

Research Article

Stocking and Harvesting Patterns Influence Age Structure, Growth, and Body Condition of Bighead Carp Populations From Two Large Subtropical Reservoirs

Xuemei Chen ^{1,2}, Lei Yang ^{1,2}, Hang Zhang,^{1,2} Xiang Ji ^{1,2}, Chuansong Liao ¹, Thomas Mehner ³, Chuanbo Guo ^{1,2}, Tanglin Zhang,^{1,2} and Jiashou Liu^{1,2}

¹Key Laboratory of Breeding Biotechnology and Sustainable Aquaculture, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China

²College of Advanced Agricultural Sciences, University of Chinese Academy of Sciences, Beijing, China

³Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

Correspondence should be addressed to Chuansong Liao; liaocs@ihb.ac.cn

Received 27 November 2024; Accepted 17 May 2025

Academic Editor: Pronob Das

Copyright © 2025 Xuemei Chen et al. Journal of Applied Ichthyology published by John Wiley & Sons Ltd. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Understanding the density-dependent effects is essential for sustainable fishery management. Stocking and harvesting activities directly influence fish abundance and associated density-dependent responses. In this study, we compared the body size, age structure, growth patterns, and body condition of bighead carp (*Hypophthalmichthys nobilis*) from two large subtropical reservoirs in China: Shanmei Reservoir (SMR) ($n = 161$) and Liuxihe Reservoir (LXHR) ($n = 257$), which have different stocking and harvesting patterns. In SMR, annual stocking and harvesting maintain a lower bighead carp biomass (catch per unit effort, $0.62 \pm 0.03 \text{ g/m}^2/24 \text{ h}$), whereas in LXHR, annual stocking without harvesting results in higher fish biomass ($0.84 \pm 0.01 \text{ g/m}^2/24 \text{ h}$). Plankton biomass and abundance, particularly zooplankton, were significantly higher in SMR than in LXHR. The SMR population exhibited a more stable age structure, faster growth, and better body condition, whereas the LXHR population showed the opposite trends under higher fish density. Both populations exhibited isometric growth and included individuals aged one to five, but dominant age groups differed. The SMR population had a larger inflection age and greater standard length (SMR: 4.7 years and 591 mm; LXHR: 3.5 years and 456 mm). In addition, total mortality, fishing mortality, and exploitation rates were higher in SMR than in LXHR. These findings highlighted the role of stocking and harvesting in shaping fish density and hence inducing density-dependent effects. A balanced fisheries strategy integrating both practices is crucial for sustainable fish population management.

Keywords: density-dependent effects; fishery management; food availability; subtropical reservoir

1. Introduction

Density-dependent effects are a common phenomenon in natural populations, critically influencing population growth and persistence [1]. Fluctuations in population density affect individual survival and growth primarily through changes in resource availability, such as food or habitat [2, 3]. Density-dependent effects are influenced by

multiple factors, primarily including the interaction between human activities [4], biological factors (e.g., resource availability and competition [5]), and environmental factors (e.g., climate change and water quality [6]). Human activities, especially stocking and harvesting, directly influence fish density in aquatic ecosystems [7]. Overharvesting or inappropriate stocking can lead to imbalances in population density, affecting the growth and competition dynamics

[8, 9]. Overstocking may lead to high fish density and intensify competition for resources, resulting in slower growth rate and poorer body condition [10]. Conversely, overfishing can significantly reduce population density, simplify age structure, destabilize population dynamics, and threaten long-term sustainability [11, 12]. Environmental changes can also affect resource availability and modulate the strength of density-dependent effects [13]. For example, increased water temperature promotes fish metabolism, intensifying resource competition and enhancing negative density dependence in high-density populations, while potentially fostering growth and weakening these effects in low-density populations [14]. Decreased water levels may compress habitat space, intensifying competition [15]. Extreme weather events may disrupt habitats, increase mortality, and further complicate density-dependent effects [16]. In conclusion, a comprehensive understanding of density-dependent effects is crucial for sustainable fisheries management [4].

Bighead carp (*Hypophthalmichthys nobilis*) belong to the order Cypriniformes and the family Cyprinidae [17]. As one species of the four major Chinese carp [18], bighead carp had a total production of 3.3×10^6 tons in China, contributing 12% to the country's total freshwater fishery output in 2022 [19]. Bighead carp inhabit pelagic zones and primarily feed on zooplankton and phytoplankton [20]. They are commonly stocked to increase fishery outcomes and control algal blooms in lakes and reservoirs [21, 22]. Due to their inability to spawn in lentic reservoir ecosystems, the population densities of bighead carp are mainly managed through stocking and harvesting activities [23]. Therefore, understanding and accounting for density-dependent effects is essential for optimizing fisheries management strategies. Despite the economic and ecological importance of bighead carp, current research primarily focuses on their age and growth [24, 25], whereas the effects of fisheries management strategies on their biological traits remain poorly understood.

China possesses the highest number of reservoirs globally (24,089; [26]). Among the most widely applied fishery models in these reservoirs are enhanced fisheries, particularly for silver carp (*H. molitrix*) and bighead carp. However, the stocking and management strategies vary significantly across different reservoirs [27]. Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR), both large subtropical reservoirs located in southeastern China, illustrate two different stocking and harvesting patterns for bighead carp. In the SMR, bighead carp are annually stocked and harvested [28]. In contrast, bighead carp are also stocked annually, but harvesting has been thoroughly prohibited in the LXHR since 2017 due to its designation as a national aquatic germplasm resource conservation area for the endangered fish species *Spinibarbus hollandi*. The different management strategies make them ideal systems for analyzing how the biological traits of bighead carp respond to different stocking and harvesting patterns.

In this study, we compared the body size, growth patterns, age structure, body condition, mortality, and exploitation rate of bighead carp populations in the SMR and

LXHR. We primarily focused on exploring the effects of stocking and fishing activities, as well as plankton resources, on the growth of bighead carp from both top-down (fishing pressure) and bottom-up (food resources) perspectives. We hypothesized that the bighead carp population in SMR with regular stocking and harvesting would have a lower density, faster growth, better body condition, and more stable population dynamics according to the theory of density dependence.

2. Materials and Methods

2.1. Study Area. SMR and LXHR are located in subtropical areas of China (Figure 1). Both reservoirs have large capacities and areas and are vital drinking water sources for downstream residents, but they differ in fisheries stocking and harvesting patterns (Table 1). In the SMR, bighead carp are annually stocked and harvested, while in the LXHR, bighead carp are likewise stocked annually, but not harvested. Due to the fishing ban in LXHR, our sampling was approved by the management office. Similarly, sampling in SMR was carried out with authorization from the reservoir management authority.

2.2. Fish Sampling and Data Collection. According to official records, the initial body weight (BW) of the bighead carp stocked was approximately 150–250 g in both reservoirs (unpublished data). From April to July 2022, we conducted monthly fish sampling using the same experimental gillnets in both reservoirs. The gillnets, measuring 50 m in length and 5 m in height, consisted of four different mesh sizes (8, 10, 12, and 14 cm, stretched). At each of the six designated sampling sites per reservoir, we deployed four gillnets (totaling 200 m in length) for 12 h each night (18:00–19:00 to 6:00–7:00). To improve our capture efficiency, this sampling procedure was repeated at each site over the next 2 days, resulting in a cumulative sampling duration of 36 h per site. Catch per unit effort (CPUE) was estimated based on the biomass (BPUE, $\text{g}/\text{m}^2/24\text{h}$) and abundance (NPUE, $\text{ind.}/\text{m}^2/24\text{h}$), representing the total biomass and number of individuals captured per unit effort, respectively.

