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RESEARCH ARTICLE

Reproductive biology of thin sharpbelly, *Toxabramis swinhonis* Günther, 1873 in a shallow lake (Biandantang Lake) along the middle reach of the Yangtze River basin (China): implications for fisheries management

Xianghong Dong[1,2,3,4], Gaël Grenouillet[3,5], Tao Ju[6], Tao Xiang[1,2], Zhan Mai[1], Pascal Laffaille[4], Sovan Lek[3] and Jiashou Liu[1,*]

[1] State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, PR China
[2] University of Chinese Academy of Sciences, Beijing, PR China
[3] EDB, Université de Toulouse, CNRS, ENFA, UPS, Toulouse, France
[4] Ecolab, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France
[5] Institut Universitaire de France, Paris, France
[6] Key Laboratory of Freshwater Biodiversity Conservation, Ministry of Agriculture of China, Yangtze River Fisheries Research Institute, Chinese Academy of Fishery Science, Wuhan, PR China

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Abstract – The reproductive biology of *Toxabramis swinhonis*, one of the most abundant bycatch species in freshwater fishery in China, was first reported based on 783 specimens collected in Biandantang Lake, central China from October 2016 to September 2017. The overall sex ratio (female/male) was 1.03:1, not significantly different from the expected value 1:1. Nevertheless, sex ratio varied with seasons: 1.32:1 in the early stage of the spawning season (March–April), while 0.46:1 in the later stage (July–August). The monthly succession of the average gonadosomatic index (GSI) and percentages of mature individuals co-indicated that *T. swinhonis* was a spring-summer (March–August) spawner. Further, the bimodal distribution of the size of eggs from one gravid ovary and histological analysis of mature gonads suggested that *T. swinhonis* was a multiple spawner with indeterminate fecundity and high degree of spawning asynchronicity. The sizes and ages at first maturity for females and males were 84.47 and 81.86 mm, and 1.62 and 1.56 yr, respectively. The batch fecundity (F_B) of this species varied in a wide range from 2006 to 73592 eggs per fish with a mean value of 26487.15 ± 2675.61 (S.E.) eggs and increased with the increasing of the gonad weight (W_G), eviscerated weight (W_E), total length (L_T) and age (A). Overall, *T. swinhonis* in Biandantang (BDT) Lake is characterized by high fecundity and prolonged spawning season, resulting in easy population explosion. Thus, to remove *T. swinhonis* moderately or release predator fish discreetly to control its population is proposed considering its reproductive characteristics.

Keywords: Fisheries management / reproductive biology / Biandantang Lake / *Toxabramis swinhonis* / Yangtze River basin

1 Introduction

Toxabramis swinhonis Günther, 1873 (family Cyprinidae, subfamily Cultrinae), commonly known as thin sharpbelly, is a small pelagic and gregarious fish widely distributed in the Yangtze River, Yellow River and other freshwater bodies in China (Chen *et al.*, 1998; Zheng, 1998). The species mainly feeds upon copepods, cladocerans and insect larvae (Xie *et al.*, 2001; Zhang, 2005), whilst it is the common prey of many larger economic piscivorous fishes such as *Siniperca chuatsi* (Basilewsky, 1855), *Culter alburnus* (Basilewsky, 1855), *Culetr dabryi dabryi* (Bleeker, 1871) and *Cultrichthys erythropterus* (Basilewsky, 1855) (Anonymous, 1976; Yang *et al.*, 2002; Zhang, 2005; Cui *et al.*, 2013). Consequently, despite not being a fish of fishing interest, *T. swinhonis* is an important species in terms of ecological aspects and fisheries management as it is one of the main by-catch species in

*Corresponding author: jsliu@ihb.ac.cn

freshwater fishery in inland China and plays a key role in the energy flows of these hydro-ecosystems, linking zooplankton to higher trophic levels (Li *et al.*, 1988; Ye *et al.*, 2014). Further, recent studies have documented that *T. swinhonis* is gradually becoming the most abundant small fish species in many rivers, lakes and reservoirs of China, and this phenomenon exhibits a trend of further increasing (Ge *et al.*, 2009; Li *et al.*, 2018), questioning the sustainability of fisheries resources and fish biodiversity conservation in these water bodies.

Hence, it is the time that much more attentions should be paid on the biology, ecology and fisheries management of this species. However, as far as the authors are aware, the limited documented studies on the above-mentioned aspects of *T. swinhonis* mainly focused on its age, growth, mortality, feeding habits and community ecology (Li *et al.*, 1988; Xie *et al.*, 2001; Zhang, 2005; Ye *et al.*, 2014, 2015). To date, researches on reproductive biology of this species are either unpublished or unavailable though reproductive traits are essential for fish population dynamics modeling, fish stock assessment and fisheries management (King and McFarlane, 2003; Tracey *et al.*, 2007).

