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PRIMARY RESEARCH PAPER

Comparative study of the reproductive biology of two congeneric and introduced goby species: implications for management strategies

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Abstract A full understanding of life history characteristics of invasive species is a fundamental prerequisite for the development of management strategies. Two introduced goby species (*Rhinogobius cliffordpopei* and *Rhinogobius giurinus*) have established highly abundant populations in Lake Erhai (China). In the present study, we examined the reproductive biology of these two species with the aim of improving the efficiency of management strategy. The results indicated that *R. cliffordpopei* spawned from February to June, whereas *R. giurinus* spawned from April to August. *Rhinogobius cliffordpopei* showed higher gonado-somatic indices and had larger eggs than *R. giurinus*. The adult sex ratio of *R. cliffordpopei* was female skewed, but that of *R. giurinus* was equal. *Rhinogobius cliffordpopei* showed a male-skewed sexual size dimorphism, whereas the body size of *R. giurinus* varied only slightly between males and females. The different reproductive traits appear as a crucial biologic aspect for developing control programs. Specifically, control measures should be implemented and/or intensified from September to February for *R. cliffordpopei* and from January to April for *R. giurinus*. The body size of the smaller *R. cliffordpopei* females is the determinant for minimal mesh size of the nets used in physical removals of *R. cliffordpopei*.

Keywords Goby · Biological invasion · Reproductive strategy · Invasive species management

Introduction

As more and more introduced species are establishing invasive populations worldwide and impacting recipient ecosystems (Karatayev et al., 2009; Cucherousset & Olden, 2011; Winfield et al., 2011), increasing attention

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has been devoted to their management during the last decade (Sutherland et al., 2009; Gozlan et al., 2010; Britton et al., 2011). Specifically, several measures have been developed and implemented to control, contain, or eradicate a wide range of invasive species, including physical removal (Ludgate & Closs, 2003; Wimbush et al., 2009), chemical eradication (e.g., rotenone; Ling, 2002), the use of sex pheromones (Li et al., 2002; Arbuckle et al., 2005), and bio-manipulation (Saunders et al., 2010; Britton et al., 2011). The effectiveness of these measures is, however, highly dependent upon the life history characteristics of the target invasive species (Ludgate & Closs, 2003; Taylor & Hastings, 2004; Britton et al., 2011; Yeates et al., 2012). For instance, the eggs of fish species such as salmonids are around 100 times less sensitive to rotenone than juveniles and adults (Marking & Bills, 1976), and therefore eradications using rotenone should account for different vulnerabilities among life stages (Ling, 2002; Britton et al., 2011). Consequently, a full understanding of life history characteristics of invasive species is crucial to develop economically and/or ecologically effective management strategies (Ludgate & Closs, 2003; Taylor & Hastings, 2004; Yeates et al., 2012). Reproduction characteristics can have substantial effects on invasion success, and a thorough knowledge of the reproduction biology of invasive species is a fundamental prerequisite for developing appropriate management strategies.

Many goby species have been introduced worldwide and have become established outside of their native ranges, including North America (Dillon & Stepien, 2001; Copp et al., 2005), Europe (Copp et al., 2005; Antsulevich, 2007) and Asia (Du & Li, 2001; Yuan et al., 2010). In the Great Lakes, for instance, several goby species native to the Ponto-Caspian area (e.g., round goby *Apollonia melanostoma*, tubenose goby *Proterorhinus semilunaris*, racer goby *Neogobius gymnotrachelus*) have spread in the entire system (Dillon & Stepien, 2001; Kolar & Lodge, 2002). In Europe, several goby species (e.g., round goby, bighead goby *Neogobius kessleri*, monkey goby *Neogobius fluviatilis,* and racer goby) have also invaded other ecosystems (Copp et al., 2005). In China, introduced gobies of the genus *Rhinogobius* have established in most lakes of Yunnan-Guizhou Plateau (Xie et al., 2001, Yuan et al., 2010). The rapid proliferation of these species has raised serious concerns regarding their long-term negative impacts on native species and ecosystems (Xie et al., 2001; Cooper et al., 2007; Krakowiak & Pennuto, 2008; Yuan et al., 2010), but few studies have paid attention to the development of specific management strategies for these invasive goby species.

