SEASONAL GROWTH IN TWO SPECIES OF *THAIS* (MOLLUSCA, GASTROPODA, MURICIDAE) ON THE EAST COAST OF PENINSULAR MALAYSIA - A PRELIMINARY STUDY

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ABSTRACT

Growth in *Thais clavigera* (Küster) and *T. jubilaea* Tan & Sigurdsson (Mollusca, Gastropoda, Muricidae) was studied at a rocky shore near Kuantan, peninsular Malaysia by monitoring the shell heights of marked individuals. Based on measurements recorded at monthly or bimonthly intervals for a period of 16 months, the two species showed nearly identical seasonal growth patterns. Maximum shell growth in both species occurred during the Northeast Monsoon (November to March), while there was little or no increase in shell height during the other months of the year. Production of egg capsules appeared to predominate during the "no-growth" period. These preliminary results do not support the paradigm that animals in the tropics grow and reproduce continuously throughout the year. Competition for energy resources utilized during growth and egg capsule production, as well as physical constraints imposed by the monsoons, may be possible factors responsible for the observed patterns.

INTRODUCTION

Very little is known about the ecology of intertidal molluscs in the Malayan archipelago. Published literature concerning littoral gastropods of this region are mainly restricted to systematic lists of species (e.g., Lim, 1963; Way & Purchon, 1981; Angot, 1984) and descriptions of faunal zonation (Purchon & Enoch, 1954; Berry, 1964; Chuang, 1973). Others have concentrated on the morphology, reproductive activity and population biology of common mangrove and sandy shore gastropods, e.g., *Littoraria* (Berry & Chew, 1973; Vermeij, 1973; Berry, 1986), *Nerita* (Berry, Lim & Sase Kumar, 1973) and *Umbonium* (Berry & Othman, 1983; Berry, 1987). However, predatory species in the neogastropod family Muricidae (Caenogastropoda) have received relatively little attention. This is in spite of the fact that they can be numerically abundant and therefore important in the biological structure of coastal ecosystems as predators of barnacles, polychaetes, mussels and other invertebrates (Taylor, 1976, 1984). New muricid species were recently described from Malaysia and Singapore (Tan & Sigurdsson, 1990; 1996a, b). Recent work on the basic ecology of Malayan muricids such as *Chicoreus capucinus* (Lamarck) (Nielsen, 1976; Gribsholt, 1997), *Bedeva blosvillei* (Deshayes) (Vermeij, 1980), and *Thais carinifera* (Lamarck) (Broom, 1982) have revealed interesting predator-prey relationships. However, in general, our knowledge concerning muricid biology in the Malayan region remains fragmentary and much remains to be discovered.

Thais clavigera (Küster, 1858) and *T. jubilaea* Tan & Sigurdsson, 1990 are two of several common rocky shore muricids found along the eastern shoreline of peninsular Malaysia (Tan, 1995). The shells of the two species are somewhat similar and *T. jubilaea* may have previously been confused with *T. clavigera* (see Tan & Sigurdsson, 1990). The two species also have similar radular morphology and lay identical egg capsules. Morphologically the adults appear to differ only in the shape of the penis, pigmentation pattern on the sides of the foot, and minor anatomical features associated with the reproductive system (pers. obs.). According to prevailing ecological theory, differences in diet, foraging behaviour and life history patterns may allow two or more related species to coexist when resources are limited (Kohn & Orians, 1962; Spight, 1979; Taylor, 1984). In this study, *T. clavigera* and *T. jubilaea* were monitored simultaneously in the field to see if differences in growth patterns were discernible. The data were correlated with environmental conditions and hypotheses proposed to account for the prevailing patterns.

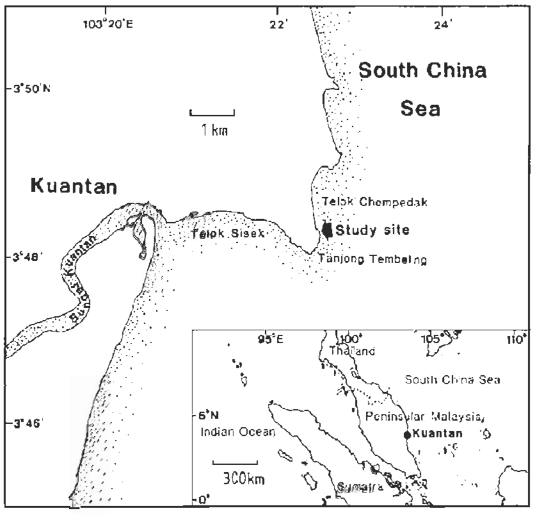


Fig. 1. Location of study site.

