

## Article

# In Situ Ecological Floating Bed Remediation Alters Internal Trophic Structure: A Case Study of Meiliang Bay, Lake Taihu

Bingyin Cao <sup>1,2</sup>, Long Ren <sup>2</sup>, Yuan Wang <sup>2</sup>, Xuwen Bing <sup>1,2</sup>, Zhen Kuang <sup>2</sup>  and Dongpo Xu <sup>1,2,\*</sup>

<sup>1</sup> Wuxi Fisheries College, Nanjing Agricultural University, Wuxi 214081, China; cx01200224@163.com (B.C.); bingxw@ffrc.cn (X.B.)

<sup>2</sup> Key Laboratory of Freshwater Fisheries and Germplasm Resources Utilization, Ministry of Agriculture and Rural Affairs, Freshwater Fisheries Research Center, Chinese Academy of Fishery Sciences, Wuxi 214081, China; renlong@ffrc.cn (L.R.); wangyuan@ffrc.cn (Y.W.); kuangzhen@ffrc.cn (Z.K.)

\* Correspondence: xudp@ffrc.cn

**Abstract:** Ecological floating beds are effective in mitigating lake eutrophication. To examine the effects of their in situ remediation processes on the food sources and trophic structures of consumers, particularly fish, this study used stable isotope techniques to compare cage enclosures, net enclosures, and natural lake area in Meiliang Bay, Lake Taihu. The results revealed that among basic carbon sources, only the  $\delta^{13}\text{C}$  values of phytoplankton and POM differed significantly, while most consumers showed no significant differences in carbon and nitrogen stable isotope characteristics across the three remediation areas. In cage enclosures, the food chain transitioned from being grazing-based, dominated by phytoplankton, to detritus-based, primarily relying on SOM. In contrast, net enclosures enhanced the utilization of phytoplankton. The trophic levels of most consumers in cage enclosures were significantly lower than those in net enclosures and the natural lake area. Trophic niche indices indicated that cage enclosures exhibited the highest trophic diversity and the lowest trophic redundancy. The in situ remediation using ecological floating beds altered the food resource conditions within the remediation areas due to differences in the degree of enclosure provided by the floating beds and interception facilities. These changes have consequently reshaped the internal trophic structure through trophic cascade effects.



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**Keywords:** eutrophication; food resources; remediation facilities; ecological floating beds; trophic structure

**Key Contribution:** This study is the first to apply stable isotope analysis to verify changes in basal carbon sources within habitats following net and cage enclosure implementation and to investigate how these changes influence fish trophic structures through bottom-up effects.

## 1. Introduction

Lakes form the essential constituents of the Earth's freshwater resources and hold a crucial position in the survival and development of humanity [1]. They also play remarkable roles in aspects such as climate regulation, alleviating floods and droughts, as well as supporting transportation [2,3]. However, human activities have led to substantial changes in water quality and biodiversity. Lake eutrophication, in particular, has become a global issue [4–6]. Lake Taihu, China's third-largest freshwater lake, has experienced severe eutrophication due to increased pollutant discharge, even causing a city-wide drinking water crisis in Wuxi [7]. Meiliang Bay, Lake Taihu, has specifically emerged as a prime area

with frequent occurrences of cyanobacterial blooms due to its geographical features and wind patterns [8].

The construction of eco-floating beds and other aquatic vegetation is effective in suppressing algal blooms. This is achieved by competing with phytoplankton for nutrients, thus leading to an improvement in water quality and an enhancement of water clarity [9]. This method has been widely applied in places such as China, Europe, Japan, Mexico, the United States, and so on, and the effects have been remarkable [10–14]. In situ restoration typically includes two approaches: net enclosure restoration and cage enclosure remediation. Cage enclosures hinder the exchange of water, resulting in the formation of isolated ecosystems. Their main application lies in assessing the impacts of water purification and the control of algal growth [15–17]. On the other hand, the net enclosure facilities intercept fish and carry out the stocking of filter-feeding fish, thus conducting ecological aquaculture for controlling algae with fish [18]. There is a transitional relationship among the cage enclosure, net enclosure, and natural lake area. The net enclosure has some artificial interventions compared to the natural lake area but remains closely connected, serving as a transition zone between the two. In contrast, the cage enclosure is more heavily influenced by human interventions and is more isolated. This creates a gradient of increasing artificial modification from the natural lake area to the net enclosure, and finally to the cage enclosure.

For the purpose of exploring more comprehensively the issue of lake eutrophication, the current studies in the literature focus on remediation methods and their impacts on water quality, plankton, and plants in lakes. For example, Liang et al. [19] found that eco-floating beds, particularly those combining *Canna indica*, *Acorus calamus*, and *Phragmites australis*, effectively improve water quality. Lin et al. [15] demonstrated that as silver carp grow larger, grazing pressure decreases, thereby weakening their control over phytoplankton populations. Ni et al. [20] proposed an eco-dam system using floating beds for pollution control and bioremediation, which showed slight improvements in water quality during Chinese mitten crab breeding in Yangcheng Lake. However, relatively few studies have explored the broader and more systemic impacts of these methods on food webs and trophic structures. Zhao et al. [21] found differences in food web structures inside and outside silver carp and bighead carp stocking areas, while Zuo et al. [22] employed in situ experimental ecology methods and found that increasing the stocking density of *Fenneropenaeus chinensis* influences fish community composition and niche overlap. Research focusing on the entire process—from changes in food resources to the triggering of trophic cascades and their subsequent effects on trophic structures—is even more limited.

In lake ecosystems, interspecies relationships have been essentially reflected in trophic interactions. These interactions are mutually constraining and interdependent, forming a complex food web [23]. The evaluation of trophic structure quantifies patterns of biodiversity and energy flow, enabling comparative analysis [24]. The application of remediation facilities and ecological floating beds undoubtedly brings about a series of complex changes to the aquatic ecosystem. We speculate that, due to the isolation effect of remediation facilities on food resources and the control effect of ecological floating beds on algae, the nutrient cycling and energy flow within the restoration area may be altered, thus triggering an adjustment of the trophic structure. Consequently, we employ the stable isotope technique to compare the stable isotope characteristics of the basal carbon sources and fish both inside and outside the remediation area, aiming to reveal the changes in material flow. We also evaluate the utilization of carbon sources by fish and shrimp, exploring how different species respond to the changes in the food resource pattern. Moreover, we analyze the dynamic adjustments of the trophic levels and trophic niches of fish so as to assess the potential impacts of the remediation process on the fish-dominated trophic structure. The