We measured the standard length (SL) and BW of all freshly caught fish with precision to the nearest 1 mm and 1 g, respectively. Then, all samples were euthanized by immersion in about 250–350 mg/L of tricaine methanesulfonate (MS-222). In addition, we collected 5–10 scales below the pectoral fin, which were stored in scale clips for subsequent analysis. The scales were soaked in a 50 mL 10% NaOH solution for approximately 5 min to remove any adhering tissues and then rinsed with distilled water. Using a dissecting microscope (Olympus CX33), we determined the fish ages by examining the cleaned scales (Silva and Stewart, 2006). We read at least three scale samples from each individual, and each scale was read twice to ensure the accuracy of the results. We randomly dissected subsamples of 88 and 150 individuals to obtain the eviscerated BW (W_E) from the SMR and LXHR Reservoirs, respectively. In addition, at each sampling site, we used a YSI Pro Plus

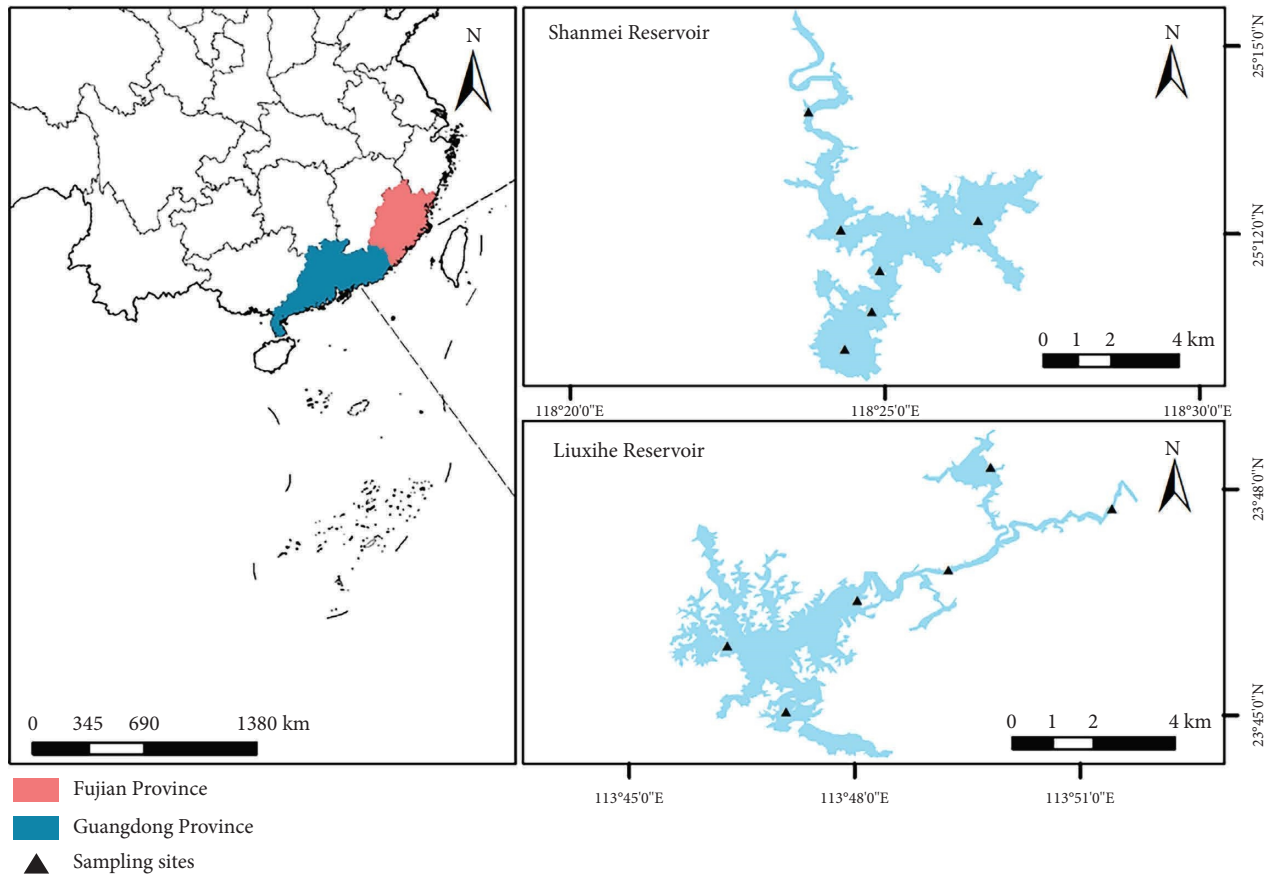


FIGURE 1: Location and shape of Shanmei Reservoir and Liuxihe Reservoir. Triangles represent sampling sites.

multiparameter water quality analyzer to record the water temperature (T , °C) at a depth of 1 m around midday. We also collected samples of zooplankton and phytoplankton at each site, determining their respective densities and biomasses according to the methods described by Zhang and Huang [29].

2.3. Data Analysis. We applied the Shapiro–Wilk test to assess data normality and Levene’s test to evaluate the homogeneity of variances. We used nonparametric tests (Mann–Whitney U test) for variables that did not meet the normality assumptions to reduce bias, and parametric tests (t -test) for variables that were normally distributed or became normally distributed after transformation. Bonferroni correction was applied for multiple comparisons. To compare the differences in CPUE, SL, and growth rate between the two reservoirs, we first used the Shapiro–Wilk test to assess data normality. Since the data did not follow a normal distribution, we conducted the Mann–Whitney U test. Then, we assessed the similarity of length frequency distributions between the two populations with the Kolmogorov–Smirnov test. We also applied chi-square tests to evaluate the differences in age structures of the bighead carp populations. Since there was only one sample for the 5-year-old group in SMR, we analyzed SL differences for the remaining four age groups using the Mann–Whitney U test. We log-transformed ($\log [x + 1]$) the

plankton biomass and density data to achieve a normal distribution, and then compared the means between the reservoirs using an independent samples t -test. A significance level of 0.05 was used.

We established the length–weight relationship using an exponential regression equation ($BW = aSL^b$ [30]), where a is the proportionality constant and b is the exponent of the power. To determine the growth pattern, we analyzed the b values according to Ricker [30] and conducted a t -test to assess whether these values significantly deviated from three [31]. We estimated the growth constant (K) and the asymptotic SL (L_∞) based on SL-at-age data collected over 4 months using FAO-ICLARM Fish Stock Assessment Tools (FiSAT II), Version 1.2.2 [32]. We determined t_0 using the formula, $\ln(-t_0) = -0.3922 - 0.2752 \ln(L_\infty) - 1.038 \ln(K)$, proposed by Pauly [33], and it fitted the von Bertalanffy growth equation ($L_t = L_\infty [1 - e^{-K(t-t_0)}]$), where K is the growth factor and L_t is the predicted SL of t -aged fish [34]. We calculated the growth rates and growth acceleration equations for the two bighead carp populations [35]. In addition, we calculated the condition factor (CF) using $CF = 100W_E / (SL/10)^3$ [36], where W_E is the eviscerated BW.

We employed the length-converted catch curves method to estimate the total mortality coefficient (Z , [37]) using FiSAT II. We calculated the natural mortality constant (M) by the empirical formula: $\ln(M) = -0.0066 - 0.279 \ln(L_\infty) + 0.6543 \ln(K) + 0.6463 \ln(T)$ [38]. In the equation, T

TABLE 1: Summaries of hydrological information and stocking and harvesting data of bighead carp in the Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR).

Reservoir	Total volume ($\times 10^8 \text{m}^3$)	Water-spread area (km^2)	Mean depth (m)	Stocking ($\times 10^4$ ind.)				Harvesting (t)					
				2018	2019	2020	2021	2022	2018	2019	2020	2021	2022
SMR	6.55	23.75	28	63.9	77.3	40.2	65.3	70.0	355.7	218.1	150.9	128.8	145.0
LXHR	3.25	15.25	21	83.5	24.4	22.0	0.60	0.15	0	0	0	0	0

denotes the average water temperature of the two reservoirs during our sampling (SMR: 25.6°C; LXHR: 26.2°C). The fishing mortality constant (F) and the population exploitation rate (E) were calculated by $F = Z - M$ and $E = F/Z$, respectively.

