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Effects of a Fishing Ban on the Ecosystem Stability and Water Quality of a Plateau Lake: A Case Study of Caohai Lake, China

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Abstract: Long-term fishing bans have spurred extensive debate regarding their impacts on ecosystem structures, functions, and water qualities. However, data on the effects of specific changes induced by fishing bans on ecosystem structures, functions, and water qualities in lakes are still lacking. Therefore, the present study addresses this knowledge gap by employing an Ecopath model to assess alterations in an ecosystem's structure and function before (2011) and after (2021) the implementation of the fishing ban in Caohai Lake and its association with changes in water quality. (1) We observed a substantial reduction in the area covered by submerged aquatic vegetation after the ban, amounting to a 65% decrease in coverage compared with that before the ban, and a 60% reduction in the total ecosystem's biomass. (2) Following the ban, the number of fish species increased from 7 to 14, and this was accompanied by a rise in the fish biomass from 14.16 t·km^{-2} to 25.81 t·km^{-2}; a 4.5-fold increase in the total system consumption was observed, signifying accelerated energy and material flows within the ecosystem. (3) The fishing ban exhibited no significant impact on the total nitrogen concentration; however, it significantly reduced the water's transparency and increased the total phosphorus, ammonia nitrogen, chemical oxygen demand, and chlorophyll contents ($p < 0.05$). This shift in nutrient dynamics fostered a transformation from a macrophyte-dominant lake to an alga-dominant lake. The fish abundance and diversity increase in closed-type macrophytic lakes, thereby accelerating energy and material flows within food webs. These findings present novel insights into the effective policy management of fishing bans within the Yangtze River Basin, thus enhancing our understanding of sustainable lake ecosystem management.

Keywords: fishing bans; food web; Ecopath model; ecosystem structure; water quality

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1. Introduction

Lakes constitute a critical element of Earth's surface systems, representing an intricate web of interactions and a vital component of the terrestrial hydrosphere. They play a substantial role in regulating regional climates, maintaining equilibrium within regional ecosystems, and fostering biodiversity [1]. However, a myriad of environmental stressors, including climate change and uncontrolled development, have led to a gradual decline in biodiversity within lake ecosystems [2,3]. The decline in biodiversity within lakes is a global phenomenon observed across numerous water bodies [3,4]. This widespread decline presents an unprecedented challenge, necessitating urgent attention to preserve and protect lake biodiversity [1].

The Yangtze River, Asia's longest river and a primary watercourse in China, with a length of 6397 km, encompasses an extensive watershed that serves as the primary habitat for a rich diversity of over 2000 flora and fauna species [5]. Over the past few decades, rapid population growth and overfishing have substantially contributed to a concerning decline in plant and fish biodiversity within the Yangtze River Basin [6,7]. This decline is notably exemplified by the tragic extinction of key species such as the Yangtze River sturgeon *(Acipenser dabryanus*) and the Chinese paddlefish (*Psephurus gladius*), both unique to the region, as recognized by the International Union for the Conservation of Nature in 2022. In response to the escalating decline in biodiversity and the delicate ecological balance in the Yangtze River Basin, a series of fishing bans has been progressively implemented, evolving from seasonal bans initially in 2003 to the current "decade-long fishing ban" [8,9]. Notable research endeavors have explored the impacts of fishing bans and seasonal fishing restrictions on fish communities, consistently revealing positive effects on fish species' richness and abundance [10,11]. Fishing bans have demonstrated their effectiveness in enhancing fish density and diversity within vital water bodies, such as Dongting Lake and Poyang Lake. These bans serve not only to safeguard spawning populations and juvenile fish but also to promote a balanced ecological equilibrium among various fish species [12]. However, research in the Pearl River Basin has uncovered potential ecosystem shifts [13]. After the implementation of fishing bans, phytoplankton have emerged as the dominant primary productivity source, displacing submerged aquatic plants and impacting the West River's ecosystem [13]. Consequently, the extent to which long-term fishing bans facilitate the recovery of the ecosystem structure and function remains to be elucidated.

Caohai Lake, recognized as a nationally designated natural reserve, stands as a quintessential representation of a highland wetland ecosystem in the upper reaches of the Yangtze River. This ecosystem was once endowed with prolific biodiversity resources, featuring a diverse range of habitats, such as deep-water expanses, shallow-water marshes, sedge wetlands, and meadows [14]. The aquatic biological communities within this wetland showcase high productivity, boasting an impressive nearly 70% coverage of aquatic vegetation that contributes to maintaining the integrity of the ecosystem's structure and function [15]. However, Caohai Lake has been confronted with the challenges of overfishing and the depletion of fishery resources. In 2018, the lake witnessed the commencement of extensive restoration endeavors, which encompassed the closure of all the docks and the enforcement of a fishing ban within the lake. Despite these restoration measures, the persistent and thriving population of exotic fish species, including carp, silver carp, and grass carp, which were previously introduced by local fishermen, has posed a substantial challenge. Following the year 2019, Caohai Lake witnessed a rapid surge in fish and shrimp populations. However, this growth was accompanied by a gradual decline in submerged aquatic plant coverage and a reduction in water transparency. Particularly concerning is the severe reduction in the aquatic vegetation, with an overall coverage of less than 10%. Since the initiation of the fishing ban in Caohai Lake, a lingering uncertainty persists regarding the trajectory of the ecosystem's structural and functional aspects, as well as the water quality within the lake [16]. Numerous factors can contribute to the degradation of submerged vegetation, including the excessive discharge of pollutants within the watershed, changes in the land-use type, resuspension of sediments, extreme climatic storms causing significant wave action, persistently high-water levels, and an overabundance of fish, all of which can lead to the demise of aquatic plants [14]. In Weining County, located upstream of Caohai Lake, the population showed a downward trend from 2018 to 2021, suggesting a potential decrease in pollution discharge, complemented by upstream ecological restoration projects. Research by Xu Lin et al. revealed that in 2020, the total inflow concentrations of COD, ammonia nitrogen, TP, and TN into Caohai Lake had decreased by 14.92%, 24.92%, 28.08%, and 18.85%, respectively, compared to 2017 [17]. Moreover, the land-use type within the Caohai watershed remained largely unchanged, with the combined area of wetlands, forests, and grasslands accounting for over 50% of the total area by 2020 [15]. Furthermore, studies by Yu Wei and others have indicated that the concentrations of nitrogen and phosphorus in the sediments of Caohai Lake were not particularly high compared to other plateau lakes, such as Erhai Lake, and nitrogen and phosphorus concentrations in the overlying water were not high during periods of vigorous growth of submerged vegetation [14]. Additionally, Xu Lin and colleagues' research indicated that the water level of Caohai Lake remained relatively stable at around 2172.2 m from 2015 to 2021, without significant fluctuations [17]. Therefore, factors such as changes in external pollutants and land use, the release of nitrogen and phosphorus from sediments, and water level variations are insufficient to explain the large-scale degradation of the submerged vegetation [16]. Existing research on fishing bans has predominantly centered on river ecosystems [12,18], leaving a noticeable research gap concerning the impact of fishing bans on closed-type lake ecosystems, specifically regarding their structures, functions, and water qualities.

