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Enhancing Fishery Management in Tanghe Reservoir, China: Insights from Food Web Structure and Ecosystem Analysis

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Abstract: Situated within China's Liaoning Province, Tanghe Reservoir stands as an exemplar in the realm of reservoirs dedicated to eco-friendly fisheries development. Regrettably, frequent incidents compromising water quality and substantial reductions in reservoir fishery profits have plagued the area due to the absence of effective stocking theory guidance. However, the internal ecosystem drivers responsible for these outcomes have remained elusive. This study, leveraging an Ecopath model, delves into an exploration of the food web structure and ecosystem characteristics inherent to Tanghe Reservoir. The findings gleaned from this research demonstrate that the Tanghe Reservoir ecosystem boasts a considerable capacity for material cycling, yet it has not reached full maturity. A multitude of fish species, zoobenthos, and even zooplankton entities exhibit eco-trophic efficiencies exceeding 0.9, indicative of their rampant overexploitation. Notably, the primary cultured species, *Aristichthys nobilis* and *Hypophthalmichthys molitrix*, command significant biomass levels but register lower nutritional conversion efficiencies, signifying their overstocked status. Drawing from the tenets of maximum sustainable yield (MSY) theory, we advocate for a heightened emphasis on the harvest of *Aristichthys nobilis* and *Hypophthalmichthys molitrix*.

Keywords: Tanghe Reservoir; food web structure; ecopath with Ecosim; fishery management

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1. Introduction

Fisheries play a vital role in supporting human livelihoods [1]. China's lakes and reservoirs have abundant ecological resources, making them crucial assets for freshwater fisheries. In 2021, the inland freshwater aquaculture area in lakes of China have reached 6634.0 km^2, while reservoirs have reached 14,393.3 km^2. Compared with previous years, the aquaculture area of lakes is experiencing a decline of 7.94%, while the aquaculture area of reservoirs increased by 1.3% [2]. In recent years, the eutrophication of water bodies has been a frequent problem due to the constant entry of nutrients such as nitrogen and phosphorus [3–5]. In order to protect the safety of water sources as well as to realize the rational use of resources, the ecological fishery model, in which bighead carp and silver carp are the main species to be cultured, has developed rapidly [6,7]. However, problems such as inappropriate technology and nonstandard operations continue to affect fishery resource enhancement, conservation, and ecological stability [8,9]. Effective fishery management is essential to ensure the long-term sustainability of fish stocks and to maintain ecological balance [10].

A wide array of ecological models has been developed to assess food web dynamics, ecosystem structure, and functioning, encompassing both traditional predator–prey models and contemporary ecosystem-based approaches. Ecopath with Ecosim is one of the most popular modeling techniques used to study the food web structure of aquatic ecosystems [11]. This methodology has been extensively employed to characterize the structure and function of aquatic food networks, as well as to assess the impact of fishery activities and environmental changes [12–15].

In the year 2021, the aggregate output of China's large water surface fishery reached 119.8 × 104 tons, reflecting a year-on-year contraction of 17.8%. In this context, Liaoning Province held the ninth position in the national rankings, contributing a total of 3.7 × 104 tons. Furthermore, concerning the per capita possession of aquatic products, Liaoning Province secured third place nationwide, boasting an impressive value of 113.7 kg per individual (China, 2022). Tanghe Reservoir is a large deep-water reservoir located in Liaoyang City, Liaoning Province (Figure 1). In recent years, the pursuit of simultaneous ecological and economic benefits has prompted the deliberate introduction and release of fish into the reservoir, aiming to foster ecologically sustainable fisheries by harnessing natural bait resources [16]. As a vital water source reservoir, the nutrient profile of the water body and the stability of its ecological milieu hold paramount importance [17]. Notably, in 2014, the Tanghe Reservoir garnered widespread attention due to the outbreak of golden algae [18,19]. Currently, the absence of well-defined theoretical guidelines for fish stocking has led to a notable trend of slow growth in individual bighead carp and silver carp [7], and the average weights of silver and bighead carp at the age of four were only 1417.5 g and 1255.6 g (unpublished data), respectively, there was also a significant declined in fishery production (Figure 2), which has inflicted a significant blow to the economic gains derived from the reservoir's operations. Therefore, it is crucial to strengthen fisheries' management by analyzing the structure and function of the food web of the Tanghe Reservoir aquatic ecosystem.

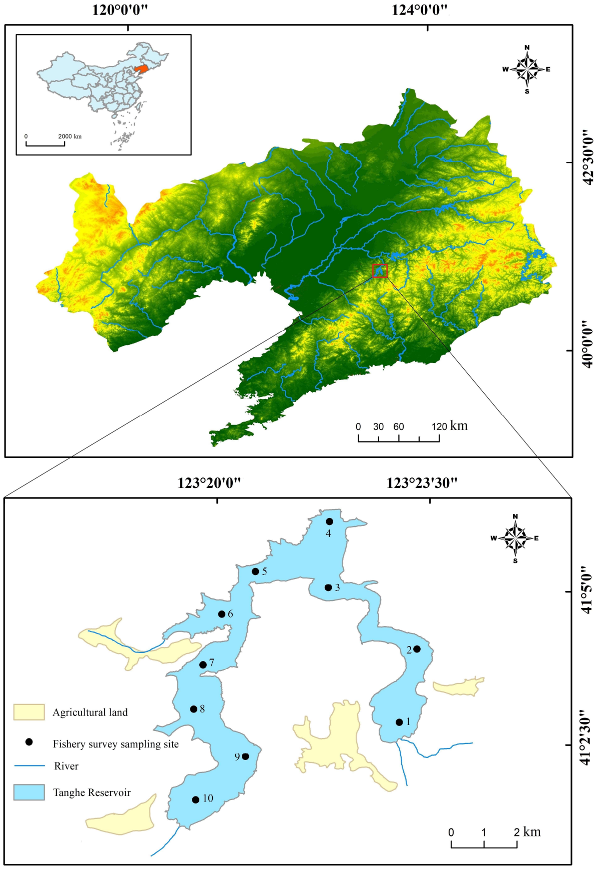

Figure 1. Location of Tanghe Reservoir and the fishery survey sampling sites.

