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Abstract: Since 2017, a fishing moratorium has been enforced in Lake Honghu as part of Chang-Jiang's biodiversity conservation strategy. However, given that the lake is a semi-closed aquatic ecosystem, and no longer serves as a habitat for certain fishes of the mid-lower Chang-Jiang basin, the efficacy of this moratorium remains uncertain. To address the question from a trophic ecology perspective, a stomach content analysis was performed on captured anchovies *C. brachygnathus*, a current predominant species in Lake Honghu, from November 2020 to October 2021. Results showed that copepods, shrimps, and macrophytes were the main components of this anchovy's diet, and had size-related shifts in diets. The dominance of *C. brachygnathus*, a pelagic-littoral omnivore in this lake, implies a lacustrine environment shift triggered by continued human disturbances. The utilization of macrophytes as the main food items by large-sized anchovies of Lake Honghu partially contributed to the rapid degradation of submerged vegetation. This highlights the need to remove large-sized individuals of *C. brachygnathus* and *Carassius auratus*, another benthic-omnivorous dominant fish, in order to effectively restore the aquatic vegetation and ecosystem of Lake Honghu. The current implementation of fishing moratoriums in subtropical shallow floodplain lakes such as Lake Honghu should be reviewed critically.

Keywords: anchovy; omnivore; plant-origin food; fisheries management; fish ban

1. Introduction

Lake Honghu is the seventh-largest freshwater lake in China, located in the middle Yangtze River (or Chang-Jiang in Chinese) basin of southern Hubei Province [1]. As a water-carrying system, it performs a crucial function in flood regulation, providing water for industry and domestic use, agricultural irrigation, transportation, and fisheries. It also serves as an important breeding and wintering habitat for East Asian migrating birds, such as *Mergus squamates* and *Ciconia boyciana* [2,3]. Lake Honghu has been listed in the Ramsar wetlands of international importance, and it is a key biodiversity region and one of the priority conservation areas set up by the Chinese Government.

Nevertheless, Lake Honghu's wetland has undergone severe human perturbations since the mid-1950s, disrupting its connectivity to the Chang-Jiang mainstem [2,3]. Prior to this, it served as nurseries, spawning, and feeding grounds to many potamodromous (e.g., silver, grass, bighead, and blunt carps) and diadromous (e.g., Japanese eel) fishes. However, due to the construction of sluice gates from 1955-1975, it has transformed into a river-isolated lake under artificial water level regulation, resulting in the decline of its aquatic environment and ecology. As a consequence, there has been a decrease in the species diversity of fish and fishery resources [1,4]. The number of fish species has drastically decreased from 73 in the 1950s-60s to 49 in the 1990s. Furthermore, fish

assemblages have shown a trend toward early sexual maturation and smaller body sizes [5]. Fish farming on a large scale from the 1990s to 2010s has caused environmental and ecological problems, including reduced water quality and aquatic vegetation [6]. These issues have been worsened by exogenous wastewater discharge into the lake, causing a continuous degradation of water quality and aquatic habitat. The lake's altered environment has had significant impacts on its fish assemblages.

Under the current biodiversity conservation strategy in the Chang-Jiang basin, Lake Honghu is designated as a non-fishing zone at both the national and provincial levels. To restore its aquatic biodiversity and fish resources, strict regulations have been implemented by the national and local governments, including a fishing ban enforced since 2017. However, as a semi-closed or river-isolated aquatic ecosystem, Lake Honghu no longer serves as nursing, feeding, or breeding ground for many diadromous and potamodromous fish species. Therefore, the question of whether a fishing moratorium remains necessary in Lake Honghu remains debatable.

Coilia brachygnathus is a significant freshwater economic fish species in China, due to its substantial biomass, especially in affiliated lakes of the mid-lower Chang-Jiang [7,9]. The anchovy, previously regarded as the landlocked form of the anadromous species *C. nasus*, has been recently confirmed as a distinct species via molecular evidence, with its occurrence extending to Lakes Taihu, Poyang, and Dongting [10,11]. While the anchovy was reported to inhabit Lake Honghu, according to local fishermen, it was not the primary catch in the lake prior to 2015. Recent field surveys in Lake Honghu conducted between 2019 and 2021 revealed that *C. brachygnathus*, followed by benthic omnivorous *Carassius auratus*, were the most abundant fish species in the lake [12]. The anchovy's flourishing in Lake Honghu may be due to life history characteristics such as a short life span, early maturity, fast growth rate, availability of ample food, low predator pressure, and the fishing moratorium [13]. Fisheries management is therefore proposed for this fish. Understanding the trophic ecology of *C. brachygnathus* in Lake Honghu would aid in the rational management and utilization of fisheries resources.

