



# Trends and mechanisms behind the invasion of *Coilia brachygnathus* (Actinopterygii, Engraulidae) in one of the world's largest reservoirs

Chuansong Liao · Jixin Yu · Jiacheng Wang · Sandra Bibiana Correa · Fei Xiong · Dongdong Zhai · Shaowen Ye · Jiashou Liu

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**Abstract** Shortjaw tapertail anchovy, *Coilia brachygnathus*, has invaded and expanded in the Three Gorges Reservoir (TGR) over the last few years. The population size and biological characteristics related to this invasion are poorly understood. To investigate its invasion mechanisms, we studied spatial and temporal changes in *C. brachygnathus* biomass and abundance and its reproductive traits and diet. Evidence of progressive directional invasion suggested that *C. brachygnathus* invaded the TGR from downstream in 2016. The TGR provided an initial blockage and later facilitated *C. brachygnathus* dispersal. In 2020 and 2021, *C. brachygnathus* accounted for 11.66%

and 16.06% of biomass and abundance, respectively, of the TGR fish community and both biomass and abundance decreased with distance to the dam. The fecundity in the TGR was higher than that in downstream native areas. Although their contributions to diet exhibited spatial differences, *C. brachygnathus* mainly consumed shrimps (*Exopalaemon modestus* and *Macrobrachium nipponensis*) and zooplankton in the TGR. Within a short period, *C. brachygnathus* has successfully colonized and expanded into the whole reservoir. Its fast maturity and high fecundity, coupled with the lentic habitats and abundant food availability, are probable key factors that explain its invasion. We propose that prevention measures to block the expansion of this species are urgently needed after the impoundment of cascaded reservoirs with navigation passages located upstream of the TGR.

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C. Liao · J. Wang · S. Ye · J. Liu (✉)  
State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, Hubei, People's Republic of China  
e-mail: jsliu@ihb.ac.cn

J. Yu · F. Xiong · D. Zhai  
School of Life Sciences, Jiangnan University, Wuhan 430058, Hubei, People's Republic of China

J. Wang  
University of Chinese Academy of Sciences, Beijing 100049, People's Republic of China

S. B. Correa  
Department of Wildlife, Fisheries, and Aquaculture, Mississippi State University, Mississippi State, Mississippi 39762, USA

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## Introduction

Currently, 58 713 large dams (i.e., height > 15 m or height of 5–15 m and impounding > 3 million m<sup>3</sup>) have been constructed in the world (ICOLD, 2019), and the concomitant river impoundment greatly influences local fish assemblage and biodiversity. Documented detrimental effects include declining migratory and rheophilic fish species (Sá-Oliveira et al.,

2015; Loures & Pompeu, 2019) and species invasions. In some cases, dams can hinder the spread rate of invasive aquatic species into new areas (e.g., Dana et al., 2011), but the dam-driven hydrological alterations can often facilitate fish invasion (Júlio Júnior et al., 2009; Casimiro et al., 2017). That is because flooding, impounding, and navigation- and fish passage devices associated with impoundment infrastructure can eliminate natural barriers to fish movement and facilitate the invasion of previously disconnected catchments (e.g., Cooper et al., 2021; Kerr et al., 2021).

Both biological and environmental factors can influence the success of an invasion process. Species traits such as the ability to tolerate novel conditions, superior competitive ability, and a plastic diet are essential contributors to invasion success (Pereira et al., 2015). Moreover, the generation of suitable habitat and food resources after the dam construction expedites invasion success (Liew et al., 2016). Even so, identifying the key species traits and the eco-evolutionary mechanism that determine the success of an invasive process is still challenging due to the complexity of ecological systems (Muniz et al., 2021).

The Three Gorges Reservoir (TGR) is one of the largest reservoirs in the world (Yang et al., 2012), which was created through three filling stages in 2003, 2006, and 2009, raising the water levels to 135 m, 156 m, and 175 m, respectively (Liao et al., 2018). Its impoundment severely transformed the main-channel riverine habitats of the upper Yangtze River, China, with concomitant effects on fish assemblages (Liao et al., 2018). Nowadays, there is an overall decline of lotic fishes (Gao et al., 2010; Liao et al., 2018), whereas long distance migratory fish species are highly endangered (e.g., *Acipenser sinensis* Gray 1835 (Acipenseridae), CR; IUCN, 2021) due to the double barriers imposed by the Three Gorges Dam and the Gezhouba Dam (Zhang et al., 2020). In terms of fish invasions, a few documented outbreaks occurred after approximately 2003 (i.e., icefish *Neosalanx taihuensis* Chen 1956 and *Protosalanx hyalocranius* (Abbott 1901) (Salangidae); Gong et al., 2009). By 2012, 23 non-previously reported fish species had been sampled by different investigations in TGR, and these species were mainly introduced through aquaculture activities. Still, only *Megalobrama amblycephala* Yih 1955 (Cyprinidae) and *N. taihuensis* established populations in the reservoir

(Ba & Chen, 2012). Between 2015 and 2017, five non-native species were collected in the reservoir, and the icefish (*N. taihuensis* and *P. hyalocranius*) accounted for 1.03%, while *Coilia brachygnathus* Kreyenberg & Pappenheim 1908 (Engraulidae) accounted for 0.15% of the total fish assemblage biomass (Liao et al., 2018). The population of *C. brachygnathus* unexpectedly exploded after ≈2016 and dispersed rapidly in the whole reservoir, yet its population status and invasion mechanisms in the TGR are still poorly understood.

