Age, growth, mortality and recruitment of thin sharpbelly *Toxabramis swinhonis* Günther, 1873 in three shallow lakes along the middle and lower reaches of the Yangtze River basin, China

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ABSTRACT

Despite being the most dominant and widespread small fish species in the lakes along the middle and lower reaches of the Yangtze River basin, *Toxabramis swinhonis* has been paid little attention by fisheries scientists and little is known about its population characteristics. For this reason, we estimated age, growth, mortality and recruitment of this species based on three shallow lakes, Biandantang Lake, Shengjin Lake and Kuilei Lake (BDT, SJH and KLH, respectively) in this region. A total of 13,585 (8,818 in BDT, 2,207 in SJH and 2,560 in KLH) individuals were collected during monthly sampling from July 2016 to September 2017. The results revealed that the age structures of *T. swinhonis* consisted of four age groups (0^+–3^+), with 0^+–1^+ year old fish comprising more than 98% of the samples. Allometric growth patterns were displayed by fish from all sampling sites and the von Bertalanffy growth functions estimated were $L_t = 173.25 \, (1 - e^{-1.20 \, (t + 1.09)})$: BDT; $L_t = 162.75 \, (1 - e^{-1.20 \, (t + 1.08)})$: SJH and $L_t = 215.25 \, (1 - e^{-1.20 \, (t + 1.12)})$: KLH, respectively. The rates of total mortality (Z), natural mortality (M) and fishing mortality (F) at BDT, SJH and KLH were computed as 5.82, 5.50 and 4.55 year^{-1}; 1.89, 1.87 and 1.75 year^{-1}; 3.93, 3.63 and 2.80 year^{-1}, respectively. Meanwhile, growth performance indices (ϕ') were 0.68 (in BDT), 0.66 (in SJH) and 0.62 (in KLH), which indicated that *T. swinhonis* were overfished slightly in all study areas. Area-specific recruitment patterns were similar to each other, displaying evidence of batch spawning, with major peaks in April and August, accounting for 92.21% (BDT), 88.21% (SJH) and 88.73% (KLH) of total recruitment, respectively. These results showed that brief generation-time, fast growth rate, relatively high natural mortality rate and strong reproductive capacity (*r*-strategies) are reasons why this species became the most dominant species in many lakes of China.

INTRODUCTION

Many lakes (about 4,000) distributed along the middle and lower reaches of the Yangtze River basin (China) account for approximately 1/3 of the total area of lakes in China (*Liu & He, 1992*; *Li, 2004*). These lakes are typically shallow (no thermal stratification) with numerous submerged aquatic macrophytes and generally have higher fisheries productivity (*Li, Zhang & Li, 2010*; *Ye et al., 2014*). However, due to intensive removal of piscivores and overfishing by commercial fisheries in the past decades, short-lived small fish such as *Hyporhamphus intermedius* (Cantor, 1842), *Hemiculter leucisculus* (Basilewsky, 1855), *Coilia ectenes taihuensis* (Yen et Lin, 1976), *Cultrichthys erythropterus* (Basilewsky, 1855), *Pseudobrama simoni* (Bleeker, 1864) and *Toxabramis swinhonis* Günther, 1873 gradually become dominant species in these lakes and account for about 2/3 of total species (40–70 species in one lake) (*Li et al., 1988*; *Cao et al., 1991*; *Liu et al., 2005*; *Mao et al., 2011*; *Ye et al., 2014*). *T. swinhonis* was the most dominant of these species, accounting for more than 85% of total individuals caught in some lakes (*Ge, Zhong & Tang, 2009*) and showing an increase trend in abundance (*Li et al., 2018*), which elevated our concerns on the sustainability of fisheries resources in these water bodies.

Besides, despite not a fishery target, *T. Swinhonis* is still very valuable in terms of ecology and fisheries management as it is one of the main bycatch species in China's freshwater fishery, an important potential food resource for the carnivorous aquatic organisms (*Dai et al., 2015*; *Ye et al., 2014*) and plays a key role in the energy flows of their living hydro-ecosystems, linking zooplankton (as *T. swinhonis* mainly feeds upon copepods, cladocerans and insect larvaes) to higher trophic levels (*Zhang, 2005*). Meanwhile, many fisheries scientists pointed out that there existed a close relationship between population expansion and particular features of biology and ecology (*Peter, 1980*; *Wang et al., 2013*; *Guo et al., 2016*). Thus, it is the time that much more attentions should be paid on the biology and ecology of this outbreak species.

Published information on the biology and ecology of *T. swinhonis* is scarce. *Li et al. (1988)* defined this species as a small coarse fish and speculated on population control methods based on two reservoirs in northern China. *Xie, Cui & Li (2001a, 2001b)* investigated the relationship between diet and morphology of this species and also examined the association of submerged macrophytes in Liangzi Lake, China to density and biomass of this species. *Ye et al. (2014)* studied the growth and mortality of this species using length-based approaches in Niushan Lake, China.

In order to better understand the biology and ecology of this species and explain why it has become the most dominant fish species in many freshwater lakes of China, we conducted the present study to: (a) provide novel and comprehensive population characteristics of *T. swinhonis*, especially age structure (first report in the study regions), (b) identify demographic characteristics consistent with rapid population expansion and (c) provide potential strategies for fishery management on *T. swinhonis*.
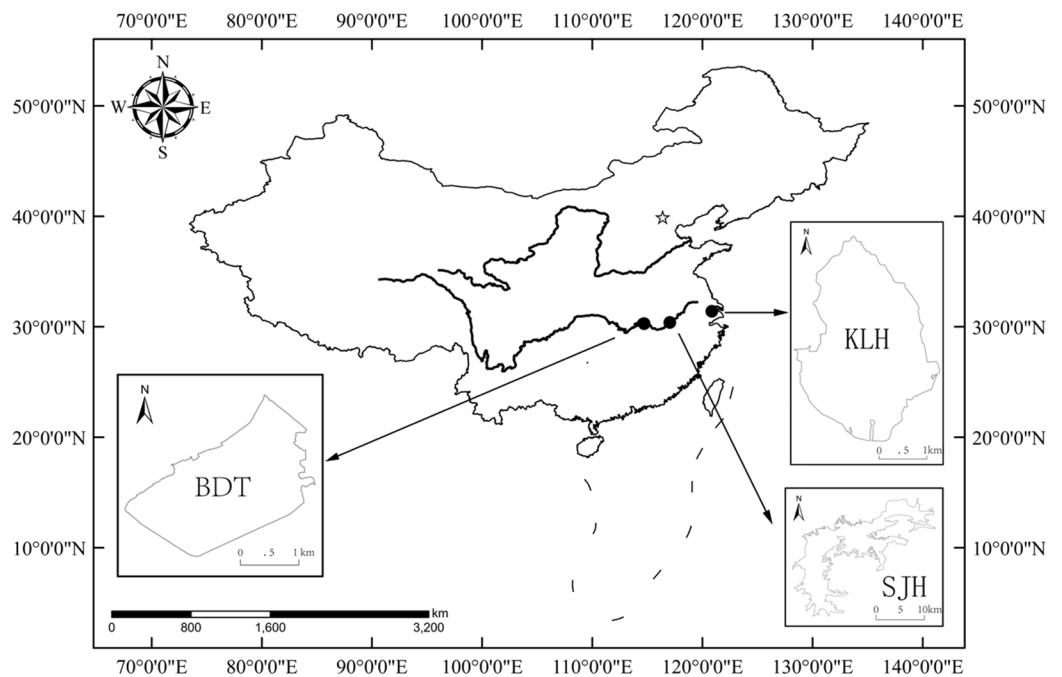
Figure 1 Map of the study area and locations of the three sampling sites for *T. swinhonis* (in the middle and lower reaches of Yangtze River basin, China). BDT, SJH and KLH are the abbreviations for Biandantang Lake, Shengjin Lake and Kuilei Lake, respectively.　　Full-size 🖼 DOI: 10.7717/peerj.6772/fig-1

MATERIALS AND METHODS

Study sites

The present study was performed in three shallow lakes (no thermal stratification), Biandantang Lake (BDT) (114°43′E, 30°15′N), Shengjin Lake (SJH) (117°03′E, 30°23′N) and Kuilei Lake (KLH) (120°51′E, 31°24′N), along the middle and lower reaches of the Yangtze River basin, China. These lakes are scattered longitudinally in this region. BDT, SJH and KLH are upstream, midstream and downstream, respectively (Fig. 1).