We performed all statistical analyses in R (V.4.0.2, [39]) using packages, including *MASS* (t -test, [40]) and *stats* (chi-square tests, [39]). All figures were created using the *ggplot2* package [41].

3. Results

3.1. Fish Abundance and Plankton Availability. The NPUE of bighead carp in the SMR (0.004 ± 0.0006 ind./m²/24 h) was significantly lower than that in the LXHR (0.007 ± 0.001 ind./m²/24 h, Mann–Whitney U test, $W = 594$, $p < 0.05$). Similarly, the BPUE of bighead carp in the SMR (0.62 ± 0.03 g/m²/24 h) was significantly lower than that in the LXHR (0.84 ± 0.01 g/m²/24 h, $W = 796$, $p < 0.001$). In contrast, both the density and biomass of phytoplankton and zooplankton were significantly higher in the SMR compared to the LXHR, respectively (Table 2).

3.2. Length Frequency Distribution and Age Structure. We measured 161 and 257 bighead carp individuals in SMR and LXHR, respectively. In the SMR, the SL of bighead carp ranged from 181 to 730 mm, with the dominant length class (250–450 mm) comprising 73.3% of the total. In the LXHR, the SL ranged from 197 to 594 mm, with the dominant length class (300–500 mm) accounting for 75.5% of the total (Kolmogorov–Smirnov test, $D = 0.3$, $p < 0.001$; Figure 2(a)). The mean SL of bighead carp in the SMR (341 ± 7 mm) was significantly smaller than that in the LXHR (394 ± 5 mm, Mann–Whitney U test, $W = 12892$, $p < 0.001$; Figure 2(b)).

The age structures of both bighead carp populations consisted of ages 1–5 (Figure 3). In the SMR population, the two-year-old age group was the most dominant one, accounting for 65.8% of the population, whereas in the LXHR population, the three-year-old age group was the most dominant, comprising 51.3% ($X^2 = 114.25$, $p < 0.001$; Figure 4(a)). The mean SL of most age groups were significantly higher in the SMR compared to the LXHR (Figure 4(b)).

3.3. Growth Pattern and Body Condition. We summarized the SL–BW relationship and the von Bertalanffy growth equation of both populations (Table 3). The b values of the SL–BW relationship were close to three in both reservoirs (SMR: $b = 2.98$, $t = 0.51 < t_{(0.05,159)}$; LXHR: $b = 3.01$, $t = 0.24 < t_{(0.05,255)}$). The mean SL growth rate was significantly higher in the SMR population compared to the LXHR population (Mann–Whitney U test, $W = 1613$, $p < 0.05$; Figure 5). In addition, in the SMR, the age and SL at the inflection point of the BW were 4.7 years and 591 mm, respectively, and both values were higher than those in the LXHR (3.5 years and 456 mm). The Z , F , and E values of the SMR population were 1.18, 0.94, and 0.80, respectively, and the three metrics also were higher than those of the LXHR

population (0.48, 0.17, and 0.35; Table 4). The mean CF of the SMR population (1.76 ± 0.20) was significantly higher than that of the LXHR population (1.66 ± 0.14) (Mann–Whitney U test, $W = 8863$, $p < 0.001$; Figure 6).

4. Discussion

Negative density dependence is primarily caused by high population density, which limits the availability of food resources for each individual, thereby impacting growth, age structure, and body condition [1]. Our study analyzed the differences in body size, age structure, growth pattern, and body condition of bighead carp populations from two large subtropical reservoirs with different fishery management strategies. We found that different stocking and harvesting patterns affected fish density and food availability and further influenced age structure, growth rate, and body condition through triggering density-dependent effects. Specifically, the population at lower density with abundant food resources exhibited a more stable age structure, faster growth rate, and better body condition compared to the population at a higher density with fewer food supplies (Figure 7).

Our study suggested that stocking and harvesting patterns play a critical role in mediating density-dependent effects on fish growth and body condition. Both bighead carp populations exhibited isometric growth, consistent with other studies in Chinese reservoirs, such as Yankou Reservoir [42] and Chitan Reservoir [43]. However, significant differences were observed in the growth rate and body condition between the two reservoirs. In SMR, the bighead carp population exhibited a faster growth rate and better body condition, aligning with the findings from Qingcaosha Reservoir [44]. In SMR, regular harvesting may reduce population density and alleviate intraspecific competition, which likely creates favorable conditions for rapid growth. Moreover, higher plankton densities, particularly zooplankton, certainly favored by lower fish densities, may further enhance growth in SMR [45]. In contrast, the fishing ban in the LXHR resulted in a higher population density, similar to the Jinshahe Reservoir (high stocking density, [46]). High fish density increases intraspecific competition, leading to a decline in growth rate and body condition [47]. Although we observed a faster growth rate in SMR, the average SL and growth factor (K) of bighead carp were lower compared to those in LXHR. The smaller size of individuals in SMR was likely due to the high fishing pressure, reflected by the fishing mortality rate of 0.94. This high fishing pressure likely contributed to the miniaturization of the population [48, 49]. The growth factor (K) of the fish was likely shaped by various factors, including water temperature, food availability, water quality, population density, fishing pressure, and habitat conditions, acting independently or interactively [50]. In SMR, intensive fishing reduced the number of large individuals, resulting in a population dominated by smaller individuals. This shift limited the overall growth potential, leading to a smaller growth factor [51].

TABLE 2: Comparison of biomass and density of zooplankton and phytoplankton (mean ± S.E.) in the Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR).

Reservoir	Zooplankton		Phytoplankton	
	Biomass (mg/L)	Density (ind./L)	Biomass (mg/L)	Density ($\times 10^6$ cells/L)
SMR	3.33 ± 1.63	3229.1 ± 1362.1	2.56 ± 0.42	20.2 ± 0.28
LXHR	0.41 ± 0.02	1137.6 ± 170.2	1.38 ± 0.30	7.39 ± 0.21
	$t = 4.60$	$t = 2.12$	$t = 2.45$	$t = 4.37$
	$p < 0.001$	$p < 0.05$	$p < 0.05$	$p < 0.05$

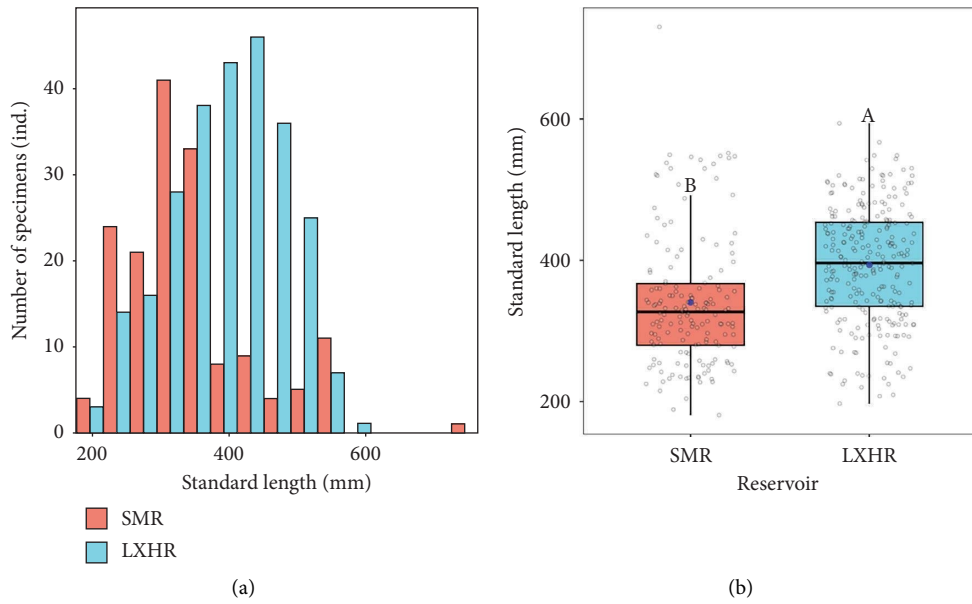


FIGURE 2: Standard length frequency distributions (a) and mean standard length (b) of bighead carp populations in Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR). Different letters in the graph represent significant differences.

