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Research Article

Life-history traits of the invasive mosquitofish (*Gambusia affinis* Baird and Girard, 1853) in the central Yangtze River, China

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Abstract

The western mosquitofish (*Gambusia affinis* Baird and Girard, 1853), which is considered one of the 100 worst invasive species in the world, has been introduced to China. However, there is little information on the biological characteristics of mosquitofish in China. To better determine how this invasive species might impact China, the life-history traits of western mosquitofish were studied in the central Yangtze River from April 2012 to March 2013. A total of 962 mosquitofish specimens were collected. The size of females and males ranged from 12 to 44 mm and 12 to 29 mm, respectively, and the maximum ages of males and females were 0+ years and 1+ years, respectively. Both sexes grew allometrically (males: negative (b = 2.593); females positive (b = 3.253)). Females were numerically dominant with an overall female-to-male sex ratio of 1.65:1. Specifically, the female-to-male sex ratio was higher in summer (2:1) and autumn (3:1) and did not deviate from the theoretical value of 1:1 in winter and spring. The smallest pregnant female had a total length of 21 mm, and fecundity ranged from 4 to 65 eggs. Compared with the findings obtained in other studies, the western mosquitofish population in the central Yangtze River is characterized by faster growth, lower fecundity and shorter life span. These traits might enable the successful invasion of mosquitofish in the central Yangtze River.

Key words: biological invasion, growth, Poeciliidae, reproduction

Introduction

Biological invasions are a serious threat to global species richness and ecosystem function (Mack et al. 2000). Freshwater ecosystems are considered especially susceptible to invading species (Cohen and Carlton 1998; Strayer 2010), and fishes are the most commonly introduced aquatic animals in the world (Gozlan et al. 2010). Additionally, many invasive freshwater fishes exhibit changes in life-history traits based on genetic differences or phenotypic plasticity that allow successful colonization in non-native ecosystems (Haynes and Cashner 1995; Bøhn et al. 2004; Alcaraz and Garcia-Berthou 2007; Gutsch and Hoffman 2016). Many life history characteristics (e.g., mortality rate, plasticity, and reproductive strategy) largely affect the invasiveness of fishes (Olden et al. 2006; Statzner et al. 2008). For instance, the potential invasiveness of pumpkinseed (*Lepomis gibbosus*) populations can be evaluated using the relationship between age at maturity and juvenile growth (Copp and Fox 2007). Hence, monitoring and improving our understanding of the life-history traits of invasive fish in different locations are necessary to advance our ability to control invasions and counteract the negative impacts caused by invasive fish species on non-native ecosystems (Mooney and Hobbs 2000; Garcia-Berthou 2007).

The western mosquitofish (*Gambusia affinis* Baird and Girard, 1853) is a small, viviparous topminnow that originates from North America. The western mosquitofish and its close relative, the eastern mosquitofish (*Gambusia holbrooki* Girard, 1859), have been introduced as a biological mosquito control agent in fresh and saline aquatic systems on every continent except Antarctica (Pyke 2008). Studies have revealed the negative effects of mosquitofish on small native fish (Goren and Galil 2005; Ayala et al. 2007), amphibians (Gamradt and Kats 1996; Goodsell and Kats 1999) and invertebrates (Margaritora 1990; Leyse et al. 2004). Mosquitofish compete with native fishes for food resources through niche overlap (Arthington 1991) and eat the eggs and larvae of fishes or amphibians (Pyke and White 2000; Meffe 1985). The western mosquitofish is in the Global Invasive Species Database and is included on the list of the 100 worst invasive alien species in the world (Lowe et al. 2000).

