

Reproductive periodicity of the tropical intertidal chiton *Acanthopleura gemmata* at One Tree Island, Great Barrier Reef, near its southern latitudinal limit

S.S. BARBOSA¹, M. BYRNE¹ AND B.P. KELAHER²

¹Anatomy and Histology, Bosch Institute, F13, University of Sydney, New South Wales 2006, Australia, ²Department of Environmental Sciences, University of Technology, Sydney, New South Wales 2007, Australia

Reproduction in the pantropical chiton Acanthopleura gemmata was examined at One Tree Island, Great Barrier Reef, near the southern limit of its distribution, using gonad histology and gonad index (GI). Gonad growth was associated with the onset of gametogenesis in mid-spring. Fully mature gonads were present from early summer until late autumn. During these months gametes at various stages of development were present in the gonads indicating a continuous pattern of gamete development and release over the six month spawning season. Following the maximum GI (March/April) there was a sharp drop in the index marking the end of spawning. In winter, the gonads entered a rest period and remained small in size. The reproductive pattern of A. gemmata at its southern limit is similar and 6 months out of phase to that reported for populations in the Gulf of Suez, at the northern limit of its distribution. This suggests that photoperiod may be an important factor in modulating reproduction. Reproduction of A. gemmata at One Tree Island is also similar to that for populations in the northern Great Barrier Reef.

Keywords: reproductive periodicity, GBR, One Tree Island, Coral reefs, *Acanthopleura*, chitons

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INTRODUCTION

A number of studies have documented chiton reproductive cycles and most of these have focused on intertidal and shallow subtidal species (Pearse, 1979; Himmelman, 1979, 1980; Soliman & Iskander, 1982; Sakker, 1986; Yoshioka, 1987; Eernisse, 1988; Currie, 1990; Gaymer *et al.*, 2004). Most chitons exhibit a distinct spawning season which may last for days or continue over several months. Short term fluctuations in spawning intensity in chitons may also be superimposed on seasonal reproductive cycles and influenced by factors such as temperature, photoperiod and lunar cycles (Glynn, 1970; Himmelman, 1979; Pearse, 1979; Yoshioka, 1989).

The genus *Acanthopleura* includes many tropical and subtropical species that are prominent in intertidal habitats. *Acanthopleura gemmata* (Blainville, 1825), the species investigated here, inhabits rocky carbonate shores where it forms home-scars that it returns to after nocturnal feeding forays (Chelazzi *et al.*, 1983). These large chitons are important members of the bioerosion guild in tropical regions (Rasmussen & Frankenberg 1990; Barbosa *et al.*, 2008). We documented reproduction in *A. gemmata*, a pantropical species with the widest geographical range known for any chiton extending from 29°N to 23°S (Ferreira, 1986).

Reproduction in *A. gemmata* has been documented for populations in the northern Great Barrier Reef (Stephenson, 1934, as *Acanthozostera gemmata*), the Gulf of Suez (Pearse, 1978, as *Acanthopleura haddoni*) and the northern Red Sea (Pearse, 1978; Soliman & Iskander, 1982, as *Acanthopleura spiniger*). The taxonomy of this widely distributed chiton has been problematic with Ferreira (1986) synonymizing the Indo-West Pacific species as *Acanthopleura gemmata*.

Despite the widespread distribution and local abundance of *A. gemmata* throughout the tropical Indo-Pacific (Ferreira, 1986), there is only scarce information on the reproductive biology of this chiton. We documented reproduction of a population of *A. gemmata* at One Tree Island, southern Great Barrier Reef, near the southern latitudinal limit of its distribution (Ferreira, 1986). It has been suggested that species at the limits of their geographical distribution may exhibit differences in reproductive periodicity compared with populations located near the centre (Billingham *et al.*, 2003). We compared our results to those reported for *A. gemmata* at Low Isles (16°S) in the more tropical northern Great Barrier Reef (Stephenson, 1934), as well as with those reported in the northern Red Sea (26°N) and Gulf of Suez (29°N), near the northern limits of the species distribution.