Therefore, the present study aims to fill this knowledge gap by thoroughly investigating the consequences of the fishing ban on Caohai Lake, utilizing the Ecopath model to analyze alterations in the ecosystem's structure, function, and water quality before and after the implementation of fishing bans. Our findings will provide foundational insights essential for the restoration of the Caohai Lake ecosystem and the effective management of lakes within the Yangtze River Basin. Understanding the impacts of conservation interventions on the ecosystem dynamics of Caohai Lake holds significant implications for the broader objective for promoting ecologically sound practices and preserving the delicate balance of lake ecosystems in the Yangtze River Basin.

2. Materials and Methods

2.1. Study Area

Caohai Lake (26°50′51.05″ N, 104°14′32.35″ E) represents the largest natural freshwater lake in Guizhou Province, strategically positioned at the central hub of the Yungui Plateau. Characterized by an average elevation of 2171.7 m above sea level, Caohai Lake typifies a classic highland wetland ecosystem. The climate of Caohai Lake, characterized by an annual mean temperature of 10.5 °C, an average annual sunshine duration of 75.2 days, and an annual average rainfall of 950 mm, plays a significant role in shaping its ecosystem. Spanning a water surface area of 31 km^2 with an average depth of 2.0 m, the lake is predominantly fed by four inflowing rivers—namely, the Sha River, Zhong River, Maojiahaizi River, and Dongshan River—to sustain its water levels and overall hydrological balance. Caohai Lake is classified as a closed-type lake owing to the presence of diversion weirs in its outflow channels and a substantial difference in elevation compared to downstream lakes. Within Caohai Lake, a diverse array of aquatic vegetations is found, encompassing 37 species of vascular plants. Noteworthy categories of aquatic plants include emergent species, such as water onion (*Scirpus validus*), sedge grass (*Cyperus rotundus*), and water bulrush (*Phragmites australis*), as well as floating-leaf species, such as water caltrop (*Trapa bispinosa*), water spinach (*Ipomoea aquatica*), and floating arrowhead (*Sagittaria natans*). Submerged species, such as hydrilla (*Hydrilla Rich.*), pondweed (*Potamogeton distinctus*), and tape grass (*Siderasis fuscata*), also contribute to the lake's vegetational composition. The lake is ecologically rich, supporting varied aquatic (including nine distinct fish species) and avian (including 142 distinct avian species) populations [19–21]. The presence of the black-necked crane, a unique highland crane species exclusive to China, holds significant ecological value and highlights the lake's importance as a habitat for endemic wildlife. Caohai Lake serves as a critical ecological resource in the Yungui Plateau region, making substantial contributions to the area's overall biodiversity and ecological significance (Figure 1).

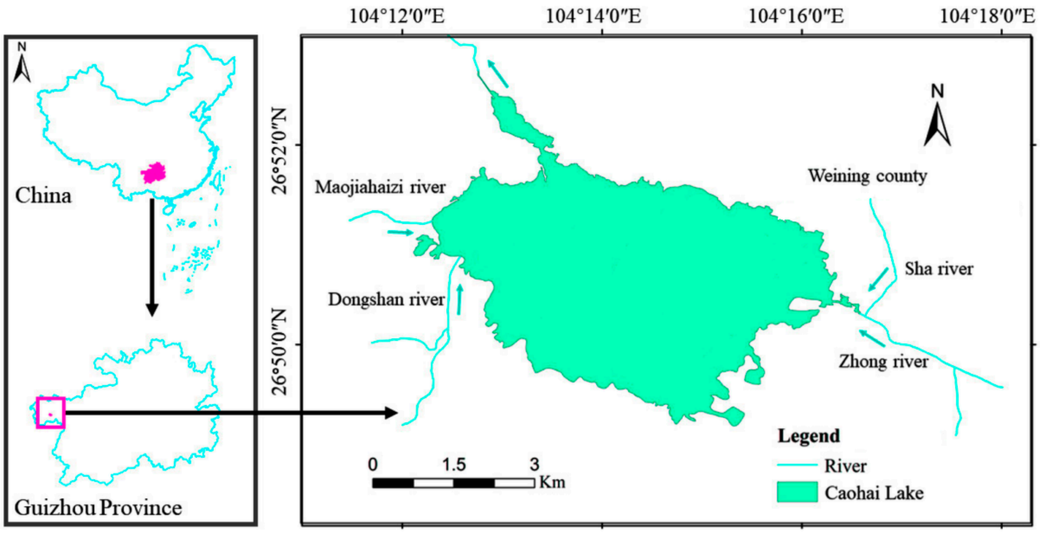

Figure 1. Location of Caohai Lake in China.

2.2. Samples

In this study, the data related to Caohai Lake in 2011 were provided by Qin Hongchao's team and the Caohai Lake Management Committee [22]. On this basis, we conducted the 2021 Caohai Lake Fish Stock Survey. To ensure a comprehensive and uniform data collection process, the current (2021) sampling locations and sampling methods are the same as those in 2011. There were 10 sampling sites included in total, with the latitude and longitude in the Supplementary Materials. Sampling was conducted from April 2011 and 10 July to 4 August 2021, with three repeated days of sampling. Samples of fish, planktonic flora and fauna, aquatic animals, and submerged plants were collected. For the qualitative and quantitative sampling of the planktonic flora and fauna, plankton nets were employed. The collected samples were characterized morphologically under 10 × 40 and 10 × 20 light microscopes, respectively, and the biomass of the plankton was calculated using the volumetric method, in which the weight of the organisms was estimated by assuming that the density of the plankton was 1 and treating the organisms as an approximate geometrical figure to obtain the biovolume according to the volumetric formula [23]. Benthic animals were collected using sediment samplers, and their biomass was determined through weighing for large benthic animals and using volumetric methods for small benthic animals, as outlined in the methodology by Chen et al. (2005) [24]. Samples of submerged plants were collected in accordance with the Technical Regulations for Lake Surveys [25]; three replicates were set for each sampling point, and the collected samples were dried to a constant weight at 70 °C within the laboratory, allowing for the accurate determination of the biomass. Fish sampling and survey methods were performed in strict adherence to the "Guidelines for the Investigation of Nutrient Enrichment in Lakes" [26] and the "Observation Methods for Lake Ecosystems" [24]. These established guidelines ensured the systematic and standardized collection of data related to fish species and population dynamics within Caohai Lake. Biomass values and annual average fish catch data were calculated based on survey data. Prior to the fishing ban, the Caohai Lake ecosystem was categorized into 14 primary functional groups (Table 1). Post ban, the ecosystem displayed a more complex structure and was delineated into 21 primary functional groups (Table 2). To assess the water's transparency at each sampling point, Secchi disk measurements were taken [25]. Water samples were also systematically collected and transported to the laboratory for the precise analysis of the key water quality parameters, including the total nitrogen (TN), total phosphorus (TP), ammonia nitrogen (NH_3-N), chemical oxygen demand (COD), and chlorophyll-a (Chl.a). The determination of the nitrogen and phosphorus contents in the water was conducted according to "Methods of Analysis for Water and Wastewater Monitoring" [27].

