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Research Article

Age Structure, Growth, and Sex Ratio of *Coilia nasus* in the Lower Yangtze River and the Estuary During the Initial Stage of Fishing Moratorium

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The comprehensive 10-year fishing moratorium implemented in the Yangtze River Basin since 2021 provides a unique opportunity to evaluate the recovery of threatened fish populations. This study assessed the recovery status of *Coilia nasus* in the lower reaches of the Yangtze River during the fourth year of the moratorium through analysis of age structure, growth parameters, and sex ratio. Field investigations were conducted at two strategic locations (Chongming and Taizhou) during the migration season (May–June 2024), yielding 3077 specimens. Results revealed significant improvements in population parameters, including increased mean age (2.64 years) and standard length (28.5 cm), alongside a higher proportion of age 3 and age 4 individuals (63.3%). Sex ratio analysis showed a pronounced female bias (3.19:1), with spatial variations between estuarine (4.99:1) and upstream (2.04:1) sites. Growth parameter analysis indicated a shift toward natural growth dynamics, with increased asymptotic length (L_∞) and altered growth rates (k) compared to premoratorium periods. Despite these positive indicators, the absence of five-year-old individuals and lower average length compared to historical records suggest incomplete recovery. Our findings provide evidence for the effectiveness of the fishing ban while highlighting the need for continued protection.

Keywords: age structure; growth parameters; Japanese grenadier anchovy; sex ratio

1. Introduction

Coilia nasus Temminck & Schlegel, 1846 (Japanese grenadier anchovy) is an anadromous fish species distributed across the Northwest Pacific Ocean, inhabiting coastal waters of China, Japan, and Korea [1–3]. In the Yangtze River Basin, anadromous populations of *C. nasus* represent the primary conservation concern due to their complex population structure and severe anthropogenic impacts [4]. The species has experienced dramatic population declines over recent decades, with fundamental changes in migration behavior, age structure, and reproductive patterns that have altered population dynamics throughout the basin.

The species exhibits complex life history traits with well-documented historical changes in the lower Yangtze River Basin. The species undertakes spawning migrations from February to September, with peak reproductive activity during May–June. Historically, in the 1970s, populations comprised individuals up to 6 years old, with 3–4-year-old fish forming dominant age classes [5]. However, exceptional market value (up to USD 1000/kg) has driven intensive overexploitation [4, 6–8]. Severe overexploitation, combined with habitat fragmentation, water pollution, and floodplain isolation from dam construction, has fundamentally altered population dynamics and resulted in significant population declines [9–12]. This overfishing has severely truncated age structure, with 2-year-old individuals becoming the primary population component during 1993–2002 [9–11], and accelerated sexual maturation from 2 to 1 year of age [13, 14]. Consequently, maximum migration distance has contracted from 1400 km (historically reaching Dongting Lake) to 844 km (currently limited to Poyang Lake) [12], spawning has been restricted to suboptimal river habitats, and the species has been designated on the IUCN Red List of Threatened Species [15].

In response to this conservation crisis, the Chinese government implemented comprehensive protective measures [16]. The Ministry of Agriculture and Rural Affairs prohibited commercial harvesting of wild *C. nasus* populations in February 2019, followed by a comprehensive 10-year fishing moratorium across the Yangtze River basin beginning in January 2021. This moratorium provides a unique opportunity to examine population recovery processes following reduced anthropogenic pressure and offers critical insights for conservation strategies of threatened migratory fishes.

Systematic assessment of biological parameters is essential for evaluating moratorium effectiveness and understanding recovery mechanisms. However, postmoratorium changes in population parameters remain poorly documented, limiting our ability to assess recovery progress. Sex-specific responses are particularly important given that habitat degradation has altered spawning habitats and potentially disrupted life history strategies [12]. Furthermore, spatial variation in recovery responses across the river system requires investigation to inform adaptive management strategies.

We examined *C. nasus* recovery in the fourth moratorium year through sampling at the Yangtze River estuary (Chongming) and upstream location (Taizhou) during migration season (May–June). Our objectives were to quantify (1) spatiotemporal sex ratio distribution; (2) gonadal development patterns; (3) sexual dimorphism in morphology and growth; and (4) age structure and sex-specific growth parameters. Comparisons with historical premoratorium data identify recovery mechanisms and provide evidence for evaluating moratorium effectiveness. This study provides baseline data using *C. nasus* as an indicator species and offers insights for adaptive conservation management of endangered migratory fishes in the Yangtze River basin.

2. Materials and Methods

2.1. Sample Collection. According to Li et al., *C. nasus* exhibits spatially and temporally variable spawning patterns: spawning occurs in the estuary during May and June, at Jingjiang in June, and at Anqing in August, with spawning migration extending upstream as the season progresses and peaking during May and August in the lower reaches of the Yangtze River and the estuary [17]. Based on this reproductive timeline, sampling of *C. nasus* was conducted during the peak migration season from May to June 2024 at two sites along the lower Yangtze River (Figure 1): Chongming (31°29′52″N, 121°36′36″E), an estuarine site located 30 km upstream of the river mouth with fluctuating surface salinity (0.16%–3.8%); and Taizhou (32°12′14″N, 119°53′40″E), a freshwater site located 210 km upstream from Chongming (approximately 240 km from the river mouth) with consistent 0% salinity. These sites were selected because they represent critical migratory corridors utilized during spawning runs. Sampling was conducted within the timeframe permitted by local fisheries authorities.

Specimens were collected using drifting gill nets (40 mm mesh size) operated by licensed local fishermen under scientific research permits issued by local fisheries authorities. A total of 3077 individuals were morphologically identified as *C. nasus*. For all specimens, we measured supermaxilla length and head length to calculate their ratio. Individuals with a supermaxilla-to-head length ratio exceeding 1.0 were confirmed as the long supermaxilla ecotype of Japanese grenadier anchovy [3].

2.2. Morphological Measurements. Each specimen was subjected to morphometric analysis, with standard length (SL) and total length (TL) measured to the nearest 0.1 cm, and total weight (W) recorded to the nearest 0.1 g using a calibrated electronic scale. Following external measurements, specimens were dissected and sexed through visual inspection of gonads. Gonadal maturity stages (GMS) were determined using a standardized six-point maturity scale [17, 18], with individuals at stages IV or V classified as mature fish [17]. Following field processing, all collected samples were transported to the laboratory for subsequent analysis.

