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Temporal changes of the food web structure and function driven by changes in hydrological regimes and water quality in a large shallow lake

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Assessing food web structural properties and energy fluxes under changing hydrological regimes and water quality reveals the temporal patterns of ecosystem dynamics in shallow lakes. Here, we studied northern China's largest shallow lake (Lake Baiyangdian) using quantitative food web models for five representative years (1958, 1980, 1993, 2009, and 2019). We analyzed the temporal patterns of food web structure and function by combining a Bayesian isotope mixing model with a food web energetics model. We further examined the temporal changes of unweighted and weighted food web topological attributes. Lake Baiyangdian changed from a detritus-based into a phytoplankton-based food web based on the relative contributions of basal food sources and energy flux distributions. The trophic position of fingerlings, large omnivorous fish, and carnivorous fish decreased with increasing eutrophication. The highest energy fluxes were from detritus to zooplankton and mollusks in 1958, from detritus and phytoplankton to zooplankton in 1980, 1993, and 2009, and from phytoplankton to zooplankton and detritus to mollusks in 2019. The highest total energy flux was in 1993, followed by 2019, with the lowest value in 1958. Unweighted food web metrics showed similar patterns. We observed more pronounced temporal variability in the node- and link-weighted food web metrics than in the unweighted metrics. In addition, hydrological factors (threshold, duration, reversals between high, and low water levels), eutrophication, and some water quality factors (chemical oxygen demand, dissolved oxygen, and pH) played important roles in the temporal changes of food web dynamics in Lake Baiyangdian. Our findings demonstrate the importance of integrating unweighted and weighted indicators to holistically comprehend how highly aggregated food webs respond to changing hydrological regimes and water quality, thereby improving management and restoration of shallow lake ecosystems.

KEYWORDS

food web structure, ecosystem functioning, energy fluxes, temporal dynamics, hydrological regimes, eutrophication

1 Introduction

Food webs describe the trophic interactions among species or trophic groups in an ecosystem (Lynam et al., 2017; Bartley et al., 2019). Their structures reflect the effects of external disturbance, community history, and resource availability and types, thereby offering insights that can guide ecosystem management and conservation (Thompson et al., 2012; Harvey et al., 2017). However, most temporal food web studies have focused on the differences in before and after scenarios (Yletyinen et al., 2016; Ibarra-García et al., 2020) or on changes in the historical food web structure without accounting for the current state (Kong et al., 2016; Xu et al., 2016). If the management objective is to alter the food web structure to promote the ecosystem's recovery from degradation, it is necessary to study the current food web and how it reached its current state before it is possible to identify effective restoration measures (Ushio et al., 2018; Griffith et al., 2019; Olivier et al., 2019).

In fact, the food web structure is intimately related to ecosystem functioning (Thompson et al., 2012; Hines et al., 2015). Clarifying the relationship between food web structure and ecosystem functioning is a key to understanding and predicting how an ecosystem responds to environmental change (Duffy et al., 2007; Ives et al., 2019). There is a growing interest in analyzing the temporal patterns of food web dynamics as well as linking changes in food web structure to changes in ecosystem functioning (Olivier et al., 2019; Ibarra-García et al., 2020; Kortsch et al., 2021). The energy fluxes can be regarded as a universal currency for ecosystem functioning because they describe the rate of energy flow among species or trophic groups (Barnes et al., 2018; Jochum and Eisenhauer, 2022). The food web energetics approach (Barnes et al., 2018; Gauzens et al., 2019; Jochum and Eisenhauer, 2022) combines food-web theory (Paine, 1980) with metabolic theory (Brown et al., 2004), and thereby provides a powerful tool for assessing energy fluxes. What's more, it permits quantification of critical ecosystem processes by summing all energy fluxes from animals, autotrophs, and detritus to their respective consumers (Kortsch et al., 2021; Li et al., 2021; Jochum and Eisenhauer, 2022).

Topological analyses are useful for summarizing the structural properties of food webs by extracting ecologically meaningful information (Xu et al., 2016). For instance, Dunne et al. (2002) showed that a food web with higher complexity, defined as higher connectance (the proportion of potential links in a food web that are realized), is more robust against species loss. However, most studies of structural properties were based on unweighted food webs (also known as binary- or topology-based food webs), which only contain information about the presence and absence of trophic links between species or trophic groups (Mor et al., 2018; Kortsch et al., 2019; Ru et al., 2020). This approach assumes a static food web, and ignores the temporal variability in trophic interactions, as well as the asymmetry of energy flux distributions, and may therefore overestimate some structural properties (Banašek-Richter et al., 2009; Poisot et al., 2015). Furthermore, most research on unweighted food webs suggests that food web metrics are essentially invariant over long time scales (Olesen et al., 2011; Trøjelsgaard and Olesen, 2016; Olivier et al., 2019). In contrast, weighted food webs offer an opportunity to capture subtle temporal fluctuations in the food web structure and function through changes in species dominance or energy fluxes rather than through changes in species richness and numbers of trophic links (Boit and Gaedke, 2014; Olivier et al., 2019; Kortsch et al., 2021; Jochum and Eisenhauer, 2022). Previous studies demonstrated this difference between food web metrics calculated from unweighted and weighted food web approaches, and although the binary food web structure may appear unchanged, the weighted food web structure and function may have changed considerably, or vice versa (Bersier et al., 2002; Banašek-Richter et al., 2009). In addition, multiple aspects of food web metrics may highlight complementary patterns of temporal variability in food web dynamics associated with different ecosystem processes (Boit and Gaedke, 2014; Olivier et al., 2019; Kortsch et al., 2021). Therefore, to understand how food web structure and function change over time, unweighted metrics (topology-based) and weighted metrics (node-weighted by biomass and link-weighted by energy fluxes) should be combined in food web research because each group of metrics provides different insights.

Understanding the underlying environmental drivers that govern the temporal variability of food web structures and functions is vital to guiding the management and conservation of shallow lake ecosystems (Trøjelsgaard and Olesen, 2016; Danet et al., 2021). Driven by anthropogenic or natural changes such as dam construction and climate change, the hydrological regimes and water quality of shallow lakes are profoundly modified from their natural condition (Marino et al., 2017; Li et al., 2019; Yan et al., 2020). As a consequence, community dynamics and various ecosystem processes have been significantly degraded (Evtimova and Donohue, 2014). In addition to adversely affecting the food web structure and ecosystem functioning, these changes can damage the associated ecosystem services that support humanity (Yang and Yang, 2014a; Evtimova and Donohue, 2016; Jackson et al., 2016; Gu et al., 2019; Zhao et al., 2019; Zhang et al., 2020). For example, Marino et al. (2017) found that the degree of hydrological stability (i.e., the magnitude of the water fluctuations) affects food web structure indirectly through changes in predator–prey interactions. Lake Chaohu has suffered from gradual eutrophication since the 1950s, and the food web has evolved progressively towards a simplified structure (Gu et al., 2011; Kong et al., 2016). Moreover, a given environmental factor may elicit different responses in different metrics of the food web structure and different ecosystem functions. In particular, eutrophication may increase an ecosystem's productivity and energy by stimulating the rapid growth of some basal organisms, such as phytoplankton, but may simultaneously decrease the trophic

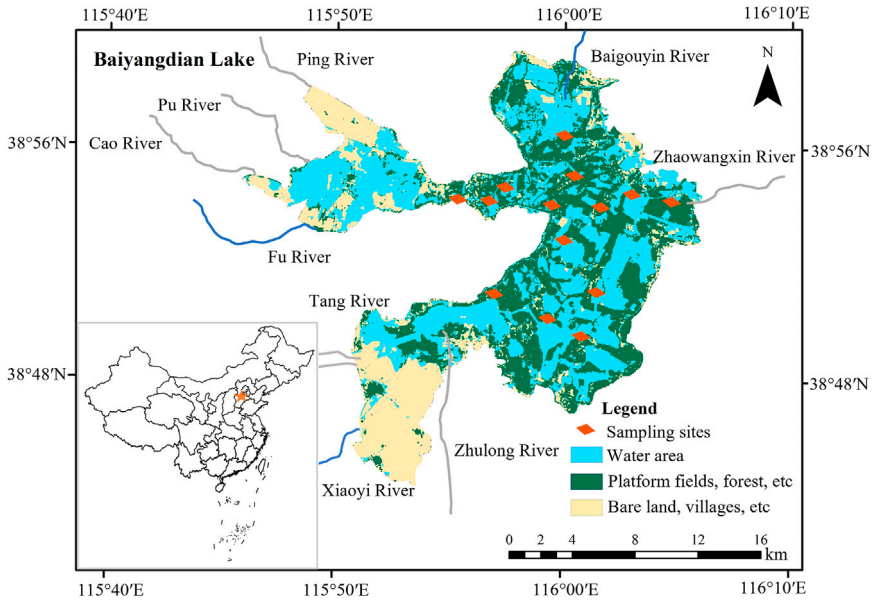

FIGURE 1
The locations of the study area, adjacent rivers, and sampling sites.

position of top predators and the food chain length (Post, 2002a; Xu et al., 2016). Hence, it is necessary to more fully understand how changes in hydrological regimes and water quality could influence food web structure and function (Ives et al., 2019).