Table 1. Functional groups of Caohai Lake prior to the fishing ban's implementation [22].

Functional Group	Group with the Main Species
Bitterling fish	*Acheilognathus macropterus* (*A. macropterus*)
Swinhoe's gudgeon	*Hypseleotris swinhonis* (*H. swinhonis*)
Crucian carp	*Carassius auratus* (*C. auratus*)
Topmouth gudgeon	*Pseudorasbora parva* (*P. parva*)
Loach	*Misgurnus anguillicaudatus* (*M. anguillicaudatus*)
Other small fishes	*Yunnanilus caohaiensis* (*Y. caohaiensis*), *Yunnanilus nigromaculatus* (*Y. nigromaculatus*)
Ricefield eel	*Monopterus albus* (*C. auratus*)
Shrimps	*Panulirus ornatus* (*C. auratus*)
Mollusks	*Cipangopaludina cathayensis* (*C. cathayensis*), *Parafossarulus striatulus* (*P. striatulus*), *Anodonta woodiana* (*A. woodiana*), etc.
Other benthos	*Pelopia*, *Monopylephoruslimosus*, *Cricotopus*, etc.
Zooplanktons	*Sinodiaptomus sarsi* (*S. sarsi*), *Limnoithona sinensis* (*L. sinensis*), etc.
Phytoplanktons	*Microcystis aeruginosa* (*M. aeruginosa*), *Synedra acusvar* (*S. acusvar*), etc.
Submerged macrophytes	Submerged macrophytes
Detritus	Detritus

Table 2. Functional groups of Caohai Lake post fishing ban's implementation.

Functional Group	Group with the Main Species
Bighead carp	*Hypophthalmichthys nobilis* (*H. nobilis*)
Silver carp	*Hypophthalmichthys molitrix* (*H. molitrix*)
Carp	*Cyprinus carpio* (*C. carpio*)
Grass carp	*Ctenopharyngodon idellus* (*C. idellus*)
Crucian carp	*Carassius auratus*
Yellow catfish	*Pelteobagrus fulvidraco* (*P. fulvidraco*)
Sharpbelly	*Hemiculter leucisculus* (*H. leucisculus*)
Bitterling fish	*A. macropterus*
Topmouth gudgeon	*P. parva*
Other small fishes	*Y. caohaiensis*, *Y. nigromaculatus*
Swinhoe's gudgeon	*H. swinhonis*
Loach	*M. anguillicaudatus*
Ricefield eel	*M. albus*
Catfish	*Clarias gariepinus* (*C. gariepinus*)
Red swamp crayfish	*Procambarus clarkii* (*P. clarkii*)
Mollusks	*C. cathayensis*, *P. striatulus*, *A. woodiana*, etc.
Other benthos	*Pelopia*, *Monopylephoruslimosus*, *Cricotopus*, etc.
Zooplanktons	*S. sarsi*, *L. sinensis*, etc.
Phytoplanktons	*M. aeruginosa*, *S. acusvar*, etc.
Submerged macrophytes	Submerged macrophytes

2.3. Ecopath Model

Among the currently applied models, the Nutrient–Phytoplankton–Zooplankton–Debris Model (NPZD) and the European Regional Sea Ecosystem Model (ERSEM) describe only the plankton at the lower trophic level of the ecosystem's food web and do not consider the effects of fisheries and cannot simulate the impacts of the disturbance of the fishing list on the ecosystem [28,29]. The Ecopath model, however, has become a worldwide tool for describing the structures, functions, and energy flows of ecosystems, and fishery activities have been introduced to the ecosystem to comprehensively evaluate the impacts of fisheries on the ecosystem.

Ecopath applies thermodynamic principles to sustain a balance of inputs and outputs for functional groups within an ecosystem [30]. The Ecopath model incorporates a fundamental equation that address both material and energy balances and is expressed as follows:

$$B_i \times (P/B)_i \times EE_i - EX_i = \sum B_j \times (Q/B)_j \times DC_{ij}$$

In the equation, "i" represents the prey functional group; "B_i" represents the biomass of the prey functional group, "i", in t·km^2; "$(P/B)_i$" represents the production-to-biomass ratio of the prey functional group, "i"; "EE_i" represents the ecological efficiency of the prey functional group, "i"; and "EX_i" signifies the net migration (emigration−immigration). Moreover, "j" represents the predator functional group; "B_j" represents the biomass of the predator functional group, "j"; "$(Q/B)_j$" indicates the consumption-to-biomass ratio of the predator functional group, "j"; and "DC_{ij}" represents the proportion of the diet of the predator group, "j", that comprises the prey group, "i". The model requires fundamental input parameters, including "B_i", "$(P/B)_i$", "$(Q/B)_i$", "EE_i", "DC_{ij}", and "EX_i". Among the first four parameters, any one can be an unknown variable that the model calculates using the other parameters. The last two parameters, "DC_{ij}" and "EX_i", are mandatory input parameters.

2.4. Parameter Determination

To estimate P/B and Q/B coefficients for functional groups within the Caohai Lake ecosystem, we utilized reference values for planktonic and submerged plants, respectively, obtained from analogous ecosystems, following the approach outlined by Li et al. (2018) [31]. In estimating P/B and Q/B parameters for benthic organisms within the Caohai Lake ecosystem, we referred to estimations from the Dianchi Lake ecosystem's model [32] and the Gehu Lake ecosystem's model [33]. Additionally, the production (P) was calculated based on the value of P/B. The conversion from the dry to the wet mass was established using a ratio of 6:1 based on previous models [34]. For the fish functional groups, we determined P/B and Q/B values using established empirical formulas [35,36]. The necessary data were sourced from the fisheries resource database available at www.fishbase.org (accessed on 25 November 2023). Default values for the unassimilated-food ratio were referenced from empirical values. The composition matrix of the functional group diets, a critical component of the food web data, was primarily sourced from the fisheries resource database (www.fishbase.org, accessed on 25 November 2023) and supplemented with data from existing historical dietary studies [37,38]. Dietary information for planktonic organisms, snails, and shrimp was referenced from previous dietary research conducted in other aquatic ecosystems [39,40].