*Coilia brachygnathus* (maximum standard length 354 mm; Qin et al., 2018) is native to the middle and lower Yangtze River basin, China and is widely distributed and an important fishing target therein (Whitehead et al., 1988; Wang et al., 2016; Qin et al., 2018). In these areas, *C. brachygnathus* is also significant prey for other larger carnivorous fishes and the Yangtze finless porpoise *Neophocaena phocaenoides* (G. Cuvier 1829) (Phocaeidae). *Coilia brachygnathus* exclusively inhabit freshwaters and is a sister taxon to a sympatric freshwater-tolerant anchovy, *C. nasus* Temminck & Schlegel 1846 (Whitehead et al., 1988). The species was first described from the Dongting Lake of the Yangtze River Basin (Kreyenberg & Pappenheim, 1908), which is about 420-km downstream of the Three Gorges Dam. The genetic distance of *C. brachygnathus* between the native Dongting Lake and the novel TGR populations is close, suggesting that the TGR population is likely derived from the downstream Dongting Lake population (Yang, 2019). *Coilia brachygnathus* has a broad diet, including zooplankton, shrimp, and small fish (Zhang et al., 2013), and has a relatively high fecundity (Luo, 2006; Liu, 2008; Wang, 2016), high growth rate (Liu, 2008; Qin et al., 2018), and early mature age (one year; Luo, 2006; Wang, 2016) in native habitats. These biological traits are similar to those of the two invasive icefish species in the TGR, indicating that these population attributes are likely related to invasion success. Understanding the invasion process and population characteristics of *C. brachygnathus* in the TGR is essential from a fisheries management perspective, particularly in response to recent management actions. For instance, it is uncertain whether this species will invade the upstream portion of the reservoir after the creation of a reservoir cascade upstream of the TGR (Cheng et al., 2015) and how will the size of the novel population change following

a ten-year fishing ban of the Yangtze River native population (Zhou et al., 2020).

This study used *C. brachygnathus* as a model system to investigate fish invasion mechanisms in the TGR. Specifically, we investigated spatial (i.e., lower, middle, and upper sections) and temporal variations (i.e., 2005–2021) in the relative abundance and biomass of *C. brachygnathus* in the TGR. We also studied several biological traits that may explain its invasion success, including body size, sex ratio, maturity size, fecundity, and diet. Our study aimed to (1) summarize processes and trends of the invasion of *C. brachygnathus* based on its current and past abundance; (2) assess the diet of *C. brachygnathus* in the TGR based on stomach contents and stable isotopes analyses; (3) compare the body size and fecundity of the *C. brachygnathus* population in the TGR with those of native populations; and (4) discuss possible implications for the management of invasive fish species in large reservoirs.

## Methods and materials

### Sampling sites

Seasonal sampling was conducted at five mainstem sites (Zigui, Wushan, Yunyang, Zhongxian, and Banan) and four secondary tributary sites (Qinggan River, Xiangxi River, Yuanshui River, Pengxi River) along the TGR (Fig. 1), during the spring (April 2020, April 2021), summer (July 2020), autumn (October 2020), and winter (January 2021) seasons. These nine sampling sites cover the lower, middle, and upper sections of the TGR (Table 1), representing current lentic, transitional, and lotic habitats. We also seasonally measured water transparency (with a Secchi disk) and water quality parameters, including pH, temperature, dissolved oxygen, and specific conductivity (with a YSI Pro Plus multi-parameter water quality analyzer) (Table 1).

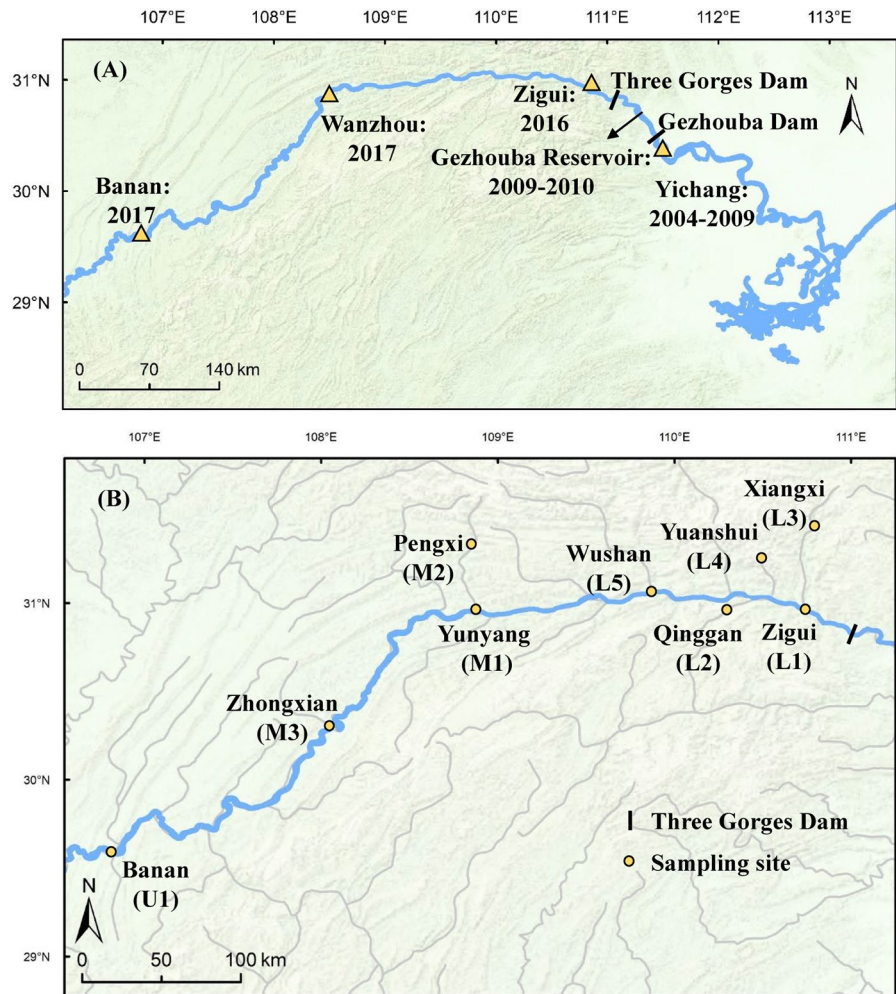
### Fish sampling and data collection

We sampled fishes in benthic and pelagic habitats using experimental multi-panel gillnets. Benthic and

