

Reproductive biology of *Schizopygopsis younghusbandi* Regan 1905 (Cyprinidae: Schizothoracinae) in the middle reaches of Yarlung Tsangpo River, China*

DUAN Youjian (段友健)¹, HUO Bin (霍斌)², MA Baoshan (马宝珊)³, YANG Xin (杨鑫)⁴, XIE Congxin (谢从新)^{2, **}

¹ School of Fisheries and Life Science, Dalian Ocean University, Dalian 116023, China

² College of Fisheries, Huazhong Agricultural University, Wuhan 430070, China

³ Yangtze River Fisheries Research Institute, Chinese Academy of Fishery Sciences, Wuhan 430223, China

⁴ Hunan Fisheries Research Institute, Changsha 410153, China

Received Jun. 9, 2017; accepted in principle Jul. 17, 2017; accepted for publication Aug. 31, 2017

© Chinese Society for Oceanology and Limnology, Science Press and Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract The reproductive biology of *Schizopygopsis younghusbandi* (Cyprinidae: Schizothoracinae) was studied by 719 individuals that collected from August 2008 to August 2009 in the middle reaches of Yarlung Tsangpo River, China. We coupled monthly variations of the gonadosomatic index (GSI), monthly proportions of the macroscopic maturity stages with size distribution of oocytes to evaluate spawning seasons. Taken as a set, these results indicated that *S. younghusbandi* spawned from March to April with high degree of the spawning synchronicity. The standard lengths and the ages at 50% maturity for male were 222 mm and 4.4 year, and 308 mm and 7.0 year for female. In addition, the estimated mean fecundity and mean relative fecundity were 18682 and 57.8 eggs per g body weight. The fecundity of *S. younghusbandi* increased linearly with increasing of standard length and body weight. This study provides details about the *S. younghusbandi* reproduction suggesting that may be this species is vulnerable to exploitation in the middle reaches of Yarlung Tsangpo River.

Keyword: reproduction; fecundity; spawning season; Tibet

1 INTRODUCTION

The Yarlung Tsangpo River originates from a glacier on the northern side of the middle Himalayas in Tibet features cold water temperature with low biological productivity. Protected by Tibetan Buddhism, who was subscribed to the belief that fish are the embodiment of the dragon god, fisheries resource is abundant (Qiu and Chen, 2009). The subfamily Schizothoracinae is the predominant group of endemic fishes living in Qinghai-Tibetan Plateau (Cao et al., 1981). With immigration from the inland areas caused lifestyle changes, recent developments in the field of fisheries have led to a renewed interest in fishing. Population decline was found for *Schizothorax waltoni*, *Ptychobarbus dipogon*, *Schizothorax o'connori*, *Oxygymnocypris stewartii*, and *Schizopygopsis younghusbandi* (Li and Chen, 2009; Qiu and Chen, 2009; Ma et al., 2011; Huo et al., 2012; Duan et al., 2014). Therefore, management

concerning the utilization and conservation of fish resources should be established base on biology and ecology.

Schizopygopsis younghusbandi (Cyprinidae: Schizothoracinae) is relatively small Schizothoracinae fishes, distributed only in the middle reaches of Yarlung Tsangpo River (Bureau of Aquatic Products, 1995). Not only are *S. younghusbandi* important to local commercial fisheries, they are also one of the most ecologically important species to structure their aquatic ecosystems by virtue of high abundance and predatory nature. Chen et al. (2009) and Duan et al. (2014) studied the age and growth of *S. younghusbandi* by otolith, revealing that it experienced a low growth

* Supported by the Finance Special Fund of Chinese Ministry of Agriculture (Fisheries Resources and Environment Survey in the Key Water Areas of Tibet)

** Corresponding author: xiecongxin@mail.hzau.edu.cn

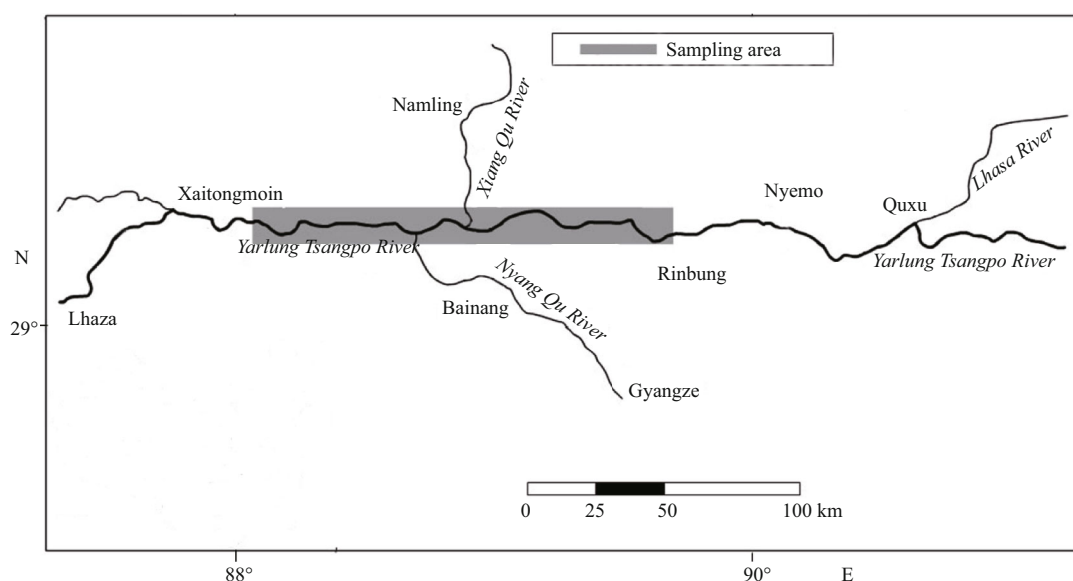


Fig.1 Sampling locations of *S. younghusbandi* in the Yarlung Tsangpo River during the period 2008–2009 (Zhou et al., 2015)

rate and could live for 18 years old for female. Xu (2011) reported that the duration of the embryonic development needed 295 h at water temperatures of 9.5–11.1°C. Like other Schizothoracinae fishes of the Tibetan Plateau (Ma et al., 2011; Huo et al., 2012), aggregation-spawning was typical characteristics of *S. younghusbandi*, which groupers were highly predictable and were often caught by commercial fisheries. The investigated found that *S. younghusbandi* as a favorite species captured from September to December when fisherman targeted them mainly using gill nets and traps. So far, however, available information on biology of *S. younghusbandi* in the Yarlung Tsangpo River is limited.