2.5. Model Equilibrium

The core output of the Ecopath model is founded on the principle for ensuring a balance between energy input and output within an ecosystem. A fundamental requirement for maintaining the model's equilibrium is that the ecological efficiency (EE) should be less than or equal to 1. In the Ecopath model, ensuring a balance is crucial where inputs and outputs for functional groups are equal. Additionally, both the total efficiency of the functional groups and EE should be less than 1, emphasizing the necessity for efficient energy utilization and transfer within the ecosystem. Therefore, the lack of equilibrium when raw data are entered into the Ecopath model necessitates iterative adjustments in the relevant parameters for the unbalanced functional groups. These adjustments continue until the model reaches its optimal state. To assess the credibility and quality of the parameters in the model designed for Caohai Lake, we employed the Ecopath pedigree (P) index. The P index is a valuable tool for evaluating the model's quality and reliability. Previous studies have established that the typical range of the P index falls between 0.16 and 0.68 [41]. The system omnivory index (SOI) is a crucial parameter within the Ecopath model, serving as an indicator of the system's stability. Higher SOI values generally signify a greater degree of system stability.

3. Results and Discussion

3.1. Ecosystem Structure and Energy Flow Distribution

The P index of the Caohai Lake Ecopath model for the pre-fishing ban was calculated at 0.411, while for the post-fishing ban model, it stood at 0.500. These P index values significantly contribute to the validation and assurance of the data reliability and quality within the respective models, affirming the credibility of our study's findings. The inputs and outputs of the Ecopath models before and after the implementation of the fishing ban in Caohai Lake are illustrated in Tables 3 and 4, respectively. After the fishing ban, there was a notable increase in the number of fish species within Caohai Lake, increasing from 7 to a total of 14 species. The additions included catfish, grass carp, common carp, silver carp, yellow catfish, snakehead, and catfish, enriching the lake's fish diversity and composition. The fish biomass increased significantly by 77.82% from 14.16 t·km^{-2} to 25.81 t·km^{-2} following the fishing ban. Concurrently, the fishing ban also induced a more intricate structure in the Caohai Lake food web, characterized by trophic levels ranging from 1 to 3.1. This was an enhancement from the pre-ban trophic level range (1–3.0). The shift toward higher trophic levels post ban indicated an improved energy transfer efficiency within the ecosystem.

Following the fishing ban, there was a notable increase in the biomass of the benthic organisms, albeit relatively minor, which rose from 77.72 t km^{-2} to 80.04 t km^{-2} (Table 4). This suggested that the fishing ban had a limited impact on benthic biomass within the ecosystem. In contrast, the phytoplankton biomass experienced a significant surge, increasing from 4.69 t·km^{-2} before the ban to 20.5 t km^{-2} after the ban, representing a remarkable four-fold increase. Furthermore, the zooplankton biomass increased substantially, surging from 2.32 t km^{-2} to 31.82 t km^{-2}, representing an approximately 13-fold increase. In contrast, the submerged plants' biomass in Caohai Lake experienced a pronounced decline, plummeting by 65% from 2552.0 t km^{-2} before the ban to 893.2 t km^{-2} after the ban. These compelling results indicate a clear transition within the Caohai Lake ecosystem—from a macrophyte-dominant, small-fish-centric system to an alga-dominant, large-fish-centric system—underscored by the significant alterations in the biomass across various trophic levels. Previous studies conducted in the Yangtze River have consistently demonstrated that managing the fishing pressure through measures such as seasonal fishing bans substantially contributes to the recovery and diversification of fish communities [42,43]. Following the trawl-fishing ban in the Arabian Gulf, marked increases in both the density and biomass of the benthic organisms in the ecosystem were observed [37]. These studies indicate that suspending fisheries and implementing fishing bans can have direct or indirect effects on aquatic organisms by reducing human interference, thereby facilitating the recovery of aquatic communities [12,18].

Table 3. Fundamental ecosystem parameters of Caohai Lake prior to the fishing ban implementation.

Functional Group	Trophic Level	Biomass (t·km^{-2})	Production/ Biomass (a^{-1})	Consumption/ Biomass (a^{-1})	Eco Trophic Efficiency	Production/ Consumption (a^{-1})
Bitterling fish	2.4	4.06	4.2	21.70	0.060	0.194
Bony fishes	2.7	4.49	1.2	6.20	0.190	0.194
Crucian carp	2.6	4.32	1.13	12.30	0.218	0.092
Topmouth gudgeon	2.8	0.93	1.2	6.20	0.345	0.194
Loach	2.5	0.156	1.2	6.20	0.090	0.194
Other small fishes	3.0	0.002	1.33	34.70	0	0.038
Ricefield eel	2.8	0.201	1.2	6.20	0.044	0.194
Shrimps	2.7	4.53	4.5	24.70	0.330	0.182
Mollusks	2.0	71.5	2.4	33.10	0.241	0.073
Other benthos	2.0	6.22	12	201.50	0.735	0.060
Zooplanktons	2.0	2.32	62.25	617.00	0.524	0.101
Phytoplanktons	1.0	4.69	420		0.538	
Submerged macrophytes	1.0	2552	2.61		0.008	
Detritus	1.0	6543			0.371	

Table 4. Fundamental ecosystem parameters of Caohai Lake post fishing ban implementation.