Several studies have investigated the diet of *C. brachygnathus* in China. For instance, stomach content analyses of 52 individuals caught between March and June 1958 from the middle Chang-Jiang revealed that copepods and insect larvae, followed by small fish and shrimps, were the anchovy's primary food items [14]. Cladocerans and oligochaetes were only occasionally consumed. Similarly, stomach content analyses of 146 individuals collected from Lake Taihu between 1982 and 1984, 87 individuals fished from Meiliang Bay from September to October 2004, and 43 individuals landed from the entire lake from September to December 2004 demonstrated that the anchovy mainly fed on animal diets such as copepods, cladocerans, aquatic insects, shrimps, and small fish [15–17]. The same findings were observed for the fish in Lake Chaohu [18]. Nonetheless, these studies mainly used snapshot surveys, and the diet composition of the anchovy was shown to be influenced by habitat trophic status [19], with the fish displaying a temporal dietary shift linked to hydrological fluctuation levels [9].

Hence, the present study aims to (1) conduct a stomach content analysis of a large number of *C. brachygnathus* caught from Lake Honghu in different sampling seasons, (2) to provide insight into the optimal utilization and management of the lake's fisheries resources, taking into account the dietary preferences of this omnivorous fish, and (3) address the issue on the necessity for fishing in this semi-closed aquatic environment.

2. Materials and Methods

2.1. Study Site

Lake Honghu, located in the southeast region of Hubei province (29°41′–29°58′N, 113°12′–113°28′E) and at an altitude of 22.75 m above sea level (Figure 1), is the largest shallow lake in the Jianghan Plain. It spans 23.4 km from east to west, 20.8 km from north to south, and has a mean water depth of 1.91m. The lake has a water surface area of 348.2 km^2 and a watershed area of 8265 km^2

[2,20]. The climate in Lake Honghu is subtropical monsoon, characterized by average annual precipitation ranging from 1000 to 1300 mm and an annual water temperature of 15.9 to 16.6^{o}C [2].
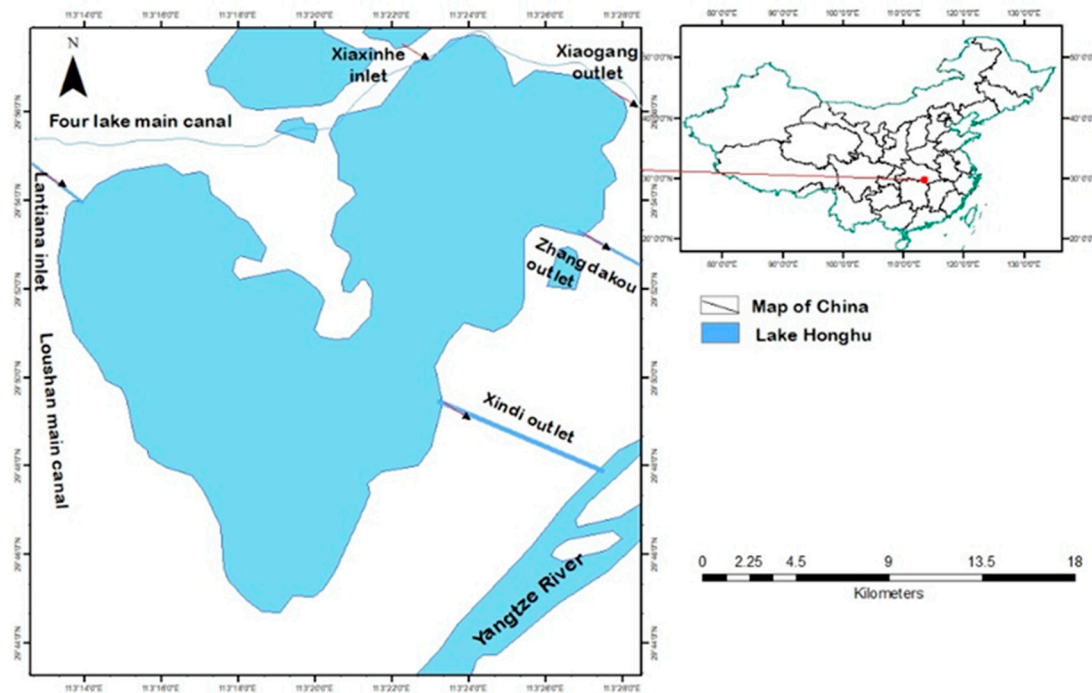

Figure 1. Location of Lake Honghu with the spatial distribution of the eight sampling sites.