Therefore, the present study aimed at filling the research gap of the reproductive biology of *T. swinhonis* with a focus on quantifiable characteristics needed for fish population dynamics modeling, fish stock assessment and fisheries management: (1) sex ratio, (2) size and age at first maturity, (3) spawning season and pattern and (4) batch fecundity. Finally, the implications of our findings for freshwater fisheries management and fish biodiversity conservation in inland China are discussed.

2 Materials and methods

2.1 Study site

Biandantang (BDT) Lake (Fig. 1; 30°17′17.03″ N, 114°43′00.68″ E) is a typical shallow macrophytic lake, which locates on the south bank of the middle reach of the Yangtze River, Hubei Province, central China (Guan, 1995). The lake, with an area of 3.86 km^2, is a sub-lake of the larger Baoan Lake (39.3 km^2) and separated from the latter by a stone dyke with one boat passage (width about 5 m) allowing water exchange (Xie *et al.*, 2000). Although this lake was historically interconnected with the mainstream of the Yangtze River by a channel, it is now an enclosed water body. Thus, the water level oscillation of this lake mainly depends on the local rainfall. Meanwhile, according to the annual investigation of the present study, the lake was slightly eutrophic (the modified Carlson's synthesis trophic state index TSI_M $(\Sigma) = 49.44$) (Aizaki *et al.*, 1981) and covered with large quantities of aquatic macrophytes such as *Potamogeton crispus* (Linn) and *Nelumbo nucifera* (Gaerth), accounting for more than 90% of the whole lake surface. More details about limnological traits of this lake during the study period can be found in Table 1.

2.2 Data collection and laboratorial procedures

T. swinhonis and limnological characteristics were collected monthly at six sites in the BDT Lake from October 2016 to September 2017 (Fig. 1). Fishes were captured using fixed multi-mesh gillnets (mesh size: 10–125 mm, 30 m long × 1.5 m high) modified from Appelberg (2000) (mesh size: 5–55 mm, 30 m long × 1.5 m high) between 17:30 and 5:30 of the next day (*i.e.*, 12 h), while the environmental factors were measured with multi-water quality meter (YSI Professional Plus; Yellow Spring Instruments, Ohio, USA), water depth finder (model SpeedTech SM-5, USA), turbidimeter (Hach 2100Q Portable Turbidimeter, Loveland, CO, USA), Secchi disk and ultraviolet spectrophotometer.

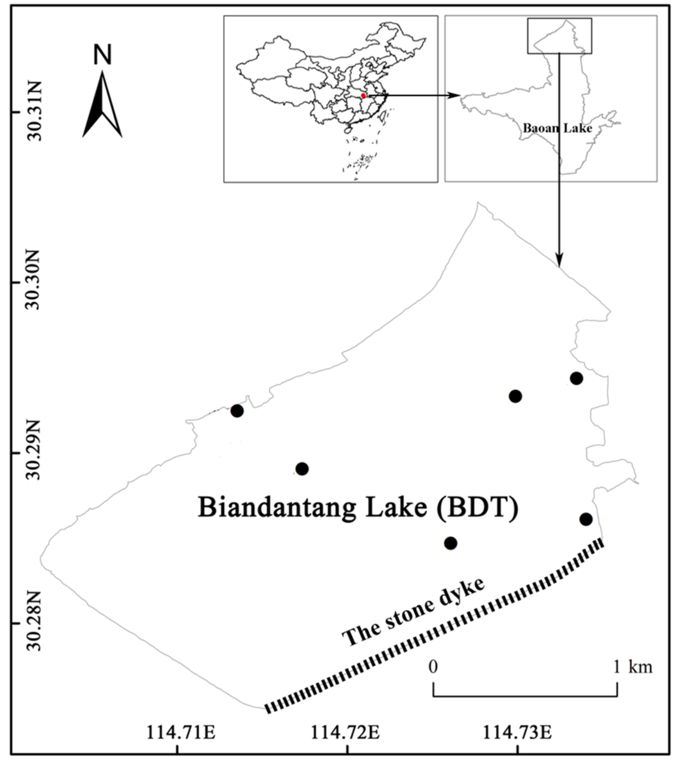

Fig. 1. Skeletons of Biandantang (BDT) Lake and larger Baoan Lake (topright). Black solid dots indicate the locations of sampling sites.

Table 1. Limnological characteristics of BDT Lake during October 2016 to September 2017.