Functional Group	Trophic Level	Biomass ($t \cdot km^{-2}$)	Production/ Biomass (a^{-1})	Consumption/ Biomass (a^{-1})	Eco Trophic Efficiency	Production/ Consumption (a^{-1})
Bighead carp	2.6	0.048	1.299	7.53	0	0.173
Silver carp	2.5	0.08	1.503	10.19	0	0.147
Carp	2.4	4.224	3.5	31.00	0.440	0.113
Grass carp	2.1	2.814	1.2	45.00	0	0.027
Crucian carp	2.4	8.672	1.13	15.00	0.840	0.075
Yellow catfish	2.9	2.262	1.47	5.70	0	0.258
Sharpbelly	2.8	2.09	4.4	15.00	0.361	0.293
Bitterling fish	2.4	0.07	4.2	21.70	0.600	0.194
Topmouth gudgeon	2.8	0.31	1.2	6.20	0.824	0.194
Other small fishes	2.8	5.2	1.33	34.70	0.156	0.038
Bony fishes	2.9	0.01	1.2	6.20	0.004	0.194
Loach	2.5	0.007	1.2	6.20	0.006	0.194
Ricefield eel	2.8	0.008	1.2	6.20	0	0.194
Catfish	3.1	0.016	1.4	6.60	0	0.212
Red swamp crayfish	2.7	4.53	4.5	24.70	0.728	0.182
Mollusks	2.0	73.4	2.4	33.10	0.801	0.073
Other benthos	2.0	6.64	12	201.50	0.780	0.060
Zooplanktons	2.0	31.82	62.25	617.00	0.063	0.101
Phytoplanktons	1.0	20.5	420		0.761	
Submerged macrophytes	1.0	893.2	2.61		0.080	
Detritus	1.0	6543			0.795	

3.2. Energy Conversion Efficiency and Trophic Relationships

3.2.1. Lindeman Energy Flow Diagram

The energy flow efficiencies among the trophic levels in Caohai Lake before and after the fishing ban are illustrated in Figure 2. Prior to the ban, the Caohai Lake ecosystem comprised six trophic levels, and post ban, it integrated an additional trophic level, resulting in a total of seven integrated trophic levels [44]. Owing to differing energy sources, the Caohai Lake ecosystem is characterized by the presence of two distinct food chains. One commences with submerged plants and other vegetation, constituting a grazing chain, while the other initiates from detritus, forming a detritus-based chain. These distinctive pathways underline the diverse energy dynamics within the Caohai ecosystem. Prior to the fishing ban, the fundamental structure of the grazing chain in the Caohai ecosystem could be described as follows: energy originating from producers flows through consumers (including mollusks, herbivorous fishes, and zooplanktons) before reaching secondary consumers (including omnivorous and carnivorous fishes). Following the ban, the detritus-based chain involves the recycling of organic matter into detritus. Energy then flows through detritus feeders (including benthic organisms and zooplankton) before reaching the carnivorous fishes. In this context, the trophic transfer efficiency at the second trophic level (II) notably increased, rising from 20.75% before the fishing ban to 42.08% after the ban. However, the transfer efficiency tends to decrease at higher trophic levels (III and beyond). This phenomenon can be attributed to the relatively small size and shallow nature of Caohai Lake, where populations at higher trophic levels tend to exhibit relatively lower biomasses. This observation aligns with findings reported for the West River in the Pearl River Basin [13].

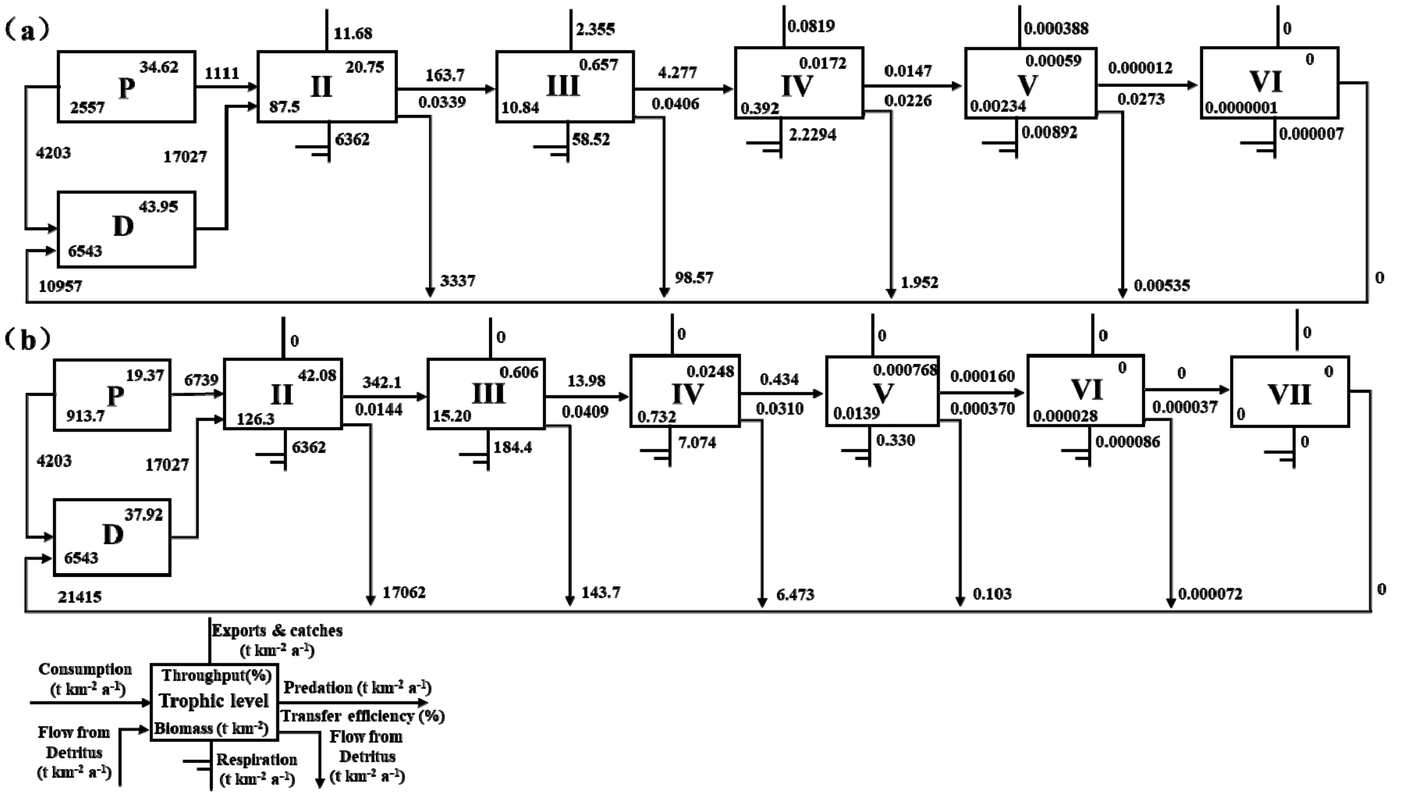

Figure 2. Energy flow efficiencies among the trophic levels in the Caohai Lake ecosystem before (**a**) and after (**b**) the implementation of the fishing ban. Trophic levels are represented by grades II, III, IV, and V.