In the present research, we selected Lake Baiyangdian, the largest shallow lake in northern China, as a case study. We aimed to 1) describe food web structure and energy fluxes in Lake Baiyangdian between 1958 and 2019 through analyzing some representative years and several sources (historical and novel data); 2) compare unweighted and weighted food web approaches to describe the food web's temporal dynamics using data obtained in Lake Baiyangdian in five representative years; and 3) determine whether the hydrological regimes and some water quality factors can explain the temporal trends of food web dynamics in Lake Baiyangdian. We hypothesized that the weighted food web approach could reveal valuable insights that are not revealed by the traditional unweighted food web approach, and that temporal variation in food web structure and function are related to changes in above mentioned environmental factors.

2 Materials and methods

2.1 Study area

Lake Baiyangdian (38°44′N to 38°59′N, 115°45′E to 116°07′E) is located near the center of Hebei Province. It is the largest freshwater lake in northern China, covering an area of around 366 km^2 at the mean surface level (Figure 1). Moreover, it is the main surface water source for the Xiong'an New Area and plays an important role in maintaining ecosystem functioning and constructing a more ecologically sustainable society. The lake lies in relatively flat terrain, with an elevation range of about 5.2–6.0 m for the lake's bottom. The macrophytes in the lake consist mainly of reeds (*Phragmites australis*). The lake plays a vital role in providing habitat for plant and bird species, protection against floods, water purification, and providing amenities and recreational opportunities for the residents of northern China. The dominant water source is surface runoff from precipitation, which averages 560 mm per year, of which 80% falls between June and September. However, the potential evaporation of 1,369 mm is much higher than precipitation.

Before 1960, Lake Baiyangdian was dominated by natural flows, but since then, dams and reservoirs have been constructed upstream for flood prevention, crop irrigation, and human consumption (Yang and Tian, 2009; Yang and Yang, 2014b; Wang et al., 2021). The resulting hydrological alterations have decreased natural flows into the lake to almost zero, which vastly reduced the water area and water level of the lake (Yang et al., 2006). Moreover, Lake Baiyangdian's watershed experienced severe drought, leading to further shrinkage of the lake, which nearly dried up from 1984 to 1988 (Song et al., 2018). Subsequently, heavy rainfall during a short period contributed to the filling of Lake Baiyangdian in July 1988. To mitigate the stress created by a shortage of water resources, the local government has intervened. From 1997 onwards, water from other sources (e.g., discharges of treated domestic wastewater, transfers from reservoirs in other watersheds) has been used to

TABLE 1 Trophic groups used to construct the food web models of Lake Baiyangdian.

Trophic groups	Taxon code	Species composition
Detritus	Detr	Particles and dissolved organic matter
Submerged macrophytes	SubM	*Ceratophyllum* L., *Charophyceae, Hydrilla verticillata*, *Myriophyllum verticillatum* L., *Najas marina* L., *Potamogeton crispus* L., *Vallisneria natans* (Lour.) Hara
Phytoplankton	Phyt	Chlorophyta, Chrysophyta, Cryptophyta, Cyanobacteria, Diatoms, Dinoflagellates, *Euglena*
Zooplankton	Zoop	Cladocera, Copepods, Protozoa, Rotifers
Meiofauna	MicZ	Chironomids, Oligochaetes
Mollusks	Moll	*Anodonta*, *Bellamya*, *Cipangopaludina*, *Planorbis*, *Radix*, *Semisulcospira*
Herbivorous fish	HerF	*Ctenopharyngodon idella*, *Parabramis pekinensis*
Filter-feeding fish	FilF	*Hypophthalmichthys molitrix*, *Hypophthalmichthys nobilis*
Fingerlings	Fing	*Abbottina rivularis*, *Hemiculter leucisculus*, *Pseudorasbora parva*
Small omnivorous fish	SomF	*Botia xanthi*, *Carassius auratus*, *Pelteobagrus fulvidraco*
Large omnivorous fish	LomF	*Cyprinus carpio*
Carnivorous fish	CarF	*Channa argus*, *Erythroculter ilishaeformis*, *Siniperca chuatsi*

sustain the lake's environmental flows, with more than 50 releases (Yang and Yang, 2014b). Due to the construction of the Xiong'an New Area in 2017 (Yuan et al., 2017), multiple sufficient artificial ecological water replenishments have promoted water level recovery in Lake Baiyangdian. Despite these inflows, the lake has become a semi-closed water body. Currently, the Fu River, Baigouyin River, and Xiaoyi River are the only three rivers that still flow into the lake. The variable frequency, quantity, and quality of the inflows have profoundly altered the hydrological regimes and water quality of Lake Baiyangdian. Consequently, changes have occurred in Lake Baiyangdian's ecosystem. We have built five quantitative food webs for Lake Baiyangdian, representative of 1958, 1980, 1993, 2009, and 2019. The reasons we focus on these 5 years in the present study are that they represent five distinct stages in the development of the lake ecosystem mentioned above, and the historical years correspond to the times when intensive investigations were conducted in Lake Baiyangdian, with relatively abundant data available in the literature.

2.2 Historical data collection

Trophic groups are defined as groups of taxa that share the same or similar predators and prey in a food web. It is widely accepted in food web studies, where it reduces the methodological biases associated with uneven resolution of taxa within and among food webs (Williams Richard and Martinez, 2000; Dunne et al., 2002; Li et al., 2021). Based on previous studies of the lake's food web structure (Yang, 2011; Zhang et al., 2022), the food web comprises 12 trophic groups (Table 1). We obtained historical biomass data for living trophic groups from the unpublished investigation reports of the Institute of Zoology of the Chinese Academy of Sciences (1958), the Department of Biology of Hebei University (1975), the Hebei Fisheries School (1980), and the Environmental Science Research Institute of Baoding (1993). We also referred to the research literature to supplement the historical biomass data in 1958, 1980, and 1993 (Jin, 1995; Yang et al., 2010; Zhang et al., 2022). We obtained biomass data for 2009 from four field surveys carried out from August 2009 to July 2010 by our research group and the published articles (Yang, 2011; Yang et al., 2014). Supplementary Table S1 shows the biomass of each trophic group in the first four representative historical years. We defined the theoretically possible feeding links among the 12 trophic groups from published information, qualitative records, and stable isotope analysis performed for consumers (Xu et al., 2016; Laigle et al., 2018; Olivier et al., 2019). The dietary preferences of consumer trophic groups in historical representative years (i.e., 1958, 1980, 1993, and 2009) were gathered from the gut content analysis in published reports and studies (Yang, 2011; Yang et al., 2014) of Lake Baiyangdian by our research group, and also referred to other relevant studies on Lake Baiyangdian (Ma et al., 2011; Zhang et al., 2022). In addition, daily water level data from 1958 to 2019 were derived by the Water Conservancy Office of Baoding City, Hebei Province. Water quality data for four historical years (i.e., 1958, 1980, 1993, and 2009) were provided by the Baoding Environmental Monitoring Center and Municipal Environmental Protection Bureau. Seasonal variations (i.e., spring, summer, and autumn) were considered, and we collected 6 samples of water quality data for each study year.

2.3 Sample collection

We performed field investigations in July and November 2018 and April 2019 (hereafter, "2019"). To improve the

comparability of the measured data and the historical dataset, we chose the same sampling sites used in the historical reports (Figure 1). We obtained 6 water samples to quantify the water quality in 2019. Each sample consisted of 14 subsamples that were collected within 14 sampling sites. We also sampled the detritus, phytoplankton, submerged macrophytes, zooplankton, meiofauna, mollusks, and fish in each sampling site during the surveys.

