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Reproduction and Juvenile Growth of the Invasive Apple Snails *Pomacea canaliculata* and *P. scalaris* (Gastropoda: Ampullariidae) in Taiwan

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Jing-Ying Wu, Yu-Ting Wu, Min-Ching Li, Yuh-Wen Chiu, Ming-Yie Liu, and Li-Lian Liu (2011) Reproduction and juvenile growth of the invasive apple snails *Pomacea canaliculata* and *P. scalaris* (Gastropoda: Ampullariidae) in Taiwan. *Zoological Studies* **50**(1): 61-68. The South American apple snails *Pomacea canaliculata* (Lamarck, 1822) and *P. scalaris* d'Orbigny, 1835 were intentionally introduced to Taiwan in 1979. *Pomacea canaliculata* is now widely distributed in Taiwan and adjacent islands but *P. scalaris* occurs only in southern Taiwan, where it coexists with *P. canaliculata*. We conducted a comparative study on the reproduction and juvenile growth characteristics of these 2 invasive species. *Pomacea canaliculata* reached a greater maximum size than *P. scalaris*. Sexual dimorphism in shell size, with females being larger than males, was found in both species. Without seasonal peaks, the percent gonad coverage varied monthly in males from 46% to 76% and 60% to 80% in *P. canaliculata* and *P. scalaris*, and in females from 19% to 52% and 22% to 32%, respectively. In the laboratory, the hatching period of *P. scalaris* (10.4 ± 1.3 d) was shorter than that of *P. canaliculata* (12.2 ± 2.3 d), and its size at hatching was also smaller. The 6-mo growth equations for *P. canaliculata* and *P. scalaris* were $y = 0.426 + 0.353x - 0.001x^2$ ($R^2 = 0.93$, $p < 0.001$) and $y = 1.428 + 0.203x - 0.001x^2$ ($R^2 = 0.86$, $p < 0.0001$) when fed dry fish feed, and the final shell lengths were 15.8-43.5 and 10.2-31.0 mm, respectively. Significant differences in growth between the 2 species were observed 2 wk after hatching and onwards. Additionally, the 1st laboratory oviposition by *P. canaliculata* and *P. scalaris* occurred on days 175 and 163, respectively. Our results indicate that a smaller hatching size and inferior growth performance of *P. scalaris* may also have played a role in shaping its distribution in Taiwan. http://zoolstud.sinica.edu.tw/Journals/50.1/61.pdf

Key words: Apple snail, Gonad coverage, Hatching rate, Juvenile growth.

The apple snails *Pomacea canaliculata* (Lamarck, 1822) and *P. scalaris* d'Orbigny, 1835 both occur naturally in South America. *Pomacea canaliculata* was illegally introduced into Taiwan as an aquaculture species in 1979 (Chang 1985, Cowie et al. 2006, Hayes et al. 2008). Because of low market demand, its use was abandoned by aquaculture farmers in the early 1980s. There was no documentation of the import of *P. scalaris*, and it was first found to coexist with *P. canaliculata* on an eel farm in southern Taiwan in 1989 (Chang 1994). It was suggested that *P. scalaris* was accidentally brought to Taiwan with *P. canaliculata* (Lee and Wu 1996).

Through irrigation drainage channels, apple snails spread into various natural waterways and are now a part of freshwater ecosystems of Taiwan. *Pomacea canaliculata* subsequently invaded

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eastern Asian waters, and has become a serious pest of aquatic crops in the region. In contrast, the distribution of *P. scalaris* is limited to southern Taiwan, which is the only recorded invasive site outside its native range (Lee and Wu 1996, Cowie et al. 2006, Hayes et al. 2008).

As an invasive species, *P. canaliculata* causes serious damage to aquatic crops in many Southeast Asian countries and Hawaii (Cowie et al. 2006). Therefore, most studies have focused on this better-known species. By comparing DNA sequences of apple snails, Hayes et al. (2008) suggested that Taiwan's *P. canaliculata* probably originated from Argentina through multiple independent introductions, while *P. scalaris* appeared to have been introduced from a single source in Argentina. Although a limited number of introductions may be the reason for the more-localized distribution of *P. scalaris* only in southern Taiwan, life history traits may also have influenced this contrasting pattern. In order to gain a better understanding of *P. canaliculata* and *P. scalaris*, the reproduction and juvenile growth characteristics of the 2 species were compared in the present study.

