

Spatial Heterogeneity of Food Webs in A River-Lake Ecotone under Flow Regulation – A Case Study in Northern China

W. Yang^{1*}, X. T. Fu¹, X. X. Li¹, B. S. Cui¹, and X. A. Yin¹

¹ State Key Laboratory of Water Environment Simulation, School of Environment, Beijing Normal University, Beijing 100875, China

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ABSTRACT. The river–lake ecotone supports diverse aquatic life, but its food web structure and topology are poorly understood. Baiyangdian Lake, northern China’s largest shallow lake, depends on external environmental flows, of which the Fu River provides the most stable water supply. Here, we used stable isotopes and topological analysis to explore the food web structure along a spatial gradient using data from field surveys from 2018 to 2019. Carbon and nitrogen stable isotopes and the food web structure were associated with environmental factors for four ecosystem types (river, river mouth, lake mouth, lake). Detritus, phytoplankton, and zooplankton $\delta^{13}\text{C}$ values became more depleted along the gradient from the river to the lake, whereas $\delta^{13}\text{C}$ of submerged macrophytes was enriched in the ecotones compared to the river and lake. Higher $\delta^{15}\text{N}$ values for basal resources and zooplankton occurred at the lake mouth and river mouth. The top consumers were omnivorous fish: *Hemiculter leucisculus* (trophic level [TL] = 3.85 ± 0.89) in the river and *Pseudorasbora parva* (TL = 4.54 ± 0.58) in the river mouth. Carnivorous *Erythroculter dabryi* occupied the highest TL (3.61 ± 0.36 and 4.46 ± 0.36 , respectively) in the lake mouth and lake. These results together led to a change from a detritus-based to phytoplankton-based food web along the gradient from the river to the lake. The species richness, number of trophic links, link density, and mean food chain length all are greatest in the lake, followed by the lake mouth, and the lowest were in the river. Our results provide a holistic view of the ecotone ecosystem and its food web, suggesting that it supports a more diverse species assemblage and more complex food web structure than the adjacent river ecosystem, rather than the adjacent lake ecosystem. Therefore, management should emphasize the combined effects of altered hydrological regimes and poor water quality on the ecotone food webs to manage the river and lake more sustainably.

Keywords: food web, stable isotopes, topology structure, river-lake ecotone, flow regulation

1. Introduction

Ecotones are the transition zones between two adjacent ecosystems and maybe biodiversity hotspots because edge effect (Holland et al., 1991; Jones, 2010; Langhans and Tockner, 2014). Rivers and lakes are naturally and organically linked (Samways and Stewart, 1997; Deng et al., 2018). Since inflowing rivers are an essential lake water source, their abiotic and ecological connections form integrated river-lake systems (Fergus et al., 2017). Among the abiotic connections, those related to the quantity and quality of water are the most important ones (Amezaga et al., 2000). The connections within a river-lake system are essential for key freshwater biogeochemical processes (e.g., exchange of energy and materials) and ecological functions (e.g., migration of organisms, water renewal, aquatic habitat diversity) as well as for the relationships between different systems (Lesack and Marsh, 2010; Mao et al., 2011). The interface where rivers meet lake systems is an ecotone that often receives plentiful organisms and nutrients from upstream riv-

ers (Naiman et al., 1988; Li et al., 2019). These ecotones are characterized by strong hydraulic exchange, which simultaneously intensifies the water purification and the transport of nutrients and sediments; these processes fundamentally control the ecological environment and the ecosystem services provided by adjacent rivers and lakes (Klosowski, 1993; Fraver, 1994; Risser, 1995). Thus, maintaining or restoring these ecotone functions is important to protect the river-lake ecosystem (Wiens, 1992; Jiang et al., 2019). In the river-lake ecotone, gradients exist in water quality, habitat, and biological variables (Huang et al., 2018; Jiang et al., 2019). These gradients tend to produce distinctive ecological communities (Ries et al., 2004) or communities that share certain compositional and structural features with adjacent aquatic systems. These features have been proposed as edge effects. The importance of ecotones as determinants of the biotic composition of ecosystems has been emphasized by researchers and lake managers (Naiman et al., 1988; Samways and Stewart, 1997), yet the systematic evidence is still missing in the ecotones between river and lake ecosystems.

Food webs comprise trophic interactions among organisms ranging from producers to top predators (Pimm, 1982), and represent essential links within communities and ecosystems. Research on food webs describes the key material and energy flow processes within ecological communities (Bukovinszky et al.,

* Corresponding author. Tel.: 86-10-5880-5053.
E-mail address: yangwei@bnu.edu.cn (W. Yang).

2008; Yen et al., 2016), and quantifies the complexity of these ecosystems using topological analysis (Montoya et al., 2006; Wood et al., 2015; Kortsch et al., 2019). Stable isotope analysis provides a powerful tool for clarifying these trophic relationships and the food web complexity (Kling et al., 1992; Vejříková et al., 2017). Stable carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are widely used to reflect the assimilated carbon sources of consumers as well as the trophic position of an organism within a food web (Post, 2002; Zimmer et al., 2020), and their patterns were influenced by biogeochemical processes and environmental factors (Francis et al., 2011). Despite a lack of consensus about the variation of isotope patterns from the river to lake ecosystems, researchers generally agree that variation in abiotic conditions and the availability of resources will be reflected in aquatic organisms along the gradient from a river to a lake. For example, Dalu et al. (2016) found the spatial differences in detritus sources along the river-estuary continuum, which provided potential food sources information for the consumers in different habitats. Samways and Stewart (1997) showed the overlapped communities in the invertebrate along the reservoir-stream gradients. Willis and Magnuson (2000) observed the highest number of fish species in stream-mouth, followed by the stream, lake mouth, and lake. Also, some researchers found that there was clear segregation of the most abundant phytoplankton populations across the ecotone along with a river-lake transitional system (Izaguirre et al., 2001). The studies above focused on a single trophic level in two adjacent ecosystems and their transition zones. Doi et al. (2013) showed small-scale spatial heterogeneity of planktonic food webs along an inflowing river and a lake gradient. However, it is critical to link environmental changes (e.g., dam construction, flow regulation, eutrophication) with multiple trophic level organisms in the community when assessing the spatial structure of the food web, including higher trophic level organisms (Middelburg, 2014; Wirta et al., 2015). Top predators are thought to impact nutrient cycling in aquatic ecosystems (Carpenter et al., 2001), but are typically ignored.