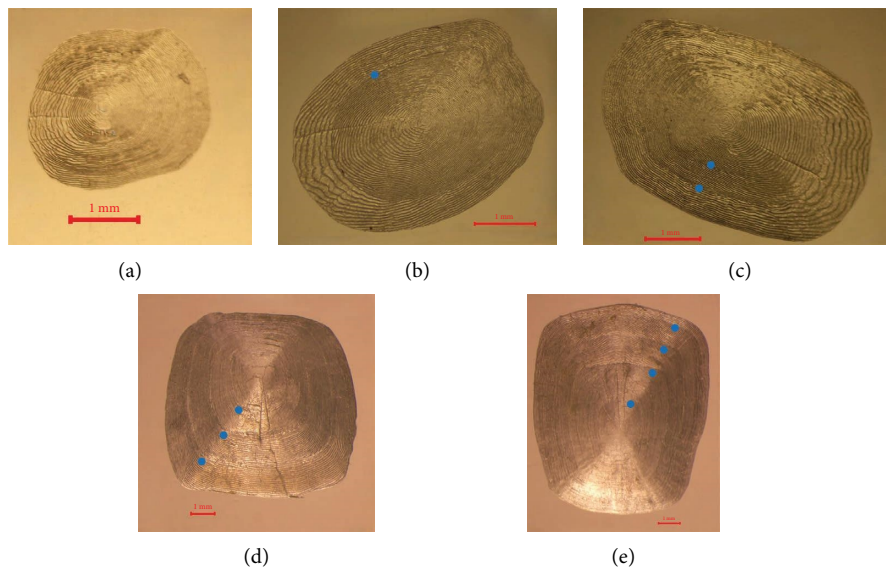


FIGURE 3: The scales of bighead carp individuals from Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR); photos (a, b, c, d, and e) represent 0⁺, 1⁺, 2⁺, 3⁺, and 4⁺ ages, respectively. Blue dots represent the annuli. Red rulers represent a size of 1 mm.

Fish growth varies significantly across regions and water bodies, driven by hydrological conditions, nutrient dynamics, food availability, population density, and fishing

pressure [25, 52]. We conducted a comparative study on the growth of bighead carp in different reservoirs and lakes located in different regions in China (Table 5,

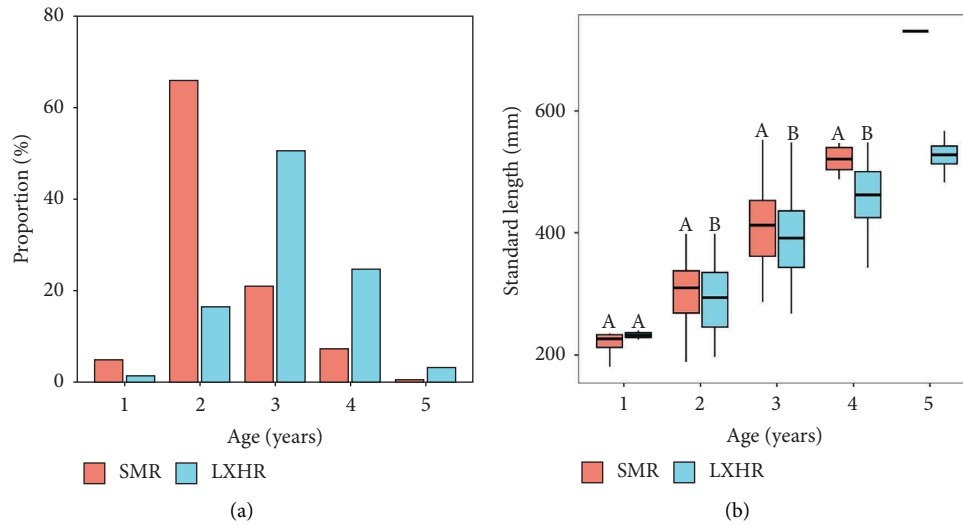


FIGURE 4: Age structure (a) and mean length in different age groups (b) of bighead carp populations in Shanmei Reservoir (SMR) and Lixihe Reservoir (LXHR). Different letters in the graph represent significant differences.

[22, 42–44, 46, 53–59]). When compared to populations in northern reservoirs, bighead carp in southern reservoirs usually grow faster, reach their growth inflection points earlier, and have a younger inflection age. These differences are largely attributed to variations in latitude and climate [60]. In northern reservoirs, higher latitudes and lower water temperatures slow the growth rates of bighead carp. In this study, both SMR and LXHR are located in southern China, where food resource availability plays a crucial role in growth [61]. Abundant food, especially in eutrophic waters with rich plankton resources, enhances growth and results in larger asymptotic lengths [62]. The higher plankton density and biomass in SMR, particularly the abundant zooplankton, contributed to the larger asymptotic length of bighead carp compared to LXHR. Furthermore, bighead carp in lakes tend to have higher inflection point ages than those in reservoirs. This may be due to the commonly higher plankton density and biomass in lakes, which provide more stable and abundant food sources for bighead carp [25].

Both bighead carp populations comprised of only five age groups. However, the two-year-old group was the most dominant in SMR, while the three-year-old group predominated in LXHR, which also has a higher proportion of older individuals. Some previous studies found that bighead carp populations exhibit more complex age structures in other subtropical reservoirs [44, 46]. Such a difference may be related to the use of fishing gear. Other reservoirs combined various gear types and also employed light trapping, which could have influenced the distribution of the age structure of fish populations. The inflection age, which marks the point where the fish growth rate reaches its peak [35], was higher in SMR (4.7 years) compared to LXHR (3.5 years). This suggested that the SMR population may possess a more stable age structure despite its higher fishing pressure. Compared to other reservoirs, the inflection ages of bighead carp in SMR and LXHR are lower than those in Biliuhe Reservoir (5.7 years, [55]) and Mengjiadun Reservoir

(5.4 years, [56]) but higher than those in Jinshahe Reservoir (3.0 years, [46]). These differences may reflect variations in fishing pressure, population density, locations, and food availability [46, 55, 56]. In this study, the majority of bighead carp individuals are younger than the growth inflection ages in both reservoirs. In SMR, this is likely due to the high fishing pressure, while in LXHR, the fishing ban likely led to the high population density, intensifying competition for food and space and limiting individual growth [63]. A more complex and balanced age structure is essential for population stability and sustainable development. Optimizing stocking and harvesting patterns would improve fisheries management and foster long-term sustainability.

Density-dependent effects play a crucial role in shaping population dynamics, particularly mortality and exploitation rates [64, 65]. We found that the total mortality and fishing mortality of the bighead carp population in SMR were higher than those in the LXHR. Specifically, the fishing mortality in SMR was 0.94/year, accounting for nearly 80% of the total mortality, indicating that fishing is the primary driver of fish mortality [66]. This was also consistent with the long-term and regular harvesting practices implemented over the years in SMR. In contrast, despite the implementation of a fishing ban in LXHR, the bighead carp population had a fishing mortality rate of 0.17/year due to the inevitability of some illegal fishing activities. The natural mortality in SMR was observed to be lower than that in LXHR. Such discrepancy likely emerges because fishing activities in SMR reduce population density, alleviating density-dependent effects, which subsequently decreases competition for resources and reduces natural mortality rates [66]. In LXHR, the higher population density intensified competition for food and habitat, leading to a higher natural mortality rate [10]. According to Peter [67], an optimal exploitation rate (E) of 0.5 is applied as a key benchmark for sustainable resource utilization. The population exploitation rates (E) of 0.80 in SMR and 0.35 in

TABLE 3: Growth equations of the bighead carp in the Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR).