2.3. Length–Weight Relationships (LWRs). The LWR was calculated using the equation $W = a \times \mathrm{SL}^b$, where W represents total weight (g), SL represents standard length (cm), and parameters a and b correspond to the intercept and slope of the regression, respectively. To linearize this relationship, parameters were estimated using log-transformed data following the equation: $\log(W) = \log(a) + b \times \log(\mathrm{SL})$. Model fit quality was assessed through the coefficient of determination (R^2). To characterize growth patterns, Student's t-test at a 95% confidence level was employed to determine if the b value significantly deviated from 3, with isometric growth defined when $b = 3$, and allometric growth when $b \neq 3$ [19]. Sex-specific differences in LWRs were evaluated using analysis of covariance (ANCOVA), with body length as a covariate affecting body weight. Additionally, Fulton's condition factor (K) was calculated as $K = 100 \times W/\mathrm{SL}^3$, where W is total weight in grams and SL is standard length in centimeters [20].

2.4. Age Determination. Scale samples were collected between the end of the pectoral fin and the beginning of the dorsal fin for age determination. For each specimen, four to six symmetrical and nonregenerated scales were carefully selected, soaked in water for 24 h, cleaned of adherent

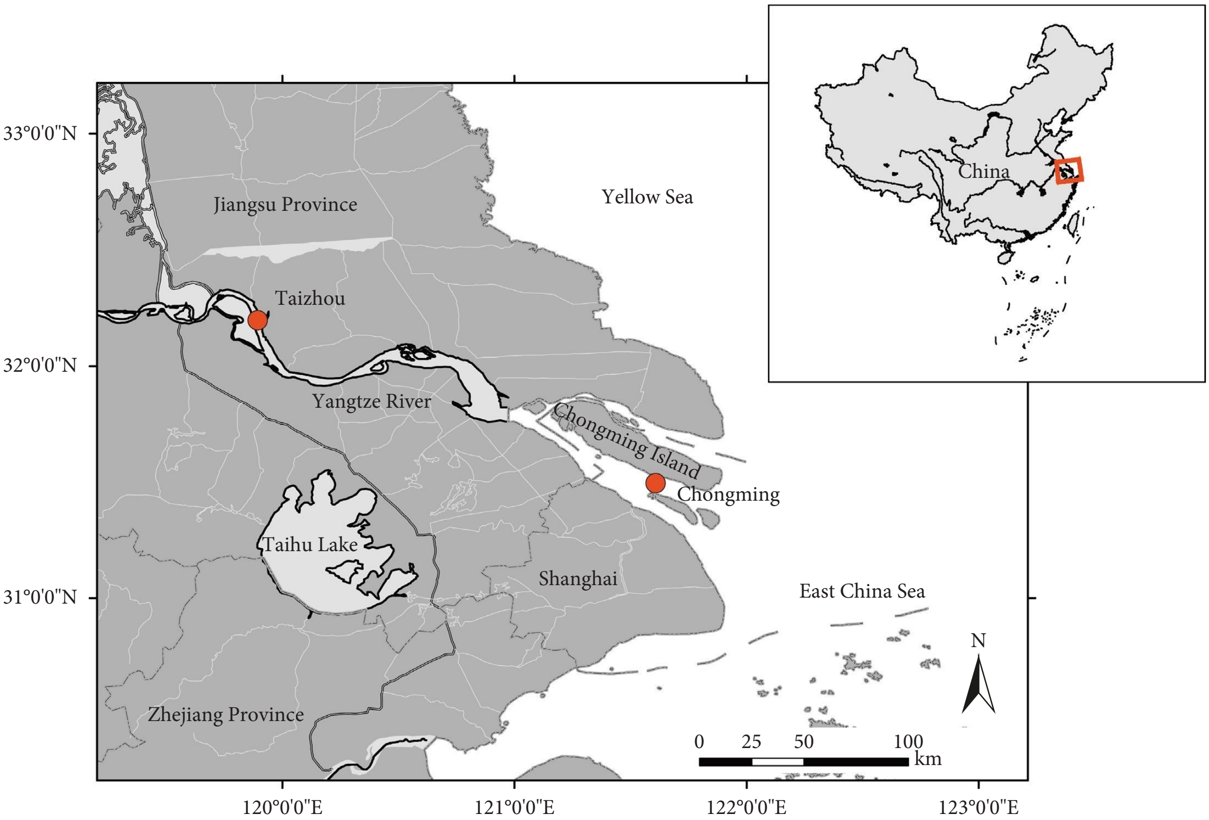


Figure 1: Sampling locations of *C. nasus* in the lower Yangtze River. Two sampling sites are shown: Chongming (estuarine site, 30 km from river mouth) and Taizhou (freshwater site, 240 km from river mouth).

tissues, and mounted between two glass slides before drying in an oven at 70°C for 3 h [18].

Age determination was conducted through microscopic examination at 10–40x magnification using transmitted light to identify alternating translucent and opaque growth zones. Fish age was determined by counting the number of annuli (thin rings) in the scales. To minimize subjective bias, all samples were independently examined by two experienced readers, and ages were accepted only when consensus was reached [21].

2.5. Growth Analysis. The length-at-age relationship was described using the von Bertalanffy growth equation: $L_s = L_\infty\,(1 - e^{-k\,(t-t_0)})$ [22], where L_s denotes the standard length at age t, L_∞ represents the asymptotic length, k is the growth rate parameter (year^{-1}), and t_0 is the theoretical age at which the fish would have a length of zero. The growth performance index (Φ') was calculated as: $\Phi' = \log_{10}(k) + 2\log_{10}(L_\infty)$ [23], where k and L_∞ are von Bertalanffy growth parameters. A chi-square test of maximum likelihood ratios [24] was employed to assess significant differences in growth functions between sexes.

2.6. Statistical Analysis. Nonparametric tests were used for statistical analyses as all variables (standard length, total length, body weight, gonadal maturity stages, and age) deviated from normality (Shapiro–Wilk test, all $p < 0.05$). The Wilcoxon rank-sum test was employed to evaluate differences in standard length, total length, body weight, GMS, and age between sampling sites, months, and sexes. The chi-square (χ^2) test was used to analyze sex ratio differences across sampling sites and months. All statistical procedures were implemented using R software (Version 4.4.1) [25].