Flow regulation by dams and reservoirs provides many social and economic benefits to most freshwater ecosystems, including irrigation, flood control or hydropower generation, and water extraction for human consumption, industry, and irrigated agriculture. The natural hydrologic conditions of lakes and rivers have been substantially altered by flow regulation (Rolls et al., 2017), and this alteration has reduced the interactions between connected rivers and lakes. It may even disrupt river-lake connectivity, threatening the ecotone areas and endangering their protective function (Poff et al., 2007). The flow regulation also negatively impacts aquatic ecosystems through interference with the natural fluxes of water, sediments, nutrients, and organisms between ecosystems (Topping et al., 2000; Nilsson et al., 2005; Gownaris et al., 2018). This can lead to shrinkage of the ecotones, deterioration of water quality, ecosystem degradation, and rapid declines in biodiversity and ecosystem service functions (Grill et al., 2019; Wang et al., 2020). Environmental flows (Arthington, 2012) are implemented to reinstate the natural flow regime elements. However, species-based flow requirements are commonly concerned with an expectation that

will achieve benefits for whole ecosystems (Rolls et al., 2017). Changes in hydrological regime and environmental factors also alter consumer assemblages, basal carbon sources availability, and their interactions (Power et al., 1996; Yang and Chen, 2013; Rolls et al., 2017). As a result, hydrological processes change and water quality deterioration due to the flow regulation represents a severe and continuing threat to the structure and functioning of the ecosystem. It may disrupt expected patterns of food web variation along the river-lake gradients. The ecotone of the interconnected river-lake systems is intrinsically hydrologically and ecologically variable, and these variations may strongly alter food web structure (Poff and Zimmerman, 2010). Few investigations have described the quantitative understanding of food web structure and topology along the gradient from a river to a lake under flow regulation (Ruhí et al., 2016; Mor et al., 2018; Ru et al., 2020).

In the present research, we studied Baiyangdian Lake, a shallow lake in northern China, and one of its inflow rivers, to reveal the spatial heterogeneity of the food webs along a gradient of four ecosystem types (river, river mouth, lake mouth, lake) in an interconnected river-lake system. The Baiyangdian Lake and its inflow rivers are affected by threats common to lakes and rivers, including insufficient environmental flows and eutrophication (Cui et al., 2010; Mao et al., 2011; Wang et al., 2012; Yang et al., 2014). Recently, managers have enhanced this system's connectivity through a variety of mechanisms, including the removal of dams, adjusting reservoir management to provide more natural flow regimes and environmental flows, and controlling the pollution of inflow rivers, thereby promoting environmental restoration and biodiversity conservation (Stanley and Doyle, 2003; East et al., 2015). In this context, the edge effect function and food web structure of ecotones of the river-lake system is worthy of attention. The objectives of this study were to (i) examine differences in stable carbon and nitrogen isotope ratios of basal resources and consumers along the gradient from the river to the lake, including their ecotones, and (ii) investigate shifts in food web structure and topological properties related to environmental variables along with the river-lake systems. According to the edge effects and studies relating to ecology in ecotones, we expected to see the highest biodiversity and food web complexity in ecotones compared to the river and the lake. Additionally, we expected to see spatial shifts in food web structure with changes in the availability of the primary carbon sources and prey items. The expected food web structure and edge effects of ecotones can be interrupted by flow regulation which affects patterns of consumer diversity and alters basal resource availability and accessibility (Power et al., 1996). Our results will help watershed managers to develop more effective environmental flows and ecosystem restoration management plans for the interconnected river-lake systems.

2. Materials and Methods

2.1. Study Area

Baiyangdian Lake (38°43' to 39°02'N, 115°45' to 116°07'E) is the largest shallow freshwater lake in northern China, covering a total surface area of 366 km² and with an average depth

that ranges from 2 to 5 m (Figure 1). The region is characterized by a temperate continental monsoon climate with an annual average precipitation of 560 mm and evaporation of 1369 mm. Baiyangdian Lake plays an important role in providing native plants and animals habitats, water purification, and biodiversity conservation in this region.

Historically, nine upstream rivers drained into Baiyangdian Lake. However, except for the natural Fu River, the rivers have dried up since the 1960s due to the construction of dams and reservoirs upstream, resulting in a decline in water levels and deterioration of the ecosystem of Baiyangdian lake. The Fu River had the most stable amount of water flowing into Baiyangdian Lake, and was located west of the lake, with a total length of 62 km and an average annual flow of about 1.44 m³/s (Tian et al., 2020). Eutrophication has been considered the major problem of Baiyangdian Lake since the 1980s (Zhao et al., 2011). Fu River is a vital pollution source for the lake, as it flows through Baoding City, a large industrial city with more than 2 million residents. Fu River constantly receives substantial effluents from urban sewage treatment plants (Zhang et al., 2020a, 2020b) and then discharges into the lake, forming a typical consecutive and interconnected river-lake system in the study area.

The government of China has attempted to restore the lake through environmental flows (Yang and Yang, 2014a). There have been 25 emergency water releases between 1997 and 2012, with volumes ranging between 0.12×10^8 and 16.0×10^8 m³ (Yang and Yang, 2014b, 2014c). The CPC Central Committee and the State Council announced the establishment of the Xiongan New Area in 2017. Its concept of “setting the city by water” highlights the importance of the Baiyangdian Lake as the center of the new area. Repeated releases of sufficient ecological water have promoted the recovery of the water level and surface area. Still, they have also changed the hydrology processes and water quality in Baiyangdian Lake from its natural state. These changes have an impact on the structure and function of river-lake ecosystem.

2.2. Sampling Methods and Stable Isotope Analysis

Five field investigations were conducted during July and November 2018 and in April, June, and September 2019 in Baiyangdian Lake, the Fu River, and the two ecotones. Sampling sites were designed to cover the lake (A1 to A13). Three (R1 to R3), nine (E1 to E9), and four (E10 to E13) sampling sites were set up for the Fu River, river mouth, and lake mouth, respectively (Figure 1). We have surveyed all the sampling sites in each season. At each sampling site in each season, water and biological samples were collected in triplicate and mixed into a comprehensive sample.

Simultaneously with the sampling, we measured the water depth (H) and Secchi depth (SD) with a Secchi disc in situ. Water temperature (T_w), dissolved oxygen (DO), and pH were measured on-site using a multiparameter handheld probe (YSI Professional Plus; YSI, Yellow Springs, OH, USA). We collected 2-L water samples 50 cm below the surface in pre-cleaned polyethylene bottles on each sampling date and then transported the

water to the laboratory in an icebox for physicochemical analysis. Total suspended solids (TSS) were measured by gravimetric methods. Total nitrogen (TN), ammonia nitrogen (NH₄), and chemical oxygen demand (COD) were determined using the alkaline potassium persulfate digestion UV spectrophotometric method, the Nessler's reagent spectrophotometry, and the potassium dichromate method, respectively. Total phosphorus (TP) and phosphate (PO₄³⁻) were both measured using ammonium molybdate tetrahydrate spectrophotometry.

We further collected samples of basal resources (i.e., detritus and primary producers such as phytoplankton and submerged macrophytes), zooplankton, zoobenthos, and fish from the four study areas: the river, river mouth, lake mouth, and lake (Figure 1). Sampling and stable isotope analysis methods are described in Text S1.

2.3. Bayesian Stable Isotope Mixing Model

Dietary proportions were estimated to quantify the trophic relationships by applying a Bayesian stable isotope mixing model with version 4.2 of the SIAR package (<https://CRAN.R-project.org/package=siar>) for the R statistical software (Parnell et al., 2010). According to the available literature, all qualitative trophic relationships among species were ecologically reasonable; therefore, we treated that knowledge as a prior, and included concentrations of carbon and nitrogen in the model to improve the results. We applied the commonly used trophic enrichment factors of $0.4 \pm 1.3\%$ (mean \pm SD) for carbon and $3.4 \pm 1.0\%$ for nitrogen in our model, as proposed by Post (2002). For the calculation formula of the trophic level of consumers, see Text S2.