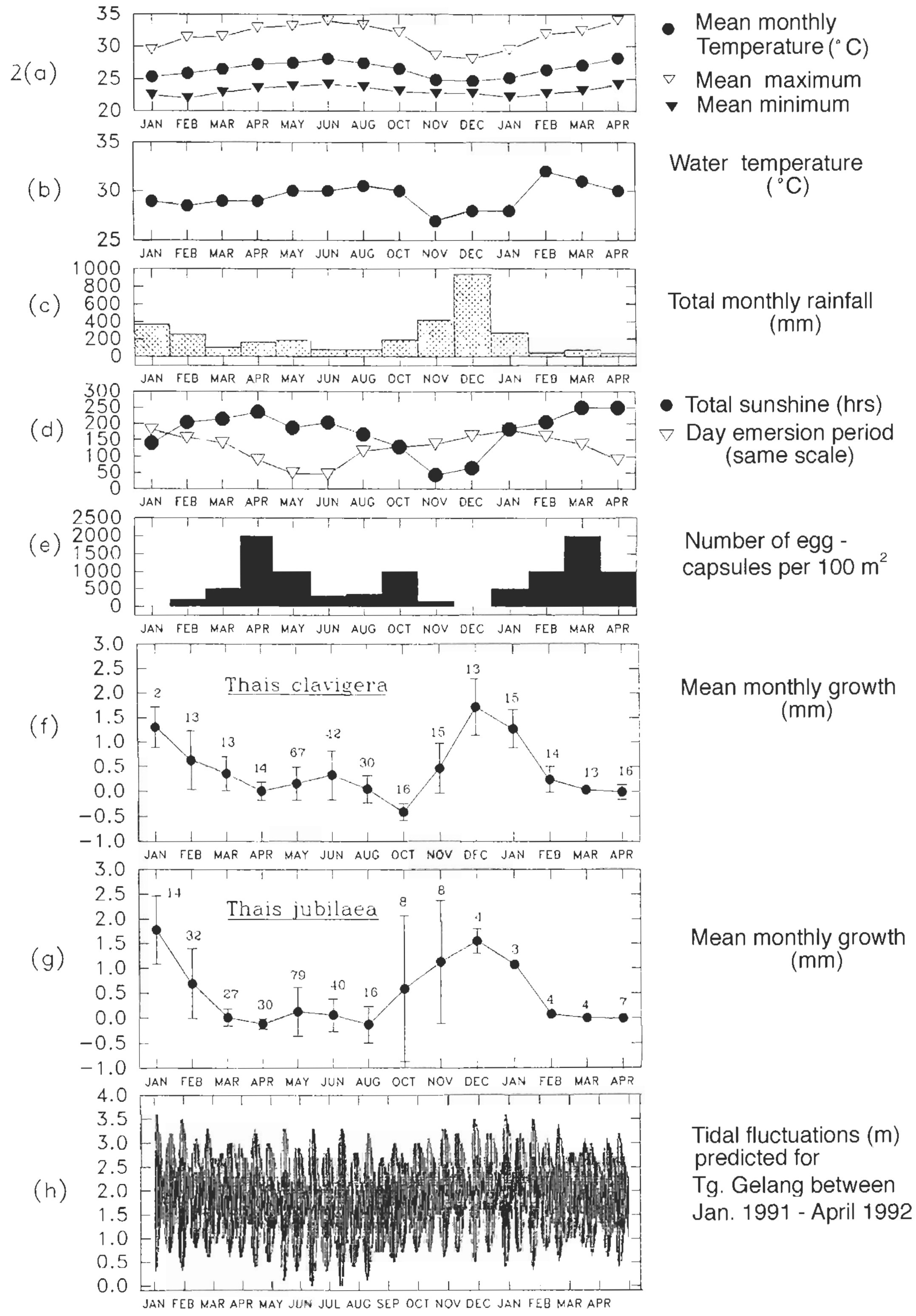
MATERIALS AND METHODS

Site description

The study site was at Tanjong Tembeling (3° 48.3'N, 103° 22.5'E) near the town of Kuantan on the east coast of peninsular Malaysia (see Fig. 1). The headland consists of wave-exposed granite outcrops and boulders on beach sand. This area was chosen as it is easily accessible while being relatively free from human disturbance. Snails were easily located on the granite boulders as there were few crevices. The tidal regime at the site is predominantly semi-diurnal with a small diurnal component. Maximum tidal range is about 3.8 m with a mean tidal height of 2.1 m (Tide Tables, 1989-1992). Water around the site is relatively turbid (8.0±0.4 NTU, n=4; Monitek nephelometer model 21 PE) due to the sandy substrate and strong wave action. Also, the site is near the mouth of Sungei Kuantan which discharges immediately south of Tanjong Tembeling (Fig. 1). However, a predominantly southerly current along the coast throughout the year (Raj, 1982) prevents the development of estuarine conditions there.

Annual variation in environmental conditions along the east coast of Malaysia is generally dictated by two monsoon periods: the Northeast (NE) Monsoon during the months of November to March, and the Southwest (SW) Monsoon, which predominates between May and September (Dale, 1956, 1959, 1960). The NE Monsoon brings heavy rainfall to the east coast of peninsular Malaysia, especially in the months of November, December and January, accompanied by strong north-northeasterly winds, overcast skies and lower temperatures (Figs. 2a-d). At the same time, there is a net rise in mean sea level brought about by these onshore winds, and

Fig. 2. Selected environmental conditions (a-d, h), egg capsule production (e) and shell growth in *Thais clavigera and T. jubilaea* (f, g) at Tanjong Tembeling (3° 45'N, 103° 23'E) for the period January 1991 through April 1992 (no observations were made in July and September 1991). Data for figs. 2a, c & d (in part) were supplied by the Malaysian Meteorological Service, based on readings obtained at the Kuantan Meteorological Station (30° 47'N, 103° 13'E). In fig. 2d, the day emersion period refers to the total number of hours the intertidal region (1 m above chart datum) is exposed to air between 0700 and 1900 hrs per month. Fig. 2e shows