Western mosquitofish were first introduced into Taiwan from Hawaii in 1911 (Liao and Liu 1989) and to the Chinese mainland (Shanghai) from the Philippines in 1924 (Ni Y 1985). In the 1940s, the mosquitofish was introduced into Hong Kong (Dudgeon and Corlett 2004), and in the 1950s, western mosquitofish were stocked in most provinces of China as a form of mosquito control (East China Sea Fisheries Research Institute 1990). The distribution of western mosquitofish in China spans Hebei, Shanxi, Yunnan, Guangxi, Sichuan, Hunan, Hainan, Guangdong, Jiangsu, Fujian, Zhejiang, Shanghai and other provinces, as well as Hong Kong and Taiwan (Pan et al. 1980; Zhu 1995; Dudgeon and Corlett 2004; Gao et al. 2017). Some southern endemic fishes (such as *Tanichthys albonubes* Lin, 1932; *Oryzias latipes* Temminck and Schlegel, 1846) and amphibians (such as *Philautus romeri* Smith, 1953) are listed in the "China Species Red List" and are threatened by mosquitofish (Dudgeon and Corlett 1994; Chen 2010). Therefore, mosquitofish are regarded as a harmful invasive species to native freshwater ecosystems in China (Xu and Qiang 2011). In the past, researchers believed that most mosquitofish were distributed in South China, and most previous studies found that mosquitofish have not established feral populations in the central Yangtze River or in Lake Poyanghu (Zhang 1988), Lake Donghu (Liu 1990), Lake Baoanhu and Lake Honghu (Liang and Liu 1995; Chen and Xu 1995). However, our 2010–2013 investigation showed that mosquitofish have successfully established feral populations and have become the dominant species in many wetlands in the central Yangtze River (unpublished data). To better manage and control feral populations of mosquitofish in the central Yangtze River, the biological traits of the species in the invaded habitat should be assessed.

The objective of the present study was to obtain information on some life-history traits of the western mosquitofish population in the central Yangtze River. In addition, we provide insights that improve our understanding of the structure of this invasive species population and contribute to the future study of the potential effects of this species on native fauna.

Material and methods

Study area

The study was performed in 18 water bodies (ponds, canals and lakes, where mosquitofish are generally found) in Wuhan, Hubei Province, China (Figure 1; Supplementary material Table S1), located in a typical middle reach of the Yangtze River. Our sampling sites were near the main river channel of the Yangtze River and the largest branch – Han River. Mosquitofish are hard to capture using dip nets in the main watercourse of the Yangtze River. Our study zone receives mostly monsoon precipitation and has an average annual rainfall greater than 1000 mm/year. The mean annual temperature ranges from 16 to 19 °C but can increase to more than 40 °C during the summer. Numerous shallow ponds, lakes and canals prevail in the floodplain of the Yangtze River.

The native ichthyofauna of the area includes *Abbottina rivularis* (Basilewsky, 1855), *Rhodeus sinensis* (Günther, 1868), *Carassius auratus* (Linnaeus, 1758), *Hypophthalmichthys nobilis* (Richardson, 1845), *Pseudorasbora parva* (Temminck and Schlegel, 1846), *Hemiculter leucisculus* (Basilewsky, 1855), *Odontobutis obscurus* (Temminck and Schlegel, 1845), *Micropercops swinhonis* (Günther, 1873), *Misgurnus anguillicaudatus* (Cantor, 1842), *Cobitis sinensis* (Sauvage and Dabry de Thiersant, 1874), *Rhinogobius giurinus* (Rutter, 1897), *Rhinogobius duospilus* (Herre, 1935), *Monopterus albus* (Zuiew, 1793), *Channa argus argus* (Cantor, 1842), and *Oryzias sinensis* (Chen et al., 1989). Alien species, such as the crayfish *Procambarus clarkii* (Girard, 1852) and the bullfrog *Lithobates catesbeianus* (Shaw, 1802), were recently introduced in the study area for aquaculture (Xu and Qiang 2011), but there are no records of western mosquitofish in this area.

Fish sampling

Fish were collected on 15–24 April (spring), 15–24 July (summer), and 1–10 November (autumn) in 2012; and 1–10 January (winter) in 2013 and identified (Table S2). Because the main objective was to assess the life-history traits of western mosquitofish in the central Yangtze River, all the samples from each season were collected within a 10-day period.

