CSIRO PUBLISHING
www.publish.csiro.au/journals/mr *Molluscan Research*, 2004, **24**, 139–148

Biology of the golden apple snail, *Pomacea canaliculata* (Lamarck, 1822), with emphasis on responses to certain environmental conditions in Sabah, Malaysia

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Abstract

This study investigated the ecology and biology of the golden apple snail in rice fields. Egg masses were produced at inconsistent intervals with the number of eggs per cluster ranging from 92 to 592 (mean 272). Regardless of clutch size, hatching success ranged from 87 to 100% (mean 95.8%). In the field, mating took place 82 days after hatching. Mean shell length at this age was 38.2 mm with females bigger than males in general. The male to female ratio was ~1: 5. Peat soils reduced egg mass production significantly and egg masses submerged in water for more than 1 week reduced hatching success significantly.

Introduction

The golden apple snail, *Pomacea canaliculata* (Lamarck, 1822), is native to South America. It was introduced from Argentina to Taiwan in the 1980s for commercial production (Mochida 1991) and was distributed widely in Asia as a dietary protein supplement and income earner for the rural poor (Matienzo 1984; Anderson 1993). Unfortunately the introduction of *P. canaliculata* was done in haste without prior studies on its ecological impact or market information (Acosta and Pullin 1989). When market demand for the snail was poor, many snail-farming projects were abandoned and in many instances the snails escaped and subsequently became a pest of crops, mainly rice (Naylor 1996). The snail is now a major rice pest in Asia (Hirai 1988; Rejesus *et al*. 1990; Halwart 1994*a*). The estimated infested area in Taiwan was 171 425 ha in 1986, 16 196 ha in Japan in 1989 and 400 000 ha in the Philippines in 1989 (Mochida 1991). When the golden apple snail began to become a pest, information on its ecology, biology and control measures was lacking. Pesticides were selected rather arbitrarily, applied inappropriately (causing environmental pollution) and were a hazard to public health with farmers suffering a range of health problems (Anderson 1993). Several control techniques have been developed, including biological (Halwart 1994*b*; Teo 2001), cultural (Teo 2003) and chemical (Litsinger and Estano 1993; Palis *et al*. 1994) controls. Information on the biology and ecology of the snail are also becoming available, most recently in a review by Cowie (2002). However, many of these reports are not species specific, with information on *P. canaliculata* sparse and dispersed. A comprehensive understanding of the biology of this species is essential for formulating an effective management strategy. Consequently, studies on the ecology of *P. canaliculata* were initiated in Sabah, Malaysia with a view to developing control measures.

In Sabah the snail is also found in rice fields with peat soils but observations suggest that it does not establish well under these conditions. In the wetlands, many of its egg masses may become submerged in water for several days during the monsoon season. The studies presented here cover growth and reproduction, the influence of water depth on snail mortality, egg submergence and viability, and effect of peat soils on egg mass production.

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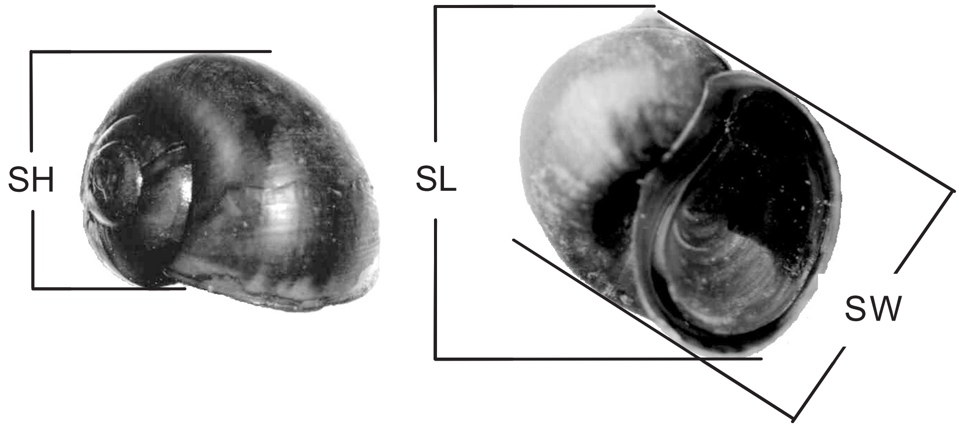

Fig. 1. Measurements of *Pomacea canaliculata* shells. SH, shell height; SL, shell length; SW, shell width.

