

RESPONSES OF TROPHIC STRUCTURE VARIATION IN FISH ASSEMBLAGE TO HYDROLOGIC REGULATION IN A TRIBUTARY OF THE THREE GORGES RESERVOIR, CHINA

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Abstract. Responses of trophic structure to reservoir regulation are important to manage and conserve the river ecosystem influenced by dams. We used stable isotope-derived community-wide metrics to describe spatiotemporal variation in trophic niches and trophic structures of fish assemblages in a tributary of the Three Gorges Reservoir (TGR) in China where water level regulation is put into operation annually. A longitudinally increasing trophic space was discovered in this tributary especially when the water level was low. Trophic diversity declined and trophic redundancy increased from the non-flood period to flood season at the upper backwater region. However, trophic space was more stable in the estuarine site. The site differences were associated with availability of food resource and pathway of consumers, as specifically, disturbance derived from flow pulse at the end of backwater site altered diet composition of the fish consumers, while immense water body in the lower confluence area limited the flood influences as well as promoted exploitation of diverse available sources. Moreover, the declined water level control facilitated the contraction of the trophic niche size at the tail backwater site because of remarkable riverine morphology alternation leading to decreasing water body whereas the rising water level regulation homogenized trophic structure along the downstream river. Our study revealed that there was different response of fish assemblages along longitudinal fluvial gradient to the water level regulation in the reservoir and targeted management and conservation measures are needed for the different sections of the tributary.

Keywords: *reservoir regulation, stable isotope, community metrics, pathway, food resource*

Introduction

For purposes of flood control, power generation and/or navigation, dams have been constructed on the majority of large rivers globally since the last century (Avakyan and Iakovleva, 1998) and these river systems have been affected spatiotemporally to varying

extent (Nilsson et al., 2005). By altering thermal and flow regimes as well as sediment transport (Kondolf, 1997; Graf, 2006), the presence of dams leads to subsequent changes in biotic assemblages (Cumming, 2004; Freedman et al., 2014) and contributions of allochthonous and autochthonous nutrients (Doi et al., 2008; Sabo et al., 2018). As a result, a variety of trophic shifts may occur resulting in alteration for trophic diversity and food web structure (Mercado-Silva et al., 2009; Gowns et al., 2014; Kaymak et al., 2018), which ultimately affect river ecosystems function. Although numerous studies have been devoted to understanding how dams influence biodiversity and food-web interactions (Holmquist et al., 1998; Bunn and Arthington, 2002; Cross et al., 2011), responses of rivers and river ecosystems to dams are intricately varied and usually show contrasting results (Gowns et al., 2014), as they depend on local geomorphic, hydrological and biologic attributes (Power et al., 1996).

Tributaries could promote the function of large river ecosystems, such as enhancing the overall biodiversity of large rivers (Fernandes et al., 2004), resetting the ecological continuum of the mainstem (Kiffney et al., 2006), and maintaining fish reproductive success with retained natural flow regime (Pracheil et al., 2009). Certain tributaries can sometimes serve as a sanctuary for many indigenous species after the mainstem has been altered by dams (Park et al., 2003; Pracheil et al., 2013). Hence, tributaries, by virtue of lower degree of alteration could provide underappreciated opportunities for conserving biodiversity (Pracheil et al., 2013) especially in the impounded reaches where lotic species are more susceptible to environmental changes. However, much research focuses on downstream effects (Cross et al., 2011; Sabo et al., 2018) or on longitudinal patterns of the river continuum (Mercado-Silva et al., 2009; Cross et al., 2013; Gowns et al., 2014) from the dam. There is a paucity of information pertaining to variation in trophic diversity in the upper tributaries which are also influenced by the regulated reservoir.

The Three Gorges Dam (TGD) is built in the middle of the Yangtze River, the largest river in China, and has created a reservoir 600 km long with a total storage capacity approaching 40 billion m³. The dam has been put into operation in 2003 and filled initially up to 175 m, the normal pool level, in 2010. Since then, the reservoir would be drawn down to 145 m water level during the flood season (May-September) for flood control, and impounded to 175 m water level after the flood season and maintained until the next year for power generation and navigation. In the Three Gorges Reservoir (TGR) region, six tributaries with the watershed area larger than 3000 km² (ten tributaries more than 1000 km²) flow into the Yangtze River. These tributaries have supported the mainstream biodiversity and possess the potential to be suitable refuges for the affected biota (Park et al., 2003). However, the same water fluctuation cycle as the mainstream occur at the lower reaches influencing the fish assemblages (Yang et al., 2013; Zhao et al., 2015) and thus would likely impact the energy flow and trophic structure as well. The Daning River is one of these important tributaries with less damaged natural landscape in particular in the pristine upper reaches. Previous study has analyzed whether the impoundment affected assimilation of carbon sources by fish consumers in this tributary (Deng et al., 2018). Isotope mixing model results indicated that riparian C₃

plants are the consistently major energy source for fish consumers irrespective of reaches or feeding strategies because of abundant standing stock of riparian vegetation and hydrologic regimes in this river (Deng et al., 2018). This tributary suffers the same hydrological regulation in the backwater accompanied by seasonal flood flows from the uppers as other tributaries in TGR. However, trophic structure shifts on account of spatiotemporal variation in environmental conditions are still unknown. The present study extends previous research on the Daning River to explore the effects of water level regulation on food web structure of local fish assemblages.

Stable isotopes, providing a concrete quantitative measure of niche width and trophic diversity (Bearhop et al., 2004; Layman et al., 2007a; Schmidt et al., 2007; Jackson et al., 2011), are widely used to examine structural features and variations of food webs influenced by species invasion (Jackson et al., 2012), overexploitation recovery (Hamilton et al., 2014), land use (de Carvalho et al., 2017), river fragmentation (Freedman et al., 2014; Kaymak et al., 2018). In this study, we employed stable isotope-derived community metrics to describe and compare trophic diversity of fish assemblages among sites and between periods. The purpose of this study was to examine the spatiotemporal variation in trophic niches and trophic structures of fish assemblages and further how local food webs responded to changes in the environmental conditions enhanced by hydrological regulation. We hypothesized that trophic niches size of fish assemblage increased along longitudinal gradient within the tributary due to the enlarged water body and the effects of flood flow on structure diversity would mitigate by water level conditions. The study on spatiotemporal variation of food web structure in association with flood flows and water level fluctuation in this important tributary could help provide the necessary references for understanding how reservoir regulation could affect overall river systems in the region. Further, this information could be benefit to ongoing management and conservation efforts in the tributaries alike.

