

## Research Article

# Phenotypic plasticity in life-history characteristics of the invasive redbelly tilapia (*Coptodon zillii*) in Shuikou Reservoir, Minjiang River, China

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## Abstract

In recent decades, the redbelly tilapia (*Coptodon zillii*) has become one of the most serious invasive alien fish species worldwide. The successful invasion of this fish may largely depend on the plasticity of its life-history traits. In order to explore the life-history traits of the invasive population of *C. zillii*, we chose Shuikou Reservoir of Minjiang River, China, as a typical invasive habitat, and 1,041 specimens were collected monthly from March 2023 to February 2024. Life-history traits were systematically investigated. The results showed that the entire population consists of individuals from age 1 to age 6, with the highest percentage (95.10%) of younger individuals at 1–2 years old. The sex ratio of males to females was 1.05:1. The equation of the length-weight relationship was  $W = 0.048 * L^{2.938}$ , and the parameters of von Bertalanffy growth equation were  $L_{\infty} = 32.937$  cm,  $W_{\infty} = 1381.010$  g,  $k = 0.131$ , and  $t_0 = -2.056$ . The breeding season ranged from March to November, and the minimum sexually mature standard lengths of females and males were 8.7 and 9.0 cm, respectively. Mean absolute fecundity was  $3854.38 \pm 254.43$  eggs, while mean relative fecundity to standard length and body weight were  $301.95 \pm 16.94$  eggs/cm and  $60.44 \pm 3.56$  eggs/g, respectively. These results indicated that the population of *C. zillii* in Shuikou Reservoir presented characteristics such as a high proportion of young individuals, low growth rate, long spawning season, high fecundity, and smaller size at first maturity compared with the native and other invasive populations. Both opportunistic and equilibrium life-history strategies might have contributed to their successful invasion, and there is a potential risk of further population expansion.

**Key words:** Age structure, fecundity, growth traits, invasion, reproductive strategies

## Introduction

Biological invasions represent a significant aspect of global change (Simberloff et al. 2013). Invasive species have resulted in significant economic losses on a global scale, in addition to negative impacts on biodiversity (Mack et al. 2000; Pimentel

et al. 2000; Moritz 2002). China is one of the countries most seriously impacted by biological invasions, with approximately 660 invasive alien species monitored in almost all ecosystems. The proliferation of invasive freshwater fishes in China is largely driven by the aquaculture and aquatic ornamental industries. There are 439 exotic freshwater fishes in China, of which 53 have established populations in the wild (Xiong et al. 2015). These invasive species pose a serious threat to both the economy and the ecosystem.

*Coptodon zillii*, also referred to as the redbelly tilapia, is classified within the Cichliformes, Cichlidae, and is indigenous to Africa and the Middle East (Geletu et al. 2024). It was introduced to China from Thailand in 1978 with the objective of becoming a target species for aquaculture (Cai 1979). However, it was subsequently abandoned by farmers due to its small size and slow growth rate. Subsequently, the fish escaped to natural water bodies, where it gradually spread to Hainan and Guangdong province due to its ecological adaptations (e.g., cold hardiness (Lu 1987), salinity tolerance (Chervinski and Hering 1973), and broad diet (Philippart and Ruwet 1982). It has established stable populations in natural water bodies in the Chinese provinces of Hainan, Guangdong, Guangxi and Fujian, and even became an dominant species in some river sections, with a tendency to spread northwards (Xing et al. 2025). The introduction of *C. zillii* has had a significant impact on the biodiversity of native fish species and the quality of the aquatic environment, due to competition for resources, predation and the transmission of parasites (Xing et al. 2025). In recent years, this species has been included in the list of 59 key invasive alien species issued by the Ministry of Agriculture and Rural Affairs of China (Gu et al. 2023). It is therefore imperative that effective measures be taken to prevent and control further outbreaks of *C. zillii*. Uncovering the mechanism of successful invasion of *C. zillii* is a prerequisite for its scientific prevention and control.

The successful invasion of exotic fishes has been demonstrated to be influenced by a multitude of factors, including the intrinsic characteristics of the species in question, the environmental conditions prevailing at the site of the invasion, and the specific circumstances of the invasion event (Capellini et al. 2015). Among these factors, life-history strategy represents a significant aspect of the species' intrinsic characteristics. Life-history traits refer to the biological characteristics of organisms in terms of growth, development and reproduction. These traits are determined by the regulation of energy allocation throughout the life process and are an important reflection of the adaptive capacity of a species to its environment and the function of the species within the ecosystem in which it is located (Roff 1992). The life-history strategy of invasive species can change when they adapt to new environments (Sakai et al. 2001; Kornis et al. 2017; Latorre et al. 2018), and exhibits considerable variability, which is conducive to population establishment (Agrawal 2001; Feiner et al. 2012; Ondrac'kova et al. 2019). Life-history strategy has been demonstrated to be an effective predictor of fish invasion (Fausch et al. 2001). In addition, age, growth and reproduction represent crucial elements of fish life-history strategy, serving as pivotal indicators for assessing phenotypic variability of exotic fish (Hetzl and Forsythe 2023).

During the 1990s, Winemiller and Rose (1992) proposed a tripartite life-history framework (later termed the W&R model), which categorizes fish reproductive strategies based on evolutionary trade-offs among three core demographic traits: age at maturation, fecundity, and juvenile survival probability. The model delineates three archetypal strategies at its vertices: a) Opportunistic Strategy (*r*-selected), characterized by early maturation, small body size, and minimal parental investment. Adaptive in unpredictable or transient habitats

where rapid colonization is advantageous. b) Periodic Strategy, exhibits high fecundity with pulsed reproduction, producing numerous small offspring. Favored in seasonally fluctuating or spatially patchy environments where reproductive timing aligns with resource pulses. c) Equilibrium Strategy (*k*-selected), prioritizes quality over quantity, with substantial energy allocated to few, well-developed offspring. Dominates in stable habitats with intense competition or predation pressure. The model's triangular continuum accommodates intermediate strategies, capturing the full spectrum of life-history variation. While all fish species—marine and freshwater—occupy a position within this framework, invasive fishes often exhibit flexible or mixed strategies, typically falling between the extreme endpoints rather than conforming rigidly to a single archetype (Winemiller and Rose 1992).

The invasive population of bluegill sunfish (*Lepomis macrochirus*) in Qiandao Lake, China, is distinguished by an opportunistic life-history, characterised by early sexual maturity, a prolonged reproductive period, high fecundity and a higher proportion of females (Ma et al. 2024). This life-history strategy is associated with high reproductive potential and high resilience of the entire population, which facilitates rapid population expansion. The combination of opportunistic (high fecundity, short lifespan) and equilibrium (male nest-keeping) life-history strategy enabled the successful invasion of the Shimofuri goby (*Tridentiger bifasciatus*) at an important node (Nansi Lake) on the East Route of the South-to-North Water Transfer Project in China (Qin et al. 2020). Amur sleeper (*Perccottus glenii*) is one of the most invasive fish species in Eastern and Central Europe. It exhibits an opportunistic life-history strategy, characterised by relatively small size, precociousness, and a medium lifespan, as well as an equilibrium strategy, including parental care (Joanna et al. 2011). The combination of opportunistic and equilibrium life-history traits has been demonstrated to contribute to successful invasion (Fox et al. 2007; Fox and Copp 2014).