Rhinogobius cliffordpopei and *R. giurinus* are two common small-bodied (maximal total length <80 mm) goby species that originate from central and eastern China. They were inadvertently introduced into most lakes of the Yunnan Province (Southern China) in the 1950–1960s and their populations have expanded greatly over the last decades (Xie et al., 2001; Yuan et al., 2010). The two species were introduced simultaneously to Lake Erhai in 1961 and since then have become the most dominant benthic fish species (Du & Li, 2001). The fishery of the lake is composed of 3,171 boats for a total of 71,982 fyke nets and the annual yield of the two species accounted for 48% (about 3,500–4,000 tons) of total fish yields of the lake in 2010 (unpublished data). The two species mainly prey on large-sized zooplanktons (Cladocera and Copepoda) and aquatic insects (Chironomid larvae), and they often prey on fish larvae and eggs, including those from native species (Xie et al., 2000; Du and Li, 2001; Zhang, 2005). They can compete with native species (e.g., *Cyprinus longipectoralis, Cyprinus barbatus, Barbodes daliensis*) for food resources (Du and Li, 2001). The two species are considered to be as one of the major causes of the decline and/or extirpation of some native fishes in the lake. In their native lakes along the middle and lower reaches of the Yangtze River (China), the two species have been described as ecologically similar with close life history characteristics and feeding habits (Zhang, 2005; Wu & Zhong, 2008). For instance, Zhang (2005) have studied the reproductive biology of the two species in a native lake, whereas Yan & Chen (2007) investigated the different spawning seasons and female fecundity of *R. giurinus* in two native lakes and an introduced lake. However, no study has compared the reproductive biology of the two species outside of their native range with the aim of developing specific management strategies.

Currently, the principal management strategy to control these two invasive species in Lake Erhai is similar for the two species (i.e., removals by the local fishery) despite the fact that they might differ in many aspects of their life history, including their reproductive biology. Therefore, quantifying the reproductive biology of the two species outside of their native range may promote the development of a more effective management strategy. Here, the reproductive biology of the two goby species was compared to test whether the species differ regarding seasonal spawning cycles, trade-offs between egg size and fecundity, adult sex ratio, size at maturity, and sexual size dimorphisms (SSD). Such a comparison is expected to facilitate a species-specific management strategy for the two invasive species.

Materials and methods

Study area

The present study was conducted in Lake Erhai (105°5–17′ E, 23°35–58′ N, surface area 250 km^2, maximal water depth of 21 m), a shallow freshwater plateau lake in northwest of the Yunnan Province in China (Fig. 1). Water temperature usually peaks at around 25–27°C in July or August without thermal or dissolved oxygen stratification and drops to approximately 6–8°C in December or January. The dominant fish species of Lake Erhai are non-native species, including the two goby species *R. giurinus* and *R. cliffordpopei*, and *Neosalanx taihuensis* (Chen 1965), *Pseudorasbora parva* (Temminck & Schlegel, 1846), *Hypseleotris swinhonis* (Günther, 1873), and *Hemiculter leucisculus* (Basilewsky, 1855). Previous investigations have demonstrated that the two species displayed strong habitat segregation whereby *R. cliffordpopei* mainly uses littoral habitat (water depth <6 m, high abundance of submerged macrophytes, submerged-macrophyte/detritus substrata) and *R. giurinus* mainly uses profundal habitat (12 m < water depth <12–20 m, no submerged macrophytes, silt, and coarse sand substrata, STable 1, Guo et al., 2012). The proportion of the two invasive gobies to native fish species captured in fyke nets was 154:1 individuals in littoral habitat and 518:1 individuals in profundal habitat.

Fish sampling and data collection

From October 2009 to October 2011, *R. cliffordpopei* and *R. giurinus* were sampled monthly using benthic fyke nets in five sites in littoral habitat (LH1–LH5) and three sites in profundal habitat (PH1–PH3), respectively (Fig. 1). The nets comprised a trunk stem with twenty traps, two end traps, and two end pockets. Total length of the net was 15 m, including 12 m of traps (0.6 m each), 2 m of end traps (1 m each), and 1 m of end pockets (0.5 m each). The framework of each trap was made of iron wire with a width of 0.35 m and a height of 0.62 m. The stretched mesh size was 0.4 cm. Four nets were deployed per site and per month from 8:00 to 12:00 and retrieved 24 h later. A stone was added in each end of the nets and two ropes with buoys were attached to each end pocket of the nets (the ropes were longer than 15 m in profundal habitat). The nets were retrieved by slowly pulling the ropes. All fishes in end pockets were collected. The sampling procedure was similar in the two habitats. All *R. cliffordpopei* collected from five sampling sites in the littoral habitat were pooled in each month. A random subsample was subsequently taken. The same procedure was used for *R. giurinus* in the profundal habitat. For each month and each species, the number of individuals subsequently analyzed ranged from 200 to 300. The subsamples were kept at −20°C in a freezer for subsequent analyses. Total body length (L_T) and body mass (M_T) were measured for each individual to the nearest mm and 0.01 g. Based on macroscopic appearances, gonads of both sexes were classified into five reproductive stages (stage I–V) following Nikolsky (1963) and Yan & Chen (2007) (Table 1). Developmental stages of ovaries and testes were assessed by visual inspection primarily based on its appearances (Table 1). Gonads (≥stage II, Table 1) were carefully removed and weighed to the nearest 0.1 mg (gonad mass, M_G). The sex (female or male) of each individual was determined by the macroscopic differences of ovaries and testes (≥stage II, Table 1). Eviscerated mass (M_E) of each individual was measured. To estimate female fecundity, about 0.1 g of mature ovaries (stage IV at the peak of the breeding season, Table 1) was sampled from the anterior, middle, and posterior sections of each lobe. The samples were weighed (M_S) and fixed with 10% formalin solution for 2 weeks and then preserved in 75% ethanol. The number of eggs in each subsample (N_S) was subsequently determined and the length and width of the eggs measured under an optical microscope. The diameter of each egg (D_E) was calculated based on the mean values of length and width. All the

