Spatial heterogeneity of food web structure in a large shallow eutrophic lake (Lake Taihu, China): implications for eutrophication process and management

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ABSTRACT
The knowledge of food web spatial heterogeneity is important for ecologists and lake managers to understand ecosystem complexity and lake management. Lake Taihu, a large shallow eutrophic lake in China, has two distinct zones: algae- and macrophyte-dominated. In this study, we assessed the spatial heterogeneity of food webs in the two lake zones using stable isotope analysis and isotope mixing model. The basal sources and consumers showed significant differences in $\delta^{13}C$ and $\delta^{15}N$ ratios between the two lake zones, except for the filter-feeding fishes. Overall, more $\delta^{13}C$-depleted and $\delta^{15}N$-enriched ratios were found in the algae- than the macrophyte-dominated zones for basal sources and consumers. Although the consumers in the algae-dominant zone had higher average $\delta^{15}N$ values, the food web of the macrophyte-dominated zone had longer food chain length and more diverse trophic linkages. These spatial differences may have resulted from resource availability and environmental stress of Lake Taihu ecosystem. Factors associated with spatial trophic heterogeneity should be considered for the management and restoration of this shallow eutrophic lake.

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1. Introduction
Food web is the network of feeding interactions and its structure may affect the entire ecosystem functions (Thompson et al. 2012). Numerous researchers have found that complex spatial heterogeneity existed in food web (Scharroba et al. 2016; Hetherington et al. 2017; Kopec et al. 2019). Theoretical analyses and modeling exercises suggest that there are two main factors shape the spatial heterogeneity of food web structure: resource
availability and environmental stress (Anderson and Cabana 2009). Resource availability hypothesis states that the wider carbon range of basal sources may bring more complex pathways for the transfer of matter and energy (Wang and Brose 2018). On the other hand, food chain length would decline with increased stress, due to reduce the energy flow to consumers or alter species compositions (Vander Zanden et al. 1999). These hypothesis explain the spatial heterogeneity formation mechanisms of food web structure, however, the related empirical evidence is still need to be supplemented.

Large shallow lakes have been recognized as one of the most productive ecosystems. They provide different ecosystem services to humans such as maintaining biodiversity, providing water sources and controlling floods (Woodward 2009). Due to variable geomorphological condition, hydrodynamic complexity, and human disturbance of different lake zones or sub-basins, multiple types of stable states often coexist in a single lake (Scheffer and Jeppesen 2007; Janssen et al. 2014). Some lake zones may be dominated by abundant macrophytes with clean water while others may be dominated by dense algae blooms with turbid water (van Nes et al. 2007; Kuiper et al. 2017). These create more complexities in the study of large shallow lakes, especially those related to eutrophication management.

The stable states in shallow lakes provide an unique perspective for exploring the spatial heterogeneity of food web structure. The various basal sources composition and environment stress (e.g., pollutant inputs or water depth) of different stable states within large shallow lakes may affect the formation of corresponding food webs (Hobbs et al. 2014). However, many food web studies of stable states in shallow lakes attempted to explore the overall ecosystem characteristics, and ignored the spatial differences of food web structure (Kong et al. 2017; Lopez Moreira Mazacotte et al. 2018). Indeed, exploring the spatial heterogeneity of the food web could help to explore the trophic structure and energy pathways under multiple stable states in one complex shallow lake ecosystem.

Stable isotope technologies have been used as powerful and complementary tools for understanding the food web structure and energy pathways in aquatic ecosystems (Syvaranta et al. 2011; Wang et al. 2013). Both δ^{13}C and δ^{15}N can reveal the assimilated portion of consumers’ diets at the time of synthesis (France 1995). On the one hand, δ^{13}C changes little when it fractionates through the food chain, so it could be used to identify the food source (Mao et al. 2016). On the other hand, δ^{15}N of the predator increases approximately 2‰–3.5‰ relative to its prey, and is usually used to estimate the trophic positions of species (Cornelissen et al. 2018). Isotope mixing models based on Bayesian procedures can be used to calculate the relative contribution of the multiple potential food sources to consumers (Solomon et al. 2011). Therefore, stable isotope analysis and isotope mixing models provide a possible strategy for quantitatively illustrating the food web structure for a large shallow lake.

