



OPEN ACCESS

EDITED BY
Pablo Presa,
University of Vigo, Spain

REVIEWED BY
Oumar Sadio,
Institut de Recherche Pour le Développement,
Senegal
Qun Liu,
Ocean University of China, China
Richard Kindong,
Shanghai Ocean University, China

*CORRESPONDENCE
Lekang Li
✉ lekangli1987@126.com
Xiaoling Gong
✉ xlgong@shou.edu.cn

†These authors have contributed
equally to this work and share
first authorship

RECEIVED 31 May 2025
ACCEPTED 21 August 2025
PUBLISHED 28 August 2025

CITATION

Luo Y, Xu Q, Wang S, Luo Z, Kong C, Peng L,
Zhang B, Bao B, Li L and Gong X (2025)
Assessing the stock recovery of *Coilia nasus*
in the Yangtze River-Poyang Lake waterway
and adjacent waters, using the length-based
Bayesian biomass method.
Front. Mar. Sci. 12:1638854.
doi: 10.3389/fmars.2025.1638854

COPYRIGHT

© 2025 Luo, Xu, Wang, Luo, Kong, Peng,
Zhang, Bao, Li and Gong. This is an open-
access article distributed under the terms of
the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/)
(CC BY). The use, distribution or reproduction
in other forums is permitted, provided the
original author(s) and the copyright owner(s)
are credited and that the original publication
in this journal is cited, in accordance with
accepted academic practice. No use,
distribution or reproduction is permitted
which does not comply with these terms.

Assessing the stock recovery of *Coilia nasus* in the Yangtze River-Poyang Lake waterway and adjacent waters, using the length-based Bayesian biomass method

Yulan Luo^{1,2†}, Qun Xu^{3†}, Sheng Wang⁴, Zhengli Luo^{1,2},
Chiping Kong³, Legen Peng⁴, Bao Zhang³, Baolong Bao^{1,2},
Lekang Li^{3*} and Xiaoling Gong^{1,2*}

¹Key Laboratory of Exploration and Utilization of Aquatic Genetic Resources (Shanghai Ocean University), Ministry of Education, Shanghai, China, ²National Demonstration Center for Experimental Fisheries Science Education, Shanghai Ocean University, Shanghai, China, ³Jiujiang Academy of Agricultural Sciences, Jiujiang, China, ⁴Aquatic Conservation and Rescue Center of Jiangxi Province, Nanchang, China

The comprehensive ten-year fishing ban implemented in the Yangtze River on January 1, 2021, represents a critical ecological conservation measure and national strategic priority in China. Assessment of the ban's effectiveness is essential to guide future long-term conservation efforts. This study systematically analyzed changes in the stock structure and biomass dynamics of *Coilia nasus* in the Yangtze River-Poyang Lake waterway and adjacent waters from 2019 to 2024 using the Length-Based Bayesian Biomass (LBB) method. Results showed a notable improvement in age structure, with the proportion of four-year-old individuals increasing from 3.2% in 2020 to 17.2% in 2024, effectively reversing the previous trend toward younger, smaller fish. The average body length and weight increased significantly, from 271.20 ± 38.44 mm, 68.52 ± 33.26 g in 2019 to 305.53 ± 37.99 mm, 88.02 ± 32.01 g in 2024 ($P < 0.05$). The dominant size classes shifted step by step, from 250 – 260 mm, 50 – 60 g in 2019 to 330 – 340 mm, 120 – 130 g in 2024. According to the LBB model, the relative biomass (B/B_0) increased from 0.17 to 0.68, and biomass relative to the maximum sustainable yield (B/B_{msy}) rose from 0.48 to 1.9, demonstrating a transition in the stock status from “outside of safe biological limits” to “healthy” from 2019 to 2024. These trends, along with increases in the L_{mean}/L_{opt} , L_c/L_{copt} ratios and other indexes, highlight improvements in size structure and a greater presence of larger individuals. In addition, the fishing mortality to natural mortality ratio (F/M) markedly declined from 2.6 in 2019 to 0.37 in 2024,

underscoring the substantial alleviation of fishing pressure under the ban. To further validate these findings, SPR was estimated using the LBSPR model, increasing from 0.19 to 0.42 and suggesting improved reproductive sustainability. These findings provide strong evidence that the fishing ban has played a critical role in the stock recovery of *C. nasus* and mitigating the effects of overfishing.

KEYWORDS

the fishing ban, *Coilia nasus*, stock structure, Yangtze River, Poyang Lake, LBB method

1 Introduction

The Yangtze River, the world's third-longest and the longest river in Asia, is China's "Mother River". It represents not only a symbol of biodiversity but also serves as the principal cradle of freshwater fisheries in China. At its peak, the river annually yielded around 450,000 tons of fish, accounting for 60% of China's freshwater fish production (Chen, 2003). In recent decades, the biological integrity index of the Yangtze River Basin declined sharply, reaching its lowest level and indicating a state of "no fish" due to overfishing, pollution, and large-scale water infrastructure development (Zhang et al., 2020; Chen et al., 2020; Dong et al., 2023). In December 2019, China's Ministry of Agriculture and Rural Affairs announced a comprehensive ten-year fishing ban, effective January 1, 2021. This ban prohibits any commercial fishing of natural aquatic resources in the Yangtze River and its connected water bodies, including Poyang Lake, Dongting Lake, and others tributaries (Mei et al., 2020; Ma et al., 2022).

Poyang Lake is the largest freshwater lake in China and one of the only two major natural lakes hydrologically connected to the Yangtze River, characterized by complex hydrology, rich biodiversity and abundant water resources. It functions as a critical ecological nexus, maintaining fishery resources across the entire Yangtze River Basin. The lake's fish species account for about 17% of China's freshwater fish and 45.4% of those in the Yangtze River system (Liu et al., 1999). In addition to sustaining numerous native species, it serves as a crucial spawning, feeding, and nursery ground for many commercially valuable and threatened migratory fish species, including but not limited to *Acipenser sinensis*, *C. nasus*, and *Anguilla japonica* (Jiang et al., 2013).

Coilia nasus, an anadromous migratory fish species, is primarily distributed around Japan and the Korean Peninsula, and in China, it inhabits the East China Sea, Bohai Sea, and Yellow Sea, as well as in the middle and lower reaches of rivers and lakes connected to the marine areas. This species typically reaches sexual maturity at approximately age one. Recognized as a critically important migratory species and economically valuable flagship fish in the Yangtze River basin, it is known as one of the "Three Delicacies of the Yangtze River" along with *Tenualosa reevesii* and *Takifugu*

obscurus. Each year, *C. nasus* migrates upstream from the East China Sea in mid-April, passing through the Yangtze River estuary into Poyang Lake, with the number of migrating individuals reaching a peak in late June (Kong et al., 2024). From the late 1950s to the early 1970s, the catches of *C. nasus* in the Yangtze River increased steadily (Yuan, 1988), peaking at approximately 4,142 tons in 1973 (Dai et al., 2020). However, by the 1980s, the average annual catch had declined to approximately 2,904 tons. It plummeted to 673 tons between 2001 and 2005, and continuously reduced to less than 30 tons in 2002 (Zhen et al., 2012; Jiang et al., 2014, 2016; Zhu et al., 2017; Shi et al., 2009). From 2010 to 2013, the average catch further decreased to 116.6 tons, an 86.40% reduction from the 1990s and a 95.98% decline from the 1970s (Xu et al., 2016). Concurrently, the *C. nasus* population demonstrated a significant demographic shift toward younger age classes and smaller body size (Jiang et al., 2017; Zhu et al., 2017) and was subsequently listed as an endangered species by the IUCN (Hata, 2018). The dominant age of spawners, which previously was 2–3 years old in the 1970s, had shifted to 1–2 years by 2018 (Luo et al., 2021). To curb the trend, the Chinese government ceased issuing special fishing license for *C. nasus* on February 1, 2019. Consequently, the effectiveness of these policies and the stock recovery of *C. nasus* should be appropriately evaluated to guide subsequent conservation efforts in the Yangtze River Basin.

Scientific and accurate assessments provide a critical foundation for developing effective fisheries management policies. Since many of the fishery resources around the world lack sufficient data, such as age, life-history parameters and so on, it is challenging to evaluate them using conventional assessment methods. Over the past decade, stock assessment models specifically designed for data-limited conditions have attracted significant attention worldwide. Simultaneously, advancements in computational modeling techniques and interdisciplinary collaboration have significantly accelerated research progress in this area (Shi et al., 2020; Geng et al., 2018; Shi et al., 2021). Currently, two primary methods are commonly applied to assess the resource status with limited data. The first is the Maximum Sustainable Yield (MSY) model, which estimates the highest sustainable yield using catch data and supplementary information (Ju et al., 2020b; Liang et al., 2020; Zhai et al., 2020). The other utilizes length-frequency analysis

(Liang et al., 2020). Representative length-based approaches include the traditional Electronic Length Frequency Analysis (ELEFAN) and its updated versions based on stochastic optimization algorithms, such as ELEFAN-GA (genetic algorithm) and ELEFAN-SA (simulated annealing), which are implemented in the TropFishR package in R. These updated versions offer improved flexibility and accuracy in estimating growth parameters, particularly under data-limited conditions. In addition to ELEFAN, the Length-Based Spawning Potential Ratio (LBSPR) model is also widely applied in length-based assessments. This method estimates spawning potential and fishing mortality based on life-history traits and length-frequency data, and is particularly useful for evaluating the sustainability of exploited fish populations (Froese et al., 2018). Furthermore, we employed the Length-Based Bayesian Biomass (LBB) model, which integrates length-frequency data with Bayesian Markov Chain Monte Carlo (MCMC) algorithms to estimate critical stock parameters including L_{inf} (asymptotic Length), L_{mean}/L_{opt} (mean length to optimal length ratio), $L_c/L_{c_{opt}}$ (length at first capture to optimal length ratio), L_{95th}/L_{inf} (95th percentile length to asymptotic length ratio), F/M (fishing mortality to natural mortality ratio), F/K (fishing mortality to growth coefficient ratio), Z/K (total mortality to growth coefficient ratio), B/B_0 (current biomass to virgin biomass ratio), and B/B_{msy} (current Biomass to biomass at maximum sustainable yield ratio). Compared to the MSY model, length-frequency methods require only representative length-frequency data from the target stock to effectively assess biological parameters and stock status. This approach provides a strong foundation for sustainable fisheries development and effective fisheries management (Liang et al., 2020; Ju et al., 2020a). Therefore,

fisheries managers can directly employ the LBB method to assess fish stocks, even with limited data.

This study investigated the stock status of *C. nasus* in the Yangtze River-Poyang Lake waterway and adjacent waters from 2019 to 2024, covering periods before and after the fishing ban. Updated length-based methods, including ELEFAN (via TropFishR), LBSPR, and LBB, were applied to estimate key biological parameters and assess the current fisheries exploitation status, with the objective of comprehensively analyzing the stock recovery of *C. nasus* following implementation of the fishing ban. This research aims to contribute empirical evidence for the sustainable utilization and scientific management of *C. nasus* resources, while simultaneously establishing baseline datasets for longitudinal monitoring and quantitative assessment of fisheries policies implemented within the framework of the ten-year fishing ban in the Yangtze River Basin.