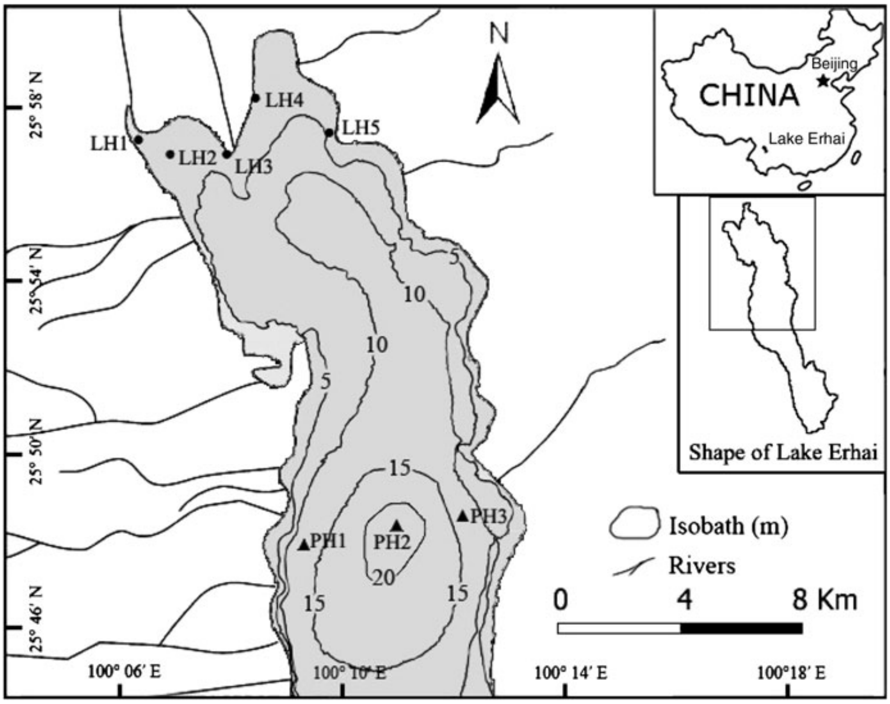

Fig. 1 Sampling sites for *R. cliffordpopei* in littoral habitat (*filled circle*, LH1–LH5) and *R. giurinus* in profundal habitat (*filled triangle*, PH1–PH3) in the central and northern parts of Lake Erhai (China)

Table 1 Macroscopic characteristics (modified from Nikolsky 1963 and Yan & Chen 2007) used to classify gonad maturity stages of *R. cliffordpopei* and *R. giurinus* in Lake Erhai (China)

Gonad maturity stages	Female	Male
I (virgin stage)	Sexes are indistinguishable by naked eye; gonads are thin, threadlike and transparent	Sexes are indistinguishable by naked eye; gonads are thin, threadlike and transparent
II (immature stage)	Ovaries are small, translucent or pale-yellow, more rod-shaped than stage-I; oocytes are indiscernible	Testes are thin, white or gray and larger than stage-I s
III (maturing stage)	Ovaries are swollen, orange in color and occupy 1/5 to 1/3 of the body cavity; vitellogenic oocytes are tightly packed in ovaries and can be visible from epithelium	Testes are firm, flat-shaped and ivory-white
IV (spawning stage)	Ovaries occupy 1/3 to 2/3 of body cavity; oocytes attain their maximum volume and can be released from genital pore with light abdominal pressure	Testes are ivory-white and milt can be released from genital pore with light pressure on the abdomen
V (spent stage)	Ovaries are flaccid and sometimes red with visible capillaries; there are often a few residual oocytes in ovaries	Testes are flaccid and decease in volume clearly; milt is found in some individuals

procedures were performed following the legislation in China.

