Effects of Aquaculture on the Shallow Lake Aquatic Ecological Environment of Lake Datong, China

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Abstract

Background: Lake Datong has undergone several stages of aquaculture from 1980 to 2017, with a rapid increase in fish production and inorganic fertilizer supplementation at every stage. Its water quality has been deteriorating since the introduction of aquaculture. The major pollutants are total phosphorus and total nitrogen, and the lake displays moderate eutrophication. In the present study, we used historical hydrobiont data, diatom inferred-total phosphorous (DI-TP) data, and an Ecopath model to explore the effects of aquaculture on the shallow lake aquatic ecological environment.

Results: According to the DI-TP data, before 1930, Lake Datong was in a mesotrophic state (50–60 μg/L DI-TP). Between 1930 and 1980, the number of nutrient-tolerant species increased slightly, which indicates an increase in nutrient enrichment in the lake (66–83 μg/L DI-TP). From the 1980s to 2010 and especially since 2000, eutrophication increased rapidly, with eutrophic species dominating the diatom assemblage. The annual average DI-TP concentration was 202 μg/L. After 2010, the nutritional level dropped to 127–152 μg/L DI-TP. In 2019, consumer biomass in Lake Datong was relatively low, and biomass of submerged hydrophytes was relatively high, indicating that a high amount of primary produce could not be exploited by consumers and therefore, could not enter the food web. This led to reduction in the energy transfer efficiency (TE) of the ecosystem. Therefore, aquatic ecology management plans ought to be formulated in future, with focus on removing macrophytes, stocking herbivorous and omnivorous fish.

Conclusions: Lake Datong has experienced four stages of nutritional succession following the introduction of aquaculture activities. Its aquatic ecological environment has experienced dramatic changes in the composition and biomass of its aquatic life. The Ecopath model illustrated the instability of the lake's ecological environment. Owing to low consumer biomass and high submerged macrophyte biomass, a substantial quantity of primary produce remained unused by consumers. It was therefore, unable to enter the food web and led to reduction in the energy TE of the ecosystem. Our results provide important reference values and theoretical support for decision-makers and stakeholders in the subsequent management of similar shallow lake water ecosystems.

1. Introduction

Aquaculture provides nearly 20% of the average daily protein intake of approximately 3.1 billion people across the world [1]. At present, nearly half (45.2%) of the world's supply of aquatic products comes from farms, and the contribution of aquaculture and fisheries continues to increase annually [2]. China produces more aquaculture products than any other country, and it accounts for nearly two-thirds (62.1%) of the total supply [2]. As per the latest statistics (2018), China produces 29.60 million t of freshwater aquaculture products. In 2018, China undertook lake aquaculture spanning approximately 750,000 ha, which amounts to almost 15% of the total freshwater aquaculture area of China [3]. Lake aquaculture production is approximately 980,000 t, which amounts to about 33% of the total freshwater aquaculture production in China [3]. In aquaculture, management measures such as supplementary feed and fertilization improve fish yield. However, in China, the feed utilization rate of aquaculture is low; when 100 kg of feed is used, about 13–15 kg of the feed is not consumed and is discharged directly into the water [4], while simultaneously, 20–30% of the feed ingested by fish is indirectly discharged into the water through feces [5]. Aquaculture wastewater contains high concentrations of nitrogen and phosphorus. Total nitrogen (TN) and total phosphorus (TP) concentrations in aquaculture areas were 219% and 150% higher than those in non-aquaculture areas, respectively [6]. The waste material influences the oxygen depletion, eutrophication, and turbidity of the receiving water [7]. The ecological balance of such an aquatic ecosystem could get disrupted resulting in hyper eutrophication in sections of lakes or even in entire lakes where aquaculture projects are undertaken [7–10].

Eutrophication not only affects the utilization of water resources and development of fisheries but can also stimulate the outbreak of harmful algae, which would impair the ecological functions and reduce the economic and ecological value of the water bodies [11]. The ecological imbalance caused by eutrophication occurs as follows: there are changes in species composition of animals and hydrophytes in the lake, development of algae gradually leads to its dominance in the water body, turbidity of water increases, food web gets simplified, and biodiversity decreases [12–14]. The middle and lower reaches of the Yangtze have the highest concentration of freshwater lake resources and the most developed aquaculture industries in China [3]; simultaneously, this region also has the highest prevalence of lake eutrophication in China [15]. At present, hyper eutrophication of lakes in China urges policy-makers and decision-makers to seek improved methods for the management of the water quality of the lakes and their restoration.

At present, the management of eutrophic shallow lakes mainly focuses on external restoration measures (reducing the external nutrient load), internal restoration measures (biological manipulation, lake dredging), and a combination of these two [16, 17]. Aquaculture mainly focuses on systems such as aquaculture ponds, cages in reservoirs and lakes, nets in lakes, and aquaculture systems on land, in offshore areas, and in shallow water [6, 18–20]. However, few studies have been undertaken to evaluate the species succession of aquaculture ecosystems in shallow lakes after the development of aquaculture and the characteristics of aquaculture in shallow lakes during the process of ecological restoration. Therefore, based on the investigations of the ecological environment of Lake Datong in 2019, combined with existing historical documents and age analysis of sediment diatoms, we comprehensively and systematically analyzed the succession process in course of the development of aquaculture in a shallow lake ecosystem. Additionally, we constructed an Ecopath model to explore the status of the ecosystem during the restoration of eutrophic shallow lakes. This model is expected to provide a basis for the management of shallow lakes after the restoration of the ecosystem and to support the management of similar shallow lakes throughout the world.

In summary, the aim of this study was to explore the effects of aquaculture on the shallow lake aquatic ecological environment of Lake Datong.

2. Materials And Methods

2.1 Study area

Lake Datong, which is located at 112° 15' 28"–112° 42' 02"E and 29° 01' 19"–29° 19' 16"N, was once the largest aquaculture lake in Hunan Province, China. The lake is 15.75 km long from east to west and 13.7 km wide from south to north. It has an area and average depth of 82.67 km^2 and 2.5 m, respectively (Figure 1). According to the Environmental Quality Standards for Surface Water (EQSSW) (Table 1), the water quality of Lake Datong was between 'Inferior' and ‘Class V’. The main pollutants that exceeded the standard values were TP and TN. The issue of water pollution is an important consideration for the Ministry of Ecology and Environment of the People's Republic of China, and it has become a key investigation target of Action Plan for Prevention and Control of Water Pollution.

Comprehensive management was undertaken by the end of 2017, when the local government launched the aquatic macrophyte restoration project for Lake Datong, which involved the planting of aquatic macrophytes to improve the quality of water.

2.2 Data collection

The data on hydrobionts are based on a survey carried out in 2019 by our research group. Phytoplankton in the water were collected using a No. 25 plankton net (pore size, 64 μm), and zooplankton were collected using a No. 13 plankton net (pore size, 86 μm). Benthic organisms were collected using mud harvesters and were washed over 0.5 mm screens. The fish resource survey adopted separate collection points. This is the traditional fishing method using a gillnet and ground cage, where the individual surveys the lake using fishing boats to count fish species. Molluscan resource survey was conducted using Peterson mud harvesters. Hydrophytes were collected using a self-made sampler. Water quality parameters and sediment TP were analyzed according to the Practical Manual of Environmental Monitoring Method Standards of China [21]. Using a gravity sampler, sediment samples were collected from the center of Lake Datong (29°12'33.40"N, 112°31'41.58"E), and borehole sediment samples were collected at 1 cm intervals on site. The ^{210}Pb and ^{137}Cs activities in the sediment samples were measured using a high-purity germanium well detector (HPGe GWL-120-15) [22]. Loss on ignition (LOI) was measured by placing the sample in a Muffle furnace and burning it at 550 °C for 4 hours. Sediment diatom samples were treated with hydrochloric acid and hydrogen peroxide to prepare slices [23]. Here, species identification mainly follows the classification system of Krammer & Lange-Bertalot [24]. At least 300 grains were identified for each sediment sample. The abundance of diatom species in each sediment sample was expressed as a percentage. The quantitative reconstruction of TP concentration in Lake Datong is based on the diatom community composition and the established diatom-TP conversion function model in the middle and lower reaches of the Yangtze River [25]. The transformation function is based on the typical correspondence analysis of diatoms and environmental databases of 45 lakes. In other words, TP is the biggest environmental factor that can explain diatom population composition. The relationship between diatom and TP was established using the weighted regression model. The process of quantitative reconstruction was run in C2 program [26]. We also collected and sorted historical data on phytoplankton, zooplankton, molluscs, hydrophytes, and fish in Lake Datong and other similar water ecosystems.

2.3 Ecosystem Model

The Ecopath with Ecosim (EwE) model is a mass-based whole-ecosystem model that takes all trophic levels of the ecosystem into account and is mainly used to simulate ecosystem status and internal energy flows [27, 28]. It is used extensively to simulate the structures of aquatic food webs and to predict the impacts of fishery activities on fishery resources. There are several examples of its application, such as the construction of the food webs of the Great Lakes and the assessment of marine fishery resources [29, 30]. However, it has rarely been used to evaluate the ecological restoration of lakes. Given the need to facilitate the ecosystem-based restoration of eutrophic lakes, we used the EwE model in the present study[31, 32].

The Ecopath model is a static model that reflects the energy balance of each component of the ecosystem, and it has been developed from the steady-state model of Polovina [33]. Therefore, at any time, any organism or functional group in the ecosystem can satisfy the following relationship [34]:

Production volume = catch + predation death + biomass accumulation + net migration + other deaths.

It can be expressed more concisely by the following equation:

$$B_i \times (P/B)_i \times EE_i - \sum_j B_j \times (Q/B)_j \times DC_{ij} - Y_i = 0 \qquad (1),$$

where B_i is the biomass of the functional group *i*; $(P/B)_i$ is the biological turnover rate of the functional group *i*, namely, the ratio of production to biomass, and its value is usually equal to the total mortality *Z* of the population under static conditions; EE_i is the ecological nutrition efficiency of the functional group *i*; B_j is the biomass of the predatory functional group *j*; $(Q/B)_j$ is the ratio of the consumption by the predatory function group *j* to its biomass; DC_{ji} is the proportion of food *i* in the diet of predator *j*; and Y_i is the fishing catch of group *i* [35, 36].