In this study, we used stable isotope analysis and an isotope mixing model to evaluate the spatial heterogeneity of the food web structure in a large shallow eutrophic lake, which has two coexisting stable states: the algae- and macrophyte-dominated stable states in two different lake zones. Our main goals were to (1) examine and compare the spatial heterogeneity of carbon and nitrogen stable isotope ratios of basal food sources and consumers; (2) elucidate the food chain length and key trophic links of energy flow through food webs in the two different lake zones. Stable isotope data will help to understand the role of resource availability and environmental stress in shaping food web structure of these two coexisting stable states.
2. Materials and methods

2.1. Study area

Lake Taihu, the third largest freshwater lake in China, is located in the lower reaches of the Yangtze River (Figure 1). It has a surface area of 2,338 km², with a length from north to south of 68.5 km, and a width from east to west of 56 km. The average water depth of the whole lake was 1.9 m, while the average water depth of the eastern bay is 0.9 m (Qin et al. 2004). As a shallow lake, its water volume was approximately $5.15 \times 10^8$ m³ (Qu et al. 2011). Influenced by the subtropical monsoon climate, the annual mean temperature of Lake Taihu varies from 14.9 to 16.2 °C, and its annual average precipitation is between 1,000 and 1,400 mm (Li et al. 2010).

Two distinct lake zones under different eutrophication conditions coexist in Lake Taihu. The northwestern zone is an algae-dominated zone that has been largely affected by industrial and agricultural pollution from its catchment (Xu et al. 2016). Since the late 1980s, this lake zone has been highly eutrophic with frequent algal blooms (Guo 2007). In contrast, the southeastern zone is macrophyte-dominated and located in the outflow area of the whole lake (Qin et al. 2007). Numerous submerged plants are present in this lake zone. The large area of these submerged plants helps clean the aquaculture-related pollution in this zone (Hu et al. 2010). The limnological parameters of these two lake zones are shown in Table 1.

2.2. Sample collection and process

Field sampling was conducted from September 12–16, 2010 from six sampling stations in Taihu Lake (Figure 1). The first three stations (ST1–3) were in the algae-dominated zone, while the other three stations (ST 4–6) were in the macrophyte-dominated zone. We collected samples of basal sources and the most abundant consumers that were broadly representative of the respective biological communities. Suspended particulate organic matter (SPOM), phytoplankton and sediment organic matter (SOM) were considered as common
basal sources in the two lake zones, and submerged plant was added as the fourth basal source in the macrophyte-dominate zone. The consumers in the two lake zones included zooplankton, zoobenthos, shrimp and fish. For zooplankton, rotifer (e.g., Brachionus calyciflorus) and cladocera (e.g., Bosmina longirostris and Moina rectirostris) were found to be the most common groups in the algae-dominated zone, whereas copepoda (e.g., Eucyclops serrulatus and Harpacticoida Sars) was the most common group in the macrophyte-dominated zone. Among zoobenthos, Corbicula fluminea was highly abundant in the algae-dominated zone while Bellamya purificata and Radix swinhoei were dominant species in the macrophyte-dominated zone. For shrimp, Macrobrachium nipponense was the dominant species in both lake zones. Furthermore, four feeding types of fishes were analyzed: herbivorous (only found in the macrophyte-dominated zone), filter-feeding, omnivorous and carnivorous fish. The carnivorous fish in the algae-dominated zone were divided into two groups: small and big. The small carnivorous fish species were mainly composed of Coilia ectenes taihuensis and Protosalanx chinensis and were dominant in the algae-dominate zone.

SPOM was collected by filtering surface lake water through pre-combusted (450 °C for 4 h) Whatman GF/F glass fiber filters with three replicates at each sampling site (Zeng et al. 2007). The Peterson Grab was used to collect sediment from the surface sediment for analysis of the stable isotope ratio of SOM. Phytoplankton was collected using a plankton net (64 μm mesh) and separated from other materials by centrifugation (Hamilton et al. 2005). Submerged plant material was collected along with the sediment, washed and then cold stored.