Materials and methods

General

Unless otherwise stated, all experiments were conducted at the Agriculture Research Centre, Tuaran. The experimental plots were all separated by bunds made of mud from the field with width 150 mm and height 200 mm. The water in the plots and fibreglass bin was maintained at 50–100 mm depth and planted with water spinach (*Ipomea aquatica* Forsk) as feed for the snails.

Shell size and sex ratio

Snails were collected at random in rice fields during the paddy-planting season in a few villages in each of the districts of Tuaran, Tambunan and Keningau, these being the main snail-infested areas. The villages are a few kilometres apart but the districts are at least 150 km away from one another. The study was carried out when the crop was ~45 cm high, just before the booting stage. The snail population density was low at the time of the study because of control measures applied by the farmers, so a larger sample would have been difficult to collect. Each sample consisted of at least 20 adult snails. Figure 1 shows the shell dimensions taken using a digital Vernier caliper.

Number of eggs per cluster

Pomacea snails lay their eggs on objects protruding above the water surface. One hundred and thirty egg masses were collected at random from the rice fields in Tuaran during the rainy season, coinciding with the breeding season of the pest. The number of eggs per mass was counted manually by separating them one by one with a needle.

Growth increment – indoor and field conditions

A fibreglass bin (0.9 m × 1.2 m × 2.4 m) was used in the indoor studies. The bin was filled with 300 mm of mud collected from the rice field. An egg cluster laid on a stick was collected from the field and was staked into the mud in the bin and allowed to hatch. Growth rate measurements were initiated 3 weeks after egg hatching when the snails were easier to handle without damage. Only ten snails were kept in the bin, excess snails were discarded. The field study was conducted in the rice field in a 1 m × 2 m plot without the paddy plants during the rainy season. An egg cluster collected from the field was staked onto the plot and allowed to hatch. Only ten snails were kept in each plot to prevent overcrowding. Shell measurements were taken daily with a digital caliper and later weekly when growth began to plateau. At each measurement event, the length, width and height (see Fig. 1) of ten snails were recorded. Growth under higher population density was also measured, in a 2 m × 2 m plot under similar environmental conditions.

Pattern and frequency of oviposition

The objective of this part of the study was to investigate the pattern of egg mass production. Single female snails in each of fourteen plots of 1 m × 1 m were observed, each collected from the field and with a shell height of ~25 mm. Each of the plots was fenced with wire mesh to a height of 600 mm to keep the snails confined. The number of egg masses produced was recorded daily for a period of 5 months.

Hatching rate

Fifty egg masses were collected at random from the rice field at the Research Centre during the breeding season. Each egg mass was placed above 5 mm of water in a beaker, and then allowed to hatch. When hatching was complete, the number of hatchlings and unhatched eggs were counted and the percentage hatched was calculated.

Effect of peat substrate on egg mass production

The objective of this part of the study was to investigate the effect of peat on egg mass production. The plots were prepared by removing the rice stubble followed by ground levelling. Five plots, each measuring 1 m × 2 m were prepared and peat soil was laid across the plot at 25, 50, 75 and 100 mm depths. One plot was untreated and served as a control. Rice was not planted in the plots and the experiment was not replicated. The peat substrate was collected from a rice field in Sipitang (200 km away from the Research Centre) at depths of 0–150 mm. This area is covered by fibrous peat consisting of undecomposed or partly decomposed woody plants with a pH of 3.5 (Bower *et al*. 1975). A total of 30 adult snails (20 female and 10 male) with a shell height of 25 mm were collected from the rice field and introduced into each plot. Stakes were placed in each plot for the snails to oviposit their eggs. Recordings were made daily for a period of 2 months.