Equation 2 represents the quantity of food consumed by all *n* species in the functional species *i*:

$$\sum_{j=1}^{n} \times (Q/B)_j \times DC_{ij} \qquad (2).$$

In this Ecopath model, *EE* represents the proportion of yield lost due to predation or fishing in each group, which can be estimated after inputting the values of *B*, *P/B*, *Q/B,* and *DC* of each functional group in the food web. We ensured that *EE* < 1 after all the Ecopath model parameters had been input.

The energy balance formula in the Ecopath model is as follows:

$$(P/Q)_i + (U/Q)_i + (R/Q)_i = 1 \qquad (3),$$

where $(P/Q)_i$ is the ratio of production to consumption; $(U/Q)_i$ is the ratio of unassimilated biomass to consumption; and $(R/Q)_i$ is the ratio of respiration to consumption. In the Ecopath model, the $(P/Q)_i$ value is calculated based on the input $(P/B)_i$ and $(Q/B)_i$ values. $(U/Q)_i$ is entered directly. $(R/Q)_i$ is calculated using equation (3). During the parameter adjustment, we ensured that energy balance in the Ecopath model (R/Q) was > 0.

3. Results

3.1 Phytoplankton

Changes in phytoplankton species composition

The abundance and biomass of the phytoplankton in Lake Datong have undergone relatively considerable changes but have, nevertheless, been at low levels (Table 2). Conversely, the resident phytoplankton species have changed markedly over the past 60 years (Figure 2). From the 1860s, dinoflagellates have been the dominant species, accounting for 69.7% of all phytoplankton species; however, these have decreased to less than 5% in recent years. In 2019, Chlorophyta formed the dominant species, accounting for 40–50%; Euglenophyta increased from 0% (prior to 2005) to 34.69% and then decreased rapidly to less than 10%. Cyanophyta increased from 0% in the 1960s to 19.08% in the 2000s, slowly increased to 23.75% in 2013–2014, and then dropped to around 20% in 2019. In addition, Bacillariophyta changed minimally from the 1960s to 2008–2009, increased to 27.59% by 2010, and then decreased gradually to 16.24% by 2019. The Shannon diversity index (H-value) decreased from 2.045 in 2008-2009 to 1.24 in 2013, and then increased to 3.549 by 2019. The Margalef richness index (D-value) decreased from 3.11 in 2008-2009 to 0.75 in 2013, and then increased to 6.773 in 2019. The Pielou evenness index (J-value) decreased from 1.037 in 2008-2009 to 0.68 in 2012-2013 and further decreased to 0.555 by 2019 (Table 2). In terms of spatial distribution, the phytoplankton abundance gradually decreased from south to north. In contrast, mollusc biomass decreased from northeast to southwest [37] (Figure 3).

Succession of diatoms in sediments

A total of 43 species from 21 genera were identified in the sedimentary column of Lake Datong. Among them, planktonic and benthic genera were dominant, and epiphytic genera were also common (Figure 4). It can be seen from Figure 4 that *Aulacoseira granulata* is one of the dominant species. At approximately 10 cm depth (approximately corresponding to the year 1980), the content of *Aulacoseira granulata* and the diatom assemblage in the sedimentary column changed significantly. Below 10 cm depth, *Aulacoseira granulata* is a dominant species, accounting for 60-80% of the total content, and it is found at the bottom of the borehole, where there are few diatoms. The populations of planktonic species with low nutrition, including *Aulacoseira ambigua* and *Cyclotella bodanica*, and epiphytic species, including *Fragilaria Capucina*, *Cocconeis placentula*, *Gyrosigma acuminatum,* and *Eunitia* accounted for less than 15% of the total population. At a depth of 10 cm, the proportion of *Aulacoseira granulata* decreased rapidly. From 1 to 9 cm in the sediment column of Lake Datong, the content of diatoms began to increase. Simultaneously, the numbers of eutrophic species such as *Cyclotelaphanos thaliformis*, *Cyclotella meneghiniana*, *Stephanodiscus hantzschii,* and *Stephanodiscus minutulus* began to increase.

3.2 Zooplankton

The zooplankton in Lake Datong have been dominated by copepods since the 1960s. Among them, Calanoids along with a few rotifers and protozoa accounted for 84% of the total biomass. In Lake Datong, during the aquaculture period, the structure of its zooplankton community was characterized by small zooplankton protozoa, and the number of species, abundance, and biomass of rotifers accounted for a higher proportion. The large and medium-sized zooplankton *Cladoceras* and *Copepods* account for a lower proportion. Especially after 2011, a trend of miniaturization is increasingly evident. However, the number of species, biomass, and abundance of zooplankton surveyed recently have shown an increase (Table 3). The average abundance of zooplankton was 19,904 ind/L and the average biomass was 966.38 mg/L. Of these, the average abundance and biomass values of small zooplankton protozoa and rotifers were 19870 ind/L and 5.471 mg/L, respectively. In case of large and medium-sized zooplankton, the average abundance and biomass of copepods were 31 ind/L and 912.91 mg/L, respectively. The highest values of abundance and biomass were 41100 ind/L and 6587.713 mg/L, respectively at the sampling point D19. The minimum value was at D5, where the abundance was 9000 ind/L, and the biomass was 5.961 mg/L. The abundance and biomass of zooplankton in Lake Datong demonstrated a significant variation in spatial distribution, with relatively high abundance in the east and relatively low abundance in the south (Figure 5). Simultaneously, the zooplankton H-index in Lake Datong was 1.06, with a range of 0.31-1.88. The average value of the D-index was 0.67, ranging from 0.11 to 1.39. The mean value of the J-index was 0.65, with a range of 0.45-0.90.

3.3 Mollusca

In the winter of 1960, there were more than 21 species of Mollusca in Lake Datong, including 11 species of Gastropoda and 10 species of bivalves. In terms of both abundance and biomass, bivalves are dominant. The composition of molluscs in Lake Datong decreased to 15 species belonging to 5 families by 2008–2009 (Table 4). *Bellamya purificata*, *Corbicula fluminea,* and *Uniodoug lasiae* are the dominant species. During the aquaculture period, Lake Datong had high abundance and high biomass of molluscs (Figure 6). However, their average abundance and biomass had evident temporal and spatial differences, showing a gradual increase over time from spring and summer to autumn and winter and a gradual decrease from northeast to southwest. During the period, the molluscs *Gyraulus albus, Segmentina nitida*,and *Radix*, which prefer habitats with aquatic macrophytes, and *Stenothyra divalis, Limnoperna lacustris, and Solenaia oleivara*, which prefer the lotic habitat, disappeared. In addition, the dominant mollusc type changed from Lamellibranchia to Gastropoda. A recent survey in 2019 demonstrated that Lake Datong had 7 species of molluscs from 2 orders, 3 families, and 7 genera. It had one gastropod species and 6 bivalve species from 1 order, 2 families, and 6 genera. A total of 163 molluscs were collected during the investigation, and the total quantity of fish caught was 2824 g. The number of ring snails of species *Bellamya purificata* was 89, and the catch was 188 g, accounting for 6.66% of the total catch. Among bivalves, the number of the Lamellibranch species *Unio douglasiae* was 50. The catch of *Cristaria plicata* was the largest, weighing 1945 g, accounting for 68.87% of the total catch; *Corbicula fluminea* was the least, weighing only 20 g, accounting for a mere 0.71% of the total catch (Table 5). Comparing the distributions of molluscs in Lake Datong during aquaculture can shed light on their distinct temporal and spatial heterogeneity. Mollusca are mostly distributed in the northern and eastern parts of the lake, with a gradual decrease from northeast to southwest. There have been significant differences in their abundance and biomass in Lake Datong over different years. In 2019, our survey revealed that the biomass of large molluscs had dropped sharply (Figure 6) to less than 90% of the biomass prevalent during aquaculture, as compared to previous years. Additionally, we investigated many sampling points that did not collect mollusca (only 55.56% of the sampling points collected molluscs), especially in the western waters where aquatic hydrophytes are abundant.

3.4 Aquatic hydrophytes

In the early 1960s, Lake Datong maintained its natural lake form, with a 30% cover of aquatic hydrophytes on the lake surface. The dominant species were *Potamogeton wrightii Morong*, *Myriophyllum spicatum Linn*., *Vallisneria natans*, and *Hydrilla verticillata*. Additionally, *Ceratophyllum demersum*, *Najas minor*, *Potamogeton maackianus*, *Trapa bispinosa*, and *Nymphoides peltatum* were associated species. *Nelumbo nucifera*, *Azolla imbricata*, *Salvinia natans*, *Phragmites communis,* and *Leersia hexandra* Swartz grew in the coastal shallow water marsh. In the 1980s, the main species of aquatic hydrophytes were *Vallisneria natans, Trapa bispinosa, Nelumbo nucifera, Potamogeton wrightii Morong, Ceratophyllum demersum, Hydrilla verticillata,* and *Zizania latifolia*. In 2000, the coverage was only 10.60%. During 2011-2012, the coverage of aquatic hydrophytes was approximately 5% (420 hm^2), and they were mainly distributed in the littoral zone of the lake and in the river–lake confluence areas. Among them, submerged macrophytes accounted for 44%, emerged macrophytes accounted for 30%, floating-leaved macrophytes accounted for 14%, and floating macrophytes accounted for 12% of the coverage. In 2017, there were no aquatic macrophytes in the entire lake. Subsequently, by the end of 2017, comprehensive management of Lake Datong was undertaken and aquatic hydrophytes were planted. By 2019, the coverage of aquatic macrophytes had reached 48% (Table 6).

As per the survey of aquatic hydrophytes from July to November in 2019, 7 species, 6 genera, and 6 families of aquatic hydrophytes were recorded. There were 5 families, 5 genera, and 5 species of dicots, namely *Myriophyllum verticillatum, Ceratophyllum demersum, Trapa bispinosa, Nelumbo nucifera,* and *Halerpestes cymbalaria*. The monocots had a representation of 1 family, 1 genus, and 1 species, namely, *Hydrilla verticillata*. *Myriophyllum verticillatum* grows faster in the summer and slower in winter, making it tolerant of low temperatures. The tolerance of water temperature for *Ceratophyllum demersum*is wider. *Trapa bispinosa* requires a warm, humid, and sunny environment and is not resistant to frost. The temperature required for its flowering and fruiting is 20-30 °C during daytime and 15 °C at night. *Nelumbo nucifera* is a hydrophyte that requires long hours of sunshine, a light and warm environment, and is intolerant to shade. Growing very slowly below 16 °C, *Hydrilla verticillata* likes an environment with sufficient light and warmth, and being cold resistant, it grows well in the temperature range of 15-30 °C. *Vallisneria natans* is a heliad and grows well at 18-22 °C. Therefore, from July to November, with the weakening of light intensity, decrease in light duration, and gradual decrease in temperature, the biomass of this aquatic hydrophyte also decreases (Table 7).