2.3.1 Water sampling

We measured the water temperature (*Tw*), dissolved oxygen content (*DO*), and pH in the field using a multiparameter handheld probe (YSI Professional Plus; YSI, Yellow Springs, OH, United States). In addition, we collected 2-L water samples from the surface to a depth of 0.5 m below the surface on each sampling date, and stored the samples on ice until analysis. We measured other parameters including total phosphorus (*TP*), soluble reactive phosphorus (SRP), ammonium (NH_4^+), total nitrogen (*TN*), nitrite-nitrate (NO^{2-}+NO^{3-}), and chemical oxygen demand (*COD*) according to standard protocols (CBEP, 2002).

2.3.2 Biological sampling

We collected samples of detritus, phytoplankton, submerged macrophytes, zooplankton, meiofauna, mollusks, and fish on the same dates and locations used for the water sampling. Water samples of detritus (1 L), phytoplankton (5 L), and zooplankton (10 L) were collected from the surface water (to a depth of 0.5 m) with a Plexiglass water collector. Subsequently, we pre-filtered the phytoplankton and zooplankton samples by passing the samples through 200-mesh and 125-mesh plankton nets, respectively, and then concentrated them into 50 ml. To obtain samples for stable isotope analysis of the detritus, phytoplankton, and zooplankton, we passed the concentrated samples through pre-combusted (450°C for 6 h) and pre-weighed Whatman GF/F filters (glass microfiber filters; 0.45-μm pore size) under a moderate vacuum using a standard filtration system.

We collected green leaves of the submerged macrophytes by hand and washed them with distilled water to remove epiphytes. For the meiofauna and mollusk samples, we used a Van Veen grab with a mouth area of 1/16 m^2, whose contents we washed through a 35-mesh filter to extract the meiofauna and mollusks and preserved the organisms in 75% ethanol. We used the whole body of the meiofauna and the muscle tissue of the mollusks for the stable isotope determination.

For the fish community, we used a multi-mesh gillnet with mesh sizes ranging from 5 to 55 mm and an overall size of 1.5 × 30 m (Mao et al., 2014), which we installed beside a ground cage. The ground cage had a mesh size of 5 mm and was 25 m long, and was partitioned into 20 sections with 10-cm openings at the front and at the back for fish to enter the trap. All fish sampling started in the late afternoon (approx. 18:00 h) and ended the following morning (approx. 06:00 h), for a total of 12 h. The duration was chosen to limit the number of fish caught per net (Prchalová et al., 2011). For each species, we chose three representative specimens, and used their muscle tissue for the stable isotope analysis. All samples were oven-dried at 60°C to a constant weight and then stored individually in a dry and ventilated place. The biomasses of trophic groups in 2019 are shown in Supplementary Table S1.

2.4 Stable isotope analysis and bayesian isotope mixing model

The stable isotope samples were crushed to a fine homogeneous powder using a ball mill. Subsamples were then pressed into ultra-pure tin capsules and analyzed using an Elementar Vario Micro-Cube elemental analyzer (Flash EA1112; Thermo Scientific, Monza, Italy) coupled with a continuous-flow isotope-ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Dreieich, Germany) (Careddu et al., 2015; Hansen et al., 2018). The elemental analyzer and spectrometer were recalibrated after every 10 measurements following the manufacturer's directions. The obtained carbon (C) and nitrogen (N) stable isotope ratios (^{13}C:^{12}C and ^{15}N:^{14}N) were expressed in δ units (deviations in ‰ from Vienna Pee Dee Belemnite (VPDB) for C and atmospheric N_2 for N) according to the following equations:

$$\delta^{15}N = \left(\frac{\left(^{15}N/^{14}N_{sample}\right)}{\left(^{15}N/^{14}N_{atmosphere}\right)} - 1\right) \times 1000 \quad (1)$$

$$\delta^{13}C = \left(\frac{\left(^{13}C/^{12}C_{sample}\right)}{\left(^{13}C/^{12}C_{VPDB}\right)} - 1\right) \times 1000 \quad (2)$$

All samples were analyzed twice. Measurement errors were typically smaller than ±0.1‰ for both $\delta^{13}C$ and $\delta^{15}N$. The values (mean ± SD) of $\delta^{13}C$ and $\delta^{15}N$ of the 2019 samples are listed in Supplementary Table S2.

To elucidate the contributions of the different potential food sources to consumer trophic groups in Lake Baiyangdian in 2019, we used the Stable Isotope Analysis in R (SIAR) model (Parnell et al., 2008) with version 4.1.2 of the R software (www.r-project.org). The SIAR model is based on a Bayesian method and is fitted using a standard Markov-chain Monte Carlo method with Metropolis–Hastings steps, and we used it to generate plausible simulations and estimate the source proportions using a Dirichlet prior distribution (Parnell et al., 2010). All the potential sources for each consumer trophic group were included in the Bayesian mixing model calculations. We applied trophic enrichment factors of 0.4 ± 1.3‰ (mean ± SD) for carbon and 3.4 ± 1.0‰ for nitrogen in our model (Post, 2002b). The SIAR model performed a total of 500 000 iterations, with the first 50 000 used as the burn-in period. The output of the model was a density distribution function for plausible values of the dietary

composition in terms of the proportion of the total diet accounted for by each diet item (Parnell et al., 2010). We considered a feeding link to be effective only if the lower limit of the 50% confidence interval for the contribution of each food source to a given consumer diet exceeded 5% (Careddu et al., 2015; Bentivoglio et al., 2016). On this basis, we compared the relative contribution of food sources to the food web in 2019 and the other four representative historical years.

We calculated the trophic position of the consumer trophic groups based on their dietary preferences. Producers and detritus were defined as trophic position 1, and the consumer trophic position was weighted based on the dietary preference:

$$TP_j = 1 + \sum_{i=1}^{s} TP_{ij} P_{ij} \quad (3)$$

where TP_j is the trophic position of trophic group j; TP_{ij} is the trophic position of the food source i of trophic group j; and P_{ij} is the relative proportion of food source i in the diet of trophic group j.

2.5 Energy fluxes among trophic groups

We calculated the energy fluxes among the trophic groups in Lake Baiyangdian's food web for each study year, with the trophic links assigned using the food web energetics approach (Barnes et al., 2018; Gauzens et al., 2019). This approach estimates how much energy flux is needed to maintain the survival of the present community. Assuming a steady-state for the ecosystem, the model calculates energy fluxes in a top-down manner; that is, all energetic losses of each trophic group (estimated based on consumption of a resource by organisms at higher trophic levels and metabolic losses) are balanced by energetic gains after accounting for the assimilation efficiency. In other words, this means first calculating the energy flux at the top trophic level, where predation losses equal zero, then calculating the energy flux at lower trophic levels based on the losses to consumers at higher trophic levels, and iterating this process until the lowest trophic level is reached.

We defined food source preferences based on the collected quantitative diet data for the historical representative years (i.e., 1958, 1980, 1993, and 2009) and the outputs of the SIAR model for 2019. To account for differences in food source quality, we defined the assimilation efficiencies for each food source type: 0.906 for animals, 0.545 for plants, and 0.158 for detritus (Lang et al., 2017; Gauzens et al., 2019). Body mass estimates for each trophic group are specific to Lake Baiyangdian and derived from local biomonitoring data in 2019. The output is a metric of the total energy fluxes through the food web, as well as a matrix of energy fluxes for the trophic links among trophic groups (Kortsch et al., 2021). Energy flux calculations were performed using version 0.2.0 of the *fluxweb* package (https://cran.r-project.org/web/packages/fluxweb/index.html) for the R software.

2.6 Food web metrics

To characterize the temporal patterns of Lake Baiyangdian's food web structure, we selected three common unweighted, topology-based metrics: connectance (C), generality (G), and vulnerability (V). We also selected six weighted metrics: the node-weighted connectance (nwC), generality (nwG), and vulnerability (nwV), and the link-weighted connectance (lwC), generality (lwG), and vulnerability (lwV). These metrics describe the complexity and horizontal dimensions of the food webs. The calculation of unweighted metrics only considered species occurrences. Connectance ($C = L/S^2$, with L and S being the number of links and nodes, respectively) represents the number of links that exist divided by the total number of possible trophic links (Dunne et al., 2002). The generality and vulnerability properties represent the mean number of food sources per consumer and the mean number of consumers per food source, respectively (Schoener, 1989; Kortsch et al., 2015). As in the unweighted food web metrics, the node- and link-weighted metrics capture changes in the biomass and energy flux distribution among the trophic groups (Bersier et al., 2002; Olivier et al., 2019; Kortsch et al., 2021).