MATERIALS AND METHODS

Samples (N = 6–10) of *Acanthopleura gemmata* were collected at 4–8 week intervals from April 2006 to May 2007

Corresponding author:
S.S. Barbosa
Email: sergio@anatomy.usyd.edu.au

from a littoral beachrock platform located along the western shore of One Tree Island (23°30'S 152°05'E), Capricorn Bunker Group, southern Great Barrier Reef. Archived preserved specimens collected in October and November 2005 were also used. To provide data for mid-summer, a sample was also collected in January 2008. Sea-surface temperatures for the Capricorn Bunker Group were obtained from the Australian Institute of Marine Science Data Centre (AIMS).

Each chiton was relaxed in 10% MgSO₄ in seawater and placed in 10% formalin in filtered seawater. The total wet body weight of each individual was measured (nearest 0.1 g). Gonads were excised after removal of the dorsal shell valves and their colour and condition were noted. The gonads were blotted dry and weighed to the nearest 0.1 g. It has been shown for other marine invertebrates that fixation does not affect the weight of the tissue and aids in their dissection (Creese, 1980). A gonad index (GI; gonad weight as a percentage of total wet weight) was determined for each animal in samples collected between 2006 and 2008. The size of the chitons collected (4th shell valve width of 25–35 mm) was based on the modal size-class present in the population (Barbosa, personal observation) and made as small as possible to limit the influence that size may exert on the GI (Tyler & Grant, 1983). The gonads were transferred to 70% ethanol for storage.

For histology, gonad tissue was dehydrated in graded ethanols and embedded in paraffin. Sections (7 µm) were stained with haematoxylin and eosin. A preliminary study of gonads from 5 individuals sectioned along their entire length revealed that the gametogenic condition was homogeneous throughout the gonad. Thereafter, we used a 5 mm portion of the central region for histology. Gonads were categorized into the maturity stages used in previous studies of chitons with slight modifications (Gaymer *et al.*, 2004). These stages included: stage I, recovery; stage II, growing; stage III, mature; stage IV, partly spawned; and stage V, spent.

In the testes, the mean width (µm) of the tissue plates was measured with an ocular micrometer. For each male, all the tissue plates in a 500 µm portion of the testis section were measured at their thickest and thinnest regions in 10-measures and the mean width calculated. In each ovary, the diameter of the first 50 oocytes observed, that were sectioned through their nucleolus, was also measured to determine the size-range of eggs present. Non-spherical eggs were measured along their longest and shortest axes and the average of these measures was used to calculate the diameter.

RESULTS

The colour of the gonads assisted in determining the sex of individuals and discerning gonad condition. Recovering gonads were small, thin and dark red. Spent ovaries were small, thin and light brown. As they progressed through the growing stage the ovaries increased in size and became dark brown or olive green. Mature ovaries were black. Late stage oocytes were dark green to black. Spent and growing testes were dark red whereas mature testes were light red and packed with white sperm.

A total of 115 *Acanthopleura gemmata* were collected including 46 females and 69 males. The sex ratio was significantly biased towards males ($\chi^2 = 4.6$; $P < 0.05$).

Histology

OVARY DEVELOPMENT

Recovery stage ovaries had a germinal epithelium lined with small pre-vitellogenic oocytes and early vitellogenic oocytes (70–90 µm diameter) (Figure 1A). In growing stage ovaries, early to mid-vitellogenic oocytes (70–130 µm diameter) were present in the germinal epithelium (Figure 1B). Vitellogenic oocytes became more eosinophilic as yolk accumulated in the cytoplasm. Several vacuoles also appeared and were distributed around the cortical cytoplasm (Figure 1C). In late vitellogenic eggs (130–172 µm diameter) one large vacuole was present and an extracellular hull developed forming spiny projections around the eggs (Figure 1D). These projections increased in length as the eggs developed producing a striking profile in advanced oocytes.