Previously, several recent studies investigating reproduction have been carried out on other subfamily Schizothoracinae (Ma et al., 2012; Huo et al., 2013; Zhou et al., 2015), while information on reproductive cycle of *S. younghusbandi* showed limited attention. Knowledge of reproductive biology, such as spawn season, sexual maturity and fecundity, is vital demographic characteristics essential to understanding of a species' life history and critical component of their management. The aim of the present study was to determine the reproductive biology of *S. younghusbandi* and answer basic questions including: (1) size and age at maturity of *S. younghusbandi*; (2) the spawning season and spawning type of the fish, based on monthly proportions of macroscopic gonadal maturity stages, variations in the gonadosomatic index (GSI), and the size distribution of oocytes; and (3) fecundity and relative fecundity of *S. younghusbandi*, and analyze relationships between length and weight. Water

temperature and photoperiod on gonadal development and sexual maturity were also considered.

2 MATERIAL AND METHOD

2.1 Sample collection

Between August 2008 and August 2009, 719 specimens of *S. younghusbandi* were caught monthly with floating gillnets (mesh size 7.5 cm) and bottom gillnets (mesh size 6.5 cm) in the Yarlung Tsangpo River (Fig.1).

Prior to standard length (SL) and body weight (BW) were measured to the nearest 1 mm and 0.1 g, fish was euthanized with MS-222 and eviscerated immediately. The gonads were removed and weighed (to the nearest 0.01 g). The gonad samples were conserved in Bouin's fluid for 48 h and then immersed in 70% ethanol until examination. Fixed gonads were dehydrated in alcohol and embedded in paraffin wax for sectioning. Embedded gonads were sectioned transversely at 7–10 µm thickness and stained with haematoxylin and eosin. Pictures were taken using a Nikon microscope at ×40–400 (Nikon Eclipse 80i photomicroscope).

2.2 Experiments for the estimation of size and age at sexual maturity

Size at sexual maturity that defined as the size at which 50% of the population attains sexual maturity (SL_{50}) was performed to assess maturity macroscopically for each sex. In other words, the size at which randomly chosen individual has a 50% chance of being mature (Somerton, 1980). A logistic function to the proportion

Table 1 Macroscopic and microscopic description of the phases in male reproductive cycle of *S. younghusbandi*

Phase	Macroscopic features	Microscopic features
Immature	Sex can not be identified macroscopically. Gonads are tiny and threadlike	Seminal lobules with predominant spermatogonia and few spermatocytes
Developing	Testes filling about 0.1 of the body cavity. Whitish in color. No visible vascularization	Seminal lobules mainly containing large number of spermatogonia and cysts of spermatocytes. Cysts of spermatids occasionally present
Maturing	Easily recognized testes. Testes plump, occupying 0.2–0.3 of the body cavity. Whitish in color	Seminal lobules containing cysts of spermatocytes and spermatids. Some spermatogonia observed along the wall of the seminal lobules
Mature	Testes larger, occupying more than half of the body cavity. Milt flowing freely when abdomen slightly compressed	Large amount of spermatozoons appears in the lumina of tubules. Spermatids also present
Spawning	Milt flow freely under slight pressure or with no pressure	Seminal lobules full of spermatozoons
Spent	Testes significantly decreased in size. Flaccid, shrunk and blooded. No milt expressible	Combined with residual spermatozoa, spermatogonias dominating in the lobule lumen

(P) of mature fish was used to estimate the size with 10 mm (SL) size intervals: $P=1/\{1+\exp[-k(\text{SL}_{\text{mid}}-\text{SL}_{50})]\}$ (Chen and Paloheimo, 1994), where SL_{mid} is the midpoint of the SL class, SL_{50} is the mean SL at sexual maturity; P is the proportion of mature fish and k is the slope. This logistic function was also performed to describe the possibilities of age at maturity (A_{50}), in which age was determined by otolith. The equation is: $P=1/\{1+\exp[-k(A-A_{50})]\}$ (Chen and Paloheimo, 1994), where A is the age of fish, A_{50} is the age at first maturity.

2.3 Experiments for the spawning season

The spawning season was determined by monthly variations of the gonadosomatic index (GSI), monthly proportions of the macroscopic maturity stages, and the size distribution of oocytes. The GSI of mature individuals was assessed using the formula: $\text{GSI}=\text{GW}/\text{BW}\times 100$, GW and BW means the gonad weight and the body weight, respectively. The diameter of all oocytes that had started vitellogenesis was measured. The monthly size-frequency distribution of oocytes was photographed (Leica EZ4D dissecting microscope) and measured to the nearest 0.001 mm in diameter (Image Pro Plus 6.0). For each individual, at least 120 oocytes were measured.

2.4 Experiments for the estimation of fecundity

In order to determine fecundity, 69 females were handled by the gravimetric method (Bagenal and Braum, 1978). Portions of each ovary, including anterior, median and posterior, were sampled. Fecundity was calculated as $F=n\times W/w$, where n is the number of oocytes in the subsamples, W is the weight of ovaries, and w is the weight of subsamples. The relative fecundity was determined by the number of vitellogenic oocytes counted per female gram of total female weight (Adebisi, 1987). Regression models

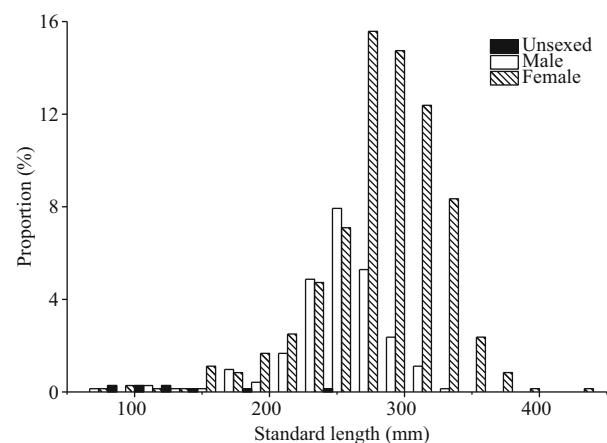


Fig.2 Size distribution for unsexed, males and females of *S. younghusbandi* in the Yarlung Tsangpo River during the period 2008–2009

were used to describe the relationships between standard length, total weight and absolute fecundity. Data and images were analyzed by means of Microsoft Excel 2003, Adobe Photoshop CS4 and Origin Lab Origin V8.0.