Materials and Methods

Study sites and sampling design

This study was conducted in the Daning River, a tributary of the Yangtze River, located in the central part of the Three Gorges Reservoir (*Fig. S1*) in China. The tributary watershed covers an area of 4426 km², and is 200 km long with 47-60 km backwater channel due to the impoundment of TGR. The backwater area vary in length and depth according to the hydrologic regulation of the TGR. The river is canyon bound scattering several open sections with less steep slopes where both C₃ and C₄ vegetation dominate the riparian areas. The valley has subtropical humid monsoon climate with mean average temperature of 16.6°C and an annual mean precipitation of 1124.5 mm, about 80% of which falls in May-October. As a result, the maximum flow in the river is generally observed from June to September (*Fig. 1*).

Three sites representing the estuary area (Wushan), the end of the backwater water region (Dachang) and the natural fluvial site (Wuxi) were selected for sampling (*Fig. S1, Table 1*). The Wushan site is located in the confluence to the reservoir, 123 km upstream of the Three Gorges Dam. This site is characterized by steep littoral zones with little vegetation cover because of the populated areas. The estuary water area is nearly 1.2 km wide and 55 m deep at the lowest water level and 1.3 km wide, 68 deep when the water level rises to 175 m (*Table 1*). The Dachang site is located 45 km above the estuary, near the end of the backwater water. In this zone, the channel is wider with less steep slopes, which forms 9 km² lacustrine environment with the depth of 33 m at the highest water level (*Table 1*).

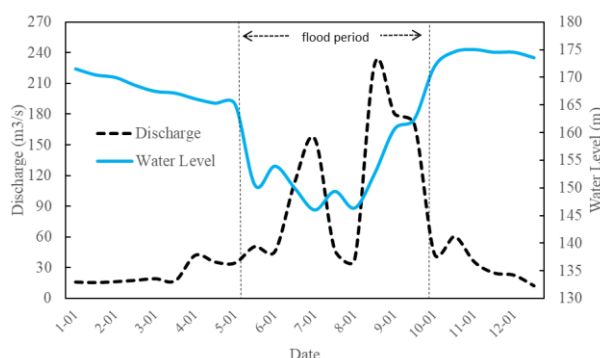


Figure 1. Water discharge (dash line) from Wuxi hydrologic gauge station (in the upper stream) and water level (solid line) at the Wushan site in Daning River

Table 1. Environmental characteristics of the sampling sites along the Daning River (NF = non-flood period or high water level; F = flood period or low water level)

	Wushan		Dachang		Wuxi	
	NF	F	NF	F	NF	F
Water depth (m)	68	55	33	19	1.5	3
Width (m)	1300	1200	1000	700	25	60
Discharge (m ³ /s)	—	—	—	—	34	122
Velocity (m/s)	0.010	0.015	0.008	0.035	0.82	1.38
Transparency(m)	1.85±0.82	0.46±0.18	1.70±0.47	0.68±0.50	—	—
Water temperature (°C)	19.1±2.9	21.5±0.2	17.8±2.0	21.3±0.1	13.6±2.1	18.3±0.2
Dissolved oxygen (mg/L)	7.9±2.8	7.4	8.2±2.1	8.6	9.6±2.7	9.8
Total phosphorus (mg/L)	0.11±0.07	0.14±0.05	0.07±0.03	0.03±0.02	0.03±0.02	0.08±0.05
Density of phytoplankton (million cells/L)	5.55±8.46	21.11±12.77	1.55±1.37	1.22±0.31	0.18±0.21	1.37±0.34

During the lower water levels, however, large lateral habitats characterized by muddy substrates expose out of the water and dense macrophyte mats would appear along the littoral zone. The Wuxi site is an upstream site where riverine system has not yet affected by the TGR. The section is characterized by lotic and shallow habitats with the substrate dominated by rock and cobble. Due to pronounced seasonality in rainfall, highest annual river discharges typically occur from June to September with an average

of 122 m³/s and the average discharge drops to 34 m³/s between October to May (*Fig. 1*). According to the water-level regulation in the TGR as well as river monthly discharges from Wuxi hydrologic gauge station, two sampling periods that reflected strong seasonal patterns in precipitation, water-level and thus, the potential for observing changes in trophic structure of fish assemblages were chosen (*Fig. 1*). In order to detect temporal differences in trophic structure based on consumer stable isotope composition, enough time need for muscle tissue to reflect any new diet (Abrantes et al., 2014). At each period, consumers were living for more than two or three months under that condition before sampling (Boecklen et al., 2011; Abrantes et al., 2014). Therefore, in the Daning River, fishes collected in September-October were referred as samples from the flood period and in December-May were referred as from the non-flood period (*Fig. 1*). All the data we used were collected from 2011 to 2013 and were classified into two periods.

Sample collection and analysis

Fish were collected from the river using 2 m by 50 m gillnets with different mesh sizes (30, 60, 80 and 120 mm). After captured, the number and weight of fish species collected were recorded. Fish were classified into five trophic groups based on available literature in Daning river (The Fish Laboratory, 1976; Zeng, 1990; Ding, 1994), which included planktivores, herbivores, benthivores, omnivores and piscivores (*Table S1*). A total of 68 fish species in this tributary were captured in our several surveys. However, the most dominant species from the different trophic groups were selected for isotopic analysis based on the abundance and frequency of capture in the surveys (Yang et al., 2013) so that the species analysed at each site during each period represented well their trophic groups. For each species, only large adult individuals were selected in case of the influence of ontogenetic diet shifts on isotopic value. For selected individuals, fish were weighed (g), measured (mm), and dissected to extract approximately 5–10 g of dorsal muscle tissue for isotopic analysis. Samples of basal carbon sources were also collected and detailed information are described in Deng et al. (2018).

All fish samples were dried at 60 °C for at least 48 h and ground into a fine powder and stored in glass vials. Carbon and nitrogen stable isotopic analysis was done at the Stable Isotope Laboratory, Chinese Academy of Forestry, Beijing, China, using a Flash EA1112 HT Elemental Analyzer coupled to a DELTA V Advantage Isotope Ratio Mass Spectrometer. Stable isotope ratios are expressed as delta (δ) and defined as parts per thousand (‰) relative to the laboratory standard material. The ratios is calculated by *Equation 1*:

$$\delta X = (R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}} \times 10^3 \text{‰} \quad (\text{Eq.1})$$

where X is ¹³C and ¹⁵N and R is the corresponding ratio ¹³C/¹²C or ¹⁵N/¹⁴N. R is the molar ratio of the heavy to light isotope of the sample and standard (‰). The standard

material used for carbon and nitrogen are Pee Dee Belemnite (PDB) limestone and atmospheric nitrogen. Precision of the isotopic analysis was 0.1‰ for carbon and 0.2‰ for nitrogen.

