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Trophic Niche Width and Overlap of Three Benthic Living Fish Species in Poyang Lake: a Stable Isotope Approach

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Abstract

An occupied niche space implies resource use, and understanding the factors that lead to change in trophic niches is vital to assess food web structures. Quantifying niches and niche overlaps are important to assess interspecies resource partitioning and competition. In this study, stable carbon and nitrogen isotopes were used to characterize trophic niche width of and niche overlap among three commercially-important benthic-living fish (*Carassius auratus*, *Pelteobagrus fulvidraco*, and *Silurus asotus*) collected from northern and southern Poyang Lake. The separation of snails and mussels on the $\delta^{13}C$ at southern part indicating the integration of terrestrial derived organic carbon, which led to larger trophic niche widths of fish in the south. The $\delta^{15}N$ ratios of fishes were significantly higher in the northern Lake than in the southern part. Furthermore, the trophic overlaps were higher in the south than in the north. Trophic niche width of *C. auratus* was the smallest as their food sources were easy to acquire, and consumers tended to specialize and narrow their trophic niches when food resource is abundant. *S. asotus*, a predator species, was short of animal food sources due to heavy fishing pressure. Therefore, its diet broadened, and the trophic niche width was the largest.

Keywords Niche width · Niche overlap · Benthic · Poyang Lake · Stable isotope

Introduction

Hutchinson's conceptualization of niche as an *n*-dimensional hypervolume is a crucial foundation for ecologists (Hutchinson 1957). An occupied niche space implies resource use, and understanding the factors that lead to change in trophic niches is important to assess food web structures, resource use, and trophic interactions. Assessing the functional role of a specie depends on quantifying its trophic niche width, which represents the richness and evenness of resources consumed (Bearhop et al. 2004). When resources are limited, coexisting species may overlap along many niche axes but must differ in at least one to avoid competitive exclusion (Hutchinson 1957).

Quantifying niches and species niche overlaps is of interest to many ecologists. Recent advances in stable isotope ecology have proven that carbon and nitrogen stable isotopes are powerful tools in this area (Bearhop et al. 2004; Newsome et al. 2007). The isotopic signature of carbon ($\delta^{13}C$) provides information on the food source of the consumer, and the isotopic signature of nitrogen ($\delta^{15}N$) is associated with the trophic level (Peterson and Fry 1987). Isotopic variation within a consumer population can be utilized to examine niche characteristics through space and time because the isotopic composition of consumer tissues predictably reflects assimilated diet (Bearhop et al. 2004; SyvÄRanta and Jones 2008). For example, Xu et al. (2012) found that Yellow catfish (*Pelteobagrus fulvidraco*) could adjust their foraging strategies to temporal changes in food availability in Taihu Lake. In summer, they tend to forage small fish and shrimp to balance the energy demand on growth and reproduction. A study on two coexisting planktivores (silver carp and bighead carp) in southern China revealed a trophic niche overlap between these

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two species in an oligotrophic system with limited resources, and a hypereutrophic system with high resource availability. No such overlap was found in mesotrophic systems as moderate watershed size and productivity allowed bighead carps to exploitatively consume zooplankton, which made silver carp shift to phytoplankton (Chen et al. 2011). Advances in mathematical techniques have made quantifying niche dimensionality among and within communities increasingly practicable (Layman et al. 2007; Jackson et al. 2011; Swanson et al. 2015). For example, a study on native and invasive fish demonstrated that narrow trophic niche areas and high overlaps with non-native species are the reasons for the decline of native species populations in Lake Patzcuaro, Mexico (Cordova-Tapia et al. 2015).