We also used the energy fluxes among the trophic groups to quantify ecosystem functioning. We considered six ecosystem functioning metrics (i.e., detritivory, phytoplanktivory, herbivory, zooplanktivory, benthivory, and piscivory) that were calculated as the sum of energy fluxes from detritus, phytoplankton, submerged macrophytes, zooplankton, benthos, and fish for their consumers. Here, we present each ecosystem functioning metric as a percentage of the total energy flux to the food web in each study year.

2.7 Statistical analysis

We conducted statistical analyses using version 26.0 of the SPSS software (https://www.ibm.com/analytics/spss-statistics-software). We used one-way ANOVA to identify significant temporal differences if the water quality variables satisfied the assumption of homogeneity of variance; if the result was significant at $p < 0.05$, we used least-significant difference (*LSD*) tests for pairwise comparison of variables between study years. We used Kruskal–Wallis tests to test for temporal differences if the water quality variables did not meet the assumption of homogeneity of variance; if the result was significant at $p < 0.05$, indicating significant differences among variables, we used the Mann–Whitney U test with Bonferroni's correction to adjust the p values for multiple comparisons.

We used the indicators of hydrologic alteration (IHA) method (Richter et al., 1996) to calculate the values of hydrological regime factors in each study year. Then, we performed a principal component analysis (PCA) on the hydrological indicators and water quality factors to investigate

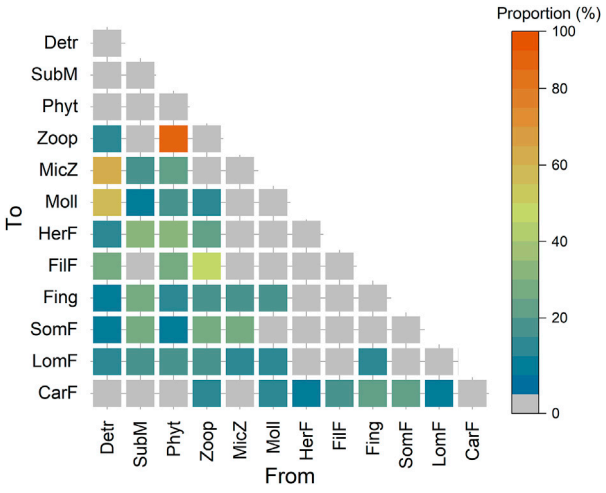

FIGURE 2
The relative contributions of the food sources to consumers in 2019. Data for the other four representative historical years are presented in Supplementary Figure S1. Abbreviations of trophic groups: CarF, carnivorous fish; Detr, detritus; FilF, filter-feeding fish; Fing, fingerlings; HerF, herbivorous fish; LomF, large omnivorous fish; MicZ, meiofauna; Moll, mollusks; Phyt, phytoplankton; SomF, small omnivorous fish; SubM, submerged macrophytes; Zoop, zooplankton.

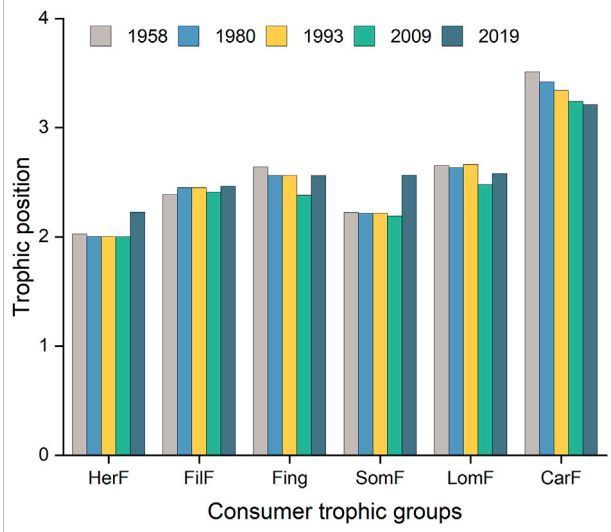

FIGURE 3
Temporal changes in the trophic positions of the six fish consumer trophic groups: CarF, carnivorous fish; FilF, filter-feeding fish; Fing, fingerlings; HerF, herbivorous fish; LomF, large omnivorous fish; SomF, small omnivorous fish.

their temporal dynamics using SPSS. We performed partial least-squares regression (PLSR) with SPSS and the *pls* package for the R software (https://cran.r-project.org/web/packages/pls/index.html) to determine the relationship between environmental factors and food web metrics. In addition, we used the variable importance in projection (*VIP*) and regression coefficient (*RC*) values from PLSR to finely screen the most important environmental factors according to their explanatory power. In our study, we considered hydrological and water quality factors with $VIP \geq 1$ to be important to the food web structure, whereas those with $VIP < 1$ were of minor importance (Wold, 1995; Onderka et al., 2012; Zhao et al., 2020).

3 Results

3.1 Quantitative food webs in lake baiyangdian

Figure 2 illustrates the relative contributions of the various potential food sources to the diets of consumers in 2019, which we estimated using the SIAR model. We found that the zooplankton diet was composed of detritus and phytoplankton in all study years (Figure 2, Supplementary Figure S1), but phytoplankton replaced detritus as the dominant food source in 2019 (Figure 2). Meiofauna and mollusks both functioned primarily as detritivores (75.7% ± 7.7% and 63.8% ± 3.0%, respectively) in all study years. The contribution of submerged macrophytes to the diet of herbivorous fish was greater than 95% until 2019, when ingested phytoplankton (32.3%) and zooplankton (22.8%) also became significant components. Filter-feeding fish mostly consumed phytoplankton and zooplankton in all study years. Fingerlings showed a dietary preference for zooplankton (39.2% ± 1.1%) in 1958, 1980, and 1993, but shifted to a phytoplankton preference (30.7%) in 2009 and a submerged macrophytes preference (27.9%) in 2019. Small omnivorous fish initially fed mainly on submerged macrophytes, but the proportion decreased from 57.4% in 1958 to 28.5% in 2019. Large omnivorous fish had a dietary preference for mollusks in the first four historical representative years but changed to a more even preference for diverse food sources in 2019. Fingerlings and small omnivorous fish comprised a major contribution to the diet of carnivorous fish during the first 4 years, accounting for 36.1% ± 1.9% and 25.6% ± 7.08% of the total, respectively; however, in 2019, the proportions of fingerlings, small omnivorous fish, and filter-feeding fish were 21.4, 20.6, and 18.6%, respectively.

We observed large interannual variations in the relative contributions of basal food sources to the food web (Supplementary Figure S2). For the first 4 years, detritus and submerged macrophytes were the main food sources in the food webs, accounting for averages of 30.1 and 22.1% of the total, respectively. However, the contributions of detritus and submerged macrophytes decreased to 21.4 and 15.2% in 2019, respectively. Furthermore, the contribution of phytoplankton increased from an average of 15.7% in the first three study