The survey results in 2019 (Figure 7) demonstrated that aquatic hydrophytes are mainly distributed in the western part of Lake Datong. In July, the aquatic hydrophytes were found to be distributed over an area of 39.67 km^2, which amounts to 48% of the total water surface area of Lake Datong. In September, they were distributed over an area of 27.2 km^2, and in November over 23.99 km^2,which amount to 33% and 29% of the total water surface area of Lake Datong, respectively. It can be observed that the range of distribution of aquatic hydrophytes gradually reduced from July to November. The total biomass of aquatic hydrophytes in Lake Datong in July, September, and November 2019 was 362000 t, 173000 t, and 70500 t, respectively, also displaying a gradual decrease.

3.5 Fish

Before 1980, Lake Datong was utilized only for natural fishing, by feeding seedlings into the river, with the development of aquaculture being established in the early 1980s. From 1981 to 1989, the average annual fish production was 585 t. At that point, there were 109 species of fish belonging to 23 families and 8 orders in Lake Datong. In 1989, fertilizers were beginning to be used in aquaculture. From 1990 to 1999, the average annual output of fish products from Lake Datong was approximately 1000 t, and the highest annual output was above 1600 t. In 1997, there were 8 orders, 23 families, and 109 species representation of fish. Since 2000, approximately 4000 ~ 5000 t of various inorganic fertilizers have been utilized in Lake Datong annually. From 2000 to 2004, the average annual output of fish products from Lake Datong was approximately 2000 t, with the highest annual output being 3000 t. After 2004, the annual input of various inorganic and compound fertilizers was approximately 12000 ~ 15000 t, and the aquatic output of Lake Datong increased rapidly. The average annual output was approximately 5000 t, and the highest annual yield exceeded 8000 t. In 2011, Lake Datong began to fence grass carp culture, adopt fertilization programs, and intensify cultivation. The fish yield that year exceeded 10000 t, with the yield maintained at approximately 12000 t. By 2012, the number of fish species declined to 45 species of 39 genera, 13 families, and 7 orders. From 2011 to 2015, 4500 ~ 5500 t of fish were placed into Lake Datong every year, of which *Hypophthalmichthys molitrix* and *Hypophthalmichthys nobilis* accounted for 60% of the species, *Ctenopharyngodon idella* accounted for 30% of the species, and other fish species accounted for approximately 10%.

There were 28 species from 24 genera, 8 families, and 5 orders represented in 2019 (Table 8). Among them, Cypriniformes have the most species of Cyprinidae, accounting for 89.29% of the total population, with 24 species belonging to 21 genera, 5 families, and 4 orders, found in the eastern part of China.

The total number and weight of the catch were 1486 fish and 43684.6 g, respectively. Among them, the most abundant species were goblins and minnows, the total number and weight of the catch being 1059 tails and 21486.7 g, respectively. There were 22 species belonging to 19 genera, 5 orders, 5 families, found in the northern part of the lake. The total number and weight of the catch were 935 and 53860 g, respectively. Among them, the largest number and weight of the carnivorous fish *Coilia brevicaudus* were 248 and 5768 g respectively, followed by *Carassius auratus*, which produced sticky eggs and omnivorous hydrophyte food, with 193 fish weighing 16022 g. There were 21 species belonging to 18 genera, 3 orders, and 4 families found in the western parts of lake. The number and total weight of the catch were 1180 and 77780 g respectively. Among them, the most omnivorous hydrophyte-feeding crucian carp was 598 and 47983 g in number and total weight of the catch, respectively, followed by the omnivorous hydrophyte-eating gobiocyphus and minnows at 204 and 2552 g, in number and weight respectively (Table 9). Simultaneously, there are no aquatic plants in the eastern lake area; however, there are more carnivorous fishes. The number of the *Culter Basilewsky* and *Erythroculter* were higher in the eastern Lake area, while the number of *Coilia brachygnathus* was the largest in the Northern Lake area, followed by *Culter Basilewsky* and *Erythroculter*. This is because of the few aquatic hydrophytes in the eastern Lake area, which is not conducive for the hiding of small fish, but conducive to the predation and survival of carnivorous fish. Conversely, there are abundant aquatic hydrophytes in the Western Lake area. Parabramis, Megalobrama, and Carassius, which produce sticky eggs and omnivorous hydrophyte food are the most abundant, while the number of carnivorous fish is lower. A large number of aquatic hydrophytes provide abundant food for the omnivorous and vegetarian fishes and a suitable habitat for their reproduction, and also provide shelter for small fish, ensuring their abundance. However, compared with other lakes of the same type, the number of predatory fish in the lake is lower.

3.6 Succession in aquatic environment

The sediment records of Lake Datong reveal the succession of its water environment, and the phosphorus trends in the sediment reflect the eutrophication trends (Figure 4). According to the criteria of trophic status, Lake Datong has experienced four different stages of nutrition. The first stage: from 1847 to 1930, Lake Datong was expansive, extending in all directions and connected with the Yangtze River. *Aulacoseira granulata* was the dominant species of diatoms, and it usually inhabited moderately eutrophicated aquatic environments. Its high silicification degree, high sedimentation rate, and a preference for strong disturbance in the water, indicated strong hydrodynamic conditions. The sediment suspension caused by hydrodynamic effects also affected the underwater light and primary productivity. At the time, the biomass of epiphytic diatoms and sample LOI were low, and the development of aquatic hydrophytes was not high. It is speculated that the water environment of the lake was good and the ecosystem was stable at this stage. The second stage: from 1930 to 1980, the TP began to increase slowly. Especially after 1949, Lake Datong began large-scale reclamations around the lake, and the deposition rate fluctuated greatly at this time and peaked; the numbers of planktonic species *Stephanodiscus hantzschii* and *Stephanodiscus minutulus* increased slightly. They are good indicators of eutrophication in the middle and lower reaches of the Yangtze River, and the epiphytic diatoms *Eunotia* and *Fragilaria* increased. This demonstrates that aquatic vegetation increased at this stage, and the LOI reached a peak. The development of aquatic vegetation can control the release of nutrients. At the time, the nutrient level had increased (DI-TP ranged from 50 to 60 μg/L). The dominant diatom was still *Aulacoseira granulata*, with the maximum abundance observed in 1930–1940. In the winter of 1949, a dike was built on Lake Datong, encircling the embankment to become an inner lake and cutting off the water exchange with Yangtze River. The hydrodynamic conditions consequently declined, with a decrease in the abundance of this species (DI-TP ranged from 66 to 83 μg/L). During the third stage, i.e., after 1980, aquaculture and fertilizer farming began in the lake in 1989. During this period, the sediment TP increased rapidly, and it rose to its highest point around 2001. Simultaneously, compared with 1960, the alkalinity of the water in Lake Datong significantly increased (from 7.0–7.5 to 8.4–8.8), and the redox potential of the water changed from + 592 ~ 859 to - 67.88 ~ -110.80 mv. Electrical conductivity increased 17-fold, from 0.138 to 2.363 mS/cm. The lake environment shifted from oxidized to reduced [44, 46] The TP content of the sediment also peaked around 2006, reaching 202 μg/L. At that time, *Aulacoseira granulata* biomass dropped sharply, and the biomass of epiphytic species, such as *Eunotia* and *Fragilaria*, decreased gradually, whereas planktonic species, such as *Stephanodiscus hantzschii* and *Stephanodiscus minutulus*, were replaced by the dominant species. It was accompanied by the emergence of typical eutrophic species such as *Cyclostephanos tholiformis* and *Cyclotella meneghiniana*. This indicates that Lake Datong was in a state of eutrophication (the annual average DI-TP concentration was 202 μg/L). The fourth stage: after 2010, the eutrophication level of the water declined (DI-TP ranged from 127 to 152 μg/L).

The latest survey in 2019 revealed that TP was higher between July and August, and lower between September and November. Conversely, July and August are wet months, with the farmland receding, causing a large quantity of TP to accumulate in the ditches and eventually enter Lake Datong. However, in July and August, the growth of aquatic hydrophytes in several areas of Lake Datong was too dense, resulting in an ecological imbalance of its water. Several aquatic hydrophytes began to decompose. Additionally, the water temperature of the lake was high in July and August, which accelerated the decomposition rate. The nutrients absorbed by aquatic hydrophytes during the growth period were released back to the water, causing secondary pollution.

3.7 Food web structure and trophic levels

The trophic level of each functional group in the aquatic food web of Lake Datong varied between 1 (primary producer) and 3.685 (mandarin fish) (Table 10). Primary producers included submerged hydrophytes and phytoplankton. Carnivorous fish, such as mandarin fish and calamari, occupied higher trophic positions of the Lake Datong ecosystem.

The Ecopath model analysis demonstrated that the theoretical trophic level of Lake Datong in 2019 was Level IV (Figure 8). The primary producers and detritus of the food web were defined as Level ▯, and the nutritional level of consumers increased sequentially [34, 36]. The trophic levels of the three primary producer functional groups in Lake Datong were all Level I, and the trophic levels of molluscs and zooplankton were all Level II. The energy flow of the Lake Datong food web had three main paths, including two pastoral food chains and one detrital food chain. Debris was the main energy source of the Lake Datong aquatic food web (Figure 9).

Lake Datong trophic Level Ⅰ had 11 functional groups. Among them, molluscs and small zooplankton were at Level Ⅱ, while the proportions of crucian, bream, cladocerans, and copepods at the second integrated trophic level were more than 50%. Twelve functional groups were occupying nutritional Level Ⅲ, and seven functional groups integrated at nutritional Level III, at more than 50%. Eight functional groups were occupying nutritional Level Ⅳ, and only three functional groups were in nutritional Level Ⅴ. The proportion of mandarin fish was 3.09%, and all other proportions were less than 1%, indicating that the energy flow of trophic Level Ⅴ and above can be ignored.