Poyang lake is a complex wetland system with the composition of water, sand, mudflat and numerous species of vegetation (Han et al. 2015). The inundation regimes and water level fluctuations are largely controlled by the dynamic balance of five major tributaries (Gan River, Fu River, Xin River, Rao River, Xiu River) and the Yangtze River. Seasonal water level fluctuation determines vegetation cover area (Wang et al. 2011, 2012; You et al. 2015) which are important spawning, feeding, and roosting habitats for fishes. Fishery in Poyang Lake provides an important source of income and protein to local people. The average annual capture of wild stocks of freshwater fish from 2000 to 2011 was 3.1×10^4 t (Jiang et al. 2013). Around 137 species of fish exist in Poyang Lake, including 53 benthic species (38.7%) (Zeng 2014). *Carassius auratus*, *Pelteobagrus fulvidraco*, and *Silurus asotus* are important commercial fishes because they are widely distributed, adapt to water regime and hace large yield. These three species account for 35% of the total fishery catch (Jiang et al. 2013). *S. asotus* is carnivorous. *P. fulvidraco* and *C. auratus* are omnivorous, but *P. fulvidraco* favors animal food and *C. auratus* favors plant food (Zhang et al. 2013). The main food sources for *C. auratus* are plant materials, zooplankton, and benthic invertebrates (Zhang 2005). *P. fulvidraco* consume small fish, shrimps, mussels, snails, and aquatic insects (Tan 1997). *S. asotus* consume fish, shrimps, crabs, and snails (Yang et al. 2002).

Studies have found that diet composition of wetland fishes varied between hydrological periods (Silva et al. 2017; Wang et al. 2011, 2012). Flow reductions in wetland systems could increase the dietary overlap between fishes (Mazumder et al. 2012). Potential food source for fishes in Poyang Lake also varied as wetland water level fluctuated (Wang et al. 2011, 2012), however it is not clear about trophic relationship during high water seasons. Although many studies have found spatial variations in water environments and nutrient concentrations in Poyang Lake (Hu et al. 2010; Wu et al. 2013; Chen et al. 2013a, b, c; Liu et al., 2016), only a few studies (Wang et al. 2009; Yang et al. 2015) have focused on whether these spatial variations influence fish niches and trophic relationships in this large and complex floodplain lake. The primary objective of this study is to determine the niche space and dietary overlap among three benthic species of fish residing northern and southern parts of Poyang Lake experiencing heavy fishing pressure during high water seasons.

Materials and methods

Sampling and pretreatment

Samples of fish and macrozoobenthos were collected on August 2011 in the northern and southern parts of Poyang Lake (Fig. 1) when the water level was high. The northern narrow part from lake outlet to Xingzi county is Hukou segment, the southern open water area belongs to Poyang Lake fault depression. *C. auratus*, *P. fulvidraco*, and *S. asotus* were collected at two sites by local fishermen in each part of the lake. The fish were preserved in ice, and their white dorsal muscle tissues were dissected in the laboratory.

Mussels and snails used in stable isotope analysis were collected by 0.05 m² modified Peterson grab at the location where fish nets were settled. At each site, 10 Peterson grab samples were taken to survey biomass and abundance of macrozoobenthos. The grab samples were pre-sieved *in situ* through a 250 μm (mesh size) sieve before being taken to the laboratory for further sorting. In the laboratory, samples were sorted on a white tray, counted, blotted dry, and weighted to determine their wet weight through an electronic balance. Foot muscle tissues of two dominant species *Corbicula fluminea* and *Bellamya aeruginosa* with wet weight more than 2.0 g were cut by scalpel. The tissues of animals were dried at 60 °C to a constant weight. These samples were then ground to fine homogeneous powder with mortar and pestle and placed in tin capsules for stable isotope analysis.

At the 20 grab sampling sites, water samples were also collected. Water depth and Secchi depth were measured in the field. Turbidity was measured with a Hydrolab DataSonde 5 (HydroLab Corporation, Austin, Texas, USA) sensor *in situ*. Water samples were collected and placed in acid-cleaned 10 L plastic containers and kept cool and shaded before transportation to the laboratory. Total nitrogen (TN), ammonium (NH_4-N), nitrate (NO_3-N), suspended solids (SS), chemical oxygen demand (COD_{Mn}), and chlorophyll a (Chl-*a*) were measured in the laboratory according to American Public Health Association (APHA) standards (2012).

