



## Reproductive biology, growth, and age composition of non-native Indian glassy fish *Parambassis ranga* (Hamilton, 1822) in Haeburu Reservoir, Okinawa-jima Island, southern Japan

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### Summary

Age composition, growth, and reproductive biology of the non-native Indian glassy fish *Parambassis ranga* (Hamilton, 1822) were surveyed in the Haeburu Reservoir on Okinawa-jima Island, southern Japan. Standard lengths (SLs) of males and females ranged from 19.7 to 44.0 mm and from 19.2 to 52.4 mm, respectively. The overall sex ratio was significantly female-biased, with the monthly percentage of females ranging from 71.4 to 100.0. Marginal growth analysis of sectioned otoliths revealed opaque zones formed annually from November to May. Observed age ranged from 0 to 3 years for both sexes, although the 1-year age class comprised the majority of the sampled population. Von Bertalanffy growth parameters were  $L_{\infty} = 48.8$  mm (SL),  $K = 0.43$  year<sup>-1</sup>, and  $t_0 = -1.47$  years for males, and  $L_{\infty} = 43.7$  mm,  $K = 0.72$  year<sup>-1</sup>, and  $t_0 = -1.29$  years for females. Length at 50% maturity was estimated to be 25.8 mm SL, and maturation was within 1 year after hatching. The main spawning season of *P. ranga* was estimated to occur from February to October, peaking in April.

### Introduction

A major pathway for non-native freshwater fish introduction is the release of ornamental aquarium fishes into the wild (Copp et al., 2005, 2007; Duggan et al., 2006; Corfield et al., 2007). Many released fishes most likely do not survive in temperate and cold zones, given their requirements for warmer environments (Gozlan et al., 2010); however, in tropical and subtropical climates, released fishes can survive and establish viable populations (e.g. Yamamoto and Tagawa, 2000; Shafland et al., 2008). On subtropical Okinawa-jima Island, southern Japan, numerous tropical fishes most likely abandoned by private aquarists have recently been discovered in natural waters, particularly in urban reservoirs (Yoshigou and Iwasaki, 2001; Tachihara et al., 2002). In 2001, the Indian glassy fish *Parambassis ranga* (Hamilton, 1822) (formerly classified as *Chanda ranga*), a small ambassid fish with a striking, transparent body, was first confirmed in the Haeburu Reservoir, southern Okinawa-jima Island (Yoshigou and Iwasaki, 2001). Another population of *P. ranga* was recently discovered in the Hiyara River, which runs through the southern part of Okinawa-jima Island (K. Tachihara, unpubl. data). *Paramb-*

*assis ranga* is native to southern Asia from Pakistan to Malaysia and has been introduced into Japan and the Philippines (Roberts, 1994; FishBase, 2011). A popular aquarium fish, it is sometimes injected with a fluorescent dye to color its transparent body for commercial purposes (Yoshigou and Iwasaki, 2001), although the fish on Okinawa-jima Island are not dyed. Many *P. ranga* individuals have been collected from both the Haeburu Reservoir and the Hiyara River; thus, this non-native fish has likely established viable populations.

Characteristics of the reproductive biology and growth of the family Ambassidae have been reported for species in the genera *Ambassis* and in *Denariusa australis* (e.g. Milton and Arthington, 1985; Semple, 1985; Coates, 1990; Bishop et al., 2001). In contrast, very little is known about the life history of *P. ranga*. Only two reports have described the growth and reproduction of native *P. ranga* in Bangladesh (Mortuza et al., 1996; Mustafa and de Graaf, 2008), while no ecological study has focused on the life history traits of non-native populations. Studies on the life history traits of non-native freshwater fishes serve as the basis for further applied studies and management planning (Sato et al., 2010). In addition, elucidating the growth and reproductive characteristics of *P. ranga* is critical to better understand their life history and to conserve native populations. The aim of this study was to estimate life history parameters associated with the reproductive biology, age, and growth of the non-native *P. ranga* population established in the Haeburu Reservoir and to compare the data collected with that of the same species in its native range and with other species of Ambassidae. It is postulated that the Haeburu Reservoir population, which has been exposed to environmental conditions different from its native environment, would have a different life history strategy than the native populations.