MATERIALS AND METHODS

Reproductive cycles of *P. canaliculata* and *P. scalaris*

Pomacea canaliculata and *P. scalaris* with shell lengths > 22 mm were collected monthly between Dec. 2004 and Mar. 2006 from Wu-Ko-sai irrigation drainage system; the water temperature was also recorded (Fig. 1). During the typhoon season, the water depth in the irrigation drainage channels can reach 80 cm within a day then drop back to about 20 cm within a week. The collected snails were brought to the laboratory and frozen at -20°C for later use. After being defrozen, the snails were put on tissue paper to remove excessive fluids on the shell surface. The shell length (measured from the tip of the apex to the lower edge of the lip) and total weight were determined. Then the shell was broken open and the snail was sexed based on the appearance of the gonad and accessory organs.

The gonad of *P. canaliculata* and *P. scalaris* is in close contact with the digestive gland, which constitutes the visceral coil. Despite being easily distinguishable from the digestive gland by the different coloration, neither the testis nor ovary can be precisely dissected from the rest of the soma without damaging the gonad. This makes the use of gonadosomatic indices based on gonad weight impractical. Thus, a method modified from Chung and Kim (1997) was used to determine the percent gonad coverage of the digestive gland. In brief, the combined digestive gland and gonad were divided into 3 areas longitudinally. The width of the gonad as a percent of the width of the digestive gland in each area was measured, and the gonad coverage (%) of the snail was obtained by averaging the 3 values.

Hatching and juvenile growth of *P. canaliculata* and *P. scalaris*

About 60 mature snails of each species with shell lengths of 35-55 mm were collected from the Cio-ru irrigation drainage system in Apr. 2008 (Fig. 1). The 2 species were reared in separate aquaria (58 × 42 × 34 cm) containing 25 L of aerated tap water and equipped with fluorescent lights. The photoperiod was 11-h L: 13-h D, and the water temperature was maintained at 26 ± 0.5°C (mean ± S.D.). During the experimental period, 3/4 of the water was changed daily, and snails were fed dry fish feed ad libitum which was provided by the Tungkang Biotechnology Research Center,

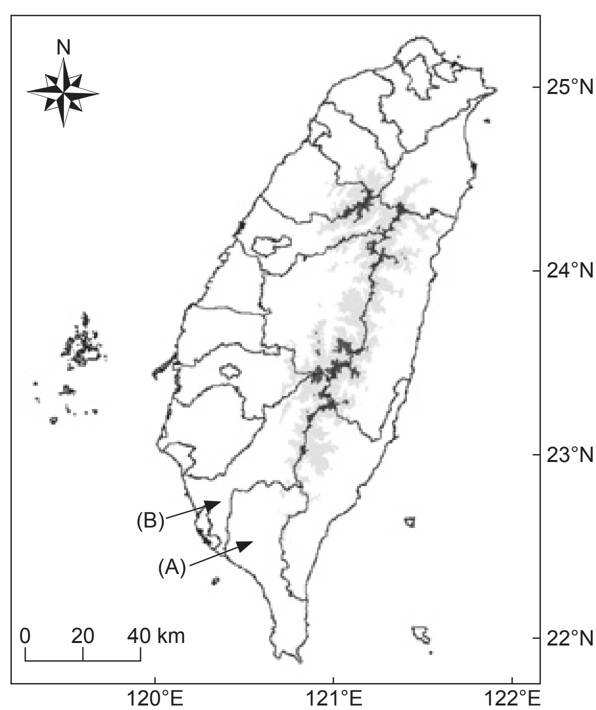

Fig. 1. Sampling sites for *Pomacea canaliculata* and *P. scalaris*. (A) Wu-Ko-sai; (B) Cio-ru.

Fisheries Research Institute (Tungkang, Taiwan). The fish feed included 46% protein, 5% lipids, 28% carbohydrates, 14% ash, and 7% moisture.

Egg masses laid were collected daily, and their overall size, number of eggs per mass (clutch size), and egg diameter were determined. For hatching experiments, egg masses were individually placed in vials (3 cm in diameter and 7 cm in height) at room temperature (27.5 ± 0.5°C). These egg masses were checked daily until hatching. The hatching period, hatching rate (percent of eggs that hatched), and size of hatchlings were subsequently determined.

In total, 8 and 14 egg masses of *P. canaliculata* and *P. scalaris* were gathered for the juvenile growth experiments. Hatchlings from different egg masses were separately reared in different aquaria (27 × 17 × 17 cm) at a density of 20 hatchlings per aquarium. The aquarium contained 2.5 L of aerated tap water and was subject to the same management regime as the system for adult snails. Snail shell length was measured with a Vernier caliper to the nearest 0.1 mm at weekly intervals. Juvenile growth and survival were calculated, and the data were analyzed by *t*-tests and polynomial regressions.