Mature ovaries had an abundance of fully-grown oocytes (160–180 µm diameter) in the lumen (Figure 1E). Pre- and mid-vitellogenic oocytes were also present in the germinal epithelium of mature ovaries. No partly spawned ovaries were observed. Spent ovaries contained pre-vitellogenic and unspawned vitellogenic oocytes which showed signs of degeneration and resorption (Figure 1F). The number and type of oocytes remaining in the ovaries at the termination of the breeding season was variable.

TESTIS DEVELOPMENT

The folds of the tissue plates are a prominent feature of testis development. These plates increase or decrease in width as sperm develop or are shed during spawning (Sakker, 1986; Currie, 1990). Growing testes had wide tissue plates (mean thickness = 57.3 µm, SE = 2.2, N = 5) with a developing spermatogenic layer. Columns of spermatocytes extended towards the testis lumen (Figure 2A). As the testes matured, spermatozoa accumulated in the lumen. Mature testes were filled with spermatozoa (Figure 2B). Spermatogenesis continued through the spawning season replacing released sperm. The tissue plates were thickest (mean thickness = 86.7 µm, SE = 8.4, N = 12) in mature testes. In partly spawned testes, spermatozoa were less densely packed and the lumen was filled with spaces due to the prior release of sperm (Figure 2C). Spent testes contained some remnant spermatocytes but their general appearance indicated that spermatogenesis had finished. Brown pigment globules accumulated along the germinal epithelium of the tissue plates and appeared to be residual lipid droplets potentially marking the end of the reproductive season (Figure 2D). In spent testes sampled in autumn to spring (May–November), the tissue plates were at their thinnest (mean thickness = 26.9 µm, SE = 1.9, N = 10). Recovery stage testes were not observed.

Gonad index

Maximum gonad indices (3.1, 2.3; Figure 3) were recorded in March and April and these were followed by a sharp decrease in the GI by May (1.1, 0.4; Figure 3) marking the end of the spawning season. Through winter to early summer (December) the gonads remained small with little change in weight. Gonad weight increased through summer. The gonad index increased as sea-surface temperature increased