the combined total number of egg capsules observed for the two species in a pre-determined area. In figs. 2f, g the means, standard deviations and sample sizes of growth increments (measured as the increase in shell heights of marked individuals) are given for each month. Predicted tidal fluctuations for the study period were obtained from the Tide Tables for Tanjong Gelang port, which is about 20 km north of the study site.


2(a)
Mean monthly Temperature (°C)
Mean maximum
Mean minimum
(b)
Water temperature (°C)
(c)
Total monthly rainfall (mm)
(d)
Total sunshine (hrs)
Day emersion period (same scale)
(e)
Number of egg - capsules per 100 m²
(f)
Thais clavigera
Mean monthly growth (mm)
(g)
Thais jubilaea
Mean monthly growth (mm)
(h)
Tidal fluctuations (m) predicted for Tg. Gelang between Jan. 1991 - April 1992
JAN FEB MAR APR MAY JUN AUG OCT NOV DEC JAN FEB MAR APR
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR

levels of spring tides are at their highest (Fig. 2h). Also, the lower of the two low tides in the semi-diumal tidal regime occurs during the day. Wave action is strong during this period.

During the SW Monsoon, the weather is generally drier and hotter (Figs. 2a, c), and the lowest spring tides are nocturnal. Winds are south-southwesterly, and during hot afternoons significant sea breezes can develop. Wave action is variable, although generally of weaker strength than during the NE Monsoon. The intermonsoonal periods occur twice a year in April and September, during which wind direction is more variable.

Besides being subjected to these seasonal changes in climate, the site experiences daily fluctuations in temperature that are usually greater than the annual range. During a sunny day at low tide, body temperatures of barnacles exposed to direct insolation can be 37° C *(Tetraclita squamosa* on vertical rock surface) and that of *Thais clavigera,* as high as 38° C, without apparent ill-effects (both at Tanjong Tembeling, March 1992, 1300 hrs, air temperature 31 °C). Strong winds during low tide (e.g., during the Northeast Monsoon) can have the reverse effect of lowering temperatures of wet surfaces due to evaporative cooling, and this can be enhanced by rain. The difference in the monthly mean maximum and minimum temperatures for Kuantan is between 7 and 10° C (ASEAN Compendium of Climatic Statistics, 1982)