Data collection and fish sampling

Toxabramis swinhonis were collected monthly from July 2016 to September 2017 using multi-mesh gillnets (1.5 × 30 m) (*Appelberg et al., 1995*). In order to obtain sufficient samples, sampling time in each lake was at least 3 days monthly. In addition, larval and juvenile *T. swinhonis* were caught by fishermen using electrofishing gear to ensure a representative and unbiased assessment of their biological characteristics. Total lengths (L) were measured to nearest 0.01 mm with a vernier caliper and body weights (W) were recorded to the nearest 0.01 g with a precision balance in the field. Sex was determined macroscopically. Scales were removed randomly from the middle portion of the lateral body of 30 individuals per month from each site and stored in small envelopes labeled with sampling site and morphometric data (*Narejo et al., 2009*; *Zhang & Li, 2002*). Lake surface temperatures (LST) were recorded every 4 h throughout the study period using HOBO Temp/Light data loggers (start time 8 am) (*da Cunha, 2015*;

Dalton et al., 2016). All the procedures described here were approved by the ethics committee of the Institute of Hydrobiology, Chinese Academy of Sciences (Y216011101).

Length distribution and length–weight relationship

Kolmogorov–Smirnov tests (K–S tests) were used to evaluate the similarity of length–frequency distribution between different sampling sites and normality of data. Differences in mean L of *T. swinhonis* among sites were evaluated using Kruskal–Wallis test with Tukey's post-hoc when the error or data was not a normal distribution. The relationship between length and weight was calculated for each site using power regression equation:

$$W = a\mathrm{L}^b e^\varepsilon, \ \varepsilon \sim \mathrm{N}\left(0, \sigma^2\right),$$

where *a* is the intercept of the regression or shape coefficient and *b* is the allometric or slope parameter (*Ricker, 1975*). The optimal regression parameters were gained by minimizing the residuals errors using the ordinary least square method (*O'Brien, 2012*). Student's *t*-test was utilized to test whether the slope of regression was significantly different from 3, indicating the growth pattern of fish: isometric ($b = 3$, no change of density and shape as one fish grows), positive allometric ($b > 3$, the fish becomes relatively stouter or deeper-bodies as it becomes longer) or negative allometric ($b < 3$, fish becomes slimmer as it grows) (*Ye et al., 2007*). Generally, the allometric coefficient (*b*) is within the range from 2 to 4 for most fish species (*Koutrakis & Tsikliras, 2003*), and thus this thumb rule can be used to corroborate the validation of the length and weight relationships of *T. swinhonis* in our study. All statistical analyses were performed using R software version 3.3.2 (*R Core Team, 2017*) with significance level (α) equal to 0.05.

Growth

Growth of a fish can be described as an increase in either length or weight. Several mathematical equations have been created to model fish growth. One of these, the von Bertalanffy growth model (VBGM), is widely used to model growth of fishes. Thus, we used the VBGM to describe the growth of *T. swinhonis* in the current study. The typical VBGM is represented by (*Von Bertalanffy, 1938*):

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right),$$

where L_t is the expected or average L at time (or age) *t*, L_∞ is the mean asymptotic L, *K* is the rate at which L_∞ is approached and t_0 is the hypothetical age at which fish L equals zero. While VBGM parameters can be estimated by length (weight)-age approach, the length-based method is most extensively adopted, especially in the tropical and subtropical regions (*Sparre & Venema, 1998*). In this study, length–frequency datasets with a constant class size (5 mm) were used to obtain the optimal growth parameters (corresponding to the maximum of the goodness of fit index, R_n) using the FiSAT II software (*Gayanilo, Sparre & Pauly, 2005*) and the module of

ELEFAN I (*Pauly, 1986*). The theoretical age (t_0) was determined by the empirical equation of *Pauly (1983)*:

$$\log_{10}(-t_0) = -0.392 - 0.275 \log_{10}(L_\infty) - \log_{10}(K).$$

In order to compare the growth performance of different geographical populations, the growth performance index (GPI) ϕ' (phi-prime) was calculated using the following formula (*Pauly & Munro, 1984*):

$$\phi' = \log_{10}(K) + 2\log_{10}(L_\infty).$$

Additionally, in order to verify the accuracy of length-based analysis, the potential or expected longevity (t_{max}) of *T. swinhonis* was calculated based on *Pauly's (1983)* empirical equation:

$$t_{max} = \frac{3}{K},$$

where t_{max} is the approximate maximum age of *T. swinhonis* at each study site, and K is the growth constant in von Bertalanffy growth function.

Age estimate

Scales of *T. swinhonis* were immersed in 10% NaOH solution for 3 h, cleaned with running water and examined under a dissecting microscope to determine age (*Steinmetz & Müller, 1991*). Four to six scales were examined from each fish, and age was eventually defined as the most frequently occurring age from the scales.

Mortality coefficients and fisheries status

To obtain the total mortality rates (Z), the length-converted catch curves were applied to the pooled length frequency datasets using the estimated growth parameters. This process was done using the FiSAT II package and mortality menu (*Gayanilo, Sparre & Pauly, 2005*).

The natural mortality rates (M) were obtained from *Pauly's (1980)* empirical equation:

$$\log_{10}M = -0.0066 - 0.279 \log_{10}L_\infty + 0.6543 \log_{10}K + 0.4634 \log_{10}T,$$

where T is the average annual LST (°C) (in the present study, along the direction of increase of longitude, $T = 17.5$, 16.6 and 17.1 °C, respectively), a proxy for the habitat temperature (*Pauly, 1980*). The validity of estimates of M can be judged by the M/K ratio as this ratio has been demonstrated to be within the range of 1.12–2.50 for most species around the world (*Beverton & Holt, 1957*).

Fishing mortality (F) was estimated from the equation $F = Z - M$ (*Gulland, 1965*).

We estimated exploitation rate (E) using the equation of *Elliott (1983)*:

$$E = \frac{F}{Z}.$$

Recruitment time and pattern

Timing and patterns of recruitment to *T. swinhonis* stocks were determined by backward projection of the length–frequency datasets onto the time axis of a time-series of
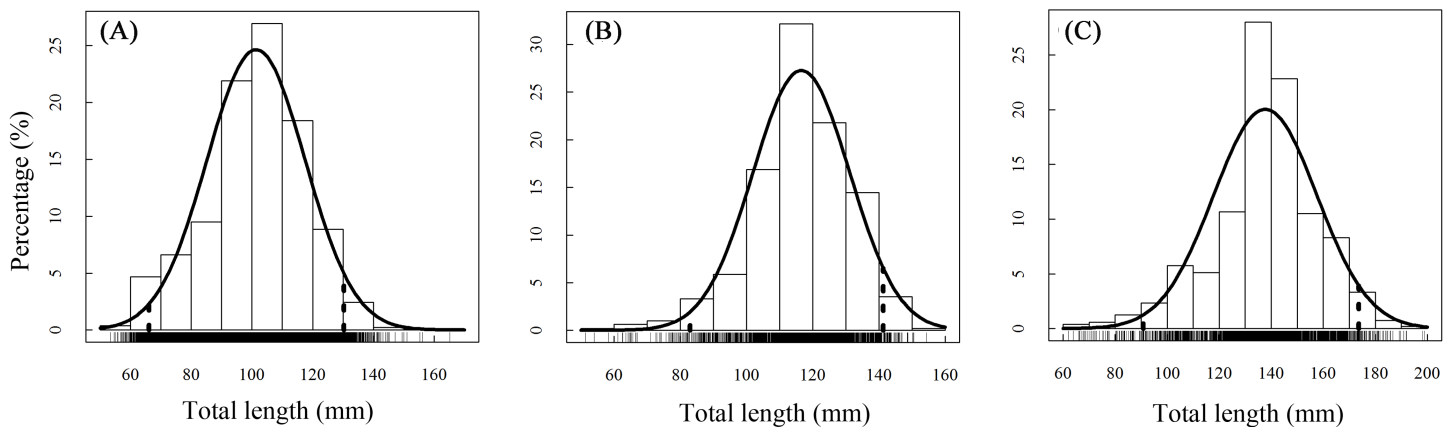
Figure 2 Annual total length frequency distribution of *T. swinhonis* in (A) BDT, (B) SJH and (C) KLH.
Full-size 🖼 DOI: 10.7717/peerj.6772/fig-2

samples as described in FiSAT II (*Moreau & Cuende, 1991*). This routine can provide the relative spawning time and the number of recruitment pulses (recruitment pattern) per year.