### Materials and methods

#### Sampling site and fish collection

The Haeburu Reservoir (26°12'N, 127°44'E) is a shallow (max. depth: approximately 3 m), small (area: approximately 30 000 m<sup>2</sup>) agricultural reservoir located in the upper reaches of the Kokuba River, which runs through the southern part of Okinawa-jima Island, central Ryukyu Archipelago, southern Japan (Fig. 1). A variety of non-native freshwater fishes has been released into this reservoir (Yoshigou and Iwasaki, 2001). *Parambassis ranga* was collected one to three times per month in the Haeburu Reservoir from May 2006 to 2007 using hand

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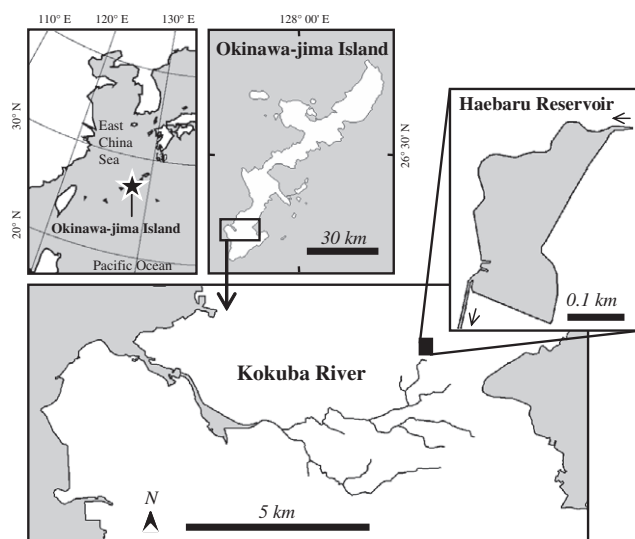


Fig. 1. Map of Okinawa-jima Island showing location of Haeburu Reservoir. Arrows = direction of flow

nets (mesh size: ca. 1.5 mm) and cast nets (stretch mesh size: 15 mm) in a shore area ( $n = 232$ ). Small sized specimens collected from November 2004 to December 2007 were also included in the analysis ( $n = 16$ ; Table 1). Surface water temperature was recorded to the nearest  $0.1^{\circ}\text{C}$  before sampling, and the mean water temperature for each month was used for the analysis. Day lengths on Okinawa-jima Island for each month were defined as the time from sunrise to sunset; data were issued by the National Astronomical Observatory of Japan (<http://www.nao.ac.jp/koyomi/>).

Collected specimens were transported on ice in a cooler box to the laboratory at the University of the Ryukyus. Standard length (SL) and body weight (BW) of each specimen were measured to the nearest 0.1 mm and 0.01 g, respectively. Gonads and **sagittal otoliths** were subsequently removed. Gonads were weighed to the nearest 0.001 g (GW), and sex was determined based on the external gonad morphology.

#### Age determination

After cleaning and drying, the right otoliths were embedded in epoxy resin and **sectioned transversely through the core into 0.20–0.25-mm-thick sections**. The sectioned otoliths were examined under a binocular microscope with reflected light against a black background, and the number of opaque zones counted (Fig. 2). **Ring counts were conducted twice by a single individual, with a 2-week interval**, without knowing the fish size and collection month. When ring counts differed between the first and second counts, an additional count was conducted and the final ages were determined. To estimate aging precision, the average percent error (APE) was calculated (Campana, 2001).

Table 1  
Standard length (SL) of additional small *P. ranga* collected November 2004–December 2007

Sex	Collection date	n	SL (mm)
Male	November 2004	1	19.7
Female	November 2004	11	19.2–29.0
Unknown	May 2005	1	16.2
	July 2006	1	15.5
	January 2007	1	23.3
	December 2007	1	13.1

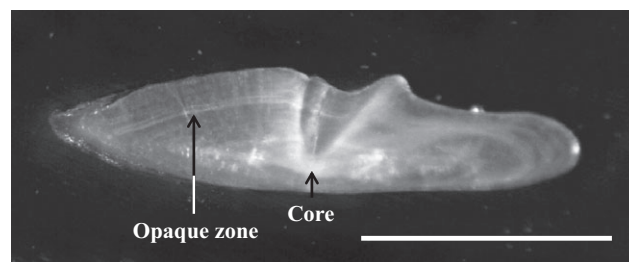


Fig. 2. Sectioned otolith, *Parambassis ranga* specimen, opaque zone and core. Scale bar = 1 mm

Annual validation of the opaque zone on the sectioned otolith was assessed through a marginal increment analysis (Campana, 2001). The widths of the translucent zone on otolith margins that were in the process of forming ( $M_n$ ) and those of the inner translucent zone that were most recently completed to form ( $M_{n-1}$ ) were measured to the nearest 0.01 mm. The opaque ring formation period was estimated based on the monthly changes in the marginal growth index (MGI):  $MGI = M_n \times 100 / M_{n-1}$ .

