

Research Article

Combined opportunistic and equilibrium life-history traits facilitate successful invasions of the Shimofuri goby (*Tridentiger bifasciatus*)Jiao Qin^{1,2}, Miao Xiang^{1,3}, Meixiang Jia^{1,3}, Fei Cheng^{1,2}, Lei Zhang^{1,2,4}, Bjorn Victor Schmidt^{1,2}, Jian Liu^{2,5} and Songguang Xie^{1,2,4,*}¹The Key Laboratory of Aquatic Biodiversity and Conservation of Chinese Academy of Sciences, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China²Weishan Lake Scientific Research Station of Environment and Fishery, Institute of Hydrobiology, Chinese Academy of Sciences, Ji'ning 277600, China³University of Chinese Academy of Sciences, Beijing 100049, China⁴Huai'an Research Center, Institute of Hydrobiology, Chinese Academy of Sciences, Huai'an, Jiangsu 223001 China⁵Fisheries Management Committee of Weishan County, Weishan County, Ji'ning 277600, China

Author e-mails: 657634710@qq.com (JQ), 2780155501@qq.com (MX), 2780155501@qq.com (MJ), chengfei@ihb.ac.cn (FC), zhanglei@ihb.ac.cn (LZ), bjorn.schmidt@ihb.ac.cn (BVS), lj688@sohu.com (JL), xiesg@ihb.ac.cn (SX)

*Corresponding author

Citation: Qin J, Xiang M, Jia MX, Cheng F, Zhang L, Schmidt BV, Liu J, Xie SG (2020) Combined opportunistic and equilibrium life-history traits facilitate successful invasions of the Shimofuri goby (*Tridentiger bifasciatus*). *Aquatic Invasions* 15(3): 514–528, <https://doi.org/10.3391/ai.2020.15.3.10>

Received: 17 December 2019**Accepted:** 20 February 2020**Published:** 7 April 2020**Thematic editor:** Ian Duggan**Copyright:** © Qin et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS**Abstract**

The life-history traits of a non-native population of Shimofuri goby (*Tridentiger bifasciatus*) were investigated in Nansi Lake, which is a storage lake on the East Route of the South-to-North Water Transfer Project, China. The results were analyzed in combination with data from other non-native populations of this species to reveal the life-history traits that caused its successful invasions. Mature gonads in April and May suggest that the species spawns in this period, and cohort tracking and age analysis revealed that individuals had a one-year lifespan. The relative fecundity was $2,825 \pm 614$ eggs/g. A short lifespan and high fecundity are opportunistic life-history traits that may enhance population establishment by promoting population increase. The male-biased sex ratio (except in April and May when the males guarding the nests) and sexual size dimorphism observed in this population may be important for males protecting nests and eggs, which is a typical equilibrium trait that facilitates establishment by increasing offspring survival. Non-native populations of this species in the San Francisco estuary system have been reported to batch spawn, have a lifespan of two years, and spawn during March and August, which in comparison with the population in Nansi Lake suggest that the species' life-history traits are phenotypically plastic. We propose that the combined equilibrium and opportunistic characteristics of the species' life-history traits and their plasticity facilitates successful invasions. Our results provide crucial information when evaluating the invasion risk of a species from its life-history traits.

Key words: goby invasion, South-to-North Water Transfer, environmental tolerance, parental care, plasticity

Introduction

Invasive fish species are a significant threat to biodiversity and freshwater ecosystems (Cucherousset and Olden 2011). Invasion success depends on the ability of a species to adapt to novel environments, which is usually relative to the life-history traits and plasticity of the species (Vila-Gispert et

al. 2005; Ribeiro et al. 2008; Fox and Copp 2014). Both opportunistic life-history traits (rapid individual growth, early maturation, and high reproductive investment) and equilibrium life-history traits (typically parental care) have been widely demonstrated to facilitate invasion success (Olden et al. 2006; Fox et al. 2007; Fox and Copp 2014). Successful invaders often exhibit life-history traits plasticity between native and non-native populations (Fox et al. 2007; Grabowska and Przybylski 2015) and different invasion stages (Marchetti et al. 2004; Olden et al. 2006), which allows the invaders to adapt to a broad range of environmental conditions (Davidson et al. 2011; Kornis et al. 2016).

Inter-Basin Water Transfers (IBWTs) have been applied worldwide to resolve the uneven distribution of water resources (Shumilova et al. 2018), and are recognized as one of the major pathways of freshwater invasions (Zhan et al. 2015; Gallardo and Aldridge 2018). IBWTs connect previously isolated catchments of donor regions and recipient regions, and facilitate the dispersal of aquatic organisms between them (Rahel 2007; Zhan et al. 2015). In addition, environmental changes caused by IBWTs may disrupt the recipient ecosystem and favor the establishment of introduced species (Bunn and Arthington 2002; Kadye and Booth 2012). Furthermore, IBWTs can entrain a great number of aquatic organisms, particularly at the early life-history stages (Grimaldo et al. 2009), creating high propagule pressure that drives invasion success (Woodford et al. 2013).

The South-to-North Water Transfer Project of China is one of the world's largest water transfer projects, and has been developed to resolve water shortages in northern China (Liu et al. 1984). It includes three routes: east, central, and west. The East Route of the South-to-North Water Transfer Project (ESNT) pumps water from the lower reaches of the Yangtze River using the Grand Canal as the main channel. The diverted water passes through five of the largest lakes in China: Gaoyou, Hongze, Luoma, Nansi, and Dongping Lakes (Jiang 2012). The first ESNT phase started in 2013, with an annual capacity of 8.9 billion m³. Biological invasions of a variety of aquatic organisms have been reported in these lakes, possibly because of water diversion, such as aquatic macrophytes, e.g., *Cabomba caroliniana* (Hou et al. 2012), mollusks, e.g., *Novaculina chinensis* (Shu et al. 2013), and fish, e.g., *Taenioides cirratus* (Qin et al. 2019).

Our previous study demonstrated that the Shimofuri goby *Tridentiger bifasciatus* (Steindachner, 1881) had successfully invaded lakes along the ESNT, with its first appearance reported in 2015 (Qin et al. 2019). It is an estuarine species that is native to Asian countries on the west Pacific from Hokkaido to Hong Kong, including the Yangtze estuary (Wu and Zhong 2008). We suggested that its invasion of the ESNT lakes originated in the Yangtze estuary because of water diversion (Qin et al. 2019). Invasions of this species have also been reported in the San Francisco estuary, USA with its first appearance in 1985 (Matern and Fleming 1995), and it has since

