RAFFLES BULLETIN OF ZOOLOGY Supplement No. **22**: 269–278
Date of Publication: 30 Dec.2009

VERTICAL DISTRIBUTION, SPAWNING AND RECRUITMENT OF *SIPHONARIA GUAMENSIS* (GASTROPODA: PULMONATA) ON A SEAWALL IN SINGAPORE

C. K. Chim and **K. S. Tan**
Tropical Marine Science Institute, National University of Singapore,
18 Kent Ridge Road, Singapore 119227, Republic of Singapore
Email: tmscck@nus.edu.sg (CCK); tmstanks@nus.edu.sg (TKS)

***ABSTRACT*. –** The abundance of the false limpet *Siphonaria guamensis* and their egg masses on a sloping intertidal seawall fronting the East Johore Strait at the mouth of Sungei Api Api, Singapore was observed between May 2003 and October 2004. Limpets and their spawn occurred over the entire length of the slope equivalent to a vertical tidal range of 0.5–2.8 m. However, the highest densities of animals (up to 166 ex.100 cm^{-2}) and egg masses (up to 29 ex.100 cm^{-2}) were concentrated at the mid-littoral zone corresponding to a narrow tidal range of between 1.2 and 2.2 m above chart datum, perhaps due to space constraints and predation at the lower shore and low food supply and high variation in physical conditions (e.g. temperature and salinity) at the higher shore. Reproduction was seasonal and egg deposition was observed primarily during the Southwest Monsoon, when limpets and egg masses were subjected to long periods of emersion, dessication and high temperature. Conversely, egg masses were almost absent during the cooler and wetter months of the Northeast Monsoon. These results suggest that egg masses were able to withstand high temperatures but not osmotic stresses resulted from rainfall. Recruits (limpets with shell lengths between 1–2 mm) appeared at the low- and mid-littoral zones some two months after deposition of egg masses.

***KEY WORDS*. –** *Siphonaria guamensis*, vertical distribution, spawning, recruitment, seawall, Singapore.

INTRODUCTION

Pulmonate limpets in the genus *Siphonaria* are common and often an abundant component of rocky intertidal habitats worldwide (see review by Hodgson, 1999). The genus comprises more than 70 species (Hubendick, 1946), most of which are widely distributed in the lower latitudes of the Indo-Pacific (Hubendick 1947). Siphonariids, like other pulmonates, are air breathers, although they also possess secondary gills for respiration in water (Yonge, 1952; De Villiers & Hodgson, 1987). These gastropods typically inhabit cleared areas within macroscopic algal mats, especially surfaces covered only by a film of microscopic algae, in large numbers (Voss, 1959; Underwood & Jernakoff, 1981). Siphonariids are capable of feeding on a wide range of microalgae, filamentous algae, foliaceous algae, macrophytous corticated algae, articulated calcareous algae and crustose algae (Underwood & Jernakoff, 1981; Jara & Moreno, 1984; Santelices & Correa, 1985; Godoy & Moreno, 1989; see also Hodgson, 1999), as well as lichens (Borland, 1950) and cyanobacteria (Chan, 2003). Not surprisingly, *Siphonaria* spp. can influence the settlement, growth and survival of algae, as well as barnacle recruitment and survival (Jara & Moreno, 1984; Hodgson, 1999) because of their occurrence in large numbers.

The vertical distribution of *Siphonaria* on intertidal shores in the temperate zone is well documented. Most species occupy the upper half of the intertidal region, although others (e.g. *S. sirius*) inhabit the low shore (Hodgson, 1999). *Siphonaria kurracheensis* has an unusual bimodal distribution, being abundant at both low and high shores on Rottnest Island in Western Australia (Black, 1979). Some species change their vertical distribution according to seasons. For example, *S. japonica* inhabits the mid shore but shifts to the low shore during winter (Abe, 1939). It is widely assumed that the vertical distribution of siphonariids is affected by both biotic (e.g. interspecific competition for space; Black, 1979; Hodgson, 1999) and abiotic factors (e.g. desiccation, temperature, salinity and wave action; Allanson, 1958; Voss, 1959; Hodgson, 1999). Although *Siphonaria* species in the lower latitudes are expected to conform in general to these observations, there is surprisingly little known about tropical species (Hodgson, 1999).

Spawning in *Siphonaria* usually involves the deposition of benthic egg masses on the shore (Abe, 1939; Chambers & McQuaid, 1994a; Ocana & Emson, 1999; Huang & Chan, 2000), although two species (*S. tasmanica* and *S. virgulata*) release pelagic egg masses (Creese, 1980; Quinn, 1983). The spawning activities of species in the temperate region are also relatively well studied. In general, spawning occurs in the summer (e.g. *S. diemenensis*, Quinn, 1988; *S. japonica*, Hirano, 1980; *S. sirius*, Iwasaki, 1993) although some species produce egg masses throughout the year (e.g. *S. concinna* and *S. serrata*, Chambers, 1994). In contrast, species from tropical regions are poorly studied. From limited information available, reproduction occurs throughout the year (*S. gigas* in Panama; Levings & Garrity, 1986; *S. hispida* in Brazil; Marcus & Marcus, 1960). However, results from other studies have shown that intertidal animals in regions near the equator (e.g. Singapore and Malaysia) display various degrees of seasonality in reproduction cycles, even though these regions experience little variation in ambient temperature. For example, reproduction in the barnacle *Chthmalus malayensis* lacked seasonality altogether (Lee et al., 2006). The gastropod *Strombus canarium* and bivalves *Anadara granosa* and *Pelecyora trigona* reproduced all year round but with distinct peaks (Broom, 1982 & 1983; Cob et al., 2008). In contrast, the gastropods *Cerithidea cingulata*, *Umbonium vestiarium* and *Thais* spp. reproduced only in restricted periods of the year (Vohra, 1970; Berry & Othman, 1983; Tan, 1999). Fluctuations in reproductive activities observed in the equatorial regions were mainly attributed to seasonal variations in rainfall intensity possibly leading to changes in salinity (Vohra, 1970; Broom, 1982). Tidal regimes and prey-predator relationships have also been considered as important factors in reproduction seasonality (Vohra, 1970; Berry & Othman, 1983; Berry, 1986a, 1987 & 1990).