2 Materials and methods

2.1 Survey area

This study focused on the Jiangxi section of the Yangtze River and Poyang Lake, which constitute a critical region for the spawning migration of *C. nasus* (Figure 1). The middle and lower reaches of the Yangtze River are characterized by flat terrain and broad river channels, with an average flow velocity of 1 – 3 m/s, resulting in generally stable and slow water flow. These hydrological characteristics provide a relatively stable environment for diadromous *C. nasus*. Poyang Lake (28°22'–29°45'N, 115°49'–116°

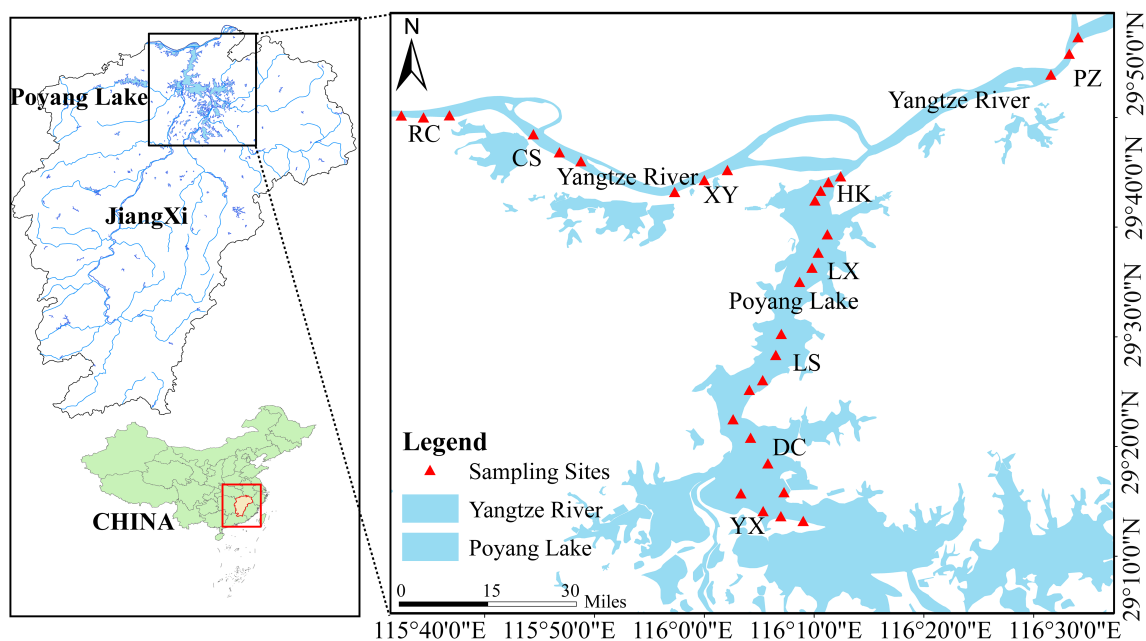


FIGURE 1

Survey sites for *C. nasus* (2019 – 2024) in the Yangtze River-Poyang Lake waterway and adjacent waters. Ruichang (RC), Chaisang (CS), Xunyang (XY), Pengze (PZ), Hukou (HK), Lianxi (LX), Lushan (LS), Duchang (DC), and Yongxiu (YX).

46°E) has a subtropical monsoon climate, featuring distinct seasons, abundant rainfall, an average annual temperature of 16–18°C, and annual precipitation between 1,000 and 1,400 mm (Cao et al., 2022). As China's largest freshwater lake, it supports well-developed lake and wetland ecosystems, with a highly indented shoreline, interlaced channels, and abundant aquatic vegetation. These ecological conditions foster high biodiversity and provide abundant nutritional resources for aquatic species. During the spawning season, *C. nasus* migrates to spawning grounds such as Hukou (HK), Lushan (LS), Duchang (DC), and Yongxiu (YX) in Poyang Lake and its connecting waterways to the Yangtze River (Jiang et al., 2013; Lu, 2015).

2.2 Material sources

The specific investigation of *C. nasus* were conducted annually during the spawning season (March to July) and foraging season (September to November) at multiple sites along the Jiangxi section of the Yangtze River and the northern part of Poyang Lake from 2019 to 2024 (Figure 1). Sampling sites were selected based on historic sampling data of *C. nasus* (Jiang et al., 2013, 2017), and remained consistent throughout the study period. Customized three-layer gillnets with multiple mesh sizes (2.0 cm, 6.0 cm, 10.0 cm, and 14.0 cm) were employed for sampling. Each net measured 50 m in length and 2 m in height, with four nets connected sequentially to form a 200 m sampling unit. Two sets of such gillnets were deployed daily at 18:00 at each sampling transect and retrieved the following morning at 6:00, and this procedure was repeated for five consecutive days. For each captured specimen of *C. nasus*, body length and body weight were measured to the nearest 1 mm and 0.1 g, respectively. Additionally, 10–20 scales were carefully extracted from the region below the dorsal fin and above the lateral line for age determination, then preserved in scale envelopes with complete specimen identification information. Due to certain special circumstances, the monitoring frequency in 2022 was reduced, resulting in a decrease in the total number of samples collected.

2.3 Research methods

2.3.1 Age identification

The scales of *C. nasus* were immersed in warm water to remove residual mucus and other impurities. Six to eight intact scales with their corresponding identification label were positioned between two glass slides. Then they were sealed with transparent adhesive tape and stored in a dry environment for subsequent analysis. The age was determined by the annuli present on the scales according to Luo et al. (2021). When the number of annuli was n and the outermost annulus extended to the scale margin, the age was recorded as n . If an incomplete annulus was visible beyond the outermost complete annulus, the age was recorded as n^+ . Scales without fully formed annuli were recorded as 0^+ . Consequently,

individual with 0^+ -1 annulus was read as age 1, those with 1^+ -2 annuli as age 2, and so forth.

2.3.2 Body length-weight relationship

SPSS 19.0 was used to perform a Pearson correlation analysis between body length and body weight. Upon finding a significant correlation ($P < 0.05$), the length-weight relationship was then fitted using the Keys equation (Keys, 1928), as given in Equation 1:

$$W = aL^b \quad (1)$$

where W represents body weight (g), L represents body length (mm), a is the condition factor, and b is the power exponent.

To further determine whether the estimated b values significantly deviated from the theoretical isometric value of 3, a one-sample t-test was performed for each year. When the difference was not significant ($P > 0.05$), growth was considered isometric; otherwise, positive ($b > 3$) or negative ($b < 3$) allometric growth was inferred.

2.3.3 Electronic length-frequency analysis

Electronic Length Frequency Analysis (ELEFAN) is a widely used approach for estimating von Bertalanffy Growth Function (VBGF) parameters from length-frequency data (Mildenberger et al., 2017). In this study, restructured length-frequency data of *C. nasus* were fitted to the VBGF using two stochastic optimization routines available in the TropFishR R package: ELEFAN-GA (based on a genetic algorithm) and ELEFAN-SA (based on simulated annealing).

The samples were grouped by body length with a 10 mm interval for length-frequency analysis. The growth relationship was fitted using the von Bertalanffy growth equation, as given in Equation 2 (von Bertalanffy, 1938):

$$L_t = Linf[1 - e^{-K(t-t_0)}] \quad (2)$$

where L_t represents the body length at age t , $Linf$ is the asymptotic length, K is the growth coefficient, t is the age, and t_0 is the theoretical age at zero length.

Among candidate parameter sets, the optimal combination was identified based on the goodness-of-fit score. R_n , as given in Equation 3 (Pauly, 1985):

$$R_n = \frac{ESP}{ASP} \quad (3)$$

where ESP is the ratio of explainable peaks, ASP is the ratio of available peaks, and R_{nmax} is the best fit.

The natural mortality coefficient (M) was estimated using Pauly's empirical formula (Pauly, 1980):

$$\lg M = -0.0066 - 0.279 \lg Linf + 0.6434 \lg K + 0.4634 \lg T \quad (4)$$

where M is the natural mortality coefficient, $Linf$ is the asymptotic length (mm), K is the growth coefficient from the von Bertalanffy growth equation, and T is the average annual water temperature (°C) in the species' habitat. In this study, the temperature of Poyang Lake was set as 18°C (Wu et al., 2015).

2.3.4 Length-based Bayesian biomass method

The LBB model is a straightforward and efficient approach that employs length-frequency data and a Markov Chain Monte Carlo (MCMC) procedure to estimate the status of fish stocks (Froese et al., 2018). The LBB method is suitable for species that exhibit continuous growth throughout their lifespan, such as most commercial fish and invertebrates, and requires only length-frequency data for assessments (Pons et al., 2020). It enables estimation of key stock parameters, including asymptotic length (L_{inf}), optimal length at first capture (L_{c_opt}), relative natural mortality (M/K), relative fishing mortality (F/K), and stock status indicators such as relative current biomass (B/B_0) and biomass at maximum sustainable yield (B/B_{msy}).

In this study, only the principal equations are presented; comprehensive methodological details are described in (Froese et al., 2018).

In LBB, it is assumed that fish growth follows the von Bertalanffy growth equation, as given in Equation 5 (von Bertalanffy, 1938):

$$L_t = L_{inf}[1 - e^{-K(t-t_0)}] \quad (5)$$

where L_t represents the body length at age t , L_{inf} is the asymptotic length, K is the growth coefficient, t is the age, and t_0 is the theoretical age at zero length.

If the fishing gear is completely selective, the catch on the body length curve is a function of the total mortality related to K . The equation of this curve is as follows:

$$N_L = N_{Lstart} \left(\frac{L_{inf}-L}{L_{inf}-Lstart} \right)^{Z/K} \quad (6)$$

where N_L is the number of survivors to length L , N_{Lstart} is the number at length $Lstart$ with full selection, i.e., from which all individuals entering the gear are retained by the gear, and Z/K is the ratio of the total mortality rate Z to K .

In addition to the parameters in Equation 6, the catch affected by partial selection is the selectivity function of fishing gear. The gear selectivity can be expressed by the following Equation 7:

$$S_L = \frac{1}{1+e^{-\alpha(L-L_c)}} \quad (7)$$

where S_L is the fraction of individuals that are retained by the gear at length L , L_c is the first capture body length, and α represents the steepness of the ogive (Quinn and Deriso, 1999).

The parameters of the selection ogive are estimated at the same time as L_{inf} , L_c , α , M/K , and F/K by fitting the relationships given in Equations 8, 9:

$$N_{L_i} = N_{L_{i-1}} S_{L_i} F \left(\frac{L_{inf}-L_i}{L_{inf}-L_{i-1}} \right)^{\frac{M}{K} + \frac{F}{K} S_{L_i}} \quad (8)$$

$$C_{L_i} = N_{L_i} S_{L_i} \quad (9)$$

where N_{L_i} and $N_{L_{i-1}}$ are the numbers of individuals in length class L_i and the previous length class L_{i-1} , respectively. C_{L_i} is the number of individuals vulnerable to the gear in length class L_i . To minimize the parameter requirements of this expand method, the

ratios M/K and F/M are output, instead of the absolute values of F , M , and K ; note that $F/M = (F/M)/(M/K)$.

The Bayesian Gibbs sampler JAGS with R statistical language (version 4.4.2) was used to fit the observed proportions-at-length to their expected values, as given in Equation 10:

$$\hat{p}_{L_i} = \frac{\hat{N}_{L_i}}{\sum \hat{N}_{L_i}} \quad (10)$$

where p_{L_i} is the observed proportions-at-length, \hat{p}_{L_i} is the mean values for p_{L_i} , \hat{N}_{L_i} denotes the mean values for N_{L_i} , which has been mentioned in Equation 8.