3. Results

3.1. Sex Ratio. In this study, we analyzed 3077 specimens, comprising 734 males and 2343 females, which yielded an overall sex ratio of 3.19:1 (females: males) during the May–June sampling period. A chi-square test indicated a significant deviation from the expected 1:1 ratio ($\chi^2 = 841.37$, $df = 1$, $p < 0.001$), thereby confirming a pronounced female bias. Spatial analysis further revealed substantial differences in sex ratios between sampling sites ($\chi^2 = 109.01$, $df = 1$, $p < 0.001$). In particular, the Chongming site exhibited a stronger female bias (4.99:1; 1429 females and 286 males) compared to the Taizhou site (2.04:1; 914 females and 448 males).

Additionally, monthly comparisons demonstrated significant fluctuations in sex ratios from May to June ($\chi^2 = 5.169$, $df = 1$, $p = 0.023 < 0.05$). Specifically, at Chongming the female ratio increased from 4.32:1 in May to 5.54:1 in June, whereas Taizhou displayed a decreasing trend from 2.73:1 to 1.89:1 (Figure 2).

3.2. Gonadal Maturity Stages. A Wilcoxon rank-sum test revealed significant differences in GMS between sexes ($W = 980{,}854$, $p < 0.001$) and among sampling sites

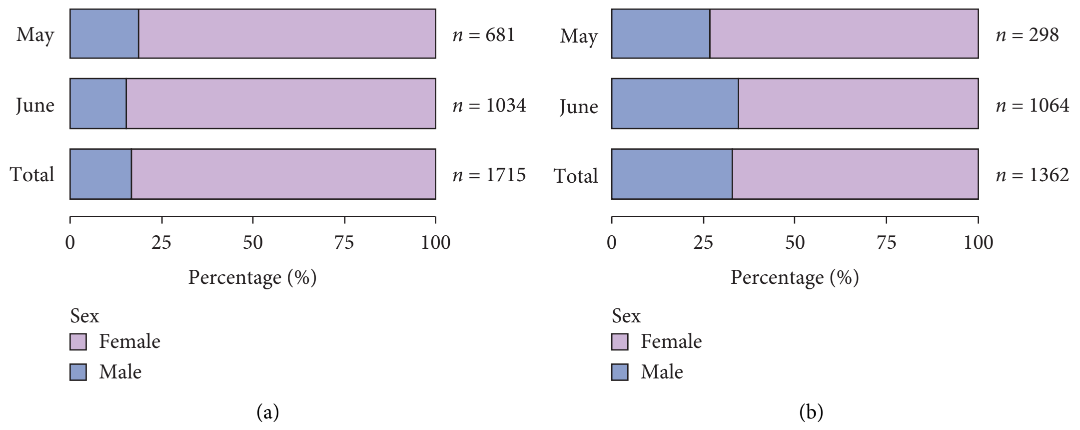


Figure 2: Sex ratio distribution of *C. nasus* in the lower Yangtze River. Percentage composition by sex at (a) Chongming and (b) Taizhou sampling sites during the May–June period. Horizontal bars display male (blue) and female (pink) proportions, and numbers on the right indicate sample sizes (n).

($W = 1{,}554{,}241$, $p < 0.001$). At the Taizhou site, the majority of females were classified at Stage II (56.8%), followed by Stage III (33.3%), while nearly half of the males were at Stage III (48.7%). Conversely, at the Chongming site, most females were observed at Stage IV (41.8%), with lower proportions at stages II (24.2%) and III (11.9%), and a predominant proportion of males remained at Stage II (62.2%). Notably, the proportion of mature individuals (Stages IV and V) was markedly higher at Chongming (females: 63.8%, males: 5.9%) compared to Taizhou (females: 10.0%, males: 32.8%).

Temporal analyses from May to June further revealed distinct patterns in gonadal development (Figure 3). At Chongming, females demonstrated accelerated maturation, as indicated by a reduction in Stage II from 30.0% to 20.5%, a decrease in Stage III from 20.1% to 6.7%, and a corresponding increase in mature stages from 49.9% to 72.7%. In contrast, males at Chongming largely remained in early developmental stages, with the prevalence of Stage II actually increasing from 50.0% to 72.2%, while Stage III decreased notably from 43.8% to 22.2%. Meanwhile, at Taizhou, both sexes exhibited clear signs of maturation: females experienced a marked decrease in Stage II from 78.9% to 49.9%, accompanied by increases in Stage III (from 18.8% to 37.8%) and mature stages (from 2.3% to 12.4%), while males showed a decline in Stage II (from 30.0% to 16.0%) alongside increases in Stage III (from 45.0% to 49.5%) and mature stages (from 25.0% to 34.5%).

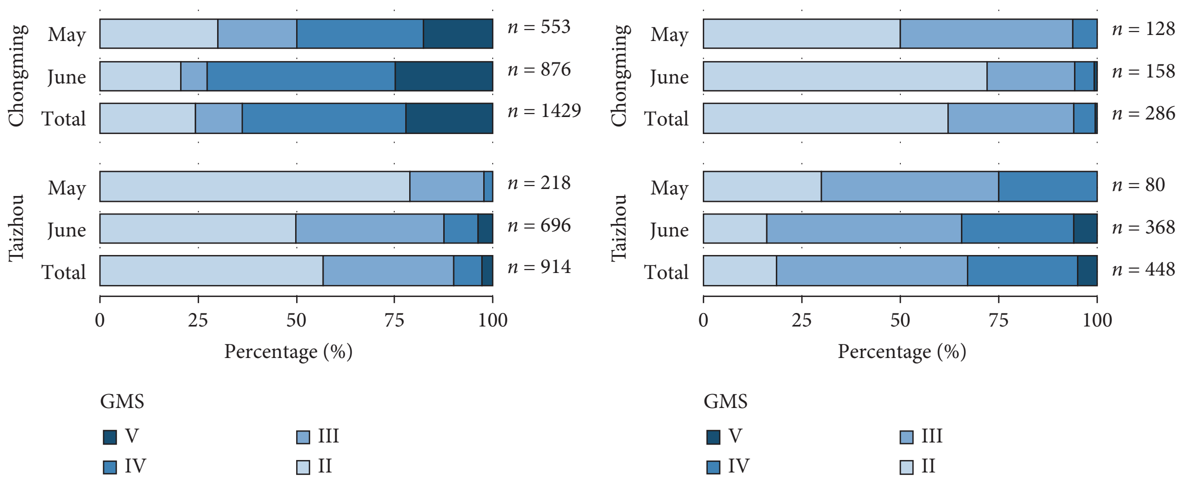
3.3. Morphometric Characteristics and Growth Patterns