RESULTS

During the sampling periods, water temperatures ranged 22.2-27.1°C (Table 1). A positive correlation between the shell length and total weight was observed in both species (Fig. 2). *Pomacea canaliculata* reached a greater maximum length than did *P. scalaris*. Sexual dimorphism, with females being larger than males, was also found, as shown by the significant difference between the slopes of the regressions for the 2 species ($p < 0.05$).

Table 1. Measurements of morphological characteristics of *Pomacea canaliculata* and *P. scalaris*. M, male; F, female; -, not examined

Species		*Pomacea canaliculata*				*Pomacea scalaris*			
Date	Sex	Sample size (*n*)	Shell length (mm)	Total weight (g)	Gonad coverage (%)	Sample size (*n*)	Shell length (mm)	Total weight (g)	Gonad coverage (%)
			Mean ± SD	Mean ± SD			Mean ± SD	Mean ± SD	
Dec. 2004 22.2°C	M	19	31.0 ± 4.6	6.7 ± 2.5	-	10	24.0 ± 1.7	3.2 ± 0.7	-
	F	11	29.1 ± 3.7	6.0 ± 2.8	-	20	24.7 ± 3.5	3.4 ± 1.5	-
Jan. 2005 24.7°C	M	12	36.8 ± 3.9	11.4 ± 4.1	68.0	11	29.6 ± 1.6	5.8 ± 1.2	60.1
	F	18	37.2 ± 4.2	12.4 ± 4.2	31.1	19	28.9 ± 2.3	6.1 ± 1.3	32.5
Feb. 2005 22.7°C	M	12	35.4 ± 4.2	10.5 ± 2.9	70.0	14	27.1 ± 2.3	7.9 ± 10.4	71.2
	F	18	35.6 ± 3.5	11.5 ± 3.3	27.8	16	27.3 ± 3.3	5.8 ± 1.8	27.2
Mar. 2005 22.9°C	M	10	35.2 ± 2.6	9.6 ± 1.8	76.2	8	29.7 ± 1.9	6.6 ± 1.0	77.5
	F	20	38.5 ± 4.0	13.6 ± 3.8	31.5	22	30.1 ± 2.9	7.2 ± 2.6	29.8
Apr. 2005 24.7°C	M	10	35.0 ± 3.7	9.1 ± 3.1	73.0	11	32.3 ± 2.4	7.1 ± 1.9	76.9
	F	20	38.6 ± 5.3	13.2 ± 5.0	31.6	19	32.2 ± 3.2	7.0 ± 2.4	31.2
June 2005 27.1°C	M	14	38.1 ± 6.0	11.2 ± 5.2	70.2	15	35.3 ± 2.3	9.6 ± 1.7	78.3
	F	16	34.1 ± 4.2	8.8 ± 3.8	25.0	15	35.7 ± 2.5	10.0 ± 2.4	30.0
Sept. 2005 26.2°C	M	11	31.9 ± 3.6	8.1 ± 2.3	64.3	14	33.1 ± 3.1	7.3 ± 1.9	79.5
	F	19	30.8 ± 4.5	8.0 ± 3.6	23.4	16	31.2 ± 3.1	6.5 ± 2.5	24.4
Oct. 2005 25.2°C	M	14	37.1 ± 5.3	11.6 ± 4.2	73.0	8	30.3 ± 2.8	6.5 ± 2.2	72.4
	F	16	36.0 ± 3.8	11.5 ± 4.1	19.1	20	30.2 ± 3.8	7.2 ± 2.8	26.0
Nov. 2005 24.5°C	M	17	36.4 ± 5.7	10.4 ± 4.3	45.8	14	32.6 ± 3.3	8.7 ± 2.9	65.9
	F	13	40.6 ± 6.7	14.6 ± 6.3	52.4	15	39.7 ± 2.5	14.8 ± 3.2	22.4
Dec. 2005 24.2°C	M	12	32.9 ± 5.4	8.0 ± 3.2	59.0	11	32.7 ± 3.6	8.7 ± 3.1	76.4
	F	18	37.2 ± 5.0	11.6 ± 4.4	20.8	19	30.5 ± 2.5	6.7 ± 2.8	23.5
Feb. 2006 23.0°C	M	9	39.9 ± 3.7	14.9 ± 3.5	-	5	35.6 ± 2.8	11.6 ± 2.7	-
	F	21	38.3 ± 5.6	14.5 ± 6.3	-	11	35.7 ± 5.5	12.6 ± 5.6	-
Mar. 2006 22.8°C	M	9	41.4 ± 3.1	16.3 ± 4.0	-	10	37.9 ± 1.9	13.2 ± 2.0	-
	F	21	40.6 ± 3.7	16.5 ± 4.2	-	18	38.3 ± 2.5	14.2 ± 3.3	-