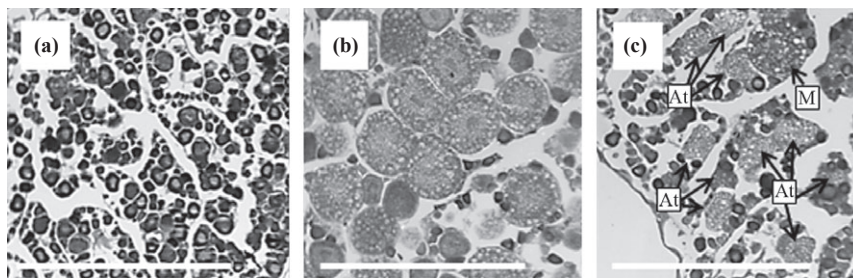
A peak birth month (April) was assumed; the age of individuals collected during the ring formation period was adjusted because fish with a 1-year age difference exhibited the same number of opaque zones in this period. To adjust for this, 1 year was added to individuals exhibiting a low MGI value before April, and 1 year was subtracted from individuals showing high MGI values after April.

Age at SL data were modeled with the von Bertalanffy growth function (VBGF) using the nonlinear least-squares method (Gauss–Newton algorithm). To derive a reliable growth curve, small individuals, including additional specimens collected during 2004–2007 (Table 1), were included in the 0-age group for calculating VBGF parameters. VBGF was derived by the equation:  $L_t = L_{\infty}(1 - e^{-K(t-t_0)})$ , where  $L_t$  is the SL at age  $t$ , and  $L_{\infty}$ ,  $K$ , and  $t_0$  are the asymptotic length, the growth coefficient, and the hypothetical age at  $SL = 0$ , respectively.

#### Gonad observations

The gonads of 205 females and 29 males, including the additional specimens (Table 1), were weighed to the nearest 0.001 g (GW), and the gonadosomatic index [GSI;  $GSI = GW \times 100 / (BW - GW)$ ] of each individual was calculated. Gonads from 195 females collected from May 2006 to 2007 and 10 females collected in November 2004 (Table 1) were stored in 10% buffered formalin and observed histologically. For these procedures, a portion of the ovary was dissected and embedded in paraffin wax; the tissues were sectioned transversely at  $5\text{--}7\text{ }\mu\text{m}$  thickness and stained with Mayer's hematoxylin and eosin. The developmental stages of the ovaries were classified according to the criteria of Yamasaki and Tachihara (2006) as: 'immature' (Fig. 3a) ovaries with immature previtellogenic oocytes, 'mature' (Fig. 3b) ovaries with mature vitellogenic oocytes, and 'atresia' (Fig. 3c) ovaries with atretic oocytes. The ovarian maturity stage was determined from the most advanced oocyte in the ovary. Because a few atretic oocytes were present in some developed mature ovaries, the percentage of atretic oocytes [=number of atretic oocytes  $\times$  100/(number of mature vitellogenic oocytes + number of atretic oocytes)] was calculated and ovaries that contained  $>10\%$  of atretic oocytes were categorized as 'atresia'.

Fig. 3. Histological classification of oocyte development in *Parambassis ranga*: (a) Immature stage; (b) mature stage; (c) atretic stage: M and At = mature oocyte and atretic oocyte, respectively. Scale bar = 1 mm



Length at 50% maturity ( $L_{50}$ ) was defined as the size when 50% of the females matured, and estimated by fitting a logistic function (generalized linear model with a logit-link function and binomial error) with a length class interval of 2 mm. In this analysis, females with atretic ovaries were used as mature individuals because individuals with atretic ovaries always had mature vitellogenic oocytes.

## Results

### Sex ratio and size composition

Collected were 28 male and 204 female specimens. The overall male to female sex ratio, 1.0 : 7.3, was significantly female-biased (chi-square goodness of fit test,  $\chi^2 = 133.5$ , d.f. = 1,  $P < 0.001$ ), and the monthly percentage of females ranged from 71.4 to 100.0 (Table 2). No *Parambassis ranga* were collected in March 2007. The size of males and females ranged from 19.7 to 44.0 mm SL (mean  $\pm$  SD =  $32.2 \pm 3.9$ ) and 19.2 to 52.4 mm SL ( $34.8 \pm 3.9$ ), respectively; the mean SLs were significantly different between sexes (Welch's  $t$ -test,  $t = -3.1$ , d.f. = 36,  $P = 0.004$ ; Fig. 4).