2.4. Topology Properties of Food Web Structure

Food web metrics (Pimm et al., 1991) were calculated by using version 1.0.0.0 of the Network 3D software (Yoon et al., 2004) and version 0.1-636 of the Cheddar package (<https://CRAN.R-project.org/package=cheddar>) implemented in the R statistical software (Hudson et al., 2013). We selected five categories of food web descriptors (species properties, link properties, the proportion of links between different trophic levels, food chain properties, and consumer-prey asymmetries) commonly addressed by topological analysis (Dunne et al., 2002; Neutel et al., 2007). Details of the topological characteristics are presented in Text S3.

2.5. Statistical Analysis

We used one-way ANOVA to test whether there were significant spatial differences if the variables satisfy the assumption of homogeneity of variance; and then if $p < 0.05$, we used least-significant difference (LSD) tests for pairwise comparison of variables between study areas. Kruskal-Wallis H tests were used to test for spatial differences if the variables do not meet the assumption of homogeneity of variance; and then if $p < 0.05$ indicating significant differences among variables, the associated Mann-Whitney U test using Bonferroni correction to adjust p values was implemented for multiple comparisons. Details of the related algorithms of each statistical test are pre-

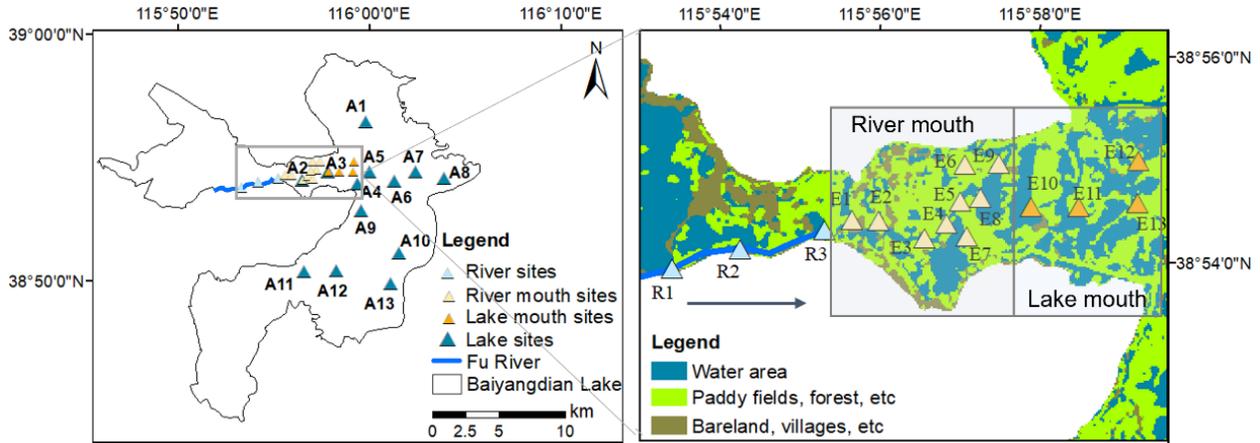


Figure 1. Location of the study areas and sampling sites.

Table 1. Mean and Standard Deviation (Mean ± SD) of The Physical and Chemical Variables Measured at The Four Ecosystem Types

Physicochemical variables	River	River mouth	Lake mouth	Lake
H (m)	1.87 ± 0.89 ^a	2.19 ± 0.40 ^a	2.41 ± 0.74 ^a	2.36 ± 0.70 ^a
T _w (°C)	21.00 ± 8.15 ^a	24.09 ± 5.39 ^a	25.10 ± 5.04 ^a	22.69 ± 6.94 ^a
SD (m)	0.63 ± 0.25 ^b	0.77 ± 0.23 ^b	0.79 ± 0.17 ^{ab}	0.88 ± 0.26 ^a
pH	8.13 ± 0.45 ^a	8.32 ± 0.24 ^a	8.35 ± 0.20 ^a	8.26 ± 0.38 ^a
TSS (mg·L ⁻¹)	15.13 ± 5.10 ^a	6.54 ± 3.42 ^b	6.47 ± 3.49 ^b	7.18 ± 5.19 ^b
DO (mg·L ⁻¹)	5.29 ± 2.44 ^a	8.39 ± 4.60 ^a	8.39 ± 4.15 ^a	6.87 ± 3.19 ^a
TN (mg·L ⁻¹)	5.96 ± 3.13 ^a	2.48 ± 2.15 ^b	2.14 ± 1.17 ^b	2.46 ± 2.00 ^b
TP (mg·L ⁻¹)	0.21 ± 0.21 ^a	0.08 ± 0.11 ^b	0.05 ± 0.03 ^b	0.07 ± 0.09 ^b
NH ₄ (mg·L ⁻¹)	0.82 ± 1.20 ^a	0.36 ± 0.43 ^a	0.45 ± 0.38 ^a	0.43 ± 0.42 ^a
PO ₄ ³⁻ (mg·L ⁻¹)	0.07 ± 0.06 ^a	0.06 ± 0.03 ^a	0.04 ± 0.03 ^a	0.04 ± 0.03 ^a
COD (mg·L ⁻¹)	30.63 ± 16.54 ^a	20.71 ± 10.82 ^a	27.15 ± 25.27 ^a	27.50 ± 16.72 ^a

Note: We labeled variables with no significant differences ($p > 0.05$) among the four ecosystem types with the same lower letter (a). Values of a variable followed by different lowercase letters (a, b) differed significantly between each ecosystem type (ANOVA followed by LSD test or Kruskal-Wallis tests followed by Mann-Whitney test, $p < 0.05$). For each variable, if a group is labeled with the letters a and b, there is no significant difference between it and all other groups labeled with a or b. Abbreviations: H, water depth; T_w, water temperature; SD, Secchi depth; TSS, total suspended solids; DO, dissolved oxygen; TN, total nitrogen; TP, total phosphorus; NH₄, ammonia nitrogen; PO₄³⁻, phosphate; COD, chemical oxygen demand.

sented in Text S4. Statistical analyses were conducted using version 26.0 of the SPSS software (<https://www.ibm.com/analytics/spss-statistics-software>).

3. Results

3.1. Spatial Variations of Physicochemical Characteristics

The values of Secchi depth (SD), total suspended solids (TSS), total nitrogen (TN), and total phosphorus (TP) differed significantly ($p < 0.05$) among the four studied ecosystems (Table 1). SD (0.88 ± 0.26 m) was highest in the lake ecosystem and was significantly higher than in the river or river mouth. The highest TSS concentration (up to 15.13 mg/L) occurred in the river, and was significantly higher than in the river mouth and lake mouth. We discovered excessive nutrient loads in the river-lake system (with mean TN and TP concentrations ranging from 2.14 to 5.96 mg/L and from 0.05 to 0.21 mg/L, respectively). Moreover, the average nutrient concentrations (TN, TP, NH₄, PO₄³⁻) were higher in the river than in downstream

ecotones and lake ecosystems. There were no significant differences among the four ecosystem types in H, T_w, DO, pH, NH₄, PO₄³⁻, and COD ($p > 0.05$).