Monthly gonad coverage of snails is shown in figure 3. Gametogenesis occurred year round without a peak season in both species. Consistently lower coverage values were observed in females. The mean gonad coverage was 46%-76% and 60%-80% in males (Table 1, Fig. 3), and 19%-52% and 22%-32% in females of *P. canaliculata* and *P. scalaris*, respectively. In addition, pink and pale brown egg masses laid on cement walls or aquatic plants by *P. canaliculata* and *P. scalaris* (Fig. 4) were observed in all sampling months.

The egg masses of *P. canaliculata* were 12-30 mm long and 9-15 mm wide, and the clutch sizes ranged 14-327 eggs (n = 97). Its eggs were round with a diameter of 2.57 ± 0.25 mm (n = 107) (Fig. 5). In *P. scalaris*, egg masses were 19-49 mm long and 12-19 mm wide, and the clutch sizes ranged 9-302 eggs (n = 70). The eggs were polygonal in shape, with a diameter of 2.69 ± 0.25 mm (n = 85). The eggs of *P. scalaris* were significantly larger than those of *P. canaliculata* ($p < 0.01$).

Significant differences in the hatching period and hatching size between the 2 species were also found (Fig. 5). Juvenile *P. canaliculata* hatched after 12.2 ± 2.3 d, which was significantly longer than for *P. scalaris* (10.4 ± 1.3 d) ($p < 0.001$). Average hatching sizes were 2.03 ± 0.22 and 1.74 ± 0.15 mm, respectively, which significantly differed ($p < 0.001$). In contrast, hatching rates did not differ between *P. canaliculata* (71.4% ± 15.4%) and *P. scalaris* (77.1% ± 14.6%) ($p > 0.05$).

In the juvenile growth experiments, the 6-mo survival rates of juvenile *P. canaliculata* and *P. scalaris* were 80% and 55%, respectively, but the difference was not significant (Fig. 6A). Variations among replicates were 45%-95%