### Age and growth

Narrow opaque and wide translucent zones were clearly visible and easily interpreted in sectioned otoliths (Fig. 2). The high and low MGI values were simultaneously observed from April to May in the one-ring group and during November to May in the two- and three-ring groups (Fig. 5). Therefore, the opaque zone on sectioned otoliths was validated as annulus forming during the November–May period. The mean APE was relatively low (4.42%), reflecting good concordance between the two counts (89%).

Table 2  
Monthly numbers of males and females, and percentage of female *Parambassis ranga*, Haeburu Reservoir, May 2006–2007

Collection date	Female	Male	%Female
May 2006	26	2	92.9
June 2006	14	0	100.0
July 2006	27	2	93.1
August 2006	8	1	88.9
September 2006	13	1	92.9
October 2006	18	7	72.0
November 2006	23	0	100.0
December 2006	5	2	71.4
January 2007	20	7	74.1
February 2007	19	2	90.5
March 2007	0	0	–
April 2007	10	2	83.3
May 2007	21	2	91.3
Total	204	28	87.9

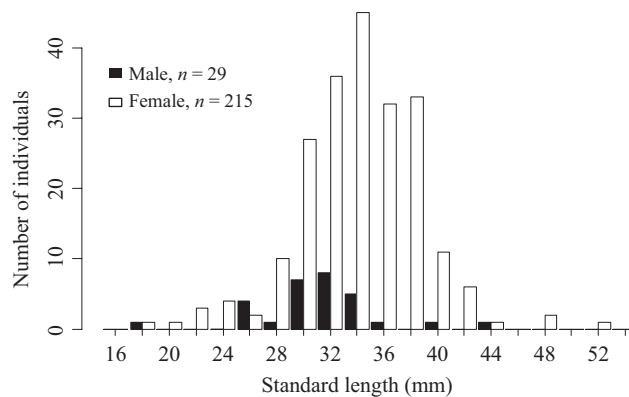


Fig. 4. Length–frequency distribution, male and female *Parambassis ranga*, Haeburu Reservoir

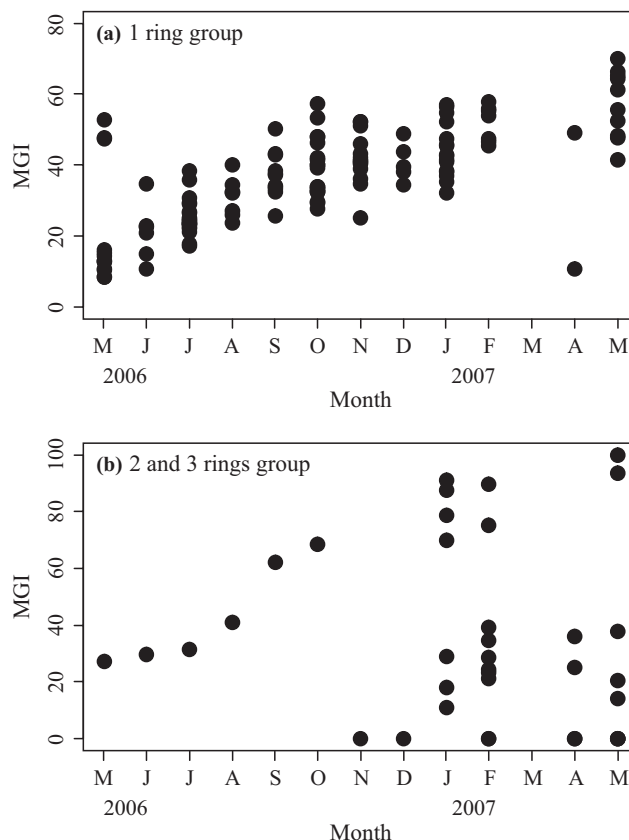


Fig. 5. Monthly changes, marginal growth index (MGI) in (a) one-ring group and (b) two- and three-ringed groups, *Parambassis ranga*, Haeburu Reservoir

The observed maximum ages of males and females were both 3 years (Table 3), although the majority of the sampling population consisted of 1-year-old fish (male: 65%, female:

Table 3  
Captured standard length (SL) per age class, *Parambassis ranga*, Haeburu Reservoir

Age class	Male SL				Female SL			
	Range	Mean $\pm$ SD	n	% to total	Range	Mean $\pm$ SD	n	% to total
0	26.8–31.4	29.3 $\pm$ 2.2	4	15	27.0–36.0	31.5 $\pm$ 2.3	13	8
1	26.4–35.2	33.5 $\pm$ 4.3	17	65	29.1–42.6	35.5 $\pm$ 3.0	122	73
2	33.4–41.0	36.5 $\pm$ 3.3	4	15	33.2–52.4	39.2 $\pm$ 4.2	31	19
3		44.0	1	4		49.6	1	1