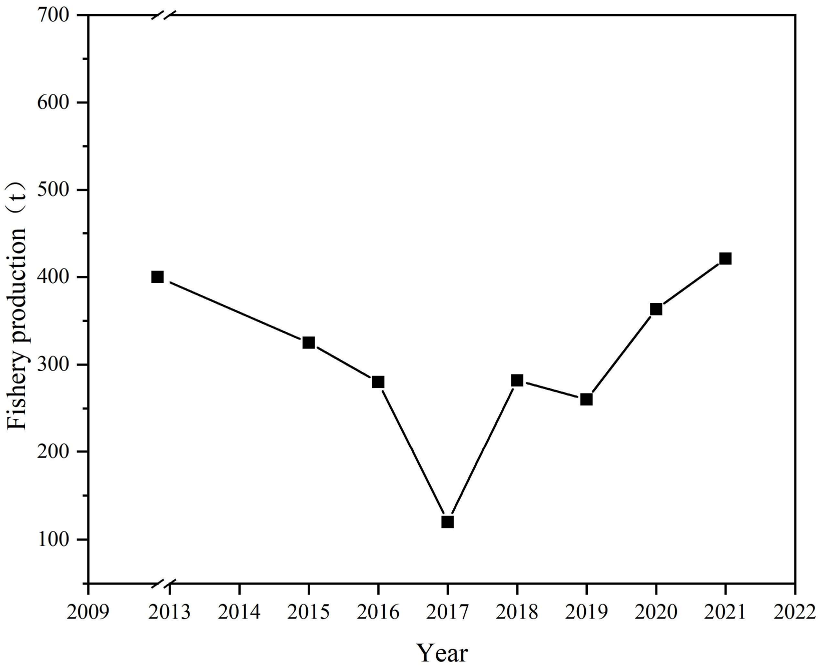

Figure 2. Inter-annual variation in fisheries production in the Tanghe Reservoir.

Therefore, an Ecopath with Ecosim model of Tanghe Reservoir has been meticulously developed, utilizing the substantial dataset available. This study holds significance not only for Tanghe Reservoir specifically but also for its broader implications on the ecological utilization and management of lake fishery resources worldwide. The current model constitutes a comprehensive case study with the objectives of (1) modeling the food web structure and energy flows in a typical deep-water reservoir, (2) describing quantitatively the ecosystem properties and maturity of Tanghe Reservoir, and (3) proposing suggestions for the improvement of fishery resource management in this kind deep-water reservoir.

2. Materials and Methods

2.1. Study Area

The Tanghe Reservoir (123°06′–123°25′ E, 41°07′–41°58′ N) is situated in the central region of Liaoning Province, China, along the tributary of the Taizi River and the main course of the Tang River. Constructed and commissioned in 1969, the Tanghe Reservoir is a typical valley-type reservoir. With a total capacity of 7.07×108 m^3, a maximum water level of 117.86 m, and a normal water level of 109.36 m [20], it is considered to be one of the large- and medium-sized reservoirs of the Liaoning Province. The annual rainfall is 789.5 mm, and the average annual sunshine duration is 2454.6 h [7]. The Tanghe Reservoir serves multiple functions, including flood control, water supply, tourism, and fisheries. The area designated for fish farming in the reservoir spans 17.4 km^2 (Figure 1).

Environmental metrics were measured from April to December 2021–2022 at 10 sampling sites of the Tanghe Reservoir. A portable YSI Professional Plus instrument was utilized for measuring conductivity (Cond), dissolved oxygen (DO), oxidation reduction potential (ORP), pH, total dissolved solids (TDS), and water temperature (WT) (Table 1). Secchi depth (SD) was also determined by using a Secchi disk. The permanganate index (COD_{Mn}) was determined using the alkaline potassium permanganate titration method (GB 11892-89, China [21]). Total nitrogen (TN) and total phosphorus (TP) were analyzed using the alkaline potassium persulfate digestion–UV spectrophotometric method and the ammonium molybdate spectrophotometric method, respectively [22], with a UV-3000 spectrophotometer (MAPADA, Shanghai, China).

Table 1. Physico-chemical characteristics (mean ± SD) in the Tanghe Reservoir.