Data analysis

Five quantitative community-wide metrics derived from stable isotope data (Layman et al., 2007a) were used to describe variation in trophic structure of fish assemblages at each site during each period. Because not all species occurred at all sites, analyses were based on fish trophic guilds. Three of these metrics are community-wide measures of trophic diversity, including $\delta^{13}\text{C}$ range (CR), which depicts basal source diversity, $\delta^{15}\text{N}$ range (NR), which gives information on trophic length, and mean distance to centroid (CD), which is calculated as the mean Euclidean distance of each assemblage component to the centroid and a measure of the average degree of trophic diversity within the assemblage (Layman et al., 2007a). Two additional metrics reflect the extent of trophic redundancy, namely mean nearest neighbour distance (NND) and standard deviation of the nearest neighbor distance (SDNND). MNND is an estimate of density and clustering of species within the community and SDNND measures the evenness of the groups' spacing in the bi-plot space (Masese et al., 2018). Smaller NND and SDNND indicate greater trophic redundancy, which means, groups have more similar trophic niches (Abrantes et al., 2014; Masese et al., 2018). Because riparian plants are the major carbon source to fishes and widespread along the river channel (Deng et al., 2018), the range in potential source $\delta^{13}\text{C}$ was similar for all sites, meaning that the community-wide metrics are comparable among sites and periods (Layman et al., 2007a). In order to provide more robust metrics that are unbiased with respect to variations in the number of groups and allow for statistical comparisons among sites and periods, Bayesian methodology was implemented to generate a posterior distribution of estimates of these metrics, thus providing a measure of uncertainty of these metrics for the fish communities at each site and period (Jackson et al., 2011). Then the comparison was conducted graphically based on the visual analysis of the credibility intervals and the degree of overlap between the Bayesian distributions was used as an indication of similarities or dissimilarities between sites and periods (Abrantes et al., 2014; Masese et al., 2018).

The area of $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ space occupied by all consumers generally represents a measure of trophic niche size and thus a proxy for the total extent of trophic diversity (Layman et al., 2007a). Instead of total area, which is highly sensitive to sample size, standard ellipse area (SEA) was used to quantify the trophic niche space of fish assemblages (Jackson et al., 2011). SEA is equivalent to bivariate standard deviations and robust to variation in sample size or the number of groups (Jackson et al., 2011). Two versions of SEA, Bayesian standard ellipse area (SEA_b), which estimate via Bayesian approach taking account of sampling error and returning probability distributions, and size-corrected standard ellipse area (SEA_c), which correct bias towards underestimation of the SEA when sample sizes are small, were calculated for

niche space comparisons of different fish assemblages. All metrics were calculated using the R statistical computing package, “Stable Isotope Analysis in R” (SIAR) and “Stable Isotope Bayesian Ellipses in R” (SIBER) (R Development Core Team, 2007; Parnell et al., 2008, 2010; Jackson et al., 2011).

T-test and ANOVA were used to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures data from different periods or sites. Pairwise differences were tested using Dunnett T3’s post hoc test. Statistical analyses were conducted using IBM SPSS Statistics (16.0). Statistical significance was determined at $p = 0.05$.

Results

Spatiotemporal differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish assemblages

At Wushan, a total of 42 fish species were found. Each 22 dominant fish species were sampled during the non-flood and flood period (*Table S1*). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of fish assemblages ranged from -29.74‰ to -17.60‰ and 4.54‰ to 17.51‰, with an average of -23.52‰ and 9.37‰ in the non-flood period and an average of -22.02‰ and 10.94‰ in the flood period, respectively. There are also 42 fish species captured at Dachang site. The 27 and 23 dominant species were sampled in the non-flood and flood period (*Table S1*). Fish $\delta^{13}\text{C}$ values varied from -28.57‰ to -16.61‰, with an average of -23.70‰ in the non-flood period and -23.51‰ in the flood period. Fish $\delta^{15}\text{N}$ values varied from 4.91‰ to 14.15‰ and the average $\delta^{15}\text{N}$ values of fish assemblages were 9.10‰ and 9.78‰ in the non-flood and flood period, respectively. At Wuxi, 35 fish species were captured during the surveys. The 13 and 15 dominant fish species were sampled in the non-flood and flood period (*Table S1*). The range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures was from -25.31‰ to -21.56‰ and 2.25‰ to 10.81‰.

There were significant differences in fish $\delta^{13}\text{C}$ between the non-flood and flood period at Wushan site (t-test, $t = 2.855$, $p < 0.01$) and no significant differences at Dachang (t-test, $t = 0.382$, $p = 0.703$) and Wuxi site (t-test, $t = 1.297$, $p = 0.201$). During the non-flood period, there are no significant differences in $\delta^{13}\text{C}$ among sites (ANOVA, $F = 0.096$, $p = 0.908$). However, the average fish $\delta^{13}\text{C}$ value displayed significant differences among sites (ANOVA, $F = 4.577$, $p < 0.05$) during the flood period. Fish assemblages at Wushan were more enriched in $\delta^{13}\text{C}$ than that at Dachang (Dunnett T3’s method, $p < 0.05$) and Wuxi (Dunnett T3’s method, $p < 0.05$) in the flood period. Similarly, differences in fish $\delta^{15}\text{N}$ signature between the non-flood and flood period were significant at Wushan (t-test, $t = 2.497$, $p < 0.05$) but not significant at Dachang (t-test, $t = 1.916$, $p = 0.058$) and Wuxi site (t-test, $t = 0.947$, $p = 0.349$). There are significant differences in $\delta^{15}\text{N}$ values among sites within each period (non-flood: ANOVA, $F = 14.129$, $p < 0.01$; flood: ANOVA, $F = 18.158$, $p < 0.01$) and only $\delta^{15}\text{N}$ values at Wushan and Dachang did not differ significantly (Dunnett T3’s method, $p = 0.07$) during the non-flood period. Overall, average $\delta^{15}\text{N}$ value of fish assemblages increased from upstream site to the downstream site.

Spatial differences in trophic diversity and structure

SEAs of fish communities differed in size, shape and position in the bi-plots (Fig. 2). Generally, standard ellipse areas sizes declined with sites upstream from the confluence. In the flood period, the SEA of the Wushan site was larger than that of Dachang site, of which was sequentially greater than the SEA of the Wuxi site. SIBER indicated that the SEA_b at the downstream sites had more than 97% probability of being larger than the SEA_b at the upstream sites for the flood period in each two-sites comparison (Table 2). In the non-flood period, however, the SEA sizes were more similar between at the Wushan and Dachang sites, which were both larger than at the Wuxi (Table 2). The probability that the SEA_b of the Wushan was larger than that of the Dachang in the non-flood period was only 56% (Table 2) and this lack of differences was also demonstrated by the high overlaps in the SEA_b 50% CIs between these two sites (Fig. 3). Besides, there was more overlap between the different SEA in the non-flood period than in the flood period (Fig. 2, Table 2). SEAs of the Wushan site showed larger overlap with the Dachang site during non-flood period than in the flood period ($14.41\%_b^2$ in the non-flood period and $4.02\%_b^2$ in the flood periods) (Table 2) and the distributions of Bayesian results (SEA_b) showed that the probability was 100%.