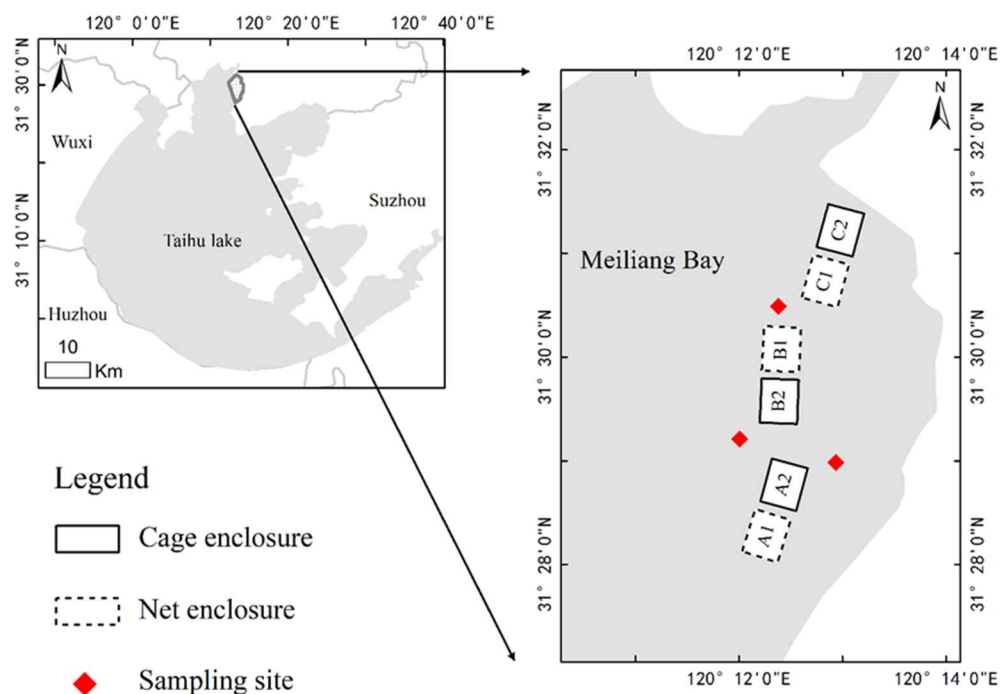
results obtained not only enhance our comprehension of ecosystem functioning but also offer guidance and serve as a reference for practical water management and ecological remediation endeavors.

## 2. Materials and Methods

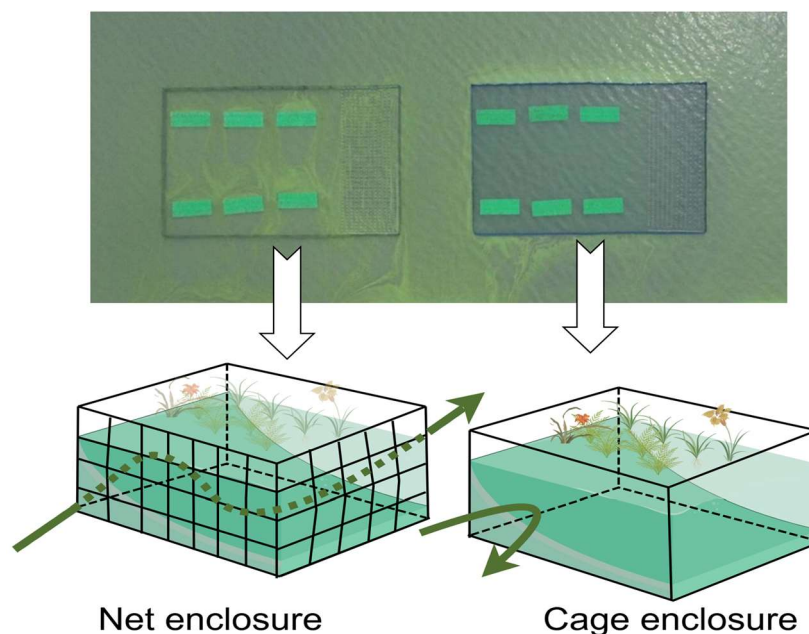
### 2.1. Study Area

Meiliang Bay ( $31^{\circ}25'27.21''$  N;  $120^{\circ}11'17.58''$  E), located in the northwestern part of Lake Taihu, is prone to algal accumulation and frequent algal blooms due to the persistent influence of southeastern winds. During May, June, August, and October 2021, samples of primary carbon sources, plankton, benthic organisms, as well as fish and shrimp were gathered from three distinct habitats.

As shown in (Figure 1), the experimental area comprised three parallel groups (A, B, and C), each covering an area of  $30 \times 50$  m<sup>2</sup>. Each group contained an equal-sized net enclosure and a waterproof cage enclosure, with the total experimental area spanning 4500 m<sup>2</sup>. Additionally, three sampling points were established in the surrounding natural lake area, all located within 100 m of the nearest restoration zone. Each cage enclosure was supported by 32 steel posts, where the waterproof fabric had a height of 3 m and its upper edge was positioned 1 m above the water surface. The bottom of the fabric was secured into the sediment using gabions, ensuring isolation between the internal and external water bodies. Similarly, each net enclosure was supported by 32 steel posts, with a 3 m high net and its upper edge 1 m above the water surface. The bottom was also anchored into the sediment with gabions. Eco-floating beds, containing aquatic plants known for their water purification properties, such as *Canna indica*, *Acorus calamus*, *Phragmites australis*, *Oenanthe javanica*, and *Sagittaria trifolia*, were cultivated within the experimental area. These plants covered 10% of the total habitat area (Figure 2).



**Figure 1.** Sampling sites for the deployment of cage enclosures, net enclosures, and the natural lake area in Meiliang Bay.



**Figure 2.** Demonstration area for net enclosure and cage enclosure. Note: The arrow indicates the direction of water flow. The net enclosure permits water exchange with the natural lake, whereas the cage enclosure does not.

## 2.2. Sample Collection and Processing

Basal carbon source samples were collected from the net enclosure, cage enclosure, and natural lake area, with 241, 227, and 34 samples, respectively. Fish and shrimp samples were collected from the same areas, totaling 459, 467, and 165, respectively. Fish and shrimp were collected using multi-mesh gillnets and stationary series traps. The gillnet had a total length of 10.5 m and a height of 1.5 m, while the stationary series trap measured 10 m in length, 0.4 meters in width, and 0.4 meters in height. The identification criteria for fish include body shape, total length, body height, the number and position of fins, scale types, coloration, patterning, and the proportions of different body parts. All specimens were identified to species-level based on the book *Fishes of Lake Taihu* [25], and basic biological data such as body length and weight were recorded. Dorsal white muscle was extracted from the fish, and abdominal muscle was extracted from the shrimp.