Statistical analyses

The gonado-somatic indices (I_G) of females were calculated for each mature specimen by the formula $I_G = 100\ M_G/M_T$. The onset and duration of reproduction seasons were quantified based on the occurrence of individuals with stage-IV ovaries (Table 1). The intensity of reproduction activities was determined by comparing I_G and the proportions of different ovary developmental stages between sampling dates. Relative fecundity of females (F_R) was determined as: $F_R = N_S\ M_G\ M_S^{-1}\ M_E^{-1}$. Mann–Whitney tests were used to test for potential differences in D_E and F_R between the two species. Absolute fecundity of females (F_A) was calculated by $F_A = N_S\ M_G\ M_S^{-1}$. Analyses of covariance (ANCOVAs) were used to test the differences in F_A between the two species with L_T as a covariate. Chi square tests (χ^2 test) were used to determine whether the ratio of adult males to females (individuals with gonad stage IV and V were classified as adults, Table 1) varied significantly from a 1:1 ratio within each species and whether adult sex ratios were significantly different between the two species. Logistic regression models were then used to quantify the proportion of mature males and females (stage IV and V, Table 1) at any L_T using binomial maturity data (immature 0, mature 1). L_T at which 50% of individuals are sexually mature was defined as the mean size of maturity (L_{m50}). Log-likelihood ratio tests were used to test the differences of L_{m50} between sexes within each species (Colonello et al., 2011). Mann–Whitney tests were used to test for potential differences in L_T between males and females within each species. Normality and homogeneity of data were assessed using one-sample Kolmogorov–Smirnov test and Levene's test. All statistical analyses were performed by means of R version 2.14.0 (R Development Core Team, 2011).

Results

Spawning seasons

Rhinogobius cliffordpopei and *R. giurinus* showed different onsets of spawning and peaks of the spawning seasons. *Rhinogobius cliffordpopei* spawned from February to June with a spawning peak occurring in March and April. Spawning activity of *R. giurinus* occurred from April to August with a peak activity during May and June. Specifically, the maturity stage of most ovaries and testes of *R. cliffordpopei* were at stage-I from July to October, and the sex of individuals was unidentifiable during this period (Table 1). Individuals with stage-IV ovaries appeared first in February. The proportions of stage-IV ovaries were higher than 90% in March and April, and decreased steadily from May to June. The gonado-somatic indices (IG) of females increased greatly in February and showed the highest values in March and April (Fig. 2). Mean I_G of females was 18.8% during the peak spawning seasons (March to April). For *R. giurinus*, gonads of most individuals were at stage-I from September to December (Table 1). Mature individuals (those with stage-IV ovaries) were first observed in April and accounted for 76–86% in May and June. I_G of females increased significantly in April, peaked in June and decreased in July (Fig. 3). Mean I_G of females during the peak spawning seasons (May to June) was 12.4%.

Egg size and fecundity

Rhinogobius cliffordpopei produced larger eggs and had a lower fecundity than *R. giurinus*. Indeed, diameter of egg (D_E) averaged 613 μm (± 93SD, $n = 2{,}303$) for *R. cliffordpopei* and 470 μm (± 94SD, $n = 1{,}902$) for *R. giurinus* (Mann–Whitney test, $W = 3{,}967{,}132$, $P < 0.001$). Relative fecundity of females (F_R) of *R. cliffordpopei* averaged 2,069 eggs g^{-1} (±3,854 SD, $n = 61$) and was significantly lower than 4,597 ± 2,368 eggs g^{-1} (±SD, $n = 50$) of *R. giurinus* (Mann–Whitney test, $W = 30$, $P < 0.001$). The absolute fecundity of females (F_A) was 1,581 ± 406 (mean ± SD, $n = 61$) for *R. giurinus* and 5,667 ± 2,025 for *R. cliffordpopei* (mean ± SD, $n = 50$). Regardless of individual body size, *R. giurinus* showed significantly higher F_A than *R. cliffordpopei* (ANCOVA, df = 1, $F = 103.79$, $P < 0.001$). Moreover, the rate at which F_A increased with increasing L_T was significantly higher in *R. giurinus* (ANCOVA, df = 1, $F = 21.01$, $P < 0.001$, Fig. 4).

Adult sex ratio

The adult sex ratio differed significantly between the two species (χ^2 test, $\chi^2 = 61.67$, df = 1, $P < 0.001$). The adult sex ratio of *R. cliffordpopei* was significantly biased toward females (1.62 female to 1 male, χ^2 test, $\chi^2 = 112.99$, df = 1, $P < 0.001$, $n = 1{,}885$), whereas the adult sex ratio of *R. giurinus* was 0.98 female to 1 male and it did not significantly differ from 1:1 (χ^2 test, $\chi^2 = 0.268$, df = 1, $P = 0.605$, $n = 2{,}467$).