2.2. Fish Sampling and Gut Content Analysis

From November 2020 to December 2021, samples of *C. brachygnathus* were collected from Lake Honghu seasonally. To collect these samples, eight different sites were used and 30- and 60-mm-stretched mesh-size monofilament gill nets and < 20 mm hoop nets were employed. Nets were set up between 14:00 and 16:00 h and were collected between 8:00 and 11:00 h the following morning. Individual fish were measured for total length to the nearest 0.1 mm, and the total weight was determined to the nearest 0.1 g using an electronic scale. Of the 800 fish sampled, their stomachs (guts) were removed, and the degree of gut fullness was recorded. Each fish was preserved individually in a buffered 4% formaldehyde solution and then transported for further diet analysis to the College of Fisheries laboratory at Huazhong Agricultural University.

At the laboratory, the entire stomach contents were emptied onto a Petri dish, and subsamples were taken to scrutinize under a microscope [21]. For large-sized food items, such as shrimp and macrophyte fragments, visual identification was performed. The inverted compound microscope (magnification: x400) was utilized to count and identify small food items up to the lowest possible taxonomic level [22,23]. Any prey items that were partially digested and consequently unidentifiable were reported as unidentified [24].

Diet composition was quantified as percentage frequency of occurrence (% O, the proportion of stomachs containing a particular prey item irrespective of amount) and percentage composition by number (%N; the proportion of the number of a particular prey item to the total number of all prey items in the entire stomach contents [25]. Given the difficult task to quantify macrophytes, the frequency of occurrence in each fish stomach was computed. The diet diversity was expressed by the Shannon-Wiener diversity index (H'). Furthermore, Pielou's evenness index (J') was calculated to measure how evenly fish rely on food resources in different seasons.

Hierarchical cluster analysis based on the Euclidean distance and prey occurrence (%O) and abundance (%N) were used for petitioning size classes into different length groups. The matrix similarity was constructed using the Bray-Curtis distance after the abundance data were log (x+1)

transformed. Canonical analysis of principal coordinates (CAP) [26] was used to distinguish variations in the diet compositions among sampling seasons and fish size classes. Besides, non-parametric permutational multivariate analysis of variance (PERMANOVA) was run to test whether the variations in diet composition among sampling periods and fish size classes were significant at 999 permutations [26]. All the statistical analyses were performed using OriginPro®2017 software (www.OriginLab.com), and PAST software.

3. Results

3.1. Food Items in Gut Contents

A total of 800 stomachs from anchovies measuring between 50 and 359 mm TL were dissected for diet analyses, which were seasonally caught from November 2020 to October 2021. Of the examined stomachs, 480 (60%) contained food, while the remaining 320 (40%) were empty. The study revealed 12 different food items, including macrophyte fragments (1 item), copepods (2 items), cladocerans (2 items), rotifers (5 items), shrimp (1 item), and the unrecognized (1 item). Table 1 presents the frequency of occurrence (%O) and abundance (%N) of these food items. Zooplankton groups were dominated by Copepods, followed by rotifers. dominated. The most frequently observed prey item in copepods remained consistent, with *Calanus* sp., making up 51.16% to 76.66% of observations. The most commonly observed prey item in cladocerans was *Bosmina* sp. The dominant prey item among rotifers was *Brachionus calyciflorus*, representing between 30.59% to 59.67% of observations throughout the sampling period. Macrophytes and shrimp were also among the most important food items throughout the entire duration of the study (Table 1). The study demonstrated a commonality of food items across all seasons, with *Calanus* sp., nauplii, *B. calyciflorus*, macrophytes, and shrimps appearing consistently as main food items.

Figure 2. Major food items identified in the stomach of *C. brachygnathus* from Lake Honghu.

Table 1. Frequency of occurrence (%O) and number (%N) of food items found in the stomach of *C. brachygnathus* between November 2020 and October 2021 in Lake Honghu.