Benthic organisms were collected using a Peterson grab sampler, sieved through a 60-mesh screen, and temporarily held for 12 h to clear their guts. Zooplankton and phytoplankton were collected using #13 and #25 plankton nets, respectively, and filtered onto Whatman GF/F glass fiber filters that had been pre-combusted at 450 °C for four hours. Particulate organic matter (POM) was collected using a 1 L water sampler, placed into 1 L polyethylene bottles, and filtered onto treated Whatman GF/F glass fiber filters. Sediment organic matter (SOM) was divided into two portions: one was acidified for carbon stable isotope analysis, and the other was left unacidified for nitrogen stable isotope analysis. These samples were rinsed with distilled water and stored at −20 °C. After lyophilization, the samples were ground into powder for further analysis.

Stable isotope analysis was conducted at the Third Institute of Oceanography China, using a Delta V Advantage isotope ratio mass spectrometer coupled with a Flash EA 1112 HT elemental analyzer. Approximately 2 mg of each sample was analyzed. One standard reference sample (IAEA-USGS24 for carbon, IAEA-USGS25 for nitrogen) was included for every 10 samples, and 1–2 samples were randomly reanalyzed. The measurement errors for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were less than 0.2‰ and 0.3‰, respectively. Vienna Pee Dee

Belemnite and atmospheric nitrogen were used as the reference materials for carbon and nitrogen isotopes.

$$\delta X (\text{‰}) = (R_{\text{samples}} - R_{\text{standard}}) / R_{\text{standard}} \times 1000$$

where  $X$  represents the sample's  $^{13}\text{C}$  or  $^{15}\text{N}$ , and  $R$  is the ratio of heavy-to-light isotopes ( $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ).

### 2.3. Data Analytics

#### 2.3.1. Trophic Level Calculations

In this study, various benthic organisms collected from the net enclosure, cage enclosure, and natural lake area were used as baseline species, and their mean  $\delta^{15}\text{N}$  values were employed to calculate the trophic levels of other aquatic organisms. The trophic level (TL) was calculated using the following formula:  $\text{TL} = (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}) / \text{TEF} + \lambda$ . Here,  $\delta^{15}\text{N}_{\text{consumer}}$  represents the nitrogen isotope ratio in the consumer,  $\delta^{15}\text{N}_{\text{baseline}}$  is the mean nitrogen isotope ratio of the baseline benthic organisms, and TEF is the nitrogen isotope fractionation factor, typically set at 3.4‰ [26]. Since the baseline organisms are primary consumers,  $\lambda$  is assigned a value of 2 [27].

The weighted mean trophic levels for the three habitats were also calculated:

$$\text{MTL} = \frac{\sum (\text{Trophic Level of Species}_i \times \text{Relative Abundance of Species}_i)}{\sum \text{Relative Abundance of Species}_i}$$

where the trophic level of species<sub>*i*</sub> refers to the trophic level of species *i*, and the relative abundance of species<sub>*i*</sub> represents the relative abundance of species *i*.

#### 2.3.2. Trophic Niche

Based on stable isotope analysis, six indicators proposed by Layman et al. [28] were employed to quantify the community trophic structure across three distinct habitats. Specifically, NR (the range of  $\delta^{15}\text{N}$  values) represents trophic level variation within the food web, and CR (the range of  $\delta^{13}\text{C}$  values) indicates the diversity of basal carbon sources. TA (the total area of the convex hull in a  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplot) reflects ecological niche width, though it can be influenced by outliers. CD (the mean distance of each species from the biplot center) captures the average level of trophic diversity. Additionally, MNND (mean nearest neighbor distance) and SDNND (standard deviation of nearest neighbor distance), respectively, indicate species packing density and measure species distribution evenness within niche space. The first four metrics describe community-wide trophic diversity through the spread in the  $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$  biplot, while the last two metrics reflect the relative positioning of species within niche space to assess trophic redundancy. To further quantify and assess the variability and confidence intervals of the trophic niche width, we employed a Bayesian approach for iterative sampling. The model parameters were specified, including 20,000 iterations, a burn-in period of 1000, and 2 chains, to ensure the robustness of the results.

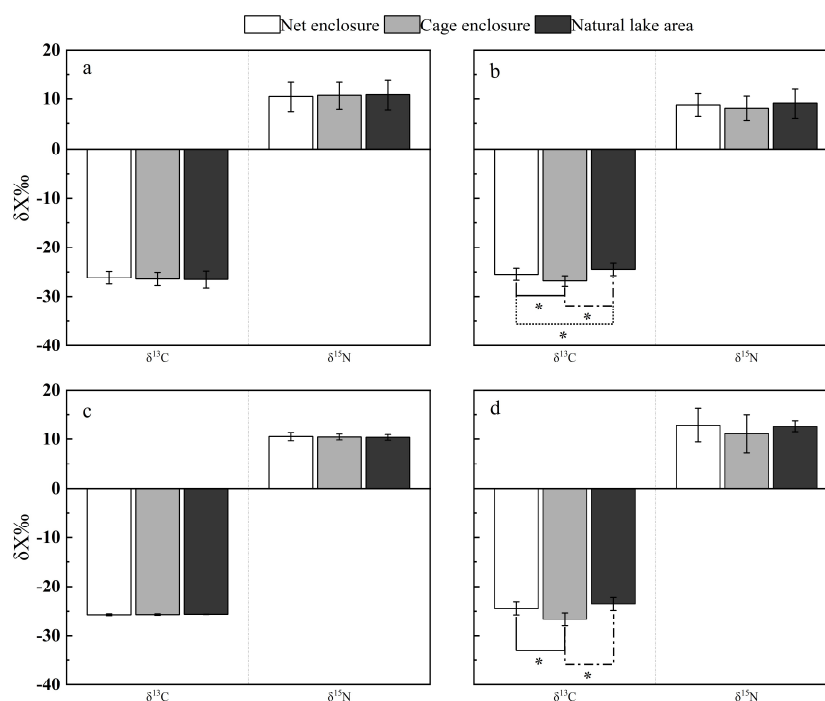
Statistical tests were conducted on four primary carbon sources—zooplankton, POM, SOM, and phytoplankton—along with fish and shrimp, within three habitats. When the data met the assumptions of normality and homoscedasticity, a one-way analysis of variance (ANOVA) was applied. If these assumptions were not satisfied, the Kruskal–Wallis one-way ANOVA (for  $K$  samples) was used. A significance level of  $\alpha = 0.05$  was adopted for all tests. All statistical analyses were performed using IBM SPSS Statistics (version 27.0.1), Excel 2019, and the R packages *SIBER* [29] and *simmr* [30]. Graphs were generated using Origin 2022 and the R package *ggplot2* (version 4.3.2).