4. Discussion

4.1 Succession and driving factors of aquatic communities

During the development of aquaculture in Lake Datong from the 1980s to 2010s, eutrophication increased, water quality deteriorated, aquatic hydrophytes degenerated, and the composition of fish communities altered significantly. These phenomena had a severe impact on the structure of the aquatic community of Lake Datong, specifically, the degradation of aquatic hydrophytes. The impact of nutritional imbalance of nitrogen and phosphorus on aquatic hydrophytes, changes in transparency, temperature, and food network consumer’s structure all affected the growth of aquatic hydrophytes both directly and indirectly. Aquatic hydrophytes underwent long-term degradation in Lake Datong and the TP content of the sediments (DI-TP increased significantly from 66–83 μg/L to 202 μg/L) indicated that the nutrient level of the lake increased significantly during this period. Upon monitoring, the TP value of the water was found to increase while the biomass of plankton did not increase significantly, which may have caused changes in the structure of the aquatic biological community. Therefore, the significant changes in the structure of aquatic communities mainly reflect the rapid change in the composition of aquatic hydrophytes. The process of eutrophication may also affect this change in the structure of aquatic communities.

Compared to other eutrophic water bodies, Lake Datong has two unique characteristics: low phytoplankton abundance and high abundance and biomass of molluscs. According to the latest reports [48], nitrogen and phosphorus concentrations in the water of Lake Datong are as high as 3.78 mg/L and 0.29 mg/L respectively, indicating moderate eutrophication. However, the biomass and abundance of phytoplankton in Lake Datong are low, and there has not been any typical bloom in recent years. The results of a survey in August 2013 revealed that there were only 29 species of phytoplankton in Lake Datong, and the phytoplankton abundance was at $10.16 \pm 5.02 \times 10^4$ ind/L [49]. Lake Datong is rich in molluscan resources, with up to 120000 t. *Bellamya purificata, Unio douglasiae, Hyriopsis cumingii* and *Corbicula fluminea* [46]. Our findings, however, are contrary to observations made in other aquaculture lakes [50-52] (Table 11). Aquaculture activities in Lake Datong did not reduce the abundance and biomass of soft-bottom animals in the aquaculture area. Studies have demonstrated that excessive consumption of zooplankton by the molluscs *Hypophthalmichthys molitrix* and *Hypophthalmichthys nobilis* is also the main reason for the low biomass of zooplankton and irregular changes in their abundance. *Anodonta woodiana* can significantly reduce the standing crop of phytoplankton and change its community structure, reduce the proportion of Cyanophyta, and increase the proportion of Chlorophyta [53]. Additionally, *Corbicula fluminea* also had indirect effects on the structure of the phytoplankton community. Zhu et al. demonstrated that filter-feeding of *Corbicula fluminea* could significantly reduce the concentration of suspended solids and the content of chlorophyll-a [54]. Molluscs such as *Corbiculidae* and *Unionidae Viviparidae* are substantial in Lake Datong. The abundant of molluscs inhibited algae bloom considerably and maintained the phytoplankton abundance of Lake Datong at a level lower than those of other eutrophic aquatic environments for a long time. In 2017, the community structure of aquatic hydrobionts in Lake Datong was significantly regulated by reducing sewage discharge, restoring aquatic hydrophytes, and prohibiting aquaculture. The loss of habitat has been established through indicators, such as decrease in the biomass and abundance of aquatic communities. It is therefore one of the main driving factors for the succession of aquatic communities in Lake Datong.

4.2 Food web structure

In mature systems, the total primary production/total respiration (TPP/TR) is close to 1, and the difference between the two is close to 0. For immature systems, respiration is lower than primary production, therefore, TPP/TR is greater than 1. As the system matures, biomass can accumulate. Therefore, immature systems have the highest total primary production to total biomass (TPP/TB) values, which gradually decreases as the system matures. Connectance index (CI) and system omnivorous index (SOI) reflect the complexity of a system's internal connections. The more mature a system is, the more complex the connections (food network) between its functional groups. Therefore, the CI and SOI are positively correlated with the maturity of the system. The more mature the ecosystem, the stronger the connections between the functional groups and the more stable the system. The CI and SOI of mature ecosystems are close to 1. The maturity of the ecosystem was also evaluated using Finn's cycling index (FCI) and Finn's mean path length (FMPL) [62].

The ecosystem statistics and key indicators of Lake Datong and five other similar lakes are presented in Table 12, including community energetics, with the accumulation and continuous increase of the system biomass. The TPP/TR ratio of Lake Datong obtained from our model was 7.544, and the net primary productivity was 20,061.23 t/(km^2.a). This demonstrates that there are many nutrients in the ecosystem of Lake Datong that have not been utilized. The TPP/TB of the Lake Datong ecosystem was 1.231. The CI of Lake Datong was 0.277 and the SOI was 0.070. This indicates that the structure of Lake Datong’s food network ecosystem was fragile, with a low-level complexity of internal connections and low maturity. The FCI of Lake Datong was 17.55%, and the FMPL was 2.923. Mature systems typically exhibit are high levels of material recycling and long paths of nutrient flows in food chains [34]. Both the characteristics were low, which indicated low degrees of material circulation in the Lake Datong ecosystem. This means that the unused components of each functional group that entered the clastic formation were separated from the system due to mineralization and deposition.

4.3 Limitations and scope for future research

Ecological restoration is not an attempt to restore the same ecological community at a certain point in time but to maximize the potential for restoration and continuous reorganization and adaptation of local species and communities to facilitate the restoration of the prior levels of various ecosystem functions [67]. There are few studies on ecological restoration of aquaculture lakes at present. Ting, et al., showed that with 50% reduction in aquaculture area, the TP concentrations of 58.7 % of the lake in summer and 63.1% of the Lake area in autumn are lower than 0.05 mg/L, and aquatic plants will recover in most areas of the lake [68]. In the restoration process of shallow lakes in the middle and lower reaches of the Yangtze River in China, Lake Dianchi [68], Lake Donghu [70], and Lake Taihu [71, 72] showed good performance through the restoration of aquatic organisms to reduce eutrophication. However, under poor management, aquatic plants were found to re-release large amounts of nutrients during the decay period, which can promote eutrophication of lakes [73, 74]. Studies have shown that in the early stages of restoring shallow eutrophic lakes, the number of fish should be reduced, and aquatic plants should be restored to reduce eutrophication. When the aquatic community tends to be stable, herbivorous and omnivorous fish should be stocked appropriately, and aquatic plants should be harvested in the early stages of decline to maintain a healthy and sustainable development of the ecosystem [14].

In short, in the process of aquatic ecological restoration of aquaculture lakes, we need to accurately control the aquatic biomass, increase the species diversity of aquatic organisms, improve the structure of food chain, make the food chain more reticular, and enhance the integrity of the aquatic ecosystem through ecosystem analysis; at the same time, the best ecological restoration plan should be determined in combination with the research results concerning other vital aspects.

5. Conclusion

1. We reconstructed four trophic succession stages of Lake Datong over the past 150 years, using the succession of sediment diatom populations and the TP concentration of the water. According to the criteria of trophic status, before 1930, Lake Datong was in a mesotrophic state (DI-TP ranged from 50 to 60 μg/L). Between 1930 and 1980, the number of nutrient-tolerant species increased slightly, which indicates an increase in nutrient enrichment in Lake Datong (DI-TP ranged from 66 to 83 μg/L). From the 1980s to 2010, eutrophication increased rapidly, especially since 2000, where the eutrophic species had been dominant in the diatom assemblage (the annual average value of DI-TP was 202 μg/L). After 2010, the nutritional level dropped (DI-TP ranged from 127 to 152 μg/L).

2. We successfully established an ecosystem model of Lake Datong for determining the nutrient structure and energy flow efficiency among its different nutrient levels after comprehensive management. The TPP/TR and TPP/TB values of Lake Datong ecosystem are higher than those of the other five lakes in the middle and lower reaches of the Yangtze River. However, TE, FCI, FMPL, CI, and SOI are lower, which indicates that the Lake Datong ecosystem is in an unstable state after comprehensive management in 2017.

3. We reproduced the succession of the water ecosystem of Lake Datong from the past by collating its historical data. At present, the consumer biomass of Lake Datong is at a relatively lower level, and the biomass of submerged hydrophytes higher, meaning a large quantity of primary produce cannot be used by consumers, cannot enter the food web, which consequently reduces the energy TE of the ecosystem. Future management needs to formulate an aquatic ecological control plan, especially Removing macrophytes, stocking herbivorous and omnivorous fish, and rational fishing can not only enhance the energy flows and nutrient cycling of the ecosystem, but also improve the food web structure.

These results of the present study could be invaluable for policy-makers and local stakeholders in facilitating the assessment of the impact of environmental change in Lake Datong and can also be used to support similar aquaculture lakes, after comprehensive management planning and strategic decision-making.

Abbreviations

CI: Connectance index

DI-TP: Diatom Inferred-Total Phosphorus

EQSSW: Environmental Quality Standards for Surface Water

FCI: Finn's cycling index

FMPL: Finn's Mean Path Length

ICPAES: Inductively Coupled Plasma Atomic Emission Spectroscopy

LOI: Loss-on-ignition

TB: Total Biomass

TE: Transfer Efficiency

TL: Trophic Grade

TN: Total Nitrogen

TP: Total Phosphorus

TPP: Total Primary Production

TR: Total Respiration

TST: Flux in the System

SOI: System omnivorous index

Declarations

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Authors' contributions

WH: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft; CHL: Validation, Resources, Writing - Review & Editing, Supervision; CY: Validation, Resources, Writing - Review & Editing, Supervision; HSC and XSL: Formal analysis, Investigation; JX: Methodology, Formal analysis; DLL: Investigation. All authors read and approved the final manuscript.