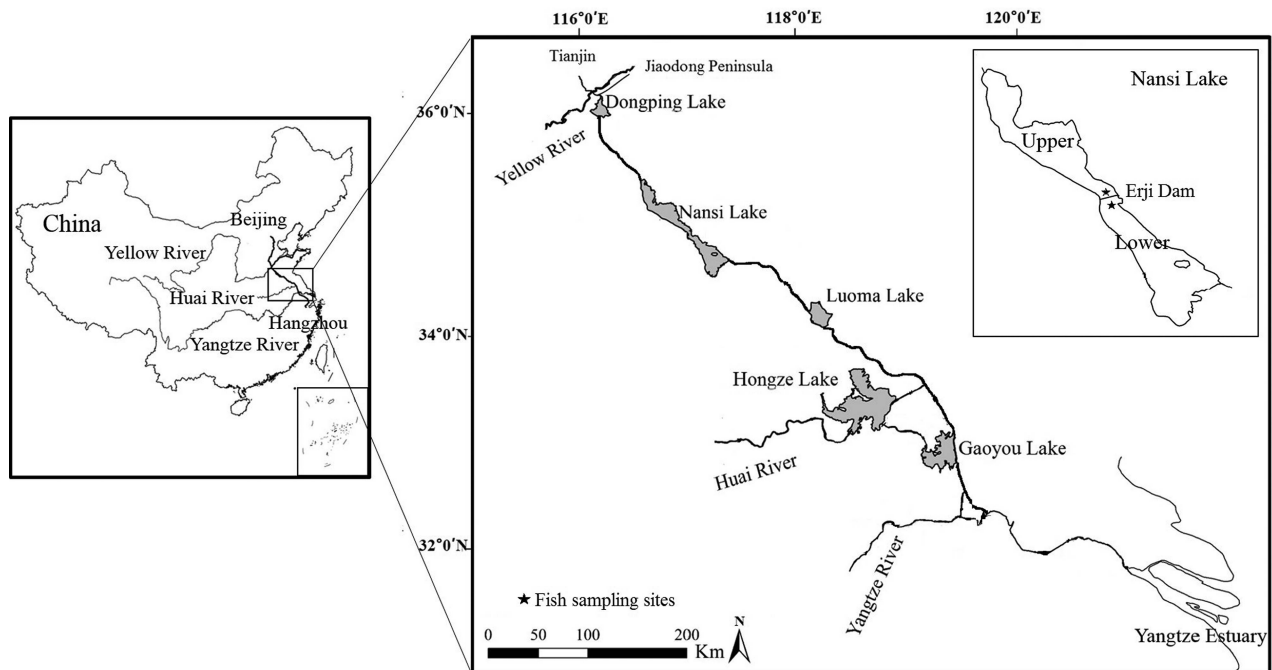


Figure 1. East Route of the South-to-North Water Transfer Project, China, showing sampling locations for the Shimofuri goby (*Tridentiger bifasciatus*) in Nansi Lake.

widely colonized brackish and freshwater bodies (Matern et al. 2002). Little is known about the life-history traits of this species, except for those of the non-native population in the San Francisco estuary: individuals are 35 to 60 mm in total length in their first year, and attain a maximum of 105 mm (Matern 1999). The spawning season is between March and August (Matern 1999), and it is a cavity nester with males guarding embryos (Moyle and Cech 1996).

In the present study, we investigated the life-history traits of a non-native population of Shimofuri goby in Nansi Lake in the ESNT, and compared them with those of the population in the San Francisco estuary. Our main objective was to identify life-history traits that contribute to the invasion success of this species. The results may provide insights into traits that favor species establishment in new areas.

Materials and methods

Nansi Lake (34°27'N–35°20'N; 116°34'E–117°21'E) belongs to the Huai River watershed, on the border between Shandong Province and Jiangsu Province, China. It has been divided into an upper part and a lower part by a sluice dam, the Erji Dam (Figure 1). Nansi Lake is the largest freshwater lake in northern China, and the area of the upper and lower parts is 582 and 571 km², respectively, with an average water depth of 1.4 m (Wang et al. 2019).

Shimofuri goby were sampled using benthic fyke nets that were 15-m long and 0.6-m wide with a 4-mm mesh size. Each net contained 20 trap cases, and each case had three entrances that fish could enter but not exit (Guo et al. 2013). Sampling was conducted monthly at one site in the upper

Table 1. Macroscopic characteristics of gonads of Shimofuri goby (*Tridentiger bifasciatus*) at different developmental stages in Nansi Lake, China.

Gonadal maturity stage	Female	Male
I (inactive)	Sexes could not be identified macroscopically. Gonads were thin, thread-like, and transparent.	Sexes could not be identified macroscopically. Testes were thin, thread-like, and transparent.
II (immature)	Ovaries were small, yellowish, and rod-shaped. Oocytes were indiscernible.	Testes were thin, white, and larger than at stage I.
III (developing)	Ovaries were swollen, with orange-yellow eggs visible. The ovary surface was covered with prominent blood vessels.	Testes were swollen and larger than at stage II.
IV (maturing)	Ovaries occupied 1/4 to 2/3 of the body cavity. Vitellogenic oocytes were tightly packed in ovaries.	Testes were firm, flat-shaped, and ivory-white.
V (spawning)	Ovaries occupied 1/2 to 3/4 of the body cavity. Oocytes attained their maximum volume and could be released from genital pores with light abdominal pressure.	Testes were ivory-white, and milt could be released from genital pores with light pressure on the abdomen.
VI (spent)	Ovaries were flaccid and red with visible capillaries, and the remains of a few residual oocytes were in the ovaries.	Testes were flaccid and small.

and one site in the lower parts of the lake (Figure 1) from September 2015 to August 2016. A total of 100 nets were deployed, with 50 in the upper part and 50 in the lower part of the lake in areas with water depth higher than 1.0 m. The nets were set at 06:00–08:00 am for 24 h, and fish were collected the following morning. The fish were anesthetized with M-222 and immediately iced. As the upper and lower parts of the lake was connected to each other with intensive water exchange and habitat was similar between them (*unpublished data*), we pooled the specimens collected from the two parts together for further analyses.

The standard lengths (SL, to 0.1-mm accuracy) and body weights (BW, to 0.001-g accuracy) of the fish were measured before they were dissected by opening the abdomen. The gonads were checked to determine sex and developmental stage. Mature stages (stages I–VI) of both sexes were classified based on their macroscopic appearance following Nikolsky (1963) (Table 1), and sex was determined from the macroscopic appearance of the gonads at stage II or later. Gonads of individuals of known sex were removed and weighed (GW, 0.001-g accuracy). After the removal of the other internal organs, the eviscerated weight (EW, 0.001-g accuracy) was measured. The gonadosomatic index (GSI) was calculated for each fish using the following equation:

$$\text{GSI} = \text{GW}/\text{EW} \times 100$$

Fecundity was determined for females with gonads at stage IV or V. Preliminary observations showed that there was no difference in developmental stage or size between the left and right ovaries based on their macroscopic appearance. Approximately 0.1 g of an ovary (usually the right one) was sampled from the anterior, middle, and posterior sections and then mixed, weighed (OW, 0.001-g accuracy), and preserved in 10% formalin solution. The number (N) of vitellogenic oocytes was counted under a dissecting microscope. Absolute fecundity (AF) was calculated in the following manner:

$$\text{AF} = \text{N} \times \text{GW}/\text{OW}$$

and relative fecundity (RF) was calculated using the following equation:

$$RF = AF/EW$$

Egg diameter was measured for 30 individuals, with ~ 100 eggs each individual.

Scales were collected above the lateral line from 30 individuals in each month if available, which covered the size range for age determination (Steinmetz and Müller 1991), and differences in SL between males and females in each month were analyzed by Student's *t*-test. The sex ratio was calculated for each month, and deviations from the theoretical value 1:1 were statistically tested using Chi-square (χ^2). The relationship between AF and SL was fitted to a linear regression function, and cohort structure was determined by tracking monthly SL values (Guo et al. 2016). The level of significance for all statistical tests was set at $P < 0.05$.