Preliminary surveys revealed that *Siphonaria guamensis* (Quoy & Gaimard, 1833) is a significant occupant of the rocky intertidal shores in Singapore, reaching densities of up to 3700 ex. m^{-2} (pers. obs.). The geographical range of *S. guamensis* includes Guam, Billiton and Java Sea (Hubendick, 1946). Despite the high abundance and wide distribution of *S. guamensis*, the ecology of this species remains poorly understood. In this study, the spatial and temporal abundance patterns of adults, egg masses, and recruits of *S. guamensis* were examined at three different littoral zones on a seawall in Singapore. Because of their relatively uniform construction as compared to natural rocky shores, seawalls provide an ideal, simple platform for ecological studies of intertidal communities.

MATERIAL AND METHODS

Study area. – A 6 m wide section of a granite seawall at the west side of the river mouth of Sungei Api Api (1°22.967'N 103°56.960'E; Fig. 1) was selected as the study site. It is located on the northeastern coast of Singapore in the East Johore Strait. Although there are no distinct wet and dry periods, Singapore experiences two monsoon seasons: the Northeast Monsoon (December–March), which is characterized by high cloud cover, generally wetter months and lower mean air temperatures, as compared to the Southwest Monsoon (June–September) during which conditions are on the whole drier and hotter. Diurnal temperature variation in Singapore is generally higher than mean monthly differences, reaching highs of 31–33°C during the day and lows of 23–25°C during the night. Rainfall and air temperature data during the study period were obtained from Singapore's Meteorological Services Department, National Environment Agency. For the purpose of this study, the seawall was divided into three littoral zones (high, mid and low) corresponding to the tidal heights for Mean High Water Spring (MHWS; 2.3–2.9 m above chart datum), Mean High Water Neap (MHWN; 1.3–2.3 m above chart datum) and Mean Low Water Neap (MLWN; 0.6–1.3 m above chart datum) at Tanjong Changi, Singapore (Maritime and Port Authority of Singapore, 2002, 2003). The seawall has a gradient of 27° with a slope length of 7.5 m. It stands relatively high above mean sea level at 0.6 m above chart datum, with an intertidal muddy sandflat beyond the base of the seawall on the seaward side. Seawater conditions were generally estuarine, with salinity values ranging between 17 and 20 ppt at high tide, and may be lower after heavy rainfall in the vicinity.

Preliminary surveys conducted between May 2002 and May 2003 revealed that the seawall at Sungei Api Api was inhabited exclusively by *Siphonaria guamensis*, unlike other rocky shores in Singapore where two or three species of *Siphonaria* co-exist. At the high littoral zone (> 2.3 m above chart datum), diversity was poor. *Siphonaria guamensis* and *Littoraria* spp. were the dominant animals, with mean densities of 31.7 and 21.7 ex.m^{-2}, respectively. The mussel *Xenostrobus* sp. and barnacle *Balanus amphitrite* were also present. The mid-littoral zone (1.3–2.3 m above chart datum) was dominated by *S. guamensis* and *B. amphitrite* (abundance: 890.0 ex. m^{-2} and 261.7 ex. m^{-2}, respectively). Other animals included littorinids (*L. articulata*, *L. strigata*, *Echinolittorina vidua*, *Peasiella* sp.), patellogastropod limpets (*Patelloida saccharinoides*, *Patelloida* sp.), oysters (*Saccostrea cuccullata*) and mussels (*Xenostrobus* sp.). Cyanobacteria as well as encrusting brown and green algae were also common. At the low littoral zone (0.6–1.3 m above chart datum), *S. guamensis*, *B. amphitrite* and the anemone *Anthopleura* sp. dominated with mean densities of 1527.6, 1226.0 and 1100.3 ex. m^{-2}, respectively. Cyanobacteria and macroalgae such as *Enteromorpha* sp., *Ulva* sp. and *Gracilaria* sp. were also present. Some 28 species of sessile and motile fauna were recorded from the seawall.

Sampling and data analysis. – A total of 27 observations were carried out approximately twice every month during daytime low tides (< 1.0 m above chart datum) between 14 May 2003 and 1 Oct.2004 on the seawall. The position of the belt-transect (6 × 7.5 m) was fixed with a paint mark and the same area monitored throughout the sampling period. During each sampling occasion, a graduated transect line was laid down the slope perpendicular to the top edge of the seawall, such that the 0 metre mark coincided with the bottom of the wall.

To determine the abundance of *Siphonaria guamensis*, ten 30 × 10 cm quadrats were placed haphazardly within each of the three littoral zones and within 3 m on either side of the transect line. All *Siphonaria guamensis* individuals and