Size at maturity and sexual size dimorphism (SSD)

Rhinogobius cliffordpopei showed different size at maturity and a strong SSD, whereas there was no significant SSD in *R. giurinus*. Specifically, the mean size of maturity (L_{m50}) of males in *R. cliffordpopei* was 37.6 mm, which was significantly larger than 33.9 mm for females (Likelihood ratio test, df = 2, Chi squared = 259.82, $P < 0.001$). *Rhinogobius giurinus* showed similar L_{m50} between males (46.7 mm) and females (47.2 mm, Likelihood ratio test, df = 2, Chi

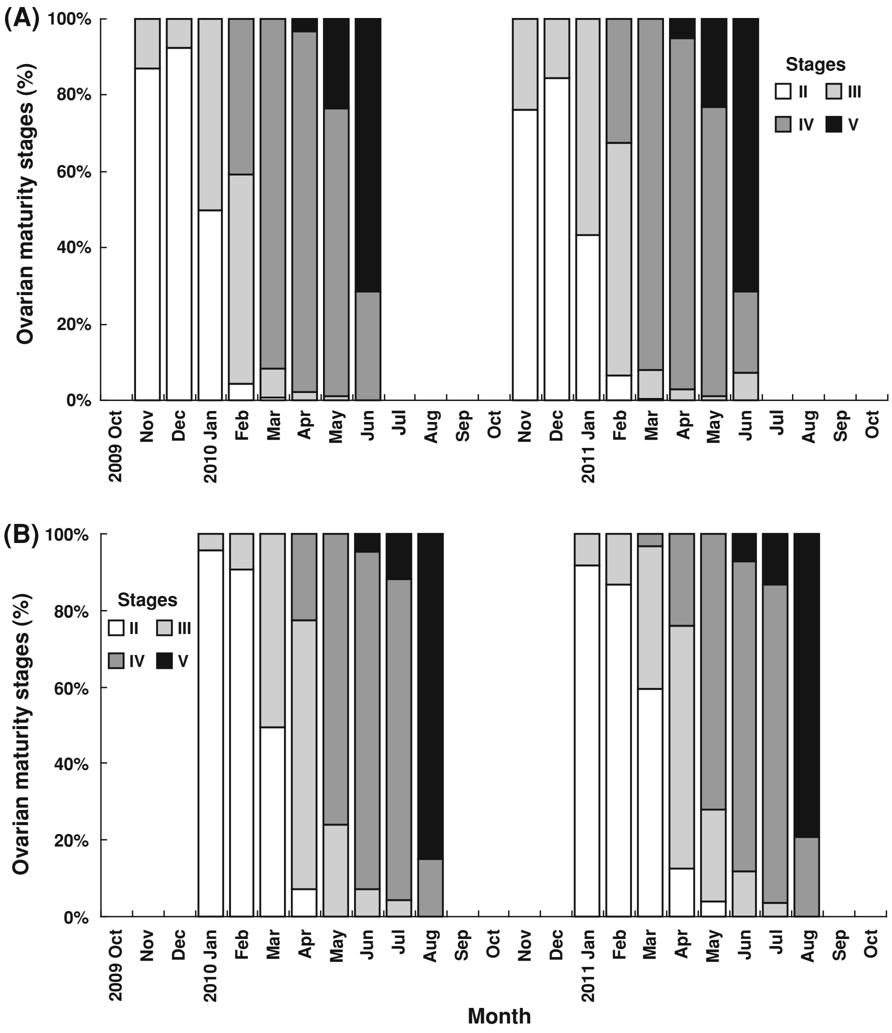

Fig. 2 Monthly changes in the percentage of ovarian maturity stages for **A** *R. cliffordpopei* and **B** *R. giurinus* from October 2009 to October 2011 in Lake Erhai (China). The absence of data indicates that individuals' sex was unidentifiable

squared = 4.62, $P = 0.099$) (Fig. 5). Moreover, males of *R. cliffordpopei* had a significantly higher mean L_T (33.4 mm) over females (30.5 mm, Mann–Whitney test, $W = 324{,}832$, $P < 0.001$), whereas L_T was not significantly different between the sexes in *R. giurinus* (38.5 mm for males and 38.9 mm for females, Mann–Whitney test, $W = 1{,}046{,}996$, $P = 0.392$).

Discussion

The present study demonstrated that *R. cliffordpopei* and *R. giurinus* differed in their reproductive biology, notably in the spawning cycles with differences in the onset of spawning and the peak of spawning seasons in Lake Erhai. The spawning cycles of the two species are highly variable in their native range along the middle and lower reaches of the Yangtze River. In Lake Biandangtang, for instance, spawning seasons of both species occur from the middle of April to late July (Zhang, 2005), whereas *R. giurinus* spawns from July to September in Lake Chaohu (coexisting with *R. cliffordpopei*) and Lake Dongting (without *R. cliffordpopei*, Yan & Chen, 2007). When introduced into Lake Fuxian, *R. giurinus* spawned from July to October (Yan & Chen, 2007). Therefore, regionally specific investigations of the spawning cycles of these two species will be critical before any control operations are put into effect. In Lake Erhai, our study was the first to demonstrate that the two