Results

The SLs of 1,219 individuals were measured, and two cohorts were identified by tracking the monthly SL frequency distribution (Figure 2). The first cohort appeared from September 2015 to June 2016, and the second appeared in samples from July and August 2016 (Figure 2). It indicated that the first cohort died out in June, the second cohort was the offspring of the first cohort, and lifespan of the fish was one year. Meanwhile, there was no annulus observed in the scales.

The sexes of all individuals examined from November 2015 to June 2016 could be determined. Males were significantly larger than females in each month (Table 2). The SL values of the largest male and female were 95.3 and 70.1 mm, respectively (Table 2). The sex of specimens collected in September and October 2015 and July and August 2016 could not be determined.

The monthly sex ratio from November 2015 to March 2016 was biased towards males (0.30:0.46, female:male), and was significantly different to 1:1 except in February 2016, when very few individuals were collected. The sex ratio in April and May 2016 was biased towards females with a ratio (female:male) of 2.14:2.07, which was also significantly different to 1:1 (Table 2). Only five females and no males were collected in June 2016 (Table 2).

The GSI of females at stage II was very low (ranging from 0.28 to 9.30, with a mean of 1.85 ± 1.56), increased slightly at stage III (ranging from 1.76 to 34.15, with a mean of 9.64 ± 5.21), dramatically increased at stage IV (ranging from 18.52 to 51.68, with a mean of 31.30 ± 7.87) and stage V (ranging from 21.00 to 56.83, with a mean of 43.88 ± 8.61), before dramatically decreasing at stage VI (ranging from 1.29 to 23.09, with a mean of 7.52 ± 4.90) (Figure 3a). The male GSI was much lower than that of the females at every stage (Figure 3b).

All of the gonads were at stage I from July to October. From November to February, the gonads were at stage II (Figure 4), and the GSI was very low

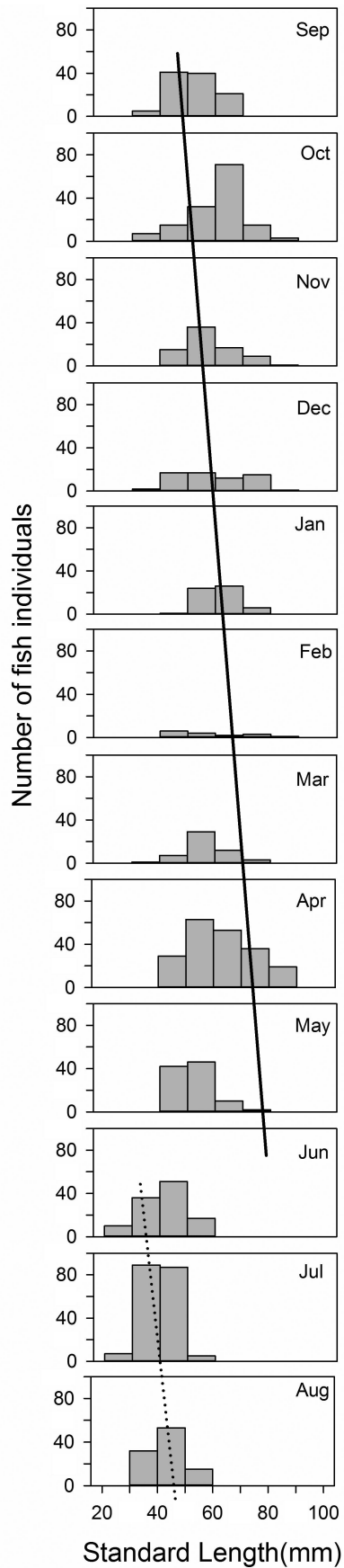


Figure 2. Monthly standard-length frequency distribution of Shimofuri goby (*Tridentiger bifasciatus*) from September 2015 to August 2016 in Nansi Lake, China. Two cohorts were identified. The solid line connects the first cohort, and the dashed line connects the second cohort.

Table 2. Monthly standard length of females and males of Shimofuri goby (*Tridentiger bifasciatus*) and sex ratio (F/M) from November 2015 to June 2016 in Nansi Lake, China. P values of the Student's *t*-tests for difference of standard length between female and male, and of the χ^2 -tests for divergence of the sex ratio from the expected 1:1 value, are presented.

Month	Standard Length (mm)				Sex ratio		
	Female		Male		p-value	F/M	p-value
	Number	Range/mean \pm SD	Number	Range/mean \pm SD			
November	25	35.0–66.0/46.3 \pm 7.3	54	40.0–80.0/56.5 \pm 9.0	< 0.05	0.46	< 0.05
December	18	41.0–63.0/51.8 \pm 6.5	47	34.0–79.0/55.5 \pm 13.5	< 0.05	0.38	< 0.05
January	13	41.0–57.0/52.2 \pm 4.5	44	45.0–73.0/57.7 \pm 6.4	< 0.05	0.3	< 0.05
February	5	43.0–53.0/47.8 \pm 4.2	11	37.0–76.0/55.1 \pm 14.5	0.15	0.45	0.13
March	40	35.0–68.0/51.8 \pm 8.9	87	42.0–95.0/67.3 \pm 9.7	< 0.05	0.46	< 0.05
April	126	38.0–70.0/50.9 \pm 7.2	59	39.0–84.0/62.9 \pm 12.0	< 0.05	2.14	< 0.05
May	73	36.0–61.0/46.3 \pm 4.8	27	38.0–74.0/50.5 \pm 10.1	< 0.05	2.7	< 0.05
June	5	41.0–50.0/44.7 \pm 3.0	–	–	–	–	–
Overall	305	34.8–70.1/49.5 \pm 7.1	329	34.4–95.3/60.0 \pm 11.8	–	–	–