pelagic gillnets have different heights (2 and 5 m, respectively) but the same length and mesh size structures. The total length of each gillnet was 30 m and consisted of 12 panels (2.5 m each) of different mesh sizes (10, 16, 20, 25, 31, 39, 48, 58, 70, 86, 110, 125 mm, knot-to-knot). We randomly selected three locations ( $\approx 500$  m apart) at each sampling site described above and deployed three benthic gillnets and three pelagic gillnets for 12 h (18:00–19:00 to 6:00–7:00) per location. To increase our sample size, we repeated our sampling the next day at each sampling site per season, amounting to an effort of 3780 m<sup>2</sup>-over 24 h (1890 m<sup>2</sup>·12 h in one day) of gillnets per season. To shed light on the temporal variations in the abundance of *C. brachygnathus*, we compared the present relative biomass with historical data (2005–2006, 2013–2014, and 2015–2017). Specifically, we retrieved relative biomass data of *C. brachygnathus* in 2005–2006 and 2013–2014 from published literatures (Wu et al., 2007; Lian, 2016). Data for 2015–2017 were obtained from our past surveys of fish assemblages in the upper (Banan), middle (Wanzhou), and lower sections (Zigui) of the TGR, using gillnets and trawl nets (Liao et al., 2018).

In the present study, all fishes collected were identified to species, and we randomly chose a subset of individuals and measured their total length (TL), standard length (SL), and body weight (BW) to 0.1 mm, 0.1 mm, and 0.01 g, precision, respectively. We dissected a sub-sample of *C. brachygnathus* to characterize reproductive traits, including size at first maturity ( $N=192$ ; April 2020, July 2020, and April 2021) and diet (April 2021). For each specimen, we identified its sex by visual inspection of the gonads, recorded reproductive stage (in a scale from I to VI, where stage I-immature stage, stage II-quiescent stage, stage III-ripening stage, stage IV-ripeness stage, stage V-reproduction stage, stage VI-spent stage; West, 1990, Yin, 1995) and weighed the eviscerated body to the nearest 0.01 g. For mature female individuals (Stage IV–V), we sampled about 0.1 g of mature ovaries from each ovary lobe's anterior, middle, and posterior sections and then weighed ( $W_{\text{egg}}$ ) and preserved the ovaries in a 10% formalin solution. We counted the number of eggs per sub-sample under a light microscope (Leica S8APO), measured the length ( $D_L$ ) and width ( $D_W$ ) of eggs, and calculated egg diameter ( $D_M$ ) from the mean  $D_L$  and  $D_W$  values. We removed and preserved the entire stomach

**Fig. 1** Map of detected sites and times of *C. brachygnathus* at the upper reach of the Yangtze River (A), and the current sampling sites in the mainstem and secondary tributaries of the Three Gorges Reservoir, located in the upper reach of the Yangtze River, China (B). For site codes, capital letter L represents the lower section, M represents the middle section, and U represents the upper section



in a 10% formalin solution for further dietary analysis. Food contents were removed from stomachs in the laboratory and identified to the lowest taxonomic level possible using a dissecting microscope. We weighed each food type to the nearest 0.01 g. We randomly sampled three to five fish individuals per sampling site and collected muscle samples to analyze stable isotope ratios of C ( $\delta^{13}\text{C}$ ) and N ( $\delta^{15}\text{N}$ ). Based on the results of stomach content analyses, we also sampled potential food resources for isotope analyses, including zooplankton and two shrimp species (*Exopalaemon modestus* (Heller, 1862) and *Macrobrachium nipponensis* (De Haan, 1849)). Tissue samples were analyzed by the Analyses and Testing Center, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China. For some individuals with C:N ratio higher than 3.5, we corrected their  $\delta^{13}\text{C}$

signature to remove the influence of lipids (Skinner et al., 2016), following the method described by McConnaughey & MaRay (1979) and Kiljunen et al. (2006).

#### Data analysis

To assess the spatial changes in population status of *C. brachygnathus* in 2020–2021 across the TGR, we implemented linear mixed-effects modeling (LMM) with relative abundance or biomass (e.g., abundance of *C. brachygnathus* / total abundance per sampling site per season) as a function of distance from the dam. We included sampling site as a random factor to control for the lack of independence among sites sampled during multiple seasons (Bates et al., 2015). Prior to model implementation, we logit transformed



**Table 1** Localities and the mean annual ( $\pm$  standard error) water transparency (WTr), pH, water temperature (WT), dissolved oxygen (DO), and conductivity (CON) of different sampling sites in the Three Gorges Reservoir

Area	Site	Site code	Altitude/ longitude	Distance (km)	WTr (m)	pH	WT (°C)	DO (mg/L)	CON ( $\mu$ s/cm)
Mainstem	Zigui	L1	30.854289° N, 110.994675° E	4.5	2.87 $\pm$ 0.07	8.03 $\pm$ 0.02	22.37 $\pm$ 0.04	7.35 $\pm$ 0.06	400.19 $\pm$ 0.52
	Wushan	L5	31.067719° N, 109.890351° E	130	1.80 $\pm$ 0.24	7.98 $\pm$ 0.01	19.00 $\pm$ 0.23	8.83 $\pm$ 0.04	332.24 $\pm$ 1.21
	Yunyang	M1	30.934613° N, 108.678354° E	258	1.51 $\pm$ 0.17	7.89 $\pm$ 0.01	19.22 $\pm$ 0.21	7.84 $\pm$ 0.05	318.04 $\pm$ 0.88
	Zhongxian	M3	30.306569° N, 108.057607° E	378	1.65 $\pm$ 0.22	7.92 $\pm$ 0.01	18.57 $\pm$ 0.26	8.18 $\pm$ 0.08	319.15 $\pm$ 0.53
	Banan	U1	29.579245° N, 106.839511° E	599	1.56 $\pm$ 0.26	7.93 $\pm$ 0.01	18.64 $\pm$ 0.01	8.33 $\pm$ 0.02	316.82 $\pm$ 0.71
Tributary	Qinggan	L2	30.964580° N, 110.543389° E	46	2.49 $\pm$ 0.14	8.00 $\pm$ 0.01	16.96 $\pm$ 0.30	9.23 $\pm$ 0.08	322.01 $\pm$ 1.40
	Xiangxi	L3	31.118924° N, 110.787687° E	50	1.92 $\pm$ 0.38	8.06 $\pm$ 0.01	16.46 $\pm$ 0.25	9.22 $\pm$ 0.06	314.88 $\pm$ 2.11
	Yuanshui	L4	31.047324° N, 110.690052° E	55	2.61 $\pm$ 0.12	8.01 $\pm$ 0.01	17.91 $\pm$ 0.45	9.42 $\pm$ 0.15	328.56 $\pm$ 2.18
	Pengxi	M2	31.094968° N, 108.674940° E	278	1.15 $\pm$ 0.18	7.78 $\pm$ 0.01	20.48 $\pm$ 0.29	7.36 $\pm$ 0.13	307.76 $\pm$ 2.62