Stable isotope analysis

Stable isotopic analysis was performed with Finnegan MAT 253 (Thermo Scientific, USA) continuous-flow isotope ratio mass spectrometer coupled with a Flash Elemental Analyzer 1112 system (Institute of Geographic Sciences

Fig. 1 Locations of the sampling sites for fish, macrozoobenthos and environmental parameters in Poyang Lake, China
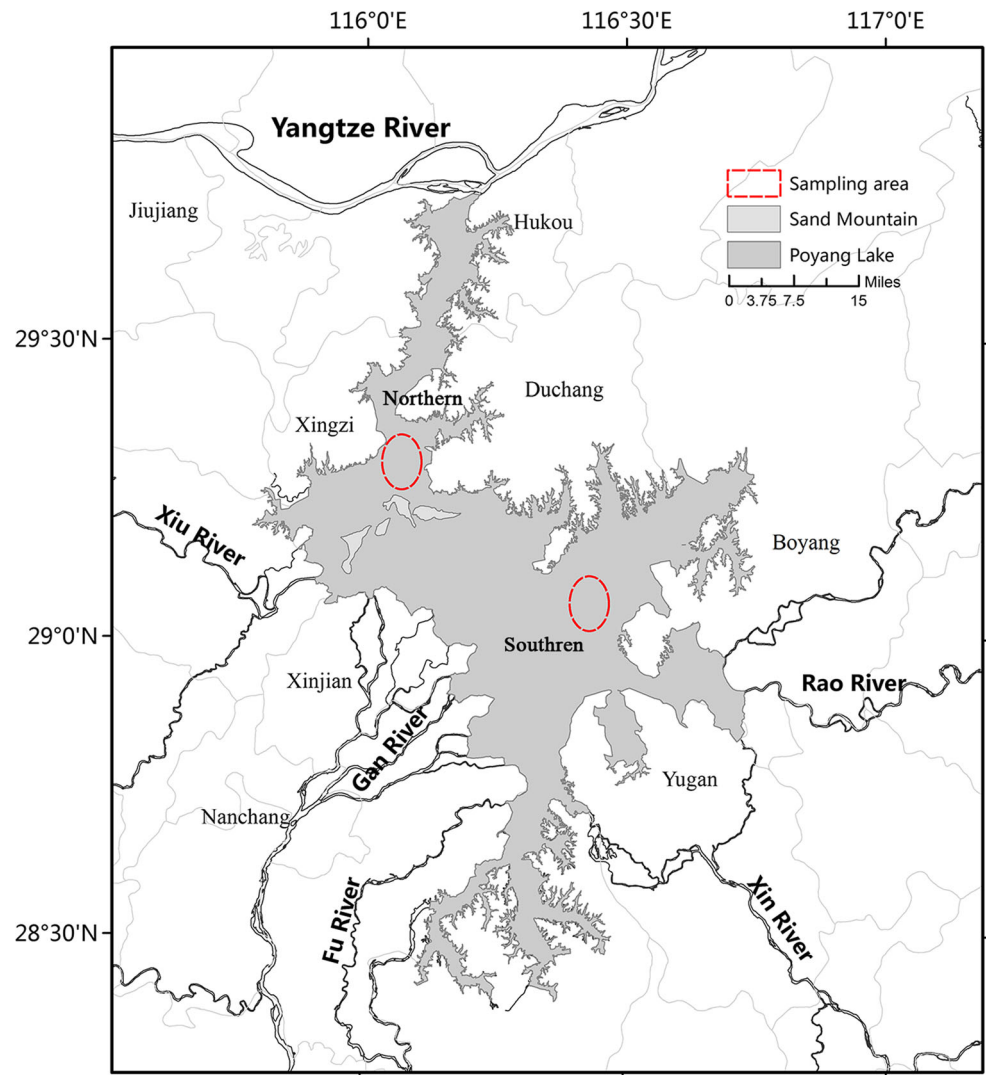
and Natural Resources Research, Chinese Academy of Sciences). The isotope ratios were expressed as δ^{13}C and δ^{15}N (per thousand percent) with the following equation: $\delta X = [(R\text{sample}/R\text{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N and R is the corresponding ratio of ^{13}C/^{12}C or ^{15}N/^{14}N. The reference standard for δ^{13}C was Pee Dee Belemnite limestone and atmospheric nitrogen for δ^{15}N. Based on replicates of laboratory standards (urea), the observed analytical precisions of δ^{13}C and δ^{15}N were ±0.1% and ±0.3%, respectively. Due to low lipid content (C:N of all fish samples <3.5), lipid content for muscle tissues was normalized (Post et al. 2007).