3.2. Stable Isotope Characterization of Basal Resources and Consumers

3.2.1. Variation of δ¹³C and δ¹⁵N in Basal Resources

The δ¹³C value of detritus and phytoplankton differed significantly ($p < 0.05$) among the four studied ecosystem types (Figure 2, Table S1). There was a more depleted δ¹³C value in detritus and phytoplankton along the gradient from the river to the lake. The mean δ¹³C value for submerged macrophytes was enriched in the two ecotones compared with the river and lake. As basal resources, the submerged macrophytes exhibited much higher δ¹³C values (-24.71 ± 5.89 to -21.09 ± 2.73 ‰) than the detritus (-33.93 ± 2.32 to -27.68 ± 3.43 ‰) and phytoplankton (-29.28 ± 1.71 to -22.95 ± 3.08 ‰) in most cases, except for lower δ¹³C values than phytoplankton in the river. There were significant differences among the four ecosystem types in δ¹⁵N

of detritus, phytoplankton, and submerged macrophytes ($p < 0.05$). $\delta^{15}\text{N}$ of detritus, phytoplankton, and submerged macrophytes were typically between 8.47 ± 3.66 and $16.14 \pm 2.14\text{‰}$, between 6.00 ± 2.97 and $11.98 \pm 2.08\text{‰}$, and between 8.29 ± 5.14 to $15.14 \pm 0.95\text{‰}$, respectively. The highest $\delta^{15}\text{N}$ values for all basal resources occurred in the lake mouth, followed by the river mouth, with the lowest values in the lake.

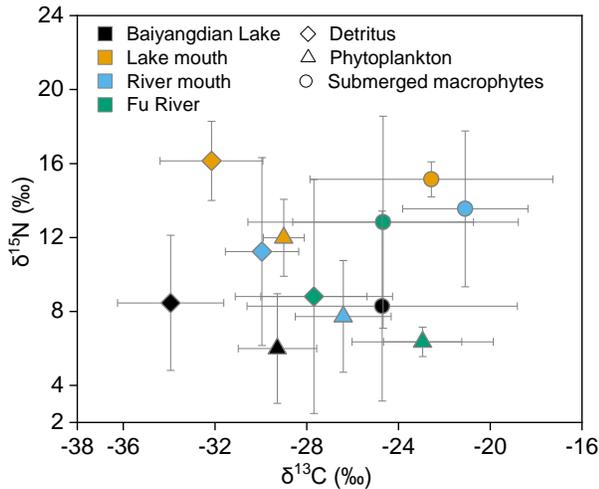


Figure 2. Stable isotope biplots for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (representing means and standard deviations) for basal resources at each site.

3.2.2. Variations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in Consumers

The $\delta^{13}\text{C}$ of zooplankton gradually became depleted along the gradient from the river to the lake, with values decreasing from $-25.16 \pm 2.31\text{‰}$ to $-28.40 \pm 2.60\text{‰}$, whereas $\delta^{15}\text{N}$ was higher in the two ecotones where these waters mixed than in the river and lake (Figure 3). The common functional group of zoobenthos in all four study ecosystem types, including oligochaetes, insects, mollusks, and shrimp, showed a consistent depletion of $\delta^{13}\text{C}$ from the river to the lake mouth, but became enriched in the lake. In comparison, $\delta^{15}\text{N}$ of the oligochaetes and insects were higher in the river mouth and lake mouth than in the river or lake. Shrimp $\delta^{15}\text{N}$ was highest in the river and lowest in the lake, with values of $14.23 \pm 3.58\text{‰}$ and $12.02 \pm 2.93\text{‰}$, respectively.

The $\delta^{13}\text{C}$ values for fish in the lake and lake mouth, *Erythroculter dabryi* had the lowest $\delta^{13}\text{C}$ ($-31.67 \pm 1.68\text{‰}$), whereas *Red crucian carp* had the highest value ($-23.53 \pm 0.11\text{‰}$). The $\delta^{13}\text{C}$ range for fish in the river mouth (-31.50 ± 0.85 to $-28.25 \pm 0.75\text{‰}$) was slightly more negative than in the river (-31.27 ± 0.76 to $-26.73 \pm 1.96\text{‰}$). The widest $\delta^{15}\text{N}$ value range for fish, 8.50‰ (from $11.50 \pm 0.50\text{‰}$ to $20.00 \pm 1.96\text{‰}$), occurred in the river mouth; the narrowest range was in the river, with a range of 5.44‰ . *Macropodus ocellatus*, *Carassius auratus*, *Hemiculter leucisculus*, and *Cyprinus carpio* were the only four fish species present in all ecosystems. $\delta^{13}\text{C}$ of *Macropodus ocellatus* in the river and river mouth was slightly more positive than in the lake and lake mouth. However, *Hemiculter leucisculus* and *Cyprinus carpio* $\delta^{13}\text{C}$ values showed the opposite

pattern. The $\delta^{15}\text{N}$ values of these four common fish were greatly depleted in both the lake and the lake mouth, but relatively enriched in the other ecosystems.

3.3. Trophic Level of Consumers

Based on the $\delta^{15}\text{N}$ values, the trophic levels of most zoobenthos in the four ecosystems were estimated to be between 1 and 3 (Figure 4). Insects occupied slightly higher trophic levels than the oligochaetes and mollusks in all ecosystems. Omnivorous fish occupied the highest trophic level in the river (*Hemiculter leucisculus*, $\text{TL} = 3.85 \pm 0.89$) and river mouth (*Pseudorasbora parva*, $\text{TL} = 4.54 \pm 0.58$) food webs. In contrast, carnivorous fish (*Erythroculter dabryi*) had the highest trophic level in the lake mouth ($\text{TL} = 3.61 \pm 0.36$) and lake ($\text{TL} = 4.46 \pm 0.36$) food webs.

Of the four common fish species (*Macropodus ocellatus*, *Hemiculter leucisculus*, *Carassius auratus*, and *Cyprinus carpio*), *Macropodus ocellatus* and *Hemiculter leucisculus* had the highest trophic levels in the river (2.25 ± 0.15 and 3.84 ± 0.89 , respectively), whereas *Carassius auratus* and *Cyprinus carpio* had the highest trophic levels in the river mouth (3.98 ± 0.24 and 2.63 ± 0.28 , respectively). Three fish species (*Pseudorasbora parva*, *Pelteobagrus fulvidraco*, and *Channa argus*) were present in all areas except the river. The highest trophic levels of *Pseudorasbora parva* and *Pelteobagrus fulvidraco* (4.54 ± 0.58 and 4.47 ± 0.10 , respectively) both appeared in the river mouth. In addition, most of the fish mentioned above had their lowest trophic level in the lake mouth, except for *Channa argus*, whose trophic level increased from the river mouth to the lake.