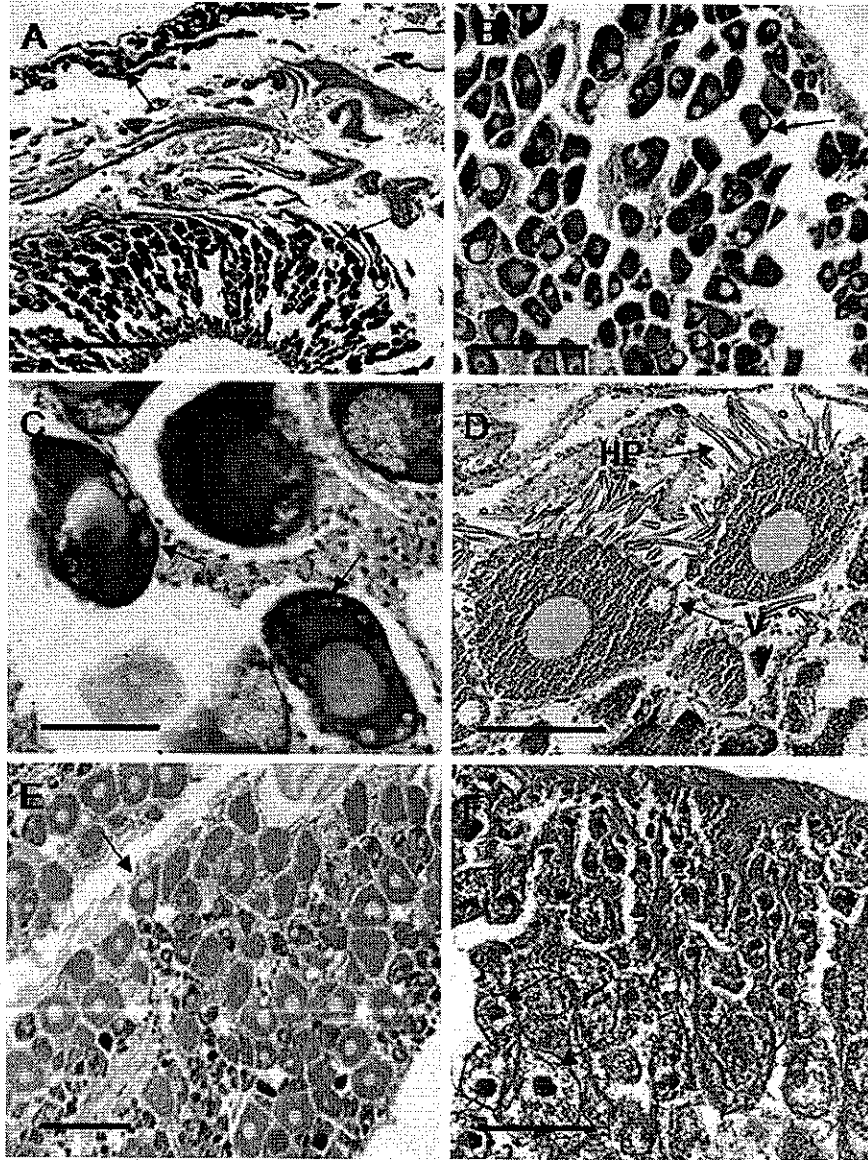


Fig. 1. *Acanthopleura gemmata*, ovary histology. (A) Stage I, recovering ovary with basophilic previtellogenic (arrow) oocytes developing along the germinal epithelium; (B) stage II, growing ovary with developing oocytes (arrow); (C) many vacuoles (arrows) are visible in the cytoplasm of developing vitellogenic oocytes; (D) stage II, growing ovary showing increased number of late vitellogenic oocytes with hull projections (HP) and a large vacuole (V). These advanced oocytes are strongly eosinophilic; (E) stage III, mature ovary filled with fully-grown oocytes (arrow); (F) stage V, spent ovary containing degenerating relict oocytes (arrows). Scales: A = 500 μm , B = 250 μm , C = 100 μm , D = 200 μm , E = 250 μm , F = 250 μm .

with the maximum GI occurring during the warmest sea temperature period (Figure 3).

Reproductive cycle

Gonad histology indicated that gametogenesis in *A. gemmata* was underway in mid-spring (October) with the presence of recovering and growing gonads containing pre- and early-vitellogenic oocytes (Figure 4). The renewal of gametogenesis was asynchronous in the population in October as indicated by the different stages of gonad maturity including the presence of spent animals.

The November gonad samples were also in a variable condition and included individuals with growing and mature gonads (Figure 4). This indicated that spawning

had started and that there was some asynchrony in gonad development and spawning activity in the population. Most chitons in mid-December had growing stage gonads. The January, March and April samples contained mature and partly-spawned specimens (Figure 4). This is also reflected in the high gonad indices recorded at these times (Figure 3). By May, post-spawned and spent individuals were present. Gonad histology indicated that *A. gemmata* spawns over the warmer months of the year from late spring (November) to autumn (May). From late autumn through winter the gonads were spent with no gametogenic activity and this is reflected by the low GI values (Figure 3). Unspawned eggs remaining in the gonads showed signs of degeneration and lysis (Figure 1F).