Standard ellipse areas (SEA) (Syväranta et al. 2013) in the δ^{13}C–δ^{15}N bi-plots of each fish were utilized to compare the isotopic niches. SEA was estimated with multivariate ellipse-based metrics, which are bivariate equivalents of SDs in univariate analysis and contain 40% of the data regardless of the sample size; therefore, they represent the core dietary niche and reveal the typical

resource use within a species or population (Jackson et al. 2011). We calculated the isotopic niche occupied by each fish by using the SIAR package in the R computing program (Jackson et al. 2011; R Development Core Team 2015). When the SEAs overlapped, we also calculated the area and percentage of overlap through the Monte Carlo method to bootstrap the same number of samples for each fish. The procedure was repeated 1000 times for each species, and the mean of each value of the trophic niche analysis and the trophic niche overlap were calculated. We calculated the isotopic niche overlap of fishes with the nicheROVER package in the R computing program (R Development Core Team 2015; Swanson et al. 2015).

Nonparametric one way ANOVA was used to determine macrozoobenthos biomass, macrozoobenthos abundance, water quality difference and isotopic variability in *B. aeruginosa*, *C. fluminea*, *C. auratus*, *S. asotus*, *P. fulvidraco* between northern and southern parts of Poyang Lake.

Table 1 Length range of fish taxa collected from northern and southern parts of Lake Poyang during August 2011

Species	Northern			Southern			p
	Length range(cm)	Mean length (cm)	n	Length range(cm)	Mean length (cm)	n	
C. auratus	11.5–13.0	12.11	8	10.5–15.5	12.15	16	0.717
P. fulvidraco	7.7–16.5	12.91	14	8.5–17	12.02	18	0.235
S. asotus	13.6–20.8	17.35	15	12.4–21.4	17.95	13	0.697

Results

Sample sizes, length range and mean length for the fishes used in the isotope analysis are shown in Table 1. The difference between body length of fishes collected at northern and southern parts was not significant (Table 1, all $p > 0.05$).

Grazing snail, *B. aeruginosa*, and filter-feeding mussel, *C. fluminea* presented in 80.0% and 63.6% of sampled sites at northern and southern Poyang Lake. These two species accounted for 67.3% and 76.5% of the biomass of macrozoobenthos in northern and southern part, respectively. Although the biomass and abundance of total macrozoobenthos were lower in the northern part than in the southern part, the difference were insignificant (Table 2, all $p > 0.05$). Only NH_4-N concentration in water was significantly lower ($p = 0.001$) in the northern part than in the southern part (Table 2), while other physical and chemical variables of the water environment during high water times showed no significant difference.

The $\delta^{13}C$ and $\delta^{15}N$ values of both mussel and snail varied significantly between northern and southern parts of the lake (Table 3). The $\delta^{15}N$ values of three fish species were significantly different between locations (Table 3). The enriched $\delta^{15}N$ value indicated that *S. asotus* was higher in the food chain in Poyang Lake (Fig. 2). The trophic niche widths of *C. auratus*, *P. fulvidraco*, and *S. asotus* were 24.7% smaller in northern than in southern Poyang Lake (Fig. 3, Table 4).

Assessment of the isotopic niche overlap showed that the probability that *C. auratus* fed within the dietary niche of the *P. fulvidraco* population was up to 90.09% in southern Poyang Lake, and the probability that *P. fulvidraco* fed from within the dietary niche of *C. auratus* was 73.39% (Table 5). The lowest isotopic niche overlap was 23.54% found between *S. asotus* and *C. auratus* in Northern Poyang Lake (Table 5). Niche overlaps among these three fish species were higher in southern part (Table 5).

Discussion

Water flow is high in northern Poyang Lake (Gu and Wan 2011). The high flow might lead to dilution of nutrients in the water and slightly reduces the concentration of nutrients (i.e., TN, NO_3-N, and NH_4-N). Chen et al. (2013c) also reported that TN concentration in the water samples of Poyang Lake had a downward trend from the south part to the north part. Meanwhile, suspended solids and turbidity are also higher at southern part.