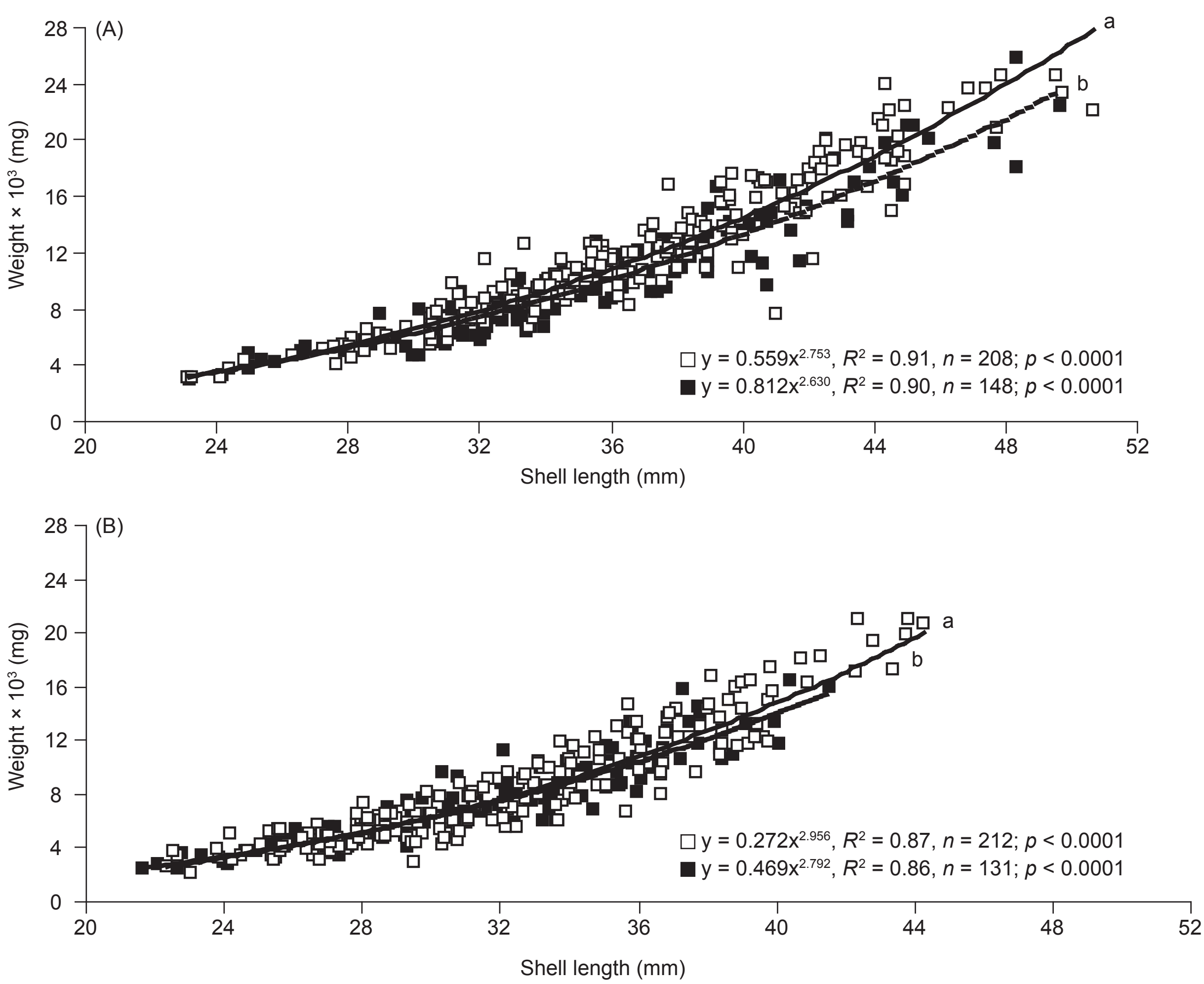

Fig. 2. Relationship between the shell length and total body weight of *Pomacea canaliculata* (A) and *P. scalaris* (B) □, Female; ■, male. Different letters indicate that the regression lines significantly differ ($p < 0.05$).

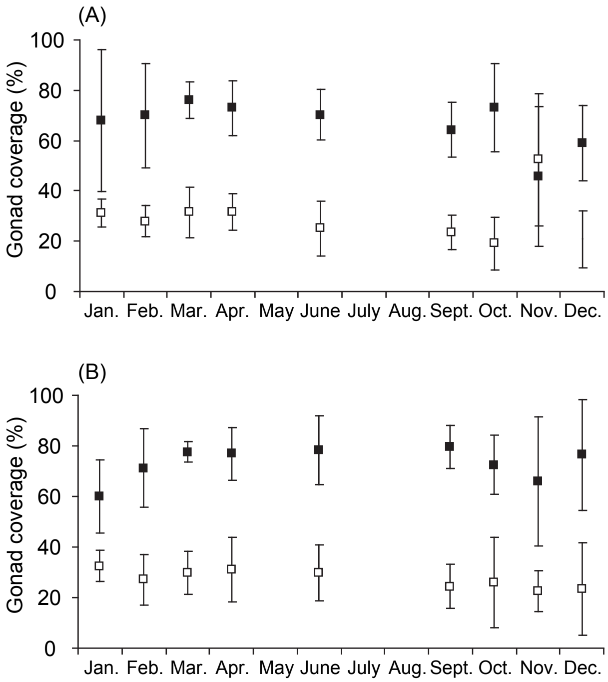

Fig. 3. Monthly variations in the percent gonad coverage of *Pomacea canaliculata* (A) and *P. scalaris* (B).

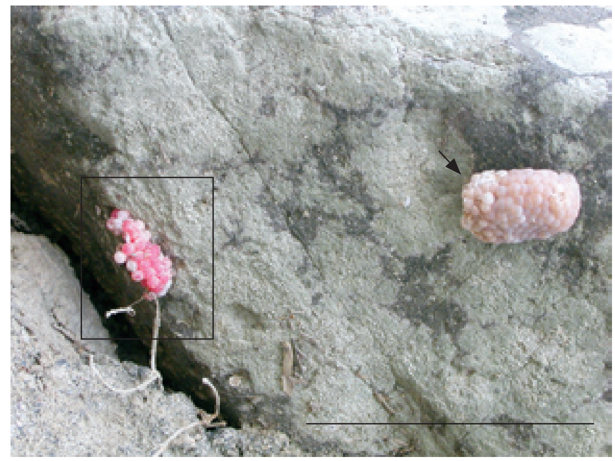

Fig. 4. Egg masses of *Pomacea canaliculata* and *P. scalaris* laid on a cement wall in Wu-Ko-sai, Taiwan. □, *Pomacea canaliculata*; —►, *Pomacea scalaris*. Scale bar = 10 cm.