3 RESULT

3.1 Size distribution

A total of 719 individuals (527 females, 183 males and 9 undetermined) were collected during the study period (Fig.2). The overall sex ratio significantly differed from 1:1 ($\chi^2=165.937$, $d.f.=1$, $P<0.05$), with 25.5% males and 73.3% females. Length-frequency distributions significantly differed between sexes (Kolmogorov-Smirnov $Z=5.198$, $n_1=527$, $n_2=183$, $P<0.05$).

3.2 The phases in the reproductive cycle of *S. younghusbandi*

Sex and maturity stage were identified based on

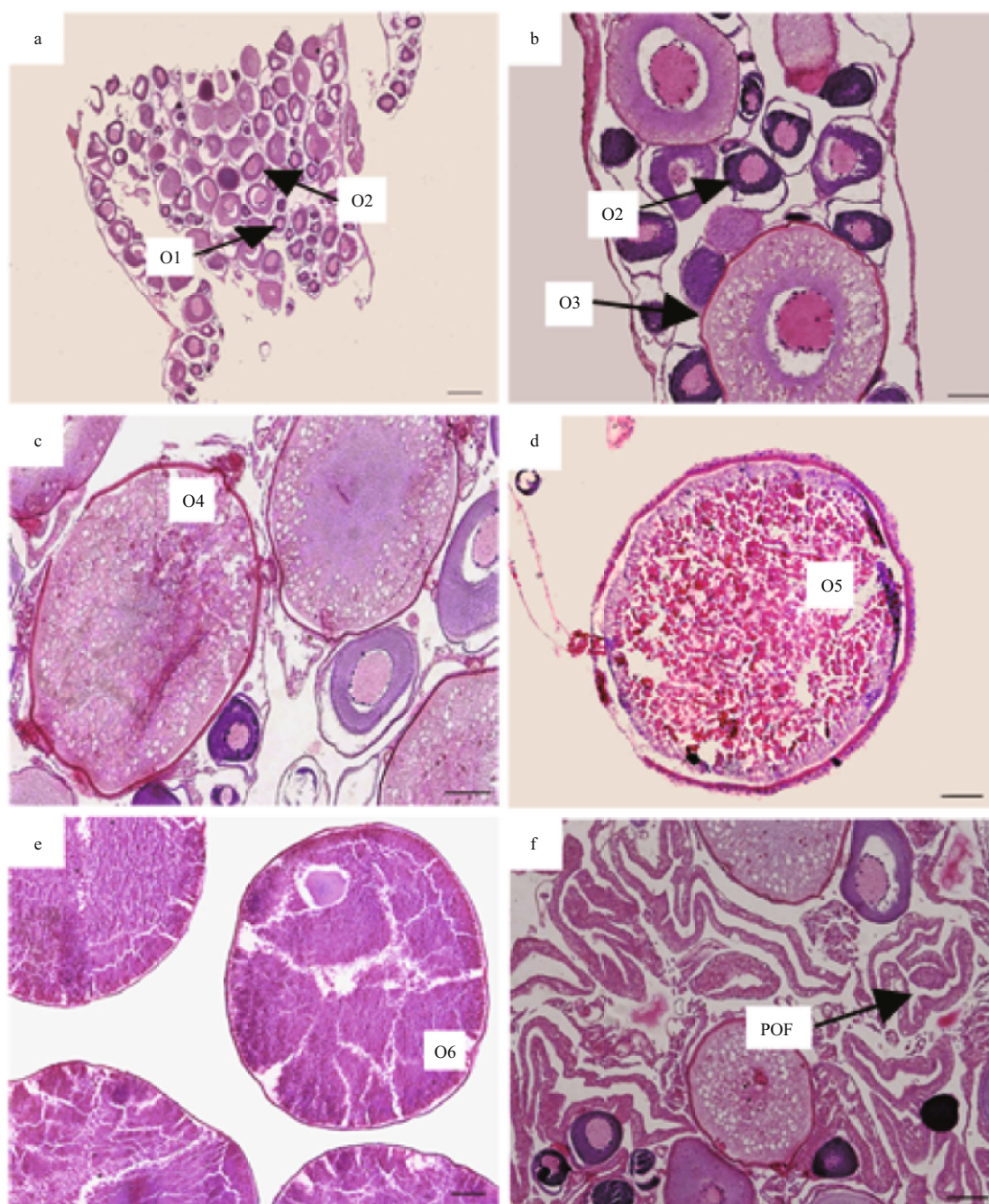


Fig.3 Ovarian development in *S. younghusbandi* in the Yarlung Tsangpo River during the period 2008–2009

a. immature ovary; b. early developing ovary; c. late developing ovary; d. maturing ovary; e. mature ovary; f. spent ovary. O1: chromatin-nucleolar oocyte; O2: peri-nucleolar oocyte; O3: cortical alveoli oocyte; O4: primary yolk oocyte; O5: second yolk oocyte; O6: tertiary yolk oocyte; ao: atretic oocyte; POF: postovulatory follicles. Scale bar: b, c, d, f: 100 μ m; a, e: 200 μ m.

macroscopic and microscopic features (Tables 1, 2). The development of gonads was categorized to six phase followed Huo et al. (2013). With regard to macroscopic features, we assigned a gross maturity stage based on the gonads. With regard to histological observation, both ovaries and testes were assigned to six microscopic developmental stages (Figs.3, 4). The

microscopic mature stage was designated when ovaries developed mainly in advanced yolked oocytes (Fig.3e). Furthermore, vitellogenic oocytes were observed in the spent ovaries (Fig.3f).