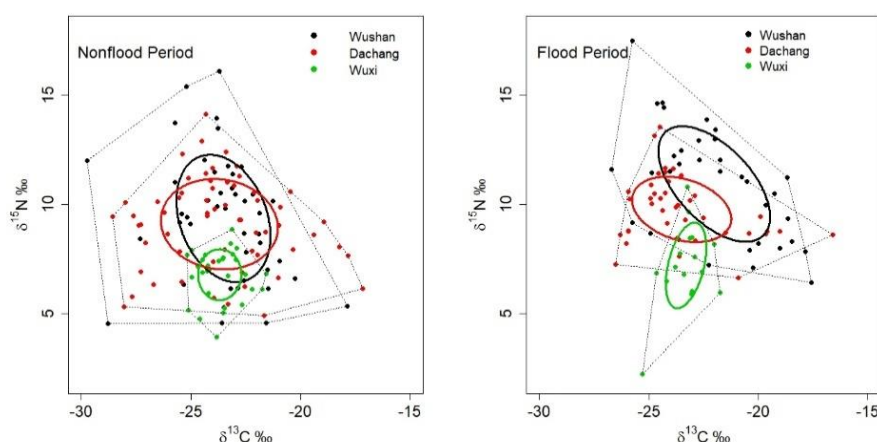


Figure 2. Mean stable isotope composition of the different fish species from the three study sites for the non-flood and flood period. Solid lines represent the standard ellipses area, and dotted lines are the convex hull areas of fish assemblages for each site

Five Layman's community metrics also varied among sites in each period (Figs. 4, 5). In the flood period, all the metrics at the Wushan were the largest than the other two sites except SDNND, whereas the metrics at the Wuxi showed the widest range of values (Figs. 4, 5). In the non-flood period, the five metrics were more similar between Wushan and Dachang, with a large overlap of the 50% CIs for each metrics in these two sites (Figs. 4, 5). However, the Wuxi site showed the smallest mode value for all the metrics compared to the two downstream sites in the non-flood period.

Table 2. Small size-corrected standard ellipse areas (SEAc), probability that the SEA in the flood period is larger than the SEA at the non-flood period, overlap in SEA between periods for the same site and overlap in SEA between pairs of sites

	SEA _c (‰ ²)	p Value SEA flood > non-flood	Overlap in SEA _c (SEA _b) between periods (‰ ²)	SEA overlap between pairs of sites (‰ ²)		
				Wushan	Dachang	Wuxi
flood period						
Wushan	17.42	0.720	5.80 (3.69-10.64)		4.02 (1.98-6.65)	0.00 (-0.06-0.89)
Dachang	10.18	0.001	9.89 (5.88-10.99)	1.00		0.83 (-0.18-1.96)
Wuxi	5.15	0.861	2.87 (1.15-3.77)	0.97	1.00	
non-flood period						
Wushan	18.87				14.41 (9.76-15.67)	1.92 (0.54-3.43)
Dachang	17.30			0.56		1.24 (0.04-2.20)
Wuxi	3.62			1.00	1.00	

Note: The top halves of the matrices show the SEA overlap between sites, in ‰². The bottom halves of the matrices with grey shading show the Bayesian probability (in %) that the SEA of group 1 (sites from the first column) is smaller than that of group two (sites from the first row). Values in brackets are 95% Bayesian credibility intervals estimates by models. Values in bold are calculated by SEAc.

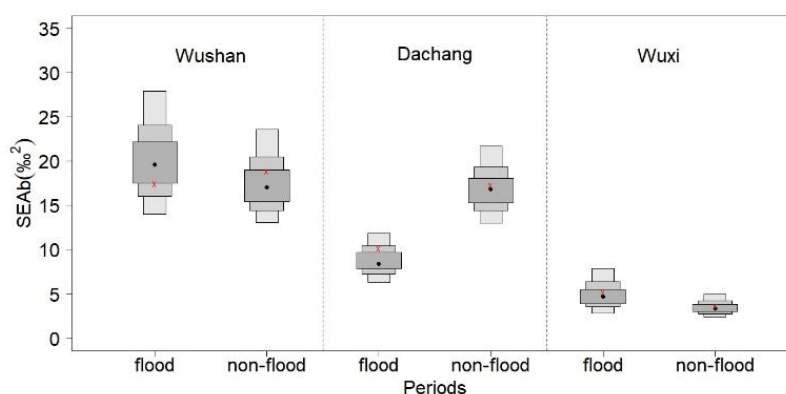


Figure 3. Density plots of the credibility intervals of the standard ellipse areas (SEA). Black dots are the mode SEA, and boxes indicate the 50%, 75% and 95% credible intervals. Red crosses are the small sample size-corrected SEA (SEAc)

Temporal variation in trophic diversity and structure

For Wushan site, there was a temporal change in SEA position with higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the flood period (Fig. 2). However, SEA did not differ in size between periods at this site (Table 2, Fig. 3). The overlap in SEA between periods was relatively low (5.85‰², corresponding to 33.32% and 30.77% of the total SEA for the flood and non-flood period, respectively; Table 2). CR, NR, CD and NND were wider in flood period than in non-flood period with the slight overlap in the 75% or 95% CIs of the distributions of Bayesian results (Figs. 4, 5), suggesting that the fluctuation of water-levels and the discharge during the flood period increases isotopic trophic diversity and decreases trophic redundancy at the Wushan site.

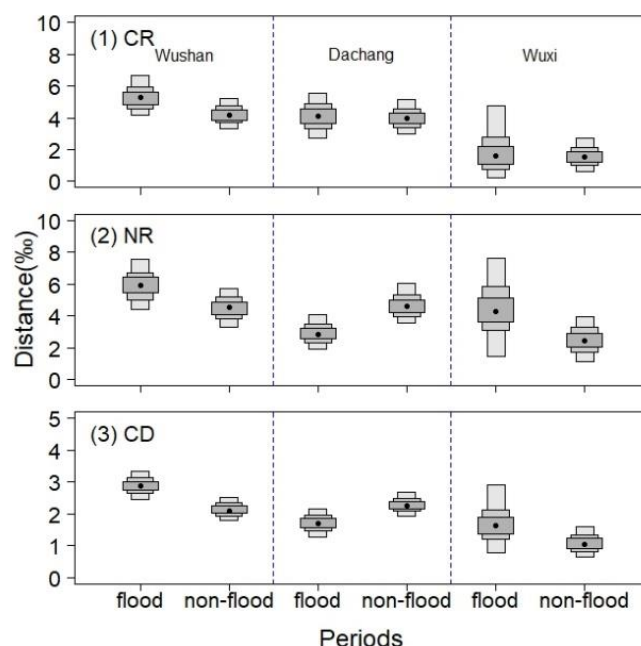


Figure 4. Bayesian results for the three Layman stable isotope-based community-wide metrics that provide information on trophic diversity at each site. CR: Stable isotope of carbon ($\delta^{13}\text{C}$) range; NR: stable nitrogen isotope ($\delta^{15}\text{N}$) range; CD: mean distance to centroid. Black dots are the mode value (%) and boxes indicate the 50%, 75% and 95% credibility intervals