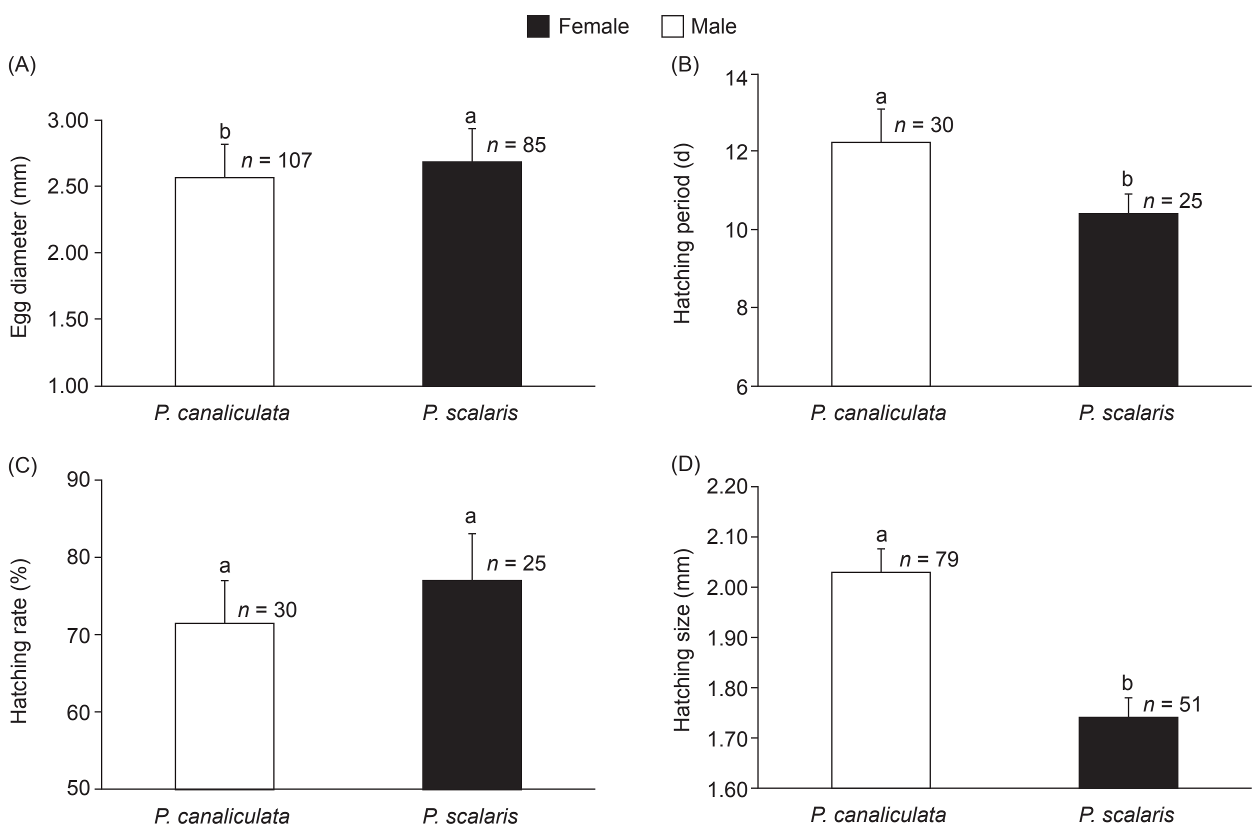

Fig. 5. Comparison of hatching characteristics between *Pomacea canaliculata* and *P. scalaris*. (A) Egg diameter; (B) hatching period; (C) hatching rate; (D) hatching size. *n*, sample size. Different letters indicate that the 2 species significantly differ ($p < 0.05$).

and 0%-100%, respectively. The growth curves of both species showed a similar pattern (Fig. 6B). A 2nd-order polynomial equation was fitted to these data which accounted for > 93% of the variance in *P. canaliculata* and 86% in *P. scalaris*. A difference between the 2 species in shell length was detected from day 14 onwards (compared by *t*-tests, $p < 0.05$). The final shell lengths ranged 15.8-43.5 mm for *P. canaliculata* and 10.2-31.0 mm for *P. scalaris* (on days 178 and 175), and the growth rates were 0.19 ± 0.02 and 0.10 ± 0.02 mm/d, respectively. In addition, the ages at 1st oviposition of *P. canaliculata* and *P. scalaris* were 175 and 163 d, respectively.