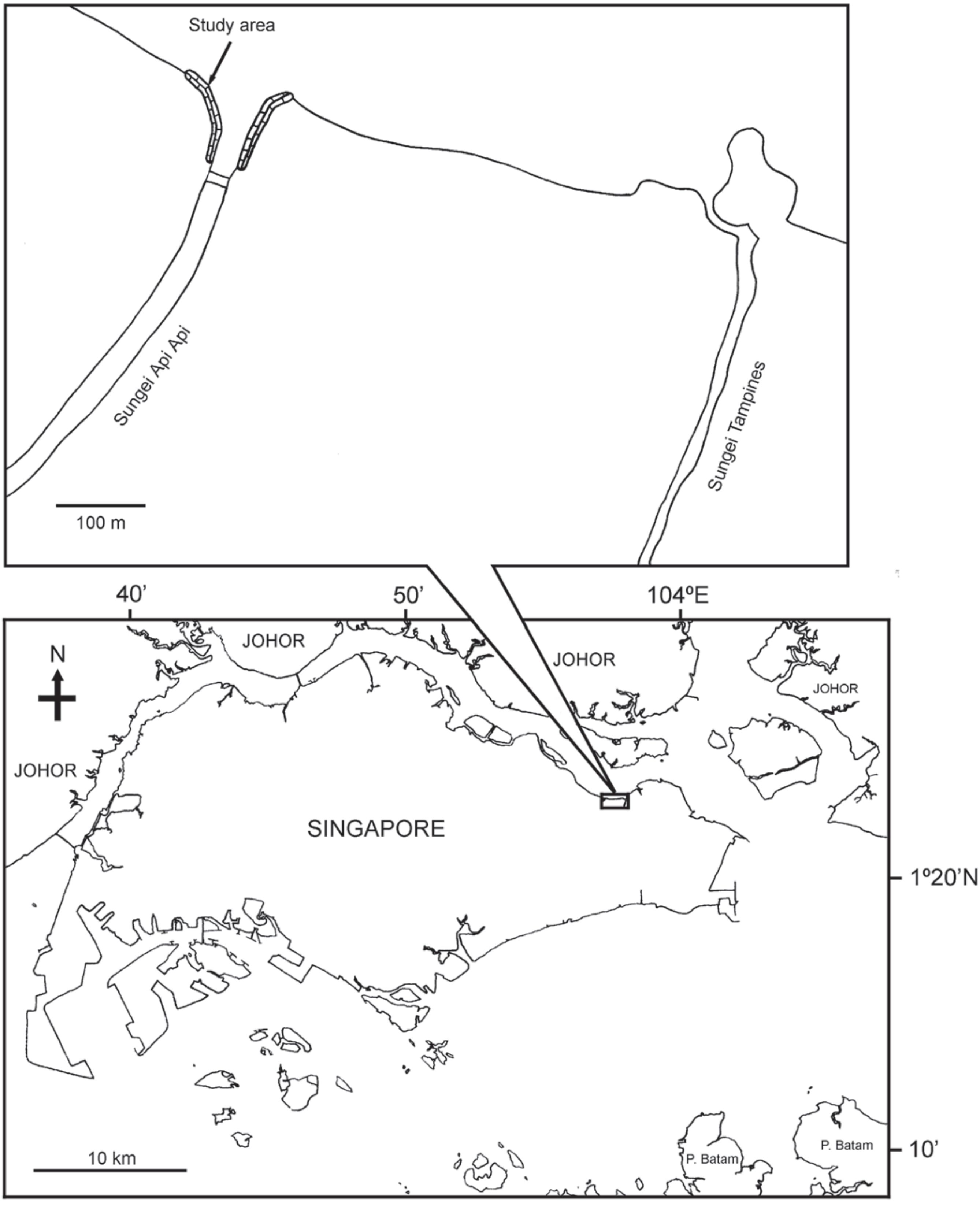

Fig. 1. Location of study site in the East Johore Strait, Singapore.

egg masses inside each quadrat were counted and recorded. Veligers are released 12–18 days after egg mass deposition, which disintegrates soon after hatching (pers. obs.). Double counting of egg masses was therefore minimal, as the interval between consecutive samplings ranged from two weeks to one month. To examine vertical distribution of limpets and egg masses, data from 27 sampling occasions were pooled for each zone and their means tested for significant difference using one-way analysis of variance (ANOVA). Temporal variation in abundance was elucidated in the same manner. Count data were square-root transformed before statistical analysis.

To enumerate the size structure of limpets at the seawall, the shell length of fifty individuals located at the transect line were measured to the nearest 1 mm. The position of each limpet along the transect line was also recorded to the nearest 0.1 m. Limpets were classified into six size-classes according to their shell length: '1–2 mm', '3–4 mm', '5–6 mm', '7–8 mm', '9–10 mm' and '> 10 mm'. Recruits refer to limpets in the '1–2 mm' size class.

RESULTS

***Vertical distribution.* –** *Siphonaria guamensis* was distributed across the entire littoral zone of the seawall (Table 1), between 0.6 m and 2.9 m above chart datum, although there was a significantly higher density of limpets in the mid-littoral zone compared to the low and high zones ($F_{2,807}$ = 119.328, P < 0.001; Tukey's HSD post-hoc test). Mean densities ranged from 1.2 ex.100 cm^{-2} in the low littoral (1.4 ex.100 cm^{-2} in the high littoral) to some 13.2 ex.100 cm^{-2} in the mid-littoral (Table 1). Similarly, *S. guamensis* egg masses were deposited at all three littoral zones of the seawall (Table 1), but the highest mean density (2 egg masses.100 cm^{-2}) occurred in the mid-littoral zone ($F_{2,807}$ = 118.981, P < 0.001; Tukey's HSD post-hoc test). During the entire period of this study, recruits were encountered at the low and mid-littoral zones but never in the high zone.

***Spawning and recruitment.* –** At the high littoral zone, mean densities of egg masses were low throughout the year (range = 0.0–3.7 egg masses.100 cm^{-2}) (Fig. 2a) and were not significantly different across months ($F_{26,243}$ = 0.872, P = 0.648). Within the same zone, mean limpet density was also low (< 1 ex. 100 cm^{-2}) during most times of the year, except between the months of Nov. and Mar. when values reached 12.7 ex.100 cm^{-2} (Fig. 2a). A significant difference in limpet density was detected across the sampling period due to the exceptionally high limpet density observed on 20 Jan.2004 ($F_{26,243}$ = 5.554, P < 0.001; post hoc Tukey's HSD test). Mean shell length of limpets at this zone during this period of high limpet density was 7.3 ± 2.7 mm (range = 3–18 mm, n = 100).

At the mid-littoral zone, there were periods of intense spawning activity from late Jul.2003 to late Oct.2003 and again from mid-Aug. to early Oct.2004 (Fig. 2b). Egg mass densities were significantly different between months ($F_{26,243}$ = 7.249, P < 0.01). Post hoc Tukey's HSD tests indicated that egg mass densities from 31 Jul. to 10 Sep.2003 and from 17 Sep.2004 to 1 Oct.2004 were significantly higher than those of other sampling dates. The ratio of egg mass density to limpet density was highest in late Jul.2003 and mid-Aug.2004, with values of 1:1 and 0.7:1, respectively. Mean limpet densities at the mid-littoral zone were relatively high throughout the sampling period (14 May 2003 to 1 Oct.2004), ranging between 6.0–25.7 ex.100 cm^{-2} (Fig. 2b). Lowest densities of limpets at this zone were observed in late Jul.2003 and mid-Aug.2004 (Fig. 2b). These reductions in limpet density coincided with the onset of the spawning season, although a significant difference in limpet density between months was barely detectable ($F_{26,243}$ = 1.539, P = 0.051). At the mid-littoral zone, limpet shell length averaged 7.1 ± 3.0 mm (n = 934) and ranged between 1–14 mm.