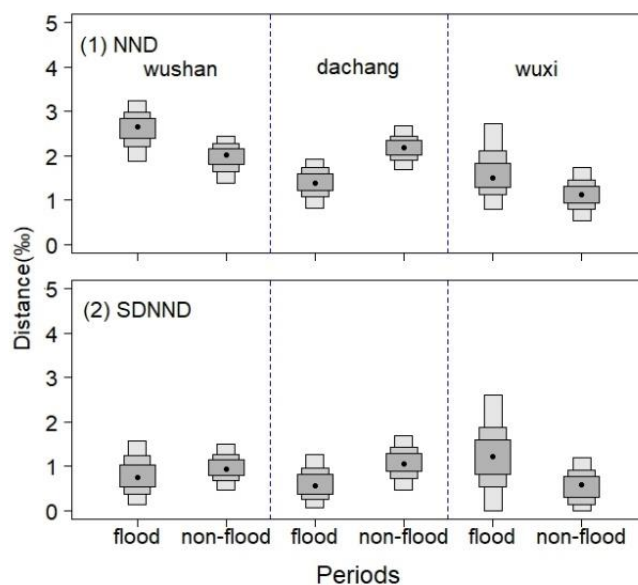


Figure 5. Bayesian results for the two Layman stable isotope-based community-wide metrics that provide information on trophic redundancy at each site. NND: mean nearest neighbor distance; SDNND: standard deviation of mean distance to centroid. Black dots are the mode value (%) and boxes indicate the 50%, 75% and 95% credibility intervals

Conversely, fish groups from the Dachang site showed no evidence of temporal changes in SEA position but increased in size in the non-flood period when 99.9% of the SEA_b was larger than that in the flood period (*Table 2, Figs. 2, 3*). The area overlap between the two periods' standard ellipses was 9.89‰², corresponding to 97.21% and 57.21% of the total SEA of the flood and non-flood period, respectively (*Table 2*). NR, CD and NND were significantly narrower in flood period (*Figs. 4, 5*) which confirmed by Bayesian results that 98.40%, 97.15% and 97.93% of the metrics in flood period were smaller than in the non-flood period, respectively. However, CR was similar for both periods and there was high overlap in the 95% CIs for SDNND (*Fig. 5*).

As for Wuxi site, there was slight seasonal differences in SEA size (*Fig. 3*). The SEA_b in the non-flood period had 89.8% probabilities of being larger than the SEA_b in the flood period and the SEA overlap between periods was 2.87 ‰² (*Table 2*), which accounted for 55.81% and 79.36% of the whole SEA in the flood and non-flood period, accordingly. As well, for the five Layman's metrics, there was little evidence of temporal differences, which were mostly a result of the large overlap in the 95% CIs between periods, due to the wide range of every value in the flood period (*Figs. 4, 5*).

Discussion

Longitudinal patterns of trophic diversity in fish assemblages

The lowest site, Wushan, displayed the largest SEA while the upper site showed the lower values (*Fig. 3*) suggesting the greater niche space in the downstream, which was also supported by higher CR and CD values implying higher trophic diversity in Wushan (*Fig. 4*). This longitudinally increasing tendency, which is also discovered in other impounded river (Kaymak et al., 2018), is much more evident in the flood season (*Fig. 3*) when the water level is relatively low and the discharge varies. It is reported that there are 42 and 35 fish species recorded at downstream and upstream respectively after the impoundment of TGR (Yang et al., 2013). Increased fish species richness in the downstream gives the opportunities for consumers to exploit more food resources and occupy new niches (Roach et al., 2009). Nevertheless, the opposite was the case in the upstream, Wuxi site, where fish community revealed a lack of planktivorous group and preponderance of omnivorous group (*Table S1*) (Ding, 1994). Besides, several fish species, such as *Coreius heterodon*, distributed mainly in the mainstream, was only found in the estuary in this tributary. These fish species could integrate the food carbon source from the mainstream. On the other hand, although the former study has verified that riparian C₃ plants are the main basal food source irrespective of reaches or feeding groups (Deng et al., 2018), the CRs, which are indicative of food source diversity in the backwater area are significantly larger than those in the upper lotic reaches (*Fig. 4*). This is likely explained by the massive backwater area as well as large periodic inundated zone in the downstream that boost diverse fish species assemblage and alternative food resource presence (Deng et al., 2018).

Temporal variation in trophic structure of fish assemblages

Seasonal differences in food web structure were observed at the downstream sites. At Wushan, the slight overlap of the SEA (*Table 2*) suggested that the position of the fish community had change substantially between two periods although the area occupied was similar. This position alternation is attributed to the change in both the base and the vertical structure of the food web influenced during the flood period (*Figs. 2, 4*). A widening of food source (larger CR) in flood season when the water level is low and fluctuant probably results from the carbon subsidies in the estuary from the mainstream where terrestrial C₄ plants is important to fish species (Wang et al., 2014). Therefore, the fish community had significantly higher $\delta^{13}\text{C}$ values in flood season (*Fig. 2*). The increase in trophic length (NR) is also likely attributed to enlarged optional food resource. There is strong evidence that food web length increases with productivity or resource availability (Pimm and Kitching, 1987; Sabo et al., 2009; Takimoto and Post, 2013). Previous reports have confirmed that planktonic algae, of which biomass in the estuary peaked in June and August during the flood season (*Table 1*) (also see Zhu et al., 2013), is an important secondary carbon source in the downstream (Deng et al., 2018). Exploitation of diverse available sources, both abundant from terrestrial and aquatic, as well as tributary and mainstream, leads to a higher trophic diversity (larger CD) and lower trophic redundancy (higher NND) at the lower water level (*Figs. 4, 5*).