Egg mass production and mortality of snails under different depths of water

The objective of this experiment was to determine egg mass production and snail mortality under different depths of water. Five plots (1 m × 2 m) were prepared, each with a water depth of 50, 300, 600, 900 or 1200 mm. The experiment was not replicated. Fifteen adult snails (shell height 25 mm) with a male to female ratio of 1 : 5 were introduced into each of the plots. Sticks were placed vertically into the plots for the snails to oviposit their eggs. The number of egg masses produced and the number of snails that died over time were recorded for 3 months. After this period, the water in the plots was removed using a water pump and the number of snails surviving in each plot was recorded. Water temperatures at each depth were recorded at 8:00 am, 12:00 pm and 3:00 pm on Monday, Wednesday and Friday in alternate weeks.

Hatching success of Pomacea canaliculata *egg masses immersed in water for different lengths of time*

The objective was to investigate the viability of egg masses after they were submerged in water for different lengths of time. A randomised design was adopted with five replicates, consisting of five egg masses per replicate. Egg masses of approximately the same size were collected from the field, with the colour giving their approximate age. Newly laid egg masses are bright pinkish-red in colour, which fades to light pinkish and then greyish before hatching. Only pinkish egg masses of approximately the same colour were selected. The egg masses were submerged in water for 0–14 nights. After each treatment, the egg masses were removed from the water and placed above 5 mm of water in a beaker for 21 days. The numbers of hatched and unhatched eggs were recorded.

Results

Shell size and sex ratio

Table 1 shows the shell size and sex ratio of snails sampled from seven different locations. The interaction between sex and shell dimensions was not significantly different. When the mean length, width and height were pooled, females were significantly bigger than males ($F_{1,30} = 14.88$; $P < 0.001$) with overall means of 27.32 ± 1.77 mm and 24.49 ± 1.81 mm respectively. Females were more numerous in the samples than were males, with an overall male to female ratio of 1 : 4.6. The number of males sampled in the studies ranged from 1 to 12 whereas females ranged from 15 to 41.

Table 1. Shell size and sex ratio of *Pomacea canaliculata*

Location	Length (mm)		Width (mm)		Height (mm)		Sample size (n)	Male : female
	Male	Female	Male	Female	Male	Female	male/female	ratio
Marabahai, Tuaran	35.63 ± 1.58	37.53 ± 1.32	30.04 ± 1.33	31.66 ± 1.17	21.02 ± 1.11	23.62 ± 1.03	12/38	1:3.2
Batangan, Tuaran	34.53 ± 1.58	37.37 ± 1.30	28.10 ± 1.41	34.03 ± 1.33	20.44 ± 1.31	22.95 ± 1.09	9/41	1:4.6
Tanaki, Tambunan	28.05 ± 2.71	32.41 ± 1.59	17.55 ± 2.04	19.42 ± 1.16	16.08 ± 2.17	19.71 ± 1.25	3/17	1:5.7
Kiawayan, Tambunan	35.14 ± 3.03	36.21 ± 1.51	20.12 ± 2.25	22.78 ± 1.19	19.25 ± 2.40	21.97 ± 1.20	3/17	1:5.7
Pupuluton, Tambunan	36.31 ± 3.34	35.89 ± 1.53	22.70 ± 2.29	22.91 ± 1.19	21.62 ± 2.31	23.55 ± 1.15	3/17	1:5.7
Lingkodou, Keningau	32.85 ± 1.95	35.15 ± 1.24	19.45 ± 1.51	21.13 ± 0.92	19.09 ± 1.56	21.39 ± 0.87	5/15	1:30
Gasabon, Keningau	25.39 ± 0.00	33.06 ± 1.90	15.74 ± 0.00	20.75 ± 1.50	15.12 ± 0.00	20.18 ± 1.57	1/19	1:19
Mean	32.56 ± 1.19	35.37 ± 0.55	21.96 ± 1.35	24.67 ± 0.94	18.95 ± 0.91	21.91 ± 0.49	5/23	1:4.6