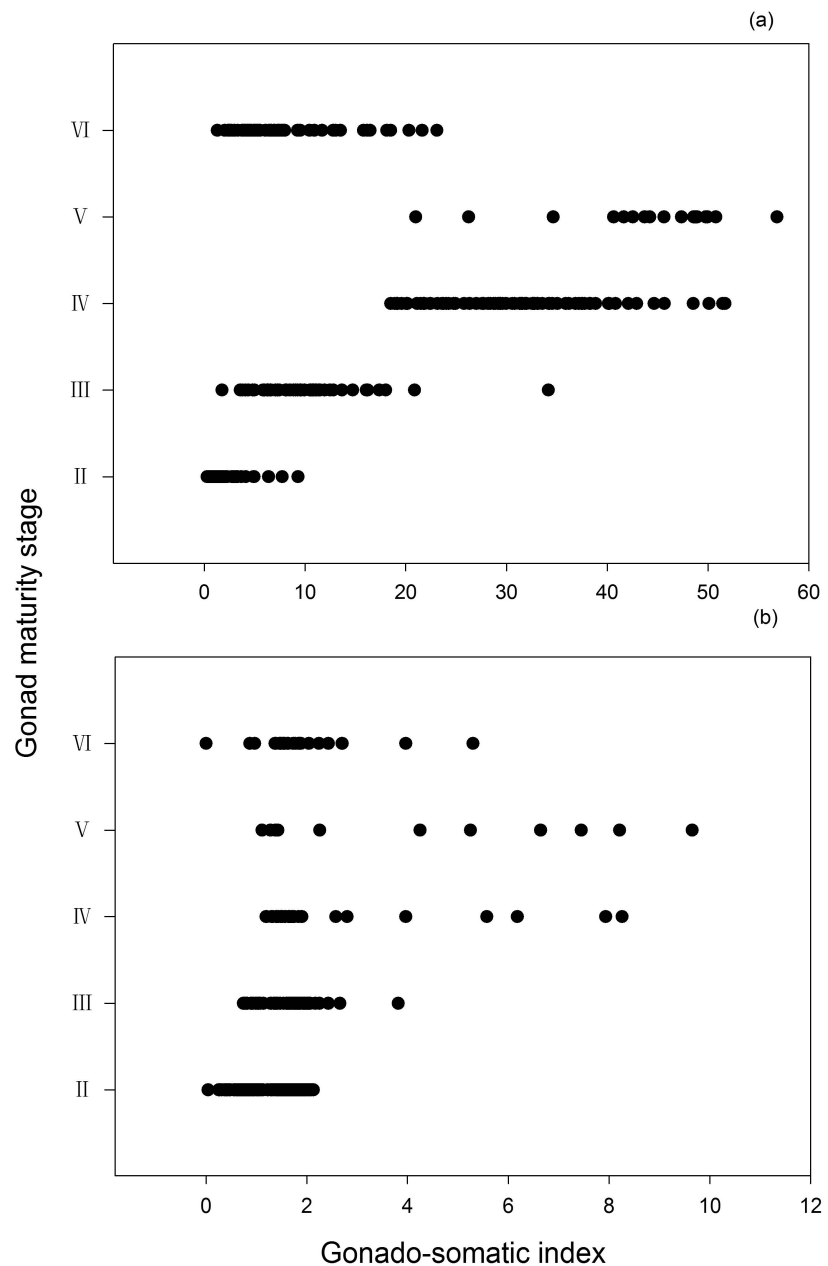


Figure 3. Relationship between the gonadosomatic index (GSI) and maturity stages of gonads in females (a) and males (b) of Shimofuri goby (*Tridentiger bifasciatus*) in Nansi Lake, China.

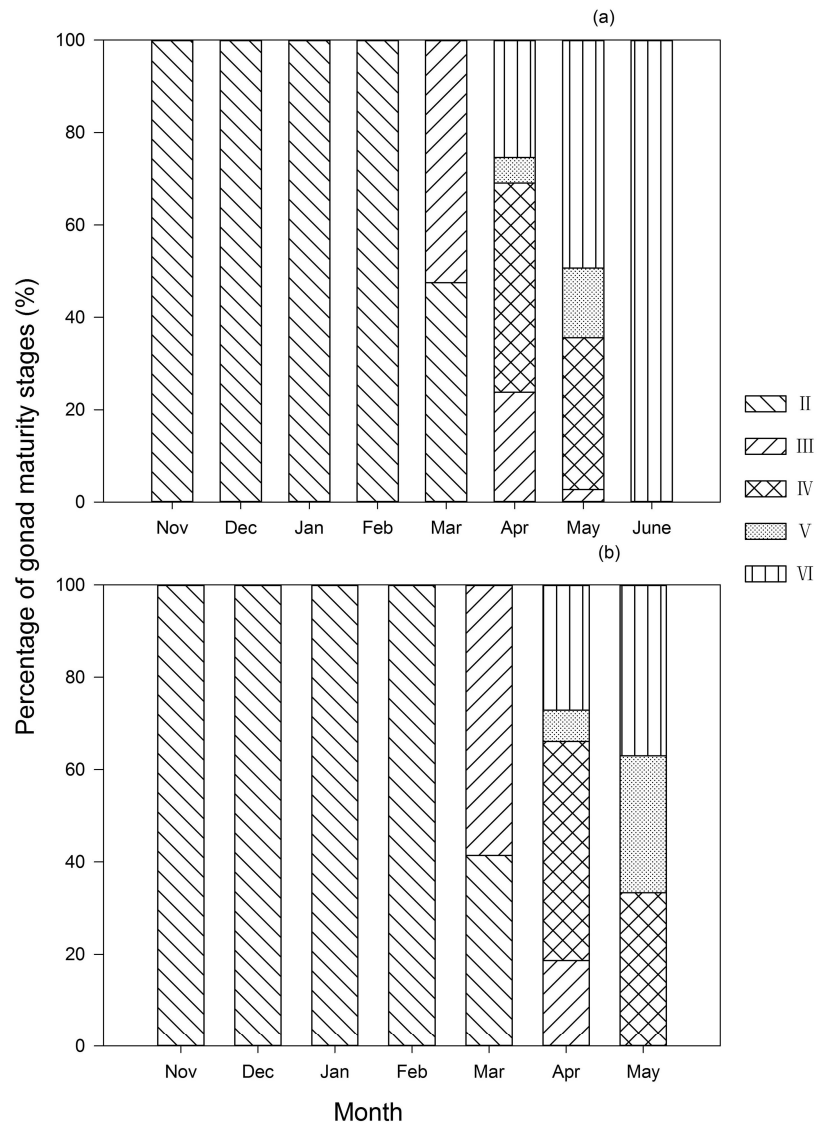


Figure 4. Monthly changes in percentage of different maturity stages of gonads for females (a) and males (b) of Shimofuri goby (*Tridentiger bifasciatus*) from November 2015 to June 2016 in Nansi Lake, China.

in both sexes (Figure 5). In April, 76% of the females and 81% of the males were mature (Figure 4), which increased to 97% of the females and 100% of the males in May. All five females collected in June were mature (Figure 4a). The GSI of both females and males increased slightly in March, before dramatically increasing in April and May (Figure 5). There were more large mature individuals of both sexes in April than in May, indicating that large individuals tend to mature early, and the largest individuals of both sexes collected in March and April were larger than those collected in May (Table 2, Figure 5).

The fecundity of 99 females with a SL of between 37.0 and 72.0 mm was recorded, and the AF ranged from 2,299 to 17,881 eggs with a mean of $8,152 \pm 3,575$ eggs. The relationship between AF and SL was fitted to the following linear function:

$$AF = 401.78SL - 12,540$$

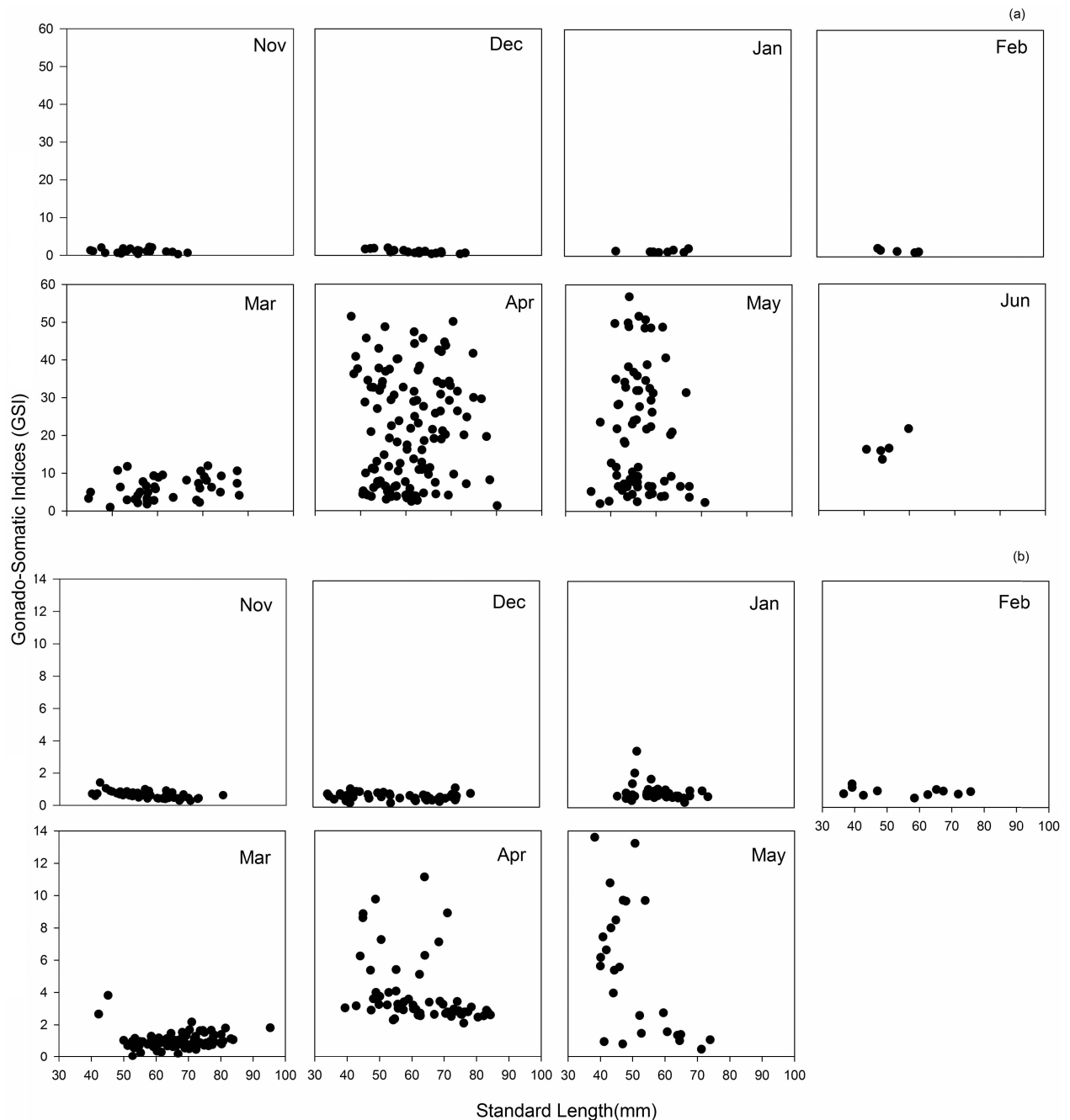


Figure 5. Monthly changes in gonadosomatic index (GSI) in females (a) and males (b) of Shimofuri goby (*Tridentiger bifasciatus*) from November 2015 to June 2016 in Nansi Lake, China.

($n = 99$, $r^2 = 0.78$) (Figure 6). The RF ranged from 1,398 to 4,360 eggs/g, with a mean of $2,825 \pm 614$ eggs/g.

Egg diameter ranged from 0.33 to 0.79 mm, with a mean of 0.54 ± 0.06 mm ($n = 4,195$), and followed a unimodal distribution, indicating synchronous oocyte development (Figure 7).

Discussion

We investigated the spawning season, age structure, longevity, and fecundity of a non-native population of Shimofuri goby in Nansi Lake, China. The increased GSI and mature gonads of both sexes in April and May suggest

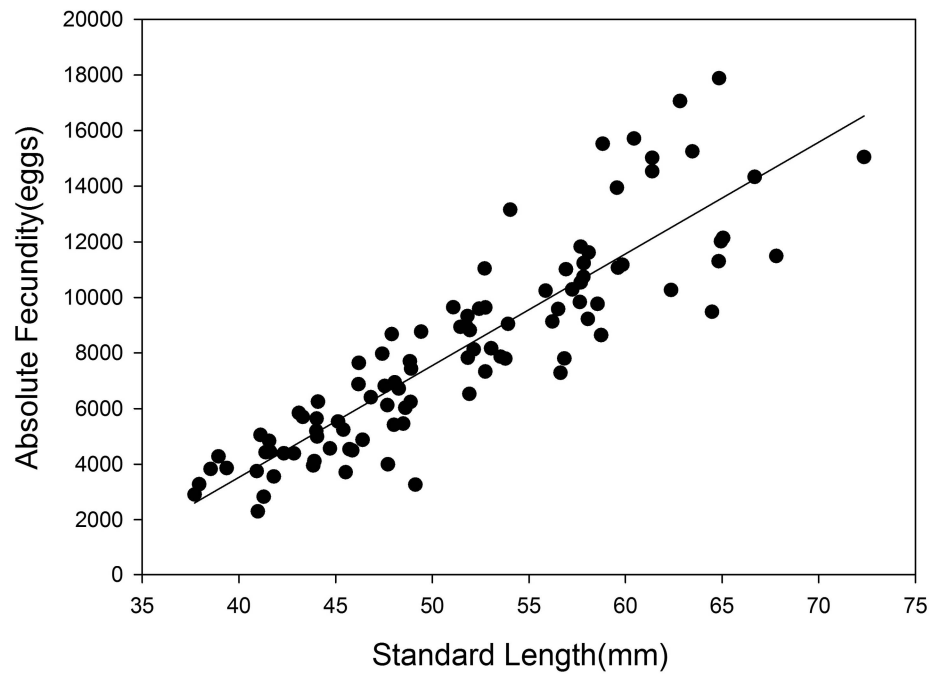


Figure 6. Relationship between absolute fecundity (AF) and standard length (SL) in Shimofuri goby (*Tridentiger bifasciatus*) in Nansi Lake, China. The linear function was fitted as $AF = 401.78SL - 12,540$ ($n = 99$, $F = 350.2$, $p < 0.05$)