Parameters	April (n = 10)	August (n = 10)	October (n = 10)	December (n = 10)	One-Way ANOVA
Cond (μS/cm)	312.70 ± 10.71 ^{b}	368.96 ± 11.45 ^{a}	293.14 ± 5.29 ^{c}	268.72 ± 3.38 ^{d}	$p = 0.000$
DO	12.48 ± 0.76 ^{a}	7.28 ± 0.64 ^{d}	7.99 ± 0.60 ^{c}	11.26 ± 0.55 ^{b}	$p = 0.000$
ORP (mV)	84.26 ± 14.12 ^{a}	79.33 ± 4.26 ^{a}	79.52 ± 4.87 ^{a}	80.57 ± 13.78 ^{a}	$p = 0.727$
pH	8.96 ± 0.08 ^{a}	8.60 ± 0.48 ^{b}	8.64 ± 0.05 ^{b}	8.50 ± 0.20 ^{b}	$p = 0.005$
SD (m)	1.67 ± 0.29 ^{c}	2.20 ± 0.47 ^{b}	1.69 ± 0.15 ^{c}	2.84 ± 0.54 ^{a}	$p = 0.000$
TDS (mg/L)	274.37 ± 1.89 ^{a}	238.81 ± 1.31 ^{d}	243.56 ± 4.30 ^{c}	267.22 ± 3.29 ^{b}	$p = 0.000$
WT (°C)	11.45 ± 1.22 ^{c}	26.14 ± 0.32 ^{a}	13.61 ± 0.09 ^{b}	6.74 ± 0.43 ^{d}	$p = 0.000$
COD_{Mn} (mg/L)	1.79 ± 0.35 ^{c}	1.40 ± 0.18 ^{bc}	2.17 ± 1.06 ^{ab}	2.60 ± 0.73 ^{a}	$p = 0.004$
TN (mg/L)	1.87 ± 0.57 ^{b}	0.86 ± 0.30 ^{c}	2.74 ± 0.15 ^{a}	0.79 ± 0.21 ^{c}	$p = 0.000$
TP (mg/L)	0.02 ± 0.01 ^{b}	0.04 ± 0.00 ^{a}	0.03 ± 0.01 ^{ab}	0.03 ± 0.02 ^{b}	$p = 0.007$

Notes: n: the number of sampling sites. Cond: conductivity. DO: dissolved oxygen. ORP: oxidation reduction potential. SD: Secchi depth. TDS: total dissolved solids. WT: water temperature. COD_{Mn}: the permanganate index. TN: total nitrogen. TP: total phosphorus. Least significant difference (LSD), one-way ANOVA, and Duncan's method were employed for multiple comparisons. Values bearing the different letters demonstrate a significant difference between months ($p < 0.05$), while the same letters demonstrate no significant difference ($p > 0.05$).

2.2. Trophic Modeling Method

A static mass-balance trophic model for the Tanghe Reservoir was constructed using Ecopath with Ecosim 6.6.5.17202. The Ecopath model simplifies the intricate food web within an ecosystem by partitioning it into distinct ecologically connected functional groups. These groups encompass various components, including detritus, phytoplankton, and several fish groups with similar ecological characteristics. The purpose is to replicate the complete material cycling and energy flow processes within the ecosystem. Adhering to the principle of trophic balance, each functional group in the model ensures that the sum of mortality and output is equal to production. The following formula can describe the model:

$$B_i \cdot (P/B) - \sum_{j=1}^{n} B_j(P/B)DC_{ji} - Y_i - E_i - BA_i = 0 \tag{1}$$

where B is the biomass of group i. P/B is the production/biomass rate of group i, which is equal to the total mortality Z [23]; Q/B is the food consumption per unit of biomass for predator j; and DC_{ji} is the fration of i in the diet of j [24,25]. To balance the model, DC_{ji}, B, P/B, Q/B, and EE should be used. The remaining unknown parameters can be calculated using the Ecopath model.

2.3. Functional Group and Input Data Collection

2.3.1. Functional Group Division

In the ecosystem-based modeling (EwE) approach, functional groups typically comprise species with similar eco-functional or taxonomic statuses. However, the model also allows for the inclusion of certain single species that hold significant economic value or ecological functions within functional groups. In this study, the ecological model of the Tanghe Reservoir was established by dividing it into 18 functional groups (Table 2), based on the aforementioned definitions and data derived from the fishery resources survey conducted in the reservoir. This categorization effectively captures the comprehensive framework of the ecosystem's functional structure and energy flow within the Tanghe Reservoir.

Table 2. Function groups of Tanghe Reservoir ecosystem.

NO.	Functional Group	Dominant Species Composition
1	Catfish	*Silurus asotus*
2	Other carnivorous fishes	*Cultrichthys erythropterus* *Opsariichthys bidens* *Channa argus*
3	Carp	*Cyprinus carpio*
4	Crucian carp	*Carassius auratus*
5	Pond smelt	*Hypomesus olidus*
6	Sharpbelly	*Hemiculter leucisculus*
7	Bighead carp	*Aristichthys nobilis*
8	Silver carp	*Hypophthalmichthys molitrix*
9	Acheilognathus	*Acheilognathus chankaensis* *Rhodeus lighti*
10	*Pseudorasbora parva*	*Pseudorasbora parva*
11	Other fishes	*Abbottina rivularis* *Zacco sinensis* *Hemibarbus labeo* *Misgurnus anguillicaudatus* *Pelteobagrus fulvidraco*
12	Herbivorous fishes	*Ctenopharyngodon idella* *Megalobrama amblycephala*
13	Shrimp	Shrimp
14	Zoobenthos	Oligochaeta *Chironomidae larvae*
15	Zooplankton	Protozoan Rotifer Cladocera Copepoda
16	Phytoplankton	Cyanophyta Chlorophyta Bacillariophyta Euglenophyta Pyrrophyta Cryptophyta
17	Macrophyte	*Acorus calamus* *Vallisneria natans*
18	Detritus	Organic ditritus

2.3.2. Fish

Fish population surveys were conducted in the Tanghe Reservoir in 2021–2022 to assess the composition of fish populations. Set nets were employed in the surveys, ensuring that all captured fish species were meticulously identified and weighed with a precision of 0.1 g. Biomass data for each fish functional group were sourced from the Tanghe Reservoir Management Department, while the calculation of production to biomass ratios (P/B) was carried out using the following equation:

$$B = \frac{C}{F} \tag{2}$$

$$F = Z - M \tag{3}$$

$$Z = \frac{P}{B} = K \times \left(L_\infty - \overline{L}\right) / \left(\overline{L} - L'\right) \tag{4}$$

where B is the biomass (t/km^2), C is the annual catch yield (t/(km^2·year)), F is the fishing mortality (1/year), Z is the total mortality (1/year), and M is the natural mortality (1/year). K, L_∞, $\overline{L}$, and L' represent the growth rate of the von Bertalanffy growth function, asymptotic length (cm), mean length (cm), and maximum length of the fish (cm), respectively [26].