For site codes, capital letter L represents the lower section, M represents the middle section, and U represents the upper section. Numbers represent site ID ordered by distance to the dam

proportional data ( $p'$ ) (logit transformation =  $\log [p' / (1 - p')]$ ) (Warton & Hui, 2011), using the R package car (Fox & Weisberg, 2011). We visually inspected model fit based on residuals vs. fitted value plots and standardized residuals vs. theoretical quantile plots and used the Shapiro test to check data normality. We also calculated catch per unit effort (CPUE,  $g/m^2/24$  h) of gillnet type (benthic gillnet or pelagic gillnet) per sampling event to estimate the absolute biomass of *C. brachygnathus* (Emmrich et al., 2012). We then implemented linear mixed-effects modeling (LMM) to compare the CPUE among sections and gillnet types. We included sampling site and sampling season as random factors to account for the lack of independence between multiple sampling events conducted at the same site and during the same season (Bates et al., 2015). We then performed within-section pairwise comparisons once we identified a significant difference, using the R package emmeans (Lenth et al., 2022). We also assessed spatial and seasonal differences in body size (i.e., standard length-SL, measured from the tip of the snout to the base of the caudal fin) of *C. brachygnathus* via LMM. We modeled SL as a function of sampling site and season and included sampling site as a random factor. We also retrieved SL data of *C. brachygnathus* populations from six native locations in the middle and

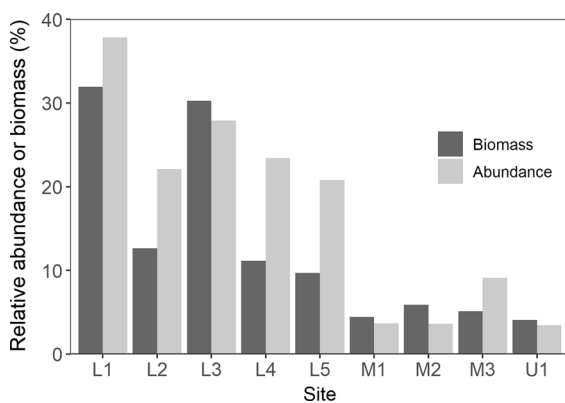
lower reaches of the Yangtze River (downstream from TGR), including Kuilei Lake, Zilang Lake, Poyang Lake, Dongting Lake, Changhu Lake, and Tianezhou Oxbow from published studies and our unpublished data (Wu et al., 2015; Wang et al., 2016; Gong et al., 2018; Qin et al., 2018). We used Wilcoxon tests to compare the mean SL between the TGR and native locations.

We retrieved data on the relative fecundity of native *C. brachygnathus* from Poyang Lake, Changhu Lake, and Swan Oxbow from the literature (Luo, 2006; Liu, 2008; Wang, 2016). We used a one-sample t test to compare relative fecundity between the TGR and native locations. We used the Chi-square test ( $X^2$  test) to test the deviation of the sex ratio of *C. brachygnathus* from the expected 1:1 ratio. Lastly, we used Bayesian stable isotope mixing models to estimate the contribution of different food sources to *C. brachygnathus* biomass (Parnell et al., 2013). We conducted all statistical analyses in R (v.4.0.2, R Foundation for Statistical Computing, Vienna, Austria). The regression models and main effects estimation (Type II and III Wald's  $X^2$  test) were conducted using the packages lme4 (Bates et al., 2015) and car (Fox & Weisberg, 2011), respectively. The Bayesian stable isotope mixing model was performed with the package siar (Parnell et al., 2013).

## Results

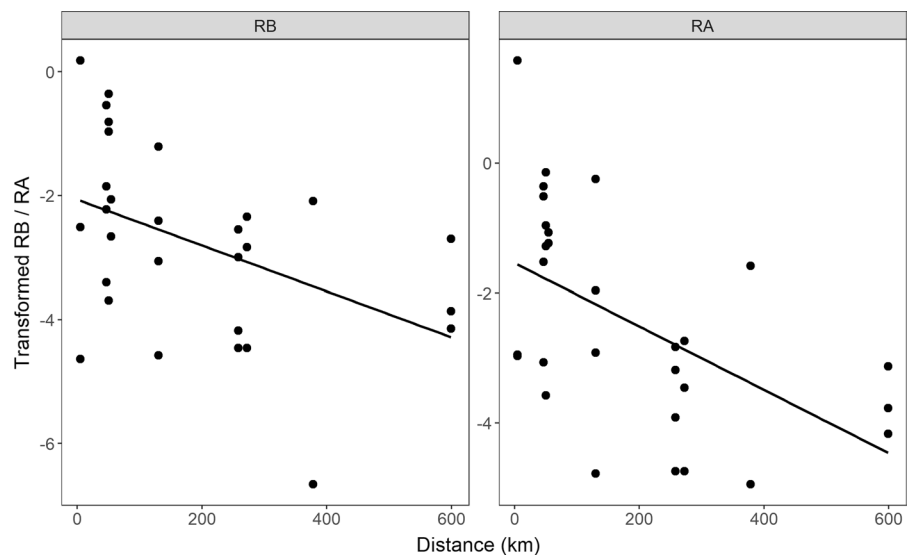
### Relative abundance, biomass, and CPUE