Zooplankton was collected using plankton nets at the surface water of each station for 10 min with three replicates. Samples were sorted in the laboratory using a stereomicroscope (Vizzini and Mazzola 2006). Zoobenthos were collected from the surface sediment using the Peterson Grab, and the muscle tissues harvested for large species, whereas the whole body was collected by removing the viscera and shells for small species. All zooplankton and zoobenthos samples were kept alive in polythene bottles for 24 h to enable them excrete the gut contents (Rawcliffe et al. 2010). Fish were obtained using a trawl net with a mesh size of 1 mm in the algae-dominated zone, and with traps in the macrophyte-dominated zone because the trawl net cannot be operated normally under dense submerged macrophyte. For large fish species (individual length > 10 cm), a small transverse sample was cut from the dorsal muscle tissue after the fish were dead (Pinnegar and Polunin 1999). For small fish species (individual length < 10 cm), the whole body of several individuals were pooled into one sample after the viscera were removed. Shrimp were collected along with fish, shucked, and the flesh posterior to the heads were excised for analysis.

To reduce disturbance of the inorganic carbon content to δ13C, we used the acidification process (i.e., adding 1 mol/L hydrochloric acid [HCl], dropwise) on SOM samples.
that were rich in carbonates prior to the analysis. Prior to stable isotope analyses, all samples were freeze-dried, powdered, sifted and weighed to the nearest 0.01 mg into tin capsules.

2.3. Stable isotope analysis

Carbon and nitrogen isotope ratios were determined at the Chinese Academy of Forestry Laboratory using isotope ratio mass spectrometry (Finnigan MAT Delta V advantage). The results are expressed in conventional delta (\(\delta\)) notation as parts per thousand (\(^{\circ}/oo\)) defined as follows:

\[
\delta^{13}C \text{ or } \delta^{15}N (^{\circ}/oo) = \left( \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 1000
\]

where \(R\) represents \(^{13}C/^{12}C\) or \(^{15}N/^{14}N\). The PeeDee Belemnite (PDB) was used as the standard for \(^{13}C\), and atmospheric \(N_2\) (AIR) was used as the standard for \(^{15}N\). The analysis precision was within 0.3\(^{\circ}/oo\) for both \(\delta^{13}C\) and \(\delta^{15}N\).

2.4. Statistical analyses

First, \(\delta^{13}C\) and \(\delta^{15}N\) values of the basal sources and consumers were compared between or within the lake zones using an analysis of variance (ANOVA). Data that did not pass the test of variance homogeneity were analyzed using the Mann-Whitney or Kruskal-Wallis non-parametric tests. A statistical significance level of \(\alpha = 0.05\) was used. Then, bio-plots of \(\delta^{13}C\) vs \(\delta^{15}N\) were used to compare the spatial heterogeneity of the food web structure between different lake zones. All statistical analyses were conducted using the software of Origin 8.5 (OriginLab Corporation, Northampton, USA, 2010).

2.5. Food web construction

To construct the food web skeletal structures of the two lake zones, we classified trophic groups by grouping consumers based on similar diets. The common trophic groups in the two lake zones were SPOM, SOM, phytoplankton, zooplankton, shrimp, zoobenthos, filter-feeding fish, omnivorous fish and carnivorous fish. Some specific trophic groups existed in the skeleton food web structures of the two lake zones. For example, the macrophyte-dominated zone had the submerged macrophyte as its specific basal source trophic group and herbivorous fish (i.e., *Ctenopharyngodon idella*), while the algae-dominated zone had the small carnivorous fish (i.e., *Coilia ectenes taihuensis* and *Protosalanx chinensis*) as its unique consumer trophic group. The empirical diet compositions of each trophic group were collected from the gut-content analysis results in Lake Taihu published previously (Institute of Zoology – Chinese Academy of Sciences 1979a, 1979b, 2000; Qi 1998; Ni and Zhu 2005).

We estimate the trophic levels of species and trophic groups according to Post (2002):

\[
\text{Trophic level} = \left[ \frac{\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{base}}}{3.4} \right] + 2
\]