Mean numbers of egg masses at the low littoral zone were generally small throughout the sampling period (Fig. 2c) although egg mass density on 31 Jul.2003 was significantly higher than those on other sampling dates ($F_{26,243}$ = 1.873, P = 0.008; post hoc Tukey's HSD test). Mean limpet densities at the low littoral zone were also relatively low throughout the sampling period, except during the periods from late Aug. to late Oct.2003 and from early Sep. to early Oct. (end of study) 2004 when limpet density reached a maximum of 35.1 ex.100 cm^{-2} (Fig. 2c). Mean shell lengths of limpets at this zone were 3.3 ± 1.6 mm (range = 1–7 mm, n = 24) and 1.6 ± 1.1 mm (range = 1–6 mm, n = 27) in the later half of 2003 and 2004, respectively. Significant difference in limpet densities between sampling dates were detected ($F_{26,243}$ = 13.037, P < 0.01). Post hoc Tukey's HSD tests indicated that limpet densities on 28 Aug.2003 and from 2 Sep.2004 to 1 Oct.2004 were significantly higher than other sampling periods.

Seasonal variation in egg mass density and juvenile recruitment is shown in Fig. 3a. Spawning and recruitment were synchronised with a two-month lag between them. Recruits emerged in late Aug.2003, about two months after the appearance of egg masses on the shore. The proportion of recruits to the total number of limpets peaked in late Oct.2003, which is about two months or less after a peak in egg mass density. There were no recruits between mid-Jan.2004 and early Aug.2004, when egg masses were either absent or occurred in small numbers. Recruits re-emerged in mid-Aug.2004, about three months after a slight increase in the number of egg masses observed on the seawall.

DISCUSSION

***Vertical distribution.* –** *Siphonaria guamensis* limpets were distributed across the entire intertidal zone of the seawall at Sungei Api Api but density was highest at the mid-littoral zone, corresponding to a tidal level of between 1 and 2 m. A distinct narrow tidal height distribution is typical of most *Siphonaria* species (Hodgson, 1999), and *S. guamensis* appears to conform to this generalization. The reasons for this tight confinement to a particular range

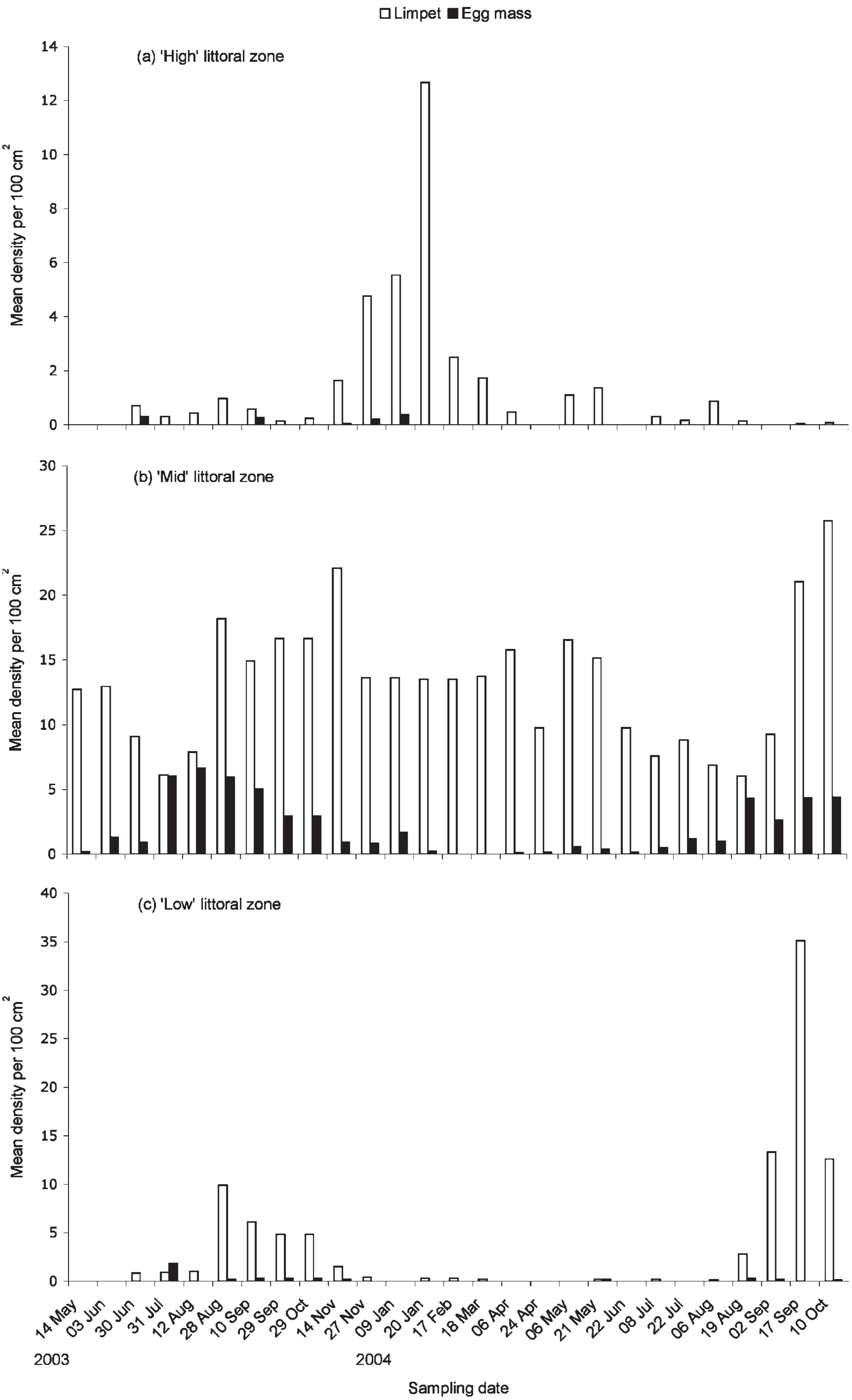

Fig. 2. Changes in the mean abundance of *Siphonaria guamensis* and their egg masses between May 2003 and Oct.2004 at: a, high; b, mid-; c, low littoral zones on a seawall at Sungei Api Api, Singapore.