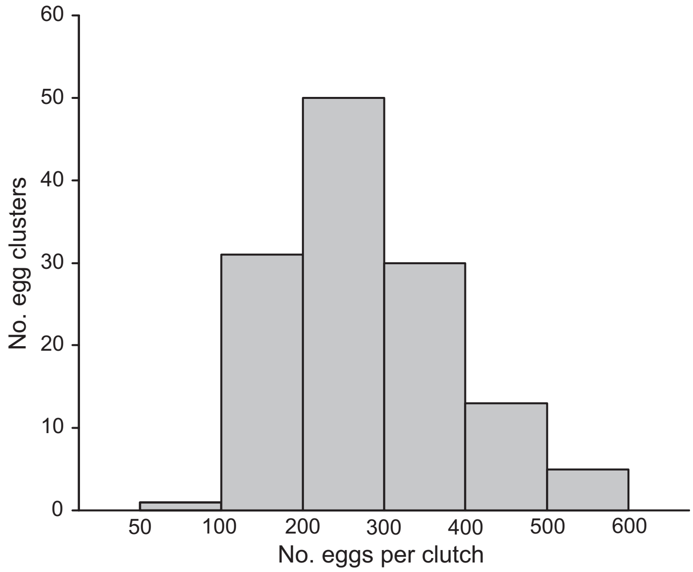

Fig. 2. Clutch size of *Pomacea canaliculata*.

Number of eggs per egg cluster

Figure 2 shows the distribution of the number of eggs per egg mass, which ranged from 92 to 592, with a mean of 272 ± 4.3. Most egg masses had more than 200 eggs, and egg masses with fewer than 100 eggs were rare. Egg masses with 500–600 eggs were not uncommon.

Growth increment – indoor and field conditions

The snails indoors grew faster than those in the field. For the indoor snails at Day 20, the length, width and height of snails kept in the bin indoors were 23.64 ± 0.60 mm, 15.56 ± 0.62 mm and 14.28 ± 0.45 mm respectively. At the corresponding age, those in the field were 6.06 ± 0.48 mm, 4.66 ± 0.50 mm and 3.95 ± 0.40 mm respectively. After Day 60, snails exhibited a continuous pattern of growth with no significant difference in growth rate under both conditions (Fig. 3). Mating was observed at Day 82 under both conditions. At this age, the length, width and height of the snails in the field were 38.2 ± 1.12 mm, 32.60 ± 1.01 mm and 26.5 ± 0.94 mm, and those of the indoor snails were 36.25 ± 0.49 mm, 30.0 ± 0.81 mm and 22.53 ± 0.41mm respectively. In contrast, in the field study, with a population density of at least 20 snails per 30 cm^2, growth was slower and no mating was observed at Day 82. At Day 82, the length, width and height of the snails were only 22.88 ± 0.91 mm, 19.11 ± 0.93 mm and 16.09 ± 0.76 mm respectively.

Pattern and frequency of oviposition

The observational study yielded no consistent pattern of oviposition among the females. Some females laid egg masses once a week for five consecutive weeks, after which they would either stop or continue to lay one or two egg masses per week. Some produced two to four egg masses per week and stopped for two to four weeks but began to lay eggs again after this period. The majority of the snails laid once a week; it was not uncommon for two egg masses to be produced per week. The number of eggs laid per clutch was typically 300–400.