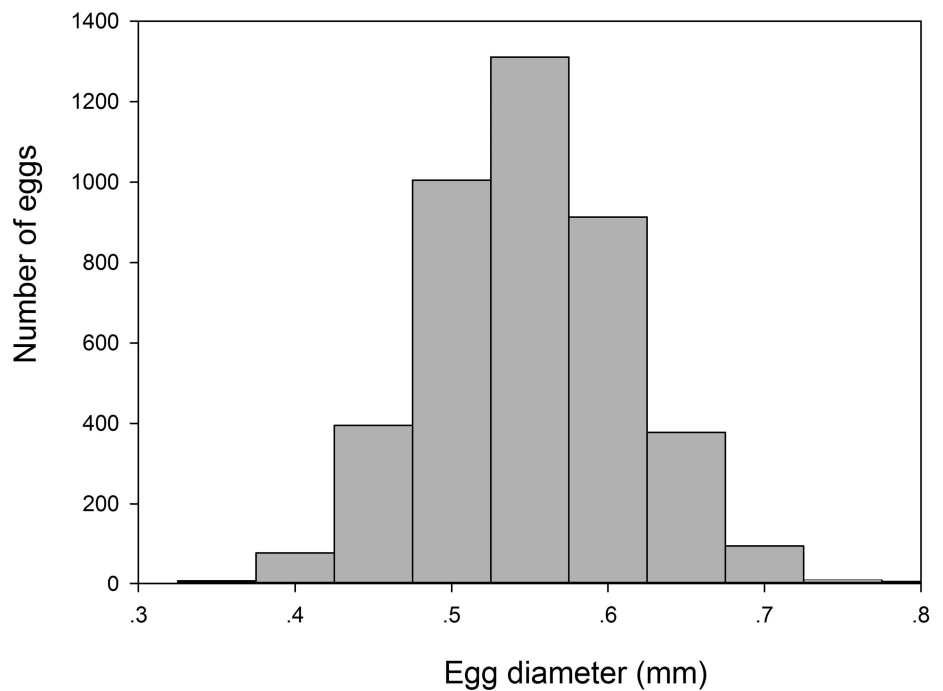


Figure 7. Frequency distribution of egg diameter of Shimofuri goby (*Tridentiger bifasciatus*) with gonads at stage IV or V in Nansi Lake, China.

that the fish spawned during this period. Cohort tracking revealed that individual longevity in the population was one year, and individuals reached maturity in the next spring of their birth and died after spawning. Mature males and females, as well as the production of a new generation, suggest that the population could successfully self-recruit. The RF of this population was 2,825 eggs/g, which is higher than that of many other

invasive gobiid species, e.g., *Proterorhinus semilunaris* (Top et al. 2018), *Padogobius bonelli* (Pompei et al. 2016), and *Neogobius kessleri* and *Neogobius melanostomus* (Kovac et al. 2009). A short lifespan and high fecundity suggest that this population has opportunistic life-history traits (Winemiller and Rose 1992) that facilitate invasions, particularly in the early stages, by ensuring population growth and establishment (Bøhn et al. 2004; Feiner et al. 2012; Gutowsky and Fox 2012; Brandner et al. 2013). Male Shimofuri gobies guard fertilized eggs and exhibit parental care (Moyle and Cech 1996), which is a typical characteristic of an equilibrium strategy that increases offspring survival (Wootton 1990; Sargent and Gross 1993). Many invasive fish species exhibit parental care, e.g., *N. melanostomus* (Wantola et al. 2013), *Rhinogobius giurinus* (Guo et al. 2013), *P. semilunaris* (Błońska et al. 2017), and *Channa argus* (Landis et al. 2011), so the Shimofuri goby may have both equilibrium and opportunistic characteristics (Winemiller and Rose 1992). These life-history traits have likely facilitated its successful invasion of Nansi Lake and other water systems (Matern et al. 2002).

Our results and those obtained from a study on a non-native population in the San Francisco estuary demonstrate that the Shimofuri goby has life-history traits plasticity. Individual longevity in the San Francisco estuary population is two years (Matern 1999), which is longer than that in the Nansi Lake population. The San Francisco estuary population spawns from March to August, and its spawning season is longer than that of the population in Nansi Lake. The San Francisco estuary population batch spawns, and females produce a series of egg batches throughout the extended spawning season. In contrast, the Nansi Lake population exhibits synchronous oocyte development, suggesting that it single spawns. Plasticity in life-history traits increase invasion success by facilitating adaptation to different environments (Fox and Copp 2014). Both abiotic and biotic conditions fluctuate dramatically in estuaries, while those in freshwater lakes are much more stable (Young et al. 2017), which may result in lower survival rates in estuaries than in freshwater lakes during early life-history stages (Winemiller 2005; Anger and Hayd 2010). The high recruitment success of batch spawners during early life-history stages may be a result of them laying a series of egg batches across an extended time period (Gozlan et al. 2003). The wide latitudinal distribution of the Shimofuri goby (both native and non-native) indicates its tolerance of a range of water temperatures (Matern 2001), and its invasion of the ENST system and San Francisco estuary, and its natural populations, demonstrate its tolerance of different salinities (Matern 2001). We suggest that these characteristics, i.e., life-history traits plasticity and high tolerance to water temperature and salinity differences, contribute to successful invasions of Shimofuri goby in both warm estuaries and cold freshwater lakes.

In Nansi Lake, the sex ratio was strongly male-biased before spawning. A male-biased sex ratio has been reported in several goby species (Corkum

et al. 2004; Guo et al. 2013; Pompei et al. 2016), including in non-native populations, e.g., *N. melanostomus* (Gutowsky and Fox 2011; Kornis et al. 2012) and *P. bonelli* (Pompei et al. 2016). With more males present, each male needs to guard relatively fewer eggs, which results in a higher offspring survival rate (Kornis et al. 2012). The sex ratio reversed to female-biased in the spawning season during April and May, when a large number of males were guarding nests and avoided capture by the trap nets (Guo et al. 2013).

The Shimofuri goby population in Nansi Lake clearly exhibited male-biased sexual size dimorphism (SSD). Male-biased SSD benefits male guarding behavior (Guo et al. 2013; Pompei et al. 2015), but results in slower female growth and smaller females than males because of higher female investment in gonadal development, which increases fecundity (Wootton 1990; Winemiller 2005). Male-biased SSD may have contributed to the successful invasion of *P. bonelli* into the River Aggia, Italy through high female reproductive investment (Pompei et al. 2016).

The Shimofuri goby spawning season (April to June) overlaps that of the ENST water diversion period (October to May), so water diversions may entrain early life-history stage individuals into the ENST system. Larval dispersal is an important method of range expansion for the Shimofuri goby in the San Francisco estuary system (Matern and Fleming 1995), and is also important in other invasive species (Beletsky et al. 2017).

In summary, the Shimofuri goby is a small species with a short lifespan and a relatively high fecundity that exhibits male parental care. Such life-history traits place the species somewhere between the opportunistic and equilibrium strategies in the three-point life-history continuum model (Winemiller and Rose 1992). Opportunistic strategies maximize colonizing capacity and promote rapid establishment (Bøhn et al. 2004; Feiner et al. 2012; Gutowsky and Fox 2012; Brandner et al. 2013), whereas equilibrium strategies (e.g., parental care) increase survival during early life-history stages (Wootton 1990; Sargent and Gross 1993). The species exhibits reproductive phenotypic plasticity among non-native populations, and its high tolerance of different water temperatures and salinities enables its adaptation to various environmental conditions (Matern 2001). These characteristics may account for the high invasion risk of Shimofuri goby. The ENST donor region is close to the Yangtze estuary, and several euryhaline fishes with life-history traits similar to the Shimofuri goby that inhabit it (e.g., *Mugilogobius myxodermus* and *Glossogobius giuris*) have a high risk of invading the ESNT system (Schmidt et al. 2019). Further studies should be conducted that monitor potential invasions of these species in the system. Our results provide crucial information concerning invasive species risks based on life-history traits. However, this is a study of a single species, and trends across species are required to more clearly determine traits that might favor establishment of non-indigenous fishes.

Acknowledgements

The authors thank the editors and reviewers for insightful comments that have helped to improve the quality of the manuscript.