In 2020–2021, the relative biomass of *Coilia brachygnathus* accounted for  $11.66\% \pm 2.91\%$  (mean  $\pm$  S.E.), and the relative abundance accounted for  $16.06\% \pm 3.80\%$  of the TGR fish community. The highest mean values were both recorded toward the dam at site L1 (biomass: 31.95%, abundance: 37.83%), while the lowest values were both found at the most upper-sampled site U1 (biomass: 4.07%,



**Fig. 2** Spatial changes in relative biomass and abundance of *C. brachygnathus* in 2020–2021 at different sampling sites in the Three Gorges Reservoir. For site codes, capital letter L represents the lower section, M represents the middle section, and U represents the upper section

**Fig. 3** Relationships between relative biomass (RB) and relative abundance (RA) of *C. brachygnathus* in 2020–2021 with distance of sampling sites from the Three Gorges Dam. Relative biomass and relative abundance were logit transformed



abundance: 3.42%; Fig. 2). Both relative biomass and relative abundance decreased with distance to the dam (LMM, biomass:  $X^2=6.46$ ,  $P<0.01$ ; abundance:  $X^2=10.83$ ,  $P<0.001$ ; Fig. 3). Based on our past sampling, individuals of *C. brachygnathus* were first recorded in 2016, right above the dam (site L1), while in 2017, individuals were recorded at the middle (site M1) and upper (site U1) sections of the TGR. Relative biomass in 2017 was low in all sections, and it had a fourfold to 40-fold increase by 2020–2021 (Table 2). The CPUE of *C. brachygnathus* was non-significantly different among sections (LMM, section: Wald's  $X^2=2.86$ ,  $P=0.24$ ; net type: Wald's  $X^2=0.01$ ,  $P=0.91$ ), neither was the interaction between section and net type (Wald's  $X^2=0.57$ ,  $P=0.75$ ). Specifically, the averaged CPUEs were  $4.75 \pm 0.05$ ,  $1.54 \pm 0.03$ , and  $1.70 \pm 0.10$  g/m<sup>2</sup>/24 h in the lower, middle, and upper sections, respectively.

### Body size

The mean standard length (SL) of *C. brachygnathus* was  $203.66 \pm 0.99$  mm (mean  $\pm$  S.E.) in the TGR. Individually, site or season did not seem to influence SL (LMM, sampling site, Wald's  $X^2=13.89$ ,  $P=0.08$ ; season, Wald's  $X^2=4.92$ ,  $P=0.18$ ). Instead, SL changed spatially across seasons, as indicated by a significant interaction between sampling site and season (LMM: sampling site \* season, Wald's  $X^2=145.11$ ,  $P<0.01$ ; Fig. 4). Specifically, the smallest mean SL was recorded at the lower section (site

**Table 2** Temporal changes in relative biomass of *C. brachygnathus* between 2005 and 2021 (except 2018 and 2019, not sampled) at the lower section (L1, Zigui), middle section

(M1, Yunyang; 2015–2017: Wanzhou), and upper section (U1, Banan) of the Three Gorges Reservoir, respectively

Site	2005–2006	2013–2014	2015	2016	2017	2020–2021
L1	0	0	0	0.07%	0.79%	31.95%
M1	0	0	0	0	1.01%	4.44%
U1	0	0	0	0	0.11%	4.07%

L5) in winter ( $164.47 \pm 14.04$  mm) and the largest mean SL at the upper section (site U1) in autumn ( $259.33 \pm 7.38$  mm). The mean SL of *C. brachygnathus* from the TGR was significantly larger than those of native fish from lakes located in the middle and lower reaches of the Yangtze River, such as Poyang Lake, Dongting Lake, Changhu Lake, Tianezhou Oxbow, Kuilei Lake, and Zilang Lake (Wilcoxon test, all  $P < 0.01$ ; SL at the TGR and native locations is summarized in Table 3).

#### Reproductive traits

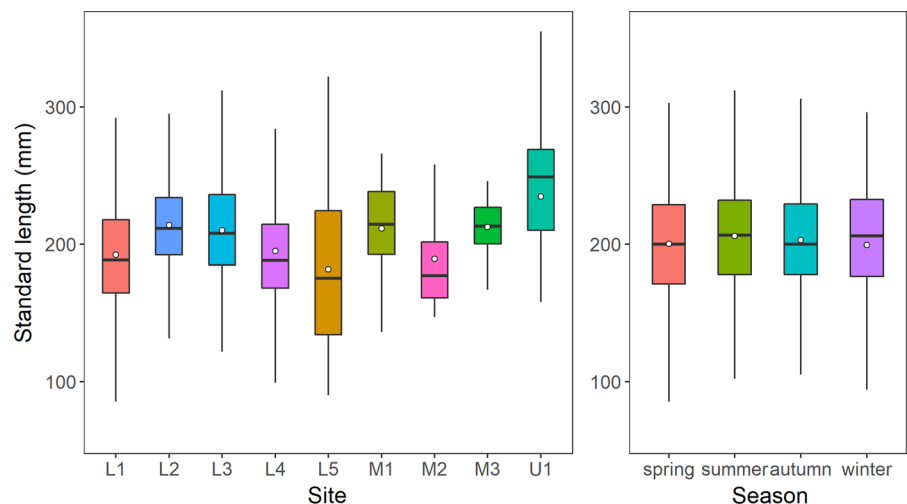
The overall sex ratio of *C. brachygnathus* was 1.49 (188 females, 126 males) in the TGR, and it was significantly different from 1 ( $X^2 = 5.79$ ,  $P = 0.02$ ). The SL at 50% maturity ( $L_{50}$ ) of *C. brachygnathus* was 224.23 mm in the TGR population. The absolute and relative fecundities in the TGR population averaged  $25,914.18 \pm 2,465.76$  eggs and  $778.6 \pm 63.2$  eggs/g (mean  $\pm$  S.E.,  $n = 32$ ), respectively, and its mature

egg size averaged  $0.40 \pm 0.001$  mm (mean  $\pm$  S.E.,  $n = 4586$ ). The relative fecundity of *C. brachygnathus* in the TGR was significantly higher than that in the native populations, including the Swan Oxbow population (RF =  $487.65 \pm 59.57$  egg/g; One sample  $t$  test,  $t = 4.68$ ,  $P < 0.001$ ) and the Changhu Lake population (RF =  $487.65$  egg/g;  $P < 0.001$ ), and was similar with that in the native Poyang Lake population (RF =  $765.83 \pm 182$  egg/g;  $P = 0.86$ ).