By substituting L_{inf} , M/K , and F/K into Equations 11, 12, the optimal length L_{opt} for unexploited generations with maximum biomass, and the optimal catch length L_{c_opt} were obtained:

$$L_{opt} = L_{inf} \left(\frac{3}{3+\frac{M}{K}} \right) \quad (11)$$

$$L_{c_opt} = \frac{L_{inf} \left(\frac{2+3\frac{F}{M}}{1+\frac{F}{M}} \right)}{\left(\frac{3+\frac{M}{K}}{1+\frac{F}{M}} \right)} \quad (12)$$

Relative yield-per-recruit Y'/R can be computed by the following equation:

$$\begin{aligned} \frac{Y'}{R} = \frac{F/M}{1+F/M} (1-Lc/L_{inf})^{M/K} & \left[1 - \frac{3(1-Lc/L_{inf})}{1+1/(M/K+F/M)} \right. \\ & \left. + \frac{3(1-Lc/L_{inf})^2}{1+2/(M/K+F/M)} - \frac{(1-Lc/L_{inf})^3}{1+3/(M/K+F/M)} \right] \end{aligned} \quad (13)$$

Assuming catch per unit effort proportional to biomass, Equation 13 divided by F/M gives the following Equation 14:

$$\begin{aligned} \frac{CPUE'}{R} = \frac{\frac{Y'}{R}}{\frac{F}{M}} = \frac{1}{1+F/M} (1-Lc/L_{inf})^{M/K} & \left[1 - \frac{3(1-Lc/L_{inf})}{1+1/(M/K+F/M)} \right. \\ & + \frac{3(1-Lc/L_{inf})^2}{1+2/(M/K+F/M)} \\ & \left. - \frac{(1-Lc/L_{inf})^3}{1+3/(M/K+F/M)} \right] \end{aligned} \quad (14)$$

Relative biomass of fish ($> L_c$) when $F = 0$ is given by Equation 15:

$$\begin{aligned} \frac{B'_0 > L_c}{R} = (1-Lc/L_{inf})^{M/K} & \left[1 - \frac{3(1-Lc/L_{inf})}{1+\frac{1}{M/K}} \right. \\ & \left. + \frac{3(1-Lc/L_{inf})^2}{1+\frac{2}{M/K}} - \frac{(1-Lc/L_{inf})^3}{1+\frac{3}{M/K}} \right] \end{aligned} \quad (15)$$

where $B'_0 > L_c$ denotes the exploitable fraction ($> L_c$) of the unfished biomass B_0 .

The ratio of fished to unfished biomass is described as:

$$\frac{B}{B_0} = \frac{\frac{CPUE'}{R}}{\frac{B'_0 > L_c}{R}} \quad (16)$$

and a proxy for the relative biomass producing B_{msy}/B_0 (the biomass at MSY) was obtained by re-running Equations 13–16 with $F/M = 1$ and $L_c = L_{c_opt}$.

An $F/M > 1$ indicates that the stock is overfished, while $B/B_0 < 1$ suggests that current biomass is below the unfished level. In particular, $B/B_0 < 0.5$ indicates critically low biomass, reflecting a severely depleted stock. If both L_{mean}/L_{opt} and L_c/L_{c_opt} are less than 1, it indicates that the length structure is truncated due to fishing pressure, with mortality concentrated on smaller individuals. When the 95th percentile length relative to asymptotic length (L_{95th}/L_{inf}) approaches 1 (> 0.9), it suggests the presence of large individuals in the stock. Stock status can be evaluated based on B/B_{msy} estimates, as shown in Table 1 (Froese et al., 2018; Palomares et al., 2018; Ju et al., 2020a; Liang et al., 2020; Wang et al., 2021, 2020). The relative biomass and length at first capture estimated using the LBB model can be directly applied to manage data-limited stocks (Wang et al., 2020). If B/B_0 is less than B_{msy}/B_0 ($B_0/B_{msy} < 1$), fishing effort should be reduced. If the mean length at capture (L_c) is less than the optimal length at first capture (L_{c_opt}), fishing should target larger individuals.

When using the LBB method for stock assessment, it is necessary to set prior values for key parameters, such as asymptotic length (L_{inf}) and the ratio of natural mortality to growth coefficient (M/K). If prior information is unavailable for the species under assessment, the model applies default priors, with M/K typically set to 1.5 (Froese et al., 2018). Alternatively, prior estimates for parameters such as L_{inf} and M/K can be derived from existing literature or independent studies, when available, and integrated into the model. In this study, L_{inf} and M/K values estimated using updated ELEFAN algorithms were used in the LBB model to minimize uncertainty.

LBB estimation was implemented in the Bayesian Gibbs sampler software JAGS (Plummer, 2003) and executed using R. The code (R-code: LBB_20.R) can be downloaded from the website (<http://oceanrep.geomar.de/44832/>, accessed on 22 February 2025).

To evaluate the robustness of model outputs under parameter uncertainty, a sensitivity analysis was conducted by varying L_{inf} and M/K values using the 2024 dataset. Detailed results are provided in the Supplementary Materials.

2.3.5 Estimation of spawning potential ratio using LBSPR

The Length-Based Spawning Potential Ratio (LBSPR) model is a data-limited stock assessment approach that estimates reproductive potential under fishing pressure using life-history parameters and length-frequency data, assuming logistic selectivity (Hordyk et al., 2015).

In this study, LBSPR was applied to independently evaluate the reproductive status of the *C. nasus* stock. Required inputs included the asymptotic length (L_{inf}), the ratio of natural mortality to growth (M/K), and the lengths at 50% and 95% maturity (L_{50} , L_{95}). Length-frequency data were binned at 10 mm intervals, and the model was implemented using the LBSPR R package.

The model estimated the spawning potential ratio (SPR), which was interpreted using a four-tier threshold system adapted from

TABLE 1 The definition of the stock status based on the B/B_{msy} .

B/ B_{msy}	F/M	Stock status
≥ 1	≤ 1	Healthy stock
0.5–1.0	≤ 1	Recovering stock
< 0.5	≤ 1	Stock outside of safe biological limits
0.5–1.0	> 1	Fully/overfished stock
0.2–0.5	> 1	Stock outside of safe biological limits
< 0.2	> 1	Severely depleted stock

previous studies (Prince et al., 2015; Hordyk et al., 2014; Richard et al., 2022). According to this framework, an SPR of ≤ 0.2 indicates critically low reproductive potential and a stock at risk of collapse. Values between 0.2 and 0.35 suggest a fully exploited population, while those between 0.35 and 0.4 indicate that the stock is operating near the maximum sustainable yield (MSY). When SPR exceeds 0.4, the stock is considered to maintain a sustainable reproductive capacity.

3 Results

3.1 Statistical results

3.1.1 The distribution of age, body length, and weight

A total of 5,844 *C. nasus* specimens were collected between 2019 and 2024, with annual sample sizes of 338, 1,165, 1,023, 389, 1,623, and 1,306, respectively. Age data could not be obtained due to the absence of scale samples in 2019 and 2022. Analysis of available samples from 2020 – 2021 and 2023 – 2024 indicated that the *C. nasus* population comprised individuals ranging from 1 to 4 years of age. In 2020, two-year-old individuals dominated, accounting for 55.8% of the sampled stock. However, from 2021 to 2024, the dominant age group shifted to three-year-old individuals, representing 76.9%, 65.8%, and 55.7% of annual samples, respectively. The proportion of four-year-old individuals gradually increased, rising from 3.2% in 2020, 7.7% in 2021, 16.2% in 2023 to 17.2% in 2024 (Table 2). These findings suggest that the fishing ban policy effectively mitigated the trend of younger, promoting a more stable and balanced age structure in the *C. nasus* stock.

Among the total of 5,844 specimens from 2019 to 2024, specimen sizes varied considerably, with body lengths ranging from 75 mm to 412 mm and weights ranging from 6.8 g to 239.0 g. Both body length and weight of *C. nasus* showed a clear increasing trend. The dominant size group gradually shifted toward longer and heavier individuals, and the overall size distribution expanded over time (Figure 2). The average body length exhibited a significant increasing trend from 2019 (271.20 ± 38.44 mm) to 2024 (305.53 ± 37.99 mm) ($P < 0.05$). Similarly, the average body weight significantly increased, ranging from 56.08 ± 25.56 g in 2020 to 88.02 ± 32.01 g in 2024 ($P < 0.05$). The dominant size group shifted from 250 – 260 mm, 50 – 60 g to 330 – 340 mm, 120 – 130 g (Table 3).

TABLE 2 Age distribution of *C. nasus* (2019 - 2024) in the Yangtze River-Poyang Lake waterway and adjacent waters.

Age class	2019	2020	2021	2022	2023	2024	Total
1-year	–	0 (0%)	0 (0%)	–	3 (2.7%)	8 (3.6%)	11
2-year	–	86 (55.8%)	8 (15.4%)	–	17 (15.3%)	52 (23.5%)	163
3-year	–	63 (41.0%)	40 (76.9%)	–	73 (65.8%)	123 (55.7%)	299
4-year	–	5 (3.2%)	4 (7.7%)	–	18 (16.2%)	38 (17.2%)	65

3.1.2 Body length and weight relationship

To investigate interannual variations in the length-weight relationship of *C. nasus* from 2019 to 2024, a power function model ($W = aL^b$) was fitted to each year's data, and variations in the model parameters were analyzed. The results indicated that the growth exponent b ranged from 2.918 to 3.431 during this period. Statistical tests against the isometric value ($b = 3$) revealed that b was not significantly different from 3 in 2019, 2022, and 2024 ($P > 0.05$), indicating isometric growth, whereas b was significantly greater than 3 in 2020, 2021, and 2023 ($P < 0.001$), indicating positive allometric growth. All models exhibited high correlation coefficients ($R^2 > 0.912$), indicating reliable and robust fits (Figure 3).

3.2 Model evaluation

3.2.1 Parameters estimated based on ELEFAN

According to the length-frequency data of *C. nasus*, the bin width was set to 10 mm, and a moving average filter of 5 classes was applied. Both ELEFAN-GA and ELEFAN-SA algorithms were implemented for growth parameter estimation. The ELEFAN-GA routine yielded a better fitting score ($R_{max} = 0.292$) and was thus selected for downstream analysis (Figure 4). The results showed that the L_{inf} was 45.33 cm and K was 0.23. Based on Equation 4 the natural mortality rate M was estimated to be 0.50. These values were then used as priors in the LBB model.