DISCUSSION

In contrast to the year-round reproduction observed in this study, reproduction of *P. canaliculata* in its native range in South America occurs during spring and summer (Oct. to Apr. in southern South America) (Andrews 1964). Similarly, *P. scalaris* in its native range reproduces from Sept. to Mar. (in Buenos Aires, Argentina) (Martín 1991 1993). This suggests that the annual reproductive output of these apple snails in Taiwan is much higher than that of their Argentinean conspecifics. Additionally, *P. scalaris* is less common than *P. canaliculata* in their native

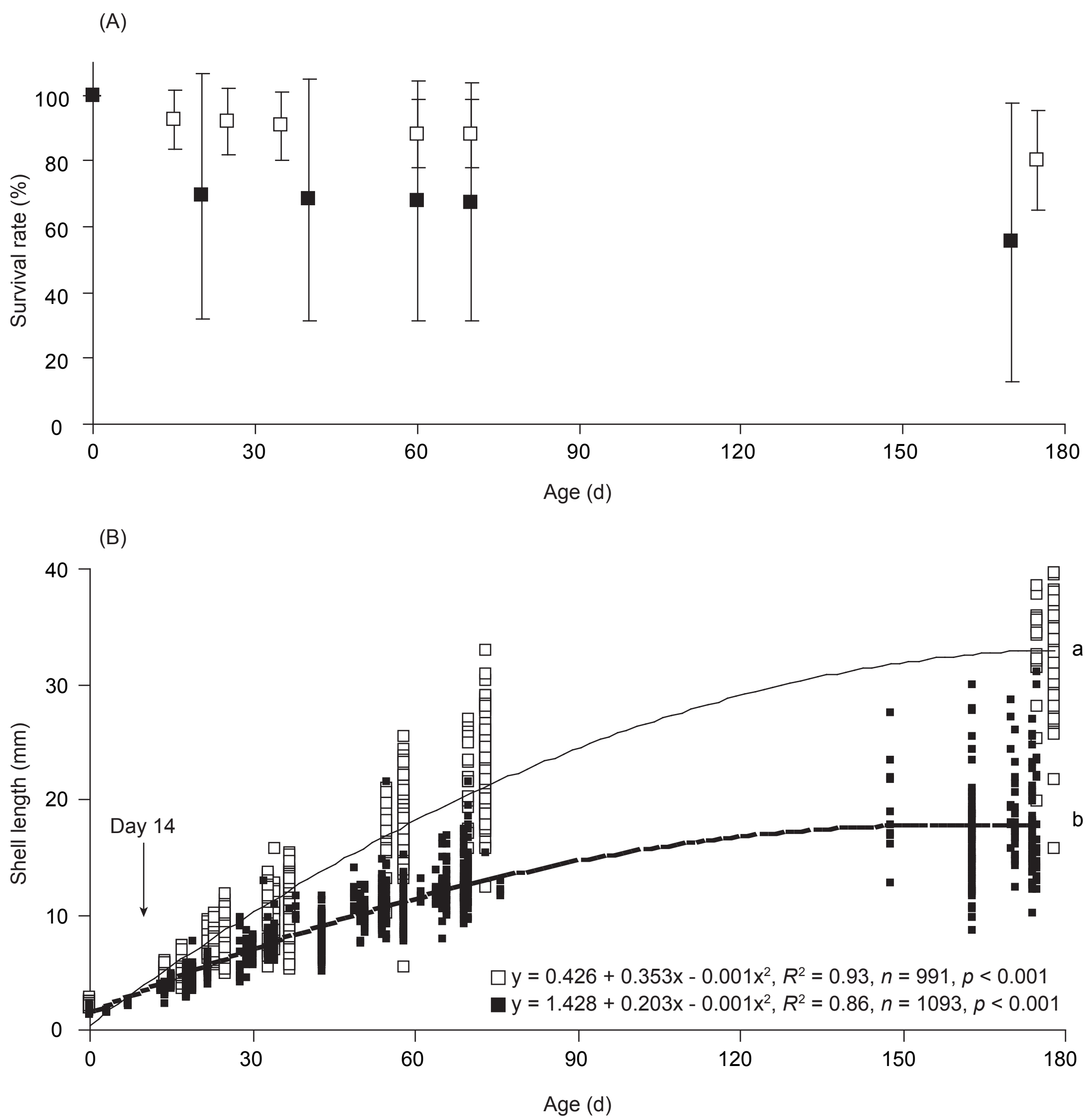

Fig. 6. Survival and growth of *Pomacea canaliculata* and *P. scalaris*. (A) Survival rate; (B) growth. □, *P. canaliculata*; ■, *P. scalaris*. Different letters indicate that the regression lines significantly differ ($p < 0.05$).

habitats (pers. comm. from Dr. S.M. Martin), similar to our observations in Taiwan.