### 3. Results

#### 3.1. Stable Isotopes and Carbon Sources

##### 3.1.1. Stable Isotopic Characteristics of Carbon Sources

The  $\delta^{13}\text{C}$  values of the four carbon sources exhibited relatively small variations, with the natural lake area showing the largest range of 3.01‰ and the cage enclosure the smallest range of 1.21‰. As shown in Figure 3, significant differences in the  $\delta^{13}\text{C}$  values of phytoplankton were observed between the cage enclosure and the net enclosure, as well as between the cage enclosure and the natural lake area ( $p < 0.05$ ). Particulate organic matter (POM) showed significant differences across all three habitats ( $p < 0.05$ ). The  $\delta^{15}\text{N}$  values varied the most in the net enclosure, with a range of 4.05‰, and the least in the cage enclosure, with a range of 2.96‰. In all three habitats, POM consistently had the lowest  $\delta^{15}\text{N}$  values, while phytoplankton exhibited the highest. The  $\delta^{15}\text{N}$  values of zooplankton were similar to those of sediment organic matter (SOM). No significant differences in  $\delta^{15}\text{N}$  values were observed across the three habitats for the four baseline carbon sources ( $p > 0.05$ ).

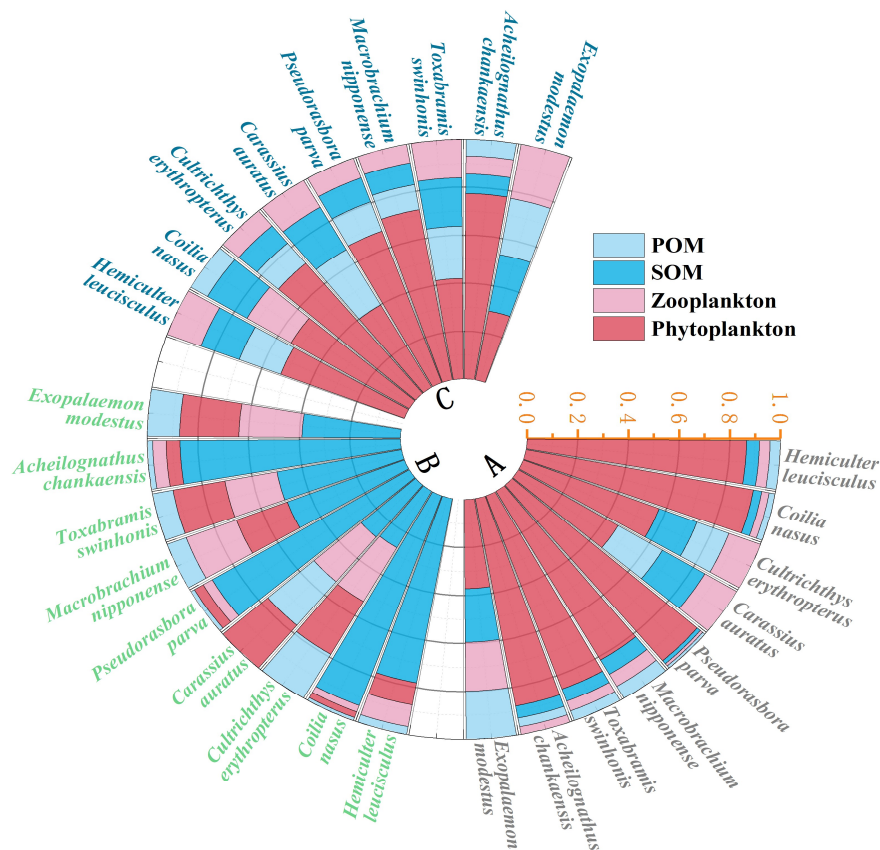


**Figure 3.**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of zooplankton, POM, SOM, and phytoplankton. Note: (a–d) indicate the differences in isotopic signatures of zooplankton, POM, SOM, and phytoplankton, respectively, and “\*” denotes a significant difference ( $p < 0.05$ ) between them.

##### 3.1.2. Contribution of Carbon Sources to Consumers

The carbon source utilization by nine consumer species—*Hemiculter leucisculus*, *Coilia nasus*, *Cultrichthys erythropterus*, *Carassius auratus*, *Pseudorasbora parva*, *Macrobrachium nipponense*, *Toxabramis swinhonis*, *Acheilognathus chankaensis*, and *Exopalaemon modestus*—was analyzed across three habitats, with particular emphasis on four carbon sources: zooplankton, phytoplankton, POM, and SOM. This study revealed notable shifts in the utilization of these carbon sources within the cage enclosure compared to the natural environment. The food chain transitioned from being a grazing-based food chain, relying on phytoplankton, to a detritus-based system dominated by SOM. In contrast, the proportion of phytoplankton as the primary carbon source in the net enclosure showed an increasing trend (Figure 4, Table S1). In the natural lake area, fish and shrimp continued to show the highest utilization

of phytoplankton, but compared to the net enclosure, their reliance on the four carbon sources was more balanced. In the net enclosure, phytoplankton contributed over 80% to all species except for *C. erythropterus*, *C. auratus*, and *E. modestus*. Within the cage enclosure, SOM emerged as the primary carbon source, significantly influencing species such as *H. leucisculus*, *C. nasus*, *P. parva*, and *A. chankaensis*.



**Figure 4.** Carbon source utilization by nine consumers in net enclosure, cage enclosure, and natural lake area. Note: where “A”, “B”, and “C” represent net enclosure, cage enclosure, and natural lake area, respectively.

### 3.2. Stable Isotopic Characteristics and Trophic Levels of Consumers

#### 3.2.1. Stable Isotope Characteristics of Consumers

The Kruskal–Wallis one-way ANOVA was performed on fish species with sample sizes greater than three collected from all three restoration zones. The results showed that most consumers did not exhibit significant differences in carbon and nitrogen stable isotope values among the net enclosure, cage enclosure, and natural lake areas ( $p > 0.05$ ) (Table 1).

The  $\delta^{13}\text{C}$  values varied across habitats: in the net enclosure, they ranged from  $-29.15 \pm 1.49\text{‰}$  to  $-20.72\text{‰}$ ; in the cage enclosure, they ranged from  $-27.00 \pm 0.97\text{‰}$  to  $-21.55 \pm 0.36\text{‰}$ ; and in the natural lake area, they ranged from  $-25.67 \pm 0.37\text{‰}$  to  $-21.63 \pm 0.17\text{‰}$ . Significant differences were observed in *A. chankaensis* and benthic organisms between the net and cage enclosures, as well as between the cage enclosure and the natural lake area ( $p < 0.05$ ). *C. nasus* showed significant differences between the net and cage enclosures, and between the net enclosure and the natural lake area ( $p < 0.05$ ).