Funding declaration

This research was financially supported by the National Natural Science Foundation of China (No. 51209202, 31870398), the Key Project in Frontier Science of Chinese Academy of Sciences (No. QYZDB-SSW-SMC041), and the Scientific Funds of Jiangsu Collaborative Innovation Center of Regional Modern Agriculture and Environmental Protection Project (No. HSXT215).

References

- Anger K, Hayd L (2010) Feeding and growth in early larval shrimp *Macrobrachium amazonicum* from the Pantanal, southwestern Brazil. *Aquatic Biology* 9: 251–261, <https://doi.org/10.3354/ab00259>
- Beletsky D, Beletsky R, Rutherford ES, Sieracki JL, Bossenbroek JM, Chadderton WL, Wittmann ME, Annis GM, Lodge DM (2017) Predicting spread of aquatic invasive species by lake currents. *Journal of Great Lakes Research* 43: 14–32, <https://doi.org/10.1016/j.jglr.2017.02.001>
- Bøhn T, Odd TS, Per-Arne A, Primicerio R (2004) Rapidly changing life-history during invasion. *Oikos* 106: 138–150, <https://doi.org/10.1111/j.0030-1299.2004.13022.x>
- Błońska D, Kobak J, Grabowska J (2017) Shelter competition between the invasive western tubenose goby and the native stone loach is mediated by sex. *Journal of Limnology* 150: 1623–1639, <https://doi.org/10.1163/1568539X-00003113>
- Brandner J, Cerwenka AF, Schliewen UK, Geist J (2013) Bigger is better: characteristics of round gobies forming an invasion front in the Danube river. *PLoS ONE* 8: e73036, <https://doi.org/10.1371/journal.pone.0073036>
- Bunn SE, Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30: 492–507, <https://doi.org/10.1007/s00267-002-2737-0>
- Cucherousset J, Olden JD (2011) Ecological impacts of non-native freshwater fishes. *Fisheries* 36: 215–230, <https://doi.org/10.1080/03632415.2011.574578>
- Corkum LD, Sapota MR, Skora KE (2004) The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. *Biological Invasions* 6: 173–181, <https://doi.org/10.1023/B:BINV.0000022136.43502.db>
- Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and if so, is it adaptive? A meta-analysis. *Ecology Letters* 14: 419–431, <https://doi.org/10.1111/j.1461-0248.2011.01596.x>
- Feiner ZS, Aday DD, Rice JA (2012) Phenotypic shifts in white perch life history strategy across stages of invasion. *Biological Invasions* 14: 2315–2329, <https://doi.org/10.1007/s10530-012-0231-z>
- Fox MG, Copp GH (2014) Old world versus new world: Life-history alterations in a successful invader introduced across Europe. *Oecologia* 174: 435–446, <https://doi.org/10.1007/s00442-013-2776-7>
- Fox MG, Vila GA, Copp GH (2007) life-history traits of introduced Iberian pumpkinseed (*Lepomis gibbosus*) relative to native populations: can differences explain colonization success? *Journal of Fish Biology* 71: 56–69, <https://doi.org/10.1111/j.1095-8649.2007.01683.x>
- Gallardo B, Aldridge DC (2018) Inter-basin water transfers and expansion of aquatic invasive species. *Water Research* 143: 282–291, <https://doi.org/10.1016/j.watres.2018.06.056>
- Gozlan RE, Pinder AC, Durand S, Bass J (2003) Could the small size of sunbleak, *Leucaspis delineates* (Pisces, Cyprinidae) be an ecological advantage in invading British waterbodies? *Folia Zoologica* 52: 99–108, <https://doi.org/10.1159/000072695>
- Grabowska J, Przybylski M (2015) Life-history traits of non-native freshwater fish invaders differentiate them from natives in the Central European bioregion. *Reviews in Fish Biology and Fisheries* 25: 165–178, <https://doi.org/10.1007/s11160-014-9375-5>
- Grimaldo L, Sommer T, Ark NV, Jone G, Holland E, Moyle PB, Herbold B, Smith Pete (2009) Factors affecting fish entrainment into massive water diversions in a tidal freshwater estuary: can fish losses be managed? *North American Journal of Fisheries Management* 29: 1253–1270, <https://doi.org/10.1577/M08-062.1>
- Guo ZQ, Cucherousset J, Lek S, Li ZJ, Zhu FY, Tang JF, Liu JS (2013) Comparative study of the reproductive biology of two congeneric and introduced goby species: implications for management strategies. *Hydrobiologia* 709: 89–99, <https://doi.org/10.1007/s10750-012-1439-8>
- Guo ZQ, Liu JS, Lek S, Li ZJ, Zhu FY, Tang JF, Julien C (2016) Age, growth and population dynamics of two congeneric and invasive gobies, *Rhinogobius giurinus* and *Rhinogobius cliffordpopei* (Actinopterygii, Gobiidae) in a plateau lake, southwestern China. *Hydrobiologia* 763: 69–79, <https://doi.org/10.1007/s10750-012-1439-8>