*Coptodon zillii* is a substrate spawner with a relatively early age of sexual maturity and a strong sense of territoriality (Cummings et al. 2017). Both males and females build and defend the nest and protect the fertilized eggs and hatched larvae until they become independent of their parents. If conditions are favourable, the parents will then proceed to the next reproductive cycle (Gophen 2016) after they completed previous cycle of reproduction. And it will only take a minimum of six to seven days for the next spawning event (Coward and Bromage 2000). It was therefore hypothesised that a variety of specialised biological traits (i.e., slow growth rate, long spawning season, high fecundity and small size at sexual maturity) might have contributed to the successful invasion of *C. zillii*. To test this hypothesis, the largest reservoir (Shuikou Reservoir) in Fujian Province in southeastern China was selected as a typical habitat due to its status as a representative of the numerous subtropical riverine reservoirs in China. Additionally, the outbreak of *C. zillii* in the reservoir has greatly increased in scale since 2011 (He et al. 2013). The age, growth and reproductive characteristics of the invasive population of *C. zillii* in this reservoir were investigated by monthly sampling from March 2023 to February 2024. To the best of our knowledge, the life-history characteristics of *C. zillii* in the natural ecosystem of the Minjiang River basin have not yet been reported. This study will provide primary data for the study of the life-history traits of *C. zillii* in the Minjiang River. The objective of this study is to elucidate life-history traits that contribute to the invasion success of the *C. zillii* in the Shuikou Reservoir of the Minjiang River. These results may provide insights for resolving key biological traits that support the population establishment of exotic fishes in new environments.

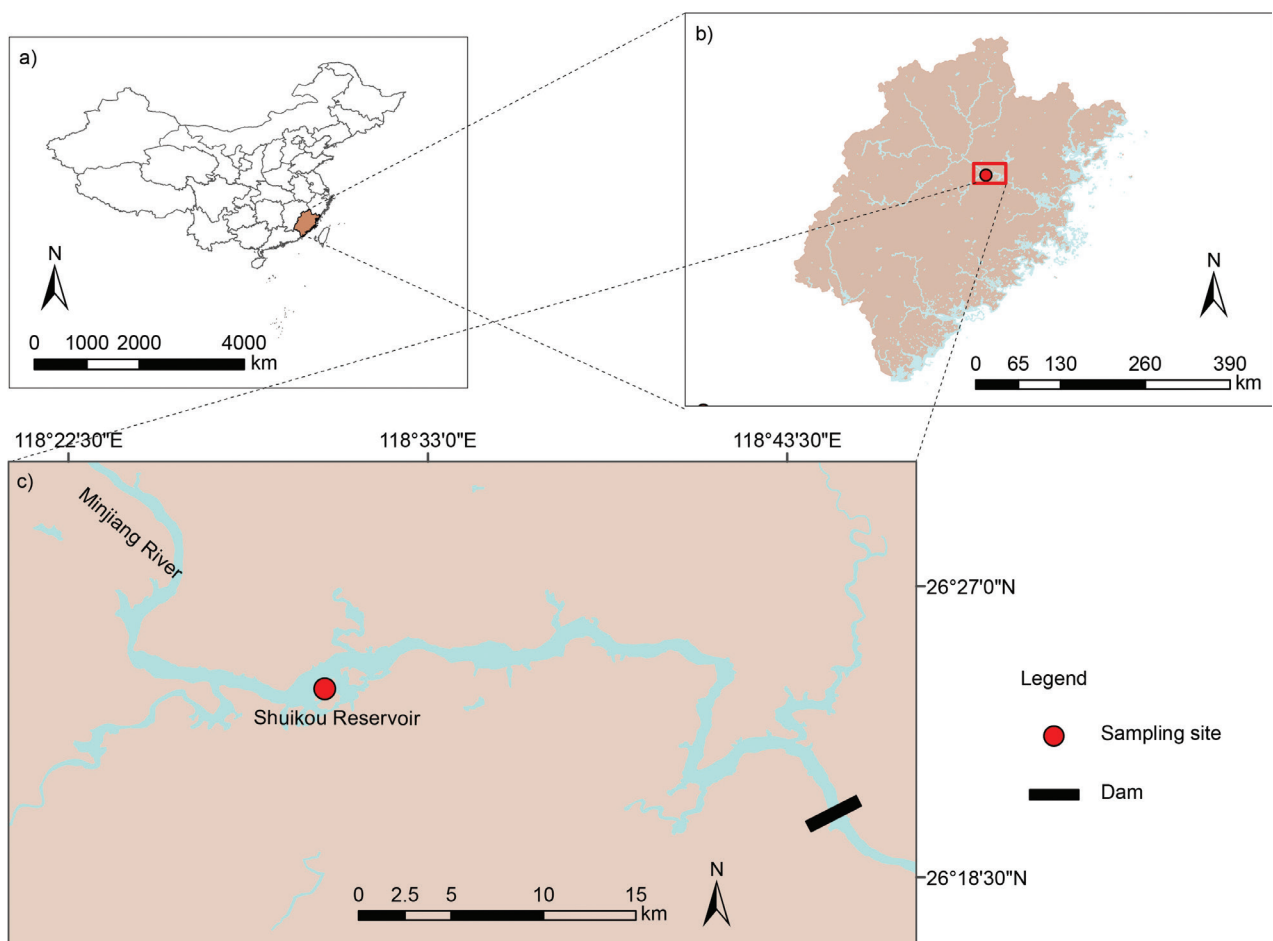
## Materials and methods

### Study area

The Shuikou Reservoir is a narrow and deep riverine reservoir located in the middle reaches of the main stream of the Minjiang River. It has a total capacity of  $2.6 \times 10^9 \text{ m}^3$ , making it the largest reservoir in Fujian Province. Following the water storage in March 1993, *C. zillii* was once farmed on a large scale around the reservoir. Escape of redbelly tilapia into the reservoir occurs from time to time due to poor culture management. In recent years, tilapia farming has ceased in the vicinity of the reservoir. However, the population of *C. zillii* within the reservoir has exhibited a notable increase year by year. In certain areas of the reservoir, *C. zillii* have become a dominant taxon (Cai 2021).