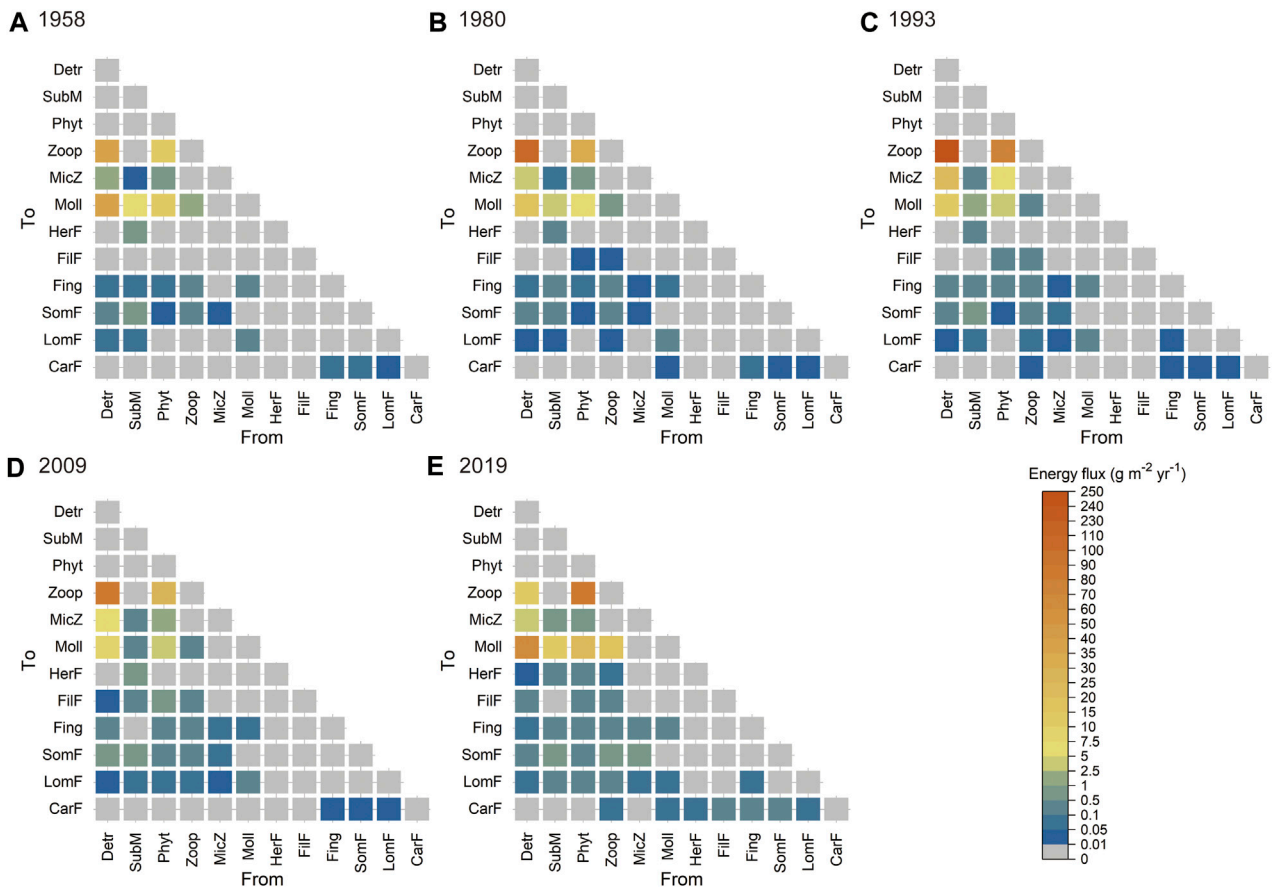

FIGURE 4
Distribution of energy fluxes from food sources to their consumers in the food webs for five representative years: **(A)** 1958, **(B)** 1980, **(C)** 1993, **(D)** 2009, and **(E)** 2019, represented as heat maps. Colour intensity represents the energy flux from the trophic groups in the column to the trophic groups in the row. Abbreviations of trophic groups: CarF, carnivorous fish; Detr, detritus; FilF, filter-feeding fish; Fing, fingerlings; HerF, herbivorous fish; LomF, large omnivorous fish; MicZ, meiofauna; Moll, mollusks; Phyt, phytoplankton; SomF, small omnivorous fish; SubM, submerged macrophytes; Zoop, zooplankton.

years to 23.7% in 2009 and then became the main food source in 2019, with a contribution of 25.3%. Together, these results demonstrate a shift of the food web from detritus-based to phytoplankton-based from 1958 to 2019.

The trophic position of the trophic groups ranged from 1 (detritus, submerged macrophytes, and phytoplankton) to an average of 3.34 ± 0.13 (carnivorous fish) (Figure 3). The trophic positions of zooplankton, meiofauna, and mollusks were relatively stable, with an average value of 2.02 ± 0.03. The carnivorous fish occupied the top trophic position, but their trophic position decreased from 3.51 in 1958 to 3.21 in 2019. This was followed by large omnivorous fish (2.60 ± 0.07) and fingerlings (2.54 ± 0.10). The highest trophic positions for small omnivorous, filter-feeding, and herbivorous fish in 2019 were 2.56, 2.46, and 2.23, respectively. The lowest trophic positions for herbivorous fish, fingerlings, and small and large omnivorous fish occurred in 2009, but these values recovered slightly in 2019.

Figure 4 illustrates the temporal changes in energy fluxes from food sources to their consumers in the food webs in the five study years. A low proportion (25.6–28.6%) of these energy fluxes was ingested by the consumer trophic groups, and a higher proportion (71.4–75.4%) of these energy fluxes entered the detritus pool. The highest total energy fluxes in the food webs were observed in 1993 (376.06 g m^{-2} yr^{-1}), followed by in 2019 (227.34 g m^{-2} yr^{-1}), with the lowest value in 1958 (107.18 g m^{-2} yr^{-1}). The ingestion by primary consumers (zooplankton, meiofauna, and mollusks) accounted for more than 90% of the total ingestion of consumers in all study years. Among the energy fluxes along specific trophic links, the energy fluxes from detritus to zooplankton (35.70 g m^{-2} yr^{-1}) and mollusks (35.24 g m^{-2} yr^{-1}) were highest in 1958. The highest values characterized energy fluxes of trophic links from detritus to

TABLE 2 Temporal changes in the unweighted and weighted (including biomass-based and flux-based) food web structure metrics. Values are the unweighted, link-weighted (*lw*), and node-weighted (*nw*) connectance (*C*), generality (*G*), and vulnerability (*V*).

Food web metrics	1958	1980	1993	2009	2019
C	0.303	0.311	0.303	0.303	0.311
nwC	0.276	0.274	0.275	0.278	0.280
lwC	0.204	0.165	0.156	0.172	0.190
G	4.444	4.556	4.444	4.444	4.556
nwG	4.402	4.321	4.139	4.291	4.322
lwG	2.157	1.877	1.796	1.856	2.381
V	3.636	3.727	3.636	3.636	3.727
nwV	5.745	5.928	5.886	5.701	5.424
lwV	2.333	1.756	1.642	1.921	1.807

zooplankton, followed by values from phytoplankton to zooplankton, in three study years (1980, 1993, and 2009). Energy fluxes from phytoplankton to zooplankton (88.55 g m^{-2} yr^{-1}) and from detritus to mollusks (67.98 g m^{-2} yr^{-1}) were higher than those of other trophic links in 2019. Supplementary Figure S3 shows the temporal variability in flux-based ecosystem functioning metrics. The proportion of detritivorous flows increased first and then decreased over time, with the highest and lowest values observed in 1993 (75.2%) and 2019 (36.5%), respectively. The percentage of planktivorous flows showed an increasing trend, from 22.0% in 1958 to 24.7% in 2009, and became the main energy flow (49.5%) in 2019. In addition, the proportions of herbivorous, zooplanktivorous, benthivorous, and piscivorous flows in food webs showed a trend of first decreasing and then increasing over time, which were relatively higher in 2019 and 1958 than in the other three study years.

The different types of food web metrics (i.e., unweighted, node-, and link-weighted) displayed temporal variability and complementary dynamics from 1958 to 2019 (Table 2). Three unweighted food web metrics (*C*, *G*, and *V*) showed similar trends, with the highest values in 1980 and 2019. The highest and lowest node-weighted connectance (*nwC*) values were observed in 2019 and 1980, respectively. Link-weighted connectance (*lwC*) was highest in 1958, after which it decreased to its lowest value in 1993. Node-weighted generality (*nwG*) and link-weighted generality (*lwG*) both decreased initially and then increased, with the highest values observed in 1958 and 2019, respectively. In contrast, node-weighted vulnerability (*nwV*) first increased and then decreased, with the highest and lowest values in 1980 and 2019, respectively. Link-weighted vulnerability (*lwV*) was highest in 1958, with all other values much lower.