Characteristics	Units	Annual average ± S.E.
Turbidity	NTU	18.39 ± 2.17
Secchi disk depth	m	0.66 ± 0.08
Water depth	m	1.55 ± 0.18
Dissolved oxygen	mg/L	7.61 ± 0.90
pH	–	7.65 ± 0.90
Conductivity	μs/cm	234.13 ± 27.59
Water temperature	°C	19.86 ± 2.34
Total nitrogen	mg/L	0.82 ± 0.10
Total phosphorus	mg/L	0.05 ± 0.01
Chlorophyll-a	mg/L	0.02 ± 0.00
Chemical oxygen demand	mg/L	5.08 ± 0.60
Ammonia nitrogen	mg/L	0.28 ± 0.03
Nitrate nitrogen	mg/L	0.15 ± 0.02

For each catch and euthanized (MS-222) fish, total length (L_T, nearest 0.01 mm), total weight (W_T, nearest 0.01 g), gonadal weight (W_G, nearest 0.01 g), eviscerated weight (W_E, nearest 0.01 g), sex, age and gonad maturity stage were determined immediately in their fresh state. Meanwhile, two subsamples, approximated 0.05 g of each, taken at anterior, middle and posterior parts of every sample fish's gonad were weighed (nearest 0.01 g) and stored separately into two labeled plastic centrifuge tubes (10 ml) with one containing Bouin's fluid and another 10% formalin neutral buffered solution (Cuellar *et al.*, 1996).

Tissue samples immersed in Bouin's solution were subsequently made into histological sections in the laboratory as the following procedure: washed with distilled water, dehydrated through increasing concentrations of ethyl alcohol, cleared in xylene, infiltrated in paraffin wax (García-Seoane *et al.*, 2014), cut into 5–6 μm thick with a microtome and stained with hematoxylin and eosin (H&E) (Lillie, 1947). In contrast, hydrated oocytes taken from the mature ovaries (stages IV to VI, collected in spawning season) infiltrated in 10% formalin neutral buffered solution were first teased apart from the connective tissue, and then counted or measured.

Fish lengths (L_T) and weights (W_T, W_G and W_E) were measured by an electronic caliper and a precision electronic balance, respectively. Age estimation was based on scalimetry, and sexes and gonad maturity stages were determined by inspecting the appearance of the gonads (shape, color and opacity) and histological analysis (whenever needed). According to Мейен (1939), gonad development stages of freshwater fish included six phases: (I) immature, (II) quiescent, (III) ripening, (IV) ripeness, (V) reproduction and (VI) spent. All microphotographs were obtained using the Olympus BX53 (Olympus Corporation, Tokyo, Japan) fluorescence microscope and all the hydrated oocytes were counted or measured under a Leica camera (DFC295) connected with a microscope (Leica S8APO).

2.3 Data analysis

Sex ratio, expressed as female:male, was computed monthly, seasonally and annually. Deviations from the theoretical value 1:1 were statistically tested using Chi-square (χ^2) test (Zar, 1999). Meanwhile, comparison of the average L_T between females and males was conducted by the Wilcoxon rank sum test.

Fish length and age at first maturity (*i.e.*, A_{50} and L_{50}, at which the probability of maturity is 50%) were estimated using specimens (125 females: 54.56–132.90 mm; 204 males: 61.76–131.94 mm) collected throughout the spawning season (April–August), von Bertalanffy growth model (VBGM) of *T. swinhonis* proposed by Ye *et al.* (2014) and the following maturity ogive (Prager *et al.*, 1989): $P = 100 \times (1 + \exp(-K\ (L_T - L_{T50})))^{-1}$, where P represents the probability of being mature at size L_T and K is the curvature of this sigmoid curve. In order to fit this maturity ogive, maturity was described in a binary configuration (0 = immature, stages I–III for both sexes; 1 = mature, stages IV–VI for both sexes) (Tracey *et al.*, 2007) and maximum likelihood estimation method was used. Further, the differences in maturity ogives between sexes were detected using the multivariate Hotelling's T-squared test (Bernard, 1981).

The spawning season and pattern were determined by analyzing the monthly values of the gonadosomatic index ($GSI = 100 \times W_G/W_E$) (Devlaming *et al.*, 1982), relative percentages of gonad maturity stages and size distribution of the oocytes. One-way ANOVA with Tukey's HSD post-hoc was used to determine whether there were significant differences in GSI among different months (Zar, 1999). The relationships between spawning season and environmental factors (water temperature and rainfall) were determined graphically using the monthly relative percentages of the gonad maturity stages.

The hydrated oocytes (stages IV and V) were used to estimate the batch fecundity (F_B) of *T. swinhonis* using the following gravimetric equation: $F_B = n \times (W_G/W_{GS})$, where W_{GS} is the weight of the subsample used for eggs counted and n is the number of hydrated oocytes within the same subsample (Bagenal and Braum, 1978; Hunter *et al.*, 1985). Further, relative fecundity was computed as fecundity divided by W_E. The relationships between F_B, and L_T, W_G, W_T and age were analyzed using linear or non-linear regression and one-way ANOVA with Tukey's HSD post-hoc, respectively.

All statistics and graphics were performed in R 3.3.2 (R Core Development Team, 2018) using the "base" and "rgdal" (Bivand *et al.*, 2018) packages. The significance level (α) was also set to 0.05 and all estimates were expressed as mean ± standard error (S.E.) in the current study unless otherwise stated.