3.3 Size and age at maturity

Size (SL_{50}) and age (A_{50}) at 50% maturity were

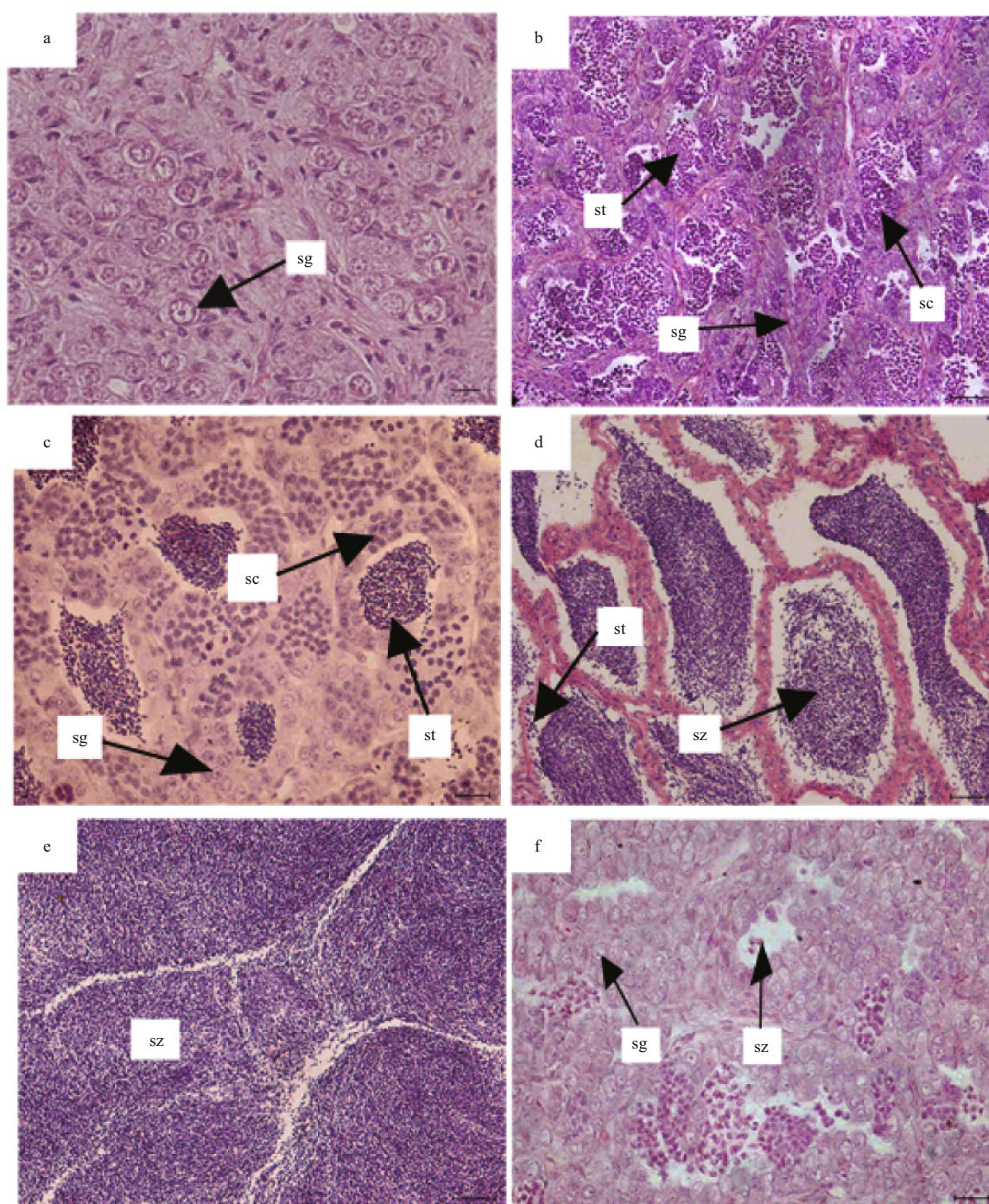


Fig.4 Testes development in *S. younghusbandi* in the Yarlung Tsangpo River during the period 2008–2009

a. immature testis; b. developing testis; c. maturing testis; d. mature testis; e. spawning testis; f. spent testis. sg: spermatogonia; sc: spermatocytes; st: spermatids; sz: spermatozoa. Scale bar: a, c, f: 20 μ m; b, d, e: 50 μ m.

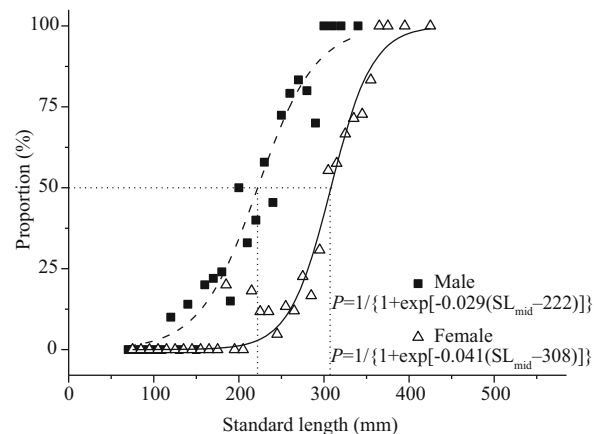
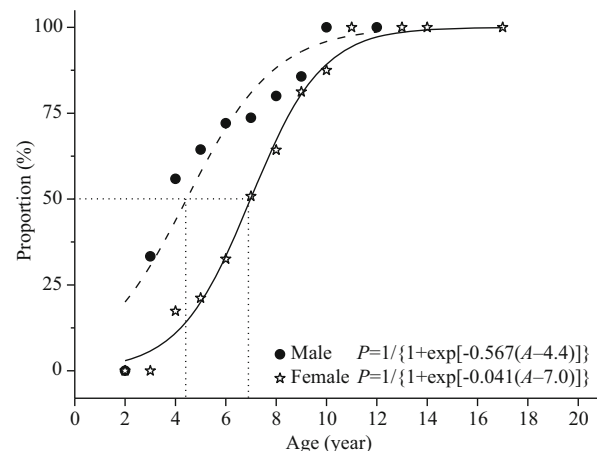
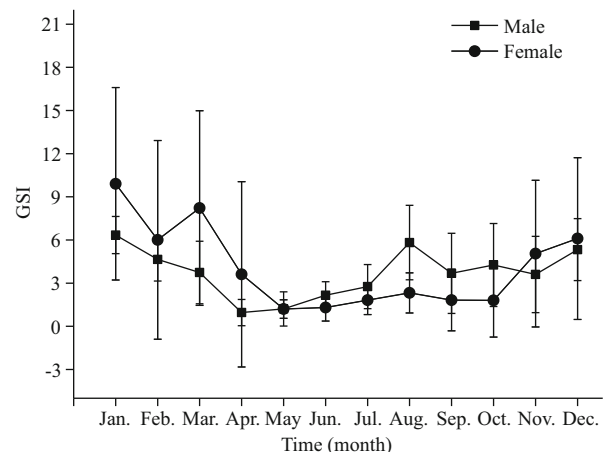
estimated by fitting a logistic function to the proportion (P) of mature fish. Size and age at maturity showed a clear difference between males and females (Figs.5, 6). Estimated SL_{50} were 222 mm and 308 mm for males and females, respectively. Estimated A_{50} are 4.4 years and 7.0 years for males and females, respectively.