3.3.1. Body Size Distribution and Condition Factor. Morphometric analysis of 3077 *C. nasus* specimens showed total lengths ranging from 13.6 to 40.9 cm (mean ± SD: 30.9 ± 4.5 cm; Figure 4(a)) and standard lengths from 12.6 to 37.8 cm (mean ± SD: 28.5 ± 4.3 cm; Figure 4(b)). Body weights ranged from 6.8 to 253.0 g (mean ± SD: 96.0 ± 40.8 g; Figure 4(c)). Size–frequency distributions indicated that 56.1% of specimens had standard lengths between 27.5 and 32.5 cm, and 50.0% had body weights between 75.0 and 125.0 g.

Spatial comparison between sampling sites (Chongming and Taizhou) revealed no significant differences in total length ($W = 1{,}135{,}773$, $p = 0.19$), standard length ($W = 1{,}120{,}538$, $p = 0.053$), or body weight ($W = 1{,}145{,}956$, $p = 0.37$).

Sexual dimorphism was evident, with females significantly larger than males across all morphometric parameters (total length: $W = 1{,}381{,}055$, $p < 0.001$; standard length: $W = 1{,}375{,}801$, $p < 0.001$; body weight: $W = 1{,}365{,}027$, $p < 0.001$). Males had standard lengths ranging from 12.6 to 37.8 cm (mean ± SD: 24.9 ± 4.3 cm), with 59.9% between 22.5 and 30.0 cm, and body weights from 6.8 to 253.0 g (mean ± SD: 64.3 ± 36.1 g), with 51.3% between 25.0 and 75.0 g. Females were larger, with standard lengths from 14.1 to 37.8 cm (mean ± SD: 29.6 ± 3.6 cm), 56.1% between 27.5 and 32.5 cm, and body weights from 8.5 to 244.0 g (mean ± SD: 106.0 ± 36.9 g), predominantly between 75.0 and 125.0 g (Figures 4(b) and 4(c)). The condition factor ranged from 0.21 to 0.69 (mean ± SD: 0.39 ± 0.06, Figure 4(d)), with females (0.39 ± 0.06) displaying significantly higher values than males (0.37 ± 0.07; $W = 1{,}078{,}023$, $p < 0.001$).

Temporal comparisons revealed significant declines in all morphometric parameters between May and June (Wilcoxon rank sum tests: standard length: $W = 1{,}262{,}459$, $p < 0.001$; body weight: $W = 1{,}318{,}279$, $p < 0.001$; condition factor: $W = 1{,}224{,}286$, $p < 0.001$). Mean standard length decreased from May to June in both females (from 30.4 ± 3.2 to 29.2 ± 3.7 cm) and males (from 27.2 ± 3.3 to 24.0 ± 4.4 cm). Mean body weight showed similar reductions, declining in females (from 116.0 ± 35.7 to 101.0 ± 36.4 g) and males (from 85.3 ± 33.7 to 56.0 ± 33.7 g). The condition factor exhibited a parallel trend, decreasing from May (0.40 ± 0.06) to June (0.37 ± 0.06) in both sexes, with females declining from 0.40 ± 0.06 to 0.39 ± 0.05 and males from 0.40 ± 0.07 to 0.36 ± 0.06 (Figure 5). Analysis by size class revealed that specimens within each length category experienced significant declines in both body weight and condition factor from May to June, with the most



(a) (b)

Figure 3: Gonadal maturity stage (GMS) composition of *C. nasus* in the lower Yangtze River. Percentage distribution of GMS for (a) female and (b) male specimens at Chongming and Taizhou sites during the May–June period. Stacked bars show proportions of maturity stages II–V, with sample sizes (n) indicated for each category.

substantial decreases observed in larger individuals (standard length classes 25–30 cm and > 30 cm; Figure 6).

3.3.2. Length–Weight Relationships. The LWRs of *C. nasus* exhibited distinct sexual patterns (Figure 7), described by the following equations: $W_{♀} = 3.42 \times 10^{-3} \times \mathrm{SL}^{3.04}$ ($R^2 = 0.89$, $n = 2343$) for females and $W_{♂} = 1.17 \times 10^{-3} \times \mathrm{SL}^{3.35}$ ($R^2 = 0.94$, $n = 734$) for males.

ANCOVA confirmed significant sexual dimorphism in both slopes ($F = 76.258$, $p < 0.001$) and intercepts ($F = 35.967$, $p < 0.001$). One-sample t-tests indicated that the female growth exponent ($b = 3.04$) did not significantly deviate from the theoretical isometric value of 3 ($t = 1.77$, $p = 0.077$), whereas males displayed positive allometric growth with an exponent ($b = 3.35$) significantly higher than 3 ($t = 11.16$, $p < 0.001$).