### Sample collection

The sampling site ( $26^\circ 40' \text{N}$ ,  $118^\circ 49' \text{E}$ ) is located in Zhanghu Town, Yanping District, Nanping City, Fujian Province (Figure 1). The research was conducted with the permission of the Fisheries Department of the Bureau of Agriculture and Rural Affairs of Nanping City, Fujian Province. During the study period, which spanned from March 2023 to February 2024, 40–200 live specimens of *C. zillii* were collected from the reservoir in the middle of each month, resulting in a total of 1,041 samples. The sampling gear employed was a three-layer drift gillnet, with a length of 30 m, a height of 1.5 m, and a mesh size of 3 cm, 5 cm, and 7 cm, respectively.



**Figure 1.** Map of the location of Shuikou Reservoir (c) in Fujian Province (b) of China (a). The sampling site for *Coptodon zillii* was indicated with a red dot.

## Sample pre-treatment and analysis

Immediately following capture, the samples were anaesthetised with MS-222 (100 mg/L), after which routine biological measurements were conducted on site. These included standard length (accurate to 0.1 cm) and weight (accurate to 0.01 g). Gender of specimens were distinguished using the morphology of the genital papilla and macroscopic examination of gonads. Gonadal development was divided into six stages (I–VI) according to the criteria of Brown-Peterson et al. (2011), which were based on the anatomical morphology, colour, volume, and histology of the gonads. The gonad weight (ovary, spermatheca) (accurate to 0.01 g) and eviscerated weight (accurate to 0.01 g) were determined. The classification of oocyte maturity was conducted in accordance with the criteria established by Coward and Bromage (2000). The ovarian maturity stage was determined by the most advanced oocyte present in the ovary. The ovaries at stages IV and V were subsequently preserved in a 5% formaldehyde solution to obtain absolute and relative fecundity.

## Age determination of samples

The scales of specimens were employed as the material for age identification. Five to ten scales of each specimen were taken from between the lateral line and first dorsal fin. They were cleaned, fixed between the two glass slides, soaked with drops of alcohol, dried and preserved. And the total scale radius and the radius of each annulus were measured under a dissection microscope, with annuli identified using criteria of Carbonara and Follesa (2019).

## Data analysis

The length-weight relationship was established using the equation  $W = aL^b$  (Froese 2006), where  $W$  is the measured weight (g),  $L$  is the measured standard length (cm), and both  $a$  and  $b$  are constants. Deviation from isometry ( $b = 3$ ) for the calculated  $b$  value was ascertained by the student's  $t$ -test. In the absence of a statistically significant deviation, the fish was deemed to exhibit isometric growth. Conversely, when a statistically significant deviation was observed, the fish was classified as anisometric (with positive anisometric growth when  $b > 3$  and negative anisometric growth when  $b < 3$ ). The von Bertalanffy growth function (VBGF) was employed to delineate the growth characteristics of *C. zillii* (Coulson and Wakefield 2022), with the following expression:  $L_t = L_\infty [1 - e^{-k(t-t_0)}]$ ;  $W_t = W_\infty [1 - e^{-k(t-t_0)}]^b$ . The growth rate of standard length and body weight were described using the following equations:  $dL/dt = L_\infty k e^{-k(t-t_0)}$ ,  $dW/dt = bW_\infty k e^{-k(t-t_0)} [1 - e^{-k(t-t_0)}]^{b-1}$ . The acceleration of growth in standard length and body weight were described using the following equations:  $d^2L/dt^2 = -L_\infty k^2 e^{-k(t-t_0)}$ ,  $d^2W/dt^2 = bW_\infty k^2 e^{-k(t-t_0)} [1 - e^{-k(t-t_0)}]^{b-2} [b e^{-k(t-t_0)} - 1]$ . Age at inflexion point was calculated using the following formula,  $t_i = \ln b/k + t_0$ .  $t$ ,  $L_t$ , and  $W_t$  represent the age, mean standard length at age  $t$ , and mean body weight at age  $t$ , respectively.  $L_\infty$  and  $W_\infty$  denote the asymptotic standard length and asymptotic body weight, respectively.  $k$  and  $t_0$  represent the growth coefficient and the theoretical onset age point, respectively. The value of  $k$  is typically employed to reflect the growth rate of the population. Branstetter (1987) classified the growth coefficients into three intervals (0.05 to 0.1, 0.1 to 0.2, 0.2 to 0.5), which represent the slow-growth type, the uniform-growth type, and the fast-growth type, respectively.

The monthly gonado-somatic index (GSI) was used to reflect the degree of gonadal development, and the intensity of reproductive activity was assessed based on the monthly trend of the GSI, estimated by the formula  $GSI (\%) = 100 \times (W_g / W_E)$ , where

$W_g$  and  $W_E$  are the gonadal weight (g) and the eviscerated weight (g), respectively. The fecundity of *C. zillii* was estimated by the standard gravimetric method. We obtained and weighed three systematic subsamples (5–20% of total ovary weight) from the anterior, middle, and posterior sections of the ovary. And the fecundity was calculated according to the following formulas:  $F = nW_O/w$ ,  $F_w = F/W_E$ ,  $F_L = F/L$ . The variables are defined as follows:  $F$  is absolute fecundity;  $n$  is the number of eggs counted;  $W_O$  is the weight of the ovary (g);  $w$  is the weight of the subsamples of the ovary (g);  $F_w$  is the relative fecundity to body weight;  $W_E$  is the eviscerated weight (g);  $F_L$  is the relative fecundity to standard length; and  $L$  is the standard length (cm). Ten ovaries on stage IV were selected for analysis of the diameter of the eggs. Eggs were extracted from the anterior, middle, and posterior sections of the ovaries, which had been fixed in a 5% formaldehyde solution. The eggs were observed and photographed under a dissection microscope. The diameters of eggs were measured under a stereomicroscope using imaging software, with an accuracy of 0.01 mm.

Statistical analysis and graphical representation of the data were conducted in Microsoft Excel 2019, SPSS 27.0.1 and ORIGIN 2021, respectively. The chi-square test was utilised to ascertain whether the sex ratio of females to males was in accordance with the expected 1:1 ratio. Significance of difference was tested using independent samples  $t$ -test and one-way analysis of variance, with a significance level  $\alpha$  of 0.05.