where \(\delta^{15}N_{\text{consumer}}\) is the stable isotope ratio of each species or trophic group, and \(\delta^{15}N_{\text{base}}\) is the baseline organisms (zooplankton in our study), 3.4 is the expected \(\delta^{15}N\) fractionation per trophic level (Post 2002), and 2 is the trophic position of baseline organisms. The maximum trophic level value was considered as the food chain length of each lake zone.
The relative contribution of food sources to diets of the consumers was estimated by using the Stable Isotope Analysis in R (SIAR) package in the R language and environment for statistical computing (Parnell et al. 2008). The SIAR is a Bayesian isotopic mixing model that evaluates the distribution probability of a given consumer’s diet composition. The input data included the stable isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) of each basal source with its stand error, the stable isotope ratio of consumer and the trophic enrichment factors (TEF) value of each source, with the associated standard error. Trophic enrichment values for C were assumed to be $0.4 \pm 1.3_{\text{ppm}}$ for $\delta^{13}C$ and $3.4 \pm 1.0_{\text{ppm}}$ for $\delta^{15}N$ (Post 2002). Mean values of dietary proportions of each species were calculated correspondingly.

3. Results

3.1. Spatial heterogeneity of carbon and nitrogen stable isotope ratios of basal sources

The basal sources in the algae-dominated zone had a relatively narrow $\delta^{13}C$ ratio range, while that of the basal sources in the macrophyte-dominated zone was wider (Table 2 and Figure 2). The Kruskal-Wallis test results revealed that basal sources of these two lake zones showed distinct $\delta^{13}C$ ratios (algae- and macrophyte-dominated zones: $H = 12.865$ and $12.699$, $P = 0.002$ and 0.005, respectively). Therefore, they could act as distinct trophic bases in the following analysis. The $\delta^{13}C$ ratio of basal sources in the algae-dominated zone ranged from $-28.13_{\text{ppm}}$ (SPOM) to $-24.06_{\text{ppm}}$ (phytoplankton), and its variation was $4.07_{\text{ppm}}$. In contrast, the $\delta^{13}C$ ratio of basal sources in the macrophyte-dominated zone ranged from $-24.89_{\text{ppm}}$ (SPOM) to $-15.18_{\text{ppm}}$ (submerged macrophyte), and its variation range reached $9.71_{\text{ppm}}$. There were more depleted $\delta^{13}C$ ratios of basal sources in the algae-dominated zone than there were in the macrophyte-dominated zone. The mean $\delta^{13}C$ ratio of basal sources in the algae-dominated zone was $-25.69_{\text{ppm}}$, which was $-4.86_{\text{ppm}}$ lower than that in the macrophyte-dominated zone was. The ANOVA of SPOM, phytoplankton and SOM showed significant differences in the $\delta^{13}C$ ratios of these three basal sources between the two lake zones (Table 3).

The $\delta^{15}N$ ratios of basal sources in the two lake zones showed opposite distribution patterns compared to those of the $\delta^{13}C$ ratios (Table 2 and Figure 2). The basal sources in the algae-dominated zone had $\delta^{15}N$ ratios between $8.44_{\text{ppm}}$ (SOM) and $12.35_{\text{ppm}}$ (phytoplankton), and the changing magnitude reached $3.91_{\text{ppm}}$. The basal sources in the macrophyte-dominated zone had relatively lower $\delta^{15}N$ ratios than those in the other zone did. Their $\delta^{15}N$ ratios ranged from $5.70_{\text{ppm}}$ (SOM) to $7.77_{\text{ppm}}$ (phytoplankton), and the changing magnitude was $2.07%$. In addition, the basal sources in the algae-dominated zone had more enriched $\delta^{15}N$ ratios than those in the macrophyte-dominated zone. The average $\delta^{15}N$ ratio of basal sources in the algae-dominated zone was $3.37_{\text{ppm}}$ higher than that in the macrophyte-dominated zone. The ANOVA showed that there were significant differences in the $\delta^{15}N$ ratios in basal sources (SPOM, phytoplankton and SOM) between the two lake zones (Table 3).