of tidal heights remain unclear. It may be advantageous for sessile organisms to live in groups (e.g. provision of substrate heterogeneity by other congeners; availability of partners for cross-fertilization; better access to grazed areas where adhesion is better, etc) and this may be one factor in their seeking a particular tidal zone, apart from being out of range from predators whilst being in an area where food is available. The mid-littoral zone was characterized by the absence of the anemone *Anthopleura* sp., as well as having lower densities of macroalgae and barnacles, as compared to the low littoral zone (pers. obs.), resulting in more suitable spaces for *S. guamensis* to utilise. Limpets seemed to prefer cleared surfaces, possibly because their foot can then make suitable contact with the substratum (pers. obs.). Egg masses were always deposited on rock surfaces devoid of macroalgae (pers. obs.). The relative lack of predators (e.g. muricids) compared to the lower littoral is another possible factor in shaping the distribution. The moderate abundance of macroalgae appeared to provide limpets with a sufficient food supply although other grazers (e.g. neritids and patellogastropods) were also present at the mid-littoral zone (pers. obs.). Physical conditions such as temperature and salinity at the mid-littoral zone are expected to be less variable than those at the higher zone.

The smaller number of limpets at the low littoral zone could be due to a combination of a lack of suitable space and the effects of predation, in spite of abundant food and the less stressful physical conditions expected of the lower littoral. Macroalgae, sea anemones and barnacles dominate the surface of the seawall in the low littoral, and these limit the availability of suitable surfaces for the limpets. Other grazers (e.g. neritids and patellogastropods) were also uncommon (pers. obs.). In addition, predatory gastropods such as *Thais clavigera* and *T. gradata* (Muricidae) were present in the low littoral zone, and empty *S. guamensis* shells with typical muricid drill holes were frequently encountered (pers. obs.). This suggests that limpets at the low littoral zone were more likely to be subjected to predators which were absent in the higher zones.

In contrast, space constraint is an unlikely contributing factor to the low density of *S. guamensis* in the high littoral zone, where generally, fewer organisms were present. Perhaps as a result of the absence of such space limitations as well as more stressful physical conditions, limpets at the high littoral zone were relatively large. Muricids were also absent at the high littoral zone, although it is possible that these mobile predators move upshore during high tides to feed on the limpets. Terrestrial or avian predators such as birds have not been observed feeding on the limpets or egg masses. Furthermore, animals in the high littoral zone are probably less prone to aquatic predators as compared to those inhabiting the lower zones. Epilithic algae were limited in supply, and potential food competitors such as *Nerita* spp. were relatively common at this zone. Environmental factors such as temperature, dessication and osmotic stress may also play significant roles in determining the upper limit of limpet distribution on the seawall (Hodgson, 1999). It is likely that limpets at the high littoral zone are migrants from the lower shores because recruits were absent at this zone.

Spawning and recruitment. – The *Siphonaria guamensis* population at Sungei Api Api demonstrated a single annual phase of reproduction, as measured by the abundance of egg masses deposited. This is typical of *Siphonaria* species that exhibits seasonal reproduction (Hodgson, 1999). Tropical marine invertebrates such as the anemone *Actinoporus elongates* (Clayton & Collins, 1992), gastropods *Cerithidea cingulata* (Vohra, 1970), *Umbonium vestiarium* (Berry & Othman, 1983), *Thais clavigera* and *T. jubilaea* (Tan, 1999) and hermit crabs *Calcinus obscurus*, *Clibanarius albidigitus* and *Pagurus* sp. (Bertness, 1981) also displayed a single annual reproduction period. Although spawning occurred over an extended period of between six and seven months, *S. guamensis* showed an intensified period of egg mass deposition lasting up to four months during the Southwest Monsoon, when a large number of egg masses (up to 29.3 egg masses 100 cm^{-2}) were deposited. Production of egg masses appeared to coincide with a period of relatively high temperature and low rainfall in Jun.–Oct.2003 and again in Jul.–Oct.2004 (Fig. 3a, b). In addition, the intertidal region above 1.3 m chart datum (i.e. where *S. guamensis* egg masses were deposited) is also characterized by long day emersion periods (~ 90 cumulative hours per month between 0900 and 1500 hrs) during this time of year in Singapore. This suggests that the egg masses were able to withstand dessication whilst exposed to high temperatures. Although egg masses at the seawall appeared to dry out considerably during the day, those collected from the field hatched viable veligers in the laboratory (pers. obs.). While spawning activities coincided with the Southwest Monsoon, it declined during the cooler and wetter Northeast Monsoon months (Fig. 3a, b). This is in spite of the observation that the intertidal region occupied by *Siphonaria* experiences shorter emersion periods (~35 cumulative hours per month

Table 1. Mean densities of *Siphonaria guamensis* and their egg masses in three littoral zones of a seawall at the mouth of Sungei Api Api, Singapore, based on 270 quadrats deployed between 14 May 2003 and 1 Oct.2004. Minimum and maximum values are in parentheses.