Reservoir	Length-weight relationship	VBGF equation	Standard length growth rate	Standard length growth acceleration
SMR	$BW = 2 \times 10^{-4} SL^{2.98}$ ($R^2 = 0.9697$)	$L_t = 886.78 [1 - e^{-0.21(t+0.53)}]$	$dL_t/dt = 186.22e^{-0.21(t+0.53)}$	$d^2L_t/dt^2 = -39.11e^{-0.21(t+0.53)}$
LXHR	$BW = 2 \times 10^{-4} SL^{3.01}$ ($R^2 = 0.9618$)	$L_t = 684.96 [1 - e^{-0.28(t+0.42)}]$	$dL_t/dt = 191.79e^{-0.28(t+0.42)}$	$d^2L_t/dt^2 = -53.70e^{-0.28(t+0.42)}$

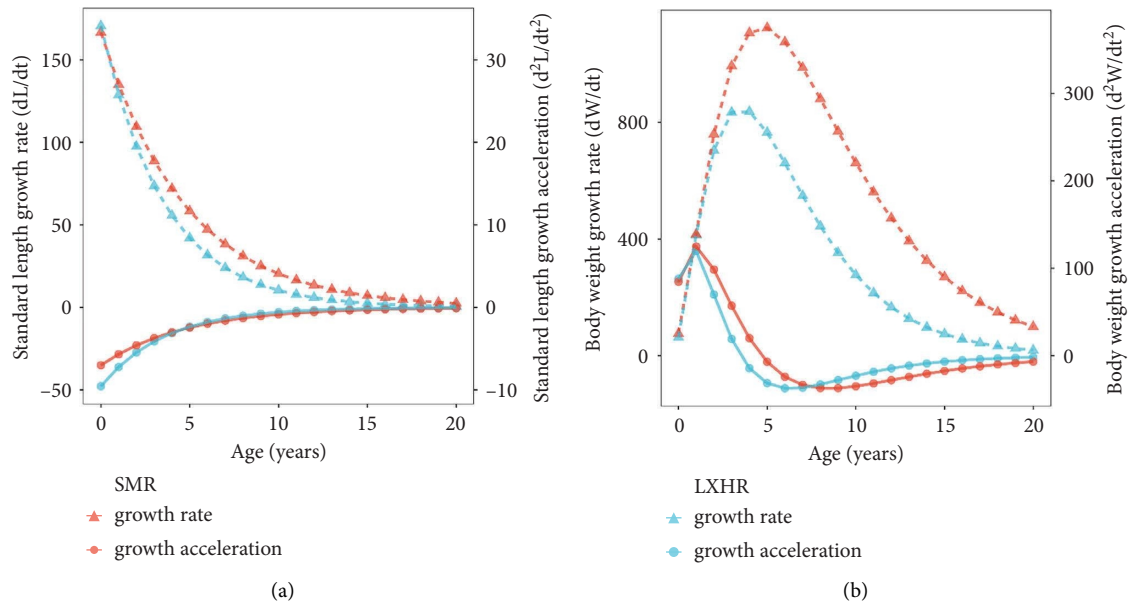


FIGURE 5: Relationship between growth rate (a), growth acceleration (b), and ages of bighead carp populations in Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR).

TABLE 4: Summaries of biological parameters of bighead carp populations in the Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR).

Biological parameters	SMR	LXHR
Asymptotic length (L_{∞} , mm)	886.8	685.0
Growth factor (K)	0.21	0.28
Age at the inflection point of BW	4.7	3.5
SL at the inflection point of BW (mm)	591.1	456.4
Total mortality (Z /year)	1.18	0.48
Natural mortality (M /year)	0.24	0.31
Fishing mortality (F /year)	0.94	0.17
Population exploitation rate (E /year)	0.80	0.35

Abbreviations: BW, body weight; SL, standard length.

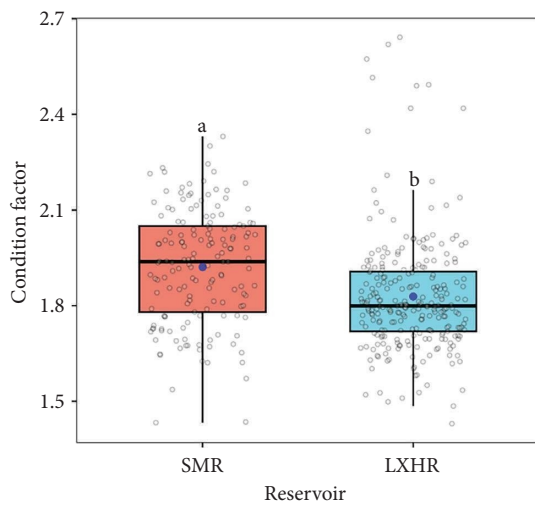


FIGURE 6: Mean condition factor of bighead carp populations in Shanmei Reservoir (SMR) and Liuxihe Reservoir (LXHR). Different letters in the graph represent significant differences.

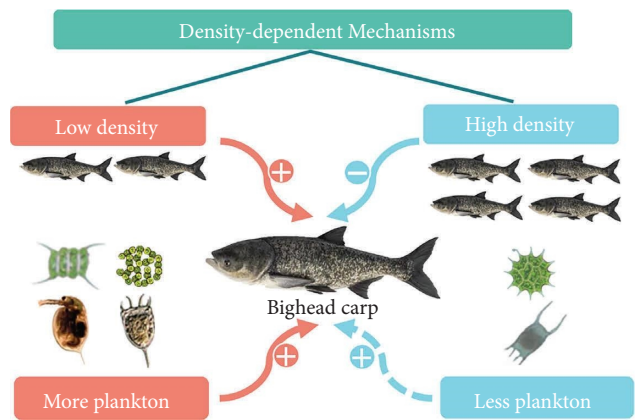


FIGURE 7: The density-dependent mechanisms affecting the growth and body condition of bighead carp populations. The red pathway represents the Shanmei Reservoir, and the blue pathway represents the Liuxihe Reservoir. “+” indicates a promoting effect, “-” indicates an inhibitory effect, and a dashed line denotes a weaker effect.

LXHR reflect different levels of population exploitation, with SMR experiencing a higher exploitation. The elevated exploitation rate in SMR suggested that continued intensive harvesting may threaten the long-term sustainability of bighead carp populations [8]. Conversely, the lower exploitation rate in LXHR indicates a lower sustainability risk, allowing the population to maintain itself more effectively [68]. However, despite the comprehensive fishing ban in the LXHR maintaining a low exploitation rate, high population density has increased interspecific competition, negatively affecting fish growth and survival [69]. Thus, continuous monitoring and effective management are crucial for maintaining the sustainability of the populations in both reservoirs.

TABLE 5: Summaries of parameters of bighead carp populations from different regions in China.

Reservoir/lake	<i>N</i>	<i>K</i>	L_{∞} (mm)	<i>t</i>	<i>b</i>	Growth pattern	Age structure (/year)	Age identification materials	Trophic state	Reference
Wudalianchi ¹	223	0.14	976	7.6	2.90	Isometric	4–9	Scale	Mesotrophic	[53]
Hongqipao Reservoir ¹	160	0.18	812	6.2	2.89	Isometric	1–6	Scale	—	[54]
Biliuhe Reservoir ¹	693	0.25	941	5.7	2.88	Isometric	2–8	Scale + fin ray	—	[55]
Mengjiaduan Reservoir ¹	43	0.16	810	5.4	2.69	Isometric	2–10	Scale + fin ray	Oli-mesotrophic	[56]
Nihe Reservoir ¹	278	0.09	1494		2.94	Isometric	1–3	Scale	Eutrophic	[57]
Qingcaosha Reservoir ²	59	0.17	921	5.0	2.95	Isometric	1–11	Scale + vertebrae	Mesotrophic	[44]
Yankou Reservoir ²	37	0.32	733	3.3	3.07	Isometric	2–7	Scale	—	[42]
Jinshahe Reservoir ²	53	0.40	685	3.0	2.87	Allometric	2–6	Scale	Oli-mesotrophic	[46]
Chitan Reservoir ²	62	0.19	684	4.9	2.97	Isometric	2–6	Scale	Mesotrophic	[43]
Shanmei Reservoir ²	161	0.21	887	4.7	2.98	Isometric	1–5	Scale	—	This study
Liuxihe Reservoir ²	257	0.28	685	3.5	3.01	Isometric	1–5	Scale	—	This study
Jili Lake ^{1,*}	68	0.14	1207	8.1	2.96	Isometric	1–8	Scale	—	[22]
Ge Lake ^{2,*}	153	0.16	1095	5.7	2.94	Isometric	2–9	Scale	Eutrophic	[58]
Hongfeng Lake ^{2,*}	243	0.13	966	7.1	2.70	Isometric	1–4	Scale	—	[59]

Note: *N*, number of specimens; *K*, growth factor; L_{∞} , asymptotic length; *t*, growth inflexion point age; *b*, growth ratio. The reservoirs and lakes in the table are arranged in order of latitude, from north to south areas.