3.2. Spatial heterogeneity of carbon and nitrogen stable isotope ratios of consumers

The $\delta^{13}C$ ratios of consumers in the algae-dominated zone were narrower than those in the other zone (Table 2 and Figure 2). The $\delta^{13}C$ range of consumers was from $-26.95_{\text{ppm}}$ (Corbicula fluminea) to $-22.40_{\text{ppm}}$ (Mylopharyngodon piceus) in the algae-dominated zone,
but it was from $-26.28\% \text{oo}$ (Hypophthalmichthys molitrix) to $-16.73\% \text{oo}$ (Ctenopharyngodon idella) in the macrophyte-dominated zone. All consumers in the algae-dominated zone had significant lower mean $\delta^{13}\text{C}$ values than those in the macrophyte-dominated zone did except for the filter-feeding fishes (Table 3 and Figure 3). The mean $\delta^{15}\text{N}$ values of consumers in the algae-dominated zone varied from $13.79\% \text{oo}$ (zooplankton) to $19.25\% \text{oo}$ (Channa argus Cantor), and from $8.96\% \text{oo}$ (zooplankton) to $14.83\% \text{oo}$ (Siniperca chuatsi) in the macrophyte-dominated zone. The average $\delta^{15}\text{N}$ values of consumers were significantly higher in the algae-dominated zone than those in the macrophyte-dominated zone (Table 3 and Figure 3). The changing magnitude of the $\delta^{15}\text{N}$ values in consumers was $5.46\% \text{oo}$ and $5.87\% \text{oo}$ in the algae- and macrophyte-dominated zones, respectively.

### 3.3. Spatial heterogeneity of food chain length and key trophic linkages

Although the consumers in the algae-dominant zone had higher average $\delta^{15}\text{N}$ values, the results of trophic level calculations showed the macrophyte-dominated zone was longer food chain length than algae-dominated zone. Using the assumption of $\delta^{15}\text{N}$ fractionation per trophic level of $3.4\% \text{oo}$ and the zooplankton as the baseline trophic level, the maximum trophic level in the algae-dominated zone was Channa argus Cantor with 3.56,
while the maximum trophic level in the macrophyte-dominated zone was *Siniperca chuatsi* with 3.73.

The relative contributions of food sources to consumers’ diets in the two lake zones are presented in Figures 4 and 5. The zooplankton in the macrophyte-dominated zone appeared to depend more on SPOM than on phytoplankton than the algae-dominated zone. The zoobenthos in the algae-dominated zone mainly fed on planktons (mean distribution, 32.29% for phytoplankton and 26.92% for zooplankton), whereas the carbon source from sediment was the major component (mean distribution was 44.99%) for the zoobenthos in the macrophyte-dominated zone. Zooplankton was the largest food source

Figure 2. Bi-plots of mean δ¹³C and δ¹⁵N values of basal sources and consumers in the (a) algae- and (b) macrophyte-dominated zones in Lake Taihu. Trophic level are given on the right y-axis, assuming a 3.4‰ increase in δ¹⁵N per level. Gray diamond: Basal food sources (Phy: Phytoplankton; SM: Submerged macrophyte); downtriangle: Zooplankton; circle: Zoobenthos (Cfl: Corbicula fluminea; Bae: Bellamya aeruginosa; Bpu: Bellamya purificata; Rsw: Radix swinhoei); righttriangle: Shrimp; black square: Fish (1: Hypophthalmichthys molitrix; 2: Aristichthys nobilis; 3: Ctenopharyngodon idella; 4: Carassius auratus; 5: Cyprinus carpio; 6: Mylopharyngodon piceus; 7: Colia ectenes taihuensis; 8: Protosalanx chinensis; 9: Erythroculter ilishaeformis; 10: Pelteobagrus fulvidraco; 11: Parasilurus asotus; 12: Channa argus Cantor; 13: Siniperca chuatsi).
for the shrimps (mean distribution was 32.62%) followed by phytoplankton, SPOM and SOM in the algae-dominated zone. In contrast, SOM became the largest food source for the shrimps (mean distribution, 26.42%) followed by phytoplankton, zooplankton and SPOM in the macrophyte-dominated zone. The filter-feeding fishes (Hypophthalmichthys molitrix and Aristichthys nobilis) in Lake Taihu were artificially stocked and fed other food sources before they were released into the lake, so their diet distributions calculated by SIAR model may reflect previous dietary contributions. Omnivorous fishes had the most diversified food sources in both lake zones. Among the various choices, the submerged macrophyte was an important food source for omnivorous fishes in the macrophyte-dominated zone where its proportion possessed the first place in two species (Carassius auratus, Cyprinus carpio). The omnivorous fish in the algae-dominated zone showed no preference on food source choice. Small carnivorous fish (Coilia ectenes taihuensis and Protosalanx chinensis) was a special trophic group in the algae-dominated zone food web. Mixing model outcomes showed that zooplankton was the most dependent food source for small carnivorous fishes: its contribution exceeded 50% for Coilia ectenes taihuensis.