RESULTS

Length–frequency distribution and age structure

A total of 13,585 individual *T. swinhonis* were measured during 15 months of field sampling. The length–frequency distributions of *T. swinhonis* are shown in Fig. 2. Lengths of *T. swinhonis* ranged from 53.32 to 165.16 mm L (mostly between 60 and 140 mm) in BDT, from 51.39 to 154.35 mm (mostly between 80 and 140 mm) in SJH and from 61.94 to 198.85 mm (mostly between 100 and 180 mm) in KLH. Results from K–S tests indicated that length frequency distribution data were non-normal in three lakes (for all three K–S tests, $D = 1$, $P \approx 0$ ($< 2.2 \times 10^{-16}$), $E = 1$). Individual comparisons of these distributions indicated statistical differences between lakes (for BDT and SJH, $D = 0.43$, $P \approx 0$ ($< 2.2 \times 10^{-16}$), $E = 0.43$; for BDT and KLH, $D = 0.75$, $P \approx 0$ ($< 2.2 \times 10^{-16}$), $E = 0.75$ and for SJH and KLH, $D = 0.56$, $P \approx 0$ ($< 2.2 \times 10^{-16}$), $E = 0.56$). Kruskal–Wallis test ($\chi^2 = 5{,}186.90$, $df = 2$, $P \approx 0$ ($< 2.2 \times 10^{-16}$), $E = 0.28$) revealed that there was a statistical difference in mean L among different sampling sites and represented a trend of L increasing with the increasing longitude (Fig. 3).

Age structure of the *T. swinhonis* specimens collected from the three lakes, as determined from scales, were simple and consisted of four age groups ranging from 0^+ to 3^+ years (Fig. 4), similar to results obtained using *Pauly's (1983)* empirical equation for maximum age ($t_{max} = 3/K$, all sites were 2.5). The dominant age group was 0^+–1^+ year old fish at all three sites (98%) (Table 1). These data suggest that *T. swinhonis* is a short-lived fish species. A chi-square test found significant differences among the age structures at the three sampling sites ($\chi^2 = 103.82$, $df = 6$, $P = 4.00 \times 10^{-20}$, $E = 0.18$).
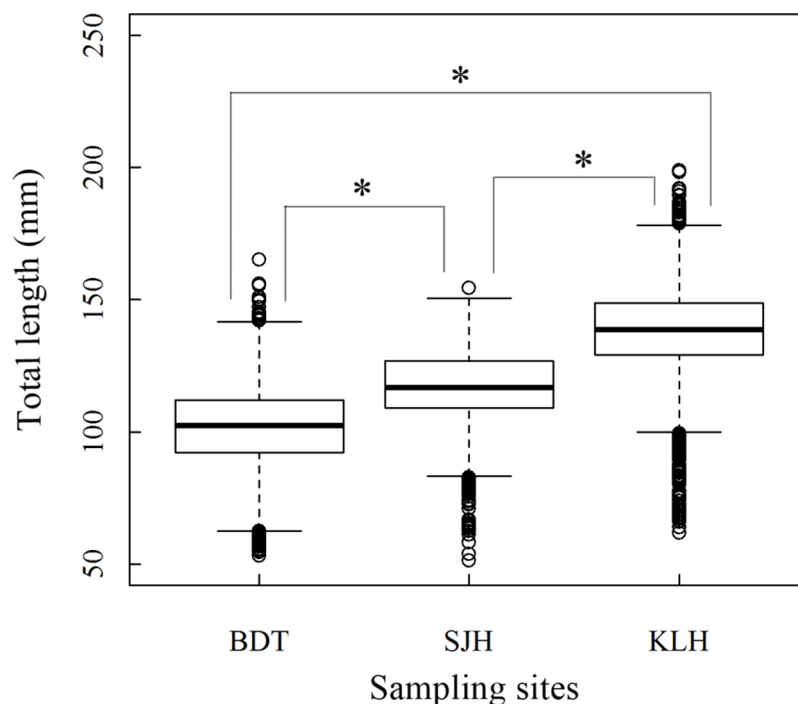
Figure 3 Boxplot (horizontal line within box: median; boundaries of the box: first and third quartiles; bars: lower and upper inner fences; circles: outliers) about Kruskal–Wallis test in the total length (L) of *T. swinhonis* at different sampling sites.　　　Full-size ☑ DOI: 10.7717/peerj.6772/fig-3

The length–weight relationships and growth pattern

Length and weight relationships for each site (sexes combined) were (Fig. 5):

BDT: $W = 0.000008 \; L^{2.906}$, $R^2 = 0.87$, $n = 8,818$;

SJH: $W = 0.00002 \; L^{2.734}$, $R^2 = 0.87$, $n = 2,207$;

KLH: $W = 0.0000001 \; L^{3.775}$, $R^2 = 0.89$, $n = 2,560$.

There were significant differences obtained from the statistical comparisons of total length and weight relationships among different sites (for BDT and SJH, $F = 58,960$, $df_1 = 1$, $df_2 = 8,816$, $P \approx 0 \; (< 2.2 \times 10^{-16})$, $E = 0.87$; for BDT and KLH, $F = 15,800$, $df_1 = 1$, $df_2 = 2,205$, $P \approx 0 \; (< 2.2 \times 10^{-16})$, $E = 0.87$ and for SJH and KLH, $F = 19,870$, $df_1 = 1$, $df_2 = 2,558$, $P \approx 0 \; (< 2.2 \times 10^{-16})$, $E = 0.89$). All slope coefficients (b values) were significantly different from the value of 3 for all three lakes (for BDT, $t = -7.84$, $df = 8,816$, $P = 5.15 \times 10^{-15}$, $E = 0.08$; for SJH, $t = -12.22$, $df = 2,205$, $P = 2.74 \times 10^{-33}$, $E = 0.26$ and for KLH, $t = 28.93$, $df = 2,558$, $P = 1.74 \times 10^{-159}$, $E = 0.57$), indicating an allometric growth pattern of *T. swinhonis* for all sampling populations.

Growth parameters

Since the age structure of *T. swinhonis* was simple, we estimated growth parameters using the methods of Powell and Wetherall, which are contained in the ELEFAN I module
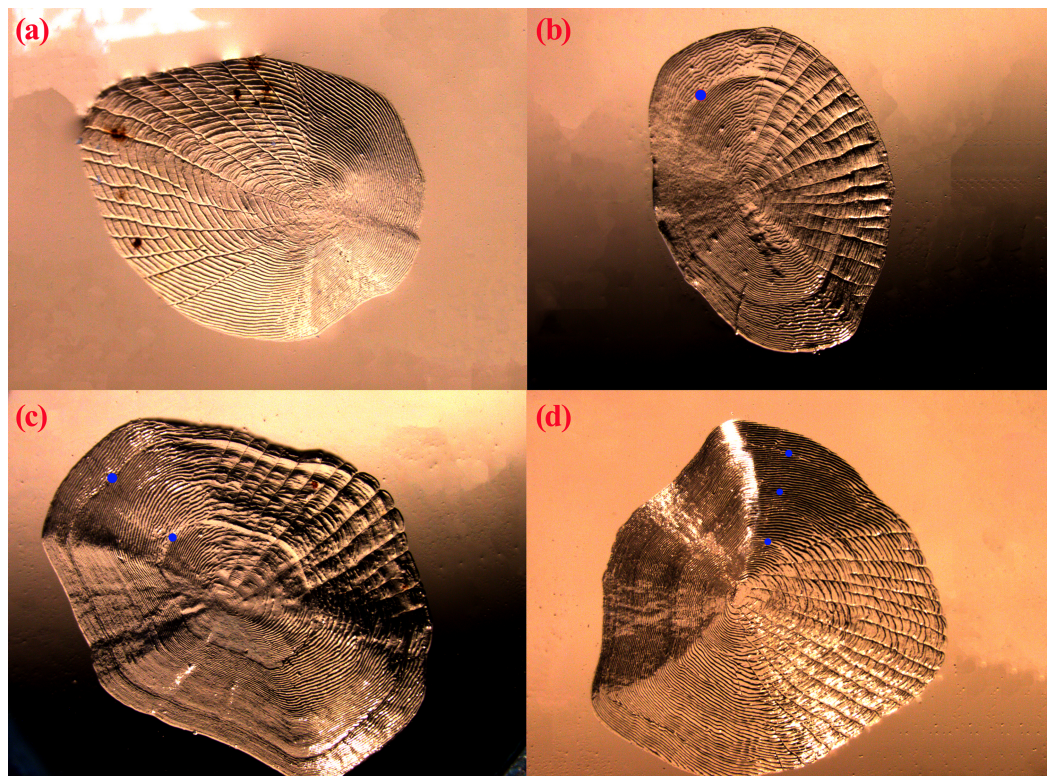
Figure 4 The scales of *T. swinhonis* from BDT Lake with (A), (B), (C) and (D) corresponded with 0⁺, 1⁺, 2⁺ and 3⁺ years, respectively. Blue dots represented the annuli.
Full-size ⬜ DOI: 10.7717/peerj.6772/fig-4

Table 1 Mean observed length (mm)-at-age for *T. swinhonis* fish from Biandantang Lake, Shengjin Lake, and Kuilei Lake.