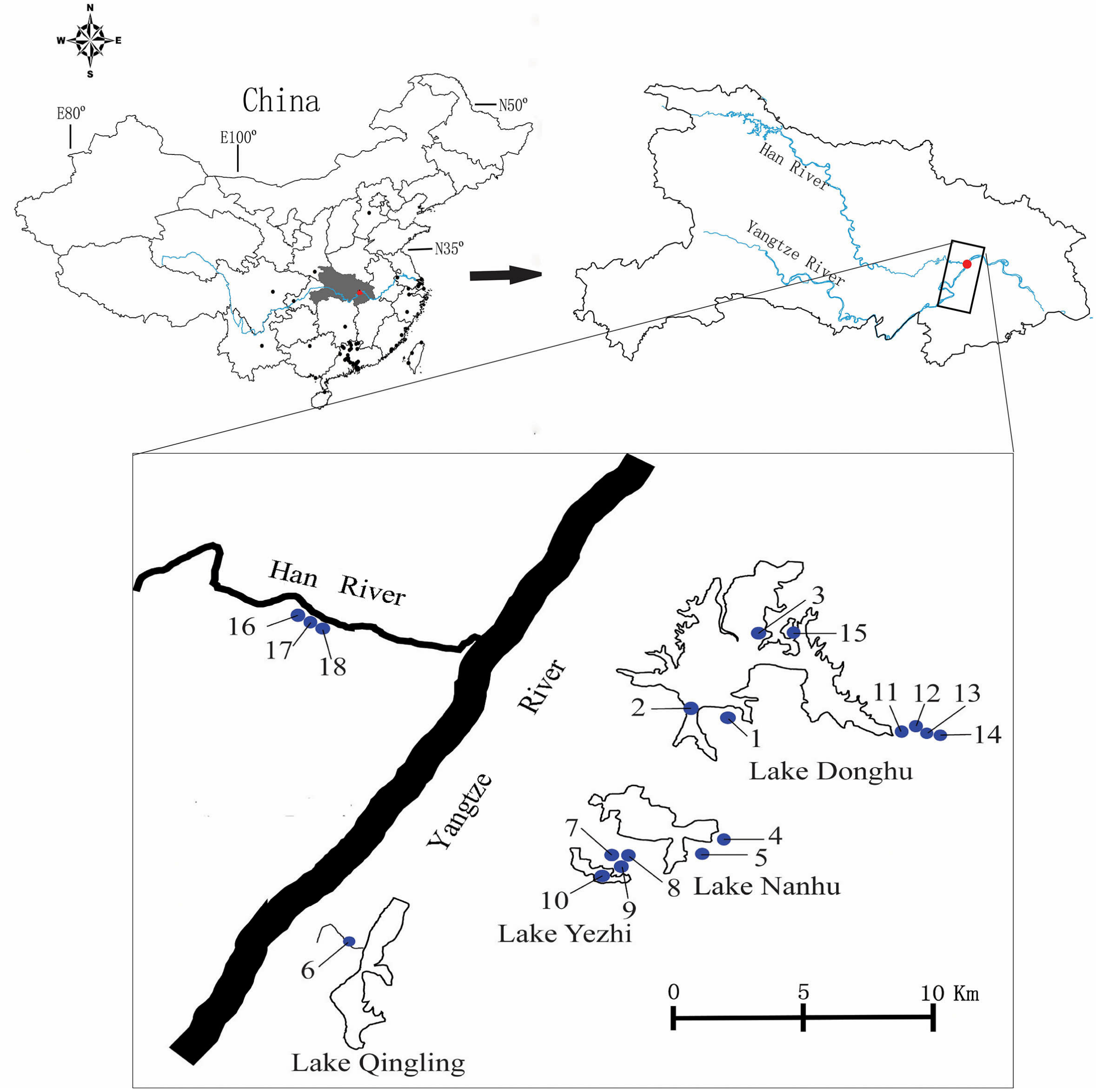

Figure 1. Distribution of western mosquitofish in China and locations recorded in this study.

All the fish were captured during daylight hours by two individuals using a dip net (0.5 m in diameter and a stretched mesh size of 1 mm). The captured fish were anaesthetized immediately with chlorobutanol and preserved in situ in 4% formalin solution for transport to the laboratory. Water temperature (°C), pH and salinity (‰) were measured in situ using a handheld multi-probe meter (YSI Corporation, USA), water depth (cm) was determined using a tape measure, and flow rate (m/s) was measured using a current meter. The habitat characteristics of the study reach are provided in Table S1.