3.4. Contribution of Food Sources to Consumers

Figure 5 illustrates the relative contributions of the various potential dietary sources to the diets of dominant consumers, which we estimated using the SIAR model. The contribution of detritus to the zooplankton and oligochaetes diets decreased greatly from the river to the lake (from 52.0 to 4.0% and from 53.7 to 23.3%, respectively). However, mollusks functioned primarily as detritivores, and the contribution of detritus to their diet was greater than 50% in all four areas. Planktivorous fish and herbivorous fish were only found in the lake mouth and lake. Planktivorous fish showed a dietary preference for phytoplankton (39.3 to 45.2%) in the lake mouth, but shifted to a zooplankton preference (41.2 to 42.6%) in the lake. Herbivorous fish mostly consumed phytoplankton in the lake mouth and lake.

Of the common fish species, *Macropodus ocellatus* fed mainly on phytoplankton, with its diet increasing from 20.4 to 36.5% from the river to the lake. *Hemiculter leucisculus* had a dietary preference for shrimp and insects in the river and river mouth, but changed to a more even preference for various potential food sources in the lake mouth and lake. Mollusks contributed most (17.63 to 17.95%) to the diet of *Cyprinus carpio* in the river and river mouth, but this changed to phytoplankton (14.87 to 21.80%) and submerged macrophytes (14.40 to 19.88%) in the lake mouth and lake.

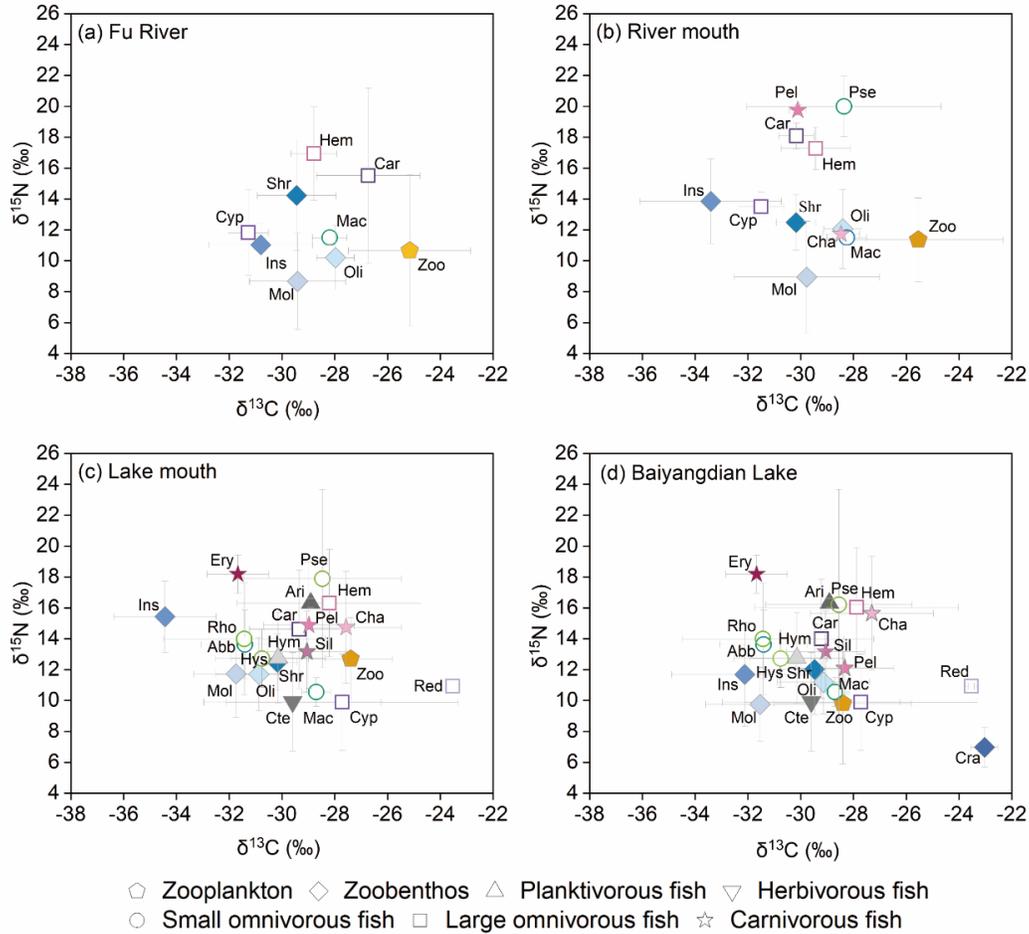


Figure 3. Stable isotope biplots for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (representing means and standard deviations) for consumers at: (a) Fu River, (b) River mouth, (c) Lake mouth, and (d) Baiyangdian Lake. Abbreviations: Abb: *Abbottina rivularis*; Ari: *Aristichthys nobilis*; Car: *Carassius auratus*; Cha: *Channa argus*; Cte: *Ctenopharyngodon idellus*; Cra: Crabs; Ery: *Erythroculter dabryi*; Hem: *Hemiculter leucisculus*; Cyp: *Cyprinus carpio*; Hym: *Hypophthalmichthys molitrix*; Hys: *Hypseleotris swinhonis*; Ins: Insects; Mac: *Macroptodus ocellatus*; Mol: Mollusks; Oli: Oligochaetes; Pel: *Pelteobagrus fulvidraco*; Pse: *Pseudorasbora parva*; Red: *Red crucian carp*; Rho: *Rhodeinae* species; Shr: Shrimp; Sil: *Silurus asotus*; Zoo: Zooplankton.

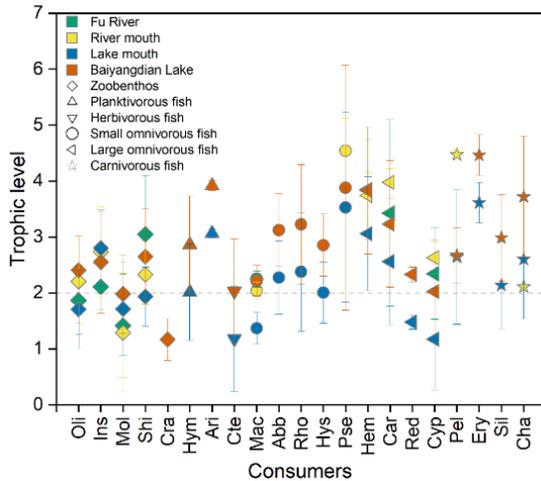


Figure 4. Differences in trophic levels of the consumers in the four study areas. The abbreviations are consistent with Figure 3.