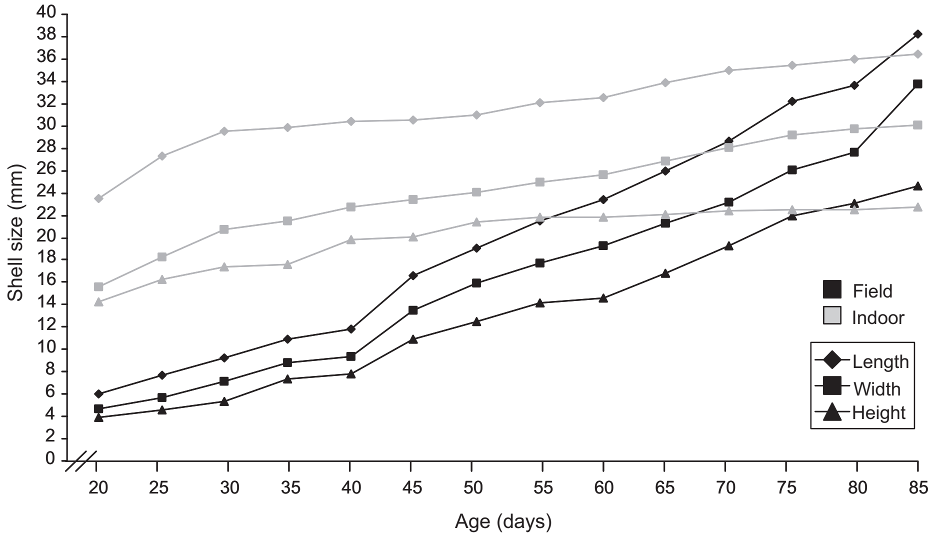

Fig. 3. Growth regression of *Pomacea canaliculata* under indoor and field conditions.

Hatching success

The eggs collected from the field took approximately ~8–12 days to hatch under laboratory conditions, with hatchlings ~2 mm in diameter. Hatching success was high, ranging from 87 to 100% (mean 95.8 ± 0.95%). Hatching rate was not dependent on clutch size; clutches of 127, 140, 148, 477, 512 and 540 eggs produced 89.4, 98.6, 99.3, 97.2, 99.4 and 94.9% hatchlings respectively.

Effect of peat soil on egg mass production

Table 2 shows the number of egg masses laid under different thicknesses of peat. There was a strong relationship between the number of egg masses laid and the thickness of peat placed in the plots. The greater the amount of peat the lesser the number of egg masses produced (fitted regression line $y = 33.35 - 4.85x$ with $r = 0.84$, F-value 15.60, significant at the 5% level). Analysis of variance showed the number of egg masses produced in all the plots treated with peat soil was significantly less than the control ($F_{4,12} = 7.04$; $P = 0.004$). The pH of the water in the plots taken at the end of the trial ranged from 6.1 to 6.7 with a mean of 6.4. These were close to the pH in the normal plots with a range of 5.9–6.4 and a mean of 6.2.

Egg mass production and mortality of snails under different depths of water

The numbers of egg masses produced at water depths of 50, 300, 600, 900 and 1200 mm were 1, 3, 11, 20 and 3, and the percentage snail mortality at the same water depths were 53.3, 26.7, 20.0, 40.0 and 66.7% respectively. While there was a tendency for higher egg mass production at 600 and 900 mm depths, the fitted quadratic regression for the number of egg masses (y) produced and water depth (x) ($y = 0.0035x^2 + 0.051x - 4.43$ with $R^2 = 0.62$) was not significant at the 5% level. Water temperatures might have caused a harmful effect on the snails. At 8:00 am, the difference in temperature was not significant among the water depths, ranging from 27 to 29°C. But at 12:00 pm and 3:00 pm, the temperature at 50 mm depth increased to a mean of 33°C (range 27.5–38°C). At a water

Table 2. Egg mass production of *Pomacea canaliculata* under different depths of peat