	Littoral Zone		
	High	Mid	Low
Limpet (individuals.100 cm^{-2} ± SD)	1.4 ± 9.1 (0–126.7)	13.2 ± 26.6 (0–166.3)	1.2 ± 3.4 (0–27.3)
Egg mass (number.100 cm^{-2} ± SD)	0.04 ± 0.4 (0–3.7)	2.0 ± 3.9 (0–29.3)	0.05 ± 0.3 (0–4.0)

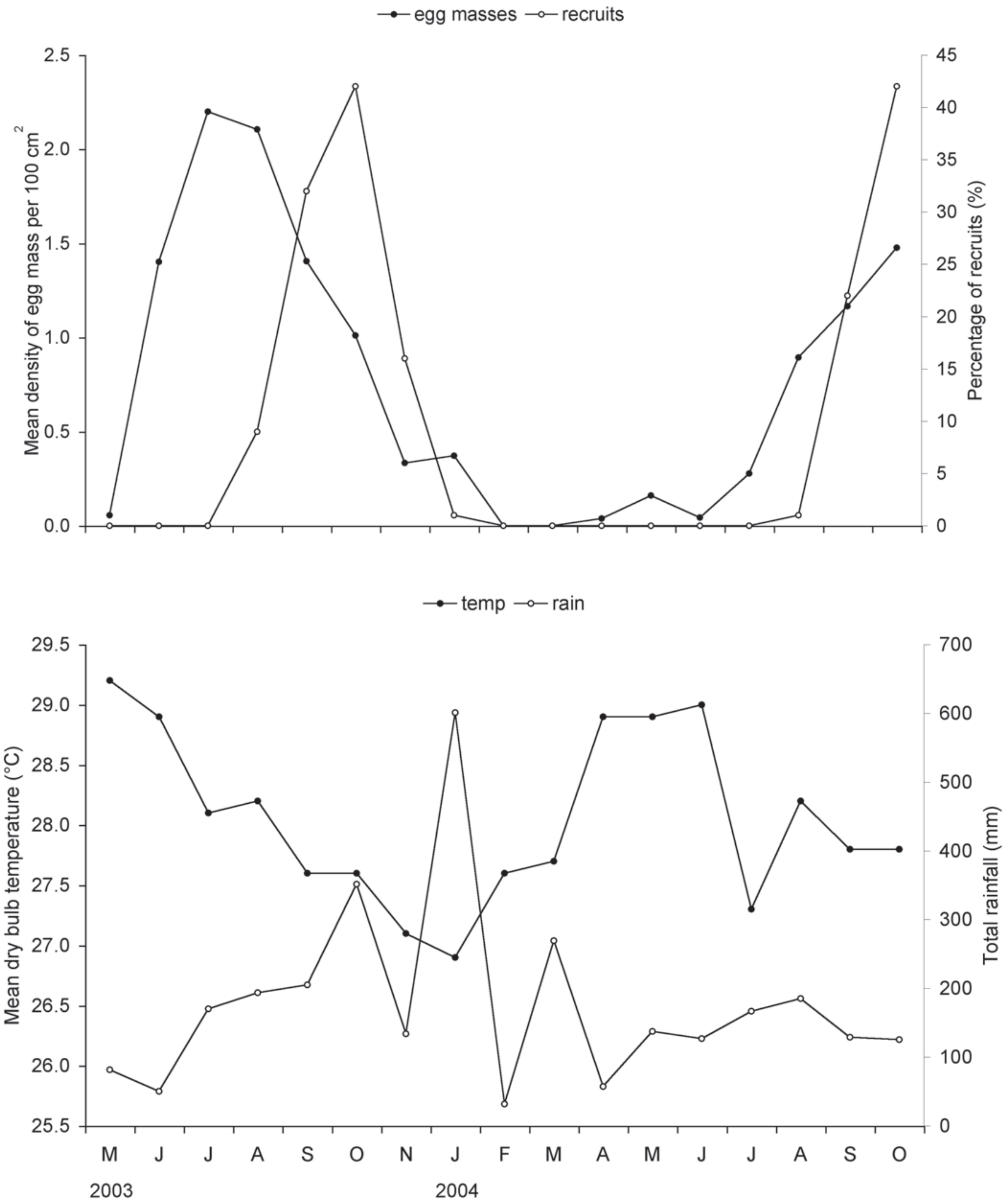

Fig. 3. Prevailing physical conditions (temperature, rainfall) in relation to abundance of *Siphonaria guamensis* egg mass and juveniles on a seawall at Sungei Api Api, Singapore: a, density of egg masses and the percentage frequency of recruits of *S. guamensis* between May 2003 and Oct.2004 (no data were collected in Dec.2003); b, mean monthly dry bulb temperature and rainfall between May 2003 and Oct.2004 at the Changi Meteorological Station, Singapore (data courtesy of the Meteorological Services Division, National Environment Agency, Singapore).

between 0900 and 1500 hrs) during the Northeast Monsoon. The low reproductive output could be in response to unfavourable salinity conditions resulting from frequent rain. Egg mass densities observed for *S. guamensis* were at their lowest after the intense rainfall in Jan.2004. Although rain may help keep egg masses damp and cool, freshwater could also be a source of osmotic stress for the embryos within. Furthermore, it may be fatal for the larvae if rain penetrates the protective jelly layer, which is presumably in a degraded condition when the larvae are about to be released. Similarly, larvae released under hypoosmotic conditions may not have a high chance of survival. Rainfall plays an important role in reproduction in other tropical intertidal invertebrates including the gastropods *Nerita birmanica* and *Cerithidea cingulata* (Berry et al., 1973; Vohra, 1970), the bivalve *Anadara granosa* (Broom, 1982, 1983), and the barnacle *Balanus amphitrite* (Desai & Anil, 2005). Biotic factors such as fluctuations in the number of competitors and predators, and food supply may also be important in contributing to the seasonal variation in the reproductive output of *S. guamensis*, although these variables were not investigated in this study.

The high density of egg mass at the mid-littoral zone could simply be a reflection of favourable conditions allowing the large number of limpets to coexist at this zone. In some *Siphonaria* species, egg masses were not deposited at the tidal height occupied by adults (see Abe, 1939, 1941; Voss, 1959). *Siphonaria guamensis* produces collar-shaped egg masses that are square in cross section, are of a firm consistency and have a thick surface layer on which sand and other debris often attach (pers. obs.). Veligers develop within relatively large egg capsules and hatch with eyes, velar swimming apparatus and a crawling foot after 12–18 days (pers. obs.). According to the classification scheme of Chambers & McQuaid (1994a), *S. guamensis* is an intermediate developer because it has a combination of reproductive traits that are characteristic of planktonic and direct developers. As planktonic developers are usually low shore species and most direct developers are high shore species (Chambers & McQuaid, 1994a), intermediate developers such as *S. guamensis* are likely to be mid shore species, which is true in this case.