Table 3. ANOVA results comparing differences of $\delta^{13}$C and $\delta^{15}$N in trophic groups between the algae- and macrophyte-dominated lake zones in Lake Taihu.

| Trophic group | $\delta^{13}$C MS | F | P | $\delta^{15}$N MS | F | P |
|--------------|------------------|---|----|------------------|---|----|
| SPOM         | 3.000            | -2.402 | 0.015$^m$ | 21.924          | 59.537 | 0.000 |
| Phytoplankton| 57.817           | 13.894 | 0.002 | 0.000           | -3.576 | 0.000$^m$ |
| SOM          | 13.394           | 11.744 | 0.006 | 22.583          | 22.184 | 0.001 |
| Zooplankton  | 117.147          | 29.123 | 0.000 | 0.000           | -3.576 | 0.000$^m$ |
| Zoobenthos   | 15.000           | -2.253 | 0.024$^m$ | 142.090         | 318.211 | 0.000 |
| Shrimp       | 26.670           | 20.829 | 0.010 | 52.274          | 406.275 | 0.000 |
| Filter-feeding fish | 5.218 | 3.170 | 0.109 | 88.625          | 32.859 | 0.000 |
| Omnivorous fish | 83.332 | 29.159 | 0.000 | 0.000           | -3.000 | 0.000$^m$ |
| Carnivorous fish | 11.000 | -3.800 | 0.000$^m$ | 0.000           | -4.342 | 0.000$^m$ |

Note: Df = 1, ‘m’ represents the data that did not pass the Levene’s test of homogeneity where the Mann-Whitney non-parametric independent – sample t test were used. Values of ‘Mann-Whitney ‘U’ and ‘Z’ were used to fill those blanks corresponding to ‘MS’ and ‘F’ where ANOVA used, respectively.

Figure 3. Comparisons of mean (±1 S.D.) carbon and nitrogen stable isotope ratios of consumers in the two lake zones (zoo. = zooplankton, zooben. = zoobenthos, Fil fish = filter-feeding fish, Omn fish = omnivorous fish, Carn fish = carnivorous fish).
and *Protosalanx chinensis*. The big carnivorous fish in the two lake zones had relatively equal food source choices. The only exception was *Erythroculter ilishaeformis* in the macrophyte-dominated zone where its diet was dominated by zooplankton (mean distribution was 63.51%).

By analyzing the complex feeding relationships in the skeleton food webs, we identified the related key trophic linkages (the mean relative contribution of each food source to its consumer diet exceeded 50%) of the two food webs (Figure 5). The key trophic linkages in the algae-dominated zone started from phytoplankton to zooplankton, and then to small zooplankton-preferred carnivorous fish (e.g., the *Coilia ectenes taihuensis* and *Protosalanx chinensis*). Moreover, three key trophic linkages existed in the food web of the macrophyte-dominated zone: (1) from SPOM to filter-feeding fish; (2) from phytoplankton to zooplankton, and then to big zooplankton-preferred fish (e.g., *Erythroculter ilishaeformis*); and (3) from submerged macrophyte to herbivorous fish (e.g., *Ctenopharyngodon idella*).

### 4. Discussion

Results based on stable isotope analyses showed large spatial heterogeneity in food web structure between the two stable states lake zones in Lake Taihu. The carbon and nitrogen stable isotopes of most trophic groups reflected significant differences in the two lake zones, and showed the trends of lower δ¹³C ratio and higher δ¹⁵N ratio in the algae-dominated than in the macrophyte-dominated zone. However, the food web in the macrophyte-dominated zone showed longer food chain length and more diverse key trophic linkages for transfer matter and energy. This similar research results can also be found in some shallow lake ecosystems (Rawcliffe et al. 2010; Ziegler et al. 2015; Iglesias et al. 2017), and river ecosystems (Roach 2013; Kaymak et al. 2018; Zheng et al. 2018).
The basal sources in the algae-dominated lake zone showed more narrow carbon range than that in the macrophyte-dominated lake zone. The submerged macrophyte expanded the carbon range of basal source in the macrophyte-dominated lake zone. Increased δ¹³C range of basal sources in food webs would be expected there are more abundant basal resources choice for consumers, and more diverse niche at the basal of food webs (Layman et al. 2007). The δ¹³C ratios of consumers also showed lighter and more concentrated trends in the algae-dominated than in the macrophyte-dominated zone. The narrow carbon range of the basal sources seems to limit the carbon source acquisition scope of consumers, and simplify the pathways for the transfer of energy and matter (Layman et al. 2012). These may have relationships with the shorter food chain length in the algae-dominated lake zone.