Depth of peat soil (cm)	Total no. egg masses laid per week 1	2	3	4	Mean[A]
0	35	39	43	28	36.3 ± 10.2[a]
2.5	14	21	26	37	24.5 ± 15.4[b,c]
5.0	22	26	28	26	25.5 ± 4.0[b]
7.5	19	18	15	10	15.5 ± 6.4[c]
10.0	7	22	17	20	16.5 ± 10.6[b,c]
Mean[NS]	19.4 ± 12.9	25.2 ± 10.2	25.8 ± 13.8	24.2 ± 12.4	23.7 ± 4.5

[A]l.s.d.$_{0.05}$ = 9.72 at 4 and 12 d.f.
[a–c]Any two means having a common letter are not significantly different to each other at the 5% level by l.s.d.
[NS]No significant difference in the total number of egg masses each week.

depth of 1200 mm, temperature fluctuation was minimal ranging from 27 to 30°C with a daily mean of 28.5°C. Temperatures above 30°C appeared to be detrimental to snails. There were more dead snails at 50 mm depth than in deeper water ($y = 0.012x^2 - 1.29x + 57.9$, $R^2 = 0.97$; significant at 5% level, $F_{2,2} = 60.98$), indicating that snail mortality was related to water depth, presumably due to heating.

Hatching success of golden apple snail egg masses after submergence in water for different periods

Table 3 shows the percentage hatching of egg masses after being submerged in water for different lengths of time. The fitted regression line was $y = 92.2 - 5.28x$ (significant at $P < 0.01$, $F_{1,13} = 80.13$, $r = 0.93$). The viability of the egg masses decreases as the duration of submersion increases. There were significant differences in percentage hatching among the treatments ($F_{14,56} = 17.08$; $P < 0.01$). There were no significant differences at the 5% level in percentage hatching with submergence up to 7 days. From Day 8 to Day 14, percentage hatching was significantly lower than in the first 7 days ($F_{14,56} = 17.08$; $P < 0.01$). At Day 14, percentage hatching was lowest, which was significantly different ($F_{14,56} = 17.08$; $P < 0.01$) from Days 0 to 13.

Discussion

Pomacea canaliculata produces numerous egg masses in areas it infests. The range of the number of eggs per egg mass was considerable, reflecting differing sizes of females (Estoy *et al*. 2002). Variability in snail size is partly related to environmental conditions, as high population density and low food availability can lead to smaller shell size and smaller egg masses (Tanaka *et al*. 1999). Diet can also affect clutch size (Lacanilao 1990).

Our samplings for estimates of ratio were done during field visits at various times of the year. The male to female ratio seemed to be consistent at approximately 1 : 5. This is possibly because of insignificant variation of climate in this region, as Banpavichit *et al*. (1994) reported that the sex ratio differed under distinctly different weather patterns. The abundance of egg masses produced in infested areas seemed to indicate that males were able to serve the larger female population successfully. The average shell height of *P. canaliculata* in Sabah is ~25 mm, with females generally larger than males. Males were often seen mating with larger sized females.

Growth was influenced significantly by environmental conditions. Snails cultured indoors grew faster than those in the field in the earlier stages probably because of better,

Table 3. Hatching percentage of *P. canaliculata* egg masses after submerging in water for varying periods

Data are mean ± s.d., with n = 5 and $t_{0.05}$ = 2.78 at 13 d.f. Square root transformed means have cv = 15.2% and s.d. = 1.08

Period of submergence (days)	Hatching %	Hatching Square root transformed mean
0	91.8 ± 1.93	9.58[a]
1	73.0 ± 4.42	8.47[a–c]
2	77.6 ± 3.73	8.79[a,b]
3	67.9 ± 5.86	8.08[a–d]
4	78.7 ± 3.61	8.86[a,b]
5	79.2 ± 4.62	8.85[a,b]
6	53.1 ± 5.39	7.13[c–e]
7	67.0 ± 3.73	8.16[a–d]
8	64.6 ± 5.03	7.93[b–d]
9	48.3 ± 4.47	6.86[d,e]
10	42.2 ± 4.02	6.43[e]
11	39.0 ± 4.49	5.94[e,f]
12	15.8 ± 4.18	4.65[f,g]
13	22.7 ± 4.16	4.43[g]
14	7.10 ± 2.57	2.50[h]