3.4 Spawning season

The reproductive cycle can be classified into three phases that contains gonad development, spawning, and resting according to monthly variations of the gonadosomatic index (GSI) (Fig.7), monthly

Table 2 Macroscopic and microscopic description of the phases in female reproductive cycle of *S. younghusbandi*

Phase	Macroscopic features	Microscopic features
Immature	Sex can not be identified macroscopically. Gonads are tiny and threadlike	Seminal lobules mainly containing spermatogonia, and few spermatocytes. The cytoplasm which stains deeply with haematoxylin. The nucleus is relatively large in size
Developing	Ovaries small, translucent and occupy less than a third of body cavity. Reddish color due to vascularization	Early developing: Ovaries with primary growth and cortical alveoli oocytes. The nucleus is spherical in form and contains many nucleoli situated on its periphery Late developing: Ovaries with dominating primary yolk oocytes. primary growth and cortical alveoli oocytes also present. Yolk globules begin to appear between the vesicles
Maturing	Easily recognized ovaries. Ovaries large and occupy almost half of body cavity. Some oocytes appear translucent	Oocytes become large, and the most second yolk oocytes are at the Ovaries
Mature	Ovaries distinctly bulge and occupy more than two third of the body cavity. Ovarian wall thin and flexible	Ovaries containing dominating tertiary oocytes that increase dramatically in size; the nucleus is moving towards the animal pole of the oocyte
Spawning	Oocytes flow freely under slight pressure or with no pressure	None
Spent	Ovaries are small and bloodshot. Body cavity is flaccid and shrunk with scattered residual vitellogenic oocytes	Ovaries with primary growth and cortical alveoli oocytes. Postovulatory follicles that failed to spawn are frequently observed, while atretic oocytes occasionally present

**Fig.5 Logistic functions fitted to percent mature by 10 mm standard length intervals of males and females *S. younghusbandi* in the Yarlung Tsangpo River during the period 2008–2009, showing the mean standard length (SL_{50}) at sexual maturity****Fig.6 Logistic functions fitted to percent mature by 1 year intervals of males and females *S. younghusbandi* in the Yarlung Tsangpo River during the period 2008–2009, showing the mean age (A_{50}) at sexual maturity****Fig.7 Monthly gonadosomatic index of males and females *S. younghusbandi* collected in the Yarlung Tsangpo River during the period 2008–2009**

Values are expressed as means and the vertical lines means±standard deviation.

proportions of the macroscopic maturity stages (Fig.8), and size distribution of oocytes (Fig.9).

The GSI of *S. younghusbandi* changed over time (Fig.7). By November males run a higher level than females and the GSI on the increase for each sex during gonad development phase. With rising water temperature and photoperiod in early spring (Fig.10), *S. younghusbandi* showed a high level from January to March. After that, the GSI level of each sex changed substantially and reached at lowest value in May (1.19% for female and 1.20% for male), which remained nearly constant to July.

According to distribution of macroscopic gonad maturity stages, we concluded that *S. younghusbandi* might spawn from March to April (Fig.8). In gonad

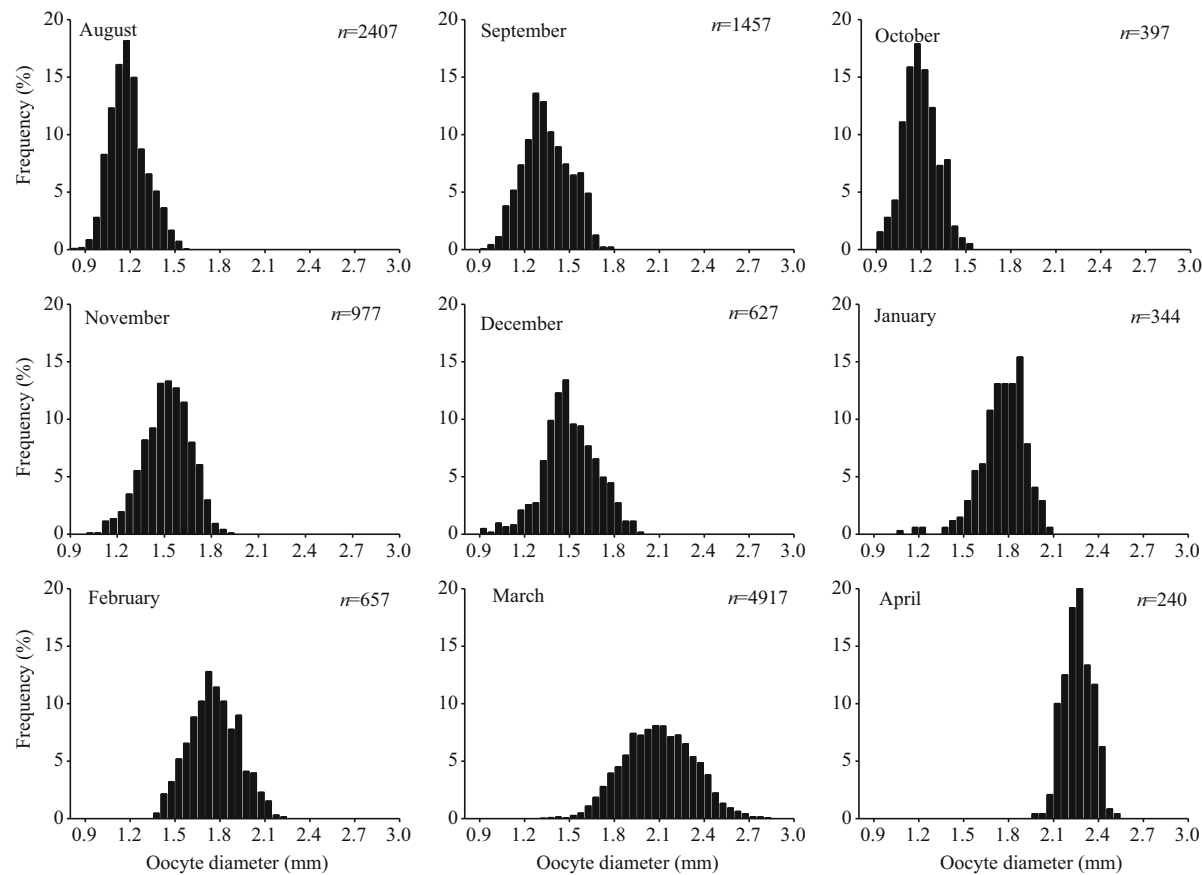


Fig.9 Monthly size-frequency of oocytes for *S. younghusbandi* in the Yarlung Tsangbo River from July 2008 to April 2009