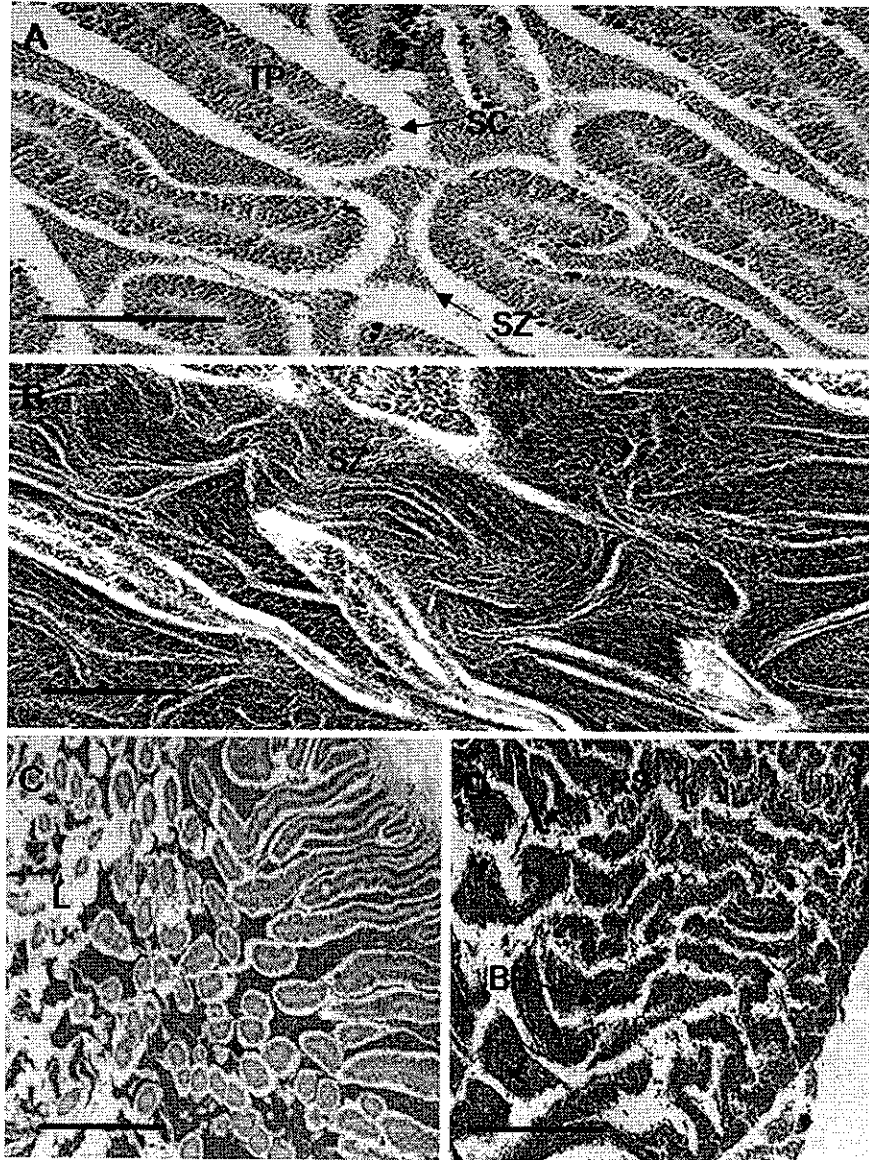


Fig. 2. *Acanthopleura gemmata*, testis histology. (A) Stage II, growing testes exhibit increased spermatogenesis with spermatocyte columns (SC) extending towards the lumen from the tissue plates (TP). As growth proceeds spermatozoa (SZ) accumulate in the lumen (B) stage III, mature testis with spermatozoa (SZ), which are strongly basophilic, densely pack the lumen; (C) stage IV, partly spawned testis showing spaces in the lumen (L) due to the release of spermatozoa; (D) stage V, spent testis with small groups of relict spermatozoa (RS) remaining in the lumen. Globules of lipid-like brown pigment (BP) accumulate along the germinal epithelium. Scales: A = 250 μm , B = 100 μm , C = 100 μm , D = 500 μm .

DISCUSSION

The condition of the gonads indicated that *A. gemmata* at One Tree Island undergo multiple spawning episodes beginning in November and continuing through to May. The most intense period of gamete release occurred in March. The reproductive pattern of *A. gemmata* at its southern limit at One Tree Island (23°S) is similar and 6 months out of phase to that reported for populations at the northern limit of the species distribution in the Gulf of Suez (29°N). In both hemispheres, gametogenesis in *A. gemmata* begins in the spring (Stephenson, 1934; Pearse, 1978; this study). These observations indicate that day length may be an important cue controlling gonad development, as suggested for other chitons (Himmelman, 1979; Yoshioka, 1989) and demonstrated for several marine

invertebrates (Pearse & Eernisse, 1982; Pearse *et al.*, 1986; Byrne *et al.*, 1997; Olive *et al.*, 1998). However, controlled photoperiod experiments, as undertaken for several echinoderm species (Pearse & Eernisse, 1982; Pearse *et al.*, 1986), are required to address this suggestion.