73%). The VBGF parameters ( $\pm$ SE) were:  $L_{\infty}$  = 48.8 ( $\pm$ 14.1) mm (SL),  $K$  = 0.43 ( $\pm$ 0.34) year<sup>-1</sup>, and  $t_0$  = -1.47 ( $\pm$ 0.67) years for males, and  $L_{\infty}$  = 43.7 ( $\pm$ 2.8) mm,  $K$  = 0.72 ( $\pm$ 0.20) year<sup>-1</sup>, and  $t_0$  = -1.29 ( $\pm$ 0.27) years for females. On average, females were larger than males in all age classes (Table 3). The growth rates of both sexes were higher in the first year, and subsequently slowed (Fig. 6; Table 3). The relationship between the SL and BW for all fish sampled during May 2006–2007 was described by a power function:  $BW = 0.00003 \times SL^{3.00}$ .

### Reproductive biology

Mature females were first recorded in the 26–28-mm SL category, and  $L_{50}$  was estimated to be 25.8 mm SL (Fig. 7). The smallest mature female identified was 27.0 mm SL (0-year age class).

During the study period (2006–2007), the water temperature in the reservoir increased from January (17.1°C), peaked in August (34.9°C), and then gradually decreased through

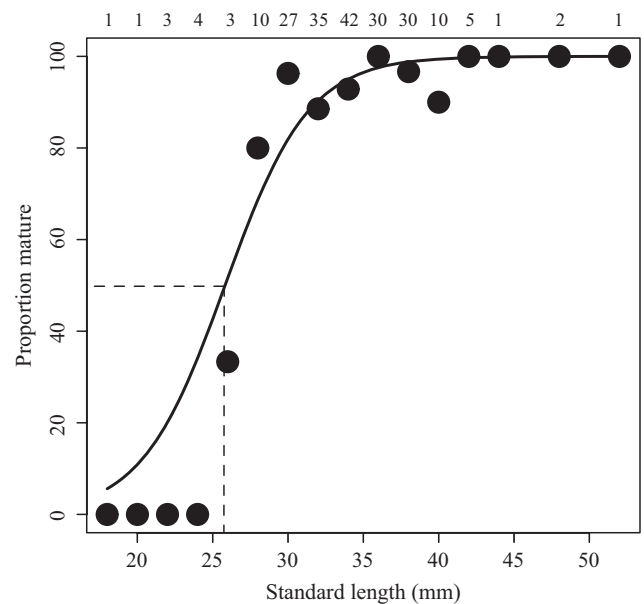


Fig. 7. Standard length at first sexual maturity ( $L_{50}$ ; dashed line) estimated by logistic function fitted to percentages of mature two females in each 2-mm size class, *Parambassis ranga*, Haeburu Reservoir. Numbers = sample sizes

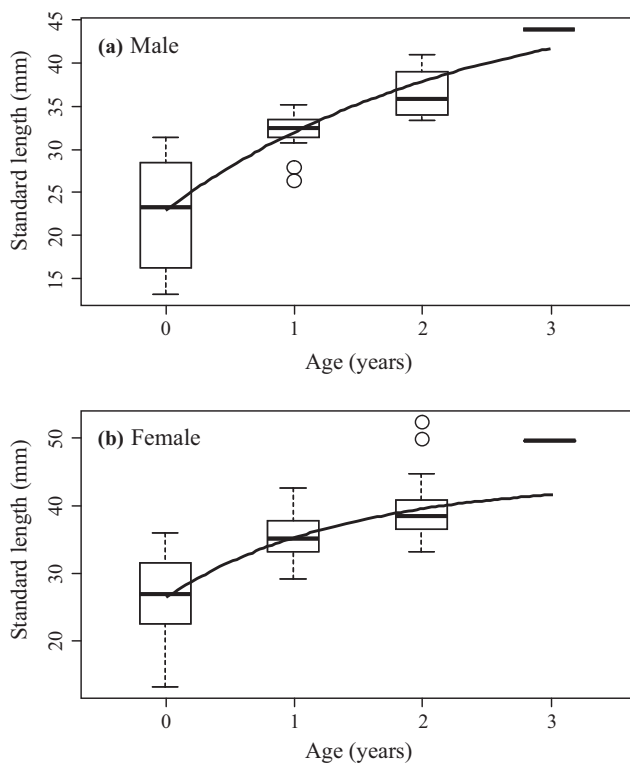


Fig. 6. Von Bertalanffy growth curves fitted to standard length (SL) and age in (a) male and (b) female *Parambassis ranga*, Haeburu Reservoir. Boxes = 25th–75th quartiles; central line = median; interval lines above and below each box = max and min distribution values, respectively; circles = outlier values

December (18.1°C; Fig. 8a). Day length increased in December (10.5 h), reached a maximum value in June (13.8 h), and decreased by November to 10.9 h (Fig. 8a).