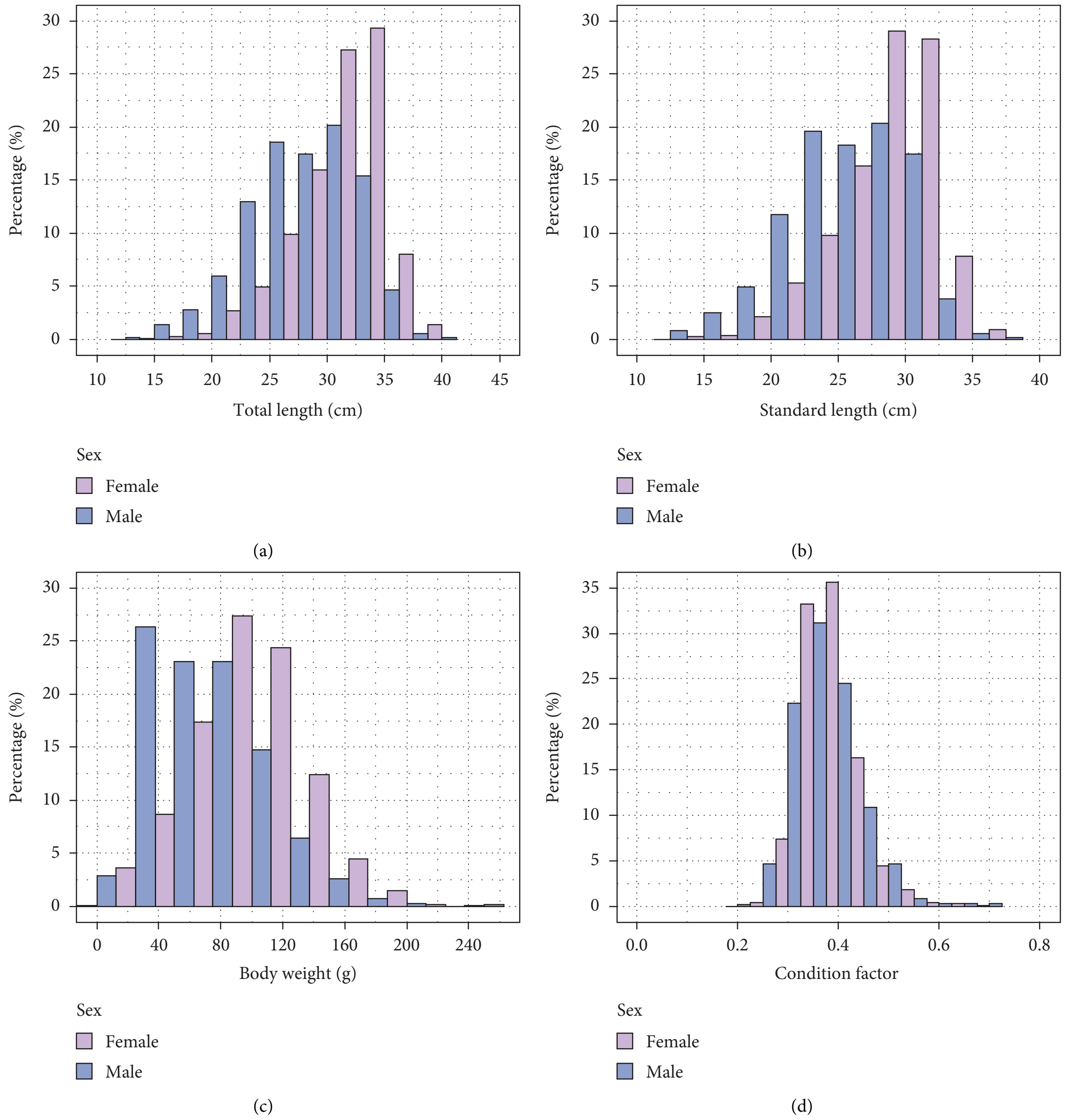
3.4. Estimated Ages and Growth Parameters. Age composition analysis of 712 *C. nasus* revealed a population structure comprising four age classes (1–4 years), with a mean age of 2.64 years. The age distribution exhibited strong dominance of age 3 individuals, comprising 52.5% ($n = 374$) of the total sample, followed by age 2 (27.0%, $n = 192$), age 4 (10.8%, $n = 77$), and age 1 (9.7%, $n = 69$).

Significant age composition differences were observed between females ($n = 532$) and males ($n = 180$) (Table 1). In females, age 3 individuals predominated (61.3%, $n = 326$), followed by age 2 (23.3%, $n = 124$), age 4 (12.4%, $n = 66$), and age 1 (3.0%, $n = 16$). Conversely, males showed a different pattern, with age 2 individuals being most prevalent (37.8%, $n = 68$), followed by age 1 (29.4%, $n = 53$), age 3 (26.7%, $n = 48$), and age 4 (6.1%, $n = 11$).

The von Bertalanffy growth functions were fitted separately for females and males (Figure 8). The growth function for females was $L_s = 42.3 \times (1 - e^{(-0.375(t+0.489))})$ ($n = 532$, $R^2 = 0.702$, $p < 0.001$) and for males was $L_s = 37.8 \times (1 - e^{(-0.493(t+0.225))})$ ($n = 180$, $R^2 = 0.859$, $p < 0.001$). The growth parameters exhibited significant differences between sexes. Females showed a higher asymptotic length ($L_\infty = 42.3 \pm 2.1$ cm) than males ($L_\infty = 37.8 \pm 2.0$ cm), while males demonstrated a higher estimated annual growth rate ($k = 0.493 \pm 0.081$ year^{-1}) than females ($k = 0.375 \pm 0.057$ year^{-1}). The theoretical age at zero length (t_0) was estimated at -0.489 ± 0.176 years for females and -0.225 ± 0.130 years for males. The growth performance index (Φ') values were similar between sexes, with females showing 2.83 and males 2.85. The likelihood ratio test indicated significant differences in growth patterns between sexes ($\chi^2 = 12.951$, $df = 3$, $p < 0.01$).

4. Discussion

During the fourth year of the 10-year comprehensive fishing ban in the Yangtze River, our study revealed substantial recovery of the *C. nasus* population in its lower reaches. The mean age reached 2.64 years, with older individuals (3- and 4-year-olds) comprising 63.3% of the population—levels approaching those recorded in 1973–1975 (mean age: 2.69 years; older individuals: 64.6%) [21] and far exceeding the degraded conditions of 1993–2002 (2.05 years; 6.4%) [9] and 2009 (2.55 years; 54.4%) [13]. Average standard length increased to 28.5 cm, an 11.8% gain over preban measurements in 2018 (25.5 cm, Figure 9). Reduced fishing pressure allowed more individuals to survive and grow larger, directly enhancing reproductive potential through the positive correlation between body size and fecundity [26]. Age-specific body size comparisons indicate that current measurements have largely recovered to historical baselines recorded in the 1970s for corresponding age classes [21], suggesting effective restoration of growth patterns in both males and females within the existing age range.



(a) (b) (c) (d)

Figure 4: Morphometric parameters of *C. nasus* in the lower Yangtze River. Percentage frequency distributions of (a) total length, (b) standard length, (c) body weight, and (d) condition factor by sex. Blue and pink bars represent male and female specimens, respectively, from combined Chongming and Taizhou samples.

However, complete recovery remains elusive. The absence of five-year-old individuals—unreported since 2009—restricts age structure diversity, and the current average length remains 9.4% below the 1973–1975 historical peak of 31.45 cm [21] due to missing large-bodied older fish. While these findings confirm fishing ban effectiveness, full restoration of historical population parameters will require additional protection years to rebuild older age classes.