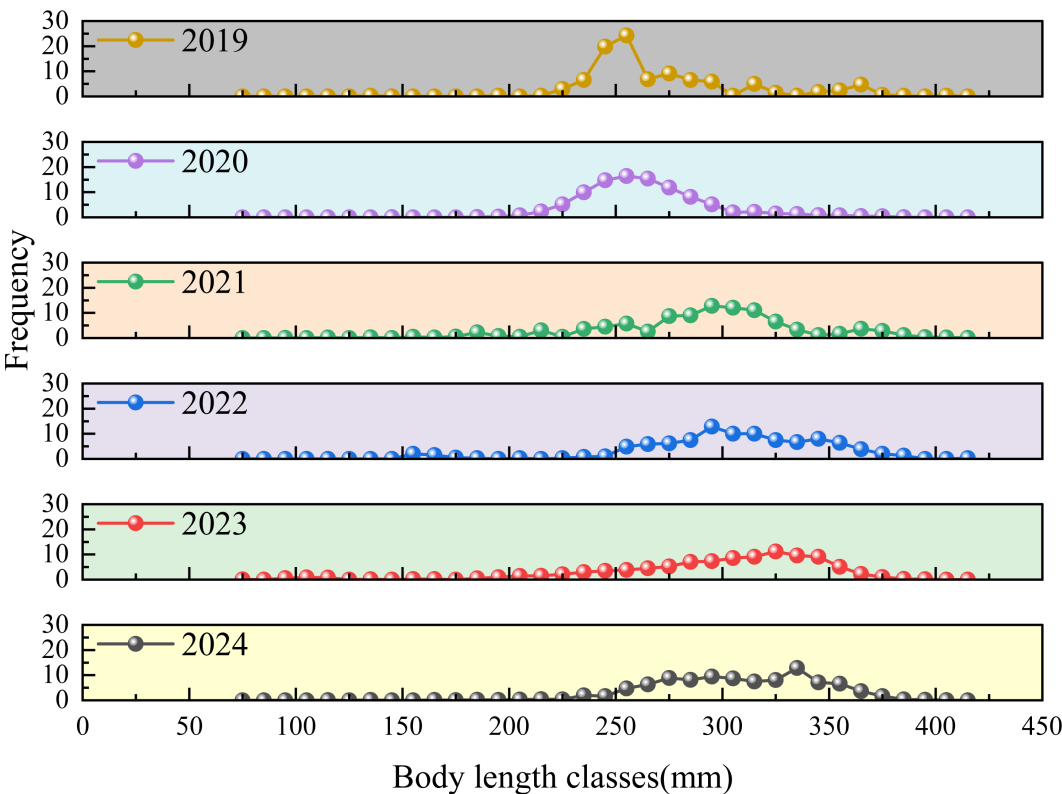


FIGURE 2 Body length classes distribution of *C. nasus* (70 – 420 mm in 10 mm intervals) from 2019 to 2024 in the Yangtze River-Poyang Lake waterway and adjacent waters. Scatter balls represent annual frequency distributions.

TABLE 3 Composition of body length and weight of *C. nasus* (2019 - 2024) in the Yangtze River-Poyang Lake waterway and adjacent waters.

Year	Individual number	Body length range (mm)	Body weight range (g)	Average body length (mm)	Average body weight (g)	Dominant length group (mm) and percentage (%)	Dominant weight group (g) and percentage (%)
2019	338	135-400	20.20-220.0	271.20 ± 38.44 ^d	68.52 ± 33.26 ^c	250-260 (24.26%)	50-60 (24.26%)
2020	1165	147-382	12.9-198.2	262.99 ± 29.76 ^e	56.08 ± 25.56 ^d	250-260 (16.39%)	40-50 (23.69%)
2021	1023	95-412	8.0-230.0	290.03 ± 46.80 ^c	79.65 ± 37.79 ^b	290-300 (12.81%)	70-80 (15.05%)
2022	389	150-410	13.3-232.8	301.79 ± 45.40 ^{ab}	86.36 ± 34.69 ^a	290-300 (12.85%)	70-80 (13.88%)
2023	1623	75-399	6.8-227.9	296.87 ± 51.62 ^b	86.50 ± 37.24 ^a	320-330 (11.21%)	90-100 (12.28%)
2024	1306	115-403	14.4-239.0	305.53 ± 37.99 ^a	88.02 ± 32.01 ^a	330-340 (12.86%)	120-130 (13.02%)

Different letters marked on the numbers indicate significant differences ($P < 0.05$).

3.2.2 Parameters estimated based on LBB

By integrating $L_{inf} = 45.38$ cm and $M/K = 2.17$ (obtained from ELEFAN-GA) as priors into LBB, a comprehensive assessment of the *C. nasus* stock from 2019 to 2024 was conducted. Key estimated parameters included L_{inf} , L_{mean}/L_{opt} , $L_c/L_{c_{opt}}$, L_{95th}/L_{inf} , F/M , F/K , Z/K , B/B_0 , and B/B_{msy} , which collectively enable quantitative assessment of the stock status and evaluation of the effectiveness of implemented conservation measures. The results indicated that L_{inf} of *C. nasus* ranged between 39.9 cm and 46.4 cm. Overall, the observed decreasing trends in F/M , F/K , and Z/K suggest a continuous decline in fishing pressure. In 2019 and 2020, both L_{mean}/L_{opt} and $L_c/L_{c_{opt}}$ ratios were below 1, indicating a truncated length structure

characterized by a predominance of smaller individuals. However, from 2021 to 2024, these ratios increased to 1.2 - 1.3 and 1.2 - 1.5, respectively, reflecting a significant rise in the proportion of larger individuals in the stock. Additionally, the L_{95th}/L_{inf} ratio approached 1 (> 0.9) in 2023, indicating the sustained presence of large individuals. The relative biomass (B/B_0) and biomass relative to MSY (B/B_{msy}) exhibited a consistent upward trend, signaling stock recovery (Table 4; Figure 5).

Figures 6, 7 present detailed results of the LBB model assessment for *C. nasus* from 2019 to 2024. The left panel show the length-frequency (L/F) distributions, while the right panels display the fitted results from the LBB master equation. The blue line represents the LBB

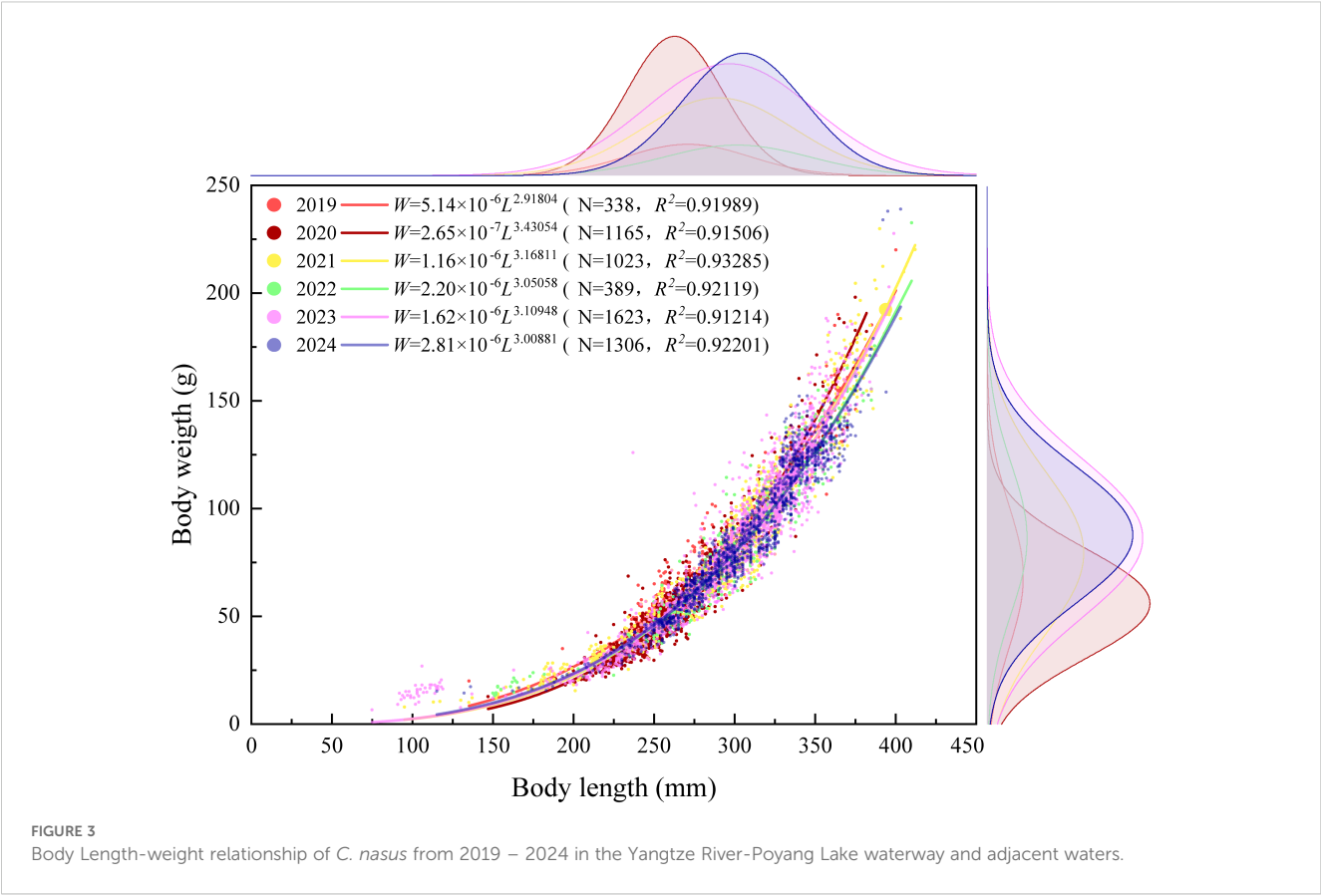


FIGURE 3 Body Length-weight relationship of *C. nasus* from 2019 – 2024 in the Yangtze River-Poyang Lake waterway and adjacent waters.

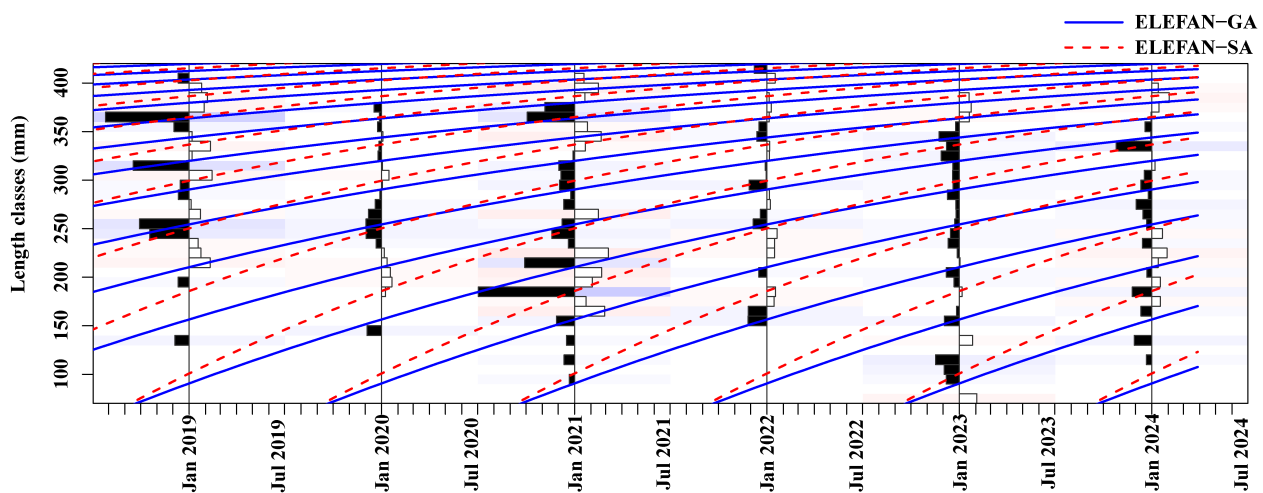


FIGURE 4

The VBGF fitted to the length frequency distribution of *C. nasus* from 2019 – 2024 using ELEFAN-GA and ELEFAN-SA in the Yangtze River-Poyang Lake waterway and adjacent waters.

TABLE 4 Summary of LBB results for *C. nasus* (2019 – 2024) in the Yangtze River-Poyang Lake waterway and adjacent waters.