3.5. Food Web Structure and Topological Properties

Detritus was the main nutrient resource in the river and river mouth food webs, accounting for 32.6 and 23.4% of the diet, respectively (Figure S1). However, the contribution of detritus decreased to 17.5 and 19.4% in the lake mouth and lake food webs, respectively. Furthermore, the contribution of phytoplankton increased from 20.6% in the river to 21.9% in the river mouth and then became the main food resource in the lake mouth and lake food webs, with contributions of 24.1 and 22.8%, respectively. Together, these results demonstrate a shift of the food web from detritus-based to phytoplankton-based along the gradient from the river to the lake. In addition, the contributions of submerged macrophytes to the river mouth and lake mouth food webs were lower (6.9 and 5.6%, respectively) than in the river and lake (8.0 and 9.0%, respectively). The topology structure of these food webs is shown in Figure S2.

Figure 6 shows the spatial trends for the main topological properties of the food webs in the four areas. The properties are

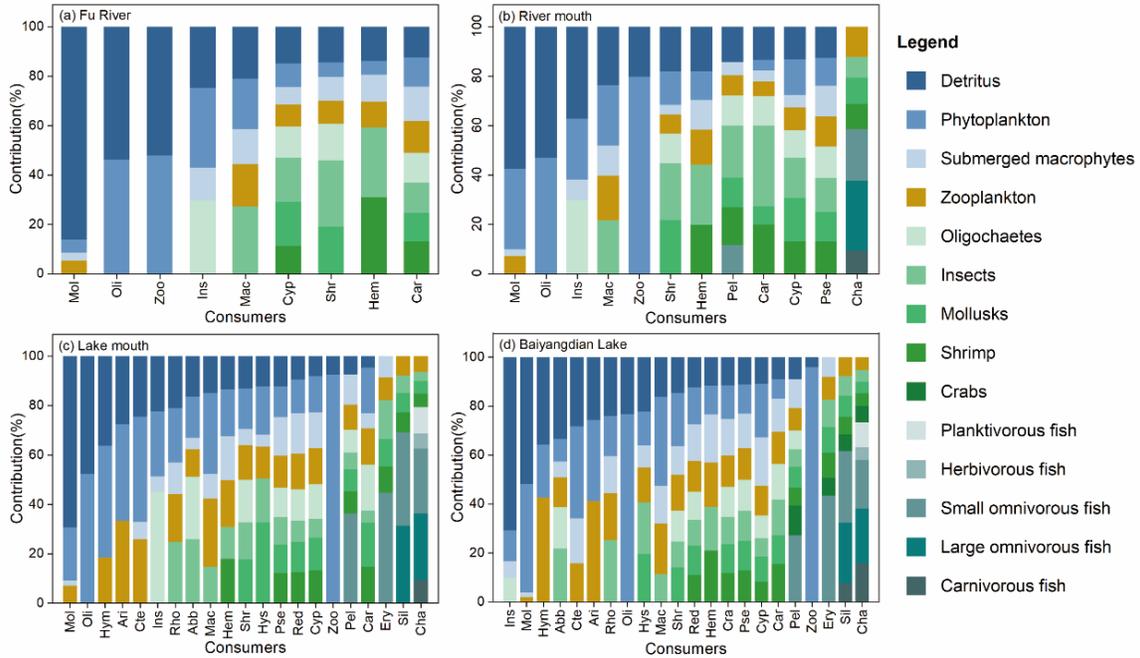


Figure 5. The contributions of the main dietary resources to consumers at: (a) Fu River, (b) River mouth, (c) Lake mouth, and (d) Baiyangdian Lake. The abbreviations are consistent with Figure 3.

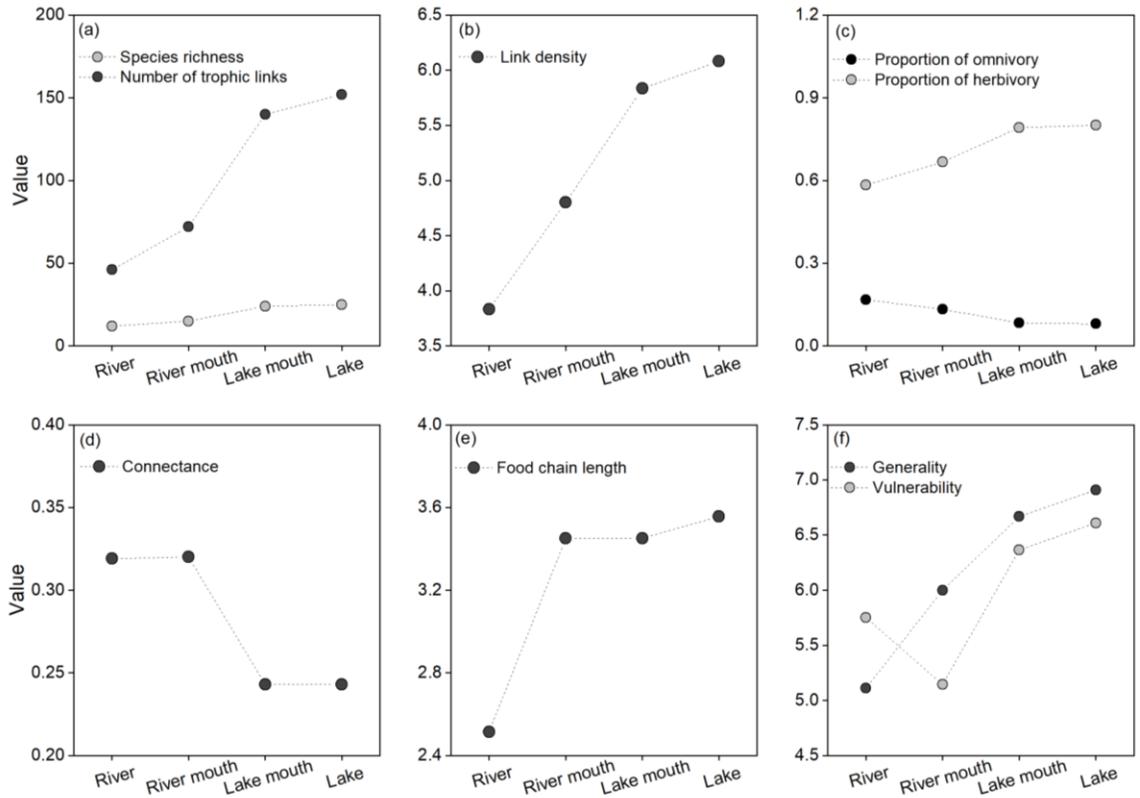


Figure 6. Topological properties of the food web structure in the study areas: (a) Species richness and the number of trophic links, (b) link density, (c) proportion of omnivory and herbivory, (d) connectance, (e) food chain length, and (f) generality and vulnerability.

defined in the supplemental text, and the values of these and other topological properties are summarized in Table S2. The species richness (S) of the food webs increased continuously from the river to the lake, increasing from 12 to 25 species. Some metrics displayed changes that were related to this pattern in species richness, such as the number of trophic links (which increased continuously from 46 to 152), link density (which increased continuously from 3.833 to 6.080), mean food chain length (which increased continuously from 2.514 to 3.556) and proportion of omnivores (which increased continuously from 0.583 to 0.800).