The transfer efficiencies among the trophic levels in the Caohai Lake ecosystem before and after the fishing ban are summarized in Table 5. During both periods, the majority of the energy distributions were concentrated at trophic levels I and II, constituting over 90% of the total energy in Caohai Lake. As trophic levels ascended, there was a notable decrease in energy, indicating a decline in the energy transfer efficiency at higher trophic levels. The energy transfer efficiencies from trophic levels III and IV were lower before the fishing ban than after the ban. This shift in the energy transfer efficiencies can be attributed to the increased diversity in fish species after the fishing ban. The total conversion efficiency of the Caohai Lake ecosystem was slightly higher before the ban (3.141%) compared to that after the ban (2.632%), which was still lower than those of other Chinese lake ecosystems, such as Qiandao Lake (6.8%) [45], Dianchi Lake (11.7%) [42], and Taihu Lake (4.1%) [46]. This difference in the conversion efficiency is primarily attributed to the shallower water and relatively fewer trophic levels in Caohai Lake compared to the deeper and more complex ecosystems of Qiandao Lake and Dianchi Lake. Qiandao Lake and Dianchi Lake are dominated by algae as the primary producers and have a higher abundance of fish, resulting in a more intricate food web and, ultimately, a higher ecosystem-wide conversion efficiency. In contrast, both Caohai Lake and Taihu Lake have shallower waters and a less complex food web, resulting in a lower overall ecosystem conversion efficiency.

3.2.2. Transfer Efficiency and Mixed Nutritional Effects

Table 6 illustrates the distributions of the energy components within the Caohai Lake ecosystem before and after the implementation of the fishing ban, encompassing predator consumption, detritus flow, and throughput parameters. Subsequent to the enforcement of the fishing ban, an overall increase was observed across these parameters. The total system flow, signifying the total energy flow within the ecosystem, underwent a substantial expansion, increasing to approximately 1.5 times its pre-ban magnitude. A significant observation is the remarkable surge in consumption by predators at trophic level II, reaching a magnitude six times higher than its pre-ban magnitude. This striking increase underscores the substantially more dynamic state of the ecosystem. In terms of trophic interactions, as described by the mixed trophic impact, the Caohai Lake ecosystem displays intricate and complex relationships. Interactions within the same functional groups typically manifest as competitive, with a negative impact on the members as they vie for resources or other ecological factors. Conversely, between predator and prey functional groups, interactions are characterized by mutual influences.

Table 5. Transfer efficiencies among trophic levels in the Caohai Lake ecosystem before and after the implementation of the fishing ban.

Source\Trophic Level	PFB					ABF				
	II	III	IV	V	VI	II	III	IV	V	VI
Producer (%)	3.496	3.853	2.262	2.723		1.193	4.251	2.794	0.037	
Detritus (%)	3.363	4.105	2.256	2.727		1.537	4.036	3.2	0.037	
All flows (%)	3.391	4.051	2.257	2.726	0.619	1.44	4.086	3.101	0.037	0.004
Proportion of total flow originating from detritus (%)	61					69				
Transfer efficiencies from primary producers (%)	3.12					2.42				
Transfer efficiencies from detritus (%)	3.15					2.71				
Total transfer efficiencies (%)	3.14					2.63				

Notes: PFB, pre-fishing ban; ABF, after the ban on fishing. Transfer efficiencies are calculated as the geometric means for trophic levels II–IV. Grades II, III, IV, and V represent trophic levels.

Table 6. Energy flow distributions across trophic levels in the Caohai Lake ecosystem before and after the implementation of the fishing ban.

Trophic Level	PFB			ABF		
	Consumption by Predators	Flow to Detritus	Throughput	Consumption by Predators	Flow to Detritus	Throughput
VI	0	0.000001	0.000002	0	0.00002	0.00004
V	0	0.0011	0.0029	0	0.0228	0.0955
IV	0.003	0.393	0.862	0.096	1.515	3.419
III	0.86	20.91	35.67	3.419	34.58	80.42
II	36	678	1111	80.42	4819	6739
I	1111	7520	8631	6739	4203	10,941
Sum	1147	8219	9778	6823	9058	17,764

Notes: PFB, pre-fishing ban; ABF, after the ban on fishing.

It needs to be emphasized that fishing activities have exerted a notable and discernible impact on the ecosystem (Figure 3). Before the fishing ban, fishing exerted a notably pronounced negative influence, particularly impacting species such as the bighead carp, silver carp, carp, grass carp, crucian carp, yellow catfish, sharpbelly, bitterling fish, topmouth gudgeon, and various other small fishes within the ecosystem. Furthermore, small shrimp and crabs also substantially negatively affected the majority of the fish species. However, post fishing ban, the Caohai Lake ecosystem exhibits a more intrinsic pattern of trophic interactions. The presence of certain species, such as the red swamp crayfish and other predatory fishes, exerts adverse effects on the fish population across the ecosystem. Conversely, phytoplankton, submerged aquatic plants, and detritus—acting as vital food sources—have a positive impact on most predator species within the ecosystem. These dynamics align with previous research findings from Taihu Lake [47], highlighting the intricate interplay of species within the Caohai Lake ecosystem before and after the implementation of the fishing ban.