In the tail of backwater region (Dachang site), there was a decrease in niche area and trophic diversity during the flood season. In general, an increased range of available food sources during the flood season, e.g. increased input of terrestrial organic matter by surface run-off, leads to a higher consumer trophic diversity and expanded niche sizes (Junk et al., 1989). However, the considerably overlapping in CR between two periods suggested that fishes exploited similar food sources, which could be consolidated by the importance of C₃ plants as the major and consistent carbon source supporting fish species because of the predominance of nutritious riparian C₃ plants in vast periodic inundated area at Dachang (Deng et al., 2018). Consequently, the decrease of niche sizes was associated with the shorter trophic length in the flood season (*Figs. 2, 4*), perhaps as a function of fluctuant water level and discharge resulting in limiting intermediate predators as prey for fish (McHugh et al., 2010). Environmental disturbance such as hydrologic variability can influence food web length in many ecosystems (Post, 2002; Sabo et al., 2009) and some argue that flood disturbance with more unpredictable flow regimes generally reduce food web length in temperate stream systems (Marty et al., 2009; Sabo et al., 2010; McHugh et al., 2010). In flood season, an effect of drastic perturbation on the backwater ecosystem in Daning River derives from dramatically descending water level and stochastic discharges from the upstream (*Fig. 1*). As a result, trophic length at Dachang would be shorten through disturbance-induced change in diet strategies according to relative accessibility of a prey (McHugh et al., 2010; Ruhí et al., 2016). In addition, the flood disturbance could further enhance fish consumers to prefer abundant C₃ plants than diverse food sources resulting in increased trophic redundancy (lower NNR) during the flood season.

The effect of hydrological regulation on the trophic structure

The larger overlap of SEA with the similar trophic metrics between Wushan and Dachang sites during non-flood period (*Table 2*) inferred that trophic structure were becoming more homogenous after the impoundment. This could be explained by expanding backward mixing processes of the whole backwater zone increasing longitudinal connectivity during the higher-water-level period (Ran et al., 2010; Zhao et al., 2015). Due to extended water retention time, it is reported that uniformity of environmental conditions (*Table 1*) (Zhu et al., 2013) and fish community (Yang et al., 2013) among different sections occur in the backwater area when the water level rises.

The hydrological regulation also could adjust response of fish assemblages from different sites to flood. After the water level declines, the significant alternation of fluvial morphology and riverside zone appears in the tail of the backwater zone but seems much less in the estuary area. The depth of water drops remarkably from an average of 33 m to 19 m at Dachang section in the flood period, which would produce a large area of inundated riparian rocky and muddy substrates outcrops and thereby compress overall ecosystem size. However, the estuary area characterized by an incised channel with steep slopes has a mean depth of more than 50 m even at the lowest water level. Accordingly, fish assemblages at Dachang site is likely more susceptible to the unpredictable flow pulse in the flood period considering comparatively smaller water body in the tail of the backwater zone than the estuary area. On the contrary, the vast water storage in the estuarine confluence zone that dampens the effect of unregulated flow pulse but likely subjects to the mixing processes with the mainstream (Ran et al., 2010). Consequently, owing to the constant contribution from C₃ source within this tributary (Deng et al., 2018), the shrinkage of ecosystem size interacting with drastic flow pulse from the upper contribute directly to contraction of the niche size and trophic diversity in Dachang region by reductions in prey diversity (Layman et al., 2007b), that is, preference of more easily accessible resources which are at lower trophic levels (Roach et al., 2009; Ruhí et al., 2016). Nevertheless, the subsidies from the mainstream and autochthonous production due to relatively stable ambient at Wushan site facilitate trophic diversity increase and maintain ecological stability.

Conclusion

Overall, river impoundment have altered the hydrology at locations in the downstream and hence the food web structure throughout the Daning River. The lower sites with larger water storage had broader trophic niches and higher trophic diversity for fish assemblages reside. The temporal variation in trophic structure changed differently according to their distinct habitats. The trophic diversity shift in the estuarine area is caused mainly by availability of basal food sources either from the mainstream or aquatic algae. However, the variation of niche diversity in the end of backwater site results from disturbance on the vertical structure of the fish food web, specifically, disturbance-induced change in diet composition based on changeless food resource

choice because nutritious vegetation contribution prevail within this tributary. The water level control promote disparate response for trophic structure of fish assemblages at different sites to the flood. The descending water level concomitant with unpredictable flow would shrunken the trophic niche size for fish assemblages in the end of backwater where considerable riverine morphology alternation resulted in water body decrease, whereas the stability of trophic size in the estuarine area were due to less perturbation mitigated by immense water body. In addition, the rising water level regulation could homogenize trophic structure along the river. The findings supplement the information of trophic ecology in the impound rivers and have important implications for development plans in this tributary.

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APPENDIX

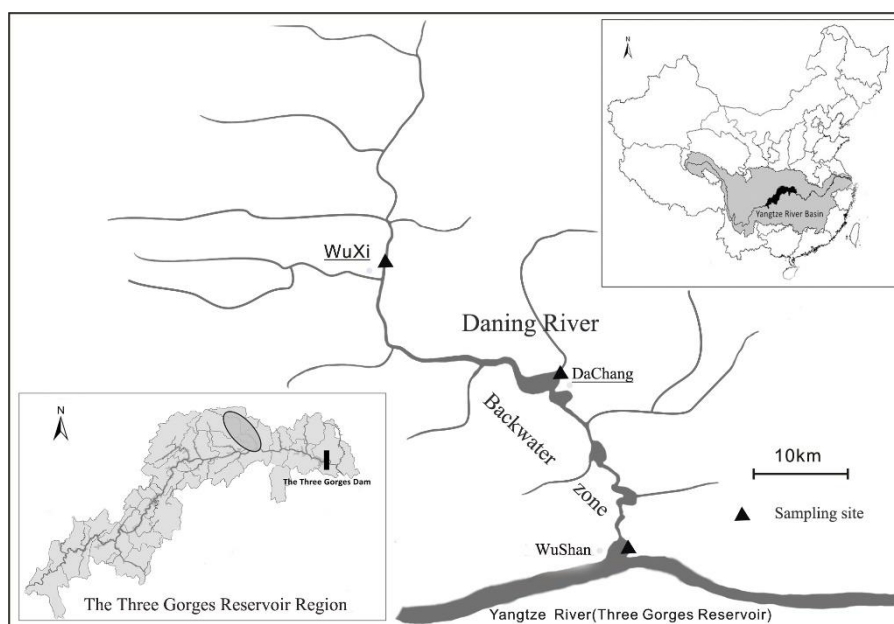


Figure S1. The location of the Daning River and the sampling sites

Table S1. Trophic group, size range and stable isotope composition (mean \pm SD) of fishes collected at each site and period (n = Number of samples analysed)