The pattern of reproduction of *A. gemmata* at One Tree Island is also similar to that documented for the northern Australian population (16°S; Stephenson, 1934). The specific timing and duration of spawning in *A. gemmata* exhibited substantial variation between the southern and northern hemisphere (Pearse, 1978; Soliman & Iskander, 1982). In the Great Barrier Reef this chiton undergoes periodic spawning over 6–7 months from mid-spring to early autumn, while in the Gulf of Suez spawning occurs over 3 months from late summer to autumn during the warmest time of the

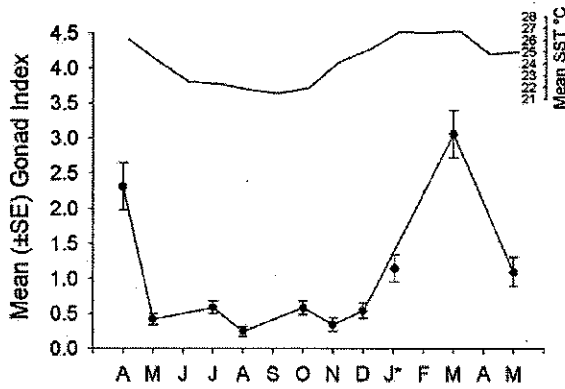


Fig. 3. *Acanthopleura gemmata*, mean (SE) gonad index from April to May (2006–2007). *Sample collected in January 2008. Ten specimens sampled for each month except November (N = 6) and December (N = 9). Insert: plot of mean sea-surface temperature (°C) for the One Tree Island region over the same time period (AIMS, 2008).

year. In the northern Red Sea it is suggested that *A. gemmata* exhibits one short, distinct breeding season in early autumn (Soliman & Iskander, 1982) although, it has also been proposed that Red Sea populations may have multiple spawning events in summer (Pearse, 1978).

Given the broad Indo-West Pacific distribution of *A. gemmata*, subtle differences in reproduction across different parts of its distribution may also be influenced by disparate taxonomy. These chitons have been a challenge for traditional taxonomy (Ferreira, 1986) and there is a possibility that *A. gemmata* may comprise a number of cryptic species. Recent molecular taxonomic studies of similarly widely distributed Indo-West Pacific invertebrates have revealed the presence of cryptic species complexes or incipient regional speciation (Dartnall *et al.*, 2003; Meyer *et al.*, 2005; O'Loughlin & Rowe, 2006). It would be interesting to undertake a phylogenetic study of *A. gemmata* through its range.

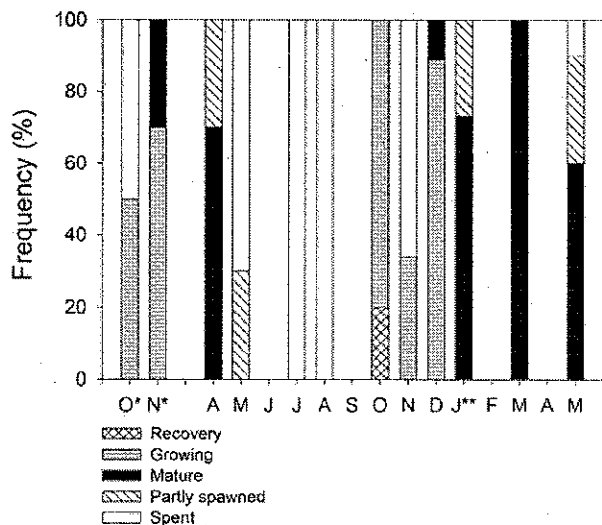


Fig. 4. *Acanthopleura gemmata*, annual gametogenic cycle. Histograms showing the frequencies of maturity stages in histological sections of gonads (males and females combined), at One Tree Island from April 2006 to May 2007. *Archived samples from October and November 2005. **Additional data sampled in January 2008. Ten specimens were sampled for each month except November (N = 6) and December (N = 9).