Age	Biandantang Lake			Shengjin Lake			Kuilei Lake		
	Mean ± S.E. (mm)	n	Percentage (%)	Mean ± S.E. (mm)	n	Percentage (%)	Mean ± S.E. (mm)	n	Percentage (%)
1	102.99 ± 1.01	307	74.15	113.85 ± 0.87	316	65.83	131.19 ± 1.09	298	45.43
2	111.05 ± 1.28	99	23.92	127.97 ± 0.79	157	32.71	153.73 ± 0.74	351	53.51
3	116.91 ± 7.16	6	1.45	131.46 ± 2.62	7	1.46	166.60 ± 8.24	7	1.06
4	131.91 ± 13.68	2	0.48	NA	NA	0.00	NA	NA	0.00

Note:
NA, not available; n, the number of specimen; S.E., standard error.

of the FiSAT II program. The results were BDT: $L_\infty = 173.25$ mm, $K = 1.20$, $t_0 = -1.09$, $R_n = 0.21$; SJH: $L_\infty = 162.75$ mm, $K = 1.20$, $t_0 = -1.08$, $R_n = 0.29$; KLH: $L_\infty = 215.25$ mm, $K = 1.20$, $t_0 = -1.12$, $R_n = 0.24$. The growth equations obtained above showed that *T. swinhonis* grew rapidly during the first year of it's life history, obtaining an average L of approximately 159.14, 149.34 and 198.34 mm with the increase of longitude during the first year, respectively, for BDT, SJH and KLH (more than 90% of L_∞ at all sites). Annual growth in L decreased sharply after this period and became relatively constant thereafter (Fig. 6). In addition, the GPI (ϕ') of *T. swinhonis* in BDT, SJH and KLH were 4.56, 4.52 and 4.75, respectively.
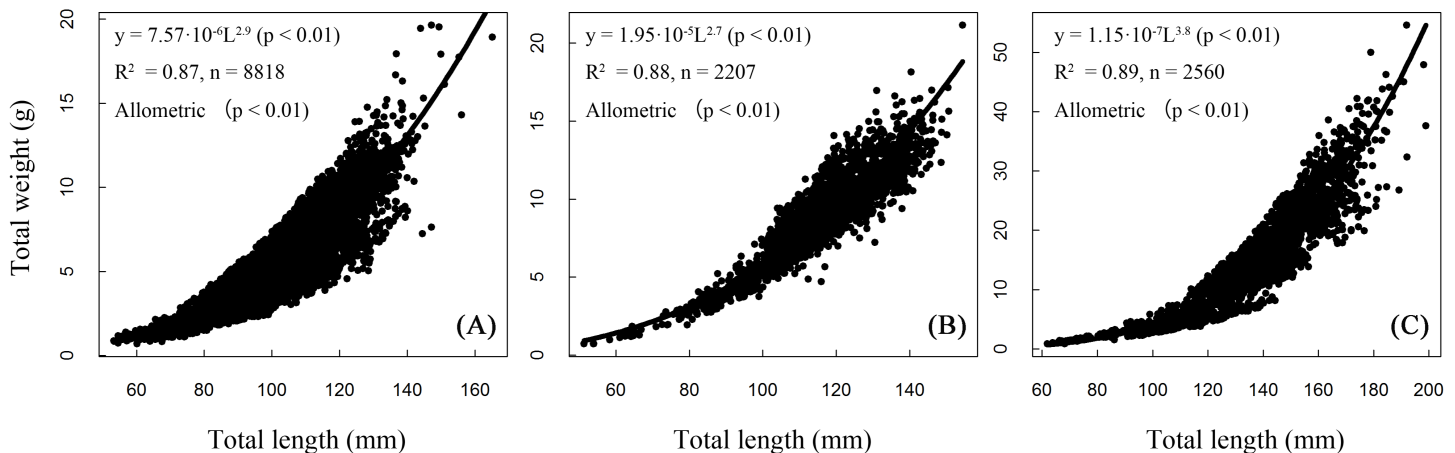
Figure 5 Total length–weight relationships of *T. swinhonis* in (A) Biandantang Lake, (B) Shengjin Lake and (C) Kuilei Lake.

Full-size ⬜ DOI: 10.7717/peerj.6772/fig-5

Mortality and exploitation rates

The total rates of mortality (Z) obtained through the length-converted catch curves were 5.82 year^{-1} (with 95% confidence interval of Z: 3.29–8.36 year^{-1}) for BDT, 5.50 year^{-1} (with 95% confidence interval of Z: 3.31–7.70 year^{-1}) for SJH and 4.55 year^{-1} (with 95% confidence interval of Z: 3.86–5.23 year^{-1}) for KLH (Fig. 7). The parameters of natural mortality rate (M) estimated by *Pauly's (1980)* empirical equation were 1.89 year^{-1} (BDT), 1.87 year^{-1} (SJH) and 1.75 year^{-1} (KLH), respectively. For BDT, SJH and KLH, the values of M/K ratio were 1.58, 1.56 and 1.46 and the fishing mortality rates (F) were 3.93, 3.63 and 2.80 year^{-1}, respectively. The exploitation rates (E) for three sampling populations of *T. swinhonis* were calculated as 0.68 (BDT), 0.66 (SJH) and 0.62 (KLH) year^{-1}, respectively, which indicated that the stocks in the present study areas have been overfished slightly.

Recruitment time and pattern

Recruitment time and pattern of *T. swinhonis* were similar at all sampling sites. The recruitment pattern was continuous and showed two major peaks throughout the year (Fig. 8), which indicated batch spawning by *T. swinhonis*. Recruitment occurred from March to September with peaks in April and August. These two peaks accounted for 92.21% (BDT), 88.21% (SJH) and 88.73% (KLH) of total recruitment, respectively.

DISCUSSION

Size and distribution of length

Knowledge about size structure would be used for understanding age, growth, recruitment and dynamics of the population, which varies with the size structure of the population (*Mirzaei, Yasin & Hwai, 2014*). Generally, the size structure of one fish species can be represented by the length–frequency distribution (*Taiwo, 2010*). In the present
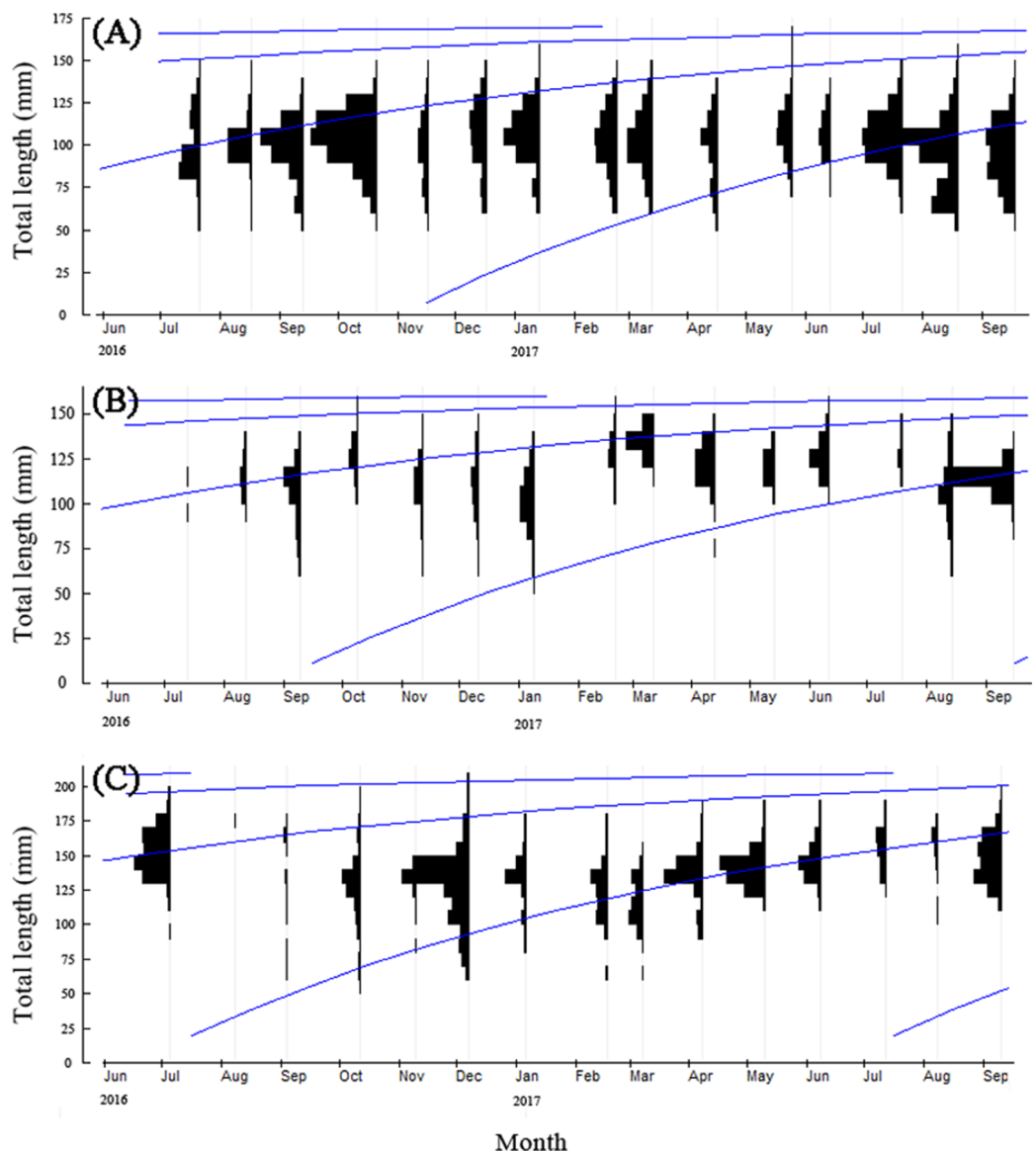
Figure 6 The von Bertalanffy growth curves of *T. swinhonis*in in (A) Biandantang Lake, (B) Shengjin Lake and (C) Kuilei Lake as superimposed on the length–frequency histograms. The different solid lines (blue) corresponded with different cohorts.   Full-size 🖾 DOI: 10.7717/peerj.6772/fig-6