The annual, single phase of recruitment follows that of egg mass deposition with a two-month time lag. This observation, supported by both field and laboratory data (pers. obs.), suggests that *S. guamensis* takes about two months to develop from an embryo to a juvenile with a shell length of 1–2 mm. Coincidently, recruits were absent during the period when ambient temperature was rising. One possible explanation for this observation is that mortality was extremely high for recruits during this period. However, this is unlikely, as limpet density did not decrease significantly. The more likely possibility is that the ‘disappearance’ of recruits is due to their rapid growth, resulting in a change in size class for the whole cohort. Spawning could be timed such that the whole cohort already has a relatively large shell size during the warmer and drier months. This strategy ensures that recruits will be subjected to minimal physiological stresses due to increased temperature and/or lowered salinities.

ACKNOWLEDGEMENTS

The 14th International Marine Biology Workshop held in Singapore was organized by Tan Koh Siang (Tropical Marine Science Institute, National University of Singapore), Lena Chan (National Biodiversity Centre, National Parks Board, Singapore), Chou Loke Ming (Department of Biological Sciences, National University of Singapore) and Peter Ng (Raffles Museum of Biodiversity Research, National University of Singapore). Publication of the workshop proceedings was made possible with funds provided by the National University of Singapore and National Parks Board. This study was partially funded by the Agency for Science Technology and Research (A*STAR) research grant 0121050037 (Marine Environment Programme) to the Tropical Marine Science Institute, National University of Singapore. We thank Hoe Li Shan and Nicholas Yap Wei Liang for reading the manuscript and providing constructive suggestions on an earlier draft of this paper.

LITERATURE CITED

Abe, N., 1939. The homing, spawning and other habits of a limpet, *Siphonaria japonica* Donovan. *Science Report of Tohoku Imperial University, 4th Series (Biology)*, **15**: 59–95.

Abe, N., 1941. Ecological observations on a limpet-like pulmonate, *Siphonaria atra* Q. & G. *Palao Tropical Biological Station Studies*, **2**: 239–278.

Allanson, B. R., 1958. Some aspects of the ecology of the molluscan genus *Siphonaria* in South Africa. *Portugaliae Acta Biologica Series B*, **6**: 179–212.

Berry, A. J., 1986a. Daily, tidal, and two-weekly spawning periodicity and brief pelagic dispersal in the tropical intertidal gastropod *Umbonium vestiarum* (L.). *Journal of Experimental Marine Biology and Ecology*, **95**: 211–223.

Berry, A. J., 1986b. Semi-lunar and lunar spawning periodicity in some tropical littorinid gastropods. *Journal of Molluscan Studies*, **52**: 144–149.

Berry, A. J., 1987. Reproductive cycles, egg production and recruitment in the Indo-Pacific intertidal gastropod *Umbonium vestiarium* (L.). *Estuarine, Coastal and Shelf Science*, **24**: 711–723.

Berry, A. J., 1990. Predator-prey interactions amd coupled annual cycles in the coastal gastropods *Umbonium vestiarium* (L.) (Trochaea) and *Natica maculosa* Lamarck (Naticidae). *Asian Marine Biology*, **7**: 109–114.

Berry, A. J., R. Lim & A. S. Kumar, 1973. Reproductive systems and breeding condition in *Nerita birmanica* (Archaeogastropoda: Neritacea) from Malayan mangrove systems. *Journal of Zoology (London)*, **170**: 189–200.

Berry, A. J. & Z. B. Othman, 1983. An annual cycle of recruitment, growth and production in a Malaysia population of the trochacean gastropod *Umbonium vestiarium* (L.). *Estuarine, Coastal and Shelf Science*, **17**: 357–363.

Bertness, M. D., 1981. Seasonality in tropical hermit crab reproduction in the Bay of Panama. *Biotropica*, **13**(4): 292–

300.

Black, R., 1979. Competition between intertidal limpets: an intrusive niche on a steep resource gradient. *Journal of Animal Ecology*, **48**: 401–411.

Borland, C., 1950. Ecological studies of *Benhamina obliquata* (Sowerby), a basommatophorous pulmonate in Otago harbour. *Transactions of the Royal Society of New Zealand*, **78**: 385–393.

Chambers, R. J., 1994. The conflict between adaptation and constraint: the case of the siphonariid limpets. PhD thesis, Rhodes University.

Chambers, R. J. & C. D. McQuaid, 1994a. Notes on the taxonomy, spawn and larval development of South African species of the intertidal pulmonate limpet genus *Siphonaria* (Gastropoda: Pulmonata). *Journal of Molluscan Studies*, **60**: 263–275.

Chambers, R. J. & C. D. McQuaid, 1994b. A review of larval development in the intertidal limpet genus *Siphonaria* (Gastropoda: Pulmonata). *Journal of Molluscan Studies*, **60**: 415–423.

Chan, K. S., 2003. Variation in cyanobacteria-dominated biofilms: consequences for the diet, growth and reproduction of an intertidal grazer, *Siphonaria japonica*, on Hong Kong shores. PhD thesis, The University of Hong Kong.

Clayton, P. D. & J. D. Collins, 1992. Reproduction and feeding ecology of a tropical, intertidal sand-dwelling anemone (*Actinoporus elongatus*, Carlgren, 1900). *Hydrobiologia*, **237**: 31–38.

Cob, Z. C., A. Arshad, J. S. Bujang, S, M. N Amin. & M. A. Ghaffar, 2008. Growth, mortality, recruitment and yield-per-recruit of *Strombus canarium* Linnaeus, 1758 (Mesogastropoda: Strombidae) from the West Johor Straits, Malaysia. *Research Journal of Fisheries and Hydrobiology*, **3**(2): 71–77.

Creese, R. G., 1980. Reproductive cycles and fecundities of two species of *Siphonaria* (Mollusca: Pulmonata) in south-eastern Australia. *Australian Journal of Marine and Freshwater Research*, **31**: 37–47.

Davenport, J., 2001. Kelp Gulls avoid siphonariid limpets because of repugnant mucus. *Ibis*, **143**(2): 304–306.

Davies, M. S. & G. A. Williams, 1997. Mucus production by species of *Siphonaria* (Mollusca: Gastropoda: Pulmonata) in Hong Kong. In: Morton, B. (ed.), *The Marine Flora and Fauna of Hong Kong and Southern China IV. Proceedings of the Eighth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1995*. Hong Kong: Hong Kong University Press. Pp. 303–314.