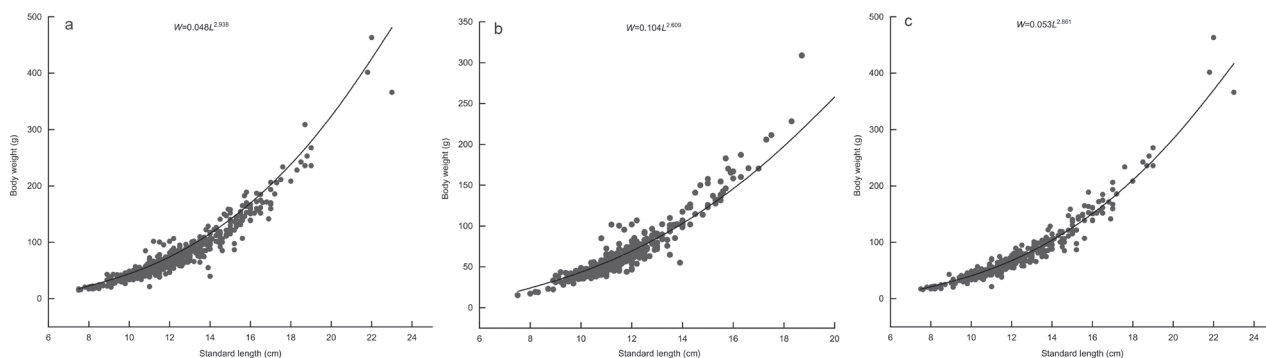
## Results

### The standard length, body weight, age composition and sex ratio

The entire population consists of individuals from age 1 to age 6, with the highest percentage (78.29%) of younger individuals at 1 years old. Individuals of age 2 constitute the second largest age group, which accounted for 16.81% of the total number of samples. The maximum ages of the female and male samples were age 4 and 6, respectively (Suppl. material 1). The standard length of females ranged from 8.7 cm to 18.7 cm, with a mean standard length of 11.51 cm. The body weight of females ranged from 23.1 g to 308.86 g, with a mean body weight of 66.34 g. The standard length of males ranged from 9.0 cm to 23.0 cm, with a mean standard length of 11.84 cm. The body weight of males ranged from 21.45 g to 463.5 g, with a mean body weight of 68.86 g. The difference in mean standard length between females and males was not statistically significant ( $P = 0.174$ ,  $t = 4.327$ ,  $df = 1039$ ), nor was the difference in mean body weight ( $P = 0.75$ ,  $t = 2.992$ ,  $df = 1039$ ). The male-to-female sex ratio of *C. zillii* was 1.05:1, which did not deviate significantly from the theoretical value of 1:1 ( $\chi^2 = 0.617$ ,  $P = 0.432$ ,  $df = 1$ ).

### Length-weight relationship

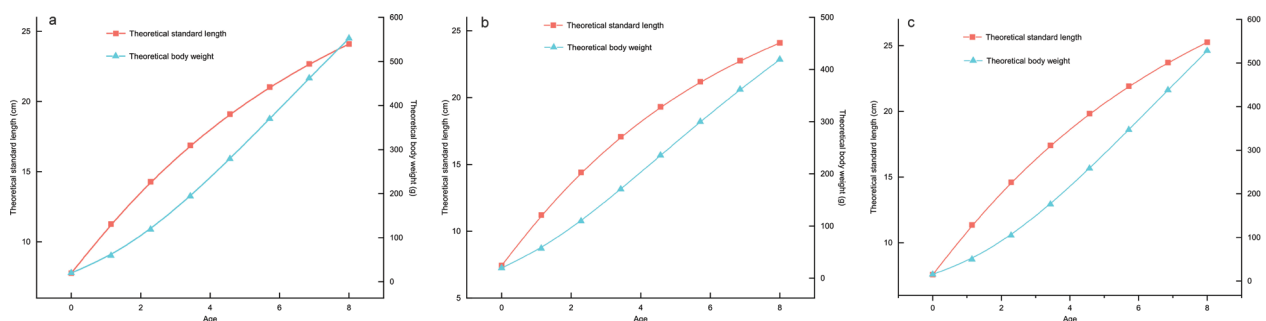
A total of 533 males and 508 females were collected for analysis in this study. The standard length and body weight of all samples ranged from 7.5 to 23.0 cm and 15.49 to 463.15 g, respectively. The length-weight relationship for all samples was determined to be  $W = 0.048 * L^{2.938}$  ( $R^2 = 0.903$ ) (Figure 2a). The length-weight relationship for female and male fish are as follows:  $W = 0.104 * L^{2.609}$  ( $R^2 = 0.718$ ) (Figure 2b) and  $W = 0.053 * L^{2.861}$  ( $R^2 = 0.837$ ) (Figure 2c). The value of the constant “ $b$ ” in the length-weight relationship were found to show negative allometry for all samples, females and males, respectively. This is consistent with the negative allometric growth type. The  $b$ -value of male samples was found to be significantly greater than that of female samples ( $t = 3.143$ ,  $P = 0.00177$ ,  $df = 506$ ).



**Figure 2.** Relationship between standard length and body weight of *Coptodon zillii* for overall samples (a), female samples (b), and male samples (c) in Shuikou Reservoir.  $W$  and  $L$  denote the expected weight and standard length, respectively.

### Growth equations

The estimated asymptotic length ( $L_{\infty}$ ) of *C. zillii* population (all samples) was determined to be 32.937 cm, while the asymptotic body weight ( $W_{\infty}$ ) was found to be 1381.010 g (Suppl. material 2; Figure 3a). Among them, the  $L_{\infty}$  of females and males were 31.041 cm and 34.934 cm, respectively (Suppl. material 2; Figure 3b, c). While the  $W_{\infty}$  of females and males were 811.883 g and 1378.825 g, respectively (Suppl. material 2; Figure 3b, c).



**Figure 3.** Theoretical standard length and body weight of *Coptodon zillii* for overall samples (a), female samples (b), and male samples (c) in Shuikou Reservoir.

### Growth rate and age at inflection point

The growth rate and growth acceleration equations for standard length and body weight of *C. zillii* are presented in Suppl. material 2. The inflection age of the *C. zillii* population was 1.05 years, corresponding to a standard length and body weight of 10.89 cm and 57.58 g, respectively (Figure 4a, d). The inflection age of females was 1.04 years, corresponding to a standard length and body weight of 10.80 cm and 55.34 g (Figure 4b, e). The inflection age of the males was 1.21 years, corresponding to a standard length and body weight of 11.44 cm and 56.33 g, respectively (Figure 4c, f). The growth rate of standard length was consistently positive and exhibited a gradual decline with age. Conversely, the growth acceleration of standard length was consistently negative and demonstrated a gradual increase with age.