Furthermore, our study revealed a significantly female-biased overall sex ratio (females: males = 3.19:1), deviating from the expected 1:1 ratio. Similar female-biased ratios have been documented in related species *C. grayii* and *C. mystus* from the Min River estuary [27]. Notably, significant geographical variation was detected along the river gradient, with the estuarine areas (Chongming) exhibiting a pronounced female bias (4.99:1), while the upstream freshwater reaches (Taizhou) showed a less pronounced female bias (2.04:1). However, this observed ratio represents migration-period demographics rather than population-wide structure, as sex ratios in anadromous species can vary seasonally due to differential migration timing and spawning behaviors.

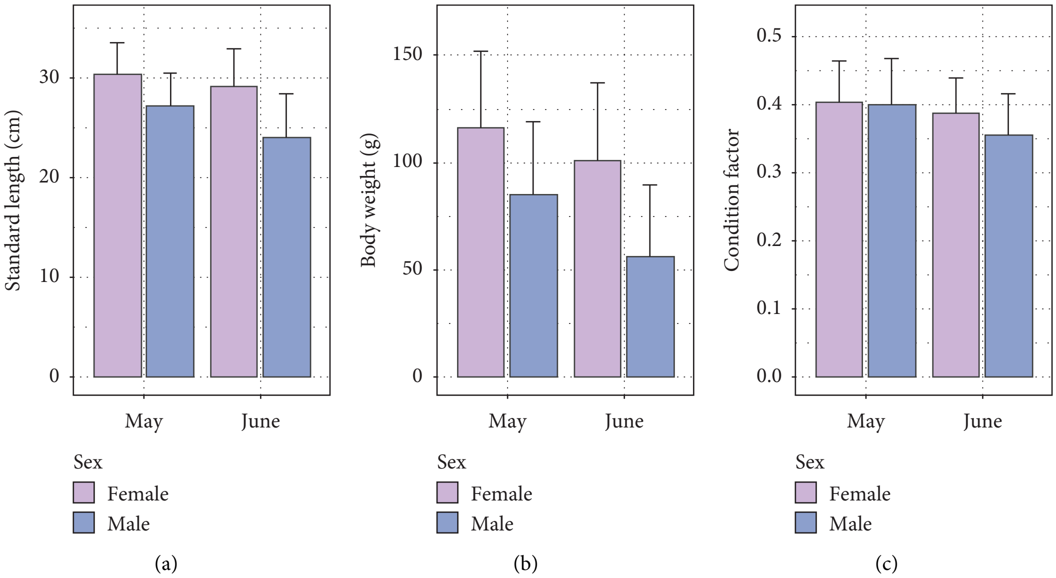


Figure 5: Monthly changes in morphometric parameters of *Coilia nasus* by sex in the lower Yangtze River. Intermonth comparison (May–June) in (a) standard length, (b) body weight, and (c) condition factor for female (pink) and male (blue) *C. nasus*. Bars represent mean values with error bars indicating standard deviation.

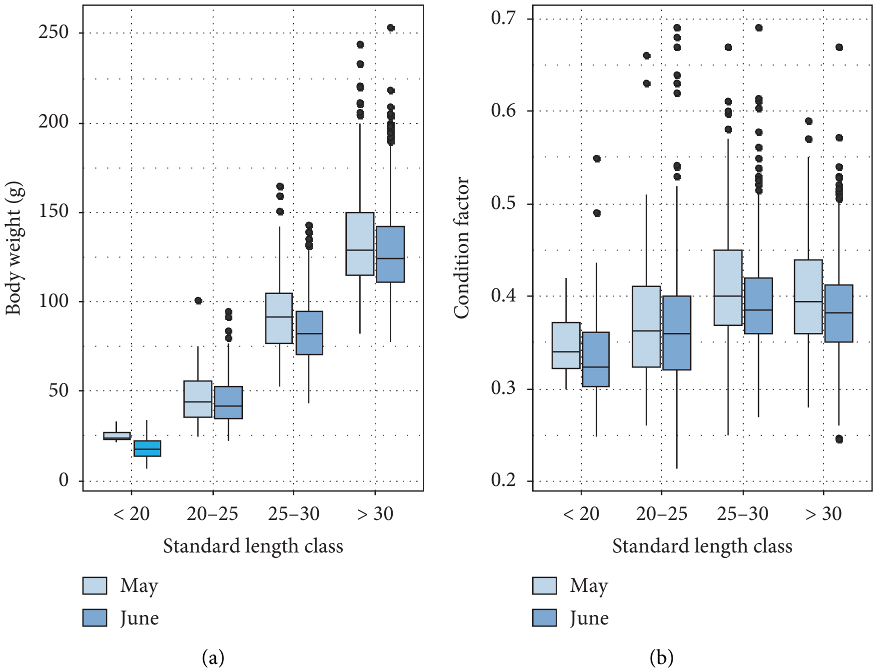


Figure 6: Monthly variation in morphometric relationships of *C. nasus* across standard length classes. Intermonth comparison (May: light blue; June: dark blue) of (a) body weight and (b) condition factor distributions among four standard length classes. Box plots display median values (horizontal lines), interquartile ranges (boxes), and statistical outliers (black dots).

Such spatial variation in sex ratios likely reflects differential migration patterns between sexes, where reproductive requirements, energy allocation, and spawning site selection create distinct demographic distributions across habitats. This spatial transition from female-dominated estuarine populations to more balanced upstream ratios occurs in *C. nasus* and other migratory fish species [28–30]. In estuarine areas, strong female biases have been documented [16, 26], whereas middle reaches such as the Wuhu section and Poyang Lake show more balanced or slightly male-biased ratios [13, 31]. Given the potential spawning sites identified by Xue et al. in the estuarine zones of Chongming Island, Haimen, Nantong, and Rugao, these estuarine environments likely serve as critical aggregation