$\overline{L}$ was obtained from the fisheries resource assessment, and K, L_∞, and L' were calculated using life history date in fish base.

Natural mortality was calculated using Pauly's empirical equation [27]:

$$logM = -0.0066 - 0.279logL_\infty + 0.6543logK + 0.4634logT \quad (5)$$

where T represents the mean annual water temperature (°C).

The Q/B ratio was calculated using the multiple regression formula as follows [28]:

$$log(Q/B) = 7.964 - 0.204 \times logW_\infty - 1965 \times T\prime + 0.083 \times A + 0.532 \times h + 0.398 \times d \quad (6)$$

where $T\prime$ is an expression for the mean annual water temperature, W_∞ is the asymptotic weight (g), A is the aspect ratio (A = h^2 (given height)/s (surface area)), h is a dummy variable expressing food type (1 for herbivores or 0 for detritivores and carnivores), and d is a dummy variable also expressing food type (1 for detritivores or 0 for herbivores and carnivores).

In the context of the Ecopath model, the proportion of unassimilated food is a crucial parameter for estimating energy balance ratios without disrupting the nutritional equilibrium. For carnivorous and omnivorous fish, this proportion was set to 0.20 and 0.41 [29], respectively. The accurate determination of this parameter is essential as it contributes significantly to the assessment of energy flow dynamics within the model, ensuring a reliable representation of trophic interactions and energy transfer in the ecosystem.

2.3.3. Plankton, Shrimp, and Zoobenthos

The biomass of phytoplankton, zooplankton, and zoobenthos from 2021 to 2022 was derived from our survey results. The consumption of biomass ratio (Q/B) values for shrimps, zoobenthos, and zooplankton were indirectly calculated using the formula Q/B = $(P/B)/(P/Q)$. The corresponding P/Q values for these functional groups were derived from reputable sources and found to be 0.075 [30], 0.02 [31], and 0.05 [32], respectively. As historical records or real-time monitoring data for shrimp biomass in the Tanghe Reservoir were not available, Ecopath employed an energy balance principle to calculate it, requiring the use of an Ecotrophic Efficiency (EE) value. In this study, the EE value for shrimp was established at 0.95, following the prevailing methodology utilized in numerous other ecosystem models [29]. The Proportions of zooplankton, zoobenthos and shrimp micro assimilated food were 0.65 [32], 0.94 [31] and 0.7 [30], respectively.

2.3.4. Macrophytes and Detritus

The biomass of macrophytes was determined using the energy balance principle in the Ecopath model, with an ecotrophic efficiency (EE) value set to 0.5 [33] and a production to biomass ratio (P/B) of 1.25 [34]. The detritus category encompasses both bacterial and organic detritus, with bacterial biomass estimated to be 17.5% of phytoplankton biomass [29]. For the biomass of particulate organic carbon, a specific volume of water sample was filtered through a Whatman GF/F glass fiber filter membrane, dried, and calcined [35]. Meanwhile, dissolved organic carbon was determined using a vario TOC cube instrument (Elementar, Langenselbold, Germany).

2.3.5. Diet Composition

In the model, diet composition is represented as the relative contribution of different food items to the predator. This contribution ratio can be computed based on weight, energy, or volume. The food matrix data for the Tanghe Reservoir were primarily sourced from pertinent references [36–40]. To improve the accuracy of the model's output trophic levels, stable isotope analysis (unpublished data) was conducted on each functional group in the reservoir. Based on the results of the stable isotope analysis, adjustments were made to the food matrix of the model to ensure that the predicted trophic levels of the functional groups closely matched the values derived from stable isotope analysis. This integration of stable isotope data helps enhance the reliability and precision of the model's trophic level predictions.

2.3.6. Model Balance and Analysis

Ecotrophic Efficiency (*EE*) was used as a critical indicator for balancing the model, where EE values cannot be higher than 1 [24]. The initial values of other uncertain parameters were slightly adjusted when EE values were higher than 1. To enhance transparency and facilitate the data evaluation process, we adopted a 'pedigree' routine [41], which serves a dual purpose by indicating the data origin and assigning confidence intervals based on their sources [42]. The resulting 'pedigree index' (*P*) is calculated by combining individual pedigree index values, providing an overall assessment of the reliability of the information used in Ecopath model. The formular is as follows:

$$P = \sum_{i=1}^{n} \sum_{j=1} \frac{l_{ij}}{n} \tag{7}$$

where l_{ij} is the pedigree index for model group i and parameter j and n is the total number of model groups [11].

The measure of fit (t^*) not only quantifies the model's uncertainty but also accounts for the number of living groups in the ecosystem, providing a description of how well the model is rooted in local data, and the formula is as given below:

$$t^* = \frac{P \cdot \sqrt{n-2}}{\sqrt{1-P^2}} \tag{8}$$

3. Results

3.1. Basic Input and Estimates

In Ecopath with Ecosim 6.6.5 software, the ecosystem model of the Tanghe Reservoir (Figure 3) was obtained by carefully adjusting the parameter values of B, P/B, and Q/B for each functional group to ensure that all ecotrophic efficiencies (EE) were less than 1. The trophic levels of the functional groups in the reservoir ranged from 1.000 to 3.357 (Table 3), with the highest trophic level observed in other carnivorous fishes (3.357), followed by catfish (3.284) and Pond smelt (3.047). The trophic levels of the main economic fishes, silver and bighead carp, were 2.197 and 2.415, respectively.