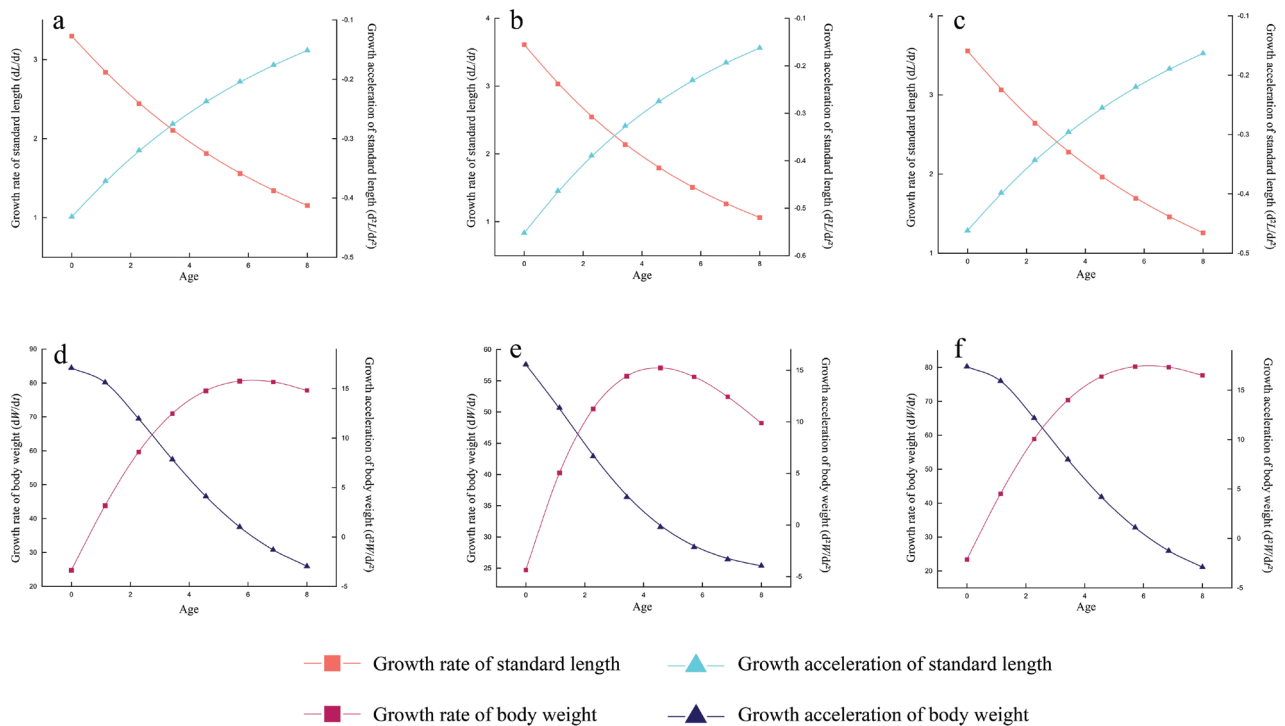
### The smallest mature specimen

Of the 1041 specimens examined, 158 had reached sexual maturity (gonads at stage IV or V) (Figure 5a), of which 54.43% were females. The standard length of the smallest sexually mature female was 8.7 cm, with a body weight of 23.097 g.

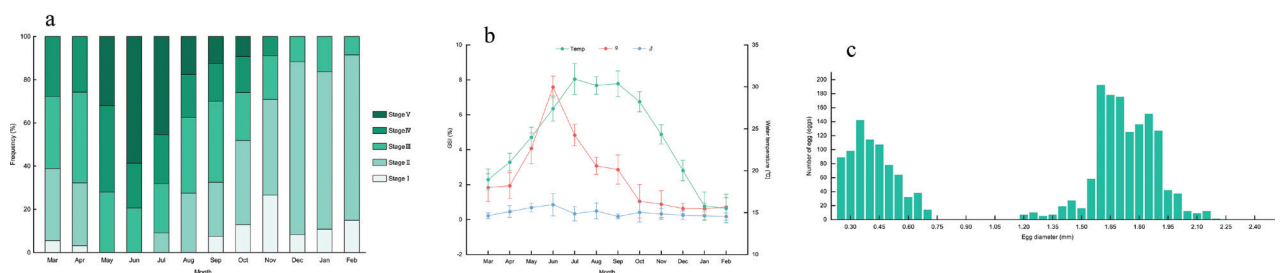
The standard length of the smallest sexually mature male was 9.0 cm, with a body weight of 28.19 g.

### Characteristics of seasonal changes in gonadal development

The gonadal weights of females ranged from 0.7 to 15.62 g, with a mean gonadal weight of 1.14 g. The gonadal weights of males ranged from 0.03 to 6.48 g, with a mean gonadal weight of 0.21 g (Suppl. material 1). The gonadal development of *C. zillii* was clearly cyclic (Figure 5b), and the changes in GSI were all in the form of a single peak (Figure 5b). There was a general consistency between the GSI and the changes in water temperature (Figure 5b). In March, 33.33% of the ovaries were in Stage III and 27.78% were in Stage IV (Figure 5a), with the GSI beginning to rise. In May, 30.20% of the ovaries were in Stage V (Figure 5a), while in June, the percentage of Stage V ovaries reached its highest point (58.62%) (Figure 5a), with a corresponding peak in the GSI. From July to October, there was a gradual decline in both the percentage of stage V ovarian and GSI. In November, the



**Figure 4.** Growth rate and acceleration of standard length and body weight of *Coptodon zillii* for overall samples (a, d), female samples (b, e) and male samples (c, f) in Shuikou Reservoir.



**Figure 5.** Annual changes in gonadal developmental stages of female samples (a), gonado-somatic index (GSI) (b) and distribution of egg diameter in stage IV ovaries (c) of *Coptodon zillii* in Shuikou Reservoir. Temp denotes water temperature. The symbol ♀ and ♂ denote GSI of female and male samples, respectively. Error bars denote standard error.

frequency of ovaries in stage V was reduced to zero, although some ovaries remained in stage IV (Figure 5a). From December to February, the majority of the ovaries were in stage I or II (Figure 5a), and the GSI reached its lowest point of the year. The breeding period of *C. zillii* in Shuikou Reservoir was estimated to span the months of March to November, with a peak observed in June.

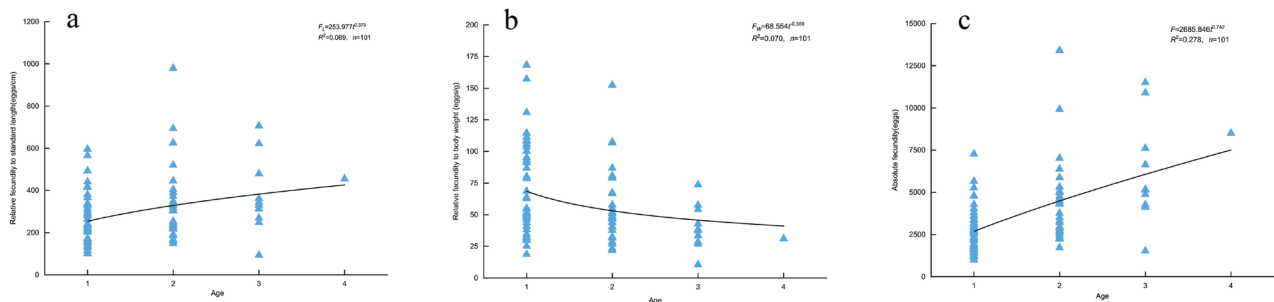
### Relationship between fecundity and age

The relative fecundity to standard length of females ( $n = 86$ ) ranged from 85.48 to 833.09 eggs/cm, with a mean value of 298.54 eggs/cm (Table 1). The relative fecundity to body weight ranged from 18.69 to 168.22 eggs/g, with a mean value of 59.89 eggs/g (Table 1). And the absolute fecundity ranged from 982 to 13413 eggs, with the mean value of 3854.38 eggs (Table 1). The relative fecundity to body weight was negatively correlated with age as in formula  $F_w = 68.554t^{-0.369}$ ,  $R^2 = 0.070$  ( $P > 0.05$ ) (Figure 6b), while the relative fecundity to standard length and absolute fecundity were positively correlated with age as in formula  $F_L = 253.977t^{0.373}$ ,  $R^2 = 0.089$  ( $P > 0.05$ ) (Figure 6a) and  $F = 2685.846t^{0.742}$ ,  $R^2 = 0.278$  ( $P > 0.05$ ) (Figure 6c), respectively.