The proportion of basal level species and herbivory showed the opposite pattern from the river to the lake, which decreased continuously from 0.250 to 0.120 and 0.167 to 0.080, respectively. Interestingly, we found higher connectance in the river and river mouth (0.319 and 0.320, respectively) than in the lake mouth and lake (both 0.243). From the perspective of predation links, we found that the proportion of links between the top and intermediate levels was highest (0.326) in the river and lowest in the river mouth (0.139). However, the proportions of links between intermediate and intermediate levels were highest (0.421 to 0.444) in the river mouth, lake mouth, and lake. The vulnerability and generality reached maximum values within the lake with the largest number of species and trophic links. On average, there were 6.609 predator species per prey species (vulnerability, SD = 1.067; Figure 6f) and 6.909 prey species per predator species (generality, SD = 0.734; Figure 6f) in the lake.

4. Discussion

In this study, food webs shifted from detritus-based to phytoplankton-based along the gradient from the river to the lake. Most of the structural complexity metrics indicated that food web complexity in the two ecotones was lower than that in the lake and higher than that in the river. These changes have occurred against a background of partial flow control (managed environmental releases from upstream reservoirs) and increasing pollution discharge into the Fu River. Therefore, management strategies should pay more attention to the combined effect of altered hydrological regimes and deteriorating water quality.

4.1. The Detritus-Based Food Web Shifted to A Phytoplankton-Based Food Web

The transition zone between the Fu River and Baiyangdian Lake is an ecotone, with a steep gradient of physicochemical variables that directly affect the distribution of organisms and with ecological processes that overlap the characteristics of the two water types (river and lake). The TSS was lower, and SD was higher in the two ecotones than in the river. In addition, nutrient concentrations (TN, TP, NH₄, and PO₄³⁻) in the two ecotones and the lake were significantly lower than those in the river, which suggests that the ecotones play a role in water purification, which is consistent with other studies (Huang et al., 2016). Subsequently, it led to variations in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the basal sources in space. Phytoplankton has a fast

turnover rate and is ubiquitous in the river-lake system. Its $\delta^{13}\text{C}$ values have highlighted differences in carbon inputs along the gradient from the river to the lake. The $\delta^{13}\text{C}$ values of phytoplankton in the river mouth and lake mouth also indicate that the river carbon dynamics influence the lower ecotones connected to the lake. Previous studies show that the phytoplankton is more depleted in $\delta^{13}\text{C}$ values than submerged macrophytes (Zimmer et al., 2020), which is consistent with our observations in most ecosystem types. Additionally, ^{13}C enrichment of basal resources and primary consumers in the river and river mouth was reflected in the $\delta^{13}\text{C}$ values of the zoobenthos and small omnivorous fish consumers but not in the large omnivorous and carnivorous fish consumers. The highest $\delta^{15}\text{N}$ values for all basal resources and primary consumers (i.e., zooplankton) occurred in the lake mouth and river mouth. This probably reflects the inflow of ^{15}N -rich nutrients in the ecotone ecosystems through natural and anthropogenic activities (Kanaya et al., 2020).

The ecotone from the river to the lake parallels a riffle-to-pool transition zone, where conditions change from relatively shallow, fast-flowing water to relatively deep, slow-flowing water, representing a transition from a lotic to a more lentic habitat. Willis and Magnuson (2000) emphasized that large-bodied fish, including piscivores, tend to occupy pools, whereas smaller fish occupy shallower, less pool-like habitats. Cyprinids and other small-bodied fish tend to be more abundant in the absence of large piscivores. Similar patterns occurred in our study ecosystems. Four species of piscivores were present in the lake and lake mouth, whereas only two piscivores were found in the river mouth and none in the Fu River. Adjacent aquatic systems and the difficulties of crossing boundaries between systems can strongly influence fish species composition and their trophic position within an ecotone (Wiens et al., 1992; Schlosser, 1995). In our study, both top consumers were omnivorous fish species in the river and river mouth, whereas carnivorous fish occupied the highest trophic level in the lake mouth and lake. The diet of the top predator (*Hemiculter leucisculus*) became more specialized in the river, where it focused on shrimp and insects. However, the top predator (*Pseudorasbora parva*) in the river mouth showed high generalist due to the increased contribution of basal resources and zoobenthos (such as mollusks and oligochaetes) to its diet.

On-going shifts in environmental factors can potentially change the assimilation of available resources in a food web and cause a shift in the nature of the main carbon source that supports the productivity of the food web. The SIAR mixing model showed that detritus in the river contributed strongly to the food web. However, the contribution of detritus decreased, and that of phytoplankton increased in the river mouth, leading to greater contributions of phytoplankton in the lake mouth and lake food webs. Previous studies concluded that suspended inorganic sediment could significantly reduce the primary production of phytoplankton through shear stress, abrasion, and light limitation during periods of high or increasing river discharge (Roach, 2013; Roach et al., 2014). In addition, Hecky and Kilham (1988) found that increased nutrient concentrations are unlikely to positively affect phytoplankton production and

biomass during periods of high flow in temperate zone rivers, because nutrients were consistently above the values required for phytoplankton growth. In addition, water velocity decreases during receding water surface levels or low discharge, and the deposition of inorganic sediment reduces turbidity, resulting in increased primary productivity in shallow habitats (Kirk, 1985; Meade, 1988). Consequently, invertebrates and fish often assimilate large fractions of phytoplankton material after long periods of deposition and reduced turbidity (Bunn and Arthington, 2002; Turner and Edwards, 2012). Moreover, the river continuum concept indicates that allochthonous matter (e.g., leaf litter) is the main energy source in shaded upper reaches of rivers (Dalu et al., 2016), along with inputs from agricultural runoff and sewage discharge, whereas the importance of autochthonous (e.g., phytoplankton) production increases in open and wider lower reaches (Vannote et al., 1980; Bunn et al., 2003). Taken together, the abiotic and biotic changes, which are ultimately controlled by the flow regime, influenced the main basal resources in the food webs along the gradient between the Fu River and Baiyangdian Lake.

4.2. Increasing Complexity of Food Webs from River to Lake

The topological properties (species richness, number of links, mean food chain length, generality, and vulnerability) of a food web reflect horizontal and vertical changes in the food web structure (Mor et al., 2018). Complexity measures for a food web incorporate the species richness, links, connectance, linkage density, and proportion of omnivory (Thompson et al., 2012; Kortsch et al., 2019). In our research, the species richness and food chain length increased along the gradient from the river to the lake. The food chain length results from the community structure, available resources, predator-prey interactions, disturbance, and ecosystem size (Lindeman, 1942; Post and Takimoto, 2007; Jake Vander Zanden and Fetzer, 2007; McHugh et al., 2010). The shift from a detritus-based to a phytoplankton-based food web, which reflects the availability of a higher quality basal resource (e.g., phytoplankton) in the lake mouth and lake, increases the diversity of primary consumers, thereby widening and lengthening the food web (Ruhí et al., 2016; Mor et al., 2018). Moreover, changes in the proportion of omnivory by predators also change the food chain length (Post and Takimoto, 2007; McHugh et al., 2010; Ruhí et al., 2016). Omnivory by top predators can let food webs shift from short to long food chains. This suggests that even if no species colonize part of the aquatic system or become locally extinct due to flow regulation, the food web structure may change via shifts in the dominant energy pathways (Ruhí et al., 2016).