The majority of individuals (93–100%) were mature from May to October 2006 and February to May 2007, but the percentage of mature females was low (0–36%) during the period November 2006–January 2007 (Fig. 8b).

No marked fluctuations in female GSI values were observed during May–December 2006 (Tukey's HSD test,  $P > 0.05$ ; Fig. 8c). The monthly GSI values were lowest in January 2007, then significantly increased in February (Tukey's HSD test,  $P = 0.002$ ) and peaked in April (Tukey's HSD test,  $P < 0.001$ ; Fig. 8c). GSI values decreased significantly in May 2007 (Tukey's HSD test,  $P < 0.001$ ; Fig. 8c).

### Discussion

#### Female-biased sex ratio

In this study, females were much more prevalent than males in all sampling months during 2006–2007. The sex ratio is not biased in *Ambassis agassizii* in Australia and *A. interrupta* in Papua New Guinea throughout the year (Milton and Arthington, 1985; Coates, 1990); male-biased sex ratios have been reported for *Ambassis macleani*, *A. agrammus*, and *Denariusa australis* in Australia, depending on season and habitat (Bishop et al., 2001). In contrast, females are more prevalent



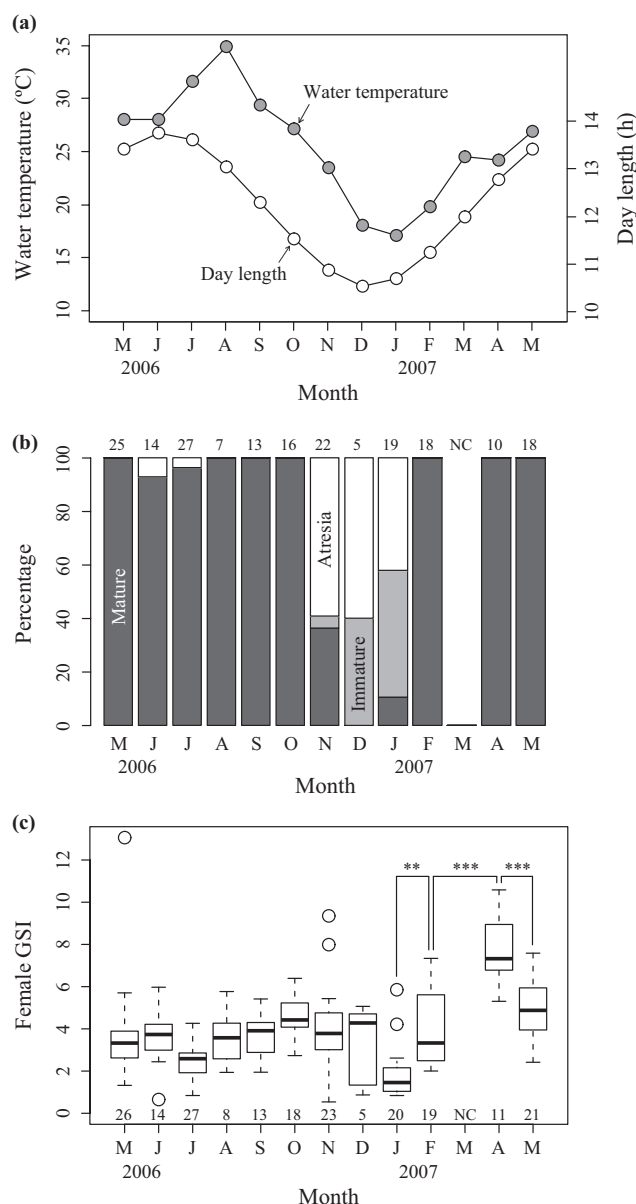


Fig. 8. (a) Monthly changes in mean water temperature and day length, Haeburu Reservoir, May 2006–2007. (b) Monthly changes in percentage of mature, immature, and atretic females, *Parambassis ranga*, May 2006–2007. Numbers on bars = sample sizes. NC, not collected. (c) Monthly changes in gonadosomatic index (GSI), female *P. ranga*, May 2006–2007. Boxes = 25th–75th quartiles; central line = median; interval lines above and below each box = max and min distribution values, respectively; circles = outlier values. Asterisks = significant differences in GSI values between two consecutive months (Tukey's HSD tests; \*\*P < 0.01, \*\*\*P < 0.001). Numbers in figure = sample sizes. NC, not collected