3 Results

3.1 Size structure

A total of 783 *T. swinhonis* (368 females, 358 males and 57 unsexed) were captured. Males were dominant in the middle size classes (80–120 mm L_T), whereas females were more abundant in other size classes (Fig. 2). Nevertheless, no significant difference was found in average L_T between females and males (F: 104.09 ± 1.06 and M: 104.13 ± 0.63 mm; Wilcoxon rank sum test, $P > 0.05$).

3.2 Sex ratio

The overall sex ratio of *T. swinhonis* was 1.03:1, not divergent significantly from the expected value 1:1 (Tab. 2; $\chi^2 = 0.14$, $P > 0.05$). Nevertheless, sex ratio varied with seasons: 1.32:1 (skewness toward females) in the early stage of spawning season (March–April), while 0.46:1 (skewness towards males) in the later stage of the spawning season (July–August). More specifically, sex ratio skewed toward females in March, August, September, November and December, whereas it reversed and biased in favor of males in June, July and October (Tab. 2). No significant differences were observed among this value with the theoretic value 1:1 for the remaining months, *i.e.* January, February, April and May (Tab. 2; $\chi^2 = 0.07$, 2.39, 0.12 and 0.09, respectively, all $P > 0.05$).

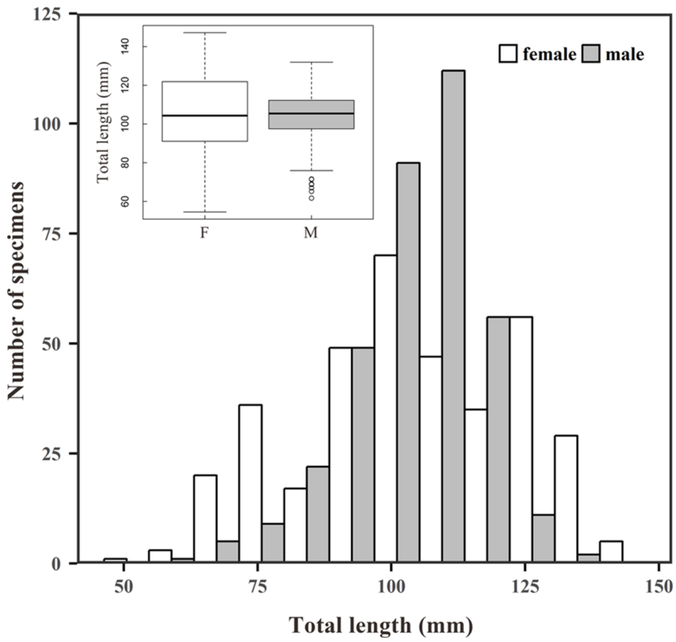

Fig. 2. Length frequency distributions of female (white) and male (gray) *Toxabramis swinhonis* collected in BDT Lake from October 2016 to September 2017. Histograms and boxplots (horizontal line within box: median; boundaries of box: 25% and 75% quantiles; bars: lower and upper inner fences; circles: outliers) are two different approaches used to characterize this information.

3.3 Size and age at first maturity

The relationships between mature probability of females and males *T. swinhonis* and their total lengths (L_T) in BDT Lake were $P = 100 \times (1 + \exp(-0.14\ (L_T - 84.47)))^{-1}$ ($n = 124$, pseudo-$R^2 = 0.65$) and $P = 100 \times (1 + \exp(-0.12\ (L_T - 81.86)))^{-1}$ ($n = 204$, pseudo-$R^2 = 0.43$), respectively. According to these two maturity ogives and VBGM of *T. swinhonis*, the estimates of L_{T50} of females and males *T. swinhonis* were 84.47 mm (accounted for 57.39% of the largest L_T of females captured) and 81.86 mm (accounted for 62.04% of the largest L_T of males captured), respectively (Fig. 3). A_{50} of females and males *T. swinhonis* were 1.62 and 1.56 yr, respectively. Further, we observed a significant difference in L_{T50} and A_{50} between sexes ($T^2 = 129.89$ and 856.62, respectively, both $P < 0.05$).

3.4 Spawning season and pattern

Monthly succession of the average GSI (Fig. 4) and the percentage of mature individual (Fig. 5) co-indicated that *T. swinhonis* was a spring-summer spawner, as both indicators increased significantly in March, peaked strongly in May, decreased sharply between June and August, then returned to quiescent period in September and maintained this state until next spawning cycle. Similarly, the relationships between abiotic variables and development of the gonad showed that the water temperature and rainfall may be two of main drivers of spawning activity, and suitable water temperatures for reproduction of *T. swinhonis* were 23–34 °C (Fig. 5). Furthermore, the histological analysis on the mature gonads of females and males (Fig. 6) combined with the distribution of egg size of one mature female (Fig. 7) collected from the spawning season proved that *T. swinhonis* was a multiple or fractional spawner (release of eggs at intervals, usually over several days or weeks) due to the fact that oocyte diameter had a bimodal distribution and all development stages of oocytes or spermatogonia co-occurred in one fully mature ovary or testis. Certainly, based on these facts, it should not be forgotten that the absolute fecundity of *T. swinhonis* estimated in this study is actually the batch fecundity (F_B).