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Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Tables

Table 1. Environmental Quality Standards for Surface Water (EQSSW) nutrient water quality standard of China (unit: mg/L)

Rank	Parameters	I	II	III	IV	V
1	TN	0.2	0.5	1	1.5	2
2	TP	0.02 (0.01/lake and reservoir)	0.1 (0.025/lake and reservoir)	0.2 (0.05/lake and reservoir)	0.3 (0.1/lake and reservoir)	0.4 (0.2/lake and reservoir)

Table 2. Phytoplankton succession in Lake Datong

Years	Number of species	Abundance and biomass	Dominant species	H value	J value	D value	References
1960 Winter	5 Domain	2 180 000 ind/L	Cyanophyta: 69.7%				[38]
1997	8 Domain, 64 Genus	1 780 000 ind/L					[39]
2005 Spring	6 Domain, 12 Genus	1 724 000 ind/L; 3.156mg/L					[40]
2008-2009	7 Domain, 54 Genus, 98 Species	1 640 000 ind/L Summer; 1 710 000 ind/L winter		Average value: 2.045 Highest in winter: 2.69 Lowest in summer: 1.26	Average value: 1.037 Highest in winter: 1.27 Lowest in summer: 0.69	Average value: 3.11 Highest in spring: 4.55 Lowest in autumn: 2.25	[37]
2011 Summer	5 Domain, 29 Species	8 560 000 ind/L	Cyanophyta: 65.34%				[41]
2011-2012		1 850 000-61 000 000 ind/L	Cryptophyta: 50-90%				[42]
2013-2014	7 Domain, 80 Species	6.58±0.66×10⁴ ind/L; 0.16±0.05 mg/L	Euglenophyta: *Euglena polymorpha;* Cryptophyta: *Cryptomonas ovata, Chroomonas acuta,* Bacillariophyta: *Cyclotlla caclotella;* Chlorophyta: *Chlorella vulgaris, Chlamydomonas incerta, Scenedesmus quadricauda*	Average value: 1.24 Highest in August: 2.08 Lowest in November: 0.72	Average value: 0.68 Highest in May: 0.86 Lowest in November: 0.31	Average value: 0.75 Highest in August: 1.15 Lowest in April: 0.38	[43]
2019 Summer	8 Phylum, 197 Species	1 020 765 ind./L; 0.871 mg/L	Chlorophyta	3.241-3.806, Average value: 3.549	0.4463-0.587, Average value: 0.555	4.093-6.792, Average value: 6.773	-

H-index: Shannon diversity index; J-index: Pielou evenness index; D-index: Margalef richness index

Table 3. Zooplankton succession in Lake Datong

Years	Number of species	Abundance and biomass	Dominant species	References
1960 Winter		371 ind/L	Calanoida: 84%	[38]
1997	45 Genus	2930 ind/L	Rotifers, Protozoa	[39]
2005 Spring	13 Genus	2205000 ind/L; 4.400 mg/L	*Brachinous urceus*, *Daphnia pulex* and *Sinocalanus sinensis*	[40]
2011 Summer	21 Species	89307 ind/L	Rotifers	[41]
2011-2012		8000-125000 ind/L	Protozoa	[42]
2013-2014	20 Genus, 46 Species	1013±198 ind/L; 5.12±1.61 mg/L	*Tintinnopsis sinensis*, *Brachionus diversicornis*, *Asplanchna priodonta*, *Polyarthra trigla*, *Filinia longiseta*, *Bosmina longirostris*, *Cyclops strenuus*	[43]
2019 Summer	3 Phylum, 15 Order, 34 Family, 60 Genus, 106 Species	Micro-zooplankton: 31 ind/L;912.91 mg/L; meso-and macro-zooplankton: 19870 ind/L;5.471 mg/L	Copepods: *Nauplii*, *Microcyclops varicans*, *Limnoithona sinensis*, *Cyclops strenuus*, *Thermocyclops hyalinus*, *Tropocyclops prasinus prasinus*, *Psammophilocyclops trispinosus*; Cladocera: Bosmina longirostris, *Bosminopsis deitersi*, *Ceriodaphnia quadrangula*, Bosmina coregoni, *Diaphanosoma leuchtenbergianum*, *Moina micrura*, *Diaphanosoma brachyurum*, *Bosmina fatalis Burckhardt.* Protozoa: *Strombidium viride*, *Halteria grandinella*, *Pleurimema cornatum*, *Pyxidicula operculata*, *Arcella arenaria*, *Pseudodifflugia gracilis*, *Difflugia urceolata*, *Acanthocystis turfacea.* Rotifers: *Trichocerca pusilla*, *Asplanchna brightwelli*, *Polyarthra euryptera.*	-

Table 4. Molluscan succession in Lake Datong

Years	Number of species	Abundance and biomass	Dominant species	References
1960 Winter	21 Species	232 ind./m^2; 97.71 g/m^2	*Hyriopsis cumingii, Arconaia lanceolate, Lanceolaria glayana, Limnoperna lacustris, Unio douglasiae, Corbicula fluminea, Sphaerium sp., Solenia oleivora, Sphaerium lacustre, Anodonta woodiana*	[38]
1997	30 Species			[39]
2008-2009	5 Family, 10 Genus, 15 Species	598 ind./m^2; 3637.71 g/m^2	*Bellamya purificata, Corbicula fluminea, Unio douglasiae*	[44]
2011 Summer	5 Family, 13 Species	566 ind./m^2; 913.375 g/m^2	*Bellamya purificata, Corbicula fluminea*	[41]
2015-2017		165.38 ind./m^2, 547.67 g/m^2, 2015; 486.02 ind./m^2, 854.77 g/m^2, 2016; 546.70 ind./m^2, 903.90 g/m^2, 2017	*Bellamya purificata, Corbicula fluminea, Unio douglasiae, Lanceolaria gladiola, Schistodesmus lampreyanus*	[45]
2019 Summer	2 Order, 3 Family, 7 Genus, 7 Species	1146.67 ind./m^2; 162.55 g/m^2	*Bellamya purificata, Cristaria plicata*	-

Table 5. Survey of molluscs in Lake Datong in 2019

Order	Family	Genus	Species	Biomass (×10^3 t)
Mesogastropoda	Viviparidae	Bellamya	*Bellamya purificata*	2.7406
Eulamellibranchia	Unionidae	Arconaia.	*Cristaria plicata*	3.86314
		Douglasiae (undetermined)	*Unio douglasiae*	2.9156
		Cuneopsis (undetermined)	*Lanceolaria gladiola*	0.80178
		Schistodesmus	*Arconaia lanceolata*	0.34987
		Lepidodesma	*Hyriopsis cumingii*	0.71431
	Corbiculidae	Corbicula	*Corbicula fluminea*	0.29156
In total				11.67686

Table 6. Succession of aquatic hydrophytes

Years	Number of species	Coverage rate	Distribution location	Biomass (wet weight)	Dominant species	References
1960 Winter		30%	Southern part	1400-1760 g/m^2	*Potamogeton wrightii Morong, Myriophyllum spicatum* Linn., *Vallisneria natans, Hydrilla verticillata*	[38]
1982	More than 50 Species			2332.1 g/m^2	*Vallisneria natans*	[46]
1997	19 Family, 41 Genus, 86 Species	16.09%				[39]
2000	26 Family, 39 Genus, 56 Species	10.60%	West part	1946.6 g/m^2		[47]
2011-2012	24 Genus, 24 Species	5%	West part		*Vallisneria denseserrulata, Potamogeton crispus, Trapa bispinosa*	[42]
2011 Summer	24 Genus, 24 Species	5%				[41]
2019 Summer	6 Family, 6 Genus, 7 Species	30-40%	West part and river–lake confluences	20 g/m^2	*Ceratophyllum demersum, Vallisneria natans, Trapa bispinosa, Hydrilla verticillate, Myriophyllum verticillatum, Nelumbo nucifera*	-

Table 7. Aquatic macrophytes survey in 2019

	Family	Genus	Species	Life form	Survey time		
					July	September	November
Dicotyledons	Haloragidaceae	Myriophyllum	*Myriophyllum verticillatum*	Submerged macrophytes	√	√	√
	Ceratophyllaceae	Ceratophyllum	*Ceratophyllum demersum*	Submerged macrophytes	√	√	√
	Trapaceae	Trapa	*Trapa bispinosa*	Floating-leaved macrophytes	√	√	
	Nymphaeaceae	Nelumbo	*Nelumbo nucifera*	Emerged macrophytes	√	√	√
	Ranunculaceae	Halerpestes	*Halerpestes cymbalaria*	Floating macrophytes		√	
Monocotyledons	Hydrocharitaceae	Hydrilla	*Hydrilla verticillata*	Submerged macrophytes	√	√	
		Vallisneria	*Vallisneria natans*	Submerged macrophytes	√		

Table 8. Fish succession in Lake Datong

Years	Number of species	Biomass	Dominant species	References
1997	8 Order, 23 Family, 109 Species	1500 t	*Hypophthalmichthys molitrix, Hypophthalmichthys nobilis*	[39]
2011-2012	7 Order, 13 Family, 39 Genus, 45 Species	16000 t	*Hypophthalmichthys nobilis, Ctenopharyngodon idella*	[42]
2011 Summer	6 Order, 12 Family, 32 Species		*Cyprinidae* is dominant: 59.4%	[41]
2019 Summer	5 Order, 8 Family, 24 Genus, 28 Species		*Cyprinidae* is dominant	-