In the northern part, mussels and snails overlapped on their $\delta^{13}C$ values but not on their $\delta^{15}N$ values, while the opposite was observed in the southern area. The separation of snails and mussels on the $\delta^{13}C$ in the southern area implied different basal resource inputs feeding the food web

Table 2 Mean and standard deviation (sd) of macrozoobenthos biomass, abundance and water quality variables of 10 sites sampled at northern and southern Poyang Lake

Variable	Units	Northern Mean ± SD	Southern Mean ± SD	p
Macrozoobentho biomass	g·m^{-2}	128.74 ± 163.37	415.33 ± 473.34	0.064
Macrozoobentho abundance	ind·m^{-2}	361.14 ± 211.59	478.40 ± 359.31	0.666
TN	mg·L^{-1}	1.70 ± 0.69	2.48 ± 1.69	0.403
COD$_{Mn}$	mg·L^{-1}	3.95 ± 0.46	4.32 ± 0.65	0.160
Suspended solids	mg·L^{-1}	25.72 ± 21.4	25.48 ± 26.49	0.860
NO$_3$-N	mg·L^{-1}	1.02 ± 0.58	1.12 ± 0.56	0.742
NH$_4$-N	mg·L^{-1}	**0.22 ± 0.1**2	**0.62 ± 0.05**	**0.001**
Chlorophyll-a	µg·L^{-1}	10.43 ± 6.05	9.02 ± 8.74	0.131
Water depth	m	2.11 ± 1.08	1.63 ± 0.80	0.193
Secchi depth	m	0.56 ± 0.34	0.56 ± 0.20	0.494
Turbidity	NTU	50.14 ± 37.06	44.98 ± 50.27	0.631

Numbers in bold indicate $p < 0.05$

Table 3 Variation of $\delta^{13}C$ and $\delta^{15}N$ for macrozoobenthos and fish collected in northern and southern Poyang Lake

Species	$\delta^{13}C$	$\delta^{15}N$
B. aeruginosa	<0.001	<0.001
C. fluminea	<0.001	<0.001
C. auratus	0.976	<0.001
P. fulvidraco	0.536	<0.001
S. asotus	0.856	<0.001

(Rossi et al. 2010). In the southern large open water area *C. fluminea* has more negative $\delta^{13}C$ values, indicating the integration of terrestrial derived organic carbon from surrounding wetlands, while the higher $\delta^{13}C$ values of *B. aeruginosa* indicating the assimilation of aquatic derived organic carbon. Both Wang et al. (2011) and Zhang et al. (2017) had reported contribution of terrestrial plants to consumers in Poyang Lake food web. *S. asotus* had the highest $\delta^{15}N$ ratio, and *C. auratus* had the lowest $\delta^{15}N$ ratio. These results confirmed the previous trophic position estimations according to records of dietary analysis (Tan 1997; Yang et al. 2002; Zhang 2005). Wang et al. (2014a) found that the $\delta^{15}N$ value of suspended particulate organic matter in Xingzi could reach 19.69‰ at high water seasons because of large amounts of domestic sewage discharge and pollution from livestock breeding. Agricultural non-point source pollution and soil erosion in the basin have caused the $\delta^{15}N$ value of sediments in Duchang to be the highest (6.72‰) (Wang et al. 2014b). Marcozoobenthos consumes suspended particulate organic matter and surface sediment organic matter, $\delta^{15}N$ value of their muscle enriched due to their food sources have high $\delta^{15}N$ ratios (Wang et al. 2014a, b). Since
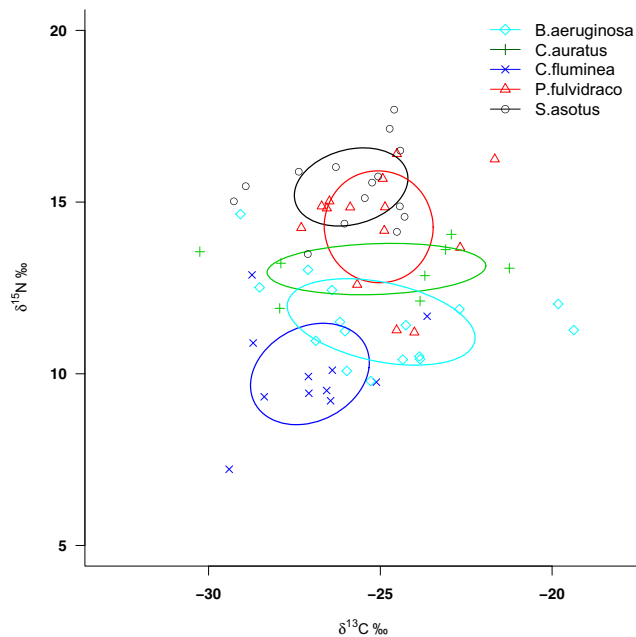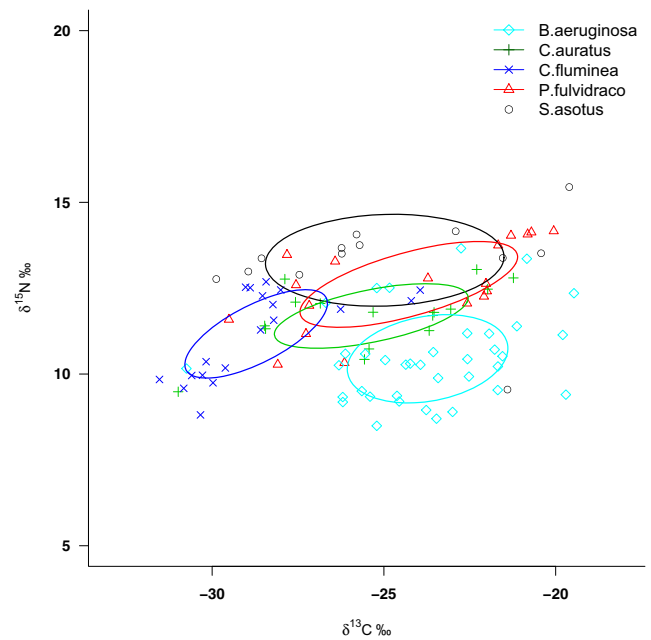