The  $\delta^{15}\text{N}$  values showed wider ranges: from  $9.76 \pm 0.64\text{‰}$  to  $20.22 \pm 1.55\text{‰}$  in the net enclosure; from  $6.60 \pm 0.72\text{‰}$  to  $20.84 \pm 2.22\text{‰}$  in the cage enclosure; and from  $10.91 \pm 1.58\text{‰}$  to  $20.14 \pm 0.79\text{‰}$  in the natural lake area. *M. nipponense* was the only species exhibiting significantly lower  $\delta^{15}\text{N}$  values in the natural lake area compared to the net and cage enclosures ( $p = 0.03$ ).

**Table 1.** Stable isotope signatures of consumers in net enclosure, cage enclosure, and natural lakes.

Species	Sample Quantity			$\delta^{13}\text{C}$ (‰)			$\delta^{15}\text{N}$ (‰)		
				Net Enclosure	Cage Enclosure	Natural Lakes	Net Enclosure	Cage Enclosure	Natural Lakes
<i>Hemiculter leucisculus</i>	31	46	6	$-22.55 \pm 0.85$	$-22.56 \pm 1.01$	$-22.64 \pm 0.83$	$17.82 \pm 0.96$	$17.66 \pm 1.41$	$17.81 \pm 0.19$
<i>Culter dabryi</i>	2	4	5	$-21.55 \pm 0.03$	$-21.55 \pm 0.36$	$-21.63 \pm 0.17$	$19.40 \pm 0.15$	$19.02 \pm 0.23$	$19.27 \pm 0.34$
<i>Paramisgurnus dabryanus</i>	1	2	2	-23.14	$-22.19 \pm 1.98$	$-23.39 \pm 0.11$	12.67	$6.60 \pm 0.72$	$13.17 \pm 0.73$
<i>Coilia nasus</i>	83	144	41	$-23.24 \pm 0.86$	$-23.74 \pm 1.10^a$	$-23.68 \pm 0.86^a$	$20.22 \pm 1.55$	$20.28 \pm 1.24$	$20.14 \pm 0.79$
<i>Cultrichthys erythropterus</i>	9	4	9	$-22.18 \pm 0.92$	$-22.02 \pm 0.21$	$-21.82 \pm 0.59$	$18.65 \pm 2.78$	$19.11 \pm 0.43$	$19.07 \pm 0.90$
<i>Carassius auratus</i>	10	5	9	$-22.84 \pm 0.61$	$-23.14 \pm 1.11$	$-23.28 \pm 0.62$	$14.32 \pm 3.40$	$13.12 \pm 4.07$	$14.71 \pm 4.29$
<i>Cyprinus carpio</i>	5	2	8	$-22.93 \pm 0.40$	$-27.00 \pm 0.97$	$-22.37 \pm 0.34$	$17.93 \pm 0.51$	$20.38 \pm 0.01$	$13.29 \pm 7.20$
<i>Pseudorasbora parva</i>	99	92	9	$-22.54 \pm 0.55$	$-22.69 \pm 1.01$	$-22.53 \pm 0.58$	$18.87 \pm 0.69$	$18.45 \pm 1.35$	$18.91 \pm 0.51$
<i>Macrobrachium nipponense</i>	15	21	9	$-22.34 \pm 0.57$	$-22.55 \pm 1.45$	$-22.27 \pm 0.69$	$19.07 \pm 0.84$	$18.96 \pm 0.85$	$18.27 \pm 0.30^{ab}$
<i>Toxabramis swinhonis</i>	42	17	5	$-22.94 \pm 1.08$	$-22.83 \pm 0.94$	$-23.07 \pm 0.45$	$17.60 \pm 1.25$	$17.70 \pm 1.03$	$17.58 \pm 0.97$
<i>Acheilognathus chankaensis</i>	73	54	12	$-22.62 \pm 0.74$	$-23.13 \pm 0.75^a$	$-22.79 \pm 0.91^b$	$17.28 \pm 0.67$	$16.57 \pm 1.12$	$16.72 \pm 0.89$
<i>Exopalaemon modestus</i>	5	11	3	$-22.48 \pm 0.67$	$-23.20 \pm 1.06$	$-22.9 \pm 0.53$	$18.68 \pm 0.82$	$18.34 \pm 1.11$	$18.91 \pm 0.83$
<i>Protosalanx hyalocranius</i>	7	5	1	$-22.39 \pm 0.50$	$-22.54 \pm 0.26$	-23.00	$18.64 \pm 2.20$	$20.84 \pm 2.22$	16.87
<i>Acheilognathus macropterus</i>	24	12	0	$-22.18 \pm 0.66$	$-23.06 \pm 0.66$	-	$17.53 \pm 1.12$	$16.49 \pm 0.68$	-
<i>Paracheilognathus himantegus</i>	1	1	0	-20.72	-21.95	-	19.70	18.92	-
<i>Hemibarbus maculatus</i>	1	0	4	-23.21	-	$-22.77 \pm 0.30$	18.85	-	$18.87 \pm 0.22$
<i>Pelteobagrus fulvidraco</i>	1	0	4	-23.04	-	$-23.07 \pm 0.37$	19.87	-	$19.28 \pm 0.55$
<i>Hemiculter bleekeri</i>	0	2	1	-	$-22.31 \pm 0.33$	-22.18	-	$17.95 \pm 0.04$	17.56
<i>Hyporhamphus intermedius</i>	0	2	1	-	$-22.19 \pm 0.24$	-22.37	-	$18.01 \pm 1.3$	18.55
<i>Hypophthalmichthys molitrix</i>	0	1	11	-	-23.04	$-23.78 \pm 0.86$	-	15.31	$15.15 \pm 1.58$
<i>Aristichthys nobilis</i>	0	4	5	-	$-22.61 \pm 0.83$	$-22.93 \pm 1.18$	-	$16.84 \pm 1.11$	$13.86 \pm 2.59$
<i>Neosalanx tangkahkeii</i>	0	2	6	-	$-23.17 \pm 0.13$	$-24.14 \pm 0.21$	-	$20.28 \pm 0.19$	$19.66 \pm 0.35$
<i>Rhinogobius giurinus</i>	0	1	0	-	-23.73	-	-	17.94	-
<i>Megalobrama amblycephala</i>	0	0	6	-	-	$-22.67 \pm 0.46$	-	-	$10.91 \pm 1.58$
<i>Megalobrama terminalis</i>	0	0	1	-	-	-24.17	-	-	13.02
<i>Pelteobagrus eupogon</i>	0	0	1	-	-	-22.95	-	-	19.33
<i>Sarcocheilichthys sinensis</i>	1	0	0	-23.21	-	-	18.63	-	-
<i>Bellamyia sp.</i>	2	0	0	$-29.15 \pm 1.49$	-	-	$9.76 \pm 0.64$	-	-
<i>Taenioides cirratus</i>	1	0	0	-24.58	-	-	18.36	-	-
benthos	46	35	6	$-25.81 \pm 0.64$	$-26.6 \pm 0.72^a$	$-25.67 \pm 0.37^b$	$14.34 \pm 1.06$	$15.38 \pm 3.46$	$14.51 \pm 0.85$

Note: “a” indicates a significant difference ( $p < 0.05$ ) from net enclosure and “b” indicates a significant difference ( $p < 0.05$ ) from cage enclosure. The first, second, and third columns of sample quantity correspond to net enclosure, cage enclosure, and natural lakes, respectively.