Parameter	2019	2020	2021	2022	2023	2024
L_{inf}	44.4 (43.5 - 45.2)	46.4 (45.3 - 47.1)	44.5 (43.8 - 45.2)	39.9 (39.3 - 40.6)	43.9 (43.2 - 44.8)	42.9 (42.2 - 43.7)
L_{mean}/L_{opt}	1	0.99	1.2	1.2	1.3	1.3
L_c/L_{c_opt}	0.99	0.97	1.2	1.4	1.5	1.5
L_{95th}/L_{inf}	0.74	0.75	0.85	0.93	0.8	0.86
F/M	2.6 (2.29 - 2.9)	2 (1.71 - 2.3)	1.4 (1.11 - 1.73)	0.5 (0.26 - 0.86)	0.46 (0.17 - 0.9)	0.37 (0.18 - 0.54)
F/K	5.6 (5.14 - 5.98)	4.3 (3.89 - 4.8)	2.7 (2.26 - 3.22)	0.63 (0.35 - 1.04)	0.94 (0.35 - 1.82)	0.71 (0.35 - 0.97)
Z/K	7.69 (7.3 - 8.1)	6.54 (6.1 - 6.91)	4.61 (4.21 - 5.11)	1.89 (1.6 - 2.29)	2.99 (2.36 - 3.86)	2.61 (2.29 - 2.89)
B/B_0	0.17 (0.14 - 0.19)	0.2 (0.17 - 0.25)	0.34 (0.25 - 0.45)	0.62 (0.21 - 1.23)	0.64 (0.07 - 1.49)	0.68 (0.19 - 1.09)
B/B_{msy}	0.48 (0.41 - 0.56)	0.59 (0.48 - 0.72)	0.96 (0.72 - 1.29)	1.6 (0.57 - 3.28)	1.8 (0.2 - 4.28)	1.9 (0.53 - 3.11)
Stock status	Stock outside of safe biological limits	Fully/overfished stock	Fully/overfished stock	Healthy stock	Healthy stock	Healthy stock

The numbers between brackets stand for 95% confidence intervals for the parameter estimates provided.

model fit, while the red line indicates the stock status derived from the LBB model. Figure 6 illustrates LBB estimates for the years 2019 - 2021, with B/B_{msy} and F/M values ranging from 0.48 to 0.96 and 2.6 to 1.4, respectively. In contrast, Figure 7 shows LBB results for 2022 - 2024, with higher B/B_{msy} values (1.6 - 1.9) and lower F/M values (0.5 - 0.37). According to the stock status classification in Table 1, the status of the *C. nasus* stock was categorized as “outside of safe biological limits” in 2019, “fully/overfished” in 2020 and 2021, and that were “healthy” from 2022 to 2024 (Figure 8).

3.2.3 LBSPR-based stock assessment

The LBSPR model yielded annual spawning potential ratio (SPR) estimates for *C. nasus* from 2019 to 2024, showing a generally increasing trend with notable interannual variation (Figure 9). In 2019, the SPR was 0.28, corresponding to a fully

exploited stock condition ($0.2 < SPR \leq 0.35$). In 2020, SPR dropped sharply to 0.19, falling into the critical depletion zone ($SPR \leq 0.2$), suggesting a high risk of recruitment impairment.

From 2021 onwards, the stock exhibited clear signs of recovery. In 2021, the SPR rose to 0.39, indicating the stock was approaching the maximum sustainable yield (MSY) level ($0.35 < SPR < 0.4$). In 2022, SPR further increased to 0.43, crossing the threshold into the sustainably reproductive range ($SPR \geq 0.4$). This favorable status was largely maintained in 2023 ($SPR = 0.39$) and 2024 ($SPR = 0.42$), both years reflecting near or above MSY-level reproductive capacity.

These findings suggest that while the stock of *C. nasus* experienced substantial overexploitation before the fishing ban, particularly in 2020, its reproductive potential has significantly improved during the post-ban period, indicating effective early-stage stock rebuilding.

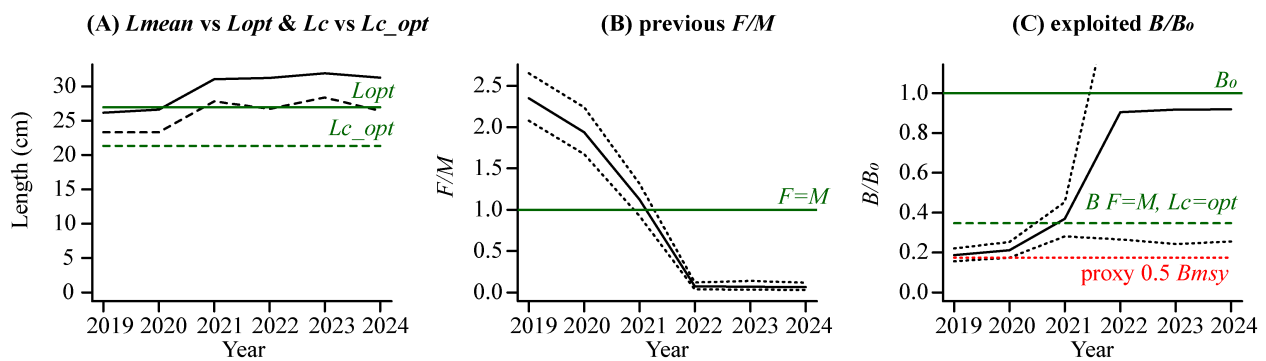


FIGURE 5

Continuous estimation results of *C. nasus* (2019 - 2024) in the Yangtze River-Poyang Lake waterway and adjacent waters using the LBB method. (A) L_{mean} (bold black curve) relative to L_{opt} , and L_c (dashed black curve) relative to L_{c_opt} . (B) Relative fishing pressure F/M (black curve), with approximate 95% confidence limits (dotted curves), with indication of the reference level where $F = M$ (green horizontal line). (C) Relative biomass B/B_0 (black curve) with approximate 95% confidence limits (dotted black curves), with indication of a proxy for B_{msy} (green dashed line) and a proxy for B_{pa} or $0.5 B_{msy}$ (red dotted line).

4 Discussion

4.1 Factors affecting fish stock structure and assessment methods

Stock structure is a key indicator reflecting the status of fish resources, influenced by multiple factors, among which fishing intensity is considered one of the most direct and significant factors affecting the stock structure of commercial fish species (Gwinn et al., 2015). Overfishing typically leads to the selective removal of large individuals, resulting in a younger age structure of the stock and a decrease in average body length and weight (Tu et al., 2018). Berkeley et al. (2004) demonstrated that fish populations under intense fishing pressure often exhibit “a truncated age structure”, characterized by the near-complete disappearance of large, older individuals. For example, studies on fish in the middle and lower reaches of the Yangtze River by Jiang et al. (2017) and Zhu et al. (2017) revealed that overfishing has led to earlier sexual maturation for major economic fish species such as *C. nasus*, with spawning populations dominated by younger individuals, thereby significantly reducing the reproductive potential of the stock. Conversely, healthy populations maintain a complete age structure, including a sufficient proportion of large, older individuals (Hixon et al., 2014), which typically exhibit higher fecundity, better egg quality, and higher offspring survival rates, factors crucial for stock recruitment and stability (Barneche et al., 2018). From the perspective of resource assessment indicators, the relative biomass (B/B_0) of a healthy stock must typically exceed 0.4, and the biomass ratio relative to maximum sustainable yield (B/B_{msy}) should exceed 1.0 (Froese et al., 2018). In addition to fishing pressures, environmental conditions such as hydrological regimes, temperature changes, and habitat quality also significantly impact stock structure (Reid et al., 2019), particularly for migratory fish like *C. nasus*, where hydraulic engineering and altered hydrological regimes influence their migration and reproductive activities (Jiang et al., 2017). Moreover, pollution, climate change, and invasive species have also been demonstrated to alter the age structure and spatial distribution of fish populations (Zhang et al., 2020).

The assessment of fish stock structure primarily includes age-based methods and length-based methods. Traditional age-based assessments determine individual age through hard tissues such as fish scales and otoliths, thereby establishing age-length relationships, which, despite their accuracy, are time-consuming and require large sample sizes (Campana, 2001). In contrast, length-based methods such as the Electronic Length Frequency Analysis (ELEFAN), Length-Based Spawning Potential Ratio model (LBSPR), and Length-Based Bayesian Biomass method (LBB) rely solely on length-frequency data, making them particularly suitable for data-limited situations (Froese et al., 2018; Liang et al., 2020). For migratory, relatively short-lived small fish species like *C. nasus*, length-based assessment methods offer substantial advantages (Wang et al., 2021). First, during resource monitoring, length data are typically more accessible than age data. Second, a strong correlation exists between length and age for fast-growing fish like *C. nasus*. Additionally, these methods can provide reliable estimates of stock parameters under data-limited conditions. Pons et al. (2020) established through simulation studies that the LBB method performs excellently in assessing the status of migratory fish resources, particularly when evaluating the effects of protection measures such as fishing bans. Therefore, this study innovatively integrated the ELEFAN, LBSPR, and LBB approaches. The asymptotic length (L_{inf}) and the ratio of natural mortality to growth coefficient (M/K) estimated from ELEFAN-GA were used as prior information for both the LBSPR and LBB models, effectively reducing parameter uncertainty and improving the robustness of the assessments (Liang et al., 2020). This multi-model framework provides strong technical support for monitoring the effectiveness of the Yangtze River fishing ban.

4.2 Impact of fishing ban on *C. nasus* stock structure and its recovery mechanism

Through systematic monitoring from 2019 to 2024, this study identified significant changes in the stock structure of *C. nasus* before and after the fishing ban, which were characterized by