Fauna

Preliminary observations revealed that the area supported a diverse array of muricid species. These include *Thais bufo* (Lamarck), *T. clavigera, T. jubilaea, T. turbinoides* (Blainville) and *Morula musiva* (Kiener). Amongst them, *T. clavigera* and *T. jubilaea* were most common and equally abundant, with densities exceeding 100 snails m^{-2} in some patches. The two species occupied the same level on the shore between 2 and 2.5 metres above chart datum amongst the barnacles *Tetraclita squamosa* (Bruguiere) and the oyster *Saccostrea cuccullata* (Born). *Thais jubilaea* were occasionally seen to forage farther down. No systematic studies on their diets were done but field observations show that both species feed on *T. squamosa and Cellana testudinaria. Thais jubilaea* (but not *T. clavigera)* was also seen to prey on *T. turbinoides.*

Methods

Between December 1990 and January 1991, the shell heights (defined as the maximum distance between the apex of the shell and tip of the siphonal canal) of a total of 150 *T. clavigera* and *T. jubilaea* were measured to the nearest 0. 1 mm using vernier calipers. The measured snails were marked using paper labels embedded in dental acrylic affixed to the dorsal surface of the shell. A further 200 snails were similarly measured and marked in April 1991. During the period January 1991 to April 1992, the study site was searched thoroughly once a month (except for July and September 1991 when no data were collected) during low tides for marked snails, and their shell heights noted. All snails were returned as far as possible to their previous positions immediately after measurement. Seawater was poured over them so that they adhered to the substrate, a method also found effective by Moran *et al.* (1984).

Reproductive activities of the two species were also monitored monthly or bimonthly from January 1991 through April 1992. This was done by estimating the total number of egg capsules seen within a pre-determined area 10 x 10 m^2 in size, either by counting them in the field or by taking photographs. The capsules adhered to the rock surfaces for about three to four weeks from the time they were laid, so there is only a small likelihood that the capsules were counted twice. Only those with developing embryos, as evidenced by their yellow or brown coloration, were counted, and those which were empty or with purple contents were ignored. While their egg capsules were conspicuous (both species lay them in communal masses), and the topography of the site allowed for a thorough search, the capsules of the two species cannot be distinguished from each other (Tan & Sigurdsson, 1990). As both species were found at spawning sites, the figures obtained are total numbers laid by *T. clavigera* and/or *T. jubilaea*. The temperature of the water surface was also noted each month. Qualitative observations on algal cover and barnacle settlement were also made.

RESULTS

Fig. 2 shows the patterns of growth and egg capsule deposition of the two *Thais* species in relation to environmental conditions experienced at Tanjong Tembeling between January 1991 and April 1992. Changes in the shell heights of *T. clavigera* and *T. jubilaea*, for the period are plotted in Figs. 2f and g. Both species had nearly identical growth characteristics. Mean positive shell growth of more than 0.5 mm month^{-1} in *T. clavigera* was apparent in January and February of 1991, and again in December 1991 and January 1992. In the case of *T. jubilaea*, mean positive shell growth greater than 0.5 mm month^{-1} took place in January and February of 1991, and again between October 1991 through to January 1992. Mean monthly maximum growth rates were 1.7 mm month^{-1} for *T. clavigera* (Fig. 2f) and 1.6 mm month^{-1} for *T. jubilaea* in December 1991 (Fig. 2g). In contrast, a general cessation of growth is apparent between the months of March and August. Mean negative values were obtained for *T. jubilaea* in April and August 1991, although for both species, positive incremental growth of less than 0.5 mm month^{-1} was observed in May 1991.

This seasonal characteristic was also apparent in the combined egg laying activities of the two species (Fig. 2e). Spawning peaks, recorded as the number of egg capsules deposited by *T. clavigera* and/or *T. jubilaea*, occurred during April and May 1991, and again in March 1992. No capsule masses were found in January 1991 and in December 1991.

The temperature of the water surface varied between 27 °C and 33 °C during the year (Fig. 2b), with lower temperatures in November and December. This coincided with short sunshine hours, high cloud cover and high rainfall that accompany the Northeast Monsoon (Figs. 2a, c, d). During the two months, low spring tides occur during the day, and the mid-littoral is usually covered by the tides at night (see Fig. 2d). Strong wave action due to onshore monsoon winds is also characteristic. Algal turf, consisting principally of the rhodophytes *Laurencia, Polysiphonia and Ceramium,* covered substantial areas of the littoral zone. Positive shell growth generally took place during this period.