Methods for collecting biological information

In the laboratory, all the collected fish were identified to the species level, their total weight (TW), eviscerated weight (EW) and gonadal weight (GW) were obtained to the nearest 0.001 g, and their total length (TL) was measured to the nearest 0.01 mm with a digital calliper. The gonadosomatic index (GSI) was calculated using the equation $GSI = 100*(GW*EW^{-1})$ (Smith and Walker 2004). The condition factor (K) was calculated using the equation $K = 10^5 TW*TL^{-3}$ (Ciotti et al. 2013). The age of each fish was determined using scales collected from the right side of the fish body, and the collected scales were reviewed for banding patterns using a binocular microscope. Mosquitofish were classified as males if they possessed any evidence of a gonopodium, as females if no gonopodium was detected and the fish were larger than the smallest male, and as juveniles if they were smaller than the smallest male and it was impossible to discern the sex. The females were considered pregnant if they possessed eggs or embryos.

Data analyses

The sex ratio was calculated as the number of females to males based on the above-described criteria used for sex determination. The sex ratios among populations were compared with the theoretical value of 1:1 using a chi-square test (χ^2) with a P value < 0.05. The fecundity of the pregnant females was determined by counting the number of embryos in the ovary. Length-frequency histograms were plotted using 2-mm size classes for females, males and juveniles (Figure 2).

The length-weight relationships were estimated by applying a power function (Eq. 1) to the data (Ricker 1973):

$$TW = a \times TL^{b} \quad (1)$$

This equation can also be expressed in its logarithmic form (Eq. 2):

$$\mathrm{Log}\,TW = \mathrm{Log}\,a + b\,\mathrm{Log}TL \quad (2)$$

where TW is the total weight (g), TL is the total length (mm), Log refers to base-10 logarithms. In the linear (after logarithmic transformation) form of the equation, a is the intercept of the y-axis of the best-fit line, and b is the slope of the line. To confirm whether the b-values obtained from the linear regressions were significantly different from the isometric value, a t-test (H_0: b = 3) (Hile 1936) with a confidence level of ± 95% was applied using Eq. 3 (Sokal and Rohlf 1987):

$$t_s = (b\text{-}3)/s_b \quad (3)$$

where t_s is the t-test value, b is the slope, and s_b is the standard error of the slope (b). The comparisons between the values obtained from the t-tests and the respective tabled critical values allowed the determination of the statistical significance of the b-values and their categorization in the isometric range (b = 3) or allometric ranges (negative allometry: b < 3; positive allometry: b > 3).

One-way analyses of variance (ANOVA) were used to test the differences in the total length, total weight, eviscerated weight and number of eggs between