**Table 1.** Fecundity of female fish of different ages.

Age	Sample size	Relative fecundity to standard length (eggs/cm)		Relative fecundity to body weight (eggs/g)		Absolute fecundity (eggs)	
		Mean±SE	Range	Mean±SE	Range	Mean±SE	Range
1	44	253.74±19.26 <sup>b</sup>	99.44-595.87	67.94±5.63 <sup>a</sup>	18.69-168.22	2765.70±207.68 <sup>c</sup>	991-7269
2	30	333.26±32.47 <sup>ab</sup>	85.48-833.09	56.61±5.24 <sup>ab</sup>	21.92-152.39	4366.76±443.03 <sup>ab</sup>	982-13413
3	11	400.67±48.42 <sup>a</sup>	93.58-402.46	42.57±4.70 <sup>b</sup>	26.74-73.65	6540.90±845.27 <sup>a</sup>	4125-11505
4	1	455.27	NA	31.12	NA	8513	NA
Total	86	298.54	85.48-833.09	59.89	18.69-168.22	3854.38	982-13413

Significant differences of fecundity between different age groups are indicated by superscript with different lowercase letters. SE denotes standard error. NA indicates that it could not be calculated because the sample size was less than 2.



**Figure 6.** Relationship between fecundity [Relative fecundity to standard length (a), Relative fecundity to body weight (b), Absolute fecundity (c)] and age of *Coptodon zillii* in Shuikou Reservoir.

### Distribution of egg diameter

The mean egg diameter was  $1.52 \pm 0.45$  mm, with a bimodal distribution of egg diameter (Figure 5c), indicating the presence of two types of oocytes in the ovaries of *C. zillii*. The first type of oocyte makes up 36.57% of the total number of eggs and its diameter varied between 0.25 and 0.70 mm. The second type of oocyte makes up 63.43% of the total number of eggs and its diameter ranged from 1.20 to 2.20 mm. It is hypothesized that this population of *C. zillii* is characterised by batch spawning.

## Discussion

### Age structure of the population

The age structure of fish populations is an important ecological characteristic, and changes in age structure reflect, to a certain extent, the adjustment of life-history strategies of fish populations in the face of ecological changes (Ma et al. 2024). In this study, the age structure of *C. zillii* population in Shuikou Reservoir was simple. Individuals of age 1 were the most numerous, accounting for 78.17% of the entire population, and the maximum age was age 6. This is similar to the age structure of *C. zillii* in Haebaru Reservoir, Okinawa, Japan (another invasion site), where the highest number of individuals was also found at age 1 (accounting for 52.38% of the entire population) and the maximum age was 7 (Ishikawa and Tachihara 2008). However, in one of the sites in its native range, Lake Nozha Hydrodrome, Egypt, individuals of age 1 accounted for only 3.96% of the entire population, while age 2 and 3 were the dominant age groups, with the number of individuals accounting for 67.84% of the entire population (Mahmoud et al. 2013). It can be seen that the population in the invasion site showed obvious rejuvenation compared with the native site, which may be attributed to the fact that the invasive population is still in the initial stage of population spread, the age structure is still not intact. It should be noted that a relatively under-aged population structure indicates that the population of *C. zillii* in Shuikou Reservoir is in a period of rapid growth, reflecting the strong potential for expansion of the population.

### Plasticity of growth characteristics

Plasticity in growth traits has been demonstrated in bleak (*Alburnus alburnus*) (Latorre et al. 2018), pumpkinseed sunfish (*Lepomis gibbosus*) (Fox et al. 2007), Amur sleeper (*Perccottus glenii*) (Joanna et al. 2011), and many other invasive fish species during the invasion process. In the present study, the growth coefficient ( $k$  value) of the *C. zillii* population in Shuikou Reservoir was 0.131, which was lower than those in both the native and invasive populations reported in the literature (see Table 2). The wide range of variation in  $k$  values (from 0.131 to 0.680) (Table 2) among different populations indicated a large inter-population variability in the growth rate of *C. zillii*. This is speculated to be the plasticity of growth performance in populations of *C. zillii* to adapt to different habitats. In addition, the two

**Table 2.** Comparison of growth characteristics of *Coptodon zillii* from native and introduced range.

Population source	Sampling site	Country	Standard length/cm	$b$	$k$	$L_{\infty}$ /cm	$W_{\infty}$ /g	Reference
Native	Wadi El-Raiyan Lakes	Egypt	8-30.5	3.088	0.49	33.5	819.33	Mehanna 2004
Native	Nozha Hydrodrom Lake	Egypt	NA	2.885	0.203	33.38	713.4	Mahmoud et al. 2013
Native	Timsah Lake	Egypt	7-16 (female)	2.975	0.680	17.83	109.54	Mahomoud et al. 2011
			8-21 (male)	3.005	0.320	22.05	201.74	
Native	Umhfein Lake	Libya	15-27	3.228	0.234	28.81	565.78	Hadi 2008
Introduced	Garmat Ali River	Iraq	7-22	3.237	0.168	28.4	455.65	Mohamed and Al-Wan 2020
Introduced	Haebaru Reservoir	Japan	3.1-13.8 (female)	NA	0.67	NA	NA	Ishikawa and Tachihara 2008
			3.3-16.8 (male)	NA	0.36	NA	NA	
Introduced	Shuikou Reservoir, Minjiang River	China	7.5-23.0	2.938	0.131	32.94	1381.01	present study

NA indicates a lack of corresponding data in the literature.

invasive populations (China, Iraq) all belonged to the medium-rate growth type, whereas the four native populations all belonged to the fast-growth type, which may reflect resource limitation and density-dependent effects acting upon the invasive populations. Similar results have been observed in invasive bighead carp (*Hypophthalmichthys nobilis*) (Coulter et al. 2018) and Indo-Pacific red lion-fish (*Pterois volitans*) (Dahl et al. 2019). At the same time, we also suggest that this is a resource allocation strategy of the invasive populations of *C. zillii* to shift energy inputs towards other physiological functions (e.g. reproduction) by sacrificing growth performance in response to the selection of abiotic or biotic factors in the new environments.

### Plasticity of reproductive characteristics

Successful reproductive strategies and their plasticity are crucial during the invasion process for fishes (Garcia-Berthou 2007). Typically, this plasticity involves higher reproductive investment (e.g. higher absolute fecundity, longer spawning seasons, earlier age at sexual maturity, etc.) compared to native populations (Bøhn et al. 2004; Britton et al. 2008; Joanna et al. 2011; Gutowsky and Fox 2012).