study, the L of *T. swinhonis* in BDT ranged from 53.32 to 165.16 mm (the majority in 60–140 mm), in SJH from 51.39 to 154.35 mm (the majority in 80–140 mm) and in KLH from 61.94 to 198.85 mm (the majority in 100–180 mm), and represented an increasing trend in L with increasing longitude. The Kolmogorov-Smirnov tests indicated that length frequencies for *T. swinhonis* were non-normally distributed at all sites and that there were statistical differences between all sites. Besides, the results obtained from the present study were much larger than the findings of all previous works (Table 2). The disparity observed in the size of *T. swinhonis* in different studies might be caused by one or more of the following elements: (1) differences of habitat (such as the temperature,
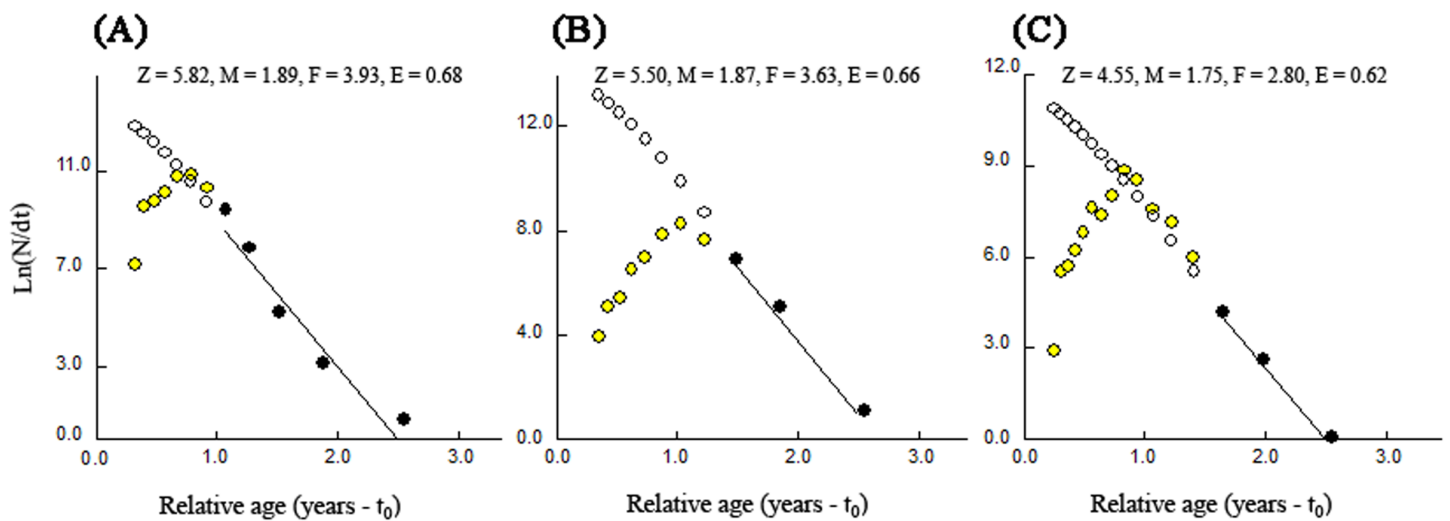
Figure 7 Length-converted catch curves used to estimate total mortality (Z) of *T. swinhonis* collected from (A) BDT, (B) SJH and (C) KLH along the middle and lower reaches of the Yangtze River basin, China. Full-size 🖼 DOI: 10.7717/peerj.6772/fig-7
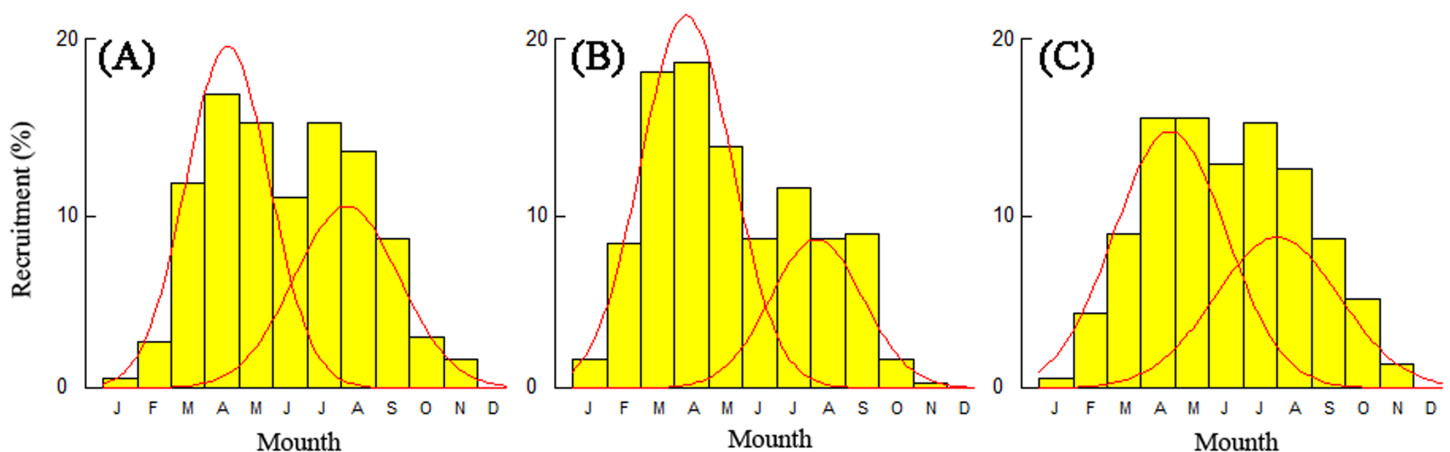

Figure 8 Annual relative recruitment patterns of *T. swinhonis* in (A) BDT, (B) SJH and (C) KLH. Full-size 🖼 DOI: 10.7717/peerj.6772/fig-8

density of food and food availability); (2) sample size differences; (3) differences in gear selectivities between studies and (4) differences in the genetic diversity of different geographical populations.

Length–weight relationship and growth pattern

The length–weight (L–W) relationship of a fish species always been considered as fundamental to further study, such as fish stock assessment (*Afrooz, Gholamreza & Seyed, 2014*). Generally, this relationship is used by freshwater ecologists and fisheries managers for (1) predicting the weight (length) for a given length (weight); (2) describing the fitness condition or morphology of one fish species; (3) estimating growth, age structure and many other aspects of a species' population dynamics and (4) mutual

Table 2 Summary of parameters of length–weight relationships of *T. swinhonis*.