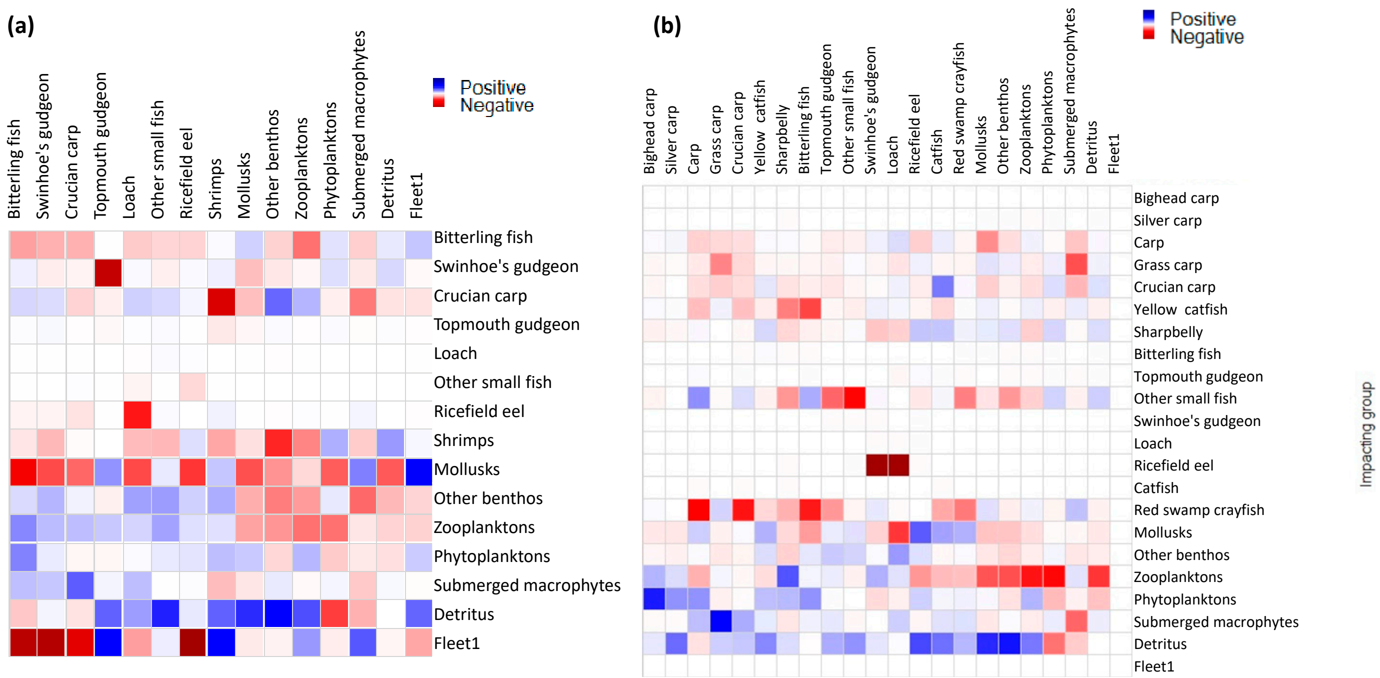

Figure 3. Mixed nutritional effects in the Caohai Lake ecosystem before (**a**) and after (**b**) the implementation of the fishing ban.

3.3. Characterization of System's Energy Flow

Following the fishing ban, the total system consumption within the Caohai ecosystem underwent a substantial 4.5-fold increase compared to the pre-ban levels (Table 7). The net production in the Caohai ecosystem demonstrated a notable rise, reaching 13,246.6 t·km^{-2}·a^{-1} after the ban, compared to the pre-ban level of 9070.4 t km^{-2}·a^{-1}. This signifies an approximately 10% increase in production post ban compared to that before the ban. The total system throughput experienced a remarkable increase, surging from 24,928.1 t km^{-2}·a^{-1} before the ban to 56,485.7 t km^{-2}·a^{-1} after the ban, marking a substantial 130% increase. Additionally, the total net primary production of the system rose from 8630.5 t km^{-2}·a^{-1} before the ban to 10,941.25 t km^{-2}·a^{-1} after the ban, representing a notable enhancement in the productivity post ban. These findings are consistent with those of a study conducted in the Pearl River Basin, which documented a shift from submerged-plant dominance to algal dominance in the ecosystem. This transition resulted in a significant increase in the calculated total net primary production [13]. Furthermore, in Erhai Lake, the invasion of alien fish species resulted in a decline in the submerged plants' biomass, subsequently elevating the calculated total net primary production from 5944.21 t km^{-2}·a^{-1} to 8837.13 t km^{-2}·a^{-1} [48]. These results provide compelling evidence that fishing bans initiate a shift in the ecosystem's composition, as characterized by a decrease in the abundance of submerged plants and a corresponding rise in the abundance of algae. This transition culminates in heightened productivity, increased energy flow, and an augmented calculated total net primary production within the Caohai ecosystem. These findings imply that fishing bans emerge as a vital strategy for bolstering fish abundance and expediting energy and material flows within the system.

The implementation of the fishing ban in Caohai Lake resulted in a decrease in the net system production from 6909.6 t·km^{-2}·a^{-1} to 4387.5 t·km^{-2}·a^{-1}. This outcome aligns with findings from the Pearl River Basin, which emphasized that an upsurge in the fish abundance within the ecosystem is linked to a substantial reduction in the net system production [43]. This decline in the net system production can be attributed to the increased foraging capacity of the fishes in the system, resulting in the increased consumption of the primary producers and, consequently, the reduced net system production. The transition from a submerged-plant-dominant macrophytic lake to an alga-dominant lake is highlighted by a substantial decrease in the total biomass of the system, excluding detritus, from 2655.4 t·km^{-2} before the ban to 1055.9 t·km^{-2} after the ban. This shift can be attributed mainly to a substantial reduction in the submerged plants' biomass. In the context of the Caohai Lake ecosystem, before the fishing ban, the SOI stood at 0.14, reflecting a certain level of stability. However, after the ban, the SOI slightly increased to 0.15, suggesting a modest enhancement in system's stability. Furthermore, the Shannon index, a measure of biodiversity, increased notably from 0.21 before the ban to 0.69 after the ban. This substantial increase in the Shannon index signifies a notable rise in the fish diversity within the lake's ecosystem. These findings from Caohai Lake are in line with those from Erhai Lake. The study in Erhai Lake, which also highlighted a decline in the submerged plants' biomass due to the invasion of alien species, showcased similar outcomes: heightened biodiversity and an increased SOI [48]. These results shed light on a fundamental ecological phenomenon, suggesting that when consumer populations within a lake's ecosystem experience explosive growth, they exert intensified pressure on the producers, often leading to a decline in the producers' productivity, while concurrently improving the system's stability.

Table 7. Comparison of statistics for the Caohai Lake ecosystem's Ecopath model before and after the implementation of the fishing ban.

Parameter	Unit	PFB	ABF	Variation
Sum of all consumptions		534.4	24,129.5	352%
Sum of all exports		6909.5	4387.4	−37%
Sum of all respiratory flows		1720.9	6553.7	281%
Sum of all flows to detritus	t·km^{-2}·a^{-1}	10,957.1	21,414.8	95%
Total system throughput		24,928.0	56,485.6	127%
Sum of all productions		9070.4	13,246.5	46%
Calculated total net primary production		8630.5	10,941.2	27%
Total primary production/total respiration	/	5.0	1.6	−67%
Net system production		6909.6	4387.4	
Total primary production/total biomass	t·km^{-2}·a^{-1}	3.2	10.3	
Total biomass/total throughput		0.106	0.018	
Total biomass (excluding detritus)	t·km^{-2}	2655.4	1055.9	
Connectance index		0.386	0.275	
System omnivory index (SOI)	/	0.143	0.151	
Shannon diversity index		0.21	0.69	

Notes: PFB, pre-fishing ban; ABF, after the ban on fishing.

3.4. Water Quality Changes

Significant changes in the water quality were observed within Caohai Lake following the fishing ban, as illustrated in Figure 4. The water's transparency significantly decreased 48.7% ($p < 0.01$), with values declining from 1.22 m before the ban to 0.63 m after the ban. Concurrently, the concentration of TP in Caohai Lake rose from 0.04 mg L^{-1} before the ban to 0.12 mg L^{-1} after the ban. No statistically significant differences were observed compared to the pre-ban levels ($p > 0.05$). After the fishing ban, the NH_3-N levels in Caohai Lake increased significantly ($p < 0.001$), reaching 1.51 mg L^{-1} from its pre-ban level of 0.19 mg L^{-1}, representing a remarkable 694.7% increase. Moreover, the COD level also saw a substantial increase after the ban, rising from 5.4 mg L^{-1} before the ban to 26.3 mg L^{-1} after the ban. Additionally, there was a significant increase in Chl.a concentration in the lake water following the ban ($p < 0.05$).