Table 9. Statistics of fish resources in Lake Datong

Order	Family	Genus	Species	First time							
				Eastern Lake area			Northern Lake area			Western Lake are	
				Species	Number	weight (g)	Species	Number	weight (g)	Species	Numbe
Cypriniformes	Cyprinidae	Megalobrama	*Megalobrama amblycephala*							+	6
		Pseudorasbora	*Pseudorasbora parva*	+	17	44.6	+	5	13		
		Hemibarbus	*Hemibarbus maculatus*	+	1	236				+	1
		Cultrichthys	*Cultrichthys erythropterus*	+	7	599.5	+	14	1158	+	14
		Hemiculter	*Hemiculter leucisculus*	+	497	6195	+	164	1877	+	167
			Hemiculter bleekeri	+	252	7931.9	+	11	428	+	6
		Hemiculter leucisculus	*Hemiculter bleekeribleekeri*	+	310	7359.8	+	13	287	+	31
		Erythroculter	*Erythroculter dabryi*	+	35	2118.9	+	28	2404	+	36
		Culter Basilewsky	*Culter alburnus*	+	21	1273.5	+	43	1974	+	64
			Culter mongolicus Basilewsky	+	38	3513	+	32	3555	+	25
		Carassius	*Carassius auratus auratus*	+	89	6200.4	+	193	16022	+	598
			Cyprinus capiofurong				+	12	4794	+	3
		Paracanthobrama	*Paracanthobrama guichenoti*	+	44	2882.5	+	22	174	+	16
		Acheilognathus	*Acheilognathus macropterus*	+	22	363.5				+	3
		Parabramis	*white bream*	+	4	475	+	1	4	+	1
		Cyprinus	*Cyprinus carpio*	+	4	1151.4	+	14	6159	+	9
		Squalidus	*Squalidus argentatus*	+	22	326.8	+	38	376	+	4
		Saurogobio	*Saurogobio dabryi*	+	3	73	+	8	148		
		Hypophthalmichthys	*Hypophthalmichthys nobilis*	+	2	117	+	26	7832	+	36
			Hypophthalmichthys molitrix							+	7
		Ctenopharyngodon	*Ctenopharyngodon idella*								
		Squaliobarbus	*Squaliobarbus curriculus*								
		Sarcocheilichthys	*Sarcocheilichthys sinensis*	+	36	580					
			Sarcocheilichthys nigripinnis	+	6	40.9	+	5	32	+	1
		Rhodeus	*Rhodeus sinensis*	+	13	156.2	+	17	36		
Siluriformes	Bagridae	Pelteobagrus	*Pelteobagrus fulvidraco*	+	54	1749.6	+	33	713	+	68
	Siluridae	Silurus	*Silurus spp*								
Perciformes	Mastacembelidae	Macrognathus	*Mastacembelus aculeatus*	+	6	88.1	+	6	100		
	Serranidae	Siniperca	*Siniperca chuatsi*	+	2	204					
	Channidae	Ophiocephalus	*Channa argus*								
Clupeiformes	Engraulidae	Coilia	*Coilia brachygnathus*				+	248	5768	+	84
Beloniformes	Belonidae	Tylosurus	*Tylosurus melanotus*	+	1	4	+	2	6		

Note "+" indicates the species investigated; "✓" indicates food habits.

Table 10. Trophic level of each functional group in Lake Datong ecosystem

Rank	Function group	Trophic level
1	Siniperca	3.685
2	Erythroculter	3.437
3	Pelteobagrus	2.66
4	Coilia	3.06
5	Megalobrama and Parabramis	2.016
6	Cyprinus	2.681
7	Carassius	2.221
8	Hypophthalmichthys nobilis	2.935
9	Hypophthalmichthys molitrix	2.603
10	Small fish	2.522
11	Mollusca	2
12	Protozoans and Rotifers	2
13	Cladocera	2.02
14	Copepods	2.02
15	Phytoplankton	1
16	Submerged Macrophytes	1
17	Detritus	1

Table 11. Comparison of mollusca biomass and abundance between Lake Datong and other lakes in the middle and lower reaches of the Yangtze River

	Area	Average water depth	Biomass	Abundance	References
Taihu Lake (2006-2007)	2338	1.9	102.2	266	[55]
Taihu Lake (2014)	2338	1.9	145	141	[56]
Gehu Lake (2009-2010)	146. 5	1.5	17. 32	8.5	[57]
Honghu Lake (2009-2010)	344	1	333.33	544	[58]
Chihu Lake (2009-2010)	90	1.7	64.32	252	[58]
Dazhi Lake (2009-2010)	69	0.9	235.15	410	[58]
Junshan Lake (2009-2010)	193	3.9	179.71	152	[58]
East Lake Wuhan (2009-2010)	34	3.5	1.34	16	[58]
South Dongting Lake (2013)	-	Maximum water depth: 23.5	279.3	173.1	[59]
Changdang Lake (2011-2012)	90	0.8-1.2	62..38 ± 65. 31	40 ± 57	[60]
Yangcheng Lake (2014-2015)	120	2.1	179.664	199.6	[61]
Lake Datong (2008-2009)	82.67	2.5	3637.71	598	[44]
Lake Datong (2019)	82.67	2.5	162.55	1146.67	-

Table 12. General characteristics of Lake Datong and five other lakes

	Lake Taihu (2008-2009)	Lake Hongze (2010)	Dianchi (2009-2010)	Lake Chaohu (2007-2010)	Lake Gehu (2010)	Lake Datong (2019)	Unit
Sum of all consumption	16760.9	9544.719	61614.648	4486.47	2665.828	13264.96	$t/(km^2{\cdot}a)$
Sum of all exports	15299.5	985.067	10418.098	16796.60	2184.73	20061.23	$t/(km^2{\cdot}a)$
Sum of all respiratory flows	4635.6	7138.957	15675.121	1308.45	829.088	3065.423	$t/(km^2{\cdot}a)$
Sum of all flows into detritus	29549.5	5473.198	56752.813	18411.37	2892.898	31203.67	$t/(km^2{\cdot}a)$
Total system throughput (TST)	66245.5	23141.94	144752.81	41003.08	8562.544	67595.28	$t/(km^2{\cdot}a)$
Sum of all production	20535.3	8620.33	30578.686	17937.42	1974.82	26214.06	$t/(km^2{\cdot}a)$
Transfer efficiency (TE)	4.1	6.43	4.9	6.9	6.4	0.339	%
Net primary production (NPP)	14903.2	8123.513	26093.305	17703.42	1815.238	23126.66	$t/(km^2{\cdot}a)$
Total primary production/total respiration TPP/TR	4.125	1.138	1.665	13.53	2.189	7.544	
Net ecosystem production (NEP)	10691.5	984.556	10418.093	16394.97	986.151	20061.23	$t/(km^2{\cdot}a)$
Total biomass (excluding detritus)		1173.547	422.141	128.36	517.286	1.231	$t/(km^2{\cdot}a)$
Connectance index (CI)	0.188	0.195	0.194	0.20	0.219	18781.15	
System omnivorous index (SOI)	0.041	0.089	0.061	0.092	0.189	0.083	
Finn's cycling index (FCI)	18.3	6.77	39.980	3.32	7.99	17.55	%
Finn's mean path length (FMPL)	3.32398	2.849	5.536	2.27	2.841	2.923	
References	[63]	[64]	[65]	[62]	[66]	-	

Figures

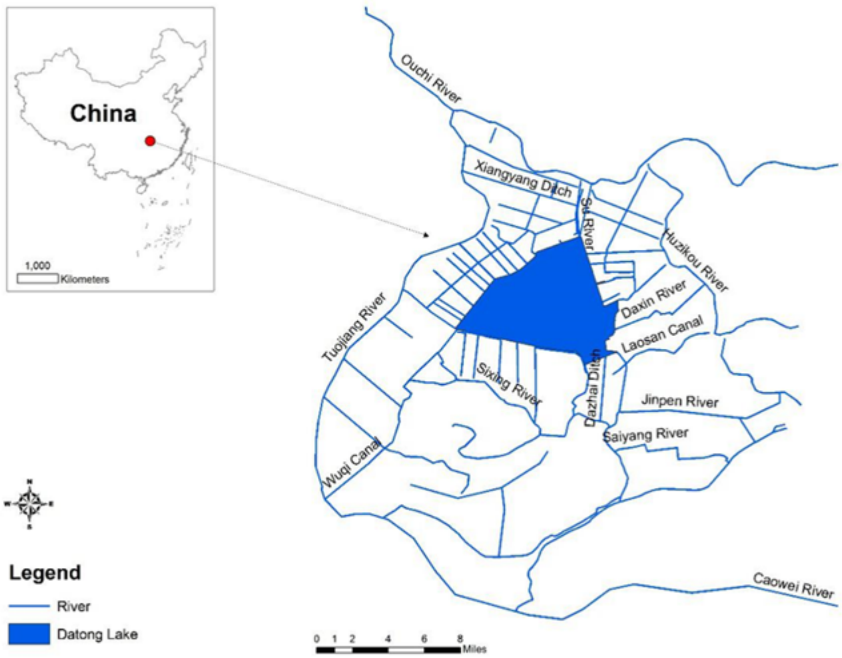

Figure 1

Location of the study area.

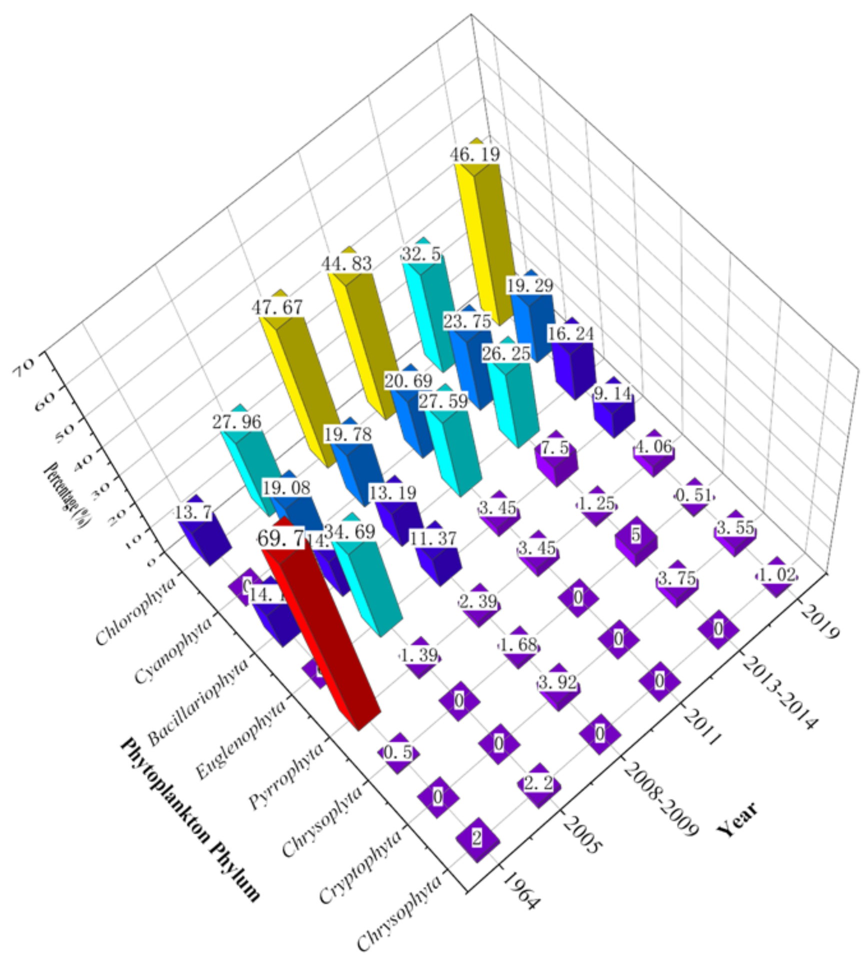

Figure 2

Succession of phytoplankton species.