*Lakes.

¹Reservoirs located in northern China.

²Reservoirs located in southern China.

Our results demonstrated that different stocking and harvesting patterns can significantly affect the age structure, growth pattern, and body condition of the bighead carp population. These effects are primarily driven by variations in fish abundance and food resource availability, further highlighting the important role of density-dependent effects in fisheries management. This is particularly relevant when formulating stocking and harvesting strategies for economically important fish species. Based on our findings, we recommend that reservoir managers implement adaptive stocking and harvesting strategies to optimize density-dependent effects and ensure the sustainability of fish populations. Specifically, for SMR, it is advisable to reduce fishing pressure, particularly on larger individuals, to prevent population miniaturization. For LXHR, adjusting stocking levels to avoid excessive population density and alleviate intraspecific competition is recommended. Regular monitoring of population density, age structure, and body condition is crucial for timely adjustments in stocking densities and fishing. Balancing stocking and harvesting patterns to optimize the density-dependent effects is essential for the sustainable management of reservoir ecosystems.

In our study, we primarily focused on exploring the effects of stocking and fishing activities, as well as plankton biomass, on the growth of bighead carp from both top-down (fishing pressure) and bottom-up (food resources) perspectives. The productivity of reservoirs is influenced by multiple factors, such as climate conditions, reservoir topography, catchment area runoff, and nutrients, which can further impact the age structure and growth of fish. In addition, the relatively short sampling period likely affected the results. Future research incorporating more influencing factors and extending the sampling period are needed to improve the comprehensiveness and reliability of the findings.

Data Availability Statement

Data are available from the authors upon request.

Ethics Statement

We confirm that the research did not involve endangered or protected species. All the procedures described in this study were in accordance with ethical standards (Guidance options on experimental animals) of the Ministry of Science and Technology of the People's Republic of China. The Institute of Hydrobiology, Chinese Academy of Sciences, reviewed and approved the study (approval file order: IHB-LL-2022047).

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

All authors read and approved the final manuscript. Xuemei Chen: writing—original draft, methodology, formal analysis, data curation, and conceptualization. Lei Yang, Hang Zhang, and Xiang Ji: investigation and data curation. Chuansong Liao, Tanglin Zhang, Chuanbo Guo, and Jiashou Liu: writing, review, editing, methodology, supervision, and conceptualization. Thomas Mehner: writing, review, editing, and methodology. Chuansong Liao and Jiashou Liu: supervision and funding acquisition.

Funding

This study was funded by the National Key Research and Development Program of China (2023YFD2400900), the Earmarked Fund for China Agriculture Research System (CARS-45), and the Reservoir Fishery Resources Survey and

Water Purification Fishery Development Planning Project of Quanzhou Shanmei Reservoir Water Resources Deployment Center (I-2019-11-2).