3.2 Relationships between water environmental factors and metrics of food web structure and function

The extreme maximum and minimum water levels were highest in 1958, followed by 2019 and 1980, respectively (Supplementary Table S3). The amplitudes of the water level fluctuation represent the difference between the maximum and minimum water levels for a given period, and they were highest in 1958 and lowest in 2019. The highest pulse duration was reported in 2009, whereas the lowest frequency of hydrologic reversals was observed in 2019. The threshold of water level pulses decreased gradually from 1958 to 2009, and then partially recovered in 2019. Since hydrological indicators of the 1-day, 3-days, 7-days, 30-days, and 90-days scale water level were significantly positively correlated with each other (Supplementary Figure S4), we have focused on the 7-days scale in our descriptions, since this period is broadly representative of the other periods. Supplementary Figure S5 and Supplementary Table S4 show the PCA results for the hydrological indicators. The first two principal component axes (i.e., PC1 and PC2) account for 81.2% of the variation in hydrological regime indicators of five representative years, 56.9% and 24.3% respectively. PC1 was strongly positively associated with *HPT* (factor loading: 0.986), *WLMaxd7* (0.981), *LPT* (0.910), *WLMind7* (0.886), and *WLAmpd7* (0.758). PC2 was strongly positively associated with *HPD* (0.935) and *LPD* (0.851).

Table 3 shows the values (mean ± SD) of the water quality variables for the five study years. All variables except for *DO* differed significantly among the five study years ($p < 0.05$). Lake Baiyangdian generally showed slightly alkaline water, with the mean pH value ranging from 7.96 to 8.72 in the five representative years, but with increasing acidity over time. T_w was highest in 2009, when it was significantly higher than in 1958 and 1980. Serious eutrophication occurred in Lake Baiyangdian, with average *TN* and *TP* concentrations ranging from 0.70 mg/L to 3.75 mg/L and from 0.03 mg/L to 0.34 mg/L, respectively, with both values increasing from 1958 to 2009, then decreasing. In addition, NO_2^-+NO_3^- was much higher in 2019 and 2009 than in the other 3 years, and this difference was significant; except for a decrease in 1993, NO_2^-+NO_3^- increased significantly from 1958 to 2019. The highest concentrations of *SRP*, *TN*, *TP*, and NH_4^+ were all observed in 2009. The average *COD* ranged from 12.0 mg/L to 59.2 mg/L, and increased to a maximum in 1993, and although it decreased thereafter, it remained much higher than in 1958. The PCA captures the relationship and associations in the dynamics among water quality factors in the five study years (Figure 5, Supplementary Table S5). The first two principal components (i.e., PC1 and PC2) together explained 62.8% of the variance, 43.0% and 19.8% respectively. PC1 was positively correlated with *SRP* (0.889), NH_4^+ (0.867), *TN* (0.827), *TP* (0.802), and T_w

TABLE 3 Mean and standard deviation (mean ± SD) for the water quality variables in the five study years. Values of a variable followed by different letters (a, b, c) differed significantly between study years (one-way ANOVA followed by *LSD* test or Kruskal–Wallis test followed by Mann-Whitney *U* test, $p < 0.05$).

Water quality factors	1958	1980	1993	2009	2019
Water temperature (T_w, °C)	17.3 ± 5.03[b]	18.0 ± 1.42[b]	18.90 ± 2.33[ab]	26.65 ± 1.43[a]	22.21 ± 4.45[ab]
pH	8.72 ± 0.18[a]	8.35 ± 0.26[ab]	8.60 ± 0.39[ab]	8.19 ± 0.14[b]	7.96 ± 0.29[b]
Dissolved oxygen (*DO*, mg/L)	7.25 ± 1.19[a]	8.72 ± 0.71[a]	7.64 ± 0.61[a]	7.71 ± 1.03[a]	6.45 ± 2.60[a]
Nitrite-nitrate (NO_2^-+NO_3^-, mg/L)	0.32 ± 0.05[bc]	0.44 ± 0.05[b]	0.08 ± 0.02[c]	1.98 ± 0.77[ab]	2.61 ± 0.45[a]
Soluble reactive phosphorus (*SRP*, mg/L)	0.01 ± 0.004[c]	0.01 ± 0.003[c]	0.13 ± 0.007[b]	0.26 ± 0.04[a]	0.02 ± 0.005[c]
Chemical oxygen demand (*COD*, mg/L)	12.0 ± 2.66[b]	25.29 ± 7.9[b]	59.15 ± 11.9[a]	21.99 ± 9.97[b]	25.76 ± 5.62[b]
Total nitrogen (*TN*, mg/L)	1.53 ± 0.16[b]	0.70 ± 0.23[b]	2.49 ± 0.34[ab]	3.75 ± 1.11[a]	2.55 ± 1.53[ab]
Total phosphorus (*TP*, mg/L)	0.03 ± 0.004[b]	0.04 ± 0.02[b]	0.27 ± 0.08[a]	0.34 ± 0.17[a]	0.08 ± 0.05[ab]
Ammonium (NH_4^+, mg/L)	0.92 ± 0.48[bc]	0.17 ± 0.06[c]	1.47 ± 0.38[b]	3.45 ± 0.58[a]	0.63 ± 0.22[c]

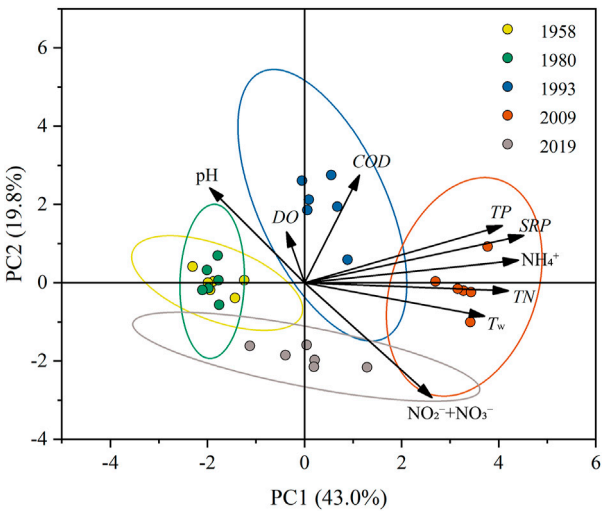

FIGURE 5
Biplot of principal component analysis (PCA) summarizing the variations in water quality factors of five representative years.

(0.730). NO_2^-+NO_3^- (−0.735) showed a negative loading on PC2, while *COD* (0.688) and pH (0.607) were positively correlated with this dimension. Furthermore, PCA arranged the five representative years into three groups according to the gradient of nutrient concentrations (i.e., *SRP*, NH_4^+, *TN*, *TP*, and NO_2^-+NO_3^-): 1958 and 1980 with low nutrients, 1993 and 2019 with relatively high nutrients, and 2009 with high nutrients.

We detected minor variations (i.e., most of them are similar) in values of the unweighted food web metrics over time. Therefore, these unweighted metrics were not appropriate for further analyses. We used the *VIP* (Table 4) and *RC* (Supplementary Table S6) values from the PLSR to select the most important environmental factors that affected the food web structure and function. *nwC* and *nwV* were mainly affected by NO_2^-+NO_3^-, *NumOfRev*, and *DO*, whereas the *RC* values showed correlations with opposite signs for these two weighted metrics. For node-weighted generality (*nwG*), the highest *VIP* was for *COD* (1.936), followed by *HPD* and *HPT* (1.684 and 1.252, respectively). Link-weighted connectance (*lwC*) and vulnerability (*lwV*) were both negatively correlated with *COD* (*VIP* = 1.486 and 1.613, respectively), and positively correlated with the threshold (*LPT* and *HPT*) and duration (*LPD* and *HPD*) of the water level pulse, respectively. Link-weighted generality (*lwG*) was negatively correlated with *DO*, and positively associated with NO_2^-+NO_3^-, *LPT*, and *WLMind7*. In addition, detritivory, phytoplanktivory, and zooplanktivory were mainly affected by NO_2^-+NO_3^-, *DO*, pH, and *NumOfRev*, whereas the RC values showed correlations with opposite signs for detritivory and the other two metrics. Herbivory was positively correlated with the threshold (*LPT* and *HPT*) of the water level pulse and *WLMind7*, and negatively correlated with *DO*. Moreover, benthivory and piscivory were both negatively correlated with *DO* (*VIP* = 1.821 and 1.551, respectively), and positively correlated with *LPT* and NO_2^-+NO_3^-.

4 Discussion

4.1 Temporal dynamics of the food web structure and function

In recent decades, Lake Baiyangdian has faced severe eutrophication (Zhao et al., 2010; Zeng et al., 2021). Nutrient over-enrichment associated with anthropogenic activities has accelerated eutrophication since the 1980s, leading to a high abundance of phytoplankton (Bumpers et al., 2017; Yang et al., 2021). Rogers et al. (2020) reported that grazing might have a negligible impact on phytoplankton dynamics at high

TABLE 4 Mean values of the variable importance in the projection (*VIP*) obtained via partial least-squares regression. Metrics are the node-weighted (nw) and link-weighted (lw) connectance (C), generality (G), and vulnerability (V), and six flow-based ecosystem functioning metrics.