#### Diet traits

Stomach content analyses revealed that zooplankton and shrimp (*Exopalaemon modestus* and *Macrobrachium nipponensis*) were the primary food types consistently consumed by *C. brachygnathus* across sampling sites, which contributed on average ( $\pm$  SE)  $65.71\% \pm 9.03\%$  (zooplankton),  $24.78\% \pm 3.40\%$  (*E. modestus*), and  $9.51\% \pm 1.31\%$  (*M. nipponensis*) to the overall diets of *C. brachygnathus* in the TGR (Table 4). The  $\delta^{13}\text{C}$  of *C. brachygnathus* ranged

**Fig. 4** Changes of mean standard length of *C. brachygnathus* in 2020–2021 among the different sampling sites and seasons in the Three Gorges Reservoir. For site codes, capital letter L represents the lower section, M represents the middle section, and U represents the upper section



**Table 3** Summary of standard length and body weight of *C. brachygnathus* populations in the Three Gorges Reservoir and native habitats, located in the middle and lower reaches of the Yangtze River

Area	Longitude and latitude	Standard length (mm)		Body weight (g)		Sample size ( <i>n</i> )	Data source
		Mean	Range	Mean	Range		
Three Gorges Reservoir	30.827194° N 111.008222° E	203.66 ± 0.99	62.01–355.01	30.02 ± 0.70	1.20–260.80	1828	This study (2020–2021)
Zilang Lake	31.969055° N 120.938138° E	160.32 ± 0.48	61.26–306.12	20.37 ± 1.12	0.76–107.80	333	Liao, C., unpublished data
Kuilei Lake	31.408472° N 120.861333° E	157.44 ± 4.77	70.50–268.24	13.13 ± 0.82	1.08–57.80	256	Liao, C., unpublished data
Poyang Lake	29.620805° N 116.165972° E	143	56–325	13.4	0.6–125.5	1403	Wu et al. 2015
Dongting Lake	29.403306° N 113.109777° E	164 ± 43	68–354	NA	NA	NA	Qin et al. (2018)
Changhu Lake	30.426750° N 112.388583° E	180	102–326	19.1	3.36–120.1	479	Wang et al. 2016
Tianezhou Oxbow	29.812888° N 112.615611° E	111 ± 37	62–271	5.6 ± 8.5	0.5–72.2	NA	Gong et al. (2018)

from -28.84‰ to -21.87‰, and the  $\delta^{15}\text{N}$  ranged from 12.04‰ to 16.60‰. Bayesian stable isotope mixing models suggested that *E. modestus* contributed the highest proportion to *C. brachygnathus* biomass in four out of seven sampling sites (i.e., lower end of the credibility intervals > 0% for sites L5, M1, M2, and U1). Zooplankton contributed the most to three out of seven sites (i.e., lower end of the credibility intervals > 0% for sites L1, L2, and L3); *M. nipponensis* contributed the lowest (i.e., lower end of the credibility intervals = 0% for six out of seven sites; Table 4; Fig. 5).

## Discussion

### Role of the dam in the invasion of *C. brachygnathus*

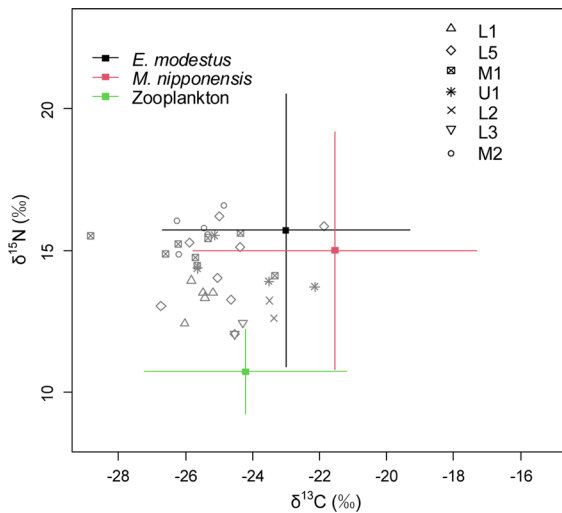
The relationship between dam construction and fish invasions is highly debated (Krieg et al., 2020; Kerr et al., 2021). Dams can prevent fishes from spreading between downstream and upstream reaches of a dammed river by limiting aquatic connectivity and fragmenting the river network (Frings et al., 2013). However, the processes of creating a reservoir, flooding, and impounding a river can facilitate invasion by

**Table 4** Predicted contribution (%) of different food types to the diet of *C. brachygnathus*, based on Bayesian stable isotope mixing model and stomach content analysis (proportional weight), at six sampling sites in the Three Gorges Reservoir

Site	Stable isotope analysis			Stomach content analysis		
	<i>E. modestus</i>	<i>M. nipponensis</i>	Zooplankton	<i>E. modestus</i>	<i>M. nipponensis</i>	Zooplankton
Zigui (L1)	40.40 (20.26–64.14)	6.25 (0.00–19.42)	53.35 (36.05–69.09)	25	12.5	62.5
Qinggan (L2)	27.50 (0.78–51.66)	26.93 (0.66–50.18)	45.57 (22.18–68.73)	12.04	7.35	80.61
Xiangxi (L3)	22.00 (0.00–46.57)	18.42 (0.00–42.24)	59.58 (34.39–82.87)	10.25	9.69	80.06
Wushan (L5)	66.02 (48.15–86.07)	5.16 (0.00–14.32)	28.82 (8.81–47.11)	53.37	13.29	33.33
Yunyang (M1)	82.50 (65.69–98.22)	3.55 (0.00–9.90)	13.95 (0.00–30.55)	30.01	3.57	66.42
Pengxi (M2)	79.47 (61.64–97.69)	7.07 (0.00–19.34)	13.46 (0.00–29.82)	–	–	–
Banan (U1)	45.07 (8.98–75.99)	24.35 (0.00–56.42)	30.58 (8.00–50.24)	–	–	–