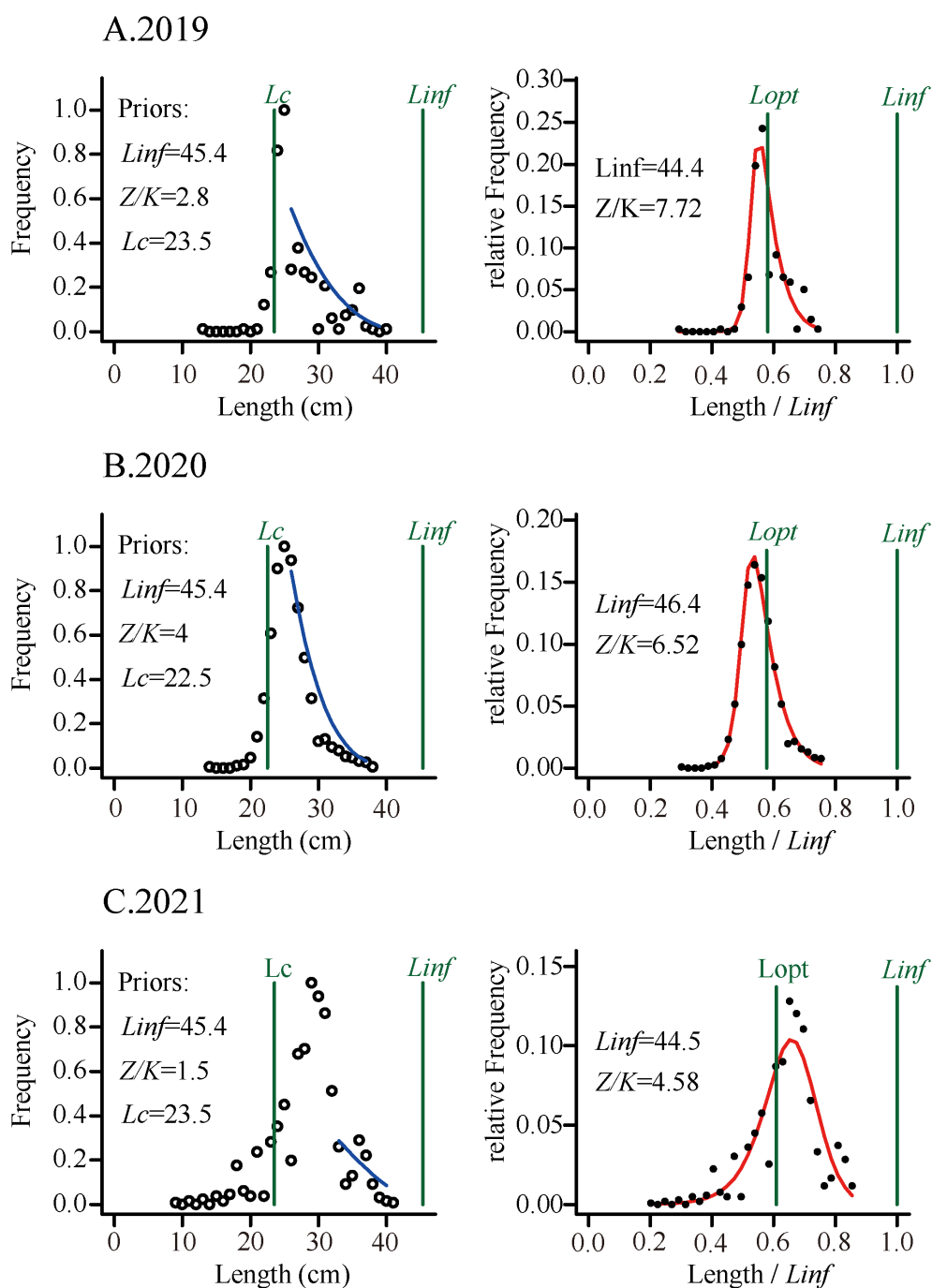


FIGURE 6

LBB estimation results for *C. nasus* (2019–2021; A–C) in the Yangtze River-Poyang Lake waterway and adjacent waters before the fishing ban. Left panels show length-frequency (L/F) data from which priors are estimated for Lc , $Linf$, and Z/K . Right panels (red curves) show the fit of the LBB master equation, which provides estimates of Z/K , M/K , F/K , Lc , and $Linf$. From $Linf$ and M/K , $Lopt$ is calculated and shown as a reference.

optimized age structure, increased individual size, and improved resource status. The proportion of four-year-old individuals increased from 3.2% in 2020 to 17.2% in 2024, representing more than a five-fold increase. The main spawning population shifted from being dominated by 1~2-year-old individuals (55.8%) to being dominated by 2~3-year-old individuals, constituting over 80% of the population. Mean body length significantly increased from 271.20 ± 38.44 mm in 2019 to 305.53 ± 37.99 mm in 2024 ($P <$

0.05), while mean body weight similarly increased from 68.52 ± 33.26 g to 88.02 ± 32.01 g ($P < 0.05$). The dominant length group shifted from 250–260 mm before the fishing ban in 2019 to 330–340 mm after implementation in 2024. Most notably, resource assessment indicators exhibited substantial improvement, with relative biomass (B/B_0) increasing from 0.14 in 2019 to 0.72 in 2024, and the biomass ratio relative to maximum sustainable yield (B/B_{msy}) rising from 0.4 to 2.0, transitioning the resource status

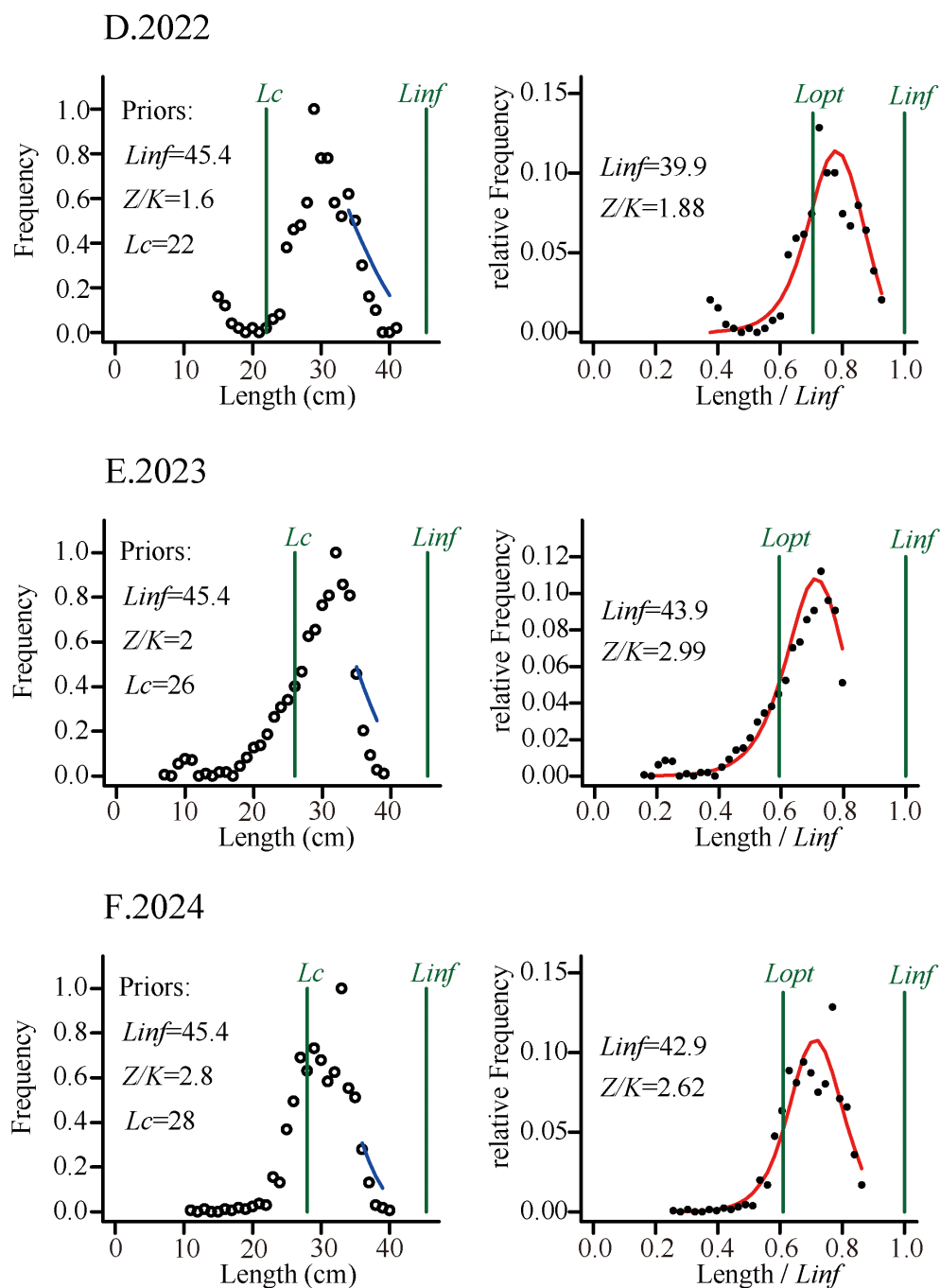


FIGURE 7

LBB estimation results for *C. nasus* (2022–2024; D–F) in the Yangtze River-Poyang Lake waterway and adjacent waters after the fishing ban. The definitions of the indicators are the same as those in Figure 6.

from “outside of safe biological limits” to “healthy”, demonstrating that the fishing ban policy was highly effective in promoting the stock recovery of the *C. nasus*. To further support the observed improvements in stock structure, the spawning potential ratio (SPR) estimated by the LBSPR model increased from 0.19 in 2020 to 0.42 in 2024, surpassing the commonly accepted sustainability threshold (SPR = 0.4). The continuous improvement in body size from year to year suggests that enhanced habitat conditions following the fishing ban have enabled individuals to achieve their growth potential,

which in turn has contributed to stock recovery. This independent model-based evidence confirms the enhancement of reproductive capacity and reinforces the effectiveness of the fishing ban in promoting the recovery of *C. nasus* stock. Further analysis incorporating environmental factors and potential sampling variations is necessary to fully understand these fluctuations.

These positive changes are primarily attributed to the substantial reduction in fishing pressure, which provided fish with extended growth cycles. The fishing ban reduced fishing mortality

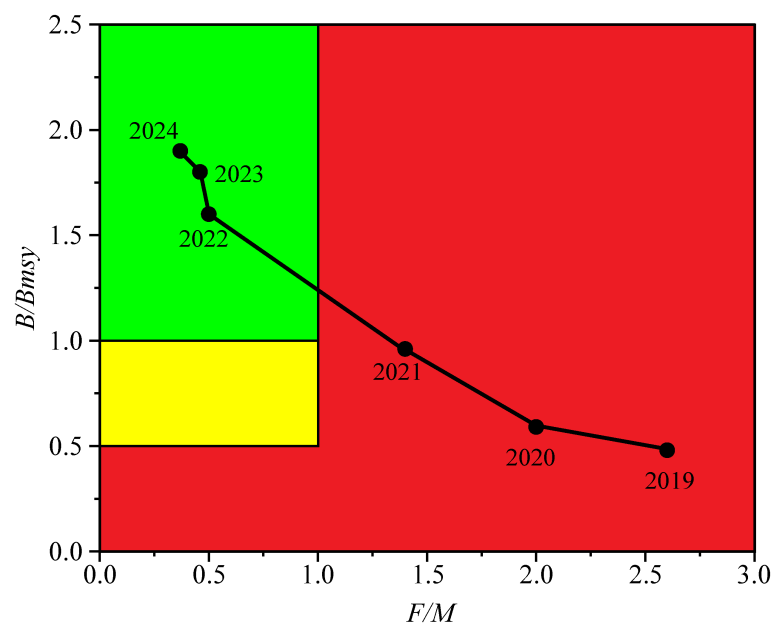


FIGURE 8

Trajectories of fishing pressure (F/M) and stock status (B/B_{msy}) for *C. nasus* (2019 - 2024) in the waterway Poyang Lake to Yangtze River and adjacent waters, China. Red area: stocks that are being overfished or are outside of safe biological limits; yellow area: recovering stocks; green area: stocks subject to sustainable fishing pressure and of a healthy stock biomass that can produce high yields close to MSY.

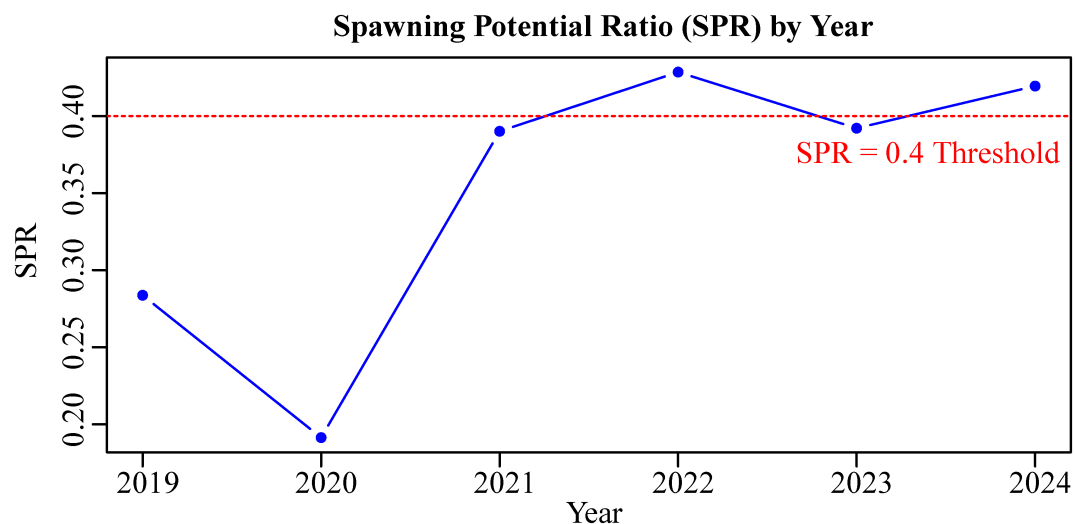


FIGURE 9

Annual variation in the spawning potential ratio (SPR) of *C. nasus* from 2019 to 2024 in the waterway Poyang Lake to Yangtze River and adjacent waters, China, estimated using the LBSPR model.