3.5 Batch fecundity

Fecundity was estimated for 98 mature females collected in spawning season whose L_T and W_T ranged from 74.77 to 111.37 mm, and 1.65 to 4.36 g, respectively. The estimates of F_B varied in a wide range from 2006 to 73 592 eggs per fish, with a mean value of 26 487.15 ± 2675.61 eggs per fish. Similarly, the estimates of relative F_B also varied within a wide range from 421 to 3608 eggs/g, with a mean value of 1730.14 ± 174.77 eggs/g of fish body weight. Meanwhile, F_B increased with increasing gonad weight (W_G), eviscerated weight (W_E), total length (L_T) and age (Fig. 8). The best-fit regression equations were $F_B = 4392.00 + 15\,314.00\ W_G$ ($n = 98$, $R^2 = 0.75$); $F_B = -3367.80 + 2038.40\ W_E$ ($n = 98$, $R^2 = 0.68$) and $F_B = 0.0002\ L_T^{3.77}$ ($n = 98$, $R^2 = 0.73$), respectively.

4 Discussion

Sex ratio is one of the most important parameters in population ecology and fisheries management as it can inform fisheries scientists and managers about population structure, reproductive potential and population dynamics (Raposo and Gurgel, 2001; Cao *et al.*, 2009). In this study, the overall sex ratio of *T. swinhonis* in BDT Lake was 1.03:1, which corresponded well with most fish populations whose sex ratios show no difference from expected 1:1 (Nikolsky, 1963). However, similar with *Abramis brama* (Linnaeus, 1758), this ratio varied with time and size, females being dominant in the early stage of spawning season (March–April) and older size groups, while males dominated in the later stage (July–August) and smaller size groups (Zhang *et al.*, 2017). According to Zhang *et al.* (2017), Türkmen *et al.* (2002) and Wang *et al.* (2013), a surplus of females in the early stage of spawning season and larger size groups, and a surplus of males in the later stage of spawning season and smaller size groups as observed here can be considered as a reproductive strategy of *T. swinhonis* to produce high number of fertilized eggs or offspring, so as to get an accelerated population growth (Nikolsky, 1963; Manorama and Ramanujam, 2017).

The size or age at first maturity (L_{T50} or A_{50}) of one fish species can directly influence its reproductive potential in population level (Beacham, 1983), being thus crucial parameter for biodiversity conservation and management strategies (Cruz *et al.*, 2000). In the present study, *T. swinhonis* got mature at the later period of their life history. Meanwhile, females matured later than males, which was similar with

Table 2. Monthly variations of sex ratio for female to male (F/M) *Toxabramis swinhonis* collected in BDT Lake from October 2016 to September 2017 (*P*-values determined by χ^2-tests).

Sampling time		Number of specimens		Sex ratio (F/M)	*P*-values
		Female	Male		
2016	October	3	16	0.19	0.003
	November	28	8	3.50	<0.001
	December	46	8	5.75	<0.001
2017	January	30	28	1.07	0.792^{ns}
	February	34	48	0.71	0.122^{ns}
	March	59	38	1.55	0.033
	April	39	36	1.08	0.729^{ns}
	May	22	24	0.92	0.768^{ns}
	June	11	32	0.34	0.001
	July	18	94	0.19	<0.001
	August	34	18	1.89	0.027
	September	44	8	5.50	<0.001
Total		368	358	1.03	0.711^{ns}

ns, stands for not significant.

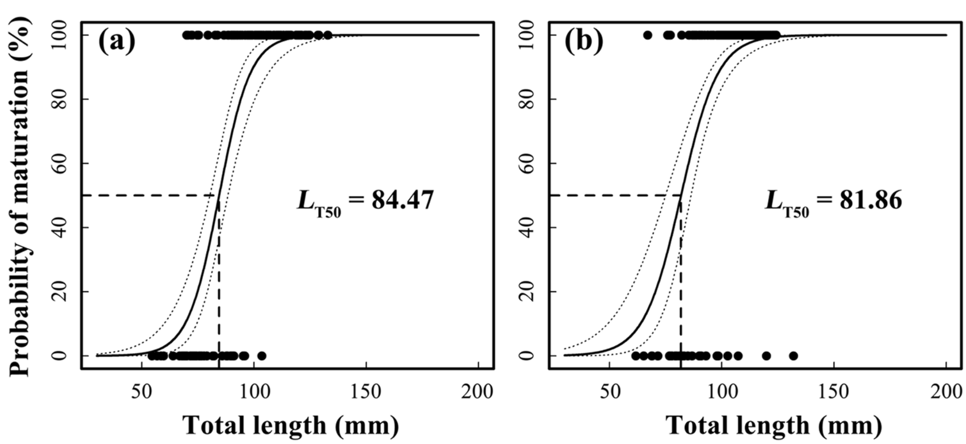

Fig. 3. Mean ± 95% C.I. logistic regression model for estimating the length at first maturity (L_{T50}) of (a) female and (b) male *Toxabramis swinhonis* collected in BDT Lake from October 2016 to September 2017. Black solid dots indicate the observed points.