Food items	November %O	November %N	January %O	January %N	June %O	June %N	October %O	October %N
Calanus sp.	75.20	23.33	54.17	23.02	51.16	20.55	76.66	23.61
Nauplii	66.43	19.22	37.75	19.16	46.99	21.84	67.23	23.22
Bosmina sp.	45.57	0.57	-	-	-	-	-	-
Alona sp.	-	-	-	-	-	-	35.42	1.64
Brachionus calyciflorus	50.98	15.83	30.59	21.66	59.67	28.64	43.98	10.07
Brachionus angularis	44.64	8.48	31.37	14.94	-	-	39.88	12.06
Brachionus caudatus	32.06	8.99	-	-	-	-	25.06	1.12
Keratella sp.	11.61	8.65	-	-	-	-	-	-
Tricocerca sp.	15.77	2.18	-	-	-	-	6.25	2.1
Macrophytes	60.76	-	70.34	-	58.46	-	65.28	-
Shrimps	55.21	12.39	51.84	21.11	45.96	24.13	68.94	25.98
Unidentified	10.23	0.36	9.85	0.11	8.96	4.84	8.53	0.2
Number of preys	11		7		6		10	
Shannon-Wiener index	2.25		1.85		1.7		2.09	
Pielou's evenness index	0.94		0.95		0.95		0.91	

3.2. Size-Related Dietary Variation

The cluster analysis conducted on collated anchovies, based on the occurrence of food items, showed size-related differences in the diet of the fish. As a result, three-sized fish classes were identified and outlined in Table 2 and Figure 3. The first group of individuals (<125 mm TL) subsisted exclusively on *Calanus* sp., Nauplii, *Brachionus* spp., *Keratella* sp., *Tricocerca* sp., *Bosmina* sp., and *Alona* sp. (Table 2). The second group (125-235 mm TL) fed mainly on *Calanus* sp., Nauplii, *Keratella* sp., *Brachionus* spp., *Tricocerca* sp., *Bosmina* sp., *Alona* sp., macrophytes, and shrimps. The third group (> 235 mm TL) foraged on larger food items such as big-sized *Calanus* sp., a few amounts of nauplii, macrophytes, and shrimps (Table 2).

Table 2. Frequency of occurrence (%O) and number (%N) of food items of the three length groups of *C. brachygnathus* in Lake Honghu.

Food items	Fish length groups < 125 mm TL O%	< 125 mm TL %N	125 – 235 mm TL O%	125 – 235 mm TL %N	>235 mm TL %O	>235 mm TL %N
Calanus sp.	57.35	27.02	76.10	30.55	58.33	35.69
nauplii	64.50	26.16	76.29	26.74	23.61	15.63
Bosmina sp.	23.11	0.13	47.06	0.04	-	-
Alona sp.	9.60	1.81	30.64	1.77	-	-
Brachionus calyciflorus	62.39	17.61	60.51	14.67	-	-
Brachionus angularis	52.66	12.8	63.24	10.45	-	-
Brachionus caudatus	22.38	6.1	36.03	5.06	-	-
Keratella sp.	9.52	5.35	6.07	2.03	-	-
Tricocerca sp.	9.52	2.11	20.34	1.9	-	-
Macrophytes	-	-	45.15	-	77.08	-
Shrimps	-	-	45.15	6.06	70.14	47.45
Unidentified	6.55	0.91	6.66	0.73	6.23	1.23

In larger-sized anchovies, it was found that only a single food source, either macrophytes or shrimps, constituted the entirety of their diet (Table 3). Out of the more than 235 mm TL individuals of *C. brachygnathus* studied, only 20 were found to feed exclusively on macrophytes, another 3

individuals of more than 248 mm TL relied entirely on shrimps, and 14 individuals with sizes ranging from181-358 mm TL (with an average of 206 mm TL) consumed both macrophytes and shrimps. However, individuals with a smaller size (125 mm TL) were observed to have a higher rate of feeding on mixed diets consisting of macrophytes, zooplankton, and shrimps (Table 3).

The findings from this study demonstrate that there are significant differences in the food composition between the three length groups ($P < 0.05$), as confirmed by the PERMANOVA analysis (Table 4). It was also affirmed by the CAP ordination plot that size differences existed among the sampled individuals (Figure 4). As shown in Figure 5, the proportion of food groups varied with fish size. In the smaller fish class, copepods and rotifers were the predominant food groups. For the medium-sized fish class, copepods, rotifers, macrophytes, and shrimps were the top food groups. Finally, macrophytes and shrimp were the two most proportioned food groups for the large-sized fish classes.