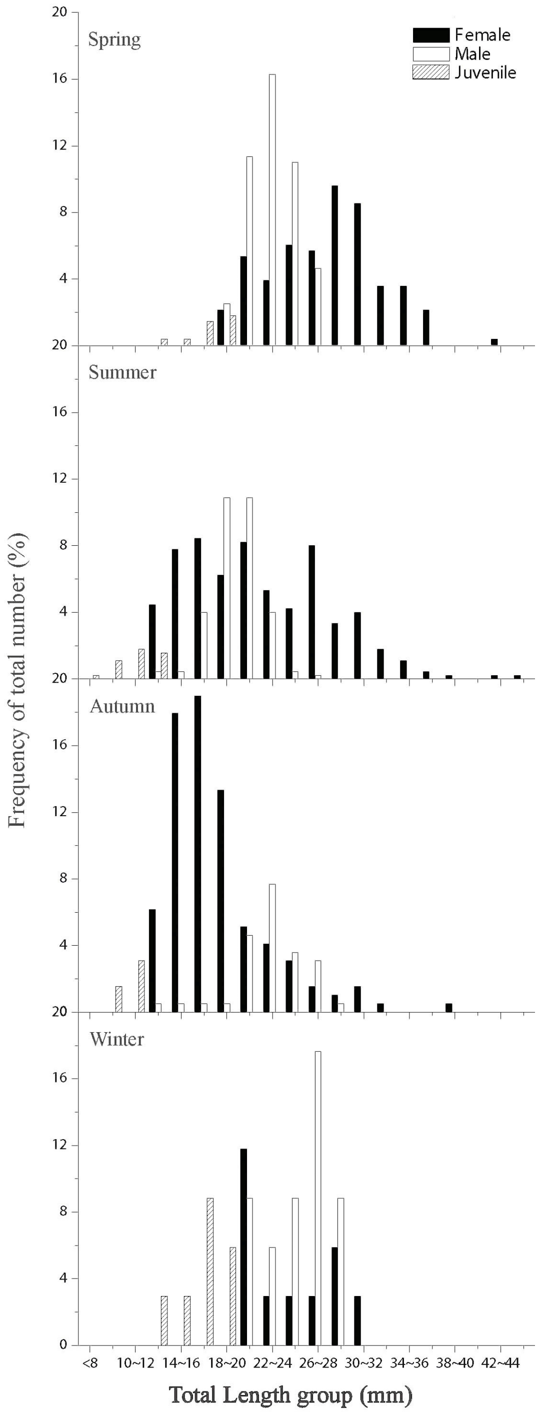

Figure 2. Seasonal patterns of the length-frequency distribution of the western mosquitofish. The cross-hatches represent juveniles, the black bars represent females, and the empty bars represent males.

Table 1. Comparison of life-history parameters of *Gambusia* spp. surveyed in different studies.

Locality	Age		Minimum size		Maximum size		Minimum size of pregnant female	Breeding season	Brood size	Sex ratio (M:F)	References
	♀	♂	♀	♂	♀	♂					
Eastern mosquitofish											
Lake Pamvotis			24.52	16.44	43.06	34.34	20.35	November-March		2.3:1	Gkenas et al. 2012
South Carolina (USA)					60	40		April–September	?-75		Meffe 1991; Meffe et al. 1995
Ebro	2+	0+			63	32		May–September	3–181	4:01	Vargas and de Sostoa 1996
Aguas de Moura	3+	1+			70	40		April–September		5:01	Paes da Franca and Da Franca 1953
Collie River					62	35		August–March		4:01	Pen and Potter 1991
Zoonar Lagoon					53	39		May–September		1:01	Fernandez-Delgado and Rossomanno 1997
Viladecans	2+	2+						May–September			Puigcerver 1992
Roma Lake	3+	3+			37	29		May–August	80–114	1.5:1	Scalici et al. 2007
Tajan River	1+	0+	17	15	50	35			7–57	2.15:1	Rahman et al. 2011
Lake Heviz			13.2	12.9	38	26.3	13.2	April–September			Specziar 2004
Tasmania					48.9	23.6					Keane and Neira 2004
Western mosquitofish											
Guadalquivir	2+	1+			65	36		May–September		2:01	Fernandez-Delgado 1989
Cook County			14	17	59	34	24	May–September			Krumholz 1948
Hovey Lake			18		54		23	April–September	3–144		Hughes 1985b
Hawaii			18.6		55.9			January–November	1–342		Stearns 1983
Wuhan	1+	0+	12.03	12.22	44.08	29.32	16.98	March–October	4–65	1.6:1	this study

the spring and summer breeding stock. The statistical analyses were performed with the statistical software SPSS 13.0 (IBM, Chicago, IL, USA).

Results

A total of 20 freshwater fish species were captured, belonging to six orders, 11 families, and 19 genera (Table S2). There was no obvious variation in the fish communities among the sampling points, and the total percentage of mosquitofish at each sampling site reached 90%. A total of 962 mosquitofish (592 females, 329 males and 41 juveniles) were caught and measured. The size of the smallest male and the smallest female was 12 mm, both collected in autumn. The largest female (collected in summer) and male (winter) were 44 mm and 29 mm respectively. The smallest female with embryos, which was collected in summer, was 21 mm. Two age groups (0+ and 1+) were identified in both sexes. Most of the collected fish belonged to the 0+ year age group, and the oldest male and female specimens were classified in the 0+ year and 1+ year age groups, respectively (Table 1). The length-frequency distributions for females and males are shown in Figure 2.

The overall female-to-male sex ratio was 1.8:1, which significantly diverges from 1:1 (χ^2 = 75.102, df = 1, P < 0.05) (Table 2). The highest ratio of females to males occurred during summer and autumn, with an approximate 1:1 ratio in winter and spring (Table 2). Unequal sex ratios were observed in the different size classes (Figure 2). In spring and summer, males were dominant in the small-size classes, whereas females dominated the mid- and large-size

Table 2. Seasonal sex ratios of *G. affinis* from Wuhan (from April 2012 to January 2013) tested by a χ^2 analysis.