Study area (source)	Total length (cm)		Parameters			n
	Minimum	Maximum	a	b	r^2	
Poyang Lake, China (*Anonymous, 1974*)[bc*]	5.3	11.1	NA	NA	NA	10
Dongting Lake, China (*Anonymous, 1980*)[bc*]	8.7	12.3	NA	NA	NA	10
Liangzi Lake, China (*Yang, 1986*)[bc*]	5.3	10.5	NA	NA	NA	10
Bashan and Zhangze reservoir, China (*Li et al., 1988*)[*]	NA	13.4	NA	NA	NA	135
Hunan, hubei, hebei and sichuan China (*Chen et al., 1998*)[bc*]	7.2	11.8	NA	NA	NA	23
Biandantang Lake, China (*Zhang, 2005*)[d*]	3.2	9.5	0.0098	3.037	0.98	61
Niushan Lake, China (*Feng et al., 2006*)[*]	2.4	9.5	NA	NA	NA	416
Niushan Lake, China (*Ye et al., 2007*)[*]	5.3	12.1	0.0061	2.845	0.897	289
The estuary of the Yangtze River, China (*Ge, Zhong & Tang, 2009*)[b*]	0.4	2.5	NA	NA	NA	91,849
Niushan Lake, China (*Ye et al., 2012*)[*]	8.4	9.4	NA	NA	NA	2
Tian-e-zhou Oxbow, China (*Wang et al., 2012*)[bc]	5.0	9.3	0.0060	3.220	0.955	103
Niushan Lake, China (*Ye et al., 2014*)	4.2	12.8	NA	NA	NA	2,132
Biandantang Lake, China (the present study)[a*]	5.3	16.5	0.0061	2.906	0.870	8,818
Shengjin Lake, China (the present study)[a*]	5.1	15.4	0.0106	2.734	0.878	2,207
Kuilei Lake, China (the present study)[a*]	6.2	19.9	0.0007	3.775	0.886	2,560

Notes:
n, the number of specimen; a, intercept; b, regression slop; r^2, coefficient of determination; NA, not available.
[a] New records of maximum total length in FishBase.
[b] Studies with very narrow total length range.
[c] Small number of specimens.
[d] Standard length was being used in the study.
[*] Materials out of FishBase.

transformation between length and weight for many stock assessment models (*Cren, 1951*; *Ye et al., 2007*). Though some fisheries scientists thought it has little value (*Hilborn & Walters, 1992*), *Froese (2006)* pointed out that a comprehensive analysis of this relationship of a large number of geographic populations can provide important insights into the biology and ecology of that species.

As previously mentioned, the values of *b* (slope coefficient) in the L–W relationships in the present study were 2.91 (in BDT), 2.73 (in SJH) and 3.78 (in KLH), respectively. Fish at all three sampling sites displayed allometric growth instead of isometric growth. The results in BDT and SJH were similar with the previous studies in this region. *Zhang & Li (2002)* reported that the value of allometric parameter was 3.07 in Biandantang Lake, China. *Ye et al. (2007)* pointed out that this value was 2.85 and presented an isometric growth pattern in Niushan Lake, China. *Wang et al. (2012)* reported that it was 3.22 in Tian-e-zhou Oxbow, China. The similarity of coefficients between the present study and the previous studies mentioned above may be due to the spatial similarity of the sampling sites in these studies.

However, the slope coefficient (*b*) estimated by power regression in KLH was 3.78, which was the highest value in all study areas. The observed difference in the value may be attributed to the difference of habitat (especially the observed temperature), the sample size used, diseases and genetic diversity (*Wootton, 1998*; *Ye et al., 2007*).

Table 3 Summary of population characteristics of *T. swinhonis* in different geographical areas.

Study area	Aging structure	L_∞ (mm)	K (year^{-1})	t_0 (year)	ϕ'	Age range (year)	R_n	n	Source
Bashan reservoir, China[a]	Scales	NA	NA	NA	NA	1–6	NA	134	*Li et al. (1988)*
Zhangze reservoir, China[a]									
Niushan Lake, China	NA	145.00	0.66	0.30	4.14	NA	0.38	2,132	*Ye et al. (2014)*
Biandantang Lake, China	Scales	173.25	1.20	−1.09	4.56	1–4	0.21	8,818	The present study
Shengjin Lake, China	Scales	162.75	1.20	−1.08	4.52	1–3	0.29	2,207	The present study
Kuilei Lake, China	Scales	215.25	1.20	−1.12	4.75	1–3	0.24	2,560	The present study

Notes:
NA, not available; R_n, the goodness of fit index.
[a] Small number of specimens.

Age structure and growth parameters

Generally, information about age structure and growth parameter of a fish population would be used for fish stock assessment (*Hollyman, 2017*; *Wells et al., 2013*), which allows fisheries scientists and managers to understand the dynamics of fish stock and how fish populations respond to the environmental changes. More specifically, it can be an indicator of fish population dynamics and help managers make more informed choices for fish conservation and fisheries management.

In view of this, we first presented the age structure of *T. swinhonis* in the middle and lower reaches of the Yangtze River basin based on scale readings and Pauly's empirical equation. These results showed that the age structure of *T. swinhonis* was very simple and dominant ages were 0^+–1^+ year old fish (more than 98% at all sites in the present study) which corresponded well with the previous work in the two reservoirs of northern China (*Li et al., 1988*). The short lifespan of *T. swinhonis* is very similar with *Pseudorasbora parva* (Temminck et Schlegel, 1842) and *H. leucisculus* (two other small dominant species in this region), whose lifespans are no more than 5 and 6 years, respectively (*Gozlan et al., 2010*; *Wang et al., 2013*). These two species are two of the most successful invasive species around the world and have been treated as an international pest fish (*Gozlan et al., 2010*; *Patimar, Abdoli & Kiabi, 2008*). The simple age structure of these two species was usually considered as one of the major reasons the species became dominant within a very short time in many new regions (*Gozlan et al., 2010*; *Wang et al., 2013*). This reason also seems likely for *T. swinhonis* in the lakes along the middle and lower reaches of the Yangtze River basin.

In terms of growth, the results of VBGMs from the present study indicated that there were some differences in the growth curves of *T. swinhonis* in different lakes and these differences are mainly reflected in the average asymptotic total length (L_∞) as the growth constants (K) were the same (1.20 year^{-1}) in all the three lakes. Moreover, the growth parameters (L_∞, K and ϕ') obtained by the current study were much larger than the values reported by *Ye et al. (2014)* in Niushan Lake, China ($L_\infty = 145$ mm, $K = 0.66$ year^{-1}, $\phi' = 4.14$) (Table 3). Many studies have documented differences in growth of a given species in different geographical areas (*SternPirlot & Wolff, 2006*; *Vakily, 1992*), and

Table 4 Estimated mortality rates of *T. swinhonis* derived from different areas.

Study areas (Source)	Z (year^{-1})	M (year^{-1})	F (year^{-1})
Biandantang Lake, China (the present study)[ad]	5.82	1.89	3.93
Shengjin Lake, China (the present study)[ad]	5.50	1.87	3.63
Kuilei Lake, China (the present study)[b]	4.55	1.75	2.80
Niushan Lake, China (*Ye et al., 2014*)[c]	2.92	1.35	1.57

Notes:
[a] National Wetland Park.
[b] Wellhead protection zone.
[c] Aquaculture base.
[d] Having fishman.

the differences might be due to the heterogeneity of habitat and diversity of genetics (*Parra et al., 2009*; *Pauly, 1986*; *Wootton, 1998*).

Mortality and fisheries status

Mortality rates are a measure of describing the rate at which fish disappear from a population and are critical parameters in formulating sustainable fishing regulations (*Ogle, 2016*). In view of this, we estimated the total mortality rates (Z), natural mortality rates (M) and fishing mortality rates (F) of *T. swinhonis* in the three shallow lakes along the middle and lower reaches of the Yangtze River basin. We present the first evaluation of exploitation rate (E).

Catch curve analysis showed that the values of Z for *T. swinhonis* were 5.82 (in BDT), 5.50 (in SJH) and 4.55 (in KLH) year^{-1}, indicating a decreasing trend with increasing longitude. We noted that the values of Z estimated in the present study were much bigger than *Ye et al. (2014)* in Niushan lake, China ($Z = 2.92$ year^{-1}). The differences of functions of these lakes and the fishing effort may explain these differences (Table 4).

Values for M were similar between lakes: BDT = 1.89, SJH = 1.87 and KLH = 1.75. These values were slightly higher than the findings of *Ye et al. (2014)* in Niushan Lake, China ($M = 1.35$). Meanwhile, the values of M/K ratio in our study were 1.58 (in BDT), 1.56 (in SJH) and 1.46 (in KLH), within the interval of 1.12–2.50 for most fish (*Pauly, 1980*), indicating our estimate of M is reasonable. However, *Pauly (1980)* also postulated that M should be in the range of 0.2–0.3, indicating *T. swinhonis* in the region of the Yangtze River basin was characterized with relatively high M, not uncommon for short-lived species.