In accounting for the structural differences between food webs, link density and connectance tend to be more important metrics than species richness (Vermaat et al., 2009; Baiser et al., 2012). The increase in link density along the gradient from the river to the lake shows that the species added to the food web in the ecotones and lake were species with relatively many interactions. More specifically, this increase can be linked to an increase in the number of generalized predators or an increase in the breadth of a predator's diet. As a result, the food web

structure changed, showing variations in the mean generality and vulnerability along the gradient. The generality and vulnerability are higher in lake mouth and lake, indicating a reduction in specialization (Chen et al., 2021).

Some research showed more food web components (auto-trophic sources, fish trophic guilds, and prey) and greater complexity within an estuary than in the adjacent river and marine systems (Careddu et al., 2015; Garcia et al., 2019). Despite the marked variability in abiotic conditions that limit the number of species that complete their life cycles within estuaries (Whitfield et al., 2012; Garcia et al., 2019), this transitional system contains diverse fish fauna and prey resources (Elliott et al., 2007; Barletta et al., 2010; de Moura et al., 2012). Nevertheless, we detected asynchronous responses between species richness and connectance of the food web in the lake mouth and lake, which agrees with previous research (Riede et al., 2010). Despite a higher number of species in the lake mouth and lake than in the other areas, these food webs had relatively low connectance, which may be related to increases in species richness and generality, and in the food chain length (Schmid-Araya et al., 2002; Woodward and Hildrew, 2002). Based on these changes, we would expect connectance to decrease if the number of links increases linearly with the number of species (Riede et al., 2010). Ecologically, increasing connectance occurs when the new taxa are prey for many predators (i.e., they increase the breadth of a predator's diet), when the new taxa represent predators for many taxa already present in the food web, or when both phenomena occur, which is the case when generalist predators are added at intermediate trophic levels in an ecotone.

4.3. Management Insights

Polis et al. (1997) emphasized that the structure and dynamics of the food web can be strongly affected by spatial patterns and movements of the locations of ecological processes. For some features of the ecotone between rivers and lakes, such as their hydrology and water quality, the effects of damming are obvious and almost immediate (Hoeinghaus et al., 2008; Cross et al., 2013; Ruhí et al., 2016; Xu et al., 2021). It is vital to pay attention to the function of such ecotones to permit sustainable management of both the river and the lake. Knowledge of the food web structure in ecotones may also be crucial for guiding conservation and restoration strategies. In our case study of Baiyangdian Lake, we found that the ecotones support a more diverse species assemblage and more complex food web structure than the adjacent river ecosystem by the background of flow control, insufficient water, and poor water quality. However, the ecotone did not show the same effect as the adjacent lake ecosystem. For instance, biodiversity in the two ecotones (i.e., species richness, number of links) is greater than that in the Fu River, but lower than that in Baiyangdian Lake. The most complexity metrics for these ecotones were lower than those in the adjacent lake. This suggests a need for improvement from the following perspectives.

The lack of ecological flows that have resulted from flow diversions to meet the human water demand is one crucial problem. To address this issue, environmental flow regulation has received increasing attention (Yang and Yang, 2014b, 2014c),

and approaches for balancing the demand for environmental flows with human water usage have been extensively proposed (Ramos et al., 2018; Xu et al., 2021). To maintain the health of the wetland ecosystem, adequate quantities of water must be transferred from upstream reservoirs and through inter-basin water transfer projects (Liao et al., 2020; Xu et al., 2021). On the other hand, fluctuations in the water level associated with specific aquatic systems (i.e., ecotones) will also affect ecosystem recovery in response to these flows, and management strategies should therefore pay more attention to these features of a system's hydrologic regime (Aharon-Rotman et al., 2017).

Since the 1970s, the water quality in Baiyangdian Lake has continued to deteriorate (Ji et al., 2019; Tao et al., 2020). Meanwhile, the reduction in the natural water purification capacity of the system's wetlands and the increase in anthropogenic pollution discharge have led to widespread eutrophication. Based on previous studies, the ecotones between the Fu River and Baiyangdian Lake have been greatly influenced by municipal wastewater discharge into the Fu River (Zhang and Liu, 2014; Zhang et al., 2020a, 2020b). The significant differences in $\delta^{15}\text{N}$ values of the basal sources among our study ecosystems can be linked to the high concentration of nutrients in the Fu River. Environmental flow management can help to improve water quality through pollutant dilution. Water releases from reservoirs are also effective ways to regulate downstream environmental flows, but the releases should be managed to ensure that water quality and water regime remain adequate for restoring the ecosystem (Liu et al., 2017). Moreover, recent research has shown that combining macrophytes with environmental flow management effectively maintains satisfactory water quality for the relatively polluted lake-marsh systems (Xu et al., 2021). In addition, food web-based flow requirements should be considered in the management plan, and food web structure in ecotones should be accounted for to improve the restoration of river and lake ecosystems. Additionally, the composition of biotic communities and the availability of the resources have great seasonal and inter-annual changes due to variations in hydrological regimes and water quality in the river-lake ecotone ecosystems. Empirical studies on understanding the temporal effects of environmental change on food web structure and topological properties are necessary for greater efforts. In the future, long-term monitoring work for hydrologic, physicochemical, and aquatic community data in the study area will be persistently performed, which is helpful to disclose the seasonal and inter-annual variation patterns in the contributions of the main dietary resources to consumers in the four ecosystem types.

5. Conclusions

In the Fu River-Baiyangdian Lake system, we found that T_w , pH, and DO had higher values, and TSS and COD had lower values in the two ecotones than in the Fu River and Baiyangdian Lake. The nutrient concentrations (TN, TP, NH_4 , and PO_4^{3-}) in the Fu River were substantially higher than those in the two ecotones and the lake. In addition, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the basal resources and consumers showed important differ-

ences among the four areas within the river-lake system. We observed a general tendency toward greater depletion of the $\delta^{13}\text{C}$ of detritus, phytoplankton, and zooplankton along the gradient from the river to the lake, but with enrichment of the mean $\delta^{13}\text{C}$ value for submerged macrophytes in the two ecotones. The highest $\delta^{15}\text{N}$ values for all basal resources and primary consumers (zooplankton) occurred in the two ecotones. The top consumers shifted from omnivorous fish in the river and river mouth to carnivorous fish in the lake mouth and lake. Together, these factors led to a shift from detritus-based food web to a phytoplankton-based food web along the gradient from the river to the lake, and most of the structural complexity metrics indicated that food web complexity in the two ecotones was lower than that in the lake and higher than that in the river. Our results provide fundamental information about the importance of the ecotone system, and suggest that its ecological functions (i.e., edge effect) have been only partially maintained or restored by the environmental flows. Therefore, the system's management strategy should pay more attention to the comprehensive impact of water shortages and deterioration of water quality on the food webs and functions in the ecotones to support more sustainable management and effective restoration of these critical ecosystems in the Baiyangdian Basin.

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