Season	♀	♂	Sex ratio (♀:♂)	χ^2	df	P
Spring	143	129	1:01	0.721	1	> 0.05
Summer	288	141	2:01	0.42	1	> 0.05
Autumn	144	42	3:01	0.581	1	> 0.05
Winter	17	17	1:01	0	1	1
Total	592	329	1.8:1	75.102	1	< 0.05

Table 3. Estimated parameters characterizing the relationship between the total length (TL, mm) and total weight (TW, g) for *G. affinis* females, males, juveniles and the entire sample.

	n	LogTW=*b*logTL+log*a*	R^2	P	sb	Relationship notes (*t*-test)
Females	585	LogTW=3.253LogTL-11.8582	0.961	< 0.05	0.026	+Allometry
Males	329	LogTW=2.593LogTL-10.3281	0.763	< 0.05	0.08	-Allometry
Juveniles	48	LogTW=2.665LogTL-10.6375	0.839	< 0.05	0.172	Isometry
All	962	LogTW=3.080LogTL-11.6944	0.934	< 0.05	0.026	+Allometry

Table 4. Comparison of some parameters of pregnant female *G. affinis* in different seasons (spring and summer). TL, total length; TW, total weight; EW, eviscerated weight; SD, standard deviation. Astrerisks denote $P < 0.05$.

	Spring		Summer		df	F	P
	n	Mean ± SD	n	Mean ± SD			
TL	43	30.4 ± 3.58	79	28.07 ± 4.15	120	8.888	0.002*
TW	43	0.37 ± 0.14	79	0.33 ± 0.18	120	1.287	0.259
EW	43	0.23 ± 0.09	79	0.22 ± 0.12	120	0.079	0.78
GSI	43	26.92 ± 11.97	79	18.18 ± 12.52	120	56.396	< 0.005*
K	43	1.26 ± 0.13	79	1.37 ± 0.15	120	13.175	< 0.0001*
Number of eggs	43	28.98 ± 11.19	79	14.84±11.68	120	41.988	< 0.0001*

groups. In autumn and winter, males were dominant in the large-size groups, and females dominated the small-size groups.

A significant relationship was found between the length and weight of both male and female mosquitofish (Table 3). The growth patterns of females, males and juveniles displayed positive allometry, negative allometry and isometry, respectively (*t*-test: t_{female} = 6.07, df = 584, $P < 0.005$; t_{male} = 5.08, df = 328, $P < 0.005$; t_{juvenile} = 3.07, df = 47, $P > 0.05$).

Females with embryos were found in spring and summer, and significant differences in fecundity were found between spring and summer. The number of eggs and the total length of the pregnant females were significantly higher in spring than in summer, although the total weight (TW) and eviscerated weight (EW) did not show any differences (Table 4).

Discussion

The life-history traits of invasive species often vary among invasion regions (Shoubridge 1977); therefore, establishing profiles of the life-history characteristics of invasive species is an emerging tool for predicting the potential success and degree of establishment (Mooney and Hobbs 2000; Bøhn et al. 2004). The population of western mosquitofish in Wuhan is located in the central Yangtze River. To the best of our knowledge, this study constitutes the first investigation of the life-history traits of western mosquitofish in the central Yangtze River, China. However, further studies are needed to confirm the extent of distribution within this region.

The age structure of western mosquitofish from the central Yangtze River was different not only within species but also among closely related species (Table 1). In our study, western mosquitofish presented short life spans, and the oldest male and female specimens were only 0+ and 1+ years of age, respectively. Although some records of eastern mosquitofish in Asia report similar short life spans (Rahman et al. 2011), most studies on western mosquitofish and closely related species report long life spans with ages of 2+ – 3+ (Table 1), and the longest life span reported for western mosquitofish is 4+ (Krumholz 1948). The life span of a species might be affected by a variety of factors, such as ecosystem productivity (Mann et al. 1984), sex differences, and environmental stability (Schlosser 1990).

The minimum TLs of the western mosquitofish (12 mm for males with a gonopodium and 12 mm for females) investigated in this study were shorter than those reported for other populations, indicating that the western mosquitofish in the central Yangtze River reach sexual maturity earlier than other populations. The maximum TLs of the western mosquitofish included in this study were shorter than those found in other studies, indicating that the western mosquitofish in the central Yangtze River have shorter life spans.