(F/M) from 3.0 in 2019 to 0.31 in 2024, directly extending individual lifespans and enabling more individuals to survive to large, older stages (Gwinn et al., 2015). The data suggest that stock recovery follows a predictable pattern: first the improvement of age structure, followed by an increase in biomass (Russ and Alcalá, 2010). Our research reveals that the age structure of *C. nasus* began to improve in the first two years after the fishing ban (2021 - 2022), while significant biomass increase emerged in the third year (2023), a pattern consistent with the findings of Sala and Giakoumi (2018)

regarding the temporal sequence of fish recovery in protected areas. Enhancement in the structure of the reproductive population constitutes another factor promoting stock recovery, as larger, older female individuals not only possess higher fecundity but also yield better offspring quality and higher survival rates (Barneche et al., 2018). This improvement, coupled with an L_{95th}/L_{inf} value approaching 0.9 indicating a significantly increased proportion of large individuals, collectively enhances the population's recruitment capacity (Froese et al., 2018).

Research by [Jaco and Steele \(2020\)](#) indicates that after reduced fishing pressure, improvements in reproductive population structure can significantly enhance population recruitment capacity within 3 – 4 years, which may explain the substantial increase in B/B_0 and B/B_{msy} observed three years after the fishing ban.

It is noteworthy that the impact of the fishing ban on the *C. nasus* stock may also involve changes in food web relationships. The fishing ban simultaneously protected the natural predators of *C. nasus*, which theoretically could increase predation pressure ([Baskett and Barnett, 2015](#)). However, [Babcock et al. \(2010\)](#) found that during the initial stages of protection measures (3 – 5 years), direct effects (target species recovery) typically precede and exceed indirect effects (changes in food web relationships) in magnitude. Our results corroborate this finding: despite the possible increase in natural predators, the *C. nasus* stock still achieved significant recovery, indicating that the positive effects of reduced fishing pressure outweighed the potential increase in predation pressure in the short term. Additionally, improved environmental conditions further facilitated stock recovery, as the implementation of the fishing ban policy was accompanied by strengthened pollution control and habitat protection measures ([Chen et al. \(2020\)](#)), with the continuous improvement of water quality in the middle and lower reaches of the Yangtze River benefiting the reproduction and growth of *C. nasus*. However, [Cooke et al. \(2021\)](#) noted that in the short term (3 – 5 years), the contribution of environmental improvements to fish population recovery typically remains subordinate to that of reduced fishing pressure, and the recovery rate observed in this study supports this view, indicating that reduced fishing pressure constitutes the dominant factor in the improvement of *C. nasus* stock structure at the current stage. By integrating changes in multiple indicators, this study demonstrates that the significant reduction in fishing pressure resulting from the fishing ban represents the main driving force for the improvement of *C. nasus* stock structure. The substantial reduction in fishing mortality has allowed more individuals to complete their natural growth cycle and establish a healthier, more balanced population structure. These findings have important implications for assessing the ecological benefits of the Yangtze River fishing ban policy and informing management of other fish resources.

4.3 Significance of *C. nasus* recovery as an ecological indicator for evaluating the Yangtze River Fishing Ban

[Dong et al. \(2023\)](#) emphasized that changes in Yangtze River fishery resources provide significant insights for global freshwater ecosystem management. As a keystone species in the Yangtze River Basin, the stock status of *C. nasus* serves as a crucial indicator for evaluating the health of the Yangtze River ecosystem and the effectiveness of fishery management ([Jiang et al., 2022](#)). The recovery of this migratory fish species spanning freshwater and

brackish environments reflects the overall improvement of river-lake-estuary multi-ecosystem complexes ([Jiang et al., 2016](#)). *C. nasus* migrates through river channels from the Yangtze River into Poyang Lake for spawning ([Jiang et al., 2017](#)), and its population condition also indicates the ecological status of lake-river connectivity systems. More importantly, as a critical component in the Yangtze River's ecological chain, the optimization of *C. nasus* stock structure and increased resource abundance may promote ecosystem balance and stability through cascade effects. Recent ecological studies further demonstrate that the recovery of keystone species can positively influence the structure and function of entire ecosystems ([Chen et al. \(2020\)](#)). Therefore, the recovery of *C. nasus* stock directly reflects the implementation effectiveness of the fishing ban policy.

From a broader perspective, the recovery data of *C. nasus* highlights the multifaceted ecological value of the Yangtze River fishing ban policy. These data confirm that large-scale freshwater ecosystem conservation measures can effectively promote the recovery of severely declined populations, providing reference for global freshwater protection efforts ([Reid et al., 2019](#)). Furthermore, the recovery rate of *C. nasus* can also serve as a benchmark for predicting the recovery potential of other fish species, particularly for long-lived, late-maturing species such as the Chinese sturgeon, which require extended protection periods. Given the complexity and diversity of the Yangtze River ecosystem, different species may respond differently to the fishing ban policy ([Zhang et al., 2020](#)), therefore the recovery of *C. nasus* represents only one aspect of the Yangtze River ecosystem restoration. Future research should be extended to other species and broader ecological indicators to comprehensively assess the ecological effects of the Yangtze River fishing ban. Based on the results of this study, we recommend that future work should include: (1) maintaining fishing ban measures, particularly for species that have shown positive recovery but have not yet reached optimal levels; (2) developing specialized monitoring systems for migratory fish species to regularly assess stock recovery status; (3) strengthening the protection of critical spawning grounds and feeding areas such as Poyang Lake; (4) establishing an ecosystem-based fishery management system following the conclusion of the fishing ban period to ensure sustainable resource utilization.

5 Conclusion

This study systematically evaluated the impact of the fishing ban policy on the resource recovery of *C. nasus* in the Yangtze River-Poyang Lake waterway and adjacent waters by using the LBB method from 2019 to 2024. The results demonstrate that the age structure of *C. nasus* has significantly improved and stabilized, with the proportion of four-year-old individuals increasing from 3.2% in 2019 to 17.2% in 2024. Relative biomass (B/B_0) exhibited a substantial increase from 0.17 to 0.68, and the ratio of biomass to maximum sustainable yield (B/B_{msy}) rose from 0.48 to 1.9, signaling a transition from the “edge of collapse” to a “healthy” stock status. These trends were independently corroborated by the LBSPR model,

which showed the spawning potential ratio (SPR) increased from 0.19 to 0.42 during the same period, surpassing the sustainability threshold (SPR = 0.4). Collectively, these findings confirm that the fishing ban policy effectively reversed stock decline through the synergistic effects of reduced fishing pressure (F/M reduced from 2.6 to 0.37) and improved habitat carrying capacity, highlighting the feasibility of coordinated human intervention and natural resilience. Based on these findings, it is recommended that the current fishing ban policy be maintained and a specialized monitoring system for migratory species be established, with particular emphasis on reproductive stock dynamics. Furthermore, a resilient, adaptive management framework should be developed to ensure sustainable resource recovery.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author/s.

Ethics statement

All procedures involving animals were approved by the Animal Ethics Committee of Jiujiang Academy of Agricultural Sciences and Shanghai Ocean University, and conducted in accordance with institutional and national guidelines. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

YL: Conceptualization, Methodology, Software, Visualization, Writing – original draft. QX: Formal analysis, Investigation, Resources, Writing – review & editing. SW: Data curation, Investigation, Resources, Writing – review & editing. ZL: Data curation, Validation, Visualization, Writing – review & editing. CK: Investigation, Resources, Writing – review & editing. LP: Resources, Writing – review & editing. BZ: Resources, Writing – review & editing. BB: Methodology, Validation, Writing – review & editing. LL: Funding acquisition, Methodology, Resources, Writing – review & editing. XG: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing.

References

- Babcock, R. C., Shears, N. T., Alcala, A. C., Barrett, N. S., Edgar, G. J., Lafferty, K. D., et al. (2010). Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *PNAS* 107, 18256–18261. doi: 10.1073/pnas.0908012107
- Barneche, D. R., Robertson, D. R., White, C. R., and Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science* 360, 642–645. doi: 10.1126/science.aao6868
- Baskett, M. L., and Barnett, L. A. K. (2015). The ecological and evolutionary consequences of marine reserves. *Annu. Rev. Ecol. Syst.* 46, 49–73. doi: 10.1146/annurev-ecolsys-112414-054424
- Berkeley, S. A., Hixon, M. A., Larson, R. J., and Love, M. S. (2004). Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29, 23–32. doi: 10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2

Funding

The author(s) declare financial support was received for the research and/or publication of this article. This research was supported by the Special Funding for the Survey and Monitoring System of Aquatic Biological Resources in Jiangxi Province (No. JXSSJC-2024-03), An Important Habitat Survey Project of *Coilia nasus* in Key Water Areas of Jiangxi Province (NY2022-C0901), the Science.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer RK declared a shared affiliation with the author(s) YL, ZL, BB and XG to the handling editor at the time of review.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2025.1638854/full#supplementary-material>

- Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.* 59, 197–242. doi: 10.1111/j.1095-8649.2001.tb00127.x
- Cao, Y. X., Xu, L. G., Fan, H. X., Mao, Z. Y., Cheng, J. X., Wang, D. C., et al. (2022). Impact of climate change and human activities on the changes of ecological flow indicators in the Lake Poyang Basin since 1960s. *J. Lake Sci.* 34, 232–246. doi: 10.18307/2022.0119
- Chen, D. Q. (2003). Current status and conservation strategies for fishery resources in the Yangtze River. *J. Fish. Sci. China.*, 17–34. doi: 10.3969/j.issn.1002-6681.2003.03.013
- Chen, T. G., Wang, Y., Gardner, C., and Wu, F. (2020). Threats and protection policies of the aquatic biodiversity in the Yangtze River. *J. Nat. Conserv.* 58, 125931. doi: 10.1016/j.jnc.2020.125931
- Cooke, S. J., Twardek, W. M., Lynch, A. J., Cowx, I. G., Olden, J. D., Funge-Smith, S., et al. (2021). A global perspective on the influence of the COVID - 19 pandemic on freshwater fish biodiversity. *Biol. Conserv.* 253, 108932. doi: 10.1016/j.biocon.2020.108932
- Dai, P., Yan, Y., Zhu, X. Y., Tian, J. L., Ma, F. J., and Liu, K. (2020). Status of *Coilia nasus* resources in the national Aquatic germplasm resources conservation area in the Anqing section of the Yangtze River. *J. Fish. Sci. China.* 27, 1267–1276. doi: 10.3724/SP.J.1118.2020.20130
- Dong, F., Fang, D. D., Zhang, H., and Wei, Q. W. (2023). Protection and development after the ten-year fishing ban in Yangtze River. *J. Fish. Sci. China.* 47, 245–259. doi: 10.11964/jfc.20221013724
- Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A. C., Dimarchopoulou, D., et al. (2018). A new approach for estimating stock status from length frequency data. *ICES J. Mar. Sci.* 75, 2004–2015. doi: 10.1093/icesjms/fsy078
- Geng, Z., Zhu, J. F., Xia, M., and Li, Y. N. (2018). Research progress in fishery stock assessment using data-poor/limited methods. *Trans. Oceanol. Limnol.*, 130–137.
- Gwinn, D. C., Allen, M. S., Johnston, F. D., Brown, P., Todd, C. R., and Arlinghaus, R. (2015). Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. *Fish Fish.* 16, 259–281. doi: 10.1111/faf.12053
- Hata, H. (2018). *Coilia nasus*: The IUCN red list of threatened species 2018. Gland, Switzerland: IUCN. doi: 10.2305/iucn.uk.2018-2.rlts.t98895427a143840780.en
- Hixon, M. A., Johnson, D. W., and Sogard, S. M. (2014). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* 71, 2171–2185. doi: 10.1093/icesjms/fst235
- Hordyk, A., Ono, K., Sainsbury, K., Loneragan, N., and Prince, J. (2015). Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio. *ICES J. Mar. Sci.* 72, 204–216. doi: 10.1093/icesjms/fst235
- Hordyk, A., Ono, K., Valencia, S., Loneragan, N., and Prince, J. (2014). A novel length-based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. *ICES J. Mar. Sci.* 72, 217–231. doi: 10.1093/icesjms/fst004
- Jaco, E. M., and Steele, M. A. (2020). Pre-closure fishing pressure predicts effects of marine protected areas. *J. Appl. Ecol.* 57, 229–240. doi: 10.1111/1365-2666.13541
- Jiang, T., Liu, H. B., Lu, M. J., Chen, T. T., and Yang, J. (2016). A possible connectivity among Estuarine tapertail anchovy (*Coilia nasus*) populations in the Yangtze River, Yellow Sea, and Poyang Lake. *Estuaries Coasts.* 39, 1762–1768. doi: 10.1007/s12237-016-0107-z
- Jiang, T., Liu, H. B., Shen, X. Q., Shimasaki, Y. H., Ohshima, Y. J., and Yang, J. (2014). Life history variations among different populations of *Coilia nasus* along the Chinese coast inferred from otolith microchemistry. *J. Fac. Agric. Kyushu Univ.* 59, 383–389. doi: 10.5109/1467650
- Jiang, T., Yang, J., Lu, M. J., Liu, H. B., Chen, T. T., and Gao, Y. W. (2017). Discovery of a spawning area for anadromous *Coilia nasus* Temminck et Schlegel 1846 in Poyang Lake, China. *J. Appl. Ichthyol.* 33, 189–192. doi: 10.1111/jai.13293
- Jiang, T., Yang, J., Xuan, Z. Y., Chen, X. B., and Liu, H. B. (2022). Preliminary report on the effects of resource recovery on anadromous *Coilia nasus* in Poyang Lake under the national 10-Year fishing ban. *Prog. Fish. Sci.* 43, 24–30. doi: 10.19663/j.issn2095-9869.20210119001
- Jiang, T., Zhou, X. Q., Liu, H. B., Liu, H. Z., and Yang, J. (2013). Two microchemistry patterns in otoliths of *Coilia nasus* from Poyang Lake, China. *J. Fish. China.* 37, 239–244. doi: 10.3724/SP.J.1231.2013.38138
- Ju, P. L., Chen, M. R., Tian, Y. J., Zhao, Y., Yang, S. Y., and Xiao, J. M. (2020a). Stock status estimating of 5 shark species in the waters around Taiwan using a length-based bayesian biomass estimation (LBB) method. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00632
- Ju, P. L., Tian, Y. J., Chen, M. R., Yang, S. Y., Liu, Y., Xing, Q. W., et al. (2020b). Evaluating stock status of 16 commercial fish species in the coastal and offshore waters of Taiwan using the CMSY and BSM methods. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00618
- Keys, A. B. (1928). The weight-length relation in fishes. *Proc. Natl. Acad. Sci. U.S.A.* 14, 922–925. doi: 10.1073/pnas.14.12.922
- Kong, C. P., Xu, Q., Huang, P., Xu, Q., Zhang, B., Gao, X., et al. (2024). Reproductive biological characteristics of the knifefish (*Coilia nasus*) in Poyang Lake. *Jiangxi Fish. Sci. Technol.*, 55–60. doi: 10.3969/j.issn.1006-3188.2024.04.013
- Liang, C., Xian, W. W., Liu, S. D., and Pauly, D. (2020). Assessments of 14 exploited fish and invertebrate stocks in Chinese waters using the LBB method. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00314
- Liu, S. P., Chen, D. Q., Qiu, S. L., and Huang, M. G. (1999). Three gorges project and dynamic monitoring of Yangtze River fishery resources. *Reserv. Fish.*, 51–54.
- Lu, M. J. (2015). *Studies on otolith morphometry and microchemistry of Coilia nasus collected from the Poyang Lake* (Shanghai: Shanghai Ocean University).
- Luo, Y. T., Dai, P., Liu, S. L., Ma, F. J., You, Y., and Liu, K. (2021). Age structure and growth characteristics of *Coilia nasus* in Anqing section of Yangtze River during fishing season in 2018. *J. Guangdong Ocean Univ.* 41, 36–43. doi: 10.3969/j.issn.1673-9159.2021.03.005
- Ma, F. J., Yang, Y. P., Fang, D. A., Ying, C. P., Xu, P., Liu, K., et al. (2022). Characteristics of *Coilia nasus* resources after fishing ban in the Yangtze River. *Acta Hydrobiol. Sin.* 46, 1580–1590. doi: 10.1016/j.marenvres.2021.105388
- Mei, Z. G., Cheng, P. L., Wang, K. X., Wei, Q. W., Barlow, J., and Wang, D. (2020). A first step for the Yangtze. *Science* 367, 1314–1314. doi: 10.1126/science.abb5537
- Mildenberger, T. K., Marc Hollis, T., and Wolff, M. (2017). TropFishR: an R package for fisheries analysis with length-frequency data. *Methods Ecol. Evol.* 8, 1520–1527. doi: 10.1111/2041-210x.12791
- Palomares, M. L. D., Froese, R., Derrick, B., Noël, S.-L., Tsui, G., Woroniak, J., et al. (2018). *A preliminary global assessment of the status of exploited marine fish and invertebrate populations*. Available online at: <https://api.semanticscholar.org/CorpusID:145910563> (Accessed February 21, 2025)
- Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES J. Mar. Sci.* 39, 175–192. doi: 10.1093/icesjms/39.2.175
- Pauly, D. (1985). On improving operation and use of the elefan programs. Part 1, avoiding “drift” of K towards low values. *Fishbyte* 3, 13–14.
- Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. Available online at: <https://api.semanticscholar.org/CorpusID:265976949> (Accessed February 24, 2025)
- Pons, M., Cope, J. M., and Kell, L. T. (2020). Comparing performance of catch-based and length-based stock assessment methods in data-limited fisheries. *Can. J. Fish. Aquat. Sci.* 77, 1026–1037. doi: 10.1139/cjfas-2019-0276
- Prince, J., Victor, S., KloulChad, V., and Hordyk, A. (2015). Length based SPR assessment of eleven Indo-Pacific coral reef fish populations in Palau. *Fish. Res.* 171, 42–58. doi: 10.1016/j.fishres.2015.06.008
- Quinn, T. J., and Deriso, R. B. (1999). *Quantitative Fish Dynamics* (New York, NY: Oxford University Press). doi: 10.1093/oso/9780195076318.001.0001
- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., et al. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* 94, 849–873. doi: 10.1111/brv.12480
- Richard, K., Ousmane, S., Wu, F., and Tian, S. (2022). Length-Based assessment methods for the conservation of a pelagic shark, *Carcharhinus falciformis* from the Tropical Pacific Ocean. *Fishes* 7, 184. doi: 10.3390/fishes7040184
- Russ, G. R., and Alcala, A. C. (2010). Decadal-scale rebuilding of predator biomass in Philippine marine reserves. *Oecologia* 163, 1103–1106. doi: 10.1007/s00442-010-1692-3
- Sala, E., and Giakoumi, S. (2018). No-take marine reserves are the most effective protected areas in the ocean. *ICES J. Mar. Sci.* 75, 1166–1168. doi: 10.1093/icesjms/fsx059
- Shi, Y. C., Fan, W., Zhang, H., Zhou, W. F., Tang, F. H., Wu, Z. L., et al. (2021). Review on stock assessment methods applicable to data-limited fisheries. *J. Fish. Sci. China.* 28, 673–691. doi: 10.12264/jfsc.2020-0309
- Shi, D. F., Zhang, K., and Chen, Z. Z. (2020). Comparison of assessment methods utilizing life-history characteristics in data-limited fisheries. *J. Fish. Sci. China.* 27, 12–24. doi: 10.3724/SP.J.1118.2020.19238
- Shi, W. G., Zhang, M. Y., Liu, K., Xu, D. P., and Duan, J. R. (2009). Stress of hydraulic engineering on fisheries in the lower reaches of the Yangtze River and compensation. *J. Lake Sci.* 21, 10–20. doi: 10.3321/j.issn:1003-5427.2009.01.002
- Tu, C. Y., Chen, K. T., and Hsieh, C. H. (2018). Fishing and temperature effects on the size structure of exploited fish stocks. *Sci. Rep.* 8, 7132. doi: 10.1038/s41598-018-25403-x
- von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws II). *Hum. Biol.* 10, 181–213.
- Wang, Y. C., Liang, C., Xian, W. W., and Wang, Y. B. (2021). Using the LBB method for the assessments of seven fish stocks from the Yangtze Estuary and its adjacent waters. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.679299
- Wang, Y., Wang, Y., Liu, S., Liang, C., Zhang, H., and Xian, W. (2020). Stock assessment using LBB method for eight fish species from the Bohai and Yellow Seas. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00164
- Wu, B., Fang, C. L., Zhang, Y. P., Fu, P. F., Chen, W. J., Xiong, X. Y., et al. (2015). The Assessment of biological parameters and stock biomass of *Siniperca chuatsi* in the Poyang Lake. *Prog. Fish Fish Sci.*, 21–26. doi: 10.11758/ykxj.20150403
- Xu, P., Xu, C. G., Liu, K., and Yang, J. (2016). *The Germplasm Resources and Artificial Regeneration Techniques of Coilia nasus in the Yangtze River*. (Beijing: Science Press).
- Yuan, C. F. (1988). The changes and causes in resources and population composition of *Coilia nasus* in the middle and lower reaches of the Yangtze River. *Chin. J. Zool.*, 12–15. doi: 10.13859/j.cjz.1988.03.005

Zhai, L., Liang, C., and Pauly, D. (2020). Assessments of 16 exploited fish stocks in Chinese waters using the CMSY and BSM methods. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.483993

Zhang, H., Kang, M., Shen, L., Wu, J. M., Li, J. Y., Du, H., et al. (2020). Rapid change in Yangtze fisheries and its implications for global freshwater ecosystem management. *Fish Fish.* 21, 601–620. doi: 10.1111/faf.12449

Zhen, F., Guo, H. Y., Tang, W. Q., Li, H. H., Liu, D., and Liu, Z. Z. (2012). Age structure and growth characteristics of anadromous populations of *Coilia nasus* in the Yangtze River. *Chin. J. Zool.* 47, 24–31. doi: 10.13859/j.cjz.2012.05.003

Zhu, G. L., Wang, L. J., Tang, W. Q., Wang, X. M., and Wang, C. (2017). Identification of olfactory receptor genes in the Japanese grenadier anchovy *Coilia nasus*. *Genes Genom* 39, 521–532. doi: 10.1007/s13258-017-0517-8