	Trophic group	Fish species	($\delta^{13}\text{C} \pm \text{SD}$)‰	($\delta^{15}\text{N} \pm \text{SD}$)‰	Size (mm)	n
Non-flood period	Wushan					
	Benthivores	<i>Pelteobagrus nitidus</i>	-23.80 ± 0.06	13.72 ± 0.33	96 - 108	2
		<i>Coreius heterodon</i>	-25.10 ± 0.68	12.83 ± 2.30	122 - 220	3
		<i>Pelteobagrus vachelli</i>	-22.87 ± 1.94	8.61 ± 2.25	130 - 185	2
	Herbivorous	<i>Ctenopharyngodon idella</i>	-22.57 ± 1.44	4.59 ± 0.01	175 - 200	2
		<i>Squaliobarbus curriculus</i>	-22.19 ± 0.51	9.20 ± 1.36	220 - 260	2
		<i>Megalobrama amblycephala</i>	-23.5	5.29	220	1
		<i>Parabramis pekinensis</i>	-23.45 ± 2.21	9.36 ± 0.34	149 - 165	2
	Omnivores	<i>Hemiculter leucisculus</i>	-22.84 ± 0.50	6.99 ± 1.18	115 - 143	2
		<i>Cyprinus carpio</i>	-20.73 ± 2.58	5.91 ± 0.47	97 - 220	3
		<i>Opsariichthys bidens</i>	-22.7	11.72	140	1
		<i>Saurogobio dabryi</i>	-23.82 ± 0.15	13.80 ± 3.29	115 - 117	2
		<i>Pseudobrama simoni</i>	-22.57	8.69	97	1
		<i>Squalidus argentatus</i>	-23.88 ± 1.84	7.97 ± 2.04	98 - 106	2
	Piscivores	<i>Carassius auratus</i>	-20.60 ± 0.49	7.03 ± 0.57	162 - 210	2
		<i>Leiocassis longirostris</i>	-21.89	8.65	112	1
		<i>Culter dabryi dabryi</i>	-22.57 ± 0.56	10.47 ± 0.01	247 - 302	2
		<i>Siniperca kneri</i>	-22.19 ± 1.29	10.77 ± 0.86	165 - 262	2
		<i>Culter alburnus</i>	-23.32	11.78	330	1
		<i>Elopichthys bambusa</i>	-23.41 ± 0.25	10.38 ± 0.48	106 - 242	3
	Planktivores	<i>Neosalanx taihuensis</i>	-27.73 ± 2.84	12.87 ± 1.24		2
		<i>Hypophthalmichthys molitrix</i>	-26.76 ± 1.61	7.93 ± 2.30	148 - 250	4
		<i>Aristichthys nobilis</i>	-24.56 ± 1.08	8.12 ± 2.55	210 - 243	2
	Dachang					
	Benthivores	<i>Pelteobagrus nitidus</i>	-24.33	14.15	106	1
		<i>Pelteobagrus vachelli</i>	-25.21 ± 3.43	9.38 ± 0.13	92 - 220	2
		<i>Silurus asotus</i>	-25.12	11.21	220	1
	Herbivorous	<i>Ctenopharyngodon idella</i>	-21.21 ± 3.58	6.05 ± 0.29	131 - 282	3
		<i>Megalobrama amblycephala</i>	-23.31	5.46	181	1
		<i>Spinibarbus sinensis</i>	-21	6.66	195	1
		<i>Parabramis pekinensis</i>	-24.75 ± 1.10	7.62 ± 0.33	170 - 202	2
	Omnivores	<i>Hemiculter bleekeri</i>	-27.35 ± 0.06	9.06 ± 0.03	95 - 104	2