The sex ratio of the western mosquitofish investigated in this study was significantly biased toward females (1.6:1); this result aligns with others found for the same and closely related species (Table 1). However, the sex ratio of mosquitofish offspring is 1:1 at birth (Krumholz 1948), which might explain why the sex ratio did not diverge from 1:1 in the winter and spring (Table 2). In winter (non-reproductive months for western mosquitofish), mortality is very high, reaching as high as 99% (Haynes 1993), and the survival rate of females was not significantly different from the survival rate of males (Table 2). Additionally, in spring, female and male western mosquitofish are born, and the mosquitofish population showed a 1:1 sex ratio at birth. In summer and autumn, females predominate in the population, perhaps because males have shorter life spans (Krumholz 1948), or due to selective mortality or differences in habitat preferences between the sexes (Britton and Moser 1982; Fernandez-Delgado 1989; Fernandez-Delgado and Rossomanno 1997).

The length-weight relationships obtained in this study suggested differences in growth between the sexes; specifically, positive allometric growth was observed in females, whereas males showed negative allometric growth. The length-weight relationships are not constant throughout the year but rather vary according to factors such as food availability, feeding rate, gonad development and spawning period (Bagenal 1978). However, the parameter *b* is characteristic of a species (Mayrat 1970) and generally does not vary significantly throughout the year. The differences in the length-weight relationships between males and females are explained by differences in sexual dimorphism and internal fecundity, among others.

The reproductive activity of the western mosquitofish population investigated in our study peaked during spring rather than summer (Table 4), which is apparently different from the occurrence of reproductive peaks during summer observed in other areas (Hughes 1985a; Fraile et al. 1992). In our study area, the temperature increases rapidly in spring, from approximately 4 °C to nearly 20 °C. Medlen (1951) found that female mosquitofish can reproduce when the water temperature reaches 16 °C. Therefore, the population of mosquitofish included in our study reproduced rapidly in spring. However, our study area floods frequently, which could disturb western mosquitofish breeding during the summer. It is well known that the fecundity of mosquitofish is positively correlated with the size of the mother (Krumholz 1948; Benejam et al. 2009; O'Dea et al. 2015). The western mosquitofish in the central Yangtze River are smaller than those of other populations; thus, the fecundity of western mosquitofish is lower than that of other populations (Table 1). Additionally, the average length of the females in spring was significantly longer than that in summer (Figure 2); therefore, the fecundity of western mosquitofish was higher in spring than in summer.

An invasive species needs several traits to be successful in a new environment, including rapid growth, rapid sexual maturity, a short life span, and a euryoecious and eurytopic nature (Morton 1996). The western mosquitofish population in the central Yangtze River is characterized by rapid growth, lower fecundity and short life span, and these traits might allow the rapid spread of western mosquitofish in the central Yangtze River. Many invasive species possess similar traits; conspicuous examples are topmouth gudgeon *Pseudorasbora parva* (Temminck and Schlegel, 1846) and pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758).

Due to its vital ecological functions and unique biodiversity, the central Yangtze River has been designated by the World Wildlife Fund (WWF) as one of the "Global 200: Priority Ecoregions for Global Conservation" (Olson and Dinerstein 1998). Two hundred and thirteen freshwater fishes, 30 amphibians and 55 reptiles, including endangered and endemic species, are distributed in the central Yangtze River (Chen et al. 2002; Yu et al. 2005a, b, c; Sui 2010). Many studies have demonstrated negative impacts of invasive mosquitofish on native fishes, amphibians and reptiles through competition and predation (Pyke 2008). Our field observations revealed that western mosquitofish prey on eggs of native fish and tadpoles. However, there is no quantitative data regarding the interactions between western mosquitofish and native species in the central Yangtze River, China. Therefore, to control invasion and the subsequent impacts of western mosquitofish in the central Yangtze River, further studies should focus on investigating the extent of the distribution region and the negative impacts that western mosquitofish might have on native species such as medaka *Oryzias latipes* (Temminck and Schlegel, 1846).

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Supplementary material

The following supplementary material is available for this article:

Table S1. Features of the 18 sites sampled in 2012-2013.

Table S2. List of fish species captured in the field.

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2018/Supplements/BIR_2018_Cheng_etal_SupplementaryTables.xlsx