Environmental factors	Food web metrics											
	nwc	***lwc***	***nwG***	***lwG***	***nwV***	***lwV***	**Detritivory**	**Herbivory**	**Phytoplanktivory**	**Zooplanktivory**	**Benthivory**	**Piscivory**
7-days minimum water level (*WLMind7*)	0.569	1.264	0.828	1.467	0.810	0.801	1.186	1.461	0.888	1.223	1.271	1.427
7-days maximum water level (*WLMaxd7*)	0.556	1.319	1.164	0.915	0.282	1.416	0.221	1.329	0.291	0.266	0.614	0.929
7-days amplitude water level (*WLAmpd7*)	0.896	0.946	1.159	0.326	0.803	1.627	0.953	0.779	1.309	0.922	0.340	0.344
Low-water pulse duration (*LPD*)	0.797	0.928	0.905	0.194	0.622	1.462	0.299	0.475	0.451	0.306	0.330	0.205
High-water pulse duration (*HPD*)	0.476	1.007	1.684	0.356	0.459	1.364	0.128	0.539	0.225	0.122	0.546	0.478
Low-water pulse threshold (*LPT*)	0.592	1.447	1.010	1.495	0.829	1.058	1.111	1.567	0.765	1.148	1.316	1.466
High-water pulse threshold (*HPT*)	0.507	1.309	1.252	1.125	0.356	1.188	0.545	1.373	0.225	0.589	0.856	1.149
Number of reversals (*NumOfRev*)	1.693	0.634	0.353	1.019	1.693	0.371	1.413	0.604	1.532	1.384	1.298	0.947
Water temperature (T_w)	1.213	0.451	0.491	0.364	1.010	0.491	0.467	0.620	0.707	0.429	0.472	0.377
pH	1.347	0.217	0.393	0.902	1.413	0.864	1.558	0.274	1.774	1.525	1.180	0.940
Dissolved oxygen (*DO*)	1.626	1.289	0.304	1.658	1.838	0.590	1.799	1.324	1.668	1.797	1.821	1.551
Nitrite-nitrate (NO_2^-+NO_3^-)	1.722	0.694	0.649	1.230	1.800	0.273	1.695	0.612	1.801	1.663	1.563	1.241
Soluble reactive phosphorus (*SRP*)	0.510	0.879	0.891	1.122	0.391	0.617	0.883	1.102	0.692	0.919	0.847	1.140
Chemical oxygen demand (*COD*)	0.614	1.486	1.936	0.950	0.732	1.613	0.506	1.107	0.216	0.508	1.061	1.055
Total nitrogen (*TN*)	1.156	0.502	0.663	0.389	0.937	0.543	0.333	0.630	0.559	0.303	0.369	0.405
Total phosphorus (*TP*)	0.486	1.027	1.203	1.117	0.368	0.773	0.766	1.161	0.538	0.801	0.872	1.165
Ammonium (NH_4^+)	0.603	0.552	0.560	0.810	0.315	0.628	0.719	0.778	0.652	0.751	0.488	0.822

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phytoplankton concentrations. In addition, nutrient enrichment often alters the elemental composition of phytoplankton (Sterner and Elser, 2002; Burson et al., 2016), and often improves its nutritional quality for potential consumers. The higher nutritional enrichment of phytoplankton relative to detritus (Guo et al., 2016; Thorp and Bowes, 2017), and the associated increase in phytoplankton production, can turn detritus-based into phytoplankton-based food webs (Power et al., 2013; Mor et al., 2018), which is what happened in our study. It is acknowledged that eutrophication promotes changes in primary productivity that could potentially affect trophic interactions and alter the dietary preferences of consumers (Bumpers et al., 2017; Zhang et al., 2018; van der Lee et al., 2021). In addition, temporal changes in dietary preferences of consumers among five representative years may also be attributed to the difference in methodologies between the gut content analysis and the stable isotope analysis. For example, in a review paper on diet tracing methods in ecology, it was concluded that these two approaches measure the diet at various stages during ingestion and assimilation, and the relative dietary contribution can vary substantially (Nielsen et al., 2018). Furthermore, the contributions of detritus were the highest with averages of 30.1% in the first four study years. This may be due to the fact that the taxonomic impediment of identifying partially digested material by the gut content analysis can render some components unknown and classify them as detritus (Nielsen et al., 2018). Recently, stable carbon isotopes values of subfossils have been successfully tracked the food sources of consumers over a long-time scale (Cheng et al., 2020), which may provide an opportunity for temporal studies of highly resolved food webs.

Consumers may change their dietary preferences to take advantage of multiple food sources based on the relative availability or nutritional quality of the resources (de Carvalho et al., 2019), and this may cause changes in their trophic positions and hence in the food web structure (Rooney and McCann, 2012; McMeans et al., 2019). In the present study, three fish trophic groups (i.e., fingerlings, large omnivorous fish, and carnivorous fish) shifted their dietary preferences toward food resources with higher nutritional quality until 2009 (fingerlings and large omnivorous fish) and until 2019 (carnivorous fish), and their trophic position decreased accordingly. Similarly, some previous studies concluded that omnivorous consumers might lower their trophic position by adjusting their diet from consumption of animal resources to increased consumption of plant resources with high nutritional quality when both resources are offered simultaneously (Zhang et al., 2018; van der Lee et al., 2021). In addition, lower trophic positions of omnivorous and carnivorous fish have been reported during the wet season in tropical floodplains, leading to increased consumption of plants or invertebrates (Blanchette et al., 2014; McMeans et al., 2019). The trophic position of the top predator or the maximum trophic position of species in a food web is conceptually similar to food chain length (Briand and Cohen, 1987). Carnivorous fish consistently occupied the highest trophic position in all five representative years, and the decrease in its trophic position over time implies a shortening of the food chain length between the top and bottom of Lake Baiyangdian's food webs, which may be caused by increased trophic omnivory and reduced dietary specialization at any or all trophic levels (Post et al., 2000; Post and Takimoto, 2007). Furthermore, the dietary preferences of consumers can shape biomass ratios between different trophic levels (McCauley et al., 2018; Burian et al., 2020). Our results showed that the biomass of trophic groups was unequally distributed across the food webs, and decreased with increasing trophic level, which is consistent with previous studies (Trebilco et al., 2013; Hatton et al., 2015).

Any changes in dietary preferences can affect energy fluxes because different food sources have different concentrations of carbon and nutrients, which leads to different assimilation efficiencies (Sterner and Elser, 2002; Jochum and Eisenhauer, 2022). The highest total energy flux in the food web was observed in 1993, followed by 2019, with the lowest in 1958. This is related to the biomass pools of phytoplankton, submerged macrophytes, and detritus, as well as the biomass flow from these pools to primary consumers. The efficiency of the energy fluxes ingested by the consumers was low, and a considerable proportion of the energy fluxes directly entered the detritus pool, where the biomass and its contained energy served as fuel for ecosystem recycling in Lake Baiyangdian's food webs, which agrees with Zeng et al. (2021). According to Barnes et al. (2018), trophic complementarity can be an important mechanism for promoting ecosystem functioning in food webs, where greater consumer diversity reduces competition for food sources, thereby increasing the total energy fluxes to consumers (Poisot et al., 2013; Peralta et al., 2014).

In addition, the distribution of energy flux is important for determining food web stability. The ingestion by primary consumers (zooplankton, meiofauna, and mollusks) accounted for more than 90% of the total ingestion of consumers in our study. The bottom-heavy food web energetics structure (i.e., larger energy fluxes at lower trophic levels) may confer greater food web stability (Rip and McCan, 2011; Barnes et al., 2018). Zooplankton and mollusks, which dominated the total energy fluxes in Lake Baiyangdian, were strongly connected to the phytoplankton and detritus energy pathways. Both energy channels can convey significant energy fluxes from basal food sources to consumers at higher trophic levels, thereby potentially stabilizing food webs (Ward et al., 2015; Mougi, 2020). However, the primary consumers that feed on more nutritious phytoplankton can use less energetically costly mechanisms to meet their nutrient uptake, assimilation, and retention needs (Sardans et al., 2012; Teurlincx et al., 2017).