many other fish species such as *A. brama* and *Raja undulate* Lacepède, 1802 (Coelho and Erzini, 2006; Zhang *et al.*, 2017). Many fishery scientists pointed out that this might be a reproductive tactic to guarantee the population growth as a larger body size often means a bigger abdominal cavity, a higher reproduction potential and a quicker speed to accumulate the fat for reproductive activities or recovery from the spawning behavior (Parker, 1992; Bisazza and Pilastro, 1997; Türkmen *et al.*, 2002; Bromley, 2003; Wang *et al.*, 2013).

Gonad development has been described for many teleost fish species to determine the spawning season and pattern (Shinkafi *et al.*, 2011; Manorama and Ramanujam, 2017), which are very important for artificial propagation and fisheries management (Cao *et al.*, 2009). The results obtained in this study indicated that *T. swinhonis* was also an asynchronous, multiple and spring-summer (*i.e.*, May and June) spawner, like many other freshwater fishes in the temperate zone (Peter and Crim, 1979). According to Malison *et al.* (1994), such a reproductive pattern may be a reproductive strategy for the larval and young *T. swinhonis* to grow quickly and survive well based on the suitable water temperature and sufficient food availability.

Fecundity is one of the most important components of fishery biology as it has direct bearing on fish production, stock recruitment and stock management (Qadri *et al.*, 2015). The batch fecundity (F_B) and relative batch fecundity of *T. swinhonis* obtained from this study were 26 487.15 eggs and 1730.14 eggs/g of fish body weight, respectively, which were obviously higher than many other freshwater fishes such as *Oxygymnocypris stewartii* (Lloyd, 1908), *A. brama* and

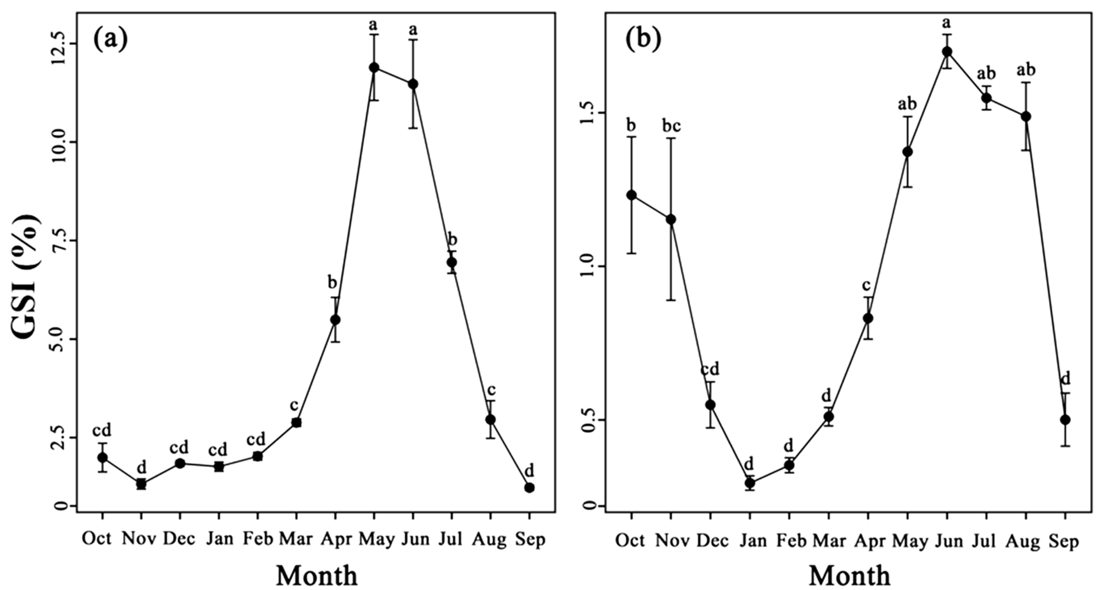

Fig. 4. Monthly variations in the gonadosomatic index (GSI) of (a) female and (b) male *Toxabramis swinhonis* collected in BDT Lake from October 2016 to September 2017. Different letters mean that there existed a statistical significance (one-way ANOVA with Tukey's HSD post-hoc). Error bars mean standard errors (S.E.).