- Gutowsky LFG, Fox MG (2011) Occupation, body size and sex ratio of round goby (*Neogobius melanostomus*) in established and newly invaded areas of an Ontario river. *Hydrobiologia* 671: 27–37, <https://doi.org/10.1007/s10750-011-0701-9>
- Gutowsky LFG, Fox MG (2012) Intra-population variability of lifehistory traits and growth during range expansion of the invasive round goby, *Neogobius melanostomus*. *Fisheries Management and Ecology* 19: 78–88, <https://doi.org/10.1111/j.1365-2400.2011.00831.x>
- Hou YT, Shu FY, Dong SX, Liu M, Xie SG (2012) *Cabomba caroliniana*, a new recorded exotic aquatic plant in Lake Nansihu and its habitat characters. *Acta Hydrobiologica Sinica* 36: 1005–1008 [in Chinese with English abstract], <https://doi.org/10.3724/SP.J.1035.2012.01005>
- Jiang YS (2012) The Environmental Impacts and Strategy of the East Route of South-to-North Water Transfer Project. Anhui Science and Technology Press, Hefei, Anhui, China, 446 pp [in Chinese]
- Kadye WT, Booth AJ (2012) Integrating stomach content and stable isotope analyses to elucidate the feeding habits of non-native sharptooth catfish *Clarias gariepinus*. *Biological Invasions* 14: 779–795, <https://doi.org/10.1007/s10530-011-0116-6>
- Kornis MS, Mercado-Silva N, Vander ZMJ (2012) Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology* 80: 235–285, <https://doi.org/10.1111/j.1095-8649.2011.03157.x>
- Kornis MS, Weidel BC, Zanden MJV (2016) Divergent life histories of invasive round gobies (*Neogobius melanostomus*) in Lake Michigan and its tributaries. *Ecology of Freshwater Fish* 26: 563–574, <https://doi.org/10.1111/eff.12300>
- Kovac VB, Copp CH, Sousa RP (2009) Life-history traits of invasive bighead goby *Neogobius kessleri* (Günther, 1861) from the middle Danube River, with a reflection on which goby species may win the competition. *Journal of Applied Ichthyology* 25: 33–37, <https://doi.org/10.1111/j.1439-0426.2009.01189.x>
- Landis AMG, Lapointe NWR, Angermeier PL (2011) Individual growth and reproductive behavior in a newly established population of northern snakehead (*Channa argus*), Potomac River, USA. *Hydrobiologia* 661: 123–131, <https://doi.org/10.1007/s10750-010-0509-z>
- Liu CM, Zuo DK, Xu YX (1984) Water transfer in China: the east route project. *International Journal of Water Resources Development* 2: 103–118, <https://doi.org/10.1080/07900628408722317>
- Matern SA (1999) The invasion of the shimofuri goby (*Tridentiger bifasciatus*) into California: establishment, potential for spread, and likely effects. PhD Thesis, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA, 167 pp
- Matern SA (2001) Using temperature and salinity tolerances to predict the success of the Shimofuri Goby, a recent invader into California. *Transactions of the American Fisheries Society* 130: 592–599, [https://doi.org/10.1577/1548-8659\(2001\)130<0592:UTASTT>2.0.CO;2](https://doi.org/10.1577/1548-8659(2001)130<0592:UTASTT>2.0.CO;2)
- Matern SA, Fleming KJ (1995) Invasion of a third Asian goby, *Tridentiger bifasciatus*, into California. *California Fish and Game* 81: 71–76
- Matern SA, Moyle PB, Pierce LC (2002) Native and alien fishes in a California estuarine marsh: twenty-one years of changing assemblages. *Transactions of the American Fisheries Society* 131: 797–816, [https://doi.org/10.1577/1548-8659\(2002\)131<0797:NAAFIA>2.0.CO;2](https://doi.org/10.1577/1548-8659(2002)131<0797:NAAFIA>2.0.CO;2)
- Marchetti MP, Moyle PB, Levine R (2004) Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications* 14: 587–596, <https://doi.org/10.1890/02-5301>
- Moyle PB, Cech JJ (1996) *Fishes: An Introduction to Ichthyology* (3rd edn). Prentice Hall, Upper Saddle River, NJ, USA, 590 pp, <https://doi.org/10.2307/1447679>
- Nikolsky GV (1963) *Ecology of Fishes*. Academic Press, London, UK, 352 pp
- Olden JD, Poff NL, Bestgen KR (2006) Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs* 76: 25–40, <https://doi.org/10.1890/05-0330>
- Pompei L, Giannetto D, Lorenzoni M (2015) Age and growth of Arno goby, *Padogobius nigricans* (Canestrini, 1867), in the Aggia River (Umbria, Central Italy). *Journal of Applied Ichthyology* 31: 494–500, <https://doi.org/10.1111/jai.12689>
- Pompei L, Giannetto D, Lorenzoni M (2016) Reproductive parameters in native and non-native areas of *Padogobius bonelliand* comparison with *P. nigricans* (Actynopterigii, Gobiidae). *Hydrobiologia* 779: 173–182, <https://doi.org/10.1007/s10750-016-2812-9>
- Qin J, Cheng F, Zhang L, Schmidt BV, Liu J, Xie SG (2019) Invasions of two estuarine gobiid species interactively induced from water diversion and saltwater intrusion. *Management of Biological Invasions* 10: 139–150, <https://doi.org/10.3391/mbi.2019.10.1.09>
- Rahel FJ (2007) Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. *Freshwater Biology* 52: 696–710, <https://doi.org/10.1111/j.1365-2427.2006.01708.x>
- Ribeiro F, Elvira B, Collares-Pereira MJ, Moyle PB (2008) Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach. *Biological Invasions* 10: 89–102, <https://doi.org/10.1007/s10530-007-9112-2>
- Sargent RC, Gross MR (1993) Williams' principle: an explanation of parental care in teleost fishes. In: Pitcher TJ (ed), *Behaviour of Teleost Fishes* (2nd edn). Chapman and Hall, London, UK, pp 333–361, https://doi.org/10.1007/978-94-011-1578-0_11

- Schmidt BV, Wang Z, Ren P, Guo CB, Qin J, Cheng F, Xie SG (2019) A review of potential factors promoting fish movement in inter-basin water transfers, with emergent patterns from a trait-based risk analysis for a large-scale project in China. *Ecology of Freshwater Fish*, <https://doi.org/10.1111/eff.12530>
- Shu FY, Zhu QC, Zhang LW, Zhang XJ, Xie SG (2013) *Novaculina chinensis* found in Lake Weishan, Shandong Province. *Chinese Journal of Zoology* 48(2): 278–280, [in Chinese with English abstract]
- Shumilova O, Tockner K, Thieme M, Koska A, Zarfl C (2018) Global water transfer megaprojects: a potential solution for the water-food-energy nexus? *Frontiers in Environmental Science* 6: 150, <https://doi.org/10.3389/fenvs.2018.00150>
- Steinmetz B, Müller R (1991) An Atlas of Fish Scales, and Other Body Structures Used for Age Determination: Non-salmonid Species Found in European Fresh Waters. Samara Publishing Ltd., Cardigan, UK, 51 pp
- Top N, Karakuş U, Gökhan TE, Robert BJ, Serhan TA (2018) Plasticity in life history traits of the native *Proterorhinus semilunaris* suggests high adaptive capacity in its invasive range. *Knowledge and Management of Aquatic Ecosystems* 419: 48, <https://doi.org/10.1051/kmae/2018032>
- Vila-Gispert A, Alcaraz C, García-Berthou E (2005) Life-history of invasive fish in small Mediterranean streams. *Biological Invasions* 7: 107–116, <https://doi.org/10.1007/s10530-004-9640-y>
- Wang F, Zhang SL, Hou HP, Yang YY, Gong YL (2019) Assessing the changes of ecosystem services in the Nansi Lake wetland, China. *Water* 11: 788, <https://doi.org/10.3390/w11040788>
- Wantola K, Corkum L, Clelland E, Grande G, Corkum LD (2013) Fin size and associated fanning behaviour as indicators of reproductive status in male round gobies (*Neogobius melanostomus*). *Behaviour* 150: 1–17, <https://doi.org/10.1163/1568539X-00003113>
- Winemiller KO (2005) Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 872–885, <https://doi.org/10.1139/f05-040>
- Winemiller KO, Rose KA (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 2196–2218, <https://doi.org/10.1139/f92-242>
- Woodford DJ, Hui C, Richardson DM, Weyl OLF (2013) Propagule pressure drives establishment of introduced freshwater fish: quantitative evidence from an irrigation network. *Ecological Applications* 8: 1926–1937, <https://doi.org/10.1890/12-1262.1>
- Wootton RJ (1990) Ecology of Teleost Fishes. Chapman and Hall, London, UK, 404 pp, <https://doi.org/10.1007/978-94-009-0829-1>
- Wu HL, Zhong JS (2008) Chinese Animals: Osteichthyes, Gobioidi. Scientific Press, Beijing, China, 951 pp [in Chinese]
- Young MJ, Berridge KA, O’Rear T, Moyle PB, Durand JR (2017) Habitat partitioning by native and alien fishes and decapods in novel habitats of the upper San Francisco Estuary. *Biological Invasions* 19: 2693–2710, <https://doi.org/10.1007/s10530-017-1477-2>
- Zhan AB, Zhang L, X, ZQ, Ni P, Xiong W, Chen YY, Haffner GD, Maclsaac HJ (2015) Water diversions facilitate spread of non-native species. *Biological Invasions* 17: 3073–3080, <https://doi.org/10.1007/s10530-015-0940-1>