References

- [1] J. C. Croll, T. Van Kooten, and A. M. De Roos, "The Consequences of Density-Dependent Individual Growth for Sustainable Harvesting and Management of Fish Stocks," *Fish and Fisheries* 24, no. 3 (2023): 427–438, <https://doi.org/10.1111/faf.12736>.
- [2] S. Raimondo, H. Rutter, B. L. Hemmer, C. R. Jackson, and G. M. Cripe, "The Influence of Density on Adults and Juveniles of the Estuarine Fish, the Sheephead Minnow (*Cyprinodon variegatus*)," *Journal of Experimental Marine Biology and Ecology* 439 (2013): 69–75, <https://doi.org/10.1016/j.jembe.2012.10.018>.
- [3] I. Arranz, T. Mehner, L. Benejam, et al., "Density-dependent Effects as Key Drivers of Intraspecific Size Structure of Six Abundant Fish Species in Lakes across Europe," *Canadian Journal of Fisheries and Aquatic Sciences* 73, no. 4 (2016): 519–534, <https://doi.org/10.1139/cjfas-2014-0508>.
- [4] K. A. Rose, J. H. Cowan, K. O. Winemiller, R. A. Myers, and R. Hilborn, "Compensatory Density Dependence in Fish Populations: Importance, Controversy, Understanding and Prognosis," *Fish and Fisheries* 2, no. 4 (2001): 293–327, <https://doi.org/10.1046/j.1467-2960.2001.00056.x>.
- [5] C. R. Hazlerigg, K. Lorenzen, P. Thorbek, J. R. Wheeler, and C. R. Tyler, "Density-Dependent Processes in the Life History of Fishes: Evidence from Laboratory Populations of Zebrafish *Danio rerio*," *PLoS One* 7, no. 5 (2012): e37550, <https://doi.org/10.1371/journal.pone.0037550>.
- [6] J.-M. Matte, D. J. Fraser, and J. W. A. Grant, "Population Variation in Density-dependent Growth, Mortality and Their Trade-Off in a Stream Fish," *Journal of Animal Ecology* 89, no. 2 (2020): 541–552, <https://doi.org/10.1111/1365-2656.13124>.
- [7] J. K. Raabe, J. A. VanDeHey, D. L. Zentner, T. K. Cross, and G. G. Sass, "Walleye Inland Lake Habitat: Considerations for Successful Natural Recruitment and Stocking in North Central North America," *Lake and Reservoir Management* 36, no. 4 (2020): 335–359, <https://doi.org/10.1080/10402381.2019.1697771>.
- [8] H. S. Embke, A. L. Rypel, S. R. Carpenter, et al., "Production Dynamics Reveal Hidden Overharvest of Inland Recreational Fisheries," *Proceedings of the National Academy of Sciences* 116, no. 49 (2019): 24676–24681, <https://doi.org/10.1073/pnas.1913196116>.
- [9] M. Lin, S. Chen, R. E. Gozlan, et al., "Stock Enhancement of culter *Mongolicus*: Assessment of Growth, Recapture and Release Size in the Yangtze Lakes," *Fisheries Research* 234 (2021): <https://doi.org/10.1016/j.fishres.2020.105809>.
- [10] M. A. Hixon and G. P. Jones, "Competition, Predation, and Density-dependent Mortality in Demersal Marine Fishes," *Ecology* 86, no. 11 (2005): 2847–2859, <https://doi.org/10.1890/04-1455>.
- [11] C. Hsieh, A. Yamauchi, T. Nakazawa, and W.-F. Wang, "Fishing Effects on Age and Spatial Structures Undermine Population Stability of Fishes," *Aquatic Sciences* 72, no. 2 (2010): 165–178, <https://doi.org/10.1007/s00027-009-0122-2>.
- [12] B. M. Huntsman, A. J. Lynch, and C. A. Caldwell, "Interacting Effects of Density-dependent and Density-independent Factors on Growth Rates in Southwestern Cutthroat Trout Populations," *Transactions of the American Fisheries Society* 150, no. 5 (2021): 651–664, <https://doi.org/10.1002/tafs.10319>.
- [13] G. D. Grossman and T. N. Simon, "Density-dependent Effects on Salmonid Populations: A Review," *Ecology of Freshwater Fish* 29, no. 3 (2020): 400–418, <https://doi.org/10.1111/eff.12523>.
- [14] K. M. Myrvold and B. P. Kennedy, "Density Dependence and its Impact on Individual Growth Rates in an Age-Structured Stream Salmonid Population," *Ecosphere* 6, no. 12 (2015): 1–16, <https://doi.org/10.1890/ES15-00390.1>.
- [15] E. Bennitt, M. C. Bonyongo, and S. Harris, "Habitat Selection by african buffalo (*Syncerus caffer*) in Response to Landscape-Level Fluctuations in Water Availability on Two Temporal Scales," *PLoS One* 9, no. 7 (2014): e101346, <https://doi.org/10.1371/journal.pone.0101346>.
- [16] M. D. Tillotson and T. P. Quinn, "Climate and Conspecific Density Trigger Pre-spawning Mortality in Sockeye Salmon (*Oncorhynchus nerka*)," *Fisheries Research* 188 (2017): 138–148, <https://doi.org/10.1016/j.fishres.2016.12.013>.
- [17] C. Zhu, J. Tong, X. Yu, and W. Guo, "Comparative Mapping for Bighead Carp (*Aristichthys nobilis*) against Model and Non-model Fishes Provides Insights into the Genomic Evolution of Cyprinids," *Molecular Genetics and Genomics* 290, no. 4 (2015): 1313–1326, <https://doi.org/10.1007/s00438-015-0992-z>.
- [18] C. Tang, Q. Yan, W. Li, X. Yang, and S. Zhang, "Impact of Dam Construction on the Spawning Grounds of the Four Major Chinese Carps in the Three Gorges Reservoir," *Journal of Hydrology* 609 (2022): <https://doi.org/10.1016/j.jhydrol.2022.127694>.
- [19] Bureau, *China Fishery Statistical Yearbook* (China Agriculture Press, 2023).
- [20] Q. Lin, Q. Chen, L. Peng, L. Xiao, L. Lei, and E. Jeppesen, "Do Bigheaded Carp Act as a Phosphorus Source for Phytoplankton in (Sub) Tropical Chinese Reservoirs?" *Water Research* 180 (2020): <https://doi.org/10.1016/j.watres.2020.115841>.
- [21] Z. Chen, D. Zhao, M. Li, W. Tu, X. Luo, and X. Liu, "A Field Study on the Effects of Combined Biomanipulation on the Water Quality of a Eutrophic Lake," *Environmental Pollution* 265 (2020): <https://doi.org/10.1016/j.envpol.2020.115091>.
- [22] J. Zhang, S. Liu, F. Ruan, Q. Ge, and H. Luo, "Studies on the Growth Characteristics of Bighead Carp in Jili Lake," *Chinese Aquaculture* 43 (2022): 12–14+44, <https://doi.org/10.3969/j.issn.1004-2091.2022.05.003>.
- [23] P. Xie, "Gut Contents of Bighead Carp (*Aristichthys nobilis*) and the Processing and Digestion of Algal Cells in the Alimentary Canal," *Aquaculture* 195, no. 1-2 (2001): 149–161, [https://doi.org/10.1016/S0044-8486\(00\)00549-4](https://doi.org/10.1016/S0044-8486(00)00549-4).
- [24] Y. Wang, Y.-C. Kao, Y. Zhou, H. Zhang, X. Yu, and G. Lei, "Can Water Level Management, Stock Enhancement, and Fishery Restriction Offset Negative Effects of Hydrological Changes on the Four Major Chinese Carps in China's Largest Freshwater Lake?" *Ecological Modelling* 403 (2019): 1–10, <https://doi.org/10.1016/j.ecolmodel.2019.03.020>.
- [25] P. Dai, F. Han, S. Yin, and H. Huang, "Research Progress on Growth Characteristics of *Hypophthalmichthys Molitrix* and *Hypophthalmichthys Nobilis*," *Chinese Aquaculture* 42 (2021): 31–35, <https://doi.org/10.3969/j.issn.1004-2091.2021.10.008>.
- [26] *ICOLD (International Commission on Large Dams)* (2023).
- [27] H. Zhang, J. Wu, H. Gorfine, et al., "Inland Fisheries Development versus Aquatic Biodiversity Conservation in China and its Global Implications," *Reviews in Fish Biology and Fisheries* 30, no. 4 (2020): 637–655, <https://doi.org/10.1007/s11160-020-09622-y>.
- [28] Q. Liu, Z. Liu, and J. Wang, "Spatial and Temporal Characteristics of Zooplankton Community Structure and its Influencing Factors in Shanmei Reservoir, Fujian Province,"