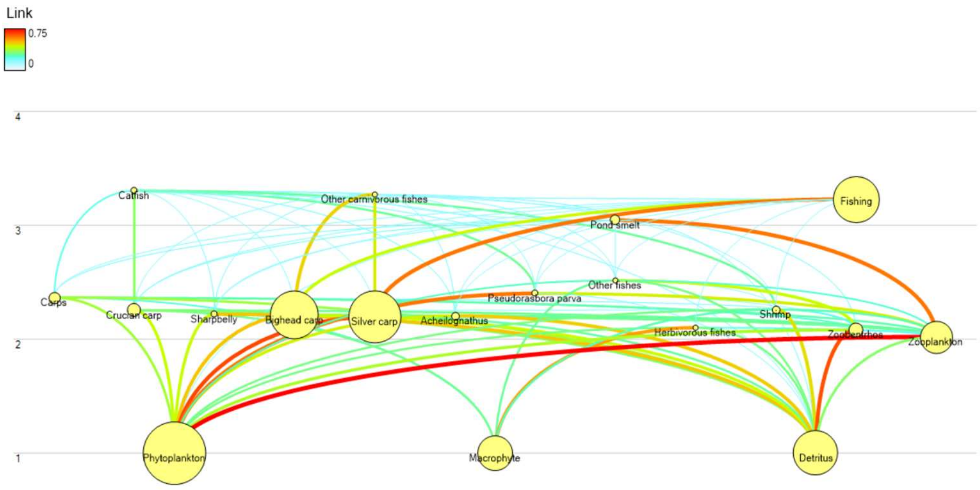

Figure 3. Schematic diagram of trophic flows and food web structure in the Tanghe Reservoir (for biomass the units are t km^{-2}).

Table 3. Basic parameter and output of Tanghe Reservoir ecosystem model in 2021.

Group Number	Group	Trophic Level	Biomass (t/km^2)	P/B (/year)	Q/B (/year)	EE	P/Q
1	Catfish	3.284	0.23	0.97	6.566	0.188	0.148
2	Other carnivorous fishes	3.357	0.14	1.95	12.61	0.937	0.155
3	Carp	2.366	1.90	0.92	4.59	0.970	0.200
4	Crucian carp	2.253	2.39	1.035	7.34	0.974	0.141
5	Pond smelt	3.047	1.32	1.38	14.34	0.615	0.096
6	Sharpbelly	2.219	0.33	2.63	12.6	0.976	0.209
7	Bighead carp	2.415	22.59	1.02	4.848	0.407	0.210
8	Silver carp	2.197	32.98	1.15	8.128	0.380	0.141
9	Acheilognathus	2.206	0.72	2.68	13.21	0.368	0.203
10	*Pseudorasbora parva*	2.402	0.31	2.83	14.46	0.998	0.196
11	Other fishes	2.516	0.17	2.55	12.65	0.987	0.202
12	Herbivorous fishes	2.102	0.11	0.71	9.388	0.685	0.076
13	Shrimp	2.261	0.89	1.83	24.4	0.950	0.075
14	Zoobentrhos	2.082	2.64	5.3	265	0.972	0.020
15	Zooplankton	2.020	11.45	24.68	493.6	0.995	0.050
16	Phytoplankton	1.000	52.30	140.2		0.637	
17	Macrophyte	1.000	13.49	1.25		0.500	
18	Detritus	1.000	22.02			0.256	

3.2. Food Web Structure and Trophic Analysis

3.2.1. Trophic Structure

To visually represent the food web relationships, trophic levels from different functional groups were amalgamated into integrated trophic levels [43], resulting in a total of four integrated trophic levels in the Tanghe Reservoir ecosystem in 2021. Lower trophic levels exhibited a more substantial proportion of energy flow within the system, forming a typical pyramid shape where the energy flow decreases as it moves up the trophic levels. In 2021, the throughput of trophic levels I and II in the Tanghe Reservoir was 14,530 t km^{-2} year^{-1} and 6516 t km^{-2} year^{-1}, respectively, accounting for 68.4% and 30.7% of the total system throughput (Table 4). Lower trophic levels thus play a dominant role in supporting the energy transfer and productivity of the entire ecosystem.

Table 4. Energy flow by aggregated trophic levels of Tanghe Reservoir ecosystem in 2021–2022.

Trophic Level	Flow to Detritus (t km^{-2} year^{-1})	Throughput (t km^{-2} year^{-1})
IV	0.896	2.992
III	98.04	180.4
II	4409	6516
I	2673	14,530
Sum	7181	21,230

3.2.2. Transfer Efficiencies

The total net primary production in the entire Tanghe Reservoir ecosystem was estimated at 7349 t km^{-2} year^{-1}. Of this, 4676 t km^{-2} year^{-1} was consumed by primary consumers (Figure 4). During the upward trophic level transfer along the entire food chain, trophic levels II, III, IV, and V accounted for 30.7%, 0.850%, 0.0141%, and 0.000530% of the total system throughput, respectively. These findings reveal the energy flow dynamics and the significant contribution of lower trophic levels to sustaining the overall ecosystem productivity in the Tanghe Reservoir. In the ecological channel model of the Tanghe Reservoir, the ecological energy transfer efficiency of phytoplankton was found to be the highest at 0.637, while that of detritus was comparatively lower at 0.256. These results suggest that the 'grazing chain' in the Tanghe Reservoir ecosystem is more efficient than the 'detritus chain'. This characteristic is also prevalent in breeding reservoir ecosystems of bighead carp and silver carp. The higher energy conversion efficiency of phytoplankton highlights their crucial role in supporting the energy flow and productivity of the ecosystem. In terms of transmission efficiency, the trophic level of II to the III was the lowest, only 3.03%, indicating that the transmission from low trophic level to high trophic level was blocked.