Desai, D. V. & A. C. Anil, 2005. Recruitment of the barnacle *Balanus amphritite* in a tropical estuary: implications of environmental perturbation, reproduction and larval ecology. *Journal of the Marine Biological Association of the United Kingdom*, **85**: 909–920.

Garrity, S. D. & S. C. Levings, 1985. Interspecific interactions and scarcity of a tropical limpet. *Journal of Molluscan Studies*, **51**: 297–308.

Giese, A. C., 1959. Comparative physiology: annual reproductive cycles of marine invertebrates. *Annual Review of Physiology*, **21**: 547–576.

Godoy, C. & C. A. Moreno, 1989. Indirect effects of human exclusion from the rocky intertidal in southern Chile: a case of cross-linkage between herbivores. *Oikos*, **54**: 101–106.

Hirano, Y., 1980. *Siphonaria* (pulmonate limpet) survey of Japan. II. Periodicity of spawning activity in *Siphonaria japonica*. *Publications of the Seto Marine Biological Laboratory*, **25**: 335–342.

Hodgson, A. N., 1999. The biology of siphonariid limpets (Gastropoda : Pulmonata). *Oceanography and Marine Biology: An Annual Review*, **37**: 245–314.

Huang, R. & B. K. K. Chan, 2000. Egg capsules and early development of *Siphonaria japonica* (Gastropoda: Pulmonata). In: Morton, B. (ed.), *The Marine Flora and Fauna of Hong Kong and Southern China V. Proceedings of the Tenth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1998*. Hong Kong: Hong Kong University Press. Pp. 129–136.

Hubendick, B., 1946. Systematic monograph of the Patelliformia. *Kungliga Svenska Vetenskapsakademiens Handingar, Tredje Serien*, **23**(5): 1–93.

Hubendick, B., 1947. Phylogenie und Tiergeographie der Siphonariidae. Zur Kenntnis der Phylogenie in der Ordnung Basommatophora und des Ursprangs der Pulmonatengruppe. *Zoolgiska Bidrag Fran Uppsala*, **24**: 1–216.

Iwasaki, K. Analyses of limpet defense and predator offense in the field. *Marine Biology*, **116**: 277–289.

Jara, H. F. & C. A. Moreno, 1984. Herbivory and structure in a midlittoral rocky community: a case in southern Chile. *Ecology*, **65**(1): 28–38.

Koh, L. L., R. M. O'Riordan & W. -J. Lee , 2005. Sex in the tropics: reproduction of *Chthamalus malayensis* Pilsbry (Class Cirripedia) at the equator. *Marine Biology*, **147**: 121–133.

Lee, W. -J., R. M. O'Riordan & L. L. Koh, 2006. Spatial and temporal patterns in the recruitment of the intertidal barnacle *Chthamalus malayensis* Pilsbry (Crustacea: Cirripedia) on the equatorial shores of Peninsular Malaysia and Singapore. *Journal of Experimental Marine Biology and Ecology*, **333**: 296–305.

Levings, S. C. & S. D. Garrity, 1986. Notes on the reproduction of a tropical pulmonate limpet *Siphonaria gigas* (Sowerby). *Veliger*, **39**: 86–90.

Marcus, E. & E. Marcus, 1960. On *Siphonaria hispida*. *Universidade de Sao Paulo*. *Faculdade de Filosofia, Ciencias e Letras*. *Boletim de Zoologia*, **23**: 107–139.

Maritime and Port Authority of Singapore (MPA), 2002. Singapore Tide Tables, year 2003. Hydrographic Department, MPA, Singapore.

Maritime and Port Authority of Singapore (MPA), 2003. Singapore Tide Tables, year 2004. Hydrographic Department, MPA, Singapore.

Ocana, T. M. J. & R. H. Emson, 1999. Maturation, spawning and development in *Siphonaria pectinata* Linnaeus (Gastropoda: Pulmonata) at Gibraltar. *Journal of Molluscan Studies*, **65**: 185–193.

Quinn, G. P., 1983. Spawning and egg masses of S*iphonaria tasmanica* Tenison Woods, 1876 from Victoria. *Journal of the Malacological Society of Australia*, **6**: 81–82.

Quinn, G. P., 1988. Ecology of the intertidal pulmonate limpet *Siphonaria diemenensis* Quoy et Gaimard. I. Population dynamics and availability of food. *Journal of Experimental Marine Biology and Ecology*, **117**: 115–136.

Quinn, G. P. & N. R. Ryan, 1989. Competitive interactions between two species of intertidal herbivorous gastropods from

Victoria, Australia. *Journal of Experimental Marine Biology and Ecology*, **125**: 1–12.

Santelices, B. & J. Correa, 1985. Differential survival of macroalgae to digestion by intertidal herbivore molluscs. *Journal of Experimental Marine Biology and Ecology*, **88**: 183–191.

Tan, K.S., 1999. Seasonal growth in two species of *Thais* (Mollusca, Gastropoda, Muricidae) on the east coast of peninsular Malaysia–a preliminary study. *Phuket Marine Biological Center Special Publication* no **19**(1): 75–84.

Underwood, A. J. & P. Jernakoff, 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia*, **48**: 221–233.

De Villiers, C. J. & A. N. Hodgson, 1987. The structure of the secondary gills of *Siphonaria capensis* (Gastropoda: Pulmonata). *Journal of Molluscan Studies*, **53**: 129–138.

Vohra, F. C., 1970. Some studies on *Cerithidea cingulata* (Gmelin, 1790) on a Singapore sandy shore. *Proceedings of the Malacological Society of London*, **39**: 187–201.

Voss, N. A., 1959. Studies on the pulmonate gastropod *Siphonaria pectinata* (Linnaeus) from the Southeast coast of Florida. *Bulletin of Marine Science of the Gulf and Caribbean*, **8**: 84–99.

Yonge, C. M., 1952. The mantle cavity in *Siphonaria alternata* (Say). *Proceedings of the Malacological Society of London*, **29**: 190–199.