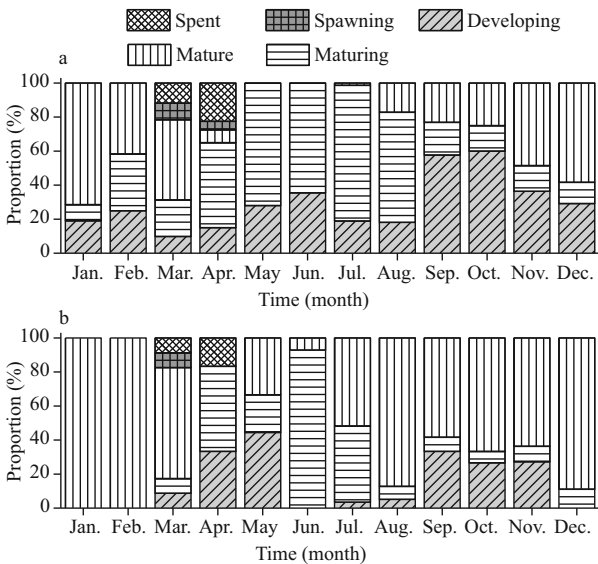


Fig.8 Distribution of macroscopic gonad maturity stages of females (a) and males (b) of *S. younghusbandi* in the Yarlung Tsangbo River between August 2008 and August 2009

development phase *S. younghusbandi* were not found mature proportions exceed 50% until to November for female, while mature proportions mainly occupied for male since early August. The highest level of

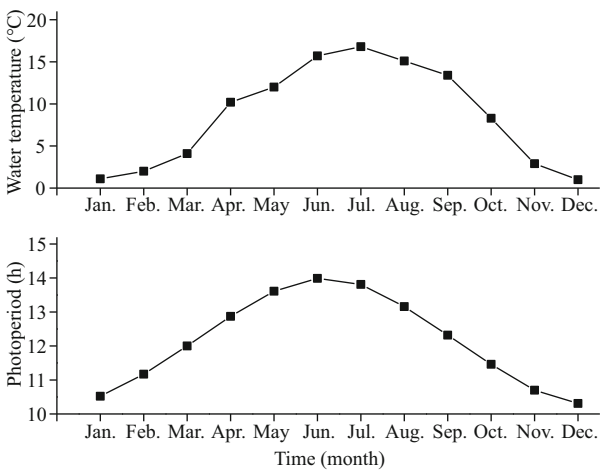


Fig.10 Monthly variation in water temperature and photoperiod in the Yarlung Tsangbo River between August 2008 and August 2009

Values are expressed as means and the vertical lines means±standard deviation.

mature proportions was well synchronized with the rising water temperature and photoperiod at spring (Fig.10), and both spent stages could be observed in March and April. Gonadal mainly consist of maturing and developing stage in resting phase. Approximately

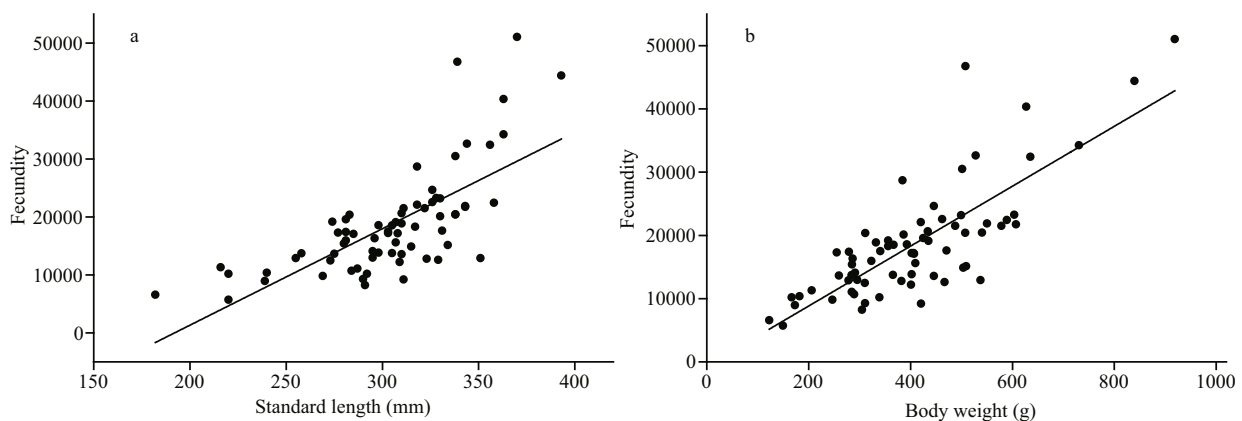


Fig.11 The relationships between ovary weight, standard length and fecundity of *S. younghusbandi* in the Yarlung Tsangbo River

60% of maturing and developing stage possessed for male, and nearly full occupied for female from May to July.

Egg sizes were measured for mature ovaries from August 2008 to April 2009 (Fig.9). Oocytes kept growing since yolk began accumulating in August. Prior to the following April, high proportion mature oocytes formed in ovaries with a diameter of >2.0 mm. Histogram of oocyte diameter showed a unimodal distribution in every month, indicating that there was a high degree of spawning synchronicity in the *S. younghusbandi* population.

3.5 Fecundity

The mean value for absolute fecundity was 18 682 (S.D.=9 038) (ranging from 5 712 to 51 037) eggs for females with standard length from 182 to 393 mm. The relative fecundity was estimated at 57.8 (S.D.=15.2) (ranging from 29.5 to 113.6) eggs/g body weight. A significantly positive correlation was found between absolute fecundity and standard length (Fig.11a, $n=69$, $R^2=0.501$), as well as body weight (Fig.11b, $n=69$, $R^2=0.624$).

4 DISCUSSION

The present study was designed to answer basic questions concerning the reproductive biology of *S. younghusbandi*. Spawning season was determined by the monthly gonadosomatic index and distribution of macroscopic maturity stages in which *S. younghusbandi* spawns over a short period each year. Our results indicate that life history of *S. younghusbandi* is typical *K*-selected traits, which characterize by relatively low fecundity and relatively late sexual maturity (Winemiller, 1992). These reproductive characteristics are in line with those of

previous studies in the middle reaches of Yarlung Tsangpo River (Qiu and Chen, 2009; Ma et al., 2012; Huo et al., 2013; Zhou et al., 2015). Fisheries based on *K*-selected species are more susceptible to growth overfishing and stock depletion (Booth and Buxton, 1997).