Conversely, during enhanced periods of egg-laying activity by *T. clavigera* and/or *T. jubilaea* (Fig. 2e), the two species showed little or no growth (Fig. 2f, g). These periods (i.e., April and October 1991; March 1992) coincided with nocturnal low tides, higher daytime temperatures, longer sunshine hours, lower rainfall, and less cloud cover. Wave action is variable during the Southwest Monsoon, but the coast generally experiences weaker wave action than during the Northeast Monsoon. In August 1991, a massive settlement of *Tetraclita squamosa* was evidenced by young barnacles on rocks and surfaces of shells.

The average annual shell growth through one growth season (April 1991 to April 1992), as measured by the increase in shell heights of marked individuals of the two species, are 3.7 ± 1.1 mm year^{-1} (n=18) for *Thais clavigera* and 4.5 ± 1.5 mm year^{-1} (n=8) for *T. jubilaea*. These growth rates were for individuals with initial shell heights of 20 mm or more. Growth rates observed were not significantly different for the two species (t-test, P>0.05). When final shell heights of marked individuals were plotted against their initial heights (Fig. 3a, b), the theoretical H_{max} values were somewhat less than the largest individuals found in the field. Juveniles with shell heights less than 20 mm were observed to grow at a higher rate compared to larger snails.

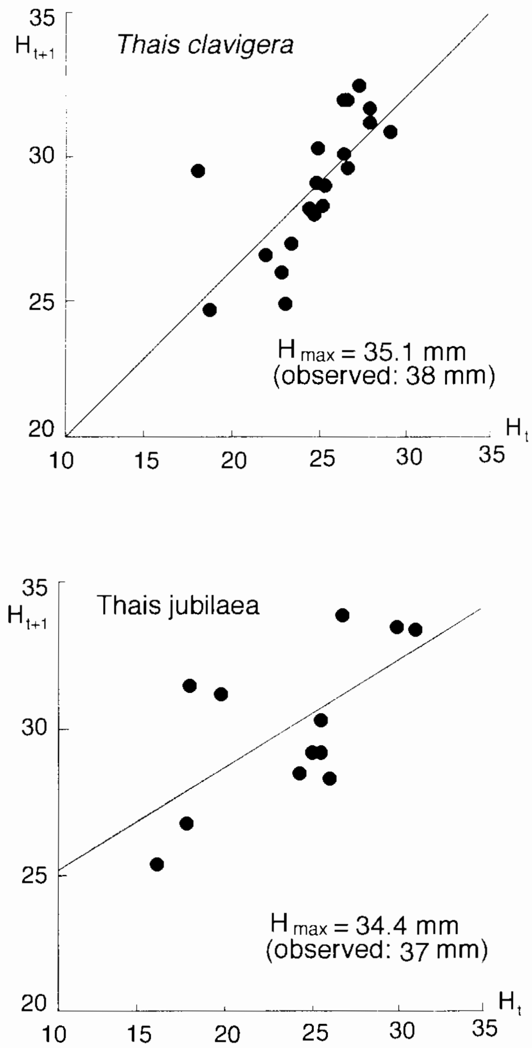


Fig. 3. Walford plots of shell heights (April 1991-April 1992) for (a) *Thais clavigera* and (b) *T. jubilaea*. H_{max} for each species was obtained by the intersection of the line of best fit with the line of no growth ($H = H_{t+1}$). Maximum shell heights observed in the field were also noted.