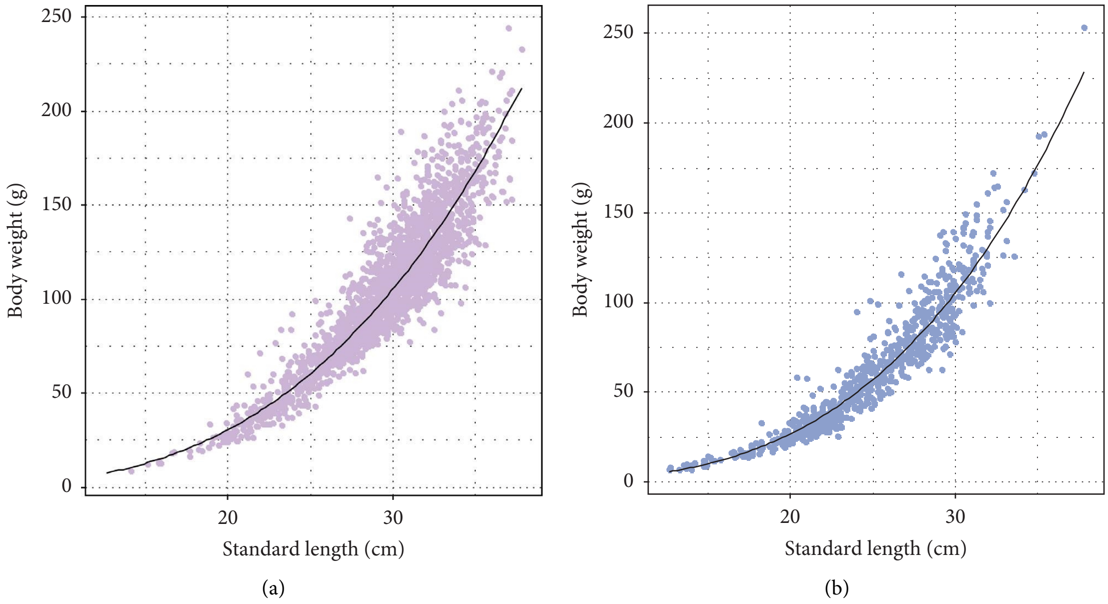


Figure 7: Sex-specific length–weight relationships of *C. nasus* in the lower Yangtze River, illustrated by scatter plots with (a) female (pink dots) and (b) male (blue dots). Black curves indicate the fitted allometric growth models.

Table 1: Age-specific standard length and body weight (mean ± SE) of female and male *C. nasus* from the lower Yangtze River.

Age (year)	Females			Males		
	Standard length (cm)	**Body weight (g)**	**No. of individuals (*n*)**	**Standard length (cm)**	**Body weight (g)**	**No. of individuals (*n*)**
1	18.2 ± 2.5	21.7 ± 9.4	16	17.1 ± 3.0	19.2 ± 11.6	53
2	25.6 ± 2.9	67.4 ± 23.8	124	25.3 ± 2.0	60.7 ± 16.5	68
3	30.9 ± 1.9	115.7 ± 23.5	326	29.8 ± 1.3	103.2 ± 21.1	48
4	34.4 ± 2.1	156.3 ± 33.0	66	33.6 ± 2.1	160.9 ± 39.8	11

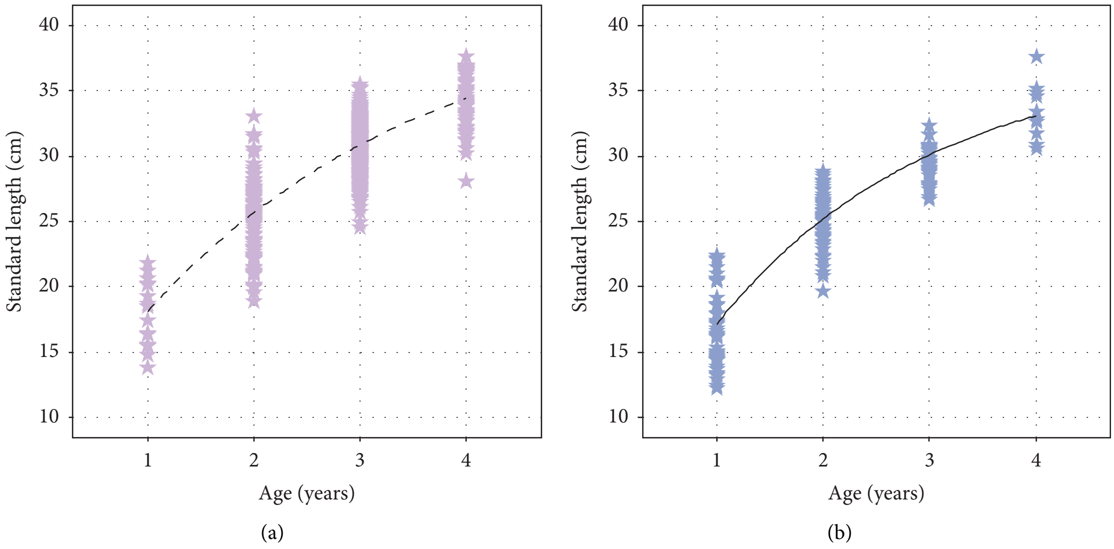


Figure 8: Sex-specific von Bertalanffy growth curves for *C. nasus* in the lower Yangtze River. Observed values are depicted by pink stars for females and blue stars for males in scatter plots. The black dashed line represents the fitted growth curve for females, while the solid black line represents the fitted growth curve for males. (a) Female. (b) Male.

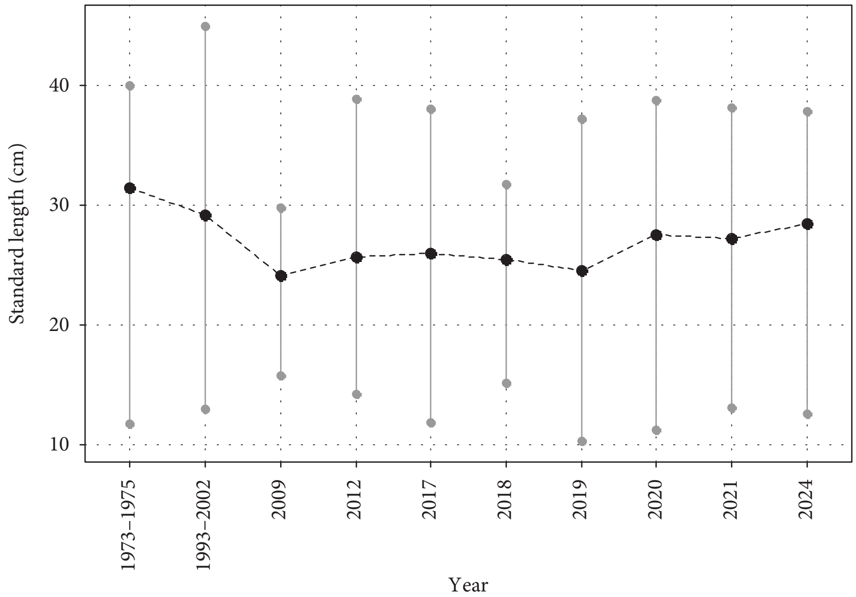


Figure 9: Temporal variations in standard length of *C. nasus* populations in the lower reaches of the Yangtze River (1973–2024).