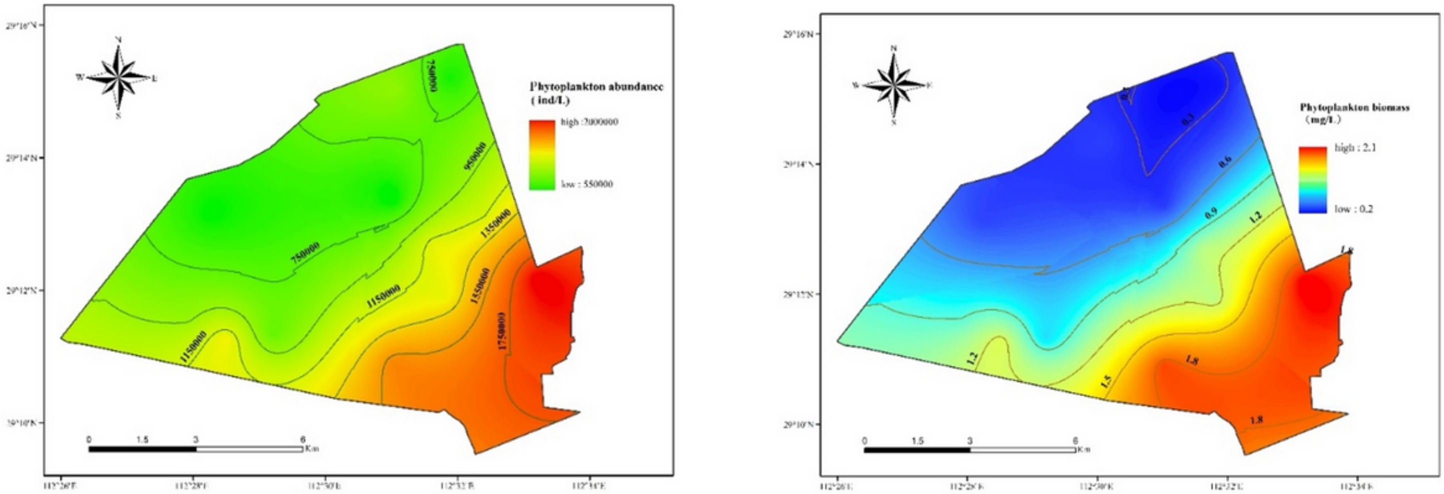

Figure 3

Spatial distribution of the abundance and biomass of phytoplankton in Lake Datong in 2019.

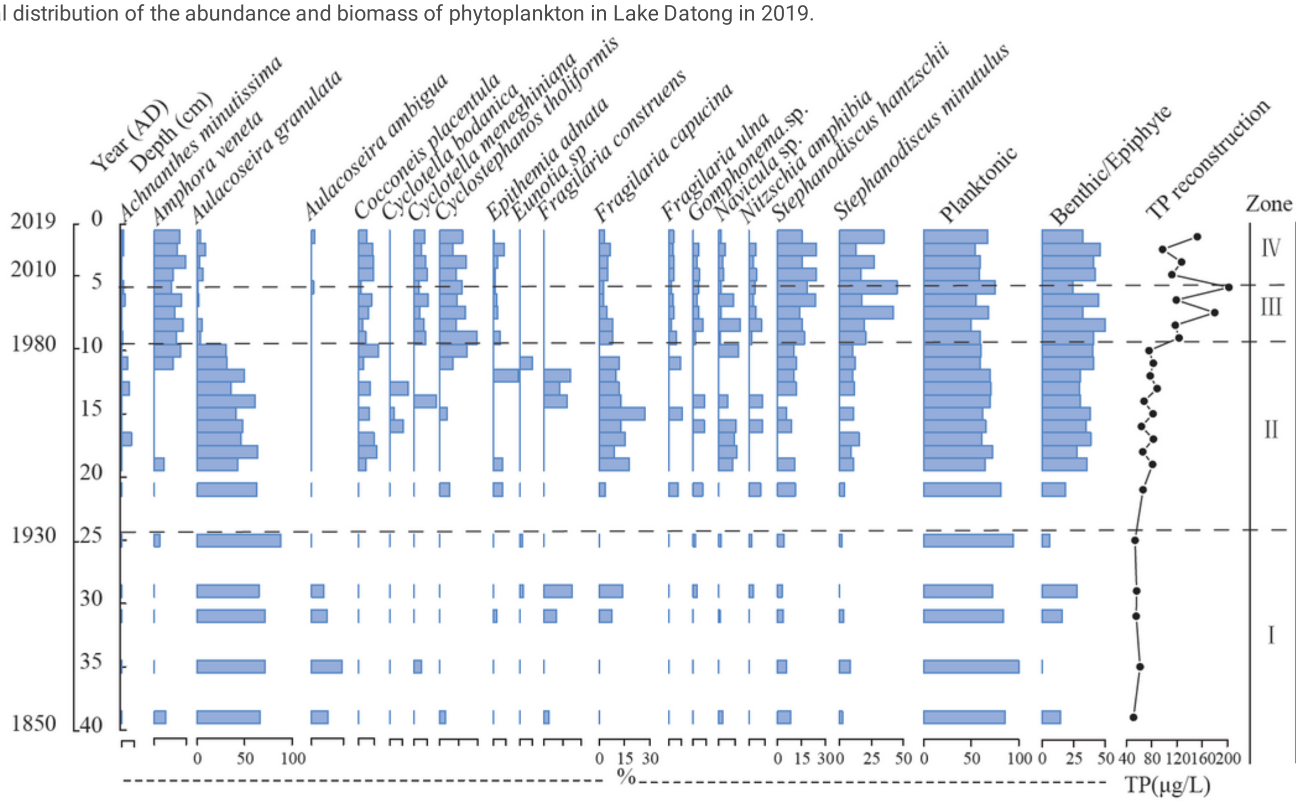

Figure 4

Succession of diatom population in sediments of Lake Datong and reconstruction of the total phosphorus (TP) concentration in the water.

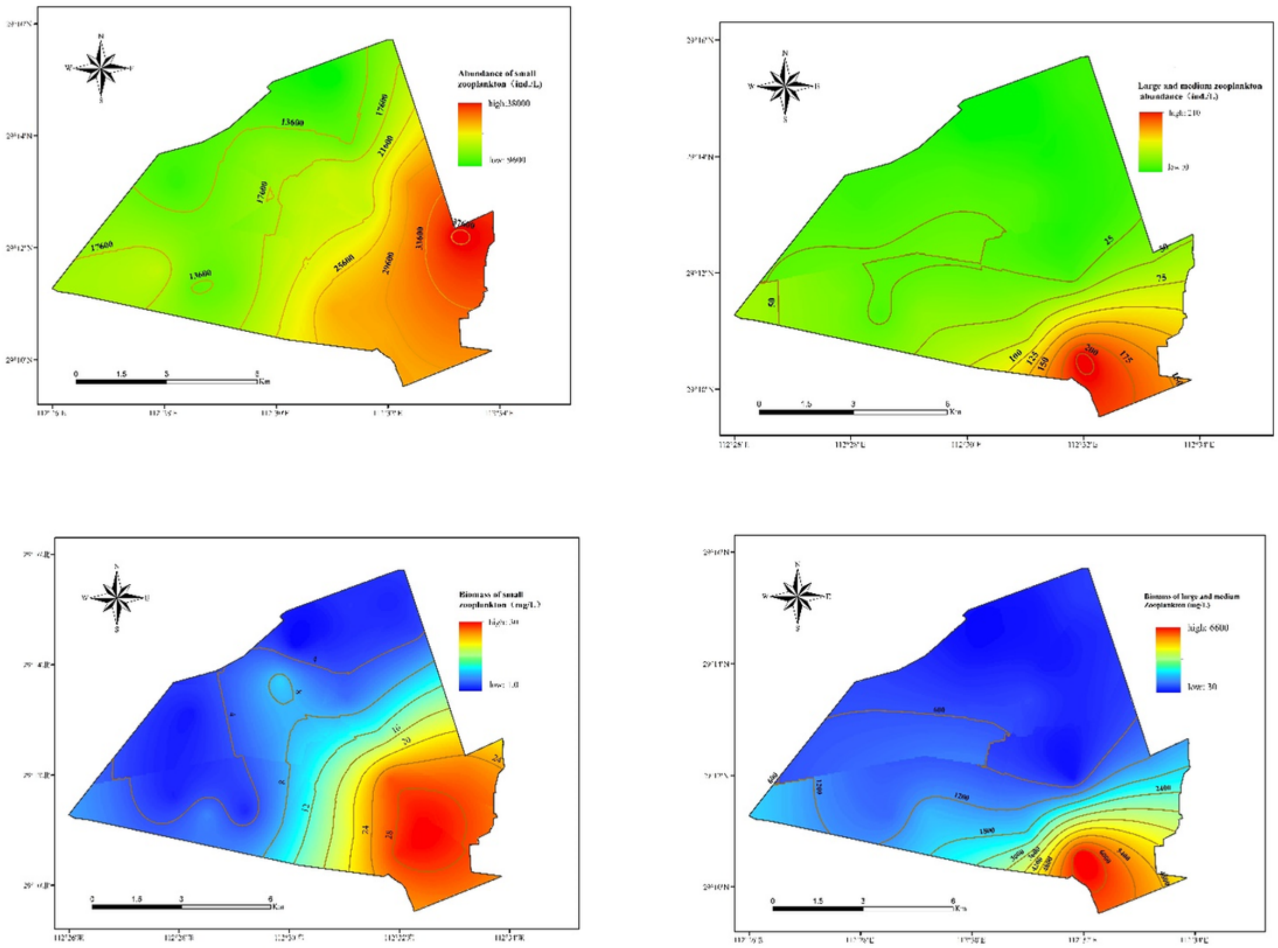

Figure 5

Spatial distribution of the abundance and biomass of zooplankton in Lake Datong.