Values are 50% contribution while values in parentheses indicate lower and upper 95% credibility intervals of food contribution. Values > 0% for the lower limit 95% credibility intervals indicate a significant predicted contribution. For site codes, capital letter L represents the lower section, M represents the middle section, and U represents the upper section





**Fig. 5** C/N stable isotope values of *C. brachygnathus* and potential food sources in different sampling sites of the Three Gorges Reservoir. For site codes, the capital letter L represents the lower section, M represents the middle section, and U represents the upper section

eliminating natural barriers that prevent fishes from dispersing among catchments disconnected before the impoundment (Júlio Júnior et al., 2009). Our study supported both arguments: the dam's initial blockage and later dispersal facilitation. Between 2010 and 2016, the Three Gorges Dam appeared to have blocked the upstream invasion of *C. brachygnathus* from the Gezhouba reservoir into the TGR. Our reasoning is based on earlier detection of non-native *C. brachygnathus* populations downstream of the TGR. The species was detected during 2004 and 2009 at the Yichang section, downstream of the Gezhouba Dam (Ma et al., 2014), and during 2009 and 2010 at the Gezhouba Reservoir, immediately downstream of the TGR (Liu et al., 2012). However, *C. brachygnathus* was not detected at five sampling sites (Low-1, Low-5, Middle-1, Middle-3, and Upper-1; downstream to upstream, respectively) within the TGR from 2013 to 2014 (Lian, 2016). Such observation suggests that the abundance of this species was below the detectability threshold at that stage of the invasion. Our past work demonstrated that *C. brachygnathus* was first detected in the lower section of the TGR during 2016 and expanded its distribution toward the upper sections in 2017. Although there is no direct evidence of how this species expanded its distribution into the TGR, the observed progressive directional invasion

suggests that *C. brachygnathus* invaded the TGR from downstream. Thus, we argue that the navigation lock should be the most likely path for the fish invasion, given that the Three Gorges project did not build a fish passage mechanism (Shi et al., 2015).

Since *C. brachygnathus* was first detected in the lower section of the TGR in 2016, it has rapidly expanded its distribution to the entire reservoir and spread into tributaries, becoming a dominant fish species in the lower and middle sections (lentic habitats) of TGR. Such rapid expansions of invasive fishes have been observed in other systems, such as *Neogobius melanostomus* (Pallas 1814) (Gobiidae) in the Laurentian Great Lakes, USA (Raad et al., 2018) and armored catfish *Loricariichthys platymetopon* Isbrücker & Nijssen 1979 (Loricariidae) in the Itaipu reservoir, Brazil (Casimiro et al., 2017). The invasion of *C. brachygnathus* likely resulted as the impoundment of the TGR eliminated the natural barriers to dispersal formed by the natural “Three Gorges” with its 120-m drop from Chongqing to Yichang and that between the Yangtze River main stem and its numerous tributaries (Zolotov & Shaitanov, 2000).

Meanwhile, longitudinally abiotic gradients created from impoundment also are likely to affect the invasion and dispersal progression (Raad et al., 2018). In our study, the lower density (i.e., relative biomass, relative abundance, but not CPUE) of *C. brachygnathus* with distance from the dam indicated that *C. brachygnathus* has different abilities to live in the longitudinal gradient of lentic, transitional, and riverine habitats along the TGR (Cheng et al., 2015). Such differential adaptations allow *C. brachygnathus* to progressively invade the lotic upper section of TGR. *Coilia brachygnathus* is an anchovy species exclusive to freshwater lakes and reservoirs (Whitehead et al., 1988), which usually inhabits pelagic waters and produces pelagic eggs in lentic habitats (Qin et al., 2018). The upper section of the TGR maintains a lotic habitat with an average water velocity of 1.28 m/s after its final impoundment in 2009 (MEP, 2017). The spatially different abundance of *C. brachygnathus* suggests that higher water velocity may create environmental restrictions making the *C. brachygnathus* expansion toward the upstream riverine areas of the TGR difficult. The persistence of fluvial-adapted species supports this argument, because lentic-adapted species do not dominate these lotic habitats after damming. For instance, the abundance

of invasive lentic-adapted species *N. melanostomus* declined from the reservoir to upstream of the Grand River (Ontario, Canada; Raab et al., 2018).

Fish communities upstream of the Yangtze River is the most species rich in China and includes numerous rare and endemic species (Liu et al., 2020). *Coilia brachygnathus* are yet to be reported in the natural Yangtze River, upstream from the TGR, and the upper cascade reservoirs (Li et al., 2020; Qu et al., 2020). However, assuming that *C. brachygnathus* can colonize the upstream cascading reservoirs through the navigation locks, it can be expected that it can differently impact its competitor and prey populations. In that case, the repeating lentic habitats formed by their impoundments are likely suitable for the colonization of *C. brachygnathus*. Monitoring and prevention measures are therefore needed. Based on the aforementioned spatial selectivity, to prevent the expansion of this invasive species, we propose that new hydropower projects should be forbidden between the tail of the TGR and the Xiangjiaba Dam to protect the remaining > 300 km of lotic stretches therein (Cheng et al., 2015). This management strategy would hinder the further upstream expansion of *C. brachygnathus*.