Table 2: Summary of the von Bertalanffy growth parameters for *C. nasus* from different studies in the Yangtze River.

Yangtze River location	Sampling year	Aging method	Sex	N	L_∞	k	t_0	Φ'	Age range (years)	References
Chongming and Taizhou	2024	Scales	Female	532	42.3	0.375	−0.489	2.83	1–4	This study
			Male	180	37.8	0.493	−0.225	2.85	1–4	
Chongming	2006	Otoliths	Both	576	32.77	0.51	−0.28	2.74	0–4	Li et al. (2010) [33]
Jingjiang	2012	Otoliths	Both	458	40.82	0.31	−0.55	2.71	1–4	Dong et al. (2014) [14]
Poyang Lake	2016	Length frequency	Both	1014	40.95	0.24	−0.57	2.61	—	Wu et al. (2016) [34]
Anqin	2018	Scales	Both	392	32.75	0.39	−0.67	2.63	1–4	Luo et al. (2021) [35]

sites for reproductive females [32], suggesting that the Yangtze River estuary may serve as an important spawning area.

Beyond demographic recovery patterns, our analysis of growth parameters across different river sections revealed additional insights into the spatial effects of historical fishing pressure. Despite methodological variations in age determination across studies (scales, otoliths, and length–frequency analysis) as shown in Table 2, the observed spatial patterns remain consistent. The growth performance index (Φ') appeared to decline from the estuary to the middle reaches of the Yangtze River, likely resulting from historical fishing pressure along the migration route before the ban. Pervasive human impacts along the river have likely driven ecological changes, including overfishing that resulted in truncated body sizes and shortened migration distances, and isolation of floodplain lakes that restricted spawning to suboptimal lotic habitats [12]. Fishing activities along the upstream gradient targeted larger fish, producing size-selective mortality that severely depleted larger individuals and potentially altered intrinsic growth characteristics. Consequently, both L_∞ and k were affected, reducing maximum body size in these upstream populations and reshaping growth patterns.

Historical comparisons with the 2006 Yangtze estuary records uncovered notable shifts in growth parameters following the fishing moratorium (Table 2). While k values fell from 0.51 to 0.375 (females) and 0.493 (males), Φ' increased from 2.74 to 2.83 (females) and 2.85 (males), along with a rise in L_∞ from 32.77 to 42.3 cm (females) and 37.8 cm (males). These seemingly contradictory changes in parameters indeed reflect ongoing recovery. The declining k indicates a return to natural growth rates free from fishing-induced selection, while the elevated φ', primarily driven by the gains in L_∞, emphasizes the re-establishment of larger specimens in the population. Such trends are consistent with the expected course of population recovery once fishing ceases.

Vertical grey lines represent the observed range (minimum to maximum) of standard lengths for each sampling period, while interconnected black dots with dashed lines indicate mean values. This comprehensive dataset integrates measurements from Yuan et al. for 1973–1975 data [21], Zhang et al. for 1993–2002 data [9], Zheng et al. for 2009 data [13], Dong et al. for 2012 data [14], Ma et al. for 2017–2021 data [16], and the present study (2024).

5. Conclusions

Our study provides evidence of early signs of recovery of the *C. nasus* population in the lower reaches of the Yangtze River during the fourth year of the comprehensive fishing moratorium. The increase in average age and size, along with a higher proportion of older individuals, indicates that the fishing ban measures are effectively facilitating population restoration. The observed female-biased sex ratio (females: males = 3.19:1) during the peak migration period and its spatial variation highlight the complex reproductive ecology and migration patterns of the species. Additionally, the analysis of growth parameters suggests a shift towards natural growth dynamics, with the re-establishment of larger individuals and alterations in growth rates. Despite these positive signs, the absence of five-year-old individuals and the lower average body length compared to historical records indicate that full recovery has not yet been achieved.

While our findings underscore the need for continued conservation and offer valuable management insights, several limitations should be acknowledged. Our data were collected in a single year, which may not reflect interannual variations. The sampling was also restricted to a limited portion of the spawning season (May–June), potentially excluding certain migration cohorts or life stages. In addition, sampling occurred only at two locations (Chongming and Taizhou), which might not adequately represent the entire Yangtze River basin. Furthermore, our sex ratio analysis represents migration-period demographics rather than population-wide structure, as sex ratios in anadromous species can vary seasonally due to differential migration timing and spawning behaviors. The temporal scope of our sampling (May–June) captures the peak reproductive period but may not reflect the complete annual population dynamics. We therefore recommend long-term monitoring over multiple years, covering the full spawning migration, and expanding the geographic focus to include additional estuarine and freshwater habitats. Adopting molecular and microelement analyses could further clarify stock structures, genetic diversity, and migratory routes. Such comprehensive approaches will support evidence-based adaptive management strategies for the continued recovery and long-term conservation of this ecologically and economically important species.

Data Availability Statement

The data supporting the findings of this study are available from the corresponding author, Kai Liu (liuk@ffrc.cn), upon reasonable request.

Ethics Statement

Specimens of *C. nasus* were collected as part of an authorized resource survey conducted with approval from the regional fisheries management authorities. All specimens were confirmed to be postmortem at the time of collection. The research protocols adhered strictly to established ethical guidelines for biological specimen handling and received formal approval from the Laboratory Animal Ethics Committee of Shanghai Ocean University (approval no. SHOU-DW-2023-207).

Disclosure

All authors reviewed the manuscript drafts and approved the final version.

Conflicts of Interest

The authors declare no conflicts of interest.

Author Contributions

Data analysis and manuscript writing: Hongyi Guo; sample collection: Xuguang Zhang; laboratory analysis: Ya Zhang; conceptualization and funding acquisition: Kai Liu. Hongyi Guo and Xuguang Zhang contributed equally to this work.

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