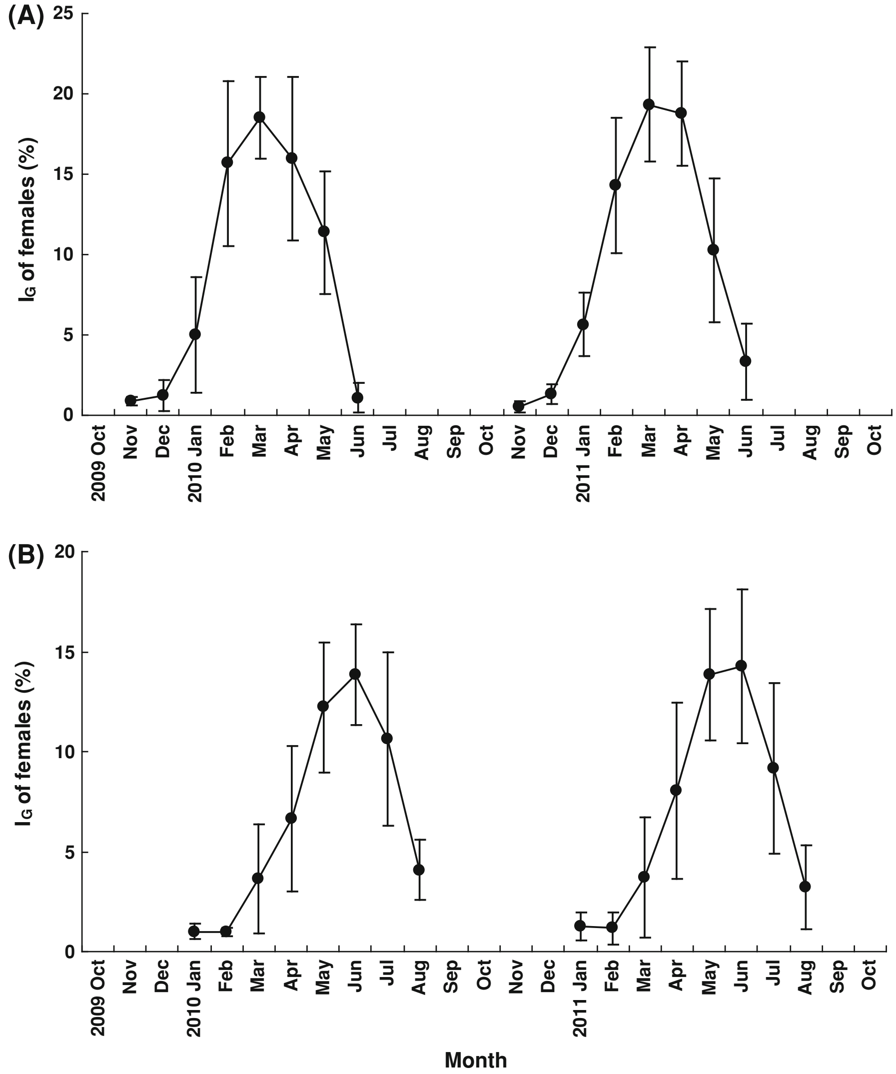

Fig. 3 Monthly changes in the gonado-somatic indices (I_G) of females for **A** *R. cliffordpopei* and **B** *R. giurinus* from Oct 2009 to Oct 2011 in Lake Erhai (China). The absence of data indicates that individuals' sex was unidentifiable. Mean ± SD

species showed clearly different spawning cycles within the same ecosystem outside of their native range, and this is a crucial issue for the timing of deployment of remediation actions (Ling, 2002; Britton et al., 2011). Management operations for fishes may often be most effective when implemented pre-spawning because offspring usually increase population size by several orders of magnitude and disperse extensively within the ecosystem (Knapp & Matthews, 1998; Ludgate & Closs, 2003; Wimbush et al., 2009; Britton et al., 2011). Moreover, the removal of adults soon after spawning may result in a population increase in juveniles (e.g., decreased intraspecific competition) rather than their decline. In New Zealand, for example, Ludgate & Closs (2003) revealed that the numbers of young-of-the-year Eurasian perch (*Perca fluviatilis*) in ponds increased markedly after the cannibalistic adult perch was removed after spawning. In the present study, control measures (e.g., eradication actions or physical removals) are probably most effective from September to February for *R. cliffordpopei*, and from January to April for *R. giurinus*.