Different anthropogenic nutrient inputs around the sub-basins were likely driving the significant spatial δ¹³C and δ¹⁵N baseline differences in food webs of these two lake zones. Lake ecosystems which received more allochthonous loading showed lower δ¹³C and higher

Figure 5. Food webs of (a) algae- and (b) macrophyte-dominated zones in Lake Taihu, based on stable isotope analysis. The line width represents proportional contribution of food source. SPOM = suspended particulate organic matter, PHY = phytoplankton, SOM = sediment organic matter, Zoo = zooplankton, Zoob = zoobenthos, Shr = shrimp, FFF = filter-feeding fish, HerF = herbivorous fish, OmnF = Omnivorous Fish, SZPCF = small carnivorous fishes (total length <10 cm) which prefer to eat zooplankton, BZPCF = big carnivorous fishes (total length >10 cm) which prefer to eat zooplankton, ZPCF = carnivorous fishes which prefer to eat zoobenthos, FPCF = carnivorous fishes which prefer to eat fishes.
The northwest area of Lake Taihu had higher allochthonous loading than the southeast area (Townsend-Small et al. 2007). In addition, the macrophyte-dominated zone is located in the outflow region of the Lake Taihu, while the algae-dominated zone is located in the inflow region where more terrestrial organic matter is received (Ngochera and Bootsma 2011). Excessive nutrient concentrations led to cyanobacteria become the important components of basal sources in algae-dominated zone, which has less negative δ13C ratios than other algae. Previous studies showed that the northwest area of Lake Taihu had more sewage-derived N than the southeast area (Mao et al. 2012, 2014). This may result in basal sources incorporating δ15N enriched NH4⁺, NO3⁻ or both that originated from waste water (Carlisle et al. 2012). Therefore, the high δ15N ratios of basal sources and consumers in the algae-dominated zone may be affected by the inputs of human-related pollutants around this zone. Similar effects can also be found in stream ecosystems (Coat et al. 2009).

Although the δ15N ratios of consumers were significantly higher, the algae-dominated zone did not exhibit a longer food chain than that of the macrophyte-dominated zone. This has relationship with the higher baseline δ15N of the food web in the algae-dominated zone, and the δ15N ratios range among consumers in the macrophyte-dominated zone was larger than that in the algae-dominated zone. A larger range in δ15N ratios generally mean more trophic levels and a greater degree of trophic diversity (Layman et al. 2012). The δ15N ratios of primary consumers are used as indicators of the catchment anthropogenic impact level when compared with reference sites, and could facilitate weighing of the nitrogen stable isotope baseline of the food web (Turschak et al. 2014). Our findings are in agreement with those of previous studies where negative relationships between anthropogenic pollution inputs and food chain length in aquatic ecosystems were reported (Winemiller et al. 2011; Sensula 2015).

The spatial distinction of water depth is also a non-negligible factor that influenced the food web structure in these two contrasting and stable lake zones. As showed in Table 1, the mean water depth was 2.46 ± 0.39 m in the algae-dominated zone, and 1.68 ± 0.38 m in the macrophyte-dominated zone. Larger water depth will result in lower light intensity absorbed and utilized by submerged plants in water body, and make against the germination, growth and distribution of submerged plants (Le Fur et al. 2018; Heidbuchel and Hussnner 2019). Furthermore, water depth also affects the underwater temperature, nutrients and dissolved oxygen (Jager et al. 2008). The difference of physical conditions within Lake Taihu decided the key component of basal source in the algae-dominated zone is algae, not submerged macrophyte. Previous studies have pointed out that the macrophyte-dominated zone also have received large amount of nutrient inputs (Liang et al. 2017). For instance, enclosure culture in East Taihu Bay (the region Site 5 located) reached its peak from 1998 to 2008 (Wang et al. 2019). Although suffered a mass of anthropogenic organic matter inputs, the water quality of East Taihu Bay was better than that of algae-dominated zone (Kong et al. 2018). It seems that the large area of submerged macrophytes and floating-leaf macrophytes play important role in maintain water quality and favorable food web structure.