The fishing mortality rate (F) in BDT, SJH and KLH were 3.93, 3.63 and 2.80 year^{-1}, values that were much higher than those found by *Ye et al. (2014)* in Niushan Lake, China ($F = 1.57$). High values of F at all sites were likely related to the morphological characteristics (barbs on the dorsal fin of *T. swinhonis* made them more susceptible to capture by multi-gillnets than other species). Certainly, the difference between the present study and previous work conducted by *Ye et al. (2014)* may be explained by the gear employed. We used the float multi-gillnets in the present study which targeted the preferred water layer (pelagic) of *T. swinhonis* while sink multi-gillnets was used by *Ye et al. (2014)* in Niushan Lake, China targeted the bottom.

Based on estimates of F and Z, the exploitation rates (E) in BDT, SJH and KLH were 0.68, 0.66 and 0.62, respectively. According to the rule of thumb (when E was more than 0.5, the fish stock was undergoing overfishing) proposed by *Gulland (1965)*, we found that the stocks in the present study areas had been overfished slightly, which should be considered by fisheries managers in the future.

Recruitment time and pattern

Recruitment is a very important period in a fish's life history and can be expressed as the number of fish that reach a certain age or length, which can give us an insight into the future viability of a fish population or predict the possible harvest from the population (*Ogle, 2016*).

The spawning time and pattern of *T. swinhonis* in the present study was identical at all sites and annual recruitment consisted of two seasonal pulses (batch spawning) which occurred between months of March to September. Long recruitment time and strong reproductive ability (L. S. Liu, 2017, unpublished data) may be the main reasons why the species became dominant in these lakes. Despite close agreement with annual changes of gonadosomatic index and distributions of egg size (L. S. Liu, 2017, unpublished data), the results in the present study are not consistent with *Ye et al. (2014)*, who found the annual recruitment only consisted of one plus (single spawning) which occurred between April and August. This is an important topic for future research.

CONCLUSIONS

This study is the first attempt to elucidate the mechanism of population outbreaks of *T. swinhonis* in the lakes along the middle and lower reaches of the Yangtze River basin based on novel and comprehensive biological data. Current results showed that, like many other freshwater fishes, brief generation-time, fast growth rate, relatively high natural mortality rates and strong reproductive capacity (*r*-strategies) may be the main causes that this fish became the most dominant fish species in many lakes of China. Thus, to control the population of *T. swinhonis*, catching it moderately before its spawning season or discreetly releasing predator fish is proposed (*Ye et al., 2006*). Certainly, more field investigations should be conducted on this species in the future, especially on the reproductive biology and population dynamics of this species.

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Competing Interests
The authors declare that they have no compting interests.

Author Contributions

- Xianghong Dong conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
- Tao Xiang performed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper.
- Tao Ju performed the experiments, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper.
- Ruojing Li performed the experiments, contributed reagents/materials/analysis tools, authored or reviewed drafts of the paper.
- Shaowen Ye performed the experiments.
- Sovan Lek analyzed the data, prepared figures and/or tables, approved the final draft.
- Jiashou Liu conceived and designed the experiments, authored or reviewed drafts of the paper, approved the final draft.
- Gaël Grenouillet authored or reviewed drafts of the paper, approved the final draft.

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Data Availability

The following information was supplied regarding data availability:

The raw datasets and the code are available in the Supplemental File.

Supplemental Information

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REFERENCES

Afrooz E, Gholamreza E, Seyed ARH. 2014. Length-weight relationship and Fulton's condition factor of *Carasobarbus luteus* (Heckel, 1843) in Hoor Al-azim wetland. *Journal of Ecology and the Natural Environment* **6(7)**:238–243 DOI 10.5897/JENE2014.0449.

Anonymous. 1974. *Fishes of the Yangtze River*. Beijing: Science Press, 103. (In Chinese).

Anonymous. 1980. *Fishes of Hunan Province*. Changsha: Science and Technology Press of Hunan Province, 42. (In Chinese).

Appelberg M, Berger H, Hesthagen T, Kleiven E, Kurkilahti M, Raitaniemi J, Rask M. 1995. Development and intercalibration of methods in nordic freshwater fish monitoring. *Water, Air, and Soil Pollution* **85**:401–406 DOI 10.1007/bf00476862.

Beverton R, Holt S. 1957. *On the dynamics of exploited fish populations*. London: Chapman and Hall.

Cao W, Zhang G, Ma J, Yu D. 1991. In: Honghu Research Group, Institute of Hydrobiology Academia Sinica. eds. *Preliminary studies on the phenomenon of size diminution of the fish resources in Lake Honghu*. Beijing: China Ocean Press. (In Chinese).

Chen Y, Chu X, Luo Y, Chen Y, Liu H, He M, Chen W, Le P, He S, Lin Y. 1998. *Cypriniformes (II), osteichthyes, fauna sinica*. Beijing: Science Presses, 159. (In Chinese).

Cren EDL. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (Perca Fluviatilis). *Journal of Animal Ecology* **20(2)**:201–219 DOI 10.2307/1540.

da Cunha AR. 2015. Evaluation of measurement errors of temperature and relative humidity from HOBO data logger under different conditions of exposure to solar radiation. *Environmental Monitoring and Assessment* **187(5)**:236 DOI 10.1007/s10661-015-4458-x.

Dai X, Li W, Fan Y, Tian S. 2015. Complete mitochondrial genome of *Toxabramis swinhonis* (Cypriniformes, Cyprinidae). *Mitochondrial DNA Part A* **28(1)**:56–57 DOI 10.3109/19401736.2015.1110796.

Dalton HA, Wood BJ, Dickey JP, Torrey S. 2016. Validation of HOBO Pendant® data loggers for automated step detection in two age classes of male turkeys: growers and finishers. *Applied Animal Behaviour Science* **176**:63–69 DOI 10.1016/j.applanim.2015.12.005.

Elliott J. 1983. Fish stock assessment. A manual of basic methods by J. A. Gulland. *Biometrics* **40(3)**:869–870 DOI 10.2307/2530936.

Feng G, Li Z, Xie C, Ye S. 2006. Structure and diversity of small-sized fish community in Lake Niushan, Hubei Province. *Journal of Lake Science* **18(3)**:299–304 DOI 10.18307/2006.0317. (In Chinese).

Froese R. 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology* **22(4)**:241–253 DOI 10.1111/j.1439-0426.2006.00805.x.

Gayanilo F, Sparre P, Pauly D. 2005. *FAO-ICLARM stock assessment tools (FISAT-II) user's guide*. Rome: Computerized Information Series, FAO.

Ge K, Zhong J, Tang J. 2009. Primarily study on species composition of fish larvae and juveniles in elver net of Yangtze River estuary. *Journal of Zhejiang Ocean University (Natural Science)* **28(6)**:298–310. (In Chinese).

Gozlan RE, Andreou D, Asaeda T, Beyer K, Bouhadad R, Burnard D, Caiola N, Cakic P, Djikanovic V, Esmaeili HR, Falka I, Golicher D, Harka A, Jeney G, Kováč V, Musil J, Nocita A, Povz M, Poulet N, Virbickas T, Wolter C, Serhan Tarkan A, Tricarico E, Trichkova T, Verreycken H, Witkowski A, Guang Zhang C, Zweimueller I, Robert Britton J. 2010. Pan-continental invasion of *Pseudorasbora parva*: towards a better understanding of freshwater fish invasions. *Fish and Fisheries* **11(4)**:315–340 DOI 10.1111/j.1467-2979.2010.00361.x.

Gulland J. 1965. Estimation of mortality rates. In: *Annex to Artic Fisheries Working Group Reports,* Copenhagen: International Council for the Exploration of the Sea (ICES).

Guo Z, Liu J, Lek S, Li Z, Zhu F, Tang J, Cucherousset J. 2016. Age, growth and population dynamics of two congeneric and invasive gobies, *Rhinogobius giurinus* and R. *Cliffordpopei* (Actinopterygii, Gobiidae) in a plateau lake, southwestern China. *Hydrobiologia* **763(1)**:69–79 DOI 10.1007/s10750-015-2361-7.

Hilborn R, Walters C. 1992. *Quantitative fisheries stock assessment*. London: Chapman and Hall.

Hollyman P. 2017. Age, growth and reproductive assessment of the whelk, *Buccinum undatum*, in coastal shelf seas. D. Phil. Thesis, Prifysgol Bangor University.

Koutrakis ET, Tsikliras AC. 2003. Length-weight relationships of fishes from three northern Aegean estuarine systems (Greece). *Journal of Applied Ichthyology* **19(4)**:258–260 DOI 10.1046/j.1439-0426.2003.00456.x.

Li Z. 2004. Adjustment of fisheries structure and resources in lakes along the middle and lower reaches of the Yangtze River. *Resource and Environment* **11**:74–77. (In Chinese).