#### Biological traits related to the establishment and spread of *C. brachygnathus*

In the present study, both stable isotope and stomach content analyses suggest that *C. brachygnathus* mainly preyed on zooplankton and shrimps (especially *E. modestus*) in the TGR. These patterns are similar to the diet of native *C. brachygnathus* populations, such as those in the Hongze Lake, the Gaoyou Lake, the Luoma Lake (Gu et al., 2019), and the Poyang Lake (Zhang et al., 2013), where zooplankton and shrimps also contributed the highest to their diet. Shrimps were available to *C. brachygnathus* at each section of the TGR (2.51, 2.65, and 2.28 kg/boat/24 h in the lower, middle, and upper sections, respectively, during 2015–2017; Liao, C., unpublished data). The densities of zooplankton were  $6.09 \times 10^4$ ,  $5.07 \times 10^4$ , and  $5.40 \times 10^4$  ind./L in the lower, middle, and upper sections, respectively, during 2016–2017 (Zhang & Huang, 1995; Wu et al., 2021), which indicates that zooplankton was also relatively abundant across the entire reservoir. The diet similarity between the native and invasive populations indicates that abundant and widely distributed zooplankton and shrimps may

satisfy the food resource requirements of *C. brachygnathus*, which should be considered a key factor explaining their successful invasion, especially at the initial stage (Blumenthal et al., 2006). This argument is consistent with the resource hypothesis, which proposes that good resource availability leads to low defense investment and high enemy damage; therefore, invasive fishes under high resource availability obtain sufficient energy to become established (Blumenthal et al., 2006).

The TGR had another invasion after its first filling, two icefish species (*N. taihuensis* and *P. hyalocranius*) were intentionally introduced to the lower section after approximately 2003 and posteriorly colonized the lower section of the reservoir (Gong et al., 2009; Ba & Chen, 2012). Considering these successful invasions and the ecological characteristics of these species, the results of our work and previous successful invasions suggest that the TGR is susceptible to invasion by exotic carnivorous and invertivorous fishes. It is worth noting that we also caught individuals of other non-native predatory species in the TGR, such as *Odontobutis obscurus* (Temminck & Schlegel 1845) (Odontobutidae), which is native to the middle and lower reaches of the Yangtze River basin. Further monitoring is needed to assess whether these species will flourish and expand their distribution in the future.

Invasive fish species usually share similar life history characteristics making them successful invaders, such as rapid growth, high fecundity, and early reproduction (Agostinho et al., 2015). *Coilia brachygnathus* has not been reported to invade other freshwater systems in China. Our study, however, demonstrated that *C. brachygnathus* shares some of these reproductive traits. TGR *C. brachygnathus* can reach 200 mm within six months of age, which indicates that females in the TGR can achieve 50% maturity (SL = 224.23 mm) within the first year of life and then spawn once a year (Tang et al., 1987; Liu, 2008). The TGR *C. brachygnathus* population has higher fecundity than some native populations, such as the Swan Oxbow and the Changhu Lake populations (Luo, 2006; Wang, 2016). Previous studies on other invasive species also found that non-native populations have higher fecundity than the native population (e.g., round goby *N. melanostomus*, Horkova & Kováč, 2014). The TGR and the native habitats are all located in the Yangtze River basin with similar latitude, and

it seems unlikely that differences in temperature and other climate conditions were large enough to explain spatial variation in fecundity. Instead, we argue that the abundant foods and low intra- and inter-specific competition at this stage of the invasion may explain such variation in fecundity (Wootton & Smith, 2015).

Invasive freshwater fishes in newly occupied areas usually allocate more energy to reproduction and offspring maintenance resulting in smaller body sizes than populations from native areas (Záhorská et al., 2009; Novomeska et al., 2013). In the present study, the body size of the population of *C. brachygnathus* examined is considerably larger than those of six native populations from the middle and lower Yangtze River (Wu et al., 2015; Wang et al., 2016; Gong et al., 2018; Qin et al., 2018). It was only five years since *C. brachygnathus* invaded the TGR. The differences in the body size between the TGR and native habitats observed in this study were unlikely to result from genetic differences but from phenotypic plasticity (Iguchi et al., 2019). We also found that standard length tends to increase from the lower to the upper section of the TGR, although the trend was statistically non-significant. Bigger invaders likely possess better adaptive and competitive abilities. Over time, the body size of the TGR population may gradually lead back to the body size typical of individuals from native populations (Novomeska et al., 2013). Such fast maturity and short generation time, large body size, and high fecundity, coupled with abundant food availability, likely formed the critical factors of the successful invasion of *C. brachygnathus* (Agostinho et al., 2015). It is no longer realistic to eliminate the *C. brachygnathus* population from the Three Gorges Reservoir, and developing mechanisms to control its abundance should be a priority. We suggest strengthening targeted fishing to increase catching effort on *C. brachygnathus* (Giakoumi et al., 2019).

In conclusion, the findings from this study revealed when *C. brachygnathus* entered the TGR and how its abundance changed spatially and temporally. Our study also highlighted biological traits of *C. brachygnathus* that facilitated their successful invasion, such as early maturity, high fecundity, and an invertivorous diet. Our results improve scientific understanding of why *C. brachygnathus* successfully colonized and expanded into the

whole reservoir within four to five years after first recorded. It is critical to further assess the potential impacts of *C. brachygnathus* on native pelagic and zooplanktivorous fishes therein, such as *Hemiculter leucisculus* (Basilewsky 1855), *H. tchangi* Fang 1942, *Pseudolaubuca sinensis* Bleeker 1864, and *P. engraulis* (Nichols 1925), as well as the potential impacts on the two native shrimp populations. The present study also issued a risk alarm that the lentic habitats formed by cascaded reservoirs in the upper reaches of the Yangtze River may facilitate *C. brachygnathus* to continue expanding upstream. Based on our findings, this invasive species could be managed through habitat conservation and fishing regulation.

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**Data availability** The datasets analyzed during the current study are available from the corresponding author on reasonable request.

**Code availability** The codes used in this study are available from the corresponding author on reasonable request.

#### Declarations

**Conflict of interest** The authors have no conflicts of interest to declare that are relevant to this article.

**Ethical approval** The manuscript has not been published or is under consideration for publication elsewhere, in whole or in part.

**Consent to participate** Not applicable.

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