Table 3. Food item contributions among different length groups of *C. brachygnathus* of Lake Honghu.

Food items	Number	Percent (%)	Total length (mm)		
			Min.	Max.	Mean
Only shrimps	3	0.38	248	308	283.2
Only macrophytes	20	2.50	235	306	278.75
Macrophytes + shrimps	14	1.75	181	359	247.71
Macrophytes + zooplankton + shrimps	121	15.13	125	309	206.92
Macrophytes + zooplankton	42	5.25	131	309	215

Table 4. Results of permutational multivariate analysis of variance (PERMANOVA) applied to diet composition.

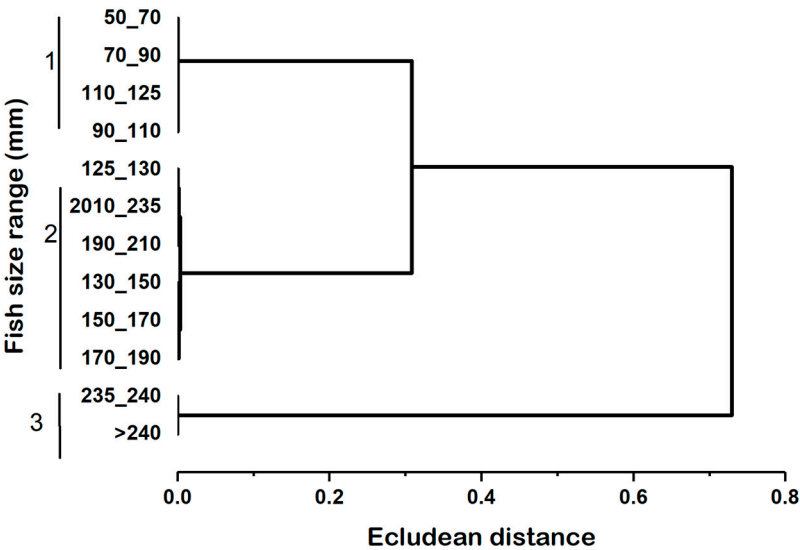| Sources	Df	SS	MS	Pseudo-*F*	*P*(perm)
Fish size	2	32593	16297	685.52	0.001
Season	3	1619.8	539.94	0.499	0.708
Fish size * season	6	1436.1	239.35	0.199	0.989

Figure 3. Cluster analysis of fish size groups based on prey occurrence based on the Euclidean distance.
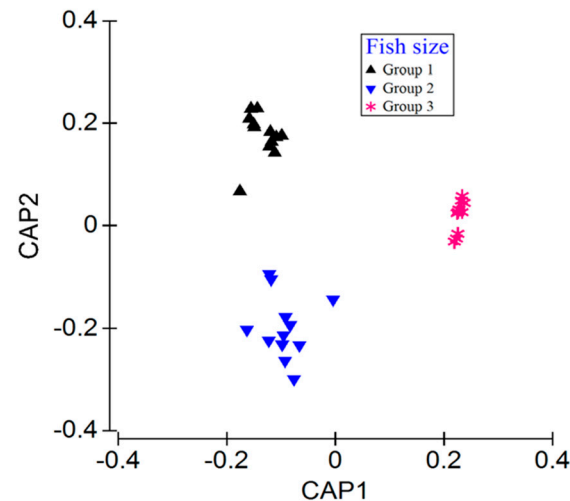
Figure 4. Canonical analysis of principal coordinates (CAP) ordination plots based on the proportion of feed compositions of the three length classes of fish.
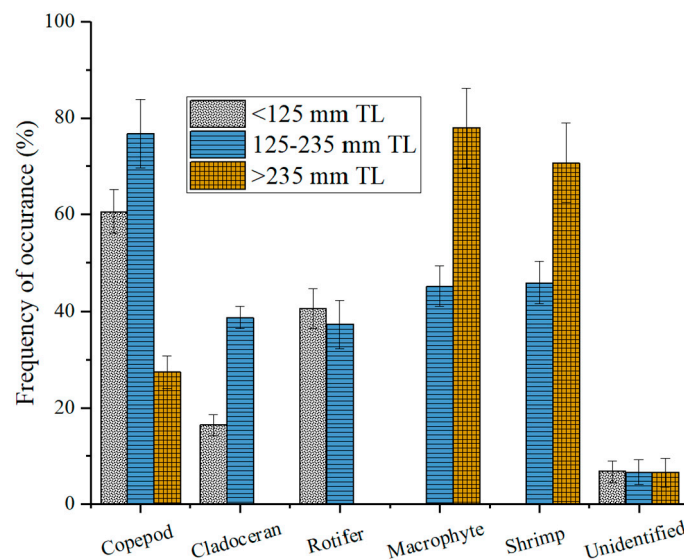

Figure 5. The percentage contribution of different food items consumed by *C. brachygnathus* in different length classes in Lake Honghu.