4.2 Changes in unweighted and weighted food web metrics

Although the food webs displayed large differences in the underlying dietary preferences and energy flux distribution in 1980 and 2019, or in 1958, 1993, and 2009, they showed similar values for the unweighted food web metrics. This suggests that unweighted food web metrics are inadequate predictors of highly aggregated food web structures and functions, since they are

limited to a static view, and are more sensitive to changes in species and link richness (Kortsch et al., 2021). However, some studies indicated that changes in community composition did not always trigger changes in the food web structure (Yletyinen et al., 2016; Griffith et al., 2019; Frelat et al., 2022). Moreover, previous studies concluded that macroscopic unweighted food web descriptors may be invariant at a broader temporal scale (spanning years to millennia), whereas strong dynamics were observed at finer temporal scales (from hours to months) (Fründ et al., 2011; Trøjelsgaard and Olesen, 2016; CaraDonna et al., 2021). We observed more pronounced temporal variability in the weighted (node- and link-weighted) food web metrics than in the unweighted food web metrics in all study years, which can be related to the fact that unweighted and weighted food web metrics likely reflect different underlying ecosystem processes (Olivier et al., 2019; Kortsch et al., 2021; Frelat et al., 2022). Previous studies show that weighted food web metrics can capture the associated consequences of energy flux distribution and thus predict ecosystem functioning (Kortsch et al., 2021). In our study, three weighted metrics (i.e., *lwC*, *lwG*, and *nwG*) showed the same trend of decreasing first and then increasing over time as most metrics of ecosystem functioning (i.e., herbivory, zooplanktivory, benthivory, and piscivory), while the detritivory showed the opposite trend. Some studies of temporal changes of node-weighted food web metrics suggest that food web structure was influenced by changes in species dominance (Olivier et al., 2019). Node-weighted connectance (*nwC*) was highest in 2019, which can be explained by the high biomass of highly connected nodes, such as mollusks and omnivorous fish, that reflect dominance of the food web by particular trophic groups in 2019.

Node-weighted vulnerability (*nwV*) was always much higher than unweighted vulnerability (*V*) in our study, which was consistent with previous studies (Olivier et al., 2019; Kortsch et al., 2021). We also found that link-weighted metrics had lower values than the corresponding unweighted metrics in Lake Baiyangdian's food webs. Similar results were observed in a previous study (Kortsch et al., 2021), which indicates that energy fluxes are not equally distributed in food webs, but rather are skewed towards a few strong fluxes and many weak fluxes. Link-weighted connectance (*lwC*) showed higher values in 1958 and 2019, which was related to the fact that several trophic groups with many interactions also had relatively high and even inflows and outflows, and this increases link-weighted food web complexity. Together these results indicate that an approach that considers the dominant species, their dietary preferences, and the energy flux distribution will challenge the conclusion about temporal changes in food web structures based only on unweighted metrics (Scotti et al., 2009; Kortsch et al., 2021; López-López et al., 2022). However, in other studies, weighted metrics were similar (Frelat et al., 2022) or complementary (Kortsch et al., 2021) to unweighted metrics in their ability to describe temporal changes in the food web structure. Therefore, it is necessary to integrate unweighted, node-weighted, and link-weighted metrics to identify the complementary temporal patterns of food web dynamics, since this provides better support for management decisions.

4.3 Effect of environmental factors on food web dynamics

The changing hydrological regimes and water quality factors that we observed can explain the temporal trends of food web dynamics. Disentangling their relationships is crucial for guiding conservation and restoration strategies in shallow lakes. Studies of ecosystem processes in shallow lakes have generally shown that water level fluctuations are a dominant force and that many other environmental factors vary concurrently with these fluctuations (Kolding and van Zwieten, 2012; Jeppesen et al., 2015). In our study, the low- and high-water level pulse thresholds (i.e., *LPT* and *HPT*) were (after *COD*) the hydrological regime indicators that most strongly affected the link-weighted connectance (*lwC*). They were positively associated with link-weighted food web complexity. Values of *LPT* and *HPT* represent variable conditions that provide a broader range of hydrologic niches that can provide conditions suitable for organisms at different trophic positions (Yan et al., 2020; Zheng et al., 2020). The number of water level reversals (*NumOfRev*) was negatively associated with node-weighted connectance (*nwC*). Frequent water level fluctuations may prevent the establishment and development of organisms, thereby decreasing biodiversity and food web complexity.

Eutrophication due to excessive nutrient loading is a common stressor for changes in food web structure and function in shallow lakes (Paerl et al., 2011). It affects the relative availability of basal resources, which further affects consumers at higher trophic positions (Bumpers et al., 2017). Eutrophication also can homogenize the composition of lake benthic assemblages (Olden et al., 2004; Donohue et al., 2009). Moreover, lakes exposed to prolonged eutrophication are prone to hypoxia, and subsequent fish kills (Bullerjahn et al., 2016). Our results showed that the biomass of phytoplankton increased from 1958 to 2009, which coincided with the intensive eutrophication in Lake Baiyangdian. As a result, most of the consumer trophic groups shifted in the direction of phytoplankton, and the food web then became more dependent on algae-based energy channels. Meanwhile, the food chain length declined from 1958 to 2009, which mean the food web structure of Lake Baiyangdian was simplified even though eutrophication brought sufficient nutrient into the ecosystem. Similar results have been reported in Lake Taihu with long-term eutrophication (Xu et al., 2016). The overall water quality of Lake Baiyangdian was better in 2019 than in 2009 and 1993, which is likely to be related to a series of governance policies and restoration projects, including a prohibition of fish breeding, water diversion projects,

wastewater treatment in villages, and dredging key channels (Zhu et al., 2019; Wang et al., 2021). The highest *lwC* value was in 1958, followed by 2019, whereas *nwC* was highest in 2019, followed by 2009. Taken together, the restoration of hydrological regimes and water quality improvements contributed to improving the lake's food web complexity by increasing the node- and link-weighted connectance in 2019. In addition, previous studies showed that most biological communities might be suppressed when a lake became eutrophication, leading to a decline in the total energy fluxes of the ecosystem (Kong et al., 2016; Wang et al., 2020). This finding is not evident in our study, as we observe the highest total energy fluxes in 1993, followed by in 2019, and the lowest value in 1958.

5 Conclusion

We confirmed our research hypotheses that the food web structure and function would vary over time in response to changes in hydrological regimes, eutrophication, and some related water quality factors. Our results revealed temporal variability of the food web structure and function in a shallow lake in northern China using both unweighted and weighted approaches and food web energetics approach. The lake changed from a detritus-based food web into a phytoplankton-based web based on the relative contributions of the basal food sources and the energy flux distribution. Fingerlings, large omnivorous fish, and carnivorous fish shifted their dietary preferences towards food sources with higher nutritional quality in the latter three study years, and their trophic position decreased accordingly. The link-weighted metrics had lower values than the corresponding unweighted topology-based metrics, which indicates that energy fluxes were not equally distributed, but rather were skewed towards a few strong fluxes and many weak fluxes. We observed more pronounced temporal variability in the weighted (node- and link-weighted) food web metrics than the unweighted food web metrics, and this may be related to the fact that unweighted and weighted food web metrics reflect different underlying ecosystem processes. Furthermore, our study demonstrated that restoring the lake's hydrological regimes and improving the water quality contributed to improving the food web complexity and function, with increased node- and link-weighted connectance and most of the flow-based ecosystem functioning metrics values in 2019. Overall, our results suggested that studies of weighted food web metrics will complement the information provided by classical topology-based (unweighted) metrics. Our approach can therefore provide useful data to support the management and restoration of the structure and functions of shallow lake ecosystems. In future research, it will be necessary to find ways to integrate the effects of additional hydrologic and water quality metrics (e.g., the differences between long- and short-term indicators, heavy metal concentrations in the water and sediments) and to expand our analysis to spatiotemporally highly resolved food webs to improve lake ecosystem management.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Author contributions

WY: Conceptualization, Resources, Supervision, Data analysis—original draft, Writing—review and editing. XF: Investigation, Methodology, Visualization, Data analysis—original draft, Writing—original draft. XL: Data analysis—original draft, Writing—review and editing. YY: Data analysis—original draft, Writing—review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.987600/full#supplementary-material.

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