The adult sex ratio of *R. cliffordpopei* was strongly female-biased, while *R. giurinus* showed similar numbers of females and males in Lake Erhai. Zhang (2005) found that they had equitable sex ratio in their native range, suggesting that the sex ratios of the two species at birth are likely to be approximate 1:1. Indeed, the sex ratio of gobies can differ in different

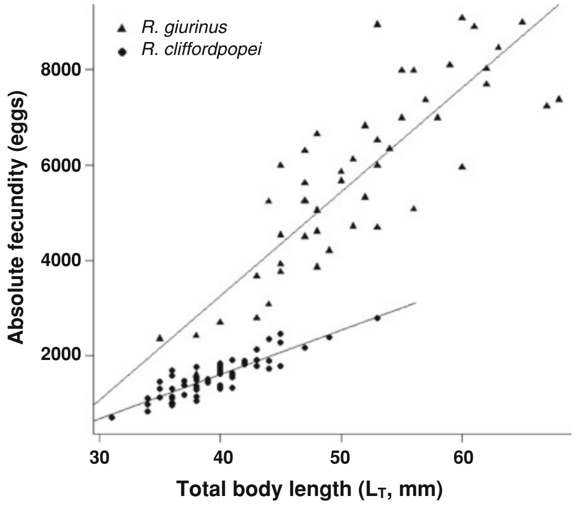

Fig. 4 Comparison of the relationships between total body length (L_T) and absolute fecundity of females (F_A) for *R. cliffordpopei* ($F_A = -2{,}100 + 92.6\ L_T$, $r = 0.88$, $n = 61$) and *R. giurinus* ($F_A = -5{,}400 + 218.7\ L_T$, $r = 0.86$, $n = 50$) from October 2009 to October 2011 in Lake Erhai (China)

environmental conditions. For instance, the operational sex ratio of *Neogobius melanostomus* was about 3:1 (male: female) in Puck Bay (Poland) and about 6:1 in the Great Lakes (Corkum et al., 2004). The monthly size frequency of the two species was analyzed (Electronic Supplementary Material, SFig. 1 & SFig. 2) and no evidence of size selectivity by fyke nets was observed. Indeed, the two goby species are congeneric species and show similar male paternal care (Takahashi et al., 2001; Ito & Yanagisawa, 2003). If the paternal caring males were less susceptible to fyke nets than females, then the adult sex ratio of *R. giurinus* would be also female biased. This was not the case here. Furthermore, benthic fyke nets have been used in the previous studies (Zhang, 2005; Yan & Chen, 2007) and the authors did not observe sex-biased adult sex ratio in the two species. Therefore, it is very unlikely that our results on sex ratio were affected by the use of fyke nets.

There are several possible mechanisms for the skewed sex ratio of *R. cliffordpopei* in littoral habitat. First, differential survival between the sexes caused by local predation of *Channa argus*, an invasive species that was found to be a potential predator of the two goby species in native lakes (Ma & Xie, 1999). The distribution *C. argus* is limited exclusively to littoral habitat in Lake Erhai where the species co-occured with *R. cliffordpopei*. Sex-specific predation resulting in biased sex ratio has been widely demonstrated in fishes. For instance, *Rivulus hartii* and *Macrobrachium crenulatum* preyed preferentially on males of *Poecilia reticulate* over females in both field and laboratory experimentations (McKellar et al., 2009; McKellar & Hendry, 2011). Selective predation on males of *R. cliffordpopei* may be due to their conspicuous visual sexual signals (e.g., bright colors; Hurtado-Gonzales et al., 2010) and/or behaviors (e.g., aggression or mobility; Costantini et al., 2007). Moreover, since adult males of *R. cliffordpopei* are significantly