### 3.2.2. Trophic Level Characteristics of Consumers

The mean trophic level of benthic organisms was used as a baseline to calculate consumer trophic levels in the cage enclosure, net enclosure, and natural lake area, resulting in a continuous trophic gradient (Figure 5). The findings revealed that the net enclosure had the highest mean trophic level (3.16), while the cage enclosure and natural lake area exhibited similar levels at 2.91 and 2.90, respectively. In the net enclosure, 60% of species had an average trophic level above 3, compared to 48% in the natural lake area and 40%



in the cage enclosure. Predatory fish, such as *C. nasus*, *P. fulvidraco*, and *Salangidae*, were at higher trophic levels, whereas herbivorous and omnivorous species like *C. carpio*, *M. amblycephala*, and *C. auratus* were at lower levels. Overall, the trophic levels of most consumers in the net enclosure, cage enclosure, and natural lake area hovered around 3. A one-way ANOVA and non-parametric test were conducted on the trophic levels of nine consumer species (Figure 6). The results indicated that most consumers in the cage enclosure had significantly lower trophic levels compared to those in the net enclosure and natural lake area ( $p < 0.05$ ). In contrast, differences between the net enclosure and natural lake area were minimal ( $p > 0.05$ ).

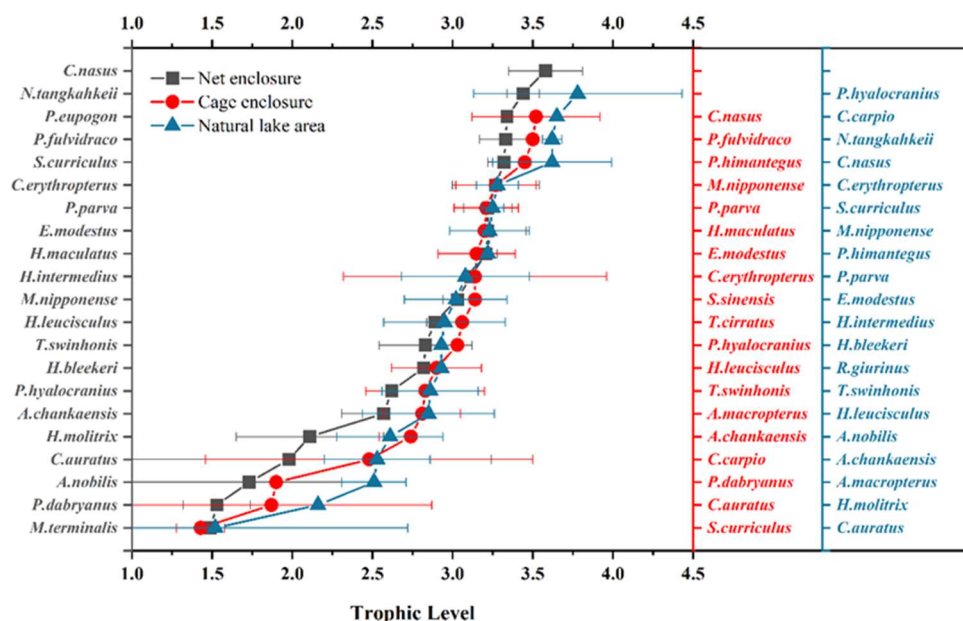


Figure 5. Trophic level gradient of net enclosure, cage enclosure, and natural lake area.

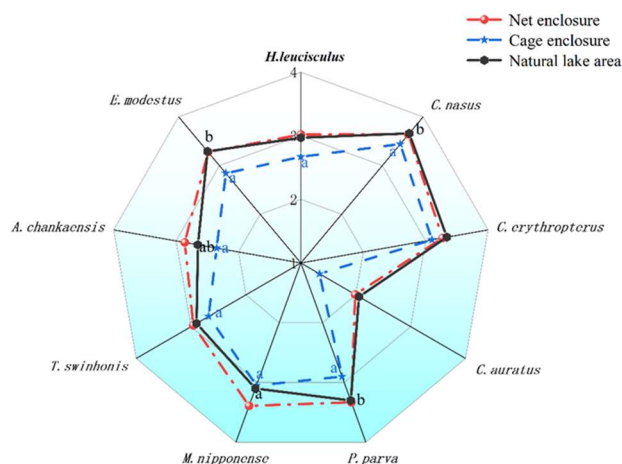


Figure 6. Trophic level differences among nine consumers in net enclosure, cage enclosure, and natural lake area. Note: “a” indicates a significant difference between the net enclosure and either the cage enclosure or the natural lake area, while “b” indicates a significant difference between the cage enclosure and the natural lake area ( $\alpha = 0.05$ ).

### 3.3. Trophic Niche of Consumers

Different habitats led to marked differences in community trophic niches (Table 2). The  $\delta^{15}\text{N}$  range reflects the vertical structure of the food web and was widest in the cage enclosure, indicating the broadest trophic level span. The  $\delta^{13}\text{C}$  range was widest in the natural lake area, suggesting the greatest diversity of carbon sources. The cage

enclosure had the largest total niche area (TA), approximately twice that of the net enclosure. The mean centroid distance (CD) was also greatest in the cage enclosure, indicating the highest level of trophic diversity. Mean nearest neighbor distance (MNND), which assesses overall community density, was largest in the cage enclosure (0.99) and smallest in the net enclosure (0.75), suggesting minimal trophic redundancy in the cage enclosure and maximum redundancy in the net enclosure. In the natural lake area, the SDNND values indicated the most even distribution of the trophic niches, whereas in the enclosures, the niches were more dispersed, with greater variation in the distances between species.