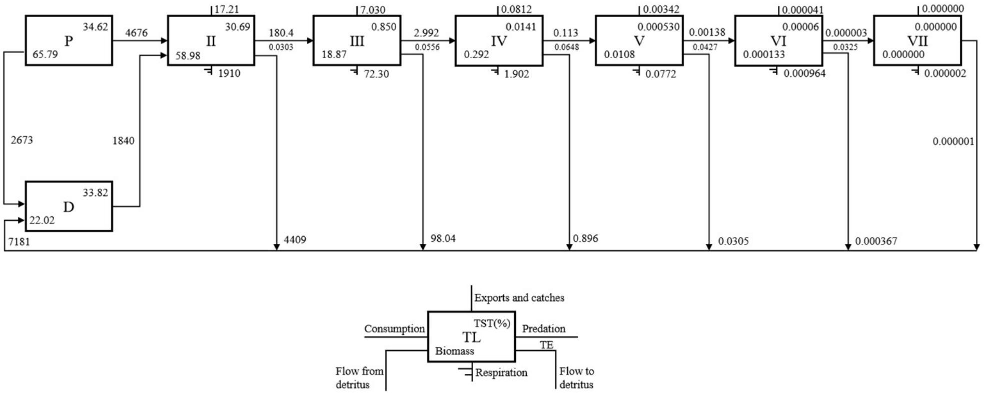

Figure 4. Lindeman spine of Tanghe Reservoir ecosystem during 2021–2022.

3.2.3. Mixed Trophic Impacts (MTI)

MTI (mixed trophic impact) analysis provides valuable insights into the trophic interactions among functional groups within an ecosystem, encompassing both direct and indirect effects (Figure 5) [11]. Phytoplankton and macrophytes, acting as producers, displayed positive effects on other functional groups. In contrast, pond smelt experienced negative impacts from catfish, other carnivorous fishes, carp, crucian carp, sharpbelly, Acheilognathus, pseudorasbora parva, and other fishes, but showed positive effects on herbivorous fishes, shrimp, and macrophytes. The main cultured species, silver and bighead carp, exhibited negative impacts on each other, whereas other carnivorous fish, sharpbellys, and fishing had positive effects on them. Consequently, the MTI analyses suggest that pond smelt, bighead, and silver carp play significant roles in shaping the structure and functioning of the Tanghe Reservoir ecosystem. These findings shed light on the intricate trophic dynamics and interrelationships among different functional groups, highlighting the ecological importance of these key species in the reservoir ecosystem.

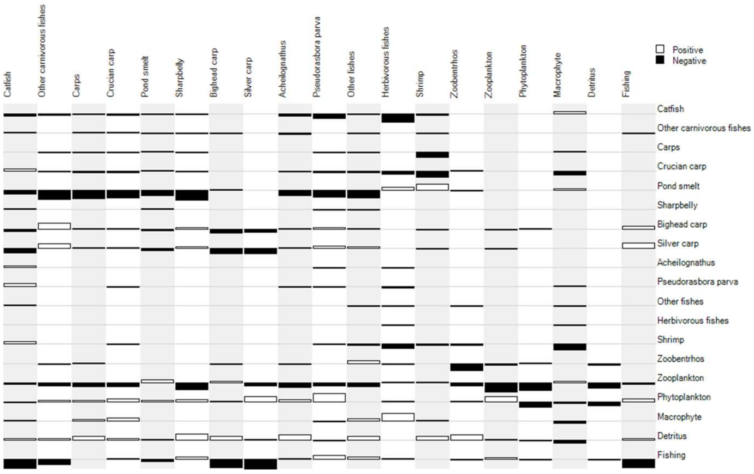

Figure 5. Mixed trophic impacts of Tanghe Reservoir ecosystem (white spaces above the line represent a positive impact, whereas black spaces underneath the line indicate a negative impact, and the heights of the bars are proportionate to the degree of the impacts).

3.3. Ecosystem Properties and Indicators

Table 5 presents summary statistics and flow indices for the Tanghe Reservoir ecosystem. The total system throughput of the reservoir reached 21,350.240 t km^{-2} year^{-1}, with 31.9% derived from consumption (6820.278 t km^{-2} year^{-1}), 25.1% from exports (5364.935 t km^{-2} year^{-1}), 9.3% from respiratory flows (1984.388 t km^{-2} year^{-1}), and 33.6% (7180.641 t km^{-2} year^{-1}) eventually flowing into detritus. The sum of all production (TP) was 7719.199 t km^{-2} year^{-1}, while the calculated total net primary production (TPP) and net system production (NSP) were 7349.324 t km^{-2} year^{-1} and 5364.936 t km^{-2} year^{-1}, respectively. Consequently, the ratio of total primary production to total respiration (TPP/TR) and total primary production to total biomass (TPP/TB) were 3.704 and 51.056, respectively. The mean trophic level of catch was computed as 2.303, and the gross efficiency (catch/net primary production) was 0.003 within the Tanghe Reservoir ecosystem. These results offer valuable insights into the energy flow and productivity dynamics of the ecosystem, emphasizing the significance of primary production in sustaining the ecosystem's trophic structure and supporting fisheries productivity.

Table 5. Summary statistics of the Tanghe Reservoir ecosystem properties in 2021–2022.