The stable isotope results indirectly demonstrated that the exchange of organisms between these two lake zones was infrequent. There are few data available on the movement of organisms in the entire Lake Taihu, and most have focused on the movement of algae bloom with special wind-field conditions (Chen et al. 2012). Stable isotope ratios reflect diets integrated over time and space, and could be a useful tool to trace the movement of organisms (Solomon et al. 2015). The carbon and nitrogen stable isotopes of most trophic groups reflected significant differences in the two lake zones, and showed
lower $\delta^{13}$C baseline and higher $\delta^{15}$N baseline in the algae-dominated than in the macrophyte-dominated zone. These results imply that the species in both lake zones might live in relatively stable habits. The only exception was the filter-feeding fishes (*Hypophthalmichthys molitrix* and *Aristichthys nobilis*). These filter-feeding fishes were artificially stocked into the whole lake as a biomanipulation strategy to control cyanobacterial blooms (Li et al. 2017). So their $\delta^{13}$C ratios may be affected by uncertain food sources before they were stocked. Further studies combining stable isotope analysis and electronic tagging may provide more accurate evidence from studying the migratory behaviors of organisms in the whole lake (Carlisle et al. 2012).

The food webs of the two lake zones depended on various food sources with a series of trophic linkages. In considering the spatial heterogeneity, our study provided a more targeted and quantitative food web for the different lake zones of Lake Taihu than previous studies (Mao et al. 2014; Li et al. 2018). In the algae-dominated zone, the small zooplankton-preferring carnivorous fishes appeared to play an important trophic role in the food web. Their proportion in the total catches of Lake Taihu have especially increased remarkably since 1980s (Xu et al. 2015). Considering their abundance and diet, small zooplankton-preferring carnivorous fishes exhibited strong predation pressure on zooplankton, and then had a trophic cascade effect on phytoplankton. The food web in the macrophyte-dominated zone had diverse key trophic links, and relatively dispersed predation pressures. It might be related to abundant food sources contributing to consumers, and consumers then have more choices to balance their diets. Predators need to adjust the diet choices to accommodate the variations of species composition and dominance in different habitats (Baudrot et al. 2016). Because of the spatial heterogeneity of ecological conditions and pollution loads, the food webs of the two studied zones showed distinct characteristics and processes. Spatial complexity of trophic structure seems to be a characteristic of complex ecosystems with heterogeneous environments in aquatic ecosystems (Nelson et al. 2015; Hetherington et al. 2017). Lake managers may consider this spatial heterogeneity of the food web in developing lake protection strategies.

Our results should be interpreted with caution because of the possible limitations of the sampling methods (for instance, we did not catch the small size fish species in the macrophyte-dominated zone due to the big mesh size of traps) or the applied methodology (such as the assumption of the fractionation rate of $\delta^{15}$N ratio). Nevertheless, they provide an empirical evidence for the hypotheses that the food web with higher resources availability and lower environmental stress, has longer food chain length and more complex key trophic linkages for the transfer of matter and energy. Previous studies have reported that these two stable states can be transfer between each other by the oscillations of ecosystem process or external fluctuations (Ibelings et al. 2007; Terborgh et al. 2018). The macrophyte-dominant zone also receives external nutrients due to agricultural practices in this zone (Cai et al. 2012), and this stable state is susceptible and could be easily transformed into the algae-dominated stable state if the water level rises suddenly (Zhao et al. 2012), the water quality decline sharply (Janssen et al. 2017) or some other interruptions. Ecological engineering strategies, such as constructing enclosures or lowering the water level, may facilitate the partial restoration of the algae-dominated stable state to the macrophyte-dominated stable state, or prevent the transformation of the latter to the former (Zhang et al. 2016).

5. Conclusions

The food web of the Lake Taihu had distinct spatial heterogeneity in two contrasting lake zones. Resources availability and environmental stress in the systems may have contributed
to this distinction. This spatially trophic heterogeneity needs to be considered by lake managers in developing strategies for the restoration of this eutrophic shallow lake ecosystem.

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