Li W, Hicks BJ, Lin M, Guo C, Zhang T, Liu J, Li Z, Beauchamp DA. 2018. Impacts of hatchery-reared mandarin fish *Siniperca chuatsi* stocking on wild fish community and water quality in a shallow Yangtze lake. *Scientific reports* **8(1)**:1–11 DOI 10.1038/s41598-017-17765-5.

Li D, Wu X, Xie Z, Lian Y. 1988. Role of minnows in the fish-farming reservoirs and control of their poupulations. *Acta Ecologica Sinica* **8**:304–310. (In Chinese).

Li W, Zhang T, Li Z. 2010. Spatial distribution and abundance of small fishes in Xiaosihai Lake, a shallow lake along the Changjiang (Yangtze) River, China. *Chinese Journal of Oceanology and Limnology* **28(3)**:470–477 DOI 10.1007/s00343-010-9082-6.

Liu J, He B. 1992. *Cultivation of the Chinese freshwater fishes*. Beijing: Science Press. (In Chinese).

Liu E, Liu Z, Chen W, Bao C, Chen K. 2005. A study on the Chaise of Lake Anchovy (*Coilia ectenes taihuensis* Yen *et* Lin) catches and its mutual relationship to the biological environment in Lake Taihu. *Journal of Lake Science* **17(4)**:340–345 DOI 10.18307/2005.0410.

Mao Z, Gu X, Zeng Q, Zhou L, Wang X, Wu L, Cao P, Sun M. 2011. Community structure and diversity of fish in Lake Taihu. *Chinese Journal of Ecology* **30(12)**:2836–2842.

Mirzaei MR, Yasin Z, Shau Hwai AT. 2014. Length-weight relationship, growth and mortality of *Anadara granosa* in Penang Island, Malaysia: An approach using length-frequency data sets. *Journal of the Marine Biological Association of the United Kingdom* **95(2)**:381–390 DOI 10.1017/S0025315414001337.

Moreau J, Cuende F. 1991. On improving the resolution of the recruitment patterns of fishes. *Fishbyte* **9(1)**:45–46.

Narejo N, Mastoi A, Lashari P, Abid M, Laghari M, Mahesar H. 2009. Age determination of a carp, *Labeo calbasu* (Hamilton) from Keenjhar Lake (District: Thatta), Sindh, Pakistan. *Sindh University Research Journal* **41(1)**:83–86.

O'Brien CM. 2012. Modelling and quantitative methods in fisheries, second edition by Malcolm Haddon. *International Statistical Review* **80(1)**:201–202 DOI 10.1111/j.1751-5823.2012.00179_26.x.

Ogle D. 2016. *Introductory fisheries analyses with R*. Boca Raton: CRC Press.

Parra I, Almodóvar A, Nicola GG, Elvira B. 2009. Latitudinal and altitudinal growth patterns of brown trout *Salmo trutta* at different spatial scales. *Journal of Fish Biology* **74(10)**:2355–2373 DOI 10.1111/j.1095-8649.2009.02249.x.

Patimar R, Abdoli A, Kiabi BH. 2008. Biological characteristics of the introduced sawbelly, *Hemiculter leucisculus* (Basilewski, 1855), in three wetlands of northern Iran: Alma-Gol, Adji-Gol and Ala-Gol. *Journal of Applied Ichthyology* **24(5)**:617–620 DOI 10.1111/j.1439-0426.2008.01080.x.

Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES Journal of Marine Science* **39(2)**:175–192 DOI 10.1093/icesjms/39.2.175.

Pauly D. 1983. *Some simple methods for the the assessment of tropical fish stock*. Rome: Food and Agriculture Organization of the United Nations.

Pauly D. 1986. Fish population dynamics in tropical waters: a manual for use with programmable calculators. *Fisheries Research* **4(2)**:171–173 DOI 10.1016/0165-7836(86)90044-5.

Pauly D, Munro J. 1984. Once more on the comparison of growth in fish and invertebrates. *Fishbyte, Newsletter of the Network of Tropical Fisheries Scientists* **2(1)**:21.

Peter B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fishery bulletin* **78(1)**:1–12.

R Core Team. 2017. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. *Available at https://www.R-project.org/*.

Ricker WE. 1975. Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**:401.

Sparre P, Venema S. 1998. *Introduction to tropical fish stock assessment*. Rome: Food and Agriculture Organization of the United Nations.

Steinmetz B, Müller R. 1991. *An atlas of fish scales and other bony structures used for age determination: non-salmonid species found in European fresh waters*. Cardigan: Samara Publishing.

SternPirlot A, Wolff M. 2006. Population dynamics and fisheries potential of *Anadara tuberculosa* (Bivalvia: Arcidae) along the Pacific coast of Costa Rica. *Revista De Biologia Tropical* **54(Suppl 1)**:87–99.

Taiwo O. 2010. Length frequency distribution and length-weight relationship of *Schilbe mystus* from Lekki Lagoon in Lagos, Nigeria. *Journal of Agricultural and Veterinary Sciences* **2**:63–69.

Vakily J. 1992. *Determination and comparison of bivalve growth, with emphasis on Thailand and other tropical areas*. Manila: The International Center for Living Aquatic Resources Management.

Von Bertalanffy L. 1938. A quantitative theory of organic growth (inquiries on growth laws. 11.). *Human Biology* **10(2)**:181–213.

Wang T, Wang H-S, Sun G-W, Huang D, Shen J-H. 2012. Length-weight and length-length relationships for some Yangtze River fishes in Tian-e-zhou Oxbow, China. *Journal of Applied Ichthyology* **28(4)**:660–662 DOI 10.1111/j.1439-0426.2012.01971.x.

Wang T, Huang D, Zhao Y, Wang H, Hu S, Shen J. 2013. Age, growth and mortality of invasive sharpbelly, *Hemiculter leu*cisculus (Basilewski, 1855) in Erhai Lake, China. *Journal of Applied Ichthyology* **29(6)**:1279–1285 DOI 10.1111/jai.12287.

Wells RJD, Kohin S, Teo SLH, Snodgrass OE, Uosaki K. 2013. Age and growth of North Pacific albacore (*Thunnus alalunga*): implications for stock assessment. *Fisheries Research* **147**:55–62 DOI 10.1016/j.fishres.2013.05.001.

Wootton R. 1998. *Ecology of teleost fishes*. Second Edition. Boston: Kluwer Academic Publishers.

Xie S, Cui Y, Li Z. 2001a. Dietary-morphological relationships of fishes in Liangzi Lake, China. *Journal of Fish Biology* **58(6)**:1714–1729 DOI 10.1111/j.1095-8649.2001.tb02325.x.

Xie S, Cui Y, Li Z. 2001b. Small fish communities in two regions of the Liangzi Lake, China, with or without submersed macrophytes. *Journal of Applied Ichthyology* **17(2)**:89–92 DOI 10.1046/j.1439-0426.2001.00248.x.

Yang G. 1986. *Fishes of Hubei Province*. Wuhan: Science and Technology Press of Hubei Province, 54. (In Chinese).

Ye S, Moreau J, Zeng W, Zhang T, Liu J, Li Z. 2014. Growth and mortality of two small fishes, *Toxabramis swinhoni*s Günther, 1873 and *Hyporhamphus intermedius* (Cantor, 1842), in a Yangtze shallow lake (China) assessed by length frequency analysis. *Journal of Applied Ichthyology* **30(3)**:479–484 DOI 10.1111/jai.12405.

Ye S, Li Z, Feng G, Cao W. 2007. Length-weight relationships for thirty fish species in Lake Niushan, a shallow macrophytic Yangtze Lake in China. *Asian Fisheries Science* **20**:217–226.

Ye S, Li Z, Lek-Ang S, Feng G, Lek S, Cao W. 2006. Community structure of small fishes in a shallow macrophytic lake (Niushan Lake) along the middle reach of the Yangtze River, China. *Aquatic Living Resources* **19(4)**:345–359 DOI 10.1051/alr:2007005.

Ye S, Zhang T, Li Z, Liu J. 2012. Relationships between spatial distribution of two dominant small-sized fishes and submerged macrophyte cover in Niushan Lake of China. *Chinese Journal of Applied Ecology* **23(9)**:2566–2572. (In Chinese).

Zhang T. 2005. Life history strategies, trophic patterns and community structure in the fishes of Lake Biandantang. D. Phil. Thesis, Institute of Hydrobiology, Chinese Academy of Sciences. (In Chinese).

Zhang T, Li Z. 2002. Age, growth, and reproduction of the bitterling (*Paracheilognatus imberbis*) in a shallow Chinese Lake. *Journal of Freshwater Ecology* **17(4)**:501–505 DOI 10.1080/02705060.2002.9663928.