Fig. 3 Isotopic bi-plot of fish and macrozoobenthos collected in southern Poyang Lake

trophic baselines in the northern part are already enriched with $\delta^{15}N$; thus, consumers, such as fish, in the food web are also enriched with $\delta^{15}N$ (Wang et al. 2009).

The range of the variance of $\delta^{13}C$ signatures of baseline species was wider in the southern part. The SEAs of *C. auratus*, *P. fulvidraco* and *S. asotus* were also larger in southern than in north part (Figs. 2 and 3), reflected the $\delta^{13}C$ range width of baseline species (Sanders et al. 2015).

Plants were relatively easy to acquire since Poyang Lake was rich in vegetation (You et al. 2015), SEA of *C. auratus* was smallest among these benthic fishes as consumers tended to specialize and narrow their trophic niches when high resource availability presence (Rossi et al. 2015). Due to heavy fishing pressure in Poyang Lake (Wang et al. 2014), even small fish were capture by local fish men, the predator *S. asotus* might be short of food sources. As a result, its diet was broadened, and had the largest trophic niche width (SEA) in both northern and southern parts (Table 4).

Trophic overlaps indicate shared diets. In Lake Poyang, the three commercially-important benthic-living fish species displayed substantial trophic niche overlaps, suggesting that they consume the same food source of aquatic macrozoobenthos. Optimal foraging theories predict trophic niche broadening as a

Fig. 2 Isotopic bi-plot of fish and macrozoobenthos collected in northern Poyang Lake

Table 4 Standard ellipse area of three benthic commercial fish species in Poyang Lake

	Northern SEA	Southern SEA
C. auratus	6.08	7.22
P. fulvidraco	8.63	9.92
S. asotus	8.48	15.53

Table 5 Trophic niche overlap (%) of three benthic living fish species in Poyang Lake

	Northern			Southern		
	C. auratus	P. fulvidraco	S. asotus	C. auratus	P. fulvidraco	S. asotus
C. auratus	–	68.21	28.86	–	90.09	83.79
P. fulvidraco	52.58	–	65.59	73.39	–	88.83
S. asotus	23.54	86.5	–	45.16	68.52	–

Trophic niche overlap is read row by row, it represents overlap in percentage of the total area

consequence of reduced food availability, where consumers relying on insufficient preferred food items are forced to add less profitable resources to their diet, hence widening their trophic niche (Rossi et al., 2015; Calizza et al. 2017). For example, in the southern part of the lake, overlapping between *S. asotus* and *C. auratus*, *S. asotus* and *P. fulvidraco* were higher than in northern part (Table 5), implied higher intraspecific competition, which would promote trophic generalization within populations due to differentiation in food use among conspecifics (Svanback and Bolnick 2007), led to increase of *S. asotus* trophic niche width.

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