than males in a non-native *Parambassis siamensis* population in Taiwan (Chen and Kuo, 2009) and in a native *P. ranga* population in Bangladesh (Mortuza et al., 1996). The biased sex ratio in *P. ranga* may be explained by two hypotheses. First, if distribution of males is in deeper or more offshore areas than females, the sampling method of cast nets and hand nets in the shore area would have failed to collect any males. Second, the female-biased sex ratio indeed represents the true sex ratio in the population. Any biological reasoning for such a phenomenon remains to be clarified, but the possibility exists that it is a specific feature of the genus *Parambassis* among Ambassidae.

### Age and growth

The opaque zone on sectioned otoliths from *P. ranga* was very clear and easily interpreted (Fig. 2). In addition, the low APE value (4.42%) and high congruence between two independent counts (89%) indicated that age was accurately estimated. Consequently, this study is the first to demonstrate that the technique of using sectioned otoliths to estimate age in fish can be applied to ambassid fishes.

In this study, the opaque zone on sectioned otoliths was formed annually between November and May, including the period when water temperature and day length decreased (November–January) and GSI value peaked (April). The opaque zone formation period of *P. ranga* is earlier and longer than that of other Okinawan freshwater fishes, where the opaque zones are formed during the spring to summer period, corresponding to their peak reproductive activity (Tachihara and Obara, 2003; Ishikawa and Tachihara, 2008, 2010; Takada and Tachihara, 2009). However, given that a variety of environmental and physiological factors may be related to ring formation (Beckman and Wilson, 1995), determining the precise factors responsible for opaque ring formation is not currently possible (Booth et al., 1995; Booth and Merron, 1996) in *P. ranga* otoliths on Okinawa-jima Island.

Sexual growth dimorphism is common in fishes, but sexual dimorphism in the growth rate of ambassids is not well known. No significant sexual difference in growth was observed in *A. agassizii*, and *A. macleayi* males generally tended to be larger than females (Milton and Arthington, 1985; Bishop et al., 2001). In the present study, estimated  $L_{\infty}$  was higher in males than in females. Judging from the high standard error value of  $L_{\infty}$  for males, this was likely a reflection of the small sample size for the males. Indeed, the observed mean SL in each age class of females was greater than that of the males in all age classes (Table 3), indicating that the growth rate of females was higher than that of males from the first year. However, as suggested previously, if the larger males inhabit more offshore and deeper areas, collection of these fishes would have failed. Therefore, whether the growth rate of females is higher than that of males remains uncertain.

The only available study on age and growth for *P. ranga* (Mustafa and de Graaf, 2008) estimated VBGF parameters using length frequency data sets obtained from Bangladesh. However, because they did not indicate which length (total length, folk length, or standard length) was measured, their estimates of  $L_{\infty}$  (70 mm) cannot be compared to the present study. Their estimate of  $K$  (0.7), however, indicated rapid growth in the first year, which was confirmed by the present analysis. Longevity in the Haeburu Reservoir (3 years) was slightly shorter than that in Bangladesh (4.3 years; Mustafa and de Graaf, 2008).

The annual growth rates of *P. ranga* in the Haeburu Reservoir are comparable to those reported for *A. agassizii* in Australia, which were aged using scales and where *A. agassizii* grew to be 31 mm SL at 1 year, 43 mm at 2 years, and 51 mm at 3 years (Milton and Arthington, 1985). Therefore, the growth rates of both species were similar in 1-year-olds, but subsequent growth was higher in *A. agassizii* than in *P. ranga*. The observed maximum ages were 3 years for both species.

### Reproductive biology

The monthly percentage of mature females and the GSI strongly suggested that the main spawning season of *P. ranga*

Table 4

Summary of reproductive study, ambassid fishes: maturation size (length at 50% maturity), maximum size, maturation size / max size as standard length (SL) or fork length (FL).