Although *P. canaliculata* in Hawaii exhibits no size dimorphism in the field (Cowie 2002), most studies demonstrated sexual dimorphism in shell length, shape, and weight. In general, females are larger than males under unlimited food conditions or in the field (Estebenet and Cazzaniga 1998, Estoy et al. 2002, Martín and Estebenet 2002). A native population of *P. scalaris* in Argentina also showed the same pattern (Martín 1993). As in those other studies, our results consistently demonstrated size dimorphism with females being larger than males in both species.

Reproduction and growth of the Ampullariidae were extensively studied (reviewed by Cowie 2002). The life history traits of apple snails are highly dependent on temperature and food. For instance, in tropical regions, the reproduction of *P. canaliculata* is continuous, and the reproductive duration decreases with latitude to a minimum of 6 mo at the southern limit of its natural distribution (Martín et al. 2001, Cowie 2002). In an outdoor experiment conducted in southern Taiwan, fewer egg masses were laid in winter (Feb.) (Chang 1985), which is similar to our finding that egg masses of both species were found year round, but fewer occurred in Jan. and Feb.

Estimation of the gonadosomatic index (GSI) based on the relative weights of the gonad and digestive gland is extensively used to study the reproductive activity of snails. The conventional index, based on the relative proportion of the gonad cross-sectional area to total cross-sectional area of the digestive gland was also successfully used to assess reproductive states in some gastropod species, e.g., *Haliotis iris*, *Hal. australis* (Poore 1973), and *Hexaplex trunculus* (Vasconcelos et al. 2008). Additionally, GSI values based on measurements of gonad thickness in relation to the diameter of the gonad and digestive gland were used for male *Rapana venosa* (Chung and Kim 1997). Although these methods differ, all of them can identify a snail's reproductive activity.

Significant differences in monthly GSI values between sexes of *Hex. trunculus* were observed, i.e., being higher in females than males in Apr., whereas males exhibited greater GSI values between Aug. and Dec. (Vasconcelos et al. 2008). Consistently higher monthly GSI values in female *R. venosa* than in males were also reported (Mann et al. 2006). In *Hal. iris*, the GSI pattern differed between years at Kaikoura, New Zealand (Poore 1973). Values were higher in males than females in 1968. In 1969, both sexes had similar GSI values. However, the cause of the inconsistent responses between years is not known. Our studies showed a general pattern in *P. canaliculata* and *P. scalaris* of higher gonad coverage in males than females. Females allocating a lot of energy to the development of oocytes and also to the albumen gland may play a role.

Hatching of *P. canaliculata* takes place 7-37 d after oviposition in Asia and Hawaii (Cowie 2002). The clutch size, hatching rate, and time from hatching to maturity vary greatly in the ranges of 25-1000, 7%-100%, and 55 d to 2 yr, respectively. A study by Chang (1985) in Taiwan indicated that the hatching rate, hatching period, and time from hatching to maturation were 60%, and 12 and 55 d, respectively, at temperatures of 25-32°C. By comparison, the time from hatching to maturation in our study was much longer, i.e., 175 d.

When *P. canaliculata* hatchlings were fed 10 macrophytes for 8 wk, their survivorship, growth, and reproduction differed on different plants (Qiu and Kwong 2009). Growth rates were high, ranging 0.27 mm/d on *Apium* to 0.36 mm/d on *Ipomoea*. In contrast, snails reared on *Eichhornia*, *Myriophyllum*, and *Polygonum* were only slightly larger than the unfed group. Another study reported highly significant differences in the sizes reached by hatchling *P. canaliculata* (initial size 2.39-2.77 mm) when supplied with fish feed, wheat germ/milk with lettuce, dog food, and fresh lettuce leaves (Estebenet and Cazzaniga 1992). The greatest growth occurred in snails fed fresh lettuce. In contrast, there was no significant difference in snail growth when the experiments were carried out with older juveniles (initial size > 17 mm). Thus, the influence of diet varies according to the growth stage of the snails tested. The growth rate of *P. canaliculata* was 0.19 mm/d in this study, which was within the range (0-0.36 mm/d) observed by Qiu and Kwong (2009). Unfortunately, the amount of food ingested by the snails was not quantified in our study. Nonetheless, it seems that dry fish feed is inappropriate, resulting in slow growth of these snails.

As Cowie (2002) stated, understanding the biology of invasive species is important if effective management strategies are to be developed. In order to gain better knowledge of freshwater ecosystems dominated by apple snails, aspects of their physiology, distribution, and behavior still require extensive study.

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