Environmental and geographical factors have an influence on fish growth and reproduction, which may lead to reaching at different sizes or at different ages of sexual maturity (Pawson et al., 2000; Yoneda and Wright, 2005; Heath et al., 2012). Indeed, our results estimate that the size and age at first sexual maturity of *S. younghusbandi* are larger and older than values reported for comparable sizes of other cyprinid fishes from plain water (Rutaisire and Booth, 2005; Tarkan, 2006). This phenomenon was also described in other Schizothoracinae fishes in the Yarlung Tsangpo River (Ma et al., 2012; Huo et al., 2013; Zhou et al., 2015). Low water temperature and lack of bait biological in high elevation water could make the fish grow slowly. Environmental characters were also considered as the primary environmental factors to synchronize the endogenous rhythms of spawning in many cyprinid fishes (De Vlaming, 1975; Papoulias et al., 2006). The fish did not spawn until the water temperature and photoperiod began increasing in March, suggesting that water temperature and photoperiod are likely mediated through its impact on the final maturation of oocytes and the initiation of reproductive activities. In addition, unimodal distributions of oocytes suggested that *S. younghusbandi* population experienced a high degree of spawning synchronicity.

The oocyte growth of spring-spawning freshwater fishes typically occurs following a relatively long phase of gonad quiescence (Peter and Crim, 1979). In contrast with this characteristic, gonadal development was initiated following a relatively short post-

spawning quiescent period in *S. younghusbandi*. A possible explanation for this might be that gonadal recrudescence occurs coincident with a period of decreasing photoperiod and water temperatures. This observation may support the hypothesis that short post-spawning quiescent period was advantageous to *S. younghusbandi* adapt to the rigorous high-elevation plateau river environment.

The *S. younghusbandi*, as one of the smallest species from Schizothoracinae fishes in the middle reaches of the Yarlung Tsangpo River, had the lowest values of absolute fecundity, because fecundity tends to increase with fish size and fish body weight increase. (Wootton, 1999; Murua and Saborido-Rey, 2003; Brouwer and Griffiths, 2005). Therefore, it is necessary to eliminate the body size effect in fecundity studies. In this study the relative fecundity of *S. younghusbandi* has 57.8 eggs/g of fish body weight. Analogously, Ma et al. (2012) found that the relative fecundity of *Schizothorax o'connori* (Cyprinidae: Schizothoracinae) in the Yarlung Tsangpo River fluctuated from 6.2 to 22.2 eggs/g, with a mean of 14.32 eggs/g of fish body weight. The mean relative fecundity of *Oxygymnocypris stewartii* in the Yarlung Zangbo River was 25.4 eggs/g of fish body weight (Huo et al., 2013). Zhou et al. (2015) reported that the relative fecundity of *Schizothorax waltoni* (Cyprinidae: Schizothoracinae) in the Yarlung Tsangpo River with 13.4 eggs/g of fish body weight. While Hotos et al. (2000) found that the relative fecundity of *Liza aurata* (Pisces Mugilidae) from a local population in the lagoon of Klisova with a mean of 1 152 eggs/g of fish body weight. The mean relative fecundity of Silver Carp in the Middle Mississippi River was 672 eggs/g of fish body weight (Williamson and Garvey, 2005). Above all, Schizothoracinae fishes represent a lower reproductive potential in the Yarlung Tsangpo River.

Schizopygopsis younghusbandi originated from primitive barbine fishes that date back to the late Tertiary, and evolved into the Qinghai-Tibet plateau fish fauna along the vicariance caused by the uplift of Tibet (Cao et al., 1981; Wu and Tan, 1991; He and Chen, 2006). The isolation made this specialized fish fauna sensitive to anthropogenic activities. Not only anthropogenic disturbance can efficiently remove large mature individuals during spawning aggregations, but could possibly progressively push the fish population towards maturation at smaller length and increase the risk of recruitment failures (Jørgensen, 1990). Thus, knowledge of the

reproductive characteristics of this species is fundamental importance to conserving this stock. Our study represents an important step in the understanding of *S. younghusbandi*'s reproductive biology. Based on those characteristics, fishery regulations should focus on the mesh size limit, the fishing closure and the proper fishing methods to prevent overfishing, should be established. Meanwhile, long-term ecological studies are needed to observe the change in size at maturity on the commercial potential of *S. younghusbandi* in the future.

5 CONCLUSION

Schizopygopsis younghusbandi spawns over a short period each year from March to April, are typically aggregation-spawning with low fecundity and late maturity. Our results indicate that *S. younghusbandi* may be vulnerable to exploitation in the middle reaches of Yarlung Tsangpo River.

6 DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

7 ACKNOWLEDGEMENT

Thanks to ZHOU Xianjun, YANG Xuefeng and HUANG Haiping for helping in sample collection and histological processing. The use of specimens in our research were carried out following the legal requirements "Instructive notions with respect to caring for laboratory animals", which was issued by the Ministry of Science and Technology of the People's Republic of China.

References

- Adebisi A A. 1987. The relationships between the fecundities, gonado-somatic indices and egg sizes of some fishes of Ogun River, Nigeria. *Archiv für Hydrobiologie*, **111**: 151-156.
- Bagenal T B, Braum E. 1978. Eggs and early life history. In: Bagenal T B ed. *Methods for Assessment of Fish Production in Fresh Waters*. Blackwell Scientific Publications, Oxford. p.165-201.
- Booth A J, Buxton C D. 1997. Management of the panga *Pterogymnus laniarius* (Pisces: Sparidae) on the Agulhas Bank, South Africa using per-recruit models. *Fisheries Research*, **32**(1): 1-11.
- Brouwer S L, Griffiths M H. 2005. Reproductive biology of carpenter seabream (*Argyrozona argyrozona*) (Pisces: Sparidae) in a marine protected area. *Fishery Bulletin*,