Species	Locality	Sex	Maturation size	Maximum size	Maturation size / maximum size	Reference
<i>Parambassis ranga</i>	Haeburu Reservoir, Japan	F	25.8 mm SL	52.4 mm SL	0.49	1
		M	—	44.0 mm SL	—	
<i>Ambassis agrammus</i>	Alligator rivers region, Australia	F	26.0 mm FL	64.0 mm FL	0.41	2
		M	27.0 mm FL	48.0 mm FL	0.56	
<i>Ambassis interrupta</i>	Sepik river, Papua New Guinea	F	70.0 mm SL	105.0 mm SL	0.67	3
		M	70.0 mm SL	105.0 mm SL	0.67	
<i>Ambassis macleayi</i>	Alligator rivers region, Australia	F	29.0 mm FL	74.0 mm FL	0.39	2
		M	33.0 mm FL	81.0 mm FL	0.41	
<i>Ambassis agassizii</i>	Brisbane River, Australia	F	37.2 mm SL	54.0 mm SL	0.69	4
		M	—	—	—	
<i>Denariusa australis</i>	Alligator rivers region, Australia	F	25.0 mm FL	38.0 mm FL	0.66	2
		M	31.0 mm FL	41.0 mm FL	0.76	

(1) Present study; (2) Bishop et al. (2001); (3) Coates (1990); (4) Milton and Arthington (1985). Note that the maturation size in Milton and Arthington (1985) are given as the mean length of ripe fish.

takes place from February to October. In addition, the maximum GSI was observed in April, indicating that peak spawning was restricted to around this month. Spawning was not active during November–January, corresponding to the decreasing water temperature and day length. The estimated spawning season and its peak in the Haeburu Reservoir was longer and earlier than those in Bangladesh, where spawning occurred during February to August, with peaks in March and July (Mortuza et al., 1996). In Australia, *A. agassizii* spawn only during October and November, and require a period of increasing water temperatures before the onset of breeding at temperatures of at least 22°C (Milton and Arthington, 1985). Reproduction of *P. ranga* was always observed to occur in the warm months (> 24°C; Fig. 8a), although the effects of day length on ambassid reproduction remain to be fully examined. However, spawning in November (23.5°C) was likely more inhibited than that in February (19.8°C), and increasing water temperature coincided with that of GSI from February to April. These observations indicate that for *P. ranga*, rising water temperature is likely more important for active spawning than high temperatures (> 24°C) alone. Other factors such as rainfall (Bishop et al., 2001) and day length may also play important roles in *P. ranga* spawning.

Maturation size ( $L_{50}$ ) of *P. ranga* females was estimated to be 25.8 mm SL, which is 49% of the maximum length recorded in this study. Maturation and maximum sizes of six ambassid fish species are summarized in Table 4. The maturation size / maximum size for each species varied between 0.39 (*A. macleayi* female) and 0.76 (*D. australis* male) irrespective of locality and gender, suggesting that this value for *P. ranga* is moderate among ambassids. Variations in maturation size / maximum size of these ambassids are likely related to differences in life history strategies. A small individual in the 0-year age class (27.0 mm SL) was found with mature ovaries, indicating that *P. ranga* in the Haeburu Reservoir matured within 1 year after hatching. Milton and Arthington (1985) reported that *A. agassizii* in Australia matured at 1 year of age. The early maturations of these ambassid fishes are thought to be a consequence of their small body size and short life cycle. During the study period, immature fishes < 20 mm SL were rarely collected (Table 1), despite a monthly sampling effort at the shore area. Therefore, small YOY (young-of-the-year) fishes are likely absent from the shore area, and may inhabit more offshore or deeper regions just

after hatching. Once reaching approximately 20 mm SL, YOY fishes would recruit to the shore area, reaching maturation soon thereafter.

#### Life history traits in non-native environments

In conclusion, life history parameters associated with reproductive biology, growth, and age composition for *P. ranga* in a non-native environment were examined. Specifically, it was found that *P. ranga* introduced into the Haeburu Reservoir exhibited rapid growth during the first year, early maturation, a short life cycle, and a long spawning season, suggesting an 'opportunistic' life history strategy (sensu Winemiller and Rose, 1992). Such traits appear to be associated with establishment success in the Haeburu Reservoir and may facilitate future dispersion success in freshwater habitats on Okinawa-jima Island. Additionally, several life history traits of *P. ranga* in the Haeburu Reservoir (longevity, duration of spawning season, and timing of peak spawning) were observed to differ from those in the native range. Non-native freshwater fishes may be able to shift their life history traits throughout several invasion stages (Bohn et al., 2004) and thereby exhibit different life history strategies than native populations (Fox et al., 2007). Therefore, additional studies examining reproduction and growth aspects in native localities, as well as ongoing monitoring of the population in the Haeburu Reservoir, will enable a more comprehensive understanding of the ecological responses of this species in a non-native environment.

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