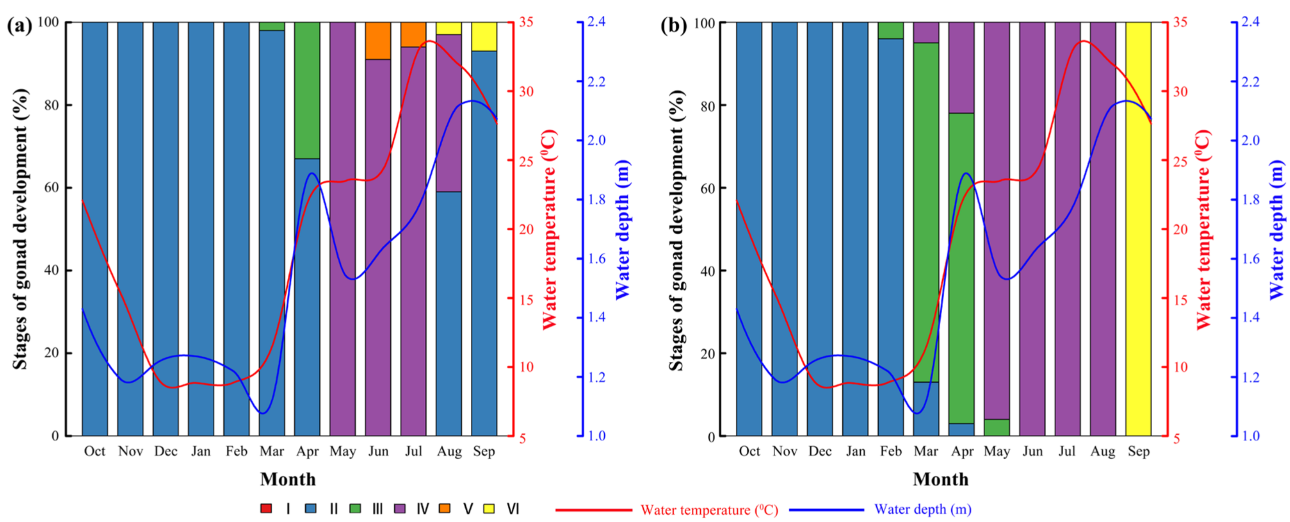

Fig. 5. Monthly successions in the pattern of gonadal maturity stages in relation to abiotic factors [water temperature (red solid lines) and water depth (blue solid lines)] for female (a) and male (b) *Toxabramis swinhonis* collected in BDT Lake from October 2016 to September 2017.

Peltobagrus fulvidraco (Richardson, 1846) (Cao *et al.*, 2009; Huo *et al.*, 2013; Zhang *et al.*, 2017). Undoubtedly, this may be another reason why *T. swinhonis* has become the most dominant fish species in many shallow lakes of China.

Based on these results, what should be noted is that the reproduction characteristics of *T. swinhonis* can lead to its population explosion which has negative effect on fish-diversity of the lake, and it has been verified that, of our catch, *T. swinhonis* took up nearly 58% in number and 22% in weight, respectively (unpublished data). To control the population of *T. swinhonis*, a very feasible or simple way we suggest, is to catch them with discretion before their spawning season and process the catch into feed (such as fish meal) for aquaculture or stock farming, or even food for human, like fried fish for sale. Besides, to release fish who prey on *T. swinhonis* with discretion is considerable as well (Ye *et al.*, 2006).

Overall, this paper is the first report about reproductive biology of *T. swinhonis*, thus comparisons cannot be conducted with either previous data for the same population in the BDT Lake or other populations of the same species elsewhere. Nevertheless, the inferences made herein can be used as the baseline information for future population modeling, fish stock assessment, fisheries management and comparison studies of *T. swinhonis*.

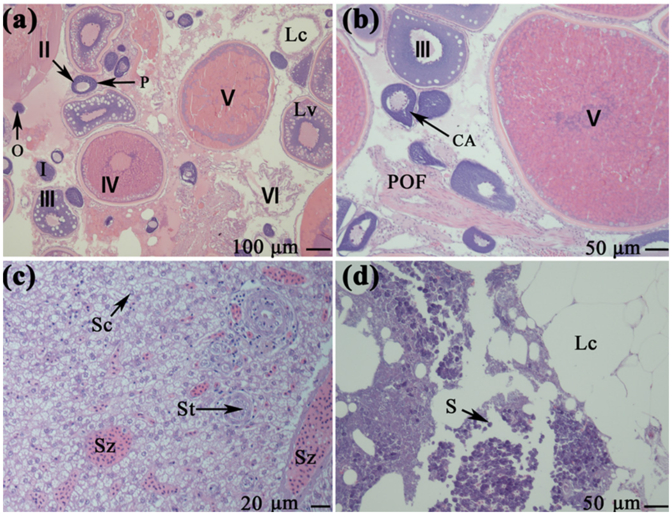

Fig. 6. Histological sections for ovary or testis of two mature *Toxabramis swinhonis* collected in spawning season. Two top figures [(a) and (b)] were ovary containing oogonia (O), perinuclear (P) oocytes, cortical alveolar (CA) oocytes, vitellogenic (V) oocytes, post-ovulatory follicles (POF), luminal cavity (Lc) and lipid vacuoles (Lv). Two bottom figures [(c) and (d)] were testis including spermatogonia (S), spermatocytes (Sc), spermatid (St), spermatozoa (Sz) and luminal cavity (Lc). Stages I to VI were gonadal development stages.