Attribute Parameter	Value	Units
Sum of all consumption (TC)	6820.278	t km^{-2} year^{-1}
Sum of all exports (TE)	5364.935	t km^{-2} year^{-1}
Sum of all respiratory flows (TR)	1984.388	t km^{-2} year^{-1}
Sum of all flows into detritus (TD)	7180.641	t km^{-2} year^{-1}
Total system throughput (TST)	21,350.240	t km^{-2} year^{-1}
Sum of all production (TP)	7719.199	t km^{-2} year^{-1}
Mean trophic level of the catch (TLc)	2.303	
Calculated total net primary production (TPP)	7349.324	t km^{-2} year^{-1}
Total primary production/total respiration (TPP/TR)	3.704	
Net system production (NSP)	5364.936	t km^{-2} year^{-1}
Total primary production/total biomass (TPP/TB)	51.056	
Total biomass (excluding detritus) (TB)	143.948	t km^{-2}
Total catch	24.326	t km^{-2} year^{-1}
Connectance index (CI)	0.299	
System omnivory index (SOI)	0.145	
Ecopath pedigree	0.481	
Measure of fit (t*)	2.122	
Shannon diversity index	1.776	
Ascendancy (A)	0.3127	
System overhead (*O*)	0.6873	
Finn's cycling index (FCI)	10.5	% of total throughput
Finn's mean path length (FML)	2.905	

The flow indices of connectance index (CI) and system omnivory index (SOI) of the Tanghe Reservoir during 2021 were 0.299 and 0.145, respectively. At the same time, the ecosystem information indices of ascendancy (A) and system overhead (O) were 31.27% and 68.73%, respectively.

4. Discussion

Reservoirs represent man-made aquatic systems with a unique blend of characteristics from both rivers and lakes [44]. The comprehensive assessment of ecological stands is crucial to safeguard the ecological integrity of these systems, given their vital role as primary water reservoirs in developing countries. Ecological models serve as valuable tools in assessing different fishery management strategies, providing the means for exploring diverse scenarios related to fishing activities, environmental variations, and trophic interactions [45]. Through the construction of Ecopath models, it was observed that the Hemavathy Reservoir in India exhibited a healthier ecosystem following appropriate fish stocking [46]. The Pasak Jolasid Reservoir in Thailand showed the underutilization of benthic and planktonic organisms, indicating the necessity for increased fish stocking [45]. Conversely, the Itaipu Reservoir in Brazil should reduce the harvest of native fish species while controlling the invasion of exotic fish species [47].

This study has established a mass-balance model to characterize the food web structure and ecosystem properties in a deep-water reservoir in the northern region of China. The primary objective is to guide the development of eco-friendly fishery practices. This model appears to be the first of its kind among the numerous deep-water reservoirs in northern China. It provides comprehensive insights into the unique features of deep-water reservoirs in this region, thereby facilitating a more sustainable approach to the development and utilization of aquatic resources. To gauge the model's quality, a comparison was conducted with 150 Ecopath models from diverse global locations, the assessment index range for these models ranged between 0.16 and 0.68 [48]. In the current study, the model's execution resulted in a pedigree index of 0.481 and a measure of fit value of 2.122. These outcomes suggest that the model's input parameters were adequately reliable, and the model itself demonstrated a high level of credibility.

In the context of the Tanghe Reservoir ecosystem, it is notable that several functional groups exhibited comparatively high EE values (Table 2), including carps (0.970), crucian carp (0.974), other carnivorous fish (0.937), sharpbelly (0.976), zoobenthos (0.972), and zooplankton (0.995). This observation suggests that these fish species had experienced overfishing, leading to significant predation pressure on zoobenthos and zooplankton, a trend akin to that observed in shallow macrophytic lakes within the Yangtze River basin [13]. In contrast, the EE values for the main stocked species, namely bighead carp (0.407) and silver carp (0.380), were relatively low. Despite the substantially higher biomass of bighead carp and silver carp in the Tanghe Reservoir compared to other locations such as Weishui Reservoir [36], Gehu Lake [49], Lake Erhai [15], and Qiandao Lake [40], these filter-feeding fish primarily relied on zooplankton as a primary food source [50,51]. The significant biomass of silver carp and bighead carp contributed to an elevated predation pressure on zooplankton. Notably, there was a distinct reduction in the size of zooplankton from 2018 to 2021, with only 12.67% and 47.12% of the average annual abundance and biomass of large zooplankton, respectively (unpublished data).

The distribution of nutrient energy flow in the integrated trophic level of the Tanghe Reservoir is typically pyramidal, with a large difference in energy conversion efficiency between high and low trophic. The total system throughput in Tanghe Reservoir (21,350.240 t km^{-2} $year^{-1}$) is much lower than in Qiandao Lake (24,698.27 t km^{-2} $year^{-1}$), Bao'an Lake (37,418.04 t km^{-2} $year^{-1}$) and Weishui Reservoir (44,254.86 t km^{-2} $year^{-1}$) (Table 6). The main reason for this is that the Tanghe River Reservoir, as a typical deep-water reservoir in northern China, lacks macrophytes and phytoplankton compared to other reservoirs. The transfer efficiency of the grazing food chain (4.819%), which begins with phytoplankton and macrophytes, is higher than that of the detritus food chain (4.693%), which begins with detritus. The average transfer efficiency of the ecosystem was 4.778%, which is much lower than the average ecosystem efficiency of 9.2% [52]. This shows that high intensity stocking has an obvious blocking effect on energy transfer.