- Journal of Lake Sciences* 34 (2022): 2039–2057, <https://doi.org/10.18307/2022.0619>.
- [29] Z. S. Zhang and X. F. Haung, *Methods in Freshwater Plankton Study* (Science Press, 1991).
- [30] W. E. Ricker, “1975 Computation and Interpretation of Biological Statistics of Fish Populations,” *Bulletin of the Fisheries Research Board of Canada*, 191, 1–382.
- [31] D. Pauly, *Fish Population Dynamics in Tropical Waters: A Manual for Use with Programmable Calculators* (1984).
- [32] Jr F. C. Gayanilo, P. Sparre, and D. Pauly, “FAO-ICLARM Stock Assessment Tools II: Revised Version: User’s Guide,” *FAO Computerized Information Series: Fisheries (Bethesda, Md.)* (2005).
- [33] D. Pauly, “1979 Theory and Management of Tropical Multispecies Stocks,” *ICLARM studies and reviews*, 1, 35.
- [34] B. L. Von, “A Quantitative Theory of Organic Growth (Inquiries on Growth Laws. II),” *Human Biology* 10 (1938): 181–213.
- [35] M. Yin, *Fish Ecology* (China Agriculture Press, 1995).
- [36] S. Chatzifotis, P. Muje, M. Pavlidis, J. Ågren, M. Paalavuo, and H. Mölsä, “Evolution of Tissue Composition and Serum Metabolites during Gonadal Development in the Common Dentex (*Dentex dentex*),” *Aquaculture* 236, no. 1-4 (2004): 557–573, <https://doi.org/10.1016/j.aquaculture.2003.12.004>.
- [37] B. Rjrh, “A Review of Methods for Estimating Mortality Rates in Fish Populations, with Special Reference to Sources of Bias in Catch Sampling,” *Reports* 140 (1956): 67–83.
- [38] D. Pauly, “A Review of the ELEFAN System for Analysis of Length-Frequency Data in Fish and Aquatic Invertebrates,” in *ICLARM Conf. Proc* (June 1987), 7–34.
- [39] R. C. Team, *R: A Language and Environment for Statistical Computing* (Foundation for Statistical Computing, 2013).
- [40] W. N. Venables and B. D. Ripley, *Modern Applied Statistics with S-PLUS* (Springer Science & Business Media, 2013).
- [41] H. Wickham, “Data Analysis,” in *ggplot2* (Cham: Springer International Publishing, 2016), 189–201, https://doi.org/10.1007/978-3-319-24277-4_9.
- [42] J. L. Yuan, J. Li, and Y. Yang, “Study on the Diversity of Fish Community Structure and Growth Performance of *Hypophthalmichthys molitrix* and *Aristichthys nobilis* in Yankou Reservoir, Zhejiang Province,” *Journal of Shanghai Ocean University* 24 (2015): 754–764.
- [43] M. He, J. Xiao, Z. Liang, L. Cui, and M. Chen, “Fish Community Structure and Growth Characteristics of Silver Carp and Bighead Carp in Jinhu Lake, Taining,” *Chinese Fisheries Research* 45 (2023): 462–472.
- [44] X. Wei, J. Gu, and M. Zhang, “Age Structure and Growth of Bighead Carp and Bighead Carp in Qingcaosha Reservoir in Shanghai,” *Journal of Shanghai Ocean University* 28 (2019): 49–57, <https://doi.org/10.12024/jso.20180502316>.
- [45] S. L. Cooke, W. R. Hill, and K. P. Meyer, “Feeding at Different Plankton Densities Alters Invasive Bighead Carp (*Hypophthalmichthys Nobilis*) Growth and Zooplankton Species Composition,” *Hydrobiologia (The Hague)* 625, no. 1 (2009): 185–193, <https://doi.org/10.1007/s10750-009-9707-y>.
- [46] J. Liu, B. Xiong, and G. J. Lv, “Captured Standard and Growth Characteristics of Bighead Carp (*Hypophthalmichthys Molotrix*) and Bighead Carp (*Hypophthalmichthys Nobilis*) in Jinshahe Reservoir,” *Resources and Environment in the Yangtze Basin* 21 (2012).
- [47] P.-A. Amundsen, R. Knudsen, and A. Klemetsen, “Intraspecific Competition and Density Dependence of Food Consumption and Growth in Arctic Charr,” *Journal of Animal Ecology* 76, no. 1 (2007): 149–158, <https://doi.org/10.1111/j.1365-2656.2006.01179.x>.
- [48] Z. Liang, P. Sun, W. Yan, L. Huang, and Y. Tang, “Significant Effects of Fishing Gear Selectivity on Fish Life History,” *Journal of Ocean University of China* 13, no. 3 (2014): 467–471, <https://doi.org/10.1007/s11802-014-2167-7>.
- [49] C. Jiang, W. Wang, S. Yan, et al., “Assessment of Tropical Fish Stocks Using the LBB Method in Dongzhaigang Bay, Hainan Island, China,” *Sustainability* 14, no. 16 (2022): 9933, <https://doi.org/10.3390/su14169933>.
- [50] S. Wagaw, A. Sisay, A. Bazezew, Y. Enawgaw, and A. Wosnie, “Biological Aspects of oreochromis Niloticus (Linnaeus, 1758) in Geray Reservoir (Ethiopia) for Effective Sustainable Fisheries,” *Fisheries and Aquatic Sciences* 27, no. 2 (2024): 100–110, <https://doi.org/10.47853/FAS.2024.e11>.
- [51] K. Enberg, C. Jørgensen, E. S. Dunlop, et al., “Fishing-induced Evolution of Growth: Concepts, Mechanisms and the Empirical Evidence,” *Marine Ecology* 33 (2012): 1–25, <https://doi.org/10.1111/j.1439-0485.2011.00460.x>.
- [52] G. Joanna, P. Dariusz, P. Mirosław, T. A. Serhan, M. Lidia, and L. K. Magdalena, “Life-history Traits of Amur Sleeper, perccottus Glenii, in the Invaded Vistula River: Early Investment in Reproduction but Reduced Growth Rate,” *Hydrobiologia (The Hague)* 661, no. 1 (2011): 197–210, <https://doi.org/10.1007/s10750-010-0524-0>.
- [53] J. Wang, W. Liu, and F. Tang, “Growth Analysis of Bighead Carp (*Hypophthalmichthys Nobilis*) in Wudalianchi,” *Chinese Journal of Zoology* 51 (2016): 543–551, <https://doi.org/10.13859/j.cjz.201604005>.
- [54] J. Zhao, W. Li, G. Zou, and W. Tian, “Age and Growth of Silver and Bighead Carp in Hongqipao Reservoir,” *Heilongjiang Fisheries* (1999): 21–25.
- [55] Z. Jiang, K. Qin, and S. Yang, “Study on the Age, Growth, and Stock of Silver Carp and Bighead Carp in Biliuhe Reservoir,” *Journal of Dalian Ocean University* 9 (1994): 8–14, <https://doi.org/10.16535/j.cnki.dlhyxb.1994.03.002>.
- [56] Y. Shen, J. Yang, and B. Qi, “Growth of Bighead Carp and Bighead Carp and Measures to Improve Fish Yield in Mengjia Reservoir,” *Water Conservancy Fishery* 5 (2001): 26–28, <https://doi.org/10.3969/j.issn.1003-1278.2001.05.014>.
- [57] H. Yu, F. Chai, and D. Xing, “Study on the Growth Patterns of Silver Carp and Bighead Carp in the Nihe Reservoir,” *Journal of Fisheries* 13 (2000): 58, <https://doi.org/10.3969/j.issn.1000-6535.2000.02.013>.
- [58] D. Li, S. Tang, and Y. Liu, “Captured Standard and Growth Characteristics of *Hypophthalmichthys molitrix* and *Aristichthys Mobilis* in Lake Gehu,” *Jiangsu Agricultural Sciences* 49 (2021): 134–139, <https://doi.org/10.15889/j.issn.1002-1302.2021.06.023>.
- [59] H. Mou, J. Yao, S. Ma, Y. Wang, and Z. Liang, “Study on the Age Structure and Growth of Silver Carp and Bighead Carp in Hongfeng Lake, Guiyang,” *Guangdong Agricultural Sciences* 39 (2012): 122–125, <https://doi.org/10.16768/j.issn.1004-874x.2012.03.073>.
- [60] D. P. Coulter, E. P. Tristano, A. A. Coulter, J. R. Seibert, and J. E. Garvey, “Role of Winter Severity on Juvenile Bighead Carp and Silver Carp Growth and Survival across Latitudes,” *Biological Invasions* 20, no. 11 (2018): 3357–3371, <https://doi.org/10.1007/s10530-018-1781-5>.
- [61] L. Persson and A. M. De Roos, “Food-dependent Individual Growth and Population Dynamics in Fishes,” *Journal of Fish Biology* 69, no. sc (2006): 1–20, <https://doi.org/10.1111/j.1095-8649.2006.01269.x>.

- [62] S. L. Cooke, "Anticipating the Spread and Ecological Effects of Invasive Bigheaded Carps (*Hypophthalmichthys* spp.) in North America: A Review of Modeling and Other Predictive Studies," *Biological Invasions* 18, no. 2 (2016): 315–344, <https://doi.org/10.1007/s10530-015-1028-7>.
- [63] K. Lorenzen and K. Enberg, "Density-dependent Growth as a Key Mechanism in the Regulation of Fish Populations: Evidence from Among-Population Comparisons," *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269, no. 1486 (2002): 49–54, <https://doi.org/10.1098/rspb.2001.1853>.
- [64] S. Gebremedhin, S. Bruneel, A. Getahun, W. Anteneh, and P. Goethals, "Scientific Methods to Understand Fish Population Dynamics and Support Sustainable Fisheries Management," *Water* 13, no. 4 (2021): 574, <https://doi.org/10.3390/w13040574>.
- [65] Y. Liu, C. Zhang, X. Wei, et al., "Coupling Dynamic Energy Budget and Population Dynamic Models to Inform Stock Enhancement in Fisheries Management," *Fish and Fisheries* 24, no. 6 (2023): 924–939, <https://doi.org/10.1111/faf.12776>.
- [66] M. S. Allen and J. E. Hightower, *Inland Fisheries Management in North America* (American Fisheries Society, 2010).
- [67] P. S. Maitland, "Fish Stock Assessment: A Manual of Basic Methods," *Biological Conservation* 56, no. 2 (1991): 241–242, [https://doi.org/10.1016/0006-3207\(91\)90020-a](https://doi.org/10.1016/0006-3207(91)90020-a).
- [68] K. Lorenzen, "Population Dynamics and Potential of Fisheries Stock Enhancement: Practical Theory for Assessment and Policy Analysis," *Philosophical Transactions of the Royal Society B: Biological Sciences* 360, no. 1453 (2005): 171–189, <https://doi.org/10.1098/rstb.2004.1570>.
- [69] C. Accolla, A. Schmolke, M. Vaugeois, and N. Galic, "Density-dependent Population Regulation in Freshwater Fishes and Small Mammals: A Literature Review and Insights for Ecological Risk Assessment," *Integrated Environmental Assessment and Management* 20, no. 5 (2024): 1225–1236, <https://doi.org/10.1002/ieam.4845>.