The onset of fish spawning and the duration of the reproductive period are usually dependent on temperature and photoperiod. However, some studies have shown that reproductive events in the same water body are not always directly related to these environmental parameters (Gertzen et al. 2016). Some invasive fish species spawn for extended periods of time in invaded water bodies to produce more offspring, thus rapidly expanding population sizes. For example, round goby (*Neogobius melanostomus*), native to the Caspian and Black Seas, spawns between May and September in their native habitat (Hôrková and Kováč 2014), but spawning time is extended in some invasive populations (Tomczak and Sopota 2006). Valiente et al. (2010) found that plasticity in spawning time gives brown trout (*Salmo trutta*) a competitive advantage when invading aquatic ecosystems in South America. In the present study, we observed that the spawning period of *C. zillii* in Shuikou Reservoir extends from March to November, exceeding the spawning periods of native populations from the Damietta tributary of the Nile River (El-Kasheif et al. 2013), the Lake Timsah in Egypt (Mahomoud et al. 2011), and Lake Kinneret in Israel (Ben-Tuvia 1978) in terms of spawning duration. While the spawning periods of *C. zillii* are highly variable in other invasion sites, for the sake of discussion, we have tabulated the spawning periods of *C. zillii* populations in the literature (Table 3). Differences in spawning time between population in the Shuikou Reservoir and other populations may depend on different environmental characteristics, such as water temperature, habitat, and food resources. However, we believe that a more important reason may be the plasticity of the reproductive characteristics of the populations. This is because the spawning time of *C. zillii* populations in two reservoirs (Shuikou Reservoir and Shanmei Reservoir), which have very similar environmental characteristics, also differed significantly. In addition, the average water temperature in Shuikou Reservoir was below 20°C (only 15–18°C) in March when spawning has just begun, and thus the water temperature at the time of the first spawning of females was below the range of water temperatures (22–28°C) reported in most literature (Li et al. 2023). We hypothesised that the invasive population in Shuikou Reservoir exhibits plasticity in the water temperature that is suitable for breeding. It has been reported in the literature (Coward and Bromage 1999) that *C. zillii* spawn on average every 26 days under favourable environmental conditions and with abundant food. So based on a spawning season of 270 days per year (from March to November), females in Shuikou Reservoir could theoretically lay an average of about 10 batches of eggs

**Table 3.** Comparison of reproductive characteristics of *Coptodon zillii* from native and introduced range.

Population source	Sampling site	Country	Breeding season	Average absolute fecundity/eggs	Reference
Native	Damietta branch of the River Nile	Egypt	May-Sep	3036	El-Kasheif et al. 2013
Native	Lake Timsah	Egypt	Jan-Aug	NA	Mahomoud et al. 2011
Native	Abu Qir bay	Egypt	NA	2139	Moharram and Akel 2007
Native	Lake Kinneret	Israel	Apr-Aug	NA	Ben-Tuvia 1978
Introduced	Lake Naivasha	Kenya	year-round	6606	Siddiqui 1979
Introduced	Lake Zwai	Ethiopia	year-round	NA	Negassa and Getahun 2003
Introduced	Garmat Ali River	Iraq	NA	2224	Mohamed and Al-Wan 2020
Introduced	Victoria Nyanza	Kenya	NA	3757.17	Lowe (McConnell) 1955
Introduced	Al-Swaib marshes	Iraq	Jun-Aug	3793	Qadoory 2012
Introduced	Aquarium keeping	Britain	NA	3606	Coward and Bromage 1999
Introduced	Pond feeding	Kenya	NA	2359	Dadzie and Wangila 1980
Introduced	Dongjiang River	China	May-Oct	7991	He et al. 2013
Introduced	Shanmai Reservoir	China	Apr-Sep	4009.85	Li et al. 2023
Introduced	Shuikou Reservoir, Minjiang River	China	Mar-Nov	3854.38	present study

NA indicates a lack of corresponding data in the literature.

per year. The extended spawning period maximises the reproductive potential of *C. zillii* in the Shuikou Reservoir and rapidly expands the population size.

Life-history theory (Stearns and Koella 1986) predicts that individuals from invasive populations will allocate more resources to reproduction than to growth (Ylikarjula et al. 1999), resulting in maturing at a much younger age compared to individuals from their native range (Philippart and Ruwet 1982). In a study conducted by Russell et al. (2012), it was observed that the age and body size at first sexual maturity of the invasive species of *Oreochromis mossambicus* in the Kewarra Beach drain in north-eastern Australia was significantly smaller than that of the native population. Fox (1994) conducted a comparative analysis of the life-history characteristics of native and non-native pumpkinseed (*Lepomis gibbosus*) populations, and observed that the non-native population exhibited earlier maturation and a smaller size than the native population. In the present study, the standard lengths of the smallest sexually mature female and male in Shuikou reservoir were 8.7 cm and 9.0 cm, respectively, and the minimum ages at sexual maturity were 0.44 and 0.41 years old, respectively. In their native range, the standard lengths at first sexual maturity of the female and male in Abu Qir Bay, Egypt, were 9.7 cm and 8.7 cm, respectively (Moharram and Akel 2007). The standard length at first sexual maturity of the female and male in Cross River, Nigeria, were 11.0 cm and 9.8 cm, respectively (Uneke and Nwani 2014). In other invaded sites, for example, in the AL-Swaib Marsh, Iraq, the standard lengths at first sexual maturity of the male and female were 13.2 cm and 12.4 cm, respectively (Qadoory 2012). In the Dongjiang River, China, the standard lengths at first sexual maturity of the male and female were 9.7 cm and 10.0 cm, respectively. The results of the above studies indicate that the standard lengths at first sexual maturity of the invasive populations are generally smaller than those of the native populations. Meanwhile, the standard lengths of the smallest sexually mature female and male in Shuikou Reservoir were observed to be smaller than those in the native and other invasion sites. The reasons for this may be attributed, on the one hand, to differences in genetic and environmental conditions between populations. However, on the other hand, it is more probable that this is an adjustment of reproductive strategies of invasive

populations in Shuikou Reservoir to adapt to the environment of their new habitats. This may be a common life-history strategy in invasive fishes, where a higher investment in fecundity in invasive populations is accompanied by a decrease in age and size at first sexual maturity compared to indigenous populations (Amundsen et al. 2012; Gutowsky and Fox 2012; Masson et al. 2016; Masson et al. 2018).