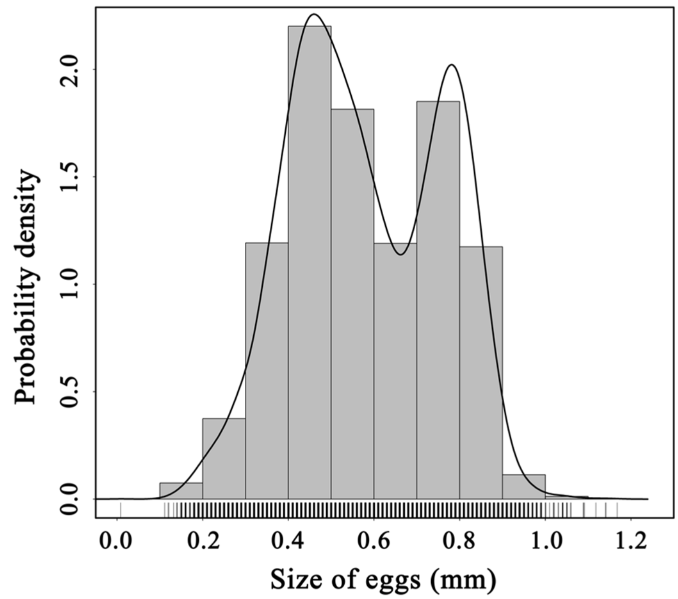

Fig. 7. Frequency distribution and kernel density estimation (solid line) of oocyte ($N = 15\,786$) diameters from a mature female (in stage IV) *Toxabramis swinhonis* collected in BDT Lake at May 2017.

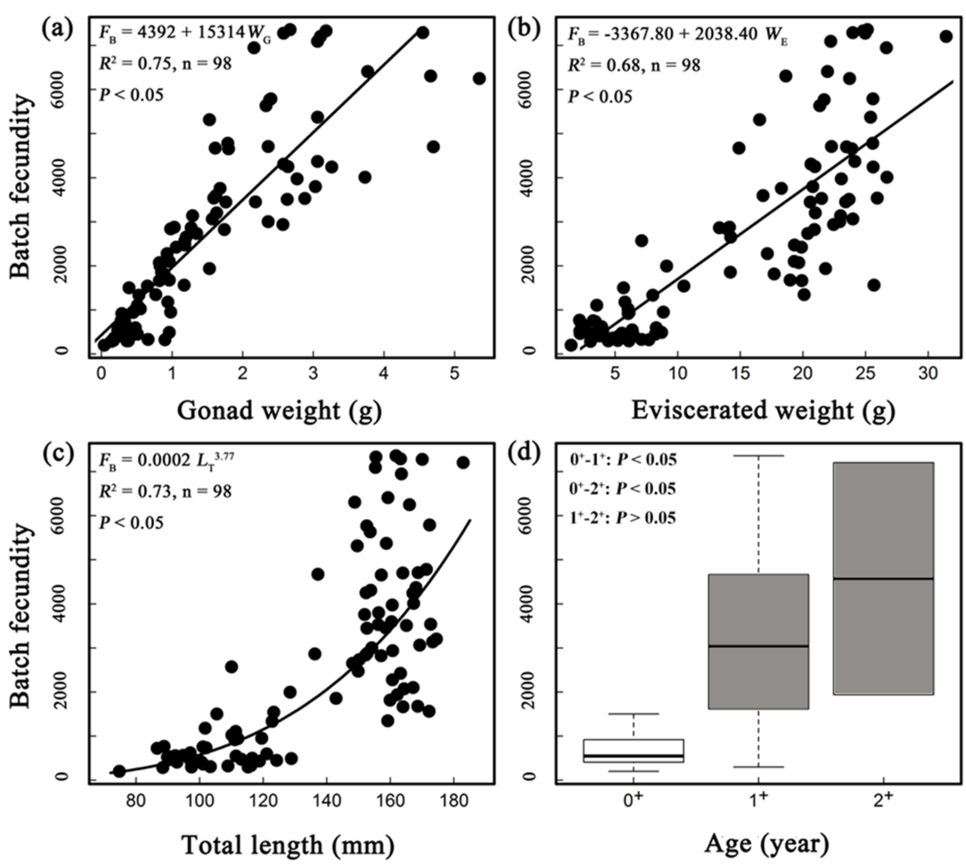

Fig. 8. Relationships between *Toxabramis swinhonis* batch fecundity and gonad weight (g), eviscerated weight (g), total length (mm) and age (year). Different colors in the boxes mean that there existed a statistical significance among different age groups (one-way ANOVA with Tukey's HSD post-hoc).

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