This model demonstrates the significant roles of pond smelt, bighead carp, and silver carp in the Tanghe Reservoir ecosystem. The concept of mixed trophic impact not only assesses the effects of fisheries or non-native species on the ecosystem but also captures the interrelations between different species within the ecosystem [24]. Previous studies have emphasized the importance of smelt in freshwater ecosystems [15,53]. In this study, smelt was found to have a moderate negative impact on other fish, likely attributed to its feeding habits, where zooplankton serves as its primary prey, and it also consumes the larvae and eggs of other fish [39]. The results of the mixed trophic impact analysis revealed that the main stocked fish, bighead carp and silver carp, exhibited a negative impact on each other, but fishing activities exerted a positive effect on both species. This implies that bighead and silver carp might have been excessively stocked in the Tanghe Reservoir, leading to elevated predation pressure on zooplankton. Such circumstances may hinder the stable development of the ecosystem.

Table 6. Comparison of ecosystem attributes in different shallow lakes in China.

Parameters	Bao'an Lake [13] (2012–2013)	Gehu Lake [49] (2010–2011)	Jinshahe Reservoir [35] (2013–2014)	Qiandao Lake [40] (2016–2017)	Tanghe Reservoir (2021–2022)	Weishui Reservoir [36] (2020–2021)
Finn's cycling index (FCI)	9.25%	7.99%	6.73%	5.15%	10.50%	11.35%
Connectance index (CI)	0.205	0.219	0.277	0.263	0.299	0.351
System omnivory index (SOI)	0.058	0.189	0.087	0.132	0.145	0.099
Total primary production/total respiration (TPP/TR)	1.64	2.761	6.735	6.509	3.704	1.394
Total system throughput (TST)	37,418.04	12,131.76	27,247.68	24,698.27	21,350.24	44,254.86
Total transfer efficiencies	8.68%	6.40%	7.60%	3.50%	4.78%	4.24%

In terms of ecosystem characteristics, several key indices of total primary production/total respiration (TPP/TR), Finn's circulation index (FCI), connectivity index (CI), and system omnivory index (SOI) provide valuable metrics to better assess the developmental status of the ecosystem [54,55]. FCI quantifies the proportion of an ecosystem's throughput that is recycled in relation to the total system throughput [56]. The FCI value for Tanghe Reservoir (10.5%) is lower than that of Weishui Reservoir (11.35%) but higher than Qiandao Lake (5.27%), Gehu Lake (7.99%), and Jinshahe Reservoir (6.74%) (Table 6), suggesting that Tanghe Reservoir exhibits a higher degree of material recycling. Additionally, CI and SOI are crucial indices reflecting system maturity, particularly as the food chain evolves from linear to web-like structures during maturation [57]. The CI and SOI values for the Tanghe Reservoir ecosystem were 0.299 and 0.145, respectively, lower than those of the Three Gorges Reservoir [58] and the Weishui Reservoir, yet higher than Bao'an Lake and Qiandao Lake. Furthermore, TPP/TR serves as a significant indicator of ecosystem maturity, with TPP/TR values closer to 1 indicating a more mature ecosystem [55]. The TPP/TR value for the Tanghe Reservoir is 3.704, surpassing the Three Gorges Reservoir (1.899) [58], Gehu Lake (2.761) and the Weishui Reservoir (1.394), yet is still lower than Qiandao Lake (6.509), the Jinshahe Reservoir (6.735), and the Itaipu Reservoir in Brazil (6.3) [59]. This comparison with other domestic and foreign reservoirs indicates that the Tanghe Reservoir ecosystem is in the developmental stage.

The adjustment of fish biomass in an ecosystem affects the EE value, and when the EE value equals 1, it signifies the ecological capacity, which is a widely utilized technique [60–62]. According to the ecological model of Tanghe Reservoir, the ecological capacities for bighead carp and silver carp were estimated to be 23.4 and 33.8, respectively, highlighting the narrow gap between the biotic chains and the ecological capacities of these species in Tanghe Reservoir. The highest rates of fish accretion and growth occur when the maximum sustainable yield is half of the ecological holding capacity [63]. With Tanghe Reservoir covering an area of 17.4 km^2, following the theory of maximum sustainable yield (MSY), the appropriate yields for bighead and silver carp in Tanghe Reservoir should be 203.6 t and 294.1 t, respectively, far exceeding the current harvests of 150.2 t and 239.1 t.

After 2022, there was an escalation in the fishing intensity for bighead carp and silver carp in Tanghe Reservoir. In comparison to 2021, an additional 100 tons of bighead carp and 120 tons of silver carp were caught. It was assumed that the biomass of other functional groups remained relatively stable, while the biomass of bighead carp decreased by 5.75 t/km^2 and silver carp by 6.90 t/km^2 in 2023 compared to 2021. Through the construction of an Ecopath model, it was observed that in 2023, the EE value of bighead carp and silver carp increased to 0.585 and 0.460, respectively, compared to the values in 2021. Concurrently, the conversion efficiencies of zooplankton and phytoplankton decreased to 0.915 and 0.631, respectively. This suggests that the heightened utilization rates of bighead carp and silver carp resulted in reduced predation pressure on zooplankton and phytoplankton.

In conclusion, this study represents the inaugural ecosystem model of a deep-water reservoir in the northern region of China. Through the construction of the Ecopath model, it was discovered that the populations of bighead and silver carp were overstocked, leading to immense predation pressure on plankton, particularly zooplankton, which could no longer fulfill the predation demand of these two species. Consequently, we recommend intensifying the harvesting of bighead and silver carp to reduce their biomass in Tanghe Reservoir.

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Data Availability Statement: This study utilized two types of data: field survey data and model-simulated data. The field survey data was collected from the Tanghe Reservoir between 2021 and 2022. The model-simulated data was generated using Ecppath with Ecosim 6.6.5 software and was employed to analyze the food web structure and aquatic ecosystem of the Tanghe Reservoir. Should there be a need for data beyond what was used in this study, researchers can reach out to the corresponding author to access the data.

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