**Table 2.** Indicators of trophic niche in net enclosure, cage enclosure, and natural lake area.

Habitat Type	NR	CR	TA	CD	MNND	SDNND
Net enclosure	5.90	1.06	2.92	1.21	0.75	0.92
Cage enclosure	7.16	1.72	5.80	1.44	0.99	1.04
Natural lake area	5.43	1.86	4.83	1.28	0.83	0.58

Using the corrected standard ellipse area (SEAc) to minimize sample bias, the trophic niche width of nine common consumers across the three habitats was analyzed (Table 3). The results showed that, except for *P. himantegus* and *T. swinhonis*, the niche width of other aquatic species was greater in the cage enclosure than in the other two habitats. For most aquatic species, except *C. auratus*, *A. chankaensis*, and *E. modestus*, the niche width was greater in the net enclosure compared to the natural lake area. Notably, *C. auratus* exhibited the largest niche width across all three habitats, while *C. erythropterus* showed significant variation, with niche widths of 6.15 %<sup>2</sup> in the net enclosure, 0.42 %<sup>2</sup> in the cage enclosure, and 1.14 %<sup>2</sup> in the natural lake area.

**Table 3.** Corrected standard ellipse areas for nine consumers areas.

Species	Net Enclosure			Cage Enclosure			Natural Lake Area		
	TA	SEA	SEAc	TA	SEA	SEAc	TA	SEA	SEAc
<i>H. leucisculus</i>	9.85	2.50	2.59	23.02	4.44	4.54	0.62	0.48	0.60
<i>C. nasus</i>	24.08	3.93	3.98	25.07	4.03	4.07	8.71	1.92	1.96
<i>C. erythropterus</i>	10.63	5.38	6.15	0.24	0.28	0.42	1.83	1.00	1.14
<i>C. auratus</i>	11.65	6.50	7.31	6.93	7.58	10.11	11.92	7.47	8.54
<i>P. parva</i>	7.66	1.13	1.14	34.97	4.18	4.23	1.61	0.92	1.06
<i>M. nipponense</i>	3.90	1.49	1.60	9.99	3.47	3.65	1.09	0.59	0.67
<i>T. swinhonis</i>	16.62	3.54	3.63	7.36	3.04	3.24	1.28	1.27	1.69
<i>A. chankaensis</i>	9.07	1.51	1.54	14.48	2.50	2.55	5.44	2.54	2.80
<i>E. modestus</i>	0.90	0.98	1.31	6.92	3.48	3.87	0.53	0.97	1.94

## 4. Discussion

### 4.1. Carbon Cycling and Feeding Dynamics in Habitat Remediation

Stable isotope analysis is a critical tool for assessing changes in carbon sources and cycling pathways within aquatic ecosystems [31]. By examining the stable isotope characteristics of carbon sources across different habitats, it is possible to gain insights into how localized habitat restorations influence the dynamics of primary carbon source cycling in aquatic systems. Similarly to another study in Meiliang Bay [21], we also found no significant difference in the isotopic characteristics of phytoplankton between the net enclosure and the natural lake area. However, we further demonstrated that the  $\delta^{13}\text{C}$  values of phytoplankton within the cage enclosure were significantly lower than those in both the net enclosure and the natural lake area. This study reveals the complex im-

pacts of localized habitat restoration on carbon cycling and carbon stable isotope characteristics. When aquatic plants in the cage enclosure absorb large amounts of nutrients, fluctuations in nutrient concentrations can significantly alter the community structure of phytoplankton [9,32–34]. These changes, in turn, lead to notable shifts in the  $\delta^{13}\text{C}$  values of phytoplankton [35,36]. Additionally, differences in carbon transport pathways and the proportion of carbon utilization by organisms can modify the  $\delta^{13}\text{C}$  ratios in phytoplankton [37]. Since there is no water exchange between the cage enclosure and the natural lake area, the inflow of terrestrial carbon, which has higher  $\delta^{13}\text{C}$  values, alters the proportion of carbon source utilization by phytoplankton in the cage enclosure compared to the net enclosure and natural lake area [38]. Inputs of external carbon sources, such as domestic water and soil erosion, elevate  $\delta^{13}\text{C}$  values in POM [39–41]. This could be a key factor behind the significantly lower  $\delta^{13}\text{C}$  values of POM within the cage enclosure compared to the net enclosure and the natural lake area. Additionally, phytoplankton detritus in the water column serves as the primary endogenous source of POM [42,43]. Both exhibited significantly lower  $\delta^{13}\text{C}$  values in the cage enclosure compared to the net enclosure and natural lake area, further confirming their close association. External nitrogen inputs can increase  $\delta^{15}\text{N}$  levels in aquatic organisms [44–46].

Primary carbon sources in lake ecosystems play a critical role in biodiversity, community structure, and stability through the transfer of energy between organisms, making them essential for ecosystem energy flow and material exchange [47,48]. This study finds that in cage enclosures, the grazing food chain based on phytoplankton transitions to a detrital food chain dominated by sedimentary organic matter (SOM). Such a shift reflects the impact of artificial interventions on the ecosystem's energy pathways. Eco-floating beds play a dual role in lake ecosystems: they improve water quality by competing with phytoplankton for nutrients [19] but also reshape ecosystem energy pathways by reducing primary productivity [49]. As a result, phytoplankton resources become insufficient to meet the energy demands of consumers, increasing the reliance on detrital food chains. This may also accelerate the material cycling at the bottom of the water body. This functional trade-off emphasizes the need for balanced ecosystem management strategies. Apart from differences in enclosure closure, the cage and net enclosures share similar baseline conditions. However, the net enclosure remains dominated by the grazing food chain based on phytoplankton, primarily due to the continuous supply of food resources from the natural lake. Similarly to the tendency of cyanobacteria to accumulate near shorelines, the net enclosure functions as a physical barrier that promotes the aggregation of phytoplankton, resulting in higher resource density within the enclosure. Additionally, the abundant carbon sources in the lake may reduce the reliance of fish on phytoplankton, thereby further contributing to the increased utilization of phytoplankton by fish in the net enclosure. Hydrodynamic conditions further shape the availability and composition of carbon sources in lakes [50]. For example, research has found that when a lagoon is in a closed state, marine organic matter decreases and autochthonous algal organic matter increases [51]. Similarly, changes in carbon source types and proportions within enclosures significantly influence consumer feeding behavior, as evidenced by alterations in stable isotope signals [52,53].

#### 4.2. Stable Isotopic Characteristics and Trophic Level Variations of Consumers

Carbon and nitrogen stable isotopes are commonly combined to analyze the contribution of food sources to consumers [54]. Figure 4 shows that the proportion of primary carbon source utilization has shifted. However, why do the carbon and nitrogen stable isotopes of most aquatic organisms show no significant differences across habitats? The isotopic mixing effect, resulting from mixed food sources or tissue turnover pathways, may

cause consumers from different food sources to exhibit similar isotopic signals [55]. This explanation should be validated through stomach content analysis to enhance scientific rigor. Additionally, fish of different lengths often show significant variations in carbon and nitrogen isotope values. Inconsistent size distributions and sample sizes among fish could also influence the results [56–58].