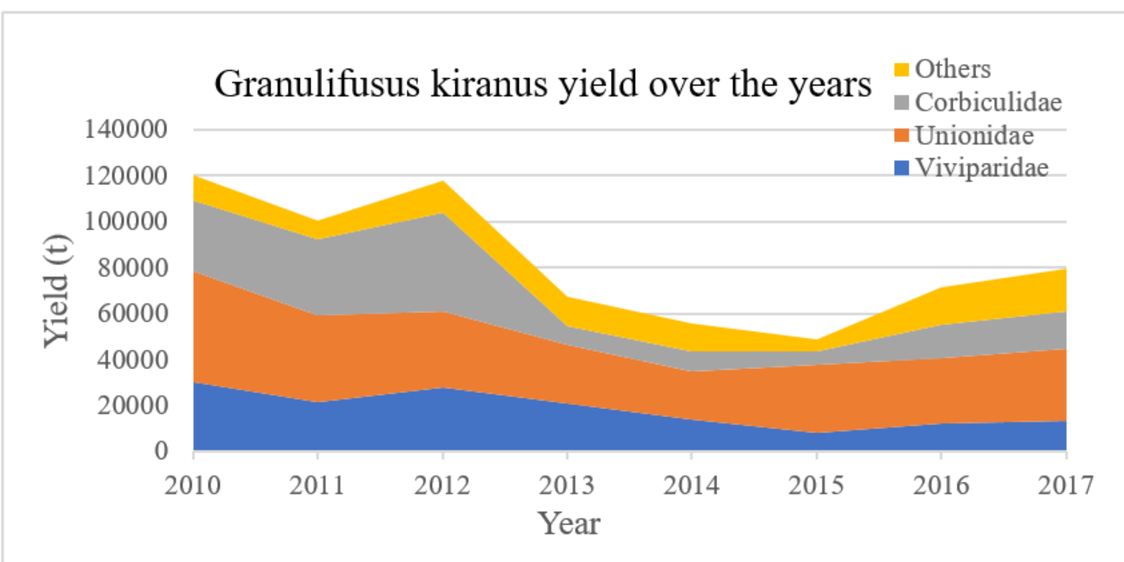

Figure 6

Mollusc production in Lake Datong (2010–2017).

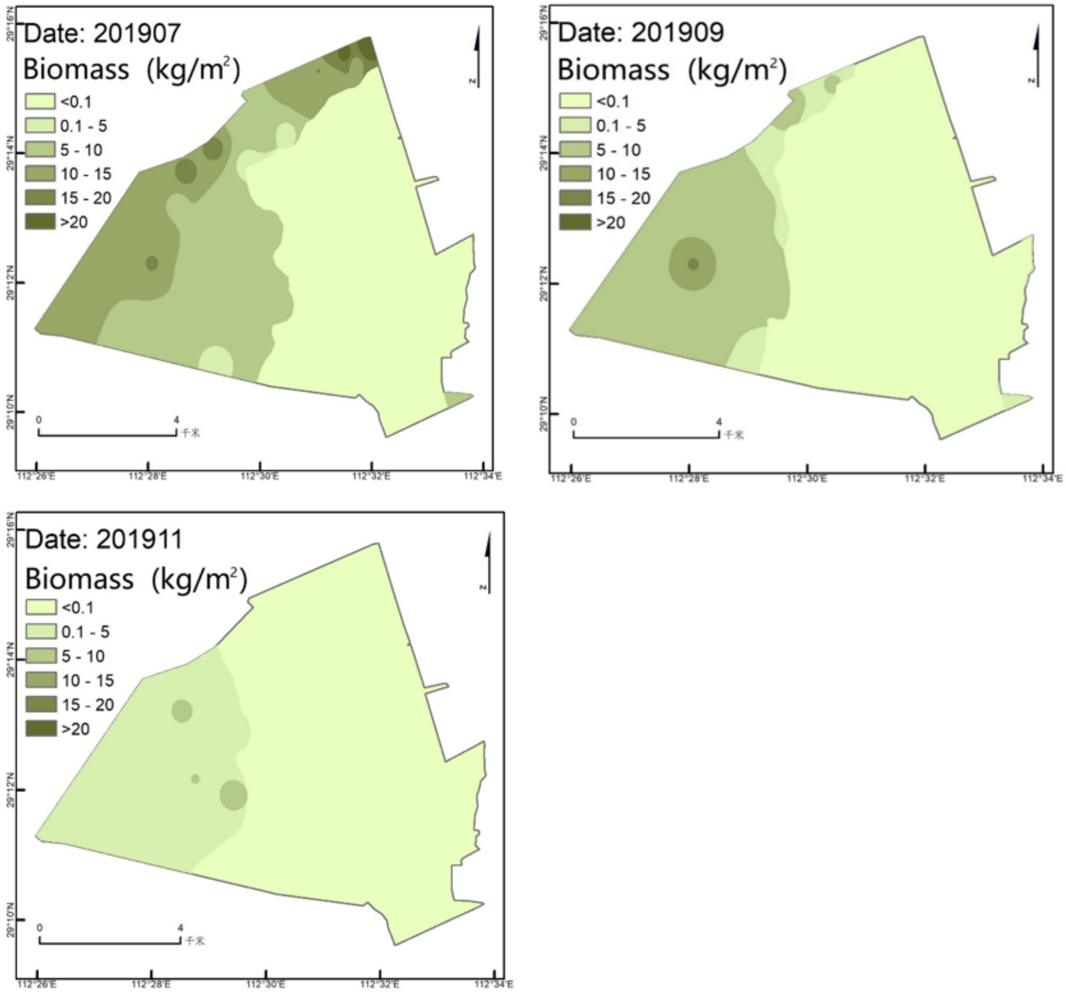

Figure 7

Distribution map of aquatic hydrophytes in Lake Datong.

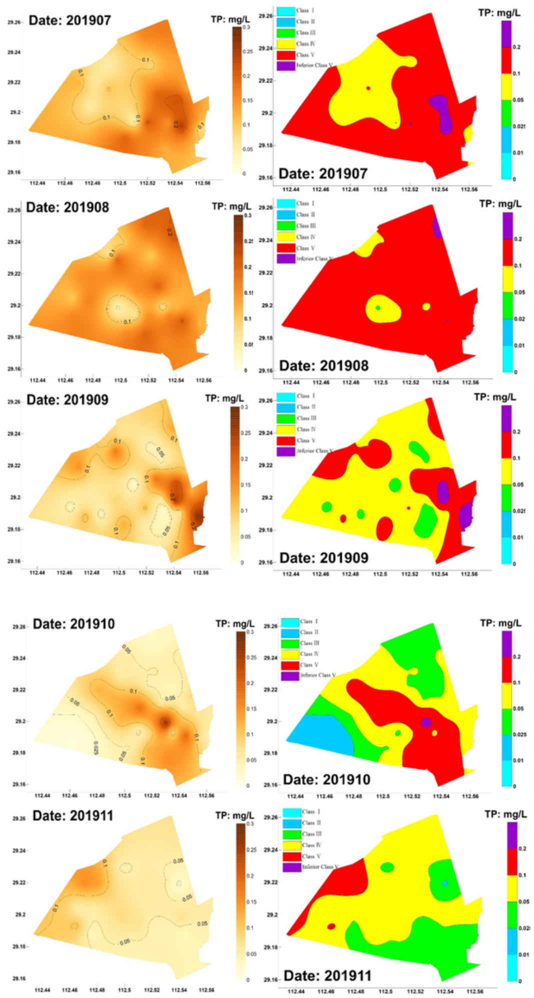

Figure 8

Spatial distribution pattern of total phosphorus (TP).

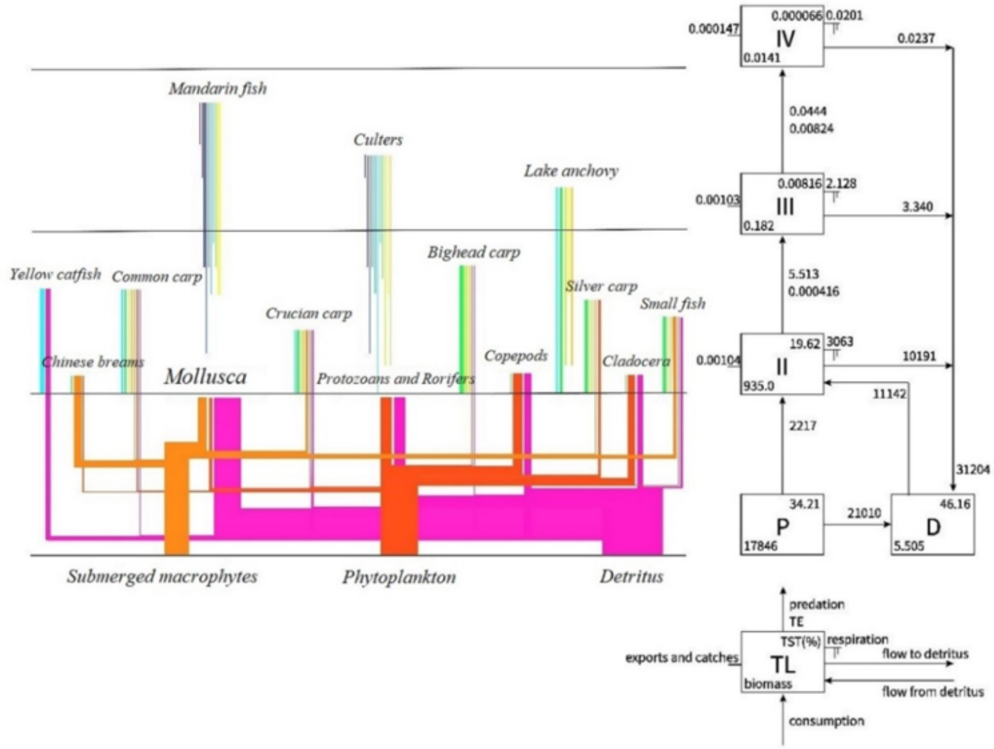

Figure 9

Structure of the food web and energy flow diagram of Lake Datong. P: producer; D: detritus; TL: trophic grade; TST (%): flux in the system (%); TE: transfer efficiency.