Orton (1920) (reviewed by Giese & Pearse, 1974; Himmelman, 1978) suggests that sea-surface temperatures may regulate reproductive cycles in chitons, especially in areas where there are large seasonal fluctuations. This may be true for populations of *A. gemmata* located in the southern Great Barrier Reef where temperatures exhibit a predictable seasonal cycle with an 8°C difference from mid-summer (~28°C) to mid-winter (~20°C; Figure 3). Similarly, sea temperatures in the Gulf of Suez fluctuate up to 10°C seasonally (Pearse, 1969). In the Great Barrier Reef, *A. gemmata* initiates gamete release in late spring when water temperatures are increasing. It has been hypothesized that populations of marine invertebrates at locations where sea-surface temperature and day length changes are minimal, might exhibit continuous spawning throughout the year (Pearse, 1978). This is true for *A. granulata* in Panama, where there is minimal fluctuation in sea temperature (Glynn, 1970). In the more tropical conditions of the northern Red Sea (with regard to temperature but not day length), *A. gemmata* spawns in the early autumn (Soliman & Iskander, 1982) but not in mid-summer (see also Pearse, 1978). This finding indicates that the species may shift spawning away from the warmest times of the year in more tropical conditions. There are, however, no data from equatorial populations of *A. gemmata* to determine whether spawning occurs throughout the year where environmental conditions are least variable.

In the northern Great Barrier Reef spawning in *A. gemmata* occurs on the full moon (Stephenson, 1934). A correlation between spawning rhythms and lunar and tidal cycles has been reported for *A. japonica* in the northern hemisphere (Yoshioka, 1989) and several other chiton species (Thorpe, 1962; Glynn, 1970; Pearse, 1979). Although we did not sample *A. gemmata* at One Tree Island with respect to lunar phases, the episodic pattern of gamete release in our study population may be influenced by lunar cues. It is likely that several factors are important in the regulation of reproduction in *A. gemmata*.

The gonad resting stage we observed in *A. gemmata* has been reported elsewhere for this species (Stephenson, 1934; Pearse, 1978; Soliman & Iskander, 1982), and is characteristic of several chiton species (Pearse, 1979; Sakker, 1986; Wells & Sellers, 1987; Yoshioka, 1987; Currie, 1990). As the gonads of the One Tree Island population prepared for spawning, gametes at various stages of development were present. This condition was evident for several months indicating a continuous pattern of gametogenesis and gamete release in spawning events. This pattern has also been documented for other chiton species (Currie, 1990).

Oocyte development in chitons is unusual in the growth of an elaborate extracellular hull during the late vitellogenic stage. In *A. gemmata*, this structure is classified as Type III (*sensu* Risbec, 1946) due to the presence of numerous projections and spines. These structures are suggested to reduce sinking rates and to facilitate the clumping of oocytes and attachment of eggs to the substratum (Pearse, 1979; Eernisse, 1988; Buckland-Nicks, 1993). A prominent feature of oogenesis in *A. gemmata*, and other chitons, is the appearance of large vacuoles at the beginning of the vitellogenic phase in the cortical cytoplasm of developing eggs (Richter, 1976; Gaymer *et al.*, 2004). By the late-vitellogenic stage these appear to coalesce to form one large vacuole. The significance of these structures is not known.

The population of *A. gemmata* at One Tree Island exhibited a bias towards males (1.5:1.0), as also reported for a population of this species in the northern Great Barrier Reef (Stephenson, 1934). Previous studies of gonochoric chitons have shown that sex ratios are often skewed towards males (Pearse, 1979). Glynn (1970) suggests that the bias towards males may be an adaptation to counter sperm dilution by the surf. It has also been suggested that female chitons may change sex with age or have different survival rates (Sakker, 1986). As yet, the adaptive significance of biased sex ratios in chitons and the regulating mechanisms remains poorly understood.

Acanthopleura gemmata in the southern Great Barrier Reef exhibited seasonal spawning in the warmer months of the year in a