4. Discussion

4.1. Dietary Variation of Anchovies in Lake Honghu

This study provides evidence supporting the omnivorous feeding habit and size-related dietary variation of *C. brachygnathus* in Lake Honghu. The size at which *C. brachygnathus* reached 50% maturity was 172 mm TL for females and 190 mm TL for males, which corresponded to one and 1.6 years, respectively [12]. Based on this, the stomach content analysis of our study, which examined a large number of anchovies (800) fished from Lake Honghu in four sampling seasons, proved that small-sized anchovies (less than 125 mm TL) were juveniles with a generalized feeding habit of zooplanktivory, while large-sized anchovies (more than 235 mm TL) were adults with a specialized feeding habit of omni-invertivory, with a greater reliance on aquatic invertebrates (shrimps) and food items of plant origin (macrophytes). Medium-sized anchovies adopted a mixed feeding strategy with varying degrees of specialization of different food items. The transition from zooplanktivory to omni-invertivory in their diet occurred in anchovies reaching 125 to 235 mm TL. This range is consistent

with the previous report for *C. brachygnathus* of the middle Chang-Jiang mainstem [14]. The minimum transition length of 131 mm TL reported by Tang [15] for Lake Taihu's anchovies was consistent with our study, but the maximum (170 mm TL) was much shorter than the 235 mm TL reported here. This variation could be explained by the smaller body size of the anchovies in Lake Taihu compared to Lake Honghu, where the anchovy has long been a dominant capture fish [15]. The trend toward body miniaturization in Lake Taihu's anchovies is likely due to high fishing pressure [17].

The study also revealed that the size-related dietary shift of *C. brachygnathus* in Lake Honghu was accompanied by a shift in spatial habitat utilization from the pelagic to the littoral zone. While small-sized fish preferred feeding on zooplankton in the pelagic zone of the lake, large-sized fish showed a preference for shrimps and/or macrophytes, indicating a preference for the well-vegetated littoral zone (Tables 1-2). The density and distribution of shrimps in Lake Bao'an, located in the middle Chang-Jiang basin of Hubei Province, was known to depend on water depth and aquatic vegetation [28]. The shrimps were found to routinely use macrophytes as a refuge under pressure from predators such as *Culter* spp. and fed on attached algae. It is, therefore, likely that large-sized *C. brachygnathus* preferentially used the well-vegetated littoral zone of Lake Honghu. Unlike in previous studies [17,19,29], zoobenthos and demersal small fish were not observed in the stomachs of anchovies from Lake Honghu (Tables 1-2). This clearly indicates that anchovies of the lake were not benthic feeders and should be referred to as pelagic or littoral omnivores instead.

In this study, no seasonal dietary difference was observed for *C. brachygnathus* of Lake Honghu (Table 4). This is in contrast to the findings of Zhang et al.'s [9] from Lake Poyang, where stable isotope analysis indicated a seasonal variation in the diet of this anchovy. The difference can be attributed to the fact that, unlike Lake Poyang, Lake Honghu is a semi-closed aquatic ecosystem where the natural sources of food are not regulated by the season. Besides, being a shallow, eutrophic floodplain lake with high productivity, Lake Honghu provides abundant food sources throughout the year for *C. brachygnathus*.