	Trophic group	Fish species	($\delta^{13}\text{C} \pm \text{SD}$)‰	($\delta^{15}\text{N} \pm \text{SD}$)‰	Size (mm)	n
		<i>Hemiculter leucisculus</i>	-22.66 ± 1.29	8.61 ± 1.23	100 - 182	5
		<i>Cyprinus carpio</i>	-20.07 ± 0.58	9.05 ± 1.39	162 - 182	3
		<i>Opsariichthys bidens</i>	-22.52 ± 0.57	11.17 ± 0.85	110 - 135	2
		<i>Saurogobio dabryi</i>	-27.07 ± 0.80	8.86 ± 2.17	99 - 135	3
		<i>Pseudobrama simoni</i>	-22.47 ± 0.37	8.60 ± 1.00	125 - 150	2
		<i>Acanthorhodeus chankaensis</i>	-18.93	9.21	82	1
		<i>Squalidus argentatus</i>	-23.32 ± 1.04	10.56 ± 0.93	117 - 130	4
		<i>Carassius auratus</i>	-19.34 ± 2.28	7.80 ± 0.22	152 - 205	3
	Piscivores	<i>Leiocassis longirostris</i>	-21.29 ± 0.42	8.90 ± 0.23	195 - 210	2
		<i>Pseudobagrus crassilabris</i>	-24.3	10.18	190	1
		<i>Culter dabryi dabryi</i>	-23.78 ± 0.40	10.63 ± 0.72	230 - 255	3
		<i>Siniperca kneri</i>	-23.91 ± 0.47	11.53 ± 0.82	150 - 210	3
		<i>Culter mongolicus</i>	-23.97 ± 0.75	11.45 ± 2.07	190 - 195	2
		<i>Culter alburnus</i>	-24.59 ± 1.55	10.72 ± 0.52	250 - 320	3
		<i>Elopichthys bambusa</i>	-25.38	12.32	350	1
	Planktivores	<i>Neosalanx taihuensis</i>	-28.57	9.46		1
		<i>Hypophthalmichthys molitrix</i>	-26.86 ± 1.33	6.69 ± 1.48	220 - 263	3
		<i>Aristichthys nobilis</i>	-25.67 ± 2.76	6.56 ± 1.61	165 - 255	4
		<i>Hyporhamphus intermedius</i>	-26.2	9.64	187	1
	Wuxi					
	Benthivores	<i>Rhinogobius cliffordpopei</i>	-23.15 ± 0.03	8.55 ± 0.46	75 - 83	2
		<i>Hemibarbus labeo</i>	-23.78 ± 0.69	6.84 ± 0.14	134 - 202	2
		<i>Paracabitis variegatus</i>	-24.49 ± 0.66	7.25 ± 0.57	92 - 115	4
	Herbivorous	<i>Discogobio yunnanensis</i>	-23.98 ± 1.09	5.10 ± 0.27	98 - 125	4
	Omnivores	<i>Trilophysa bleekeri</i>	-23.51	7.57	80	1
		<i>Onychostoma macrolepis</i>	-23.22 ± 2.06	6.65 ± 0.74	107 - 142	2
		<i>Acrossocheilus monticolus</i>	-21.89 ± 0.47	6.47 ± 0.49	77 - 145	2
		<i>Cyprinus carpio</i>	-23.47	5.26	210	1
		<i>Schizothorax prenanti</i>	-22.51	6.81	150	1
		<i>Saurogobio dabryi</i>	-22.97 ± 0.09	7.73 ± 0.25	145 - 180	3
		<i>Carassius auratus</i>	-23.84	3.93	176	1
	Piscivores	<i>Glyptothorax fukiensis</i>	-24.75 ± 0.58	7.69 ± 0.01	77 - 92	2
		<i>Zacco platypus</i>	-24.16 ± 0.26	7.02 ± 0.63	80 - 135	5
Flood period	Wushan					
	Benthivores	<i>Pelteobagrus nitidus</i>	-24.32	14.45	125	1
		<i>Coreius heterodon</i>	-25.77	17.51	231	1
		<i>Pelteobagrus vachelli</i>	-24.86	11.44	135	1
		<i>Silurus asotus</i>	-24.33 ± 0.42	13.07 ± 2.20	191 - 205	2
	Herbivorous	<i>Ctenopharyngodon idella</i>	-18.65	9.37	251	1
		<i>Squaliobarbus curriculus</i>	-20.25	7.1	244	1
		<i>Spinibarbus sinensis</i>	-20.42	7.92	318	1
		<i>Parabramis pekinensis</i>	-20.36 ± 2.69	7.77 ± 0.75	245 - 250	2
	Omnivores	<i>Hemiculter bleekeri</i>	-19.68	9.97	100	1
		<i>Hemiculter leucisculus</i>	-17.85	7.86	105	1
		<i>Cyprinus carpio</i>	-17.6	6.43	256	1
		<i>Saurogobio dabryi</i>	-23.74 ± 0.18	12.05 ± 0.28	113 - 121	2
		<i>Pseudobrama simoni</i>	-19.52 ± 0.70	8.11 ± 0.14	95 - 100	2
		<i>Squalidus argentatus</i>	-20.66 ± 0.18	11.17 ± 0.16	84 - 103	2
	Piscivores	<i>Culter dabryi dabryi</i>	-18.97 ± 0.41	10.88 ± 0.52	101 - 109	2
		<i>Siniperca kneri</i>	-22.16 ± 0.28	13.66 ± 0.32	225 - 232	2
		<i>Culter mongolicus</i>	-21.87 ± 0.16	12.52 ± 0.68	222 - 251	2
		<i>Culter alburnus</i>	-22.72 ± 0.03	12.49 ± 0.64	223 - 260	2
		<i>Elopichthys bambusa</i>	-22.63 ± 1.27	12.00 ± 0.67	174 - 203	2
	Planktivores	<i>Neosalanx taihuensis</i>	-24.38	14.65	113	1
		<i>Hypophthalmichthys molitrix</i>	-24.28 ± 0.91	8.54 ± 0.21	195 - 629	2
		<i>Aristichthys nobilis</i>	-26.23 ± 0.66	10.39 ± 1.71	227 - 772	2
	Dachang					
	Benthivores	<i>Pelteobagrus vachelli</i>	-23.57 ± 0.63	9.83 ± 0.64	168 - 210	3
		<i>Silurus asotus</i>	-24.75 ± 0.25	10.86 ± 0.79	170 - 181	2
	Herbivorous	<i>Ctenopharyngodon idella</i>	-18.76 ± 3.04	7.62 ± 1.40	190 - 245	2
		<i>Spinibarbus sinensis</i>	-23.52 ± 0.27	8.88 ± 0.57	220 - 269	2
		<i>Parabramis pekinensis</i>	-22.83 ± 0.42	9.81 ± 0.56	234 - 280	2
	Omnivores	<i>Hemiculter bleekeri</i>	-24.88	10.03	105	1
		<i>Hemiculter leucisculus</i>	-25.94	8.77		1
		<i>Cyprinus carpio</i>	-19.32 ± 0.40	8.78	226 - 230	2
		<i>Saurogobio dabryi</i>	-25.93	10.6	135	1
		<i>Pseudobrama simoni</i>	-23.63	7.62	115	1
		<i>Procypris rabaudi</i>	-22.88	8.33	130	1

	Trophic group	Fish species	($\delta^{13}\text{C} \pm \text{SD}$)‰	($\delta^{15}\text{N} \pm \text{SD}$)‰	Size (mm)	n
		<i>Squalidus argentatus</i>	-24.43 \pm 0.06	10.00 \pm 0.39	103 - 133	2
		<i>Rhinogobius giurinus</i>	-23.76	9.89	55	1
		<i>Carassius auratus</i>	-20.37 \pm 0.81	8.88 \pm 0.38	157 - 225	4
	Piscivores	<i>Culter dabryi dabryi</i>	-24.19 \pm 0.12	11.27 \pm 0.29	232 - 270	2
		<i>Siniperca kneri</i>	-23.96 \pm 0.50	12.17 \pm 1.20	178 - 227	3
		<i>Culter mongolicus</i>	-24.75	10.49	347	1
		<i>Culter alburnus</i>	-24.62 \pm 0.34	11.53 \pm 1.42	240 - 490	3
		<i>Elopichthys bambusa</i>	-25.87	10.25	270	1
	Planktivores	<i>Neosalanx taihuensis</i>	-24.27	11.68		1
		<i>Hypophthalmichthys molitrix</i>	-26.23 \pm 0.41	8.04 \pm 1.08	321 - 342	2
		<i>Aristichthys nobilis</i>	-26.32	8.62	312	1
		<i>Hyporhamphus intermedius</i>	-26.03	8.21	176	1
	Wuxi					
	Benthivores	<i>Rhinogobius cliffordpopei</i>	-23.17	9.67	68	1
		<i>Hemibarbus labeo</i>	-23.16 \pm 0.34	7.20 \pm 0.57	125 - 258	2
		<i>Paracopterus variegatus</i>	-23.12	8.47	100	1
	Herbivorous	<i>Discogobio yunnanensis</i>	-23.08	5.92	115	1
		<i>Spinibarbus sinensis</i>	-25.31	2.25	126	1
	Omnivores	<i>Trilophysa bleekeri</i>	-23.58	7.77	78	1
		<i>Onychostoma macrolepis</i>	-21.74	5.98	98	1
		<i>Acrossocheilus monticolus</i>	-23.04	8.50	123	1
		<i>Cyprinus carpio</i>	-22.58	6.93	234	1
		<i>Schizothorax prenanti</i>	-23.02	6.02	78	1
		<i>Saurogobio dabryi</i>	-22.04	8.20	140	1
		<i>Carassius auratus</i>	-24.64	6.88	87	1
	Piscivores	<i>Siniperca kneri</i>	-23.23	10.81	177	1
		<i>Glyptothorax fukiensis</i>	-23.81	7.15	91	1
		<i>Zacco platypus</i>	-24.19	6.48	116	1