DISCUSSION

The results of this study clearly show that *Thais clavigera* and *T. jubilaea* have similar seasonal growth patterns. Both species increased in shell height during the Northeast Monsoon. During the Southwest Monsoon, however, there was virtually no change in shell height. Shell growth was particularly marked in January 1991 and again in December 1991, with a second, less prominent peak during May and June 1991. Of the several studies that have examined growth patterns in tropical gastropod species, seasonality in growth has not been observed (e.g., Ward, 1967; Vohra, 1970; Balaparameswara Rao, 1976; Yamaguchi, 1977). Most other studies that document seasonal growth in molluscs were carried out in the temperate or subtropical zones. In these studies, temperature is singled out as the determining cue in triggering growth (e.g., Phillips & Campbell, 1968; Phillips, 1969; Underwood, 1974; Spight, 198 1; Kent, 1983; Moran *et al.*, 1984; Tong, 1986; Gosselin & Bourget, 1989), although availability of food (Chow, 1987), changes in salinity and photoperiod (Houston, 1971) as well as endogenous factors, may be responsible. The reasons as to why shell growth in *T. clavigera* and *T. jubilaea* at Tanjong Tembeling, is restricted to the period coinciding with the Northeast Monsoon remain speculative. During this time of the year, the east coast of peninsular Malaysia experiences strong wave action, net rise of mean sea-level due to on-shore winds (Dale, 1956; Swan, 1971; Chua, 1984), daytime low tides accompanied by heavy rainfall (Dale, 1959, 1960), increased cloud cover (Dale, 1964), and generally lower temperatures (Dale, 1963). Growth, and presumably foraging, therefore took place during periods of low dessication stress. At the same time, the snails must cope with being washed away by strong wave action, osmotic stress during periods of emersion, and perhaps lack of foot space due to high algal cover. It is difficult to relate these conditions with growth in these snails and yet both species clearly grew during this time. Unfortunately food availability was not monitored in this preliminary study, although a massive settlement of the acorn barnacle *Tetraclita squamosa* was observed in August 1991 and this may have contributed to the growth spike in the months following this increase in prey density. Nevertheless it is clear that high, relatively constant temperatures throughout the year (i.e., a mean annual range of between 3-4 °C) does not necessarily mean that tropical organisms grow throughout the year.

Annual growth rates of between 3 and 5 mm year^{-1} as determined in the present study for the two *Thais* species were comparable to those reported by Tong (1986) for *T. clavigera* in Hong Kong. She estimated their growth rates to be between 2 and 5.5 mm depending on whether they were from sheltered or exposed shores. Monthly maximum growth rates were also in line with those reported by Spight (1981) for three species of *Thais* (now *Nucella*) on the Pacific coast of North America, and by Phillips & Campbell (1968) for *Dicathais aegrota* (now *D. orbita*) in Western Australia. As noted in other studies of intertidal snails, juveniles tend to have higher growth rates compared to adults (e.g., Moore, 1938; Frank, 1965; Phillips & Campbell, 1968; Tong, 1986; Chow, 1987), and in some species, the adults stop growing altogether (Spight *et al.,* 1974). In the cases of *T. clavigera* and *T. jubilaea,* their growth characteristics seem to conform to the von Bertalanffy equation with juveniles growing faster than adults, although theoretical values for shell heights obtained from Walford plots were less than observed values. The discrepancies are probably due to the small number of juveniles and larger individuals marked at the start of the observations as well as subsequent losses due to mortality, resulting in a small sample size.

There was little or no evidence for egg capsule deposition during shell growth, while egg capsule numbers peaked during the months of April, May and October 1991 as well as in February, March and April 1992, when the snails were not growing (Figs. 2e, f, g). These periods correspond to the inter-monsoonal period, when low tides are diurnal and the eggs are subject to long periods of emersion. However, egg laying activity was not entirely restricted to the inter-monsoonal months. Smaller numbers of capsules were also deposited during the Southwest Monsoon. This period is characterized on the coast by low rainfall, increased insolation, high daytime temperatures, minimal wave action and nocturnal low tides. The lack of low tides during the day probably offsets the scorching conditions the capsules are subjected to if emersed. Low wave action may facilitate capsule deposition, which requires females to cling onto the substrate with only part of the foot in contact, the frontal part being involved in moulding the capsules to shape. This could be a possible reason as to why they form aggregates when spawning, i.e., to brace themselves against each others' shells to prevent dislodgement by waves, as suggested by Feare (1971). There is little evidence to show that the aggregations at Tanjong Tembeling are a response to predation, as reported for *T. clavigera* in Hong Kong by Abe (1985).

Reproductive seasonality has been observed in several tropical gastropod species (Berry, 1975) but these have mainly been attributed to lunar periodicity in spawning, (e.g., Berry & Chew, 1973; Berry, 1986). As the observations in this study cannot differentiate the egg capsules of the two species, it is not possible to state whether the snails exhibit seasonality in the production of egg capsules. However, it is interesting to note that peak periods of egg deposition (for either or both species) corresponded to periods of negative shell growth in both species. It is tempting to describe such a reciprocal relationship between growth and reproduction as temporal partitioning of the two activities.

Both egg-laying and shell deposition are metabolically expensive (Stickle, 1973, 1975; Palmer, 1983, 1992) and are therefore likely to compete for resources within the animal, imposing restrictions on the timing of such activities. Further studies involving gonad examination are underway to investigate the reproductive activities of muricids in the Malayan region.

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