophic than in the mesotrophic Most lake. It would be in accordance with the theory that species are forced to utilise more diverse diet with a limited number of resources in the oligotrophic environment (Araújo et al., 2011; Vejřík et al., 2017). The combination of three diet categories was practically absent. However, it is important to mention that many factors affect the optimal prey choice in natural conditions. Moreover, obtaining the diet information from only one narrow time interval is the weakness of GCA (Araújo et al., 2011;

Svanbäck & Persson, 2004). A piscivorous prey data, in particular, can be misleading, as the predator has often only one large prey present in the stomach. Such prey can often be overestimated in the results because it has a large volume and its digestion, unlike small prey such as zooplankton, takes a long time (Layman et al., 2005).

The individual specialisation of perch based on GCA (degree of IS: 0 = highest, 1 = lowest) was noticeably higher in the oligotrophic Most lake (0.25 and 0.27 in 2013 and 2014) than in the mesotrophic Milada lake (0.52 and 0.41 in 2013 and 2014). The finding is in contradiction with the theory that specialisation is affected by the food availability. Individuals are forced to be more generalist in the nutrient-poor ecosystem than in the nutrient-rich one with high food availability (Araújo et al., 2011). The reverse phenomenon could be caused by a higher variation in body size structure of perch individuals in the Most than in the Milada lake. Individuals reach significantly larger sizes in the Most lake (mean 204 mm ± 71 SD in 2013; 208 ± 79 SD in 2014) and the population in the Most lake is therefore significantly more variable than the population in the Milada lake (mean 160 mm ± 51 SD in 2013; 151 mm ± 41 SD in 2014). However, additional research, focused for example on a phenotypic plasticity (Svanbäck & Eklöv, 2006) would be necessary to support the hypothesis.

SIA, informing on long-term diet (Vander Zanden et al., 1997), did not reveal neither a clear clustering of individuals by a certain prey, nor a clear trend in body size. The specialised groups of individuals would be clearly separated in the isotopic data (Vander Zanden et al., 1997, 2010), however, the data were equally dispersed in both lakes and years without clear clusters. Thus, we cannot confirm in our study sites the observation of two subpopulations occupying their respective pelagic and littoral niches described by Svanbäck and Eklöv (2003). This long-term specialisation would be revealed by SIA (Vander Zanden et al., 2010). The interesting finding is that the total niche width (TNW) of a specific perch population in a particular location remained similar between 2 years, regardless of the perch diet composition being different or almost uniform. Thus, the overall variation in the sources utilised by the entire population remains the same between years (Araújo et al., 2011; Bolnick et al., 2003).

The diet plasticity of Eurasian perch was revealed thanks to the combination of GCA and SIA. The study clearly demonstrated the limitations of GCA when the analysis is performed over a short period of time (Hyslop, 1980), however, SIA is not as prey specific as the latter method (Nolan & Britton, 2018). Thus, a combination of both methods is highly recommended to gain the most comprehensive understanding of the issue. GCA revealed a difference in the perch diet, mainly in the most consumed prey, in the Most lake between years 2013 and 2014, but not in the Milada lake. In contrast, SIA revealed an opposite trend. Isotopic signals did not vary between years in the Most lake, whereas they significantly differed between years in the Milada lake. Due to the higher δ^{15}N of perch in the Milada lake in 2014, the individuals likely foraged primarily for YOY fish earlier that year, information that was completely missed by GCA of fish caught in September. The results of relative composition of zooplankton and YOY fish varied significantly when analysed by GCA or SIA in both lakes. Zooplankton dominated in the diet followed by YOY fish according to GCA, except in the case of the Most lake in 2013. Conversely, SIA indicated YOY fish as the prevailing diet. This difference can be explained by one or both of the following two phenomena. First, each method reflects different time periods. GCA reflects only the day the samples were collected, whereas SIA reflects long-term foraging behaviour. It is likely that predation on YOY fish was prevalent earlier in the summer leading to a decrease in YOY fish numbers, and consequently to an increase in zooplankton density. Thereafter, the abundant zooplankton was utilised by the perch and revealed by GCA at the end of summer (Persson et al., 2004; Svanbäck & Persson, 2004). Second, GCA presents the volumetric percentage of the diet categories found in the stomach, whereas SIA reflects how each diet category was converted into the consumer's body tissues depending also on the fish metabolism. The nutritional value of a diet varies, and the more similar the nutritional composition of the diet is to the consumer itself, the more efficient the conversion of the diet is (Fagan et al., 2002). Thus, it is reflected more effectively in the final isotopic signal of the consumer (Post, 2002). It implies that cannibalism is the most efficient diet source for the predator (Fagan et al., 2002; Pfennig, 2000). Cannibalism is common among perch (Persson et al., 2004). The dry matter of perch fish contains 77% of proteins and 5.8%, of lipids (Schulz et al., 2006; Xu et al., 2002), whereas the dry matter of zooplankton contains only 48% of proteins and 14% of lipids (Farhadian et al., 2013). Furthermore, the amino acid complex of YOY fish, specifically YOY perch, is more similar to the consumer than that of zooplankton (Nagai et al., 1971), and the volume percentage of water content is ca. 81% and 77% in zooplankton and YOY perch, respectively. So, the nutritional value of zooplankton is lower than that of YOY fish or zoobenthos (Meyer & Walther, 1988), however, as mentioned above, zooplankton is commonly utilised during the zooplankton-rich season due to its ready availability and higher abundance compared to the prey with the highest nutritional value (Persson et al., 2004). Further research focusing on the nutritional value based on the growth rate would help confirm how the diet is reflected in SIA.

AUTHOR CONTRIBUTIONS

Study design: IV, LV. Field work: IV, LV, MČ, PB, JP. Stable isotope analysis: IV. Statistics: LV, PB. Figures: PB, LV. Writing—original draft: IV, LV. Writing—review & editing: IV, LV, MČ, PB, JP.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The dataset analysed during the current study is available on a reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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