4.2. Plant-Origin Food Items

Food items of plant origin, like aquatic macrophytes, have never been reported for *C. brachygnathus* of Lakes Chaohu [18], Lake Dongting [9], and Taihu [19], and the congeneric species *C. nasus* of the Qingcaosha reservoir located near the estuary of the Chang-Jiang [6]. However, there have been some reports of phytoplankton and algae being found in the stomachs of anchovies. Diatoms and spirogyra have been sporadically observed in the diet of *C. brachygnathus* from the middle Chang-Jiang basin [14], while algae and a significant amount of *Microcystis* spp. were found in the diet of *C. ectenes taihuensis* (currently rendered synonymic to *C. brachygnathus*) from Lake Taihu [15] [17]. Variations in feeding habits within the same species may be due to variations in prey availability as a response to the existence of differing hydrographic conditions among surveyed areas [30]. In Lake Honghu, the presence of macrophytes in the guts of medium- to large-sized individuals of *C. brachygnathus* may be attributed to a restricting of feeding habits in response to a modified environment and available resources [30]. This shift in feeding strategy may also be driven by energetic demands, as larger-sized individuals need more energy to survive [31].

It cannot be ruled out that *C. brachygnathus* accidentally ingests macrophytes when chasing after shrimps that are attached to them. However, the majority of anchovies found with macrophytes in their guts had mixed diets consisting of macrophytes, zooplankton, and shrimps. The number of anchovies feeding only on shrimps or a combination of macrophytes and shrimps was lower than the number of anchovies that solely fed on macrophytes (Table 3). This implies that *C. brachygnathus* intentionally prefers macrophytes as a part of its diet instead of incorporating them accidentally or at random.

4.3. No Need for Fishing Ban

Omnivores are more adaptable to varying conditions than specialists [32], they are expected to be prevalent in ecosystems affected by anthropogenic and natural factors [33]. Lake Honghu exemplifies this trend, as it has undergone significant perturbations since the 1950s, resulting in the

disappearance of aquatic vegetation and the deterioration of water quality. The construction of some sluice gates in its outlets during the 1950s-1980s resulted in the hydrological disconnection from the middle Chang-Jiang mainstem, which had great influences on its fish assemblage. Following this disconnection, *Carassius auratus*, a benthic omnivore, has become one of the three dominant capture fish of Lake Honghu. So far, *C. brachygnathus* and *Carassius auratus*, two omnivorous fish species, have become the dominant capture fish of the lake [34]. The rise of *C. brachygnathus* reflects further anthropogenic disturbances [12], indicating intensified fish stocking, water pollution, and over-exploitation of aquatic vegetation during the past two decades or more [6]. As a result, Lake Honghu has already shifted from a macrophyte-dominate to an algae-dominated eutrophic lake.

Omnivorous fishes can accelerate the eutrophication process in shallow lakes and their biomass tends to increase with intensified natural and anthropogenic disturbances, such as fish stocking, water pollution, and global warming [35]. There was a positive relation between the capture of *C. brachygnathus* and the concentration of TN, TP, and DOC in Taihu Lake [17]. The removal of omnivorous fish from shallow lakes could be beneficial for improving water clarity and promoting benthic primary production [2]. In this context, the harvest of economically important omnivorous fish, such as *C. brachygnathus* and *C. auratus*, in Lake Honghu could be a viable restoration approach for this shallow eutrophic lake.

As shown here, *C. brachygnathus* of Lake Honghu can utilize macrophytes as its food items. Whether the anchovy assimilates this food item of plant origin or not, the persistence of medium- or large-sized individuals has adverse impacts on submerged macrophytes and affects the aquatic vegetation's rehabilitation and habitat promotion of the lake. The current dominance of this anchovy in the lake is partially attributed to the fishing ban implemented in 2017, which has led to a decrease in competition among fish species. This ban may have unintentionally created a breeding ground for *C. brachygnathus*, resulting in the degradation of the aquatic ecosystem [12]. Therefore, it is crucial to reevaluate the fishing ban and implement a rational approach to managing the resources of this semi-closed aquatic ecosystem. A sustainable management plan for the dominant omnivorous fish is urgently needed to promote the rehabilitation and sustainable development of Lake Honghu.

Predation by planktivorous fish on zooplankton has an adverse impact on the abundance, size, and species composition of the zooplankton community [36,37]. This, in turn, indirectly affects the phytoplankton community and physico-chemical conditions, leading to increases in phytoplankton abundance [38]. Due to weak "top-down" control exerted by zooplankton on phytoplankton communities, this can result in the flourishing of phytoplankton and the deterioration of water quality. When zooplankton abundance is low, phytoplankton can thrive, and water quality can suffer [39,40]. Fishing of big-sized anchovy in Lake Honghu is predicted to increase high zooplankton abundance, thereby providing a selective constraint on phytoplankton, ultimately facilitating the improvement of water quality and the promotion of aquatic habitats.

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