[a–h]Any two means having a common letter are not significantly different to each other at the 5% level by Duncan's Multiple Range Test.

more constant conditions (water changed frequently, food not limiting, more constant temperature). At around Day 80, growth of the indoor snails and those in the field was about the same and beginning to plateau (Fig. 3). The study showed that snails in water depths greater than 90 cm had high mortality and low egg mass production. Egg mass production was also low under peaty soil conditions. However, because these were non-replicated experiments, more studies are required to confirm the results. Whether this effect is simply due to lower pH or to substances in the peat detrimental to the snails is presently not known and requires further investigation.

Frequency of oviposition was highly variable but, because of their large numbers in the field, numerous egg masses were produced. Females kept alone in an isolated plot could lay more than once because they had the ability to store sperm (Miyahara *et al*. 1986). In Sabah, oviposition coincides with the rainy season with egg masses very abundant after heavy rain. When the dry weather returns, the number of egg masses decreases gradually. Under prolonged drought, egg masses were completely absent in the field.

During the rainy season, floods are common and many egg masses become submerged. Our results suggest submergence is not detrimental to the egg masses under natural conditions because in Sabah, floods rarely last for more than 1 week. Our study showed that submergence was potentially harmful only when it lasted for more than this period of time.

Conclusions

Pomacea canaliculata thrives under the climatic conditions in Sabah. The snail is prolific and is undoubtedly going to spread throughout the country, if not all of Borneo. It can continue to breed for as long as water is not limiting. In Sabah the dry season is short, so there is a tendency for the snail to increase in number. Growth and reproduction are not the same in different regions. The review by Cowie (2002) indicates that *P. canaliculata* in the

Philippines behaves in a similar way to the snails in Sabah, but in Japan and Argentina the snails take a longer time to reach maturity, hatching success being lower with fewer eggs in each cluster. In Argentina it took 7 months to 2 years for snails to mature (Estebenet and Cazzaniga 1992). In Hawaii a sex ratio of 1 : 1 and a maximum shell size of only 30 mm was reported by Cowie (2002), whereas in Thailand the shells can reach at least 65 mm in height (Keawjam and Upatham 1990).

Apart from being able to thrive in wet places, there are also conditions unfavourable for *P. canaliculata*. The snails cannot tolerate high water temperatures. At water depths of 5 cm with a mean temperature of 33°C mortality was high. Mochida (1991) also reported that temperatures greater than 32°C resulted in high mortality. Snails on peat soils also show a significant reduction in egg mass production.

The adaptability of *P. canaliculata* is not confined to South-East Asia, but to any place with wetlands and warm climate. Baker (1998) reported that several parts of Australia (particularly northern Australian wetlands), parts of North America, Europe, New Zealand and a few Pacific Islands are suitable for the pest to establish. Once infested, the situation is seemingly irreversible. Thus, applying strict quarantine measures at the ports of entry is the best control measure for countries still free of this pest.

Acknowledgments

The author thanks the Director of Agriculture, Sabah, Datuk Jurij Awang Yaccob, for permission to publish this paper. Thanks are also due to the Deputy Director (Research and Technology Development), Mr Phua Peh Kee, and the Assistant Director (short-term Crop Research) of Agriculture Research Centre, Mr Yong Lee Ming, for support and encouragement in carrying out the projects. The assistance of the staff of the Pest Management Division, Mr Hairie Buyug, Mr Morni Ullah, Mr Fredolin Guyang and Ms Mariana Johny, is gratefully acknowledged. Appreciation is extended to Mr Lee Nyin Kiong for composing Fig. 1.

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