Fish fecundity is a widely used indicator of reproductive capacity in breeding populations, serving as an adaptive compensation to external environmental factors (Roff 1992). The fecundity of many invasive species is regarded as a plastic trait, with females exhibiting trade-offs between the number and size of eggs spawned in response to environmental factors (Marshall and Uller 2007; Allen et al. 2008). The bighead carp (*Aristichthys nobilis*) and silver carp (*Hypophthalmichthys molitrix*) that have invaded the Upper Mississippi River in the United States have been observed to exhibit plasticity in fecundity (Lenaerts et al. 2023). The plasticity in fecundity of *Cichla kelberi* may be a principal factor responsible for its successful colonisation and invasion in the Lajes Reservoir in southeastern Brazil (Soares et al. 2021). The present study revealed that the population of *C. zillii* in Shuikou Reservoir exhibited a high level of fecundity, with a range of absolute fecundity from 991 to 13,413 eggs and a mean value of 3,809 eggs. For purposes of comparison and analysis, the results of previous studies on the fecundity of *C. zillii* in the native and invasive sites are summarized in Table 3. *C. zillii* demonstrated varying degrees of fecundity in different environmental settings, from its native tropical riverine habitat to tropical and subtropical rivers and reservoirs within its invasive range. The variation in fecundity observed among the populations in their native and invasive habitats may be attributed to differences in climatic conditions (e.g., temperature, photoperiod, etc.), age and nutritional status of the individuals, etc. However, this also reflects the ability of *C. zillii* to adapt to a variety of habitat environments and adjust the level of fecundity, indicating its strong plasticity in reproductive traits. Concurrently, our findings revealed that the absolute fecundity of populations in the invasive sites were superior to those of the populations in the native sites. When these observations were considered alongside the altered patterns of the length at the first sexual maturity (shorter in the invasive site than in the native site) and the time of spawning (longer in the invasive site than in the native site), we postulated that the *C. zillii* population in Shuikou Reservoir exhibited a high degree of plasticity in reproductive characteristics. To rapidly establish a population in the new environment of the invasive site, it is probable that they will allocate more energy required for early growth and development to gonadal development, thus maintaining a high fecundity of the population. This phenomenon has been observed in a variety of invasive fish species, including the round goby (*Neogobius melanostomus*) (Hôrková and Kovác 2014) and the bluegill sunfish (*L. macrochirus*) (Ma et al. 2024).

### Life-history strategies and invasion management

The life-histories of fish are more flexible than those of thermostats, and often adjust in response to changes in environmental stressors in order to maximise fitness (Nelson et al. 2016). Equilibrium life-history strategies provide a natural advantage to fish as they invade new habitats, but the ability to shift to opportunistic life-history strategies may facilitate the expansion of invasive fish populations (Vila-Gisper et al. 2005; Olden et al. 2006). For example, opportunistic life-history strategies facilitated the successful invasion of the pumpkinseed (*L. gibbosus*) in Europe (Fox and Copp 2014). A combination of opportunistic and equilibrium life-history strategies was identified as a key factor in the successful invasion of the Shimofuri goby

(*T. bifasciatus*) in Nansi Lake, China (Qin et al. 2020). In this study, population of *C. zillii* in Shuikou Reservoir exhibited early maturity, a prolonged reproductive period, and high fecundity, which are hallmarks of opportunistic life-history strategies. Additionally, they demonstrated parental care behaviors in an equilibrium life-history strategy. The entire population displayed high reproductive potential and recovery ability, which facilitates a rapid expansion of the population.

Given the extent of the expansion of *C. zillii* in Shuikou Reservoir, eradication is no longer a viable option. In light of the findings of this study, the following recommendations are put forth as a means of effectively curbing the rapid spread of this species. The first step is to conduct tracking and monitoring of the invasive populations of *C. zillii*. Advanced technologies such as environmental DNA (eDNA) meta-barcoding are recommended to monitor low-density populations and combined with acoustic telemetry to track dispersal patterns. Long-term monitoring must assess seasonal abundance shifts, particularly in thermally favorable zones (>24°C), where spawning aggregations occur. The second step is to use a variety of measures to effectively control the invasive populations of *C. zillii*. Regular and intensive fishing and removal of the redbelly tilapia by local people mobilised by the fisheries authorities should be carried out, so as to reduce the size of its population. At the same time, during the breeding season (March to November) of the *C. zillii*, the fishing intensity is increased in the waters where it nests and spawns to control the number of juveniles. It is recommended that the protection and restoration of native piscivores (e.g., *Culter alburnus*, *Siniperca chuatsi*, *Siniperca scherzeri*) in Shuikou Reservoir be strengthened. Scientific stocking of native piscivore in this reservoir should be put into practice based on a comprehensive resource assessment. This will inhibit the number of eggs and fry of *C. zillii* and reduce the density of its juveniles through predation and competitive effects. Breeding and releasing of indigenous fish (e.g. *Channa maculata*) with similar life-history characteristics to *C. zillii* should be considered. Furthermore, the stocking of large-size indigenous fish into the habitat of *C. zillii* may result in the reduction of the population size of *C. zillii* due to interspecific competition for resources. The third step is habitat restoration in waters invaded by *C. zillii*. A comprehensive assessment of the invaded ecosystem, including water quality analyses, biodiversity surveys, and mapping of *C. zillii* distribution, must be conducted to determine the extent of the invasion and the specific habitats degraded. Displaced or threatened native species should be reintroduced or protected through breeding programmes and habitat enhancement measures. Ecosystem stability should be maintained through restoration of aquatic vegetation at the site of invasion.

## Conclusions


In this study, we analysed the life-history traits of *C. zillii* in Shuikou Reservoir, Minjiang River. The ecological mechanisms underlying its successful invasion in terms of growth, reproduction and age composition were preliminarily explored. We found that *C. zillii* possessed opportunistic (e.g., early maturation, prolonged reproductive period and high fecundity) life-history strategies. On the other hand, previous studies have demonstrated that they also possess parental care (Geletu et al. 2024), which is associated with an equilibrium life-history strategy, suggesting that the combination of these two life-history strategies may be important for *C. zillii* in the water bodies of southern China. Our work provides, for the first time, information on the life history of *C. zillii* in the natural ecosystem of the Minjiang River Basin in Fujian Province, China, and provides a basis for elucidating the invasion mechanism and for future management and control of this species.

## Author contributions

S. Tang and J. Zhao conceived and designed the study. S. Tang and Y. Xing collected the data. S. Tang conducted the data analysis and wrote the manuscript with contributions from T. Geletu. All authors contributed to draft manuscripts and approved the final manuscript for publication.

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## Ethics and permits

The experimental protocol was approved by the Institutional Animal Care and Use Committee (IACUC) of Shanghai Ocean University (permit number: SHOUDW2024085), and complies with the Guidelines on Ethical Treatment of Experimental Animals established by the Ministry of Science and Technology, China.

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## Supplementary material 1

Standard length (SL), body weight (BW), eviscerated weight (EW), gonad weight (GW) and overall sex ratio of *Coptodon zillii* at all ages in Shuikou Reservoir

Authors: Shoujie Tang, Ying Xing, Temesgen Tola Geletu, Jinliang Zhao

Data type: docx

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## Supplementary material 2

von Bertalanffy growth equation of *Coptodon zillii* in Shuikou Reservoir

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Data type: docx

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