- 103(2): 258-269.
- Bureau of Aquatic Products. 1995. Fishes and Fish Resources in Xizang, China. China Agriculture Press, Beijing. (in Chinese)
- Cao W X, Chen Y Y, Wu Y F, Zhu S Q. 1981. Origin and evolution of schizothoracine fishes in relation to the upheaval of the Qinghai-Xizang Plateau. In: CAS ed. Studies on the Period, Amplitude and Type of the Uplift of the Qinghai-Xizang Plateau. Science Press, Beijing, p.118-130. (in Chinese)
- Chen F, Chen Y F, He D K. 2009. Age and growth of *Schizopygopsis younghusbandi younghusbandi* in the Yarlung Zangbo River in Tibet, China. *Environmental Biology of Fishes*, **86**(1): 155-162.
- Chen Y, Paloheimo J E. 1994. Estimating fish length and age at 50% maturity using a logistic type model. *Aquatic Sciences*, **56**(3): 206-219.
- De Vlaming V L. 1975. Effects of photoperiod and temperature on gonadal activity in the cyprinid teleost, *Notemigonus crysoleucas*. *The Biological Bulletin*, **148**(3): 402-415.
- Duan Y J, Xie C X, Zhou X J, Ma B S, Huo B. 2014. Age and growth characteristics of *Schizopygopsis younghusbandi* Regan, 1905 in the Yarlung Tsangpo River in Tibet, China. *Journal of Applied Ichthyology*, **30**(5): 948-954.
- He D K, Chen Y Y. 2006. Biogeography and molecular phylogeny of the genus *Schizothorax* (Teleostei: Cyprinidae) in China inferred from cytochrome *b* sequence. *Journal of Biogeogr.*, **33**(8): 1448-1460.
- Heath M R, Neat F C, Pinnegar J K, Reid D G, Sims D W, Wright P J. 2012. Review of climate change impacts on marine fish and shellfish around the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **22**(3): 337-367.
- Hotos G N, Avramidou D, Ondrias I. 2000. Reproduction biology of *Liza aurata* (Risso, 1810), (Pisces Mugilidae) in the lagoon of Klisova (Messolonghi, W. Greece). *Fisheries Research*, **47**(1): 57-67.
- Huo B, Xie C X, Ma B S, Yang X F, Huang H P. 2012. Age and Growth of *Oxygymnocypris stewartii* (Cyprinidae: Schizothoracinae) in the Yarlung Tsangpo River, Tibet, China. *Zoological Studies*, **51**(2): 185-194.
- Huo B, Xie C X, Ma B S, Yang X F, Huang H P. 2013. Reproductive biology of *Oxygymnocypris stewartii* in the Yarlung Zangbo River in Tibet, China. *Environmental Biology of Fishes*, **96**(4): 481-493.
- Jørgensen T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *ICES Journal of Marine Science*, **46**(3): 235-248.
- Li X Q, Chen Y F. 2009. Age structure, growth and mortality estimates of an endemic *Ptychobarbus dipogon* (Regan, 1905) (Cyprinidae: Schizothoracinae) in the Lhasa River, Tibet. *Environmental Biology of Fishes*, **86**(1): 97-105.
- Ma B S, Xie C X, Huo B, Yang X F, Chen S S. 2012. Reproductive biology of *Schizothorax o'connori* (cyprinidae: schizothoracinae) in the Yarlung Zangbo River, Tibet. *Zoological Studies*, **51**(7): 1 066-1 076.
- Ma B S, Xie C X, Huo B, Yang X F, Li P. 2011. Age validation, and comparison of otolith, vertebra and opercular bone for estimating age of *Schizothorax o'connori* in the Yarlung Tsangpo River, Tibet. *Environmental Biology of Fishes*, **90**(2): 159-169.
- Murua H, Saborido-Rey F. 2003. Female reproductive strategies of marine fish species of the North Atlantic. *Journal of Northwest Atlantic Fishery Science*, **33**(1): 23-31.
- Papoulias D M, Chapman D, Tillitt D E. 2006. Reproductive condition and occurrence of intersex in bighead carp and silver carp in the Missouri River. *Hydrobiologia*, **571**(1): 355-360.
- Pawson M G, Pickett G D, Witthames P R. 2000. The influence of temperature on the onset of first maturity in sea bass. *Journal of Fish Biology*, **56**(2): 319-327.
- Peter R E, Crim L W. 1979. Reproductive endocrinology of fishes: gonadal cycles and gonadotropin in teleosts. *Annual Review of Physiology*, **41**(1): 323-335.
- Qiu H, Chen Y F. 2009. Age and growth of *Schizothorax waltoni* in the Yarlung Tsangpo River in Tibet, China. *Ichthyological Research*, **56**(3): 260-265.
- Rutaisire J, Booth A J. 2005. Reproductive biology of ningu, *Labeo victorianus* (Pisces: Cyprinidae), in the Kagera and Sio Rivers, Uganda. *Environmental Biology of Fishes*, **73**(2): 153-162.
- Somerton D A. 1980. A computer technique for estimating the size of sexual maturity in crabs. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**(10): 1 488-1 494.
- Tarkan A S. 2006. Reproductive ecology of two cyprinid fishes in an oligotrophic lake near the southern limits of their distribution range. *Ecology of Freshwater Fish*, **15**(2): 131-138.
- Williamson C J, Garvey J E. 2005. Growth, fecundity, and diets of newly established silver carp in the middle Mississippi River. *Transactions of the American Fisheries Society*, **134**(6): 1 423-1 430.
- Winemiller K O. 1992. Life-history strategies and the effectiveness of sexual selection. *Oikos*, **63**(2): 318-327.
- Wootton R J. 1999. Ecology of Teleost Fishes. 2nd edn. Springer, Netherlands, 392p.
- Wu Y F, Tan Q J. 1991. Characteristics of the fish-fauna of the characteristics of Qinghai-Xizang plateau and its geological distribution and formation. *Acta Zoologica Sinica*, **37**(2): 135-152. (in Chinese with English abstract)
- Xu J. 2011. Early development of four Schizothoracinae fishes in the Yarlung Zangbo River, Tibet. Master's thesis, Huazhong Agricultural Univ., Wuhan, China. (in Chinese with English abstract)
- Yoneda M, Wright P J. 2005. Effects of varying temperature and food availability on growth and reproduction in first-time spawning female Atlantic cod. *Journal of Fish Biology*, **67**(5): 1225-1241.
- Zhou X J, Xie C X, Huo B, Duan Y J, Yang X, Ma B S. 2015. Reproductive biology of *Schizothorax waltoni* (cyprinidae: schizothoracinae) in the Yarlung Zangbo river in Tibet, China. *Environmental Biology of Fishes*, **98**(2): 597-609.