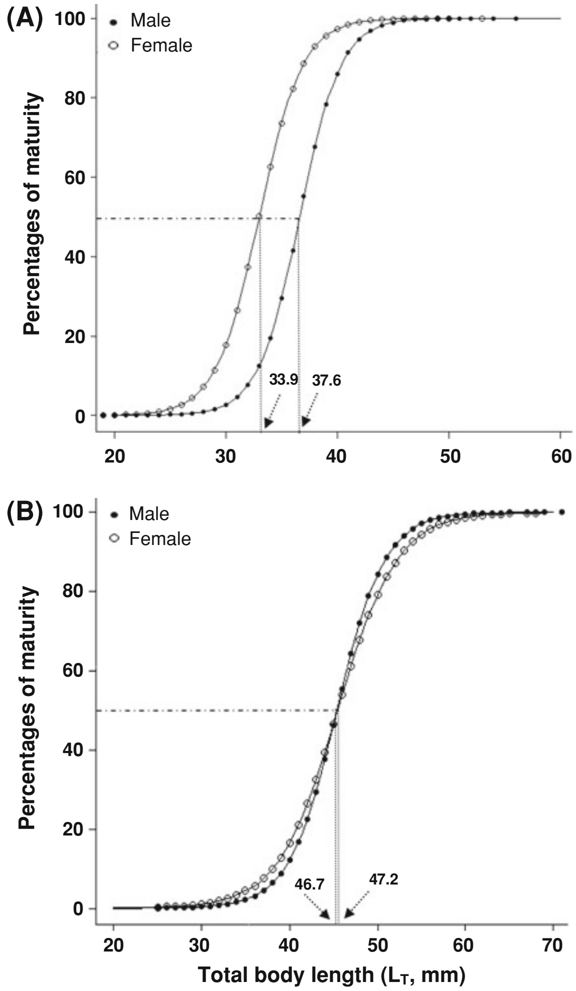

Fig. 5 Comparison of the size of maturity of **A** *R. cliffordpopei* ($n = 2{,}293$ for females and $n = 1{,}819$ for males) and **B** *R. giurinus* ($n = 2{,}237$ for females and $n = 2{,}304$ for males) from October 2009 to October 2011 in Lake Erhai (China). Mean size of maturity (L_{m50}) was 33.9 mm and 47.2 mm for females and 37.6 mm and 46.7 mm for males of *R. cliffordpopei* and *R. giurinus*, respectively

larger than females, SSD-associated size-selectivity predation on larger males can also result in a higher mortality of males (Nakazawa et al., 2007; Reardon & Thibert-Plante, 2010). Second, skewed sex ratios could be due to sex-specific mortality caused by the costs associated with parental care (Liker & Székely, 2005). Males of the genus *Rhinogobius* are nest-guarders (Takahashi et al., 2001; Ito & Yanagisawa, 2003). Parental care is not only energetically costly but also increases the vulnerability to predators, which may increase mortality of males of *R. cliffordpopei* in littoral habitat (Liker & Śzekely, 2005). Therefore, *C. argus* is probably an effective (and non-native) predator to males of *R. cliffordpopei* in the lake. After an evaluation of its potential effects on the non-target species and on the native ecosystem, *C. argus* may be a potential candidate as a bio-control agent in the lake if its ecological impacts are acceptable (Saunders et al., 2010; Britton et al., 2011). Currently, *C. argus* is the only recorded piscivorous fish in the lake with a relatively low abundance. Increasing the abundance of *C. argus* by artificially stocking and/or limiting catches by the fishery may be a synergistic operation with the physical removals.

Here, *R. cliffordpopei* showed a clearly male-biased sexual size dimorphism (SSD) while *R. giurinus* showed no SSD. Sexual selection, fecundity selection, and inter-sexual resources partitioning selection are the three major selective processes underpinning SSD (Fairbairn, 2007). As a male-guarding species, males of *R. cliffordpopei* may be subjected to a strong sexual selection because the large males often have advantages in acquiring larger and/or better nests (Malavasi et al., 2001; Takahashi et al., 2001). The large males of *R.* sp. DA, for instance, are found to occupy larger nest stones and guard more eggs in each nest over the smaller ones (Takahashi et al., 2001). However, the body size of *R. cliffordpopei* in Lake Biandangtang was similar between the sexes and males of *R. giurinus* were significantly larger than females (Zhang, 2005). The direction and magnitude of these selections often vary substantially among species as well as populations within species in highly different environments (Blanckenhorn et al., 2006). In Lake Erhai, physical removals should give a careful consideration for the male-biased SSD of *R. cliffordpopei* because the effectiveness of physical removals (e.g., intensive gill netting) may vary with different body size of the target fishes (Knapp & Matthews, 1998; Britton et al., 2011). For instance, Knapp & Matthews (1998) found that introduced adult trout were highly vulnerable to gill nets, but younger fishes were not readily captured until they reached approximately 110 mm. Thus, we suggest that the body size of the smaller *R. cliffordpopei* females is the determinant for minimal mesh size of benthic fyke and seine nets used in the physical removals of *R. cliffordpopei*.

In conclusion, our results demonstrated that the two invasive goby species showed different reproductive characteristics in Lake Erhai. Consequently, the approaches taken in the management of the two species should incorporate these differences. First, the physical removals using fyke nets should be redoubled from September to February for *R. cliffordpopei*, and from January to April for *R. giurinus* based on their spawning cycles. Second, the body size of the smaller *R. cliffordpopei* females is the determinant for minimal mesh size of benthic fyke used in the physical removals. Third, the efficiency of the control method should be improved (e.g., physical removals should be conducted mainly in profundal and sublittoral habitats for *R. giurinus,* but in littoral habitat for *R. cliffordpopei*, because the two species show a strong habitat segregation in the lake (Guo et al., 2012)). Fourth, since the presently undertaken control operations are only physical removals, application of synergistic remediation may be a complementary strategy (e.g., chemical eradication using rotenone (Ling, 2002) and sex pheromones (Li et al., 2002; Arbuckle et al., 2005) and light trapping (Meekan et al., 2001; Vilizzi et al., 2008)). In addition, further investigations on life history traits and ecological impacts are imperative for a comprehensive management strategy of these invasive fish species.

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