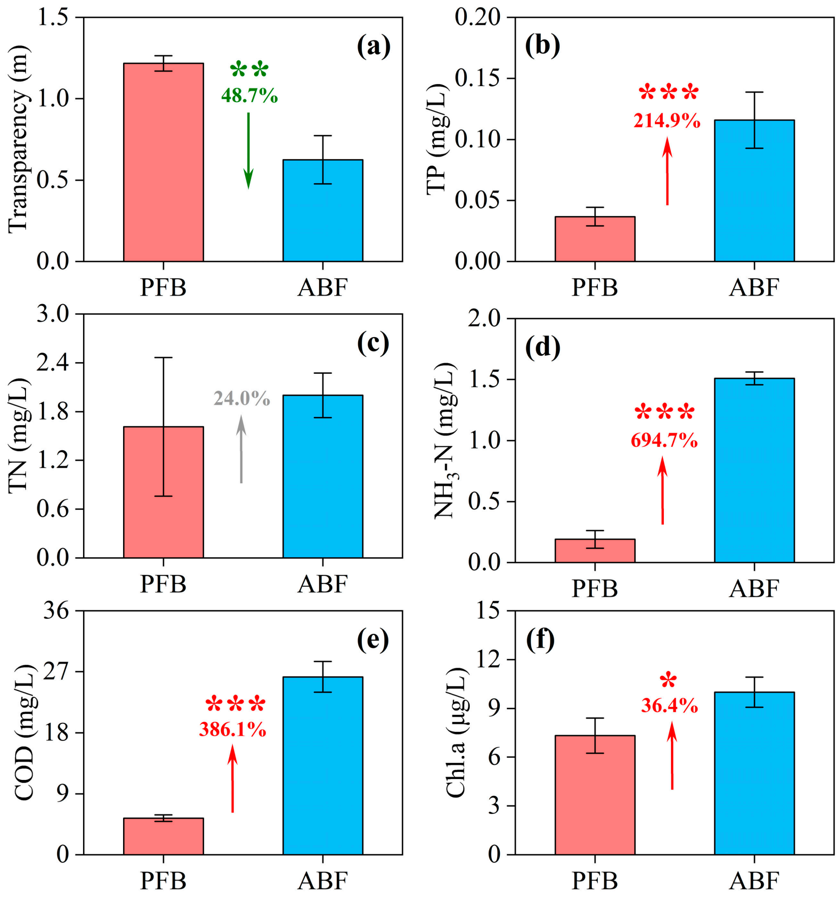

Figure 4. Changes in water transparency (**a**), total phosphorus (TP) level (**b**), total nitrogen (TN) level (**c**), ammonia nitrogen (NH_3-N) level (**d**), chemical oxygen demand (COD) level (**e**), and chlorophyll-a (Chl.a) level (**f**) in Caohai Lake before (PFB) and after (ABF) the implementation of the fishing ban. * ($p < 0.05$), ** ($p < 0.01$), and *** ($p < 0.001$) indicate significant differences in water qualities before and after the fishing ban.

These findings demonstrate that the fishing ban has brought about significant changes in the water's transparency and TP, COD, NH_3-N, and Chl.a levels in Caohai Lake. The factors influencing the water's transparency are multifaceted, including natural, biological, and human-related factors [49–51]. Although anthropogenic activities, such as fishing, decreased after the ban, the heightened fish richness and abundance in the lake can lead to sediment resuspension, facilitating the release of nutrients and stimulating algal growth. These processes ultimately contribute to the reduction in lake water's transparency [52]. Moreover, research conducted in Lake Dianchi revealed that fishing bans did not have a significant impact on water quality parameters [53]. This difference in the impact might be attributed to Caohai Lake's status as a closed-type lake with limited water flow. Additionally, the introduction of large fish species, such as silver carp, bighead carp, and grass carp, leading to a higher consumer population, could be constraining the growth and reproduction of the reducers. The present study revealed that the aquatic plant coverage in Caohai Lake significantly decreased from 70% before the fishing ban to only 10% after the ban (in 2021). This reduction in the abundance of submerged plants results in decreased nutrient removal, thus potentially leading to the deterioration of the lake water's quality.

4. Conclusions

The present study employed an Ecopath model to quantitatively assess and compare the structural characteristic, energy flow, and water quality changes in Caohai Lake's ecosystem before and after the implementation of a fishing ban. Prior to the ban, Caohai

Lake exhibited typical features of a macrophyte-dominant lake with a relatively low fish abundance, leading to slower energy and material flow within the ecosystem. However, following the ban, the fish abundance and biodiversity increased significantly, resulting in the substantial acceleration of the energy flow within the ecosystem. Furthermore, the fishing ban also had a profound impact on the water quality of Caohai Lake, as evidenced by the decreased water transparency and increased TP, NH_3-N, COD, and Chl.a levels. These alterations signify the transition from a macrophyte-dominant lake to an alga-dominant lake. Our findings underscore the implications for fishing bans in closed grass-type lakes, suggesting that although such bans can lead to an increase in fish species and abundance, thereby accelerating the energy flow through the food web, they also have a notable negative impact on lake water's quality and the reverse lake ecosystem succession. This study recommends that before formulating fishing ban policies, an in-depth analysis of the lake's fish structure, the nutrient levels of nitrogen and phosphorus in the sediments, and the hydrological conditions should be conducted. In the absence of a comprehensive assessment, the implementation of such policies should be approached with caution. When implementing a fishing ban, a phased and regional approach is advised to mitigate the impact on the ecosystem; after the implementation, real-time monitoring should be strengthened, with warning levels set to pay attention to the health of the aquatic ecosystem and prevent ecological catastrophes.

By combining previous research results with the results of this study, external causes of water quality degradation and the disappearance of submerged vegetation are essentially ruled out, and the increase in the fish population is identified as an important driving factor for the catastrophic shift in the Caohai Lake's ecosystem. The next phase could involve in-depth studies on how the increase in the fish population, nitrogen and phosphorus release from sediments, and wind-induced resuspension of suspended solids interact with each other, further revealing the detailed process of the ecosystem's degradation and providing more useful information for the restoration of the submerged vegetation in Caohai Lake.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/w16050782/s1, Table S1: Detailed locations of sampling sites in Caohai Lake.

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