Although there were no significant differences in  $\delta^{15}\text{N}$  values of fish across the three habitats, their trophic levels, as shown in Figure 5, exhibited notable variations. The average trophic levels were ranked as follows: net enclosure > cage enclosure > natural lake area. The individual development of species, spatial and temporal environmental variations, and prey availability influenced the stable isotope composition and corresponding trophic levels of species to some extent [59,60]. As shown in Figure 3, phytoplankton in the net enclosure exhibited the highest  $\delta^{15}\text{N}$  values, not only significantly higher than those in other habitats but also exceeding the  $\delta^{15}\text{N}$  values of SOM across all three habitats. Furthermore, the contribution of phytoplankton in the net enclosure was significantly higher than in other habitats. This is likely the primary factor contributing to the higher average trophic level observed in the net enclosure.

However, a high contribution of phytoplankton does not necessarily lead to significantly higher trophic levels of consumers, as trophic level changes are also influenced by other ecological factors, such as the complexity of community structure [61] and diversity of predation strategies [62]. For instance, while the  $\delta^{15}\text{N}$  value of the carbon source in the natural lake area was high, the average trophic level in the cage enclosure was still higher than in the natural lake area, which may be attributed to the presence of a mixed feeding effect. Differences in community structure likely play a critical role in this process. When the relative abundance of high-trophic-level species in the cage enclosure exceeds that in the natural lake area, such a phenomenon is likely to occur. Figure 6 shows that the trophic levels of nine common fish species were similar in the net enclosure and natural lake area and significantly higher than those in the cage enclosure. This suggests that the relative abundance of high-trophic-level fish in the cage enclosure is greater than in the natural lake area, which may be related to the barrier effect of the cage enclosure. The cage enclosure restricts fish migration and prey resource flow, enhancing predation opportunities for carnivorous fish, thereby increasing their population and elevating the overall trophic level.

#### 4.3. Trophic Niche Characteristics of Different Habitats

Using Layman's six quantitative metrics [28] to describe the community's trophic structure, the results showed that, except for the  $\delta^{13}\text{C}$  range being greater in the natural lake area, the other five metrics were highest in the cage enclosure. This indicates that the cage enclosure has the highest trophic diversity but the lowest level of trophic redundancy. The highest trophic diversity in the cage enclosure suggests a broader utilization of resources or reduced interspecific competition through resource partitioning, while the low trophic redundancy indicates a more fragile food web structure reliant on fewer species to maintain key ecological functions.

Since the natural lake area is much larger than the enclosure, it provides a wider range of carbon sources, resulting in the largest  $\delta^{13}\text{C}$  range [63]. The exogenous nutrient inputs in the natural lake area are characterized by diversity, with their components, quantities, and input methods varying considerably. Such diversity has an impact on the ways in which primary producers absorb and utilize nitrogen. In contrast, the exogenous nutrient inputs within the enclosure are relatively monotonous, which causes the selection and utilization of nitrogen sources by primary producers within the enclosure to differ from those in the natural lake area, ultimately resulting in changes in the vertical structure of the food web within the enclosure [64,65]. Higher MNND and SDNND values in the enclosures suggest

that species are more dispersed, with fewer species occupying overlapping ecological niches, leading to minimal trophic redundancy. Thus, the removal of a species could easily disrupt ecosystem stability in the enclosure, whereas removing redundant species in the natural lake area would not significantly impact ecosystem stability [66].

According to optimal foraging theory, when intraspecific competition is high and food resources are limited, individuals tend to adopt opportunistic feeding behaviors, leading to an expansion of the ecological niche width of the entire population [67]. The ecological niche width for species found across all three habitats was calculated using Jackson et al.'s bias-corrected SEAc method [29]. A wider niche width indicates a species' greater adaptability to environmental conditions. Generally, species in the enclosure exhibited the widest niche widths, whereas those in the natural lake area showed the narrowest. In the cage and net enclosures, food resources were abundant, and large top predators, such as *Elopichthys bambusa* and *Culter alburnus*, were absent. Consequently, smaller carnivorous fish, such as *Coilia nasus*, were able to adjust their feeding strategies freely, foraging across broader spatial areas and over extended time periods. Fish differentiate their resource use based on competitive relationships [68,69]. This allows them to make more efficient use of food resources across temporal and spatial dimensions, thereby further expanding their ecological niches. For omnivorous and herbivorous fish, carbon source analyses across habitats reveal a shift in the cage enclosure from plankton to SOM as the primary carbon source. This suggests that food resources for herbivorous and omnivorous fish are limited in the enclosure, as commonly observed in similar studies [70,71]. This constraint prompts them to diversify their diet in response to environmental shifts, broadening their niche width to enhance survival.

## 5. Conclusions

The restoration measures of cage and net enclosures using ecological floating beds have significantly altered the energy flow pathways within ecosystems. Compared to natural lakes, the food web in cage enclosures shifted from a grazing food chain dominated by phytoplankton to a detrital food chain relying on SOM, while net enclosures enhanced the phytoplankton-driven grazing food chain. These changes, driven by trophic cascade effects, significantly influenced the trophic levels of consumers. From a trophic niche perspective, the limited food resources in cage enclosures may force consumers to broaden their trophic niche width to cope with resource constraints, but the ecosystem also becomes more vulnerable. In contrast, net enclosures, supported by the resource supply of the lake, maintain higher trophic levels and more stable energy flows, demonstrating greater potential for application in eutrophication management in lakes. Cage enclosures primarily depend on detrital food chains, which accelerate the cycling of carbon, nitrogen, and other organic matter in sediments, contributing to short-term improvements in sediment conditions. However, the energy pathways dominated by detrital chains may be insufficient to support the long-term ecological stability of cage enclosures. Therefore, future management strategies should balance water quality improvements with ecosystem stability to develop more scientific and sustainable restoration approaches.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/fishes10020044/s1>, Table S1: The contribution rate of basic carbon sources to nine kinds of consumers.

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supervision, D.X.; project administration, Z.K.; funding acquisition, Z.K. All authors have read and agreed to the published version of the manuscript.

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**Institutional Review Board Statement:** All experiments were conducted in accordance with the Chinese national guidelines and regulations regarding appropriate research ethics (GB/T 35892-2018: Laboratory animal—Guideline for ethical review of animal welfare) [72]. However, ethical review and approval were not required for this study as the fish samples were frozen and then taken back to the laboratory. It is worth noting that no live fish were utilized over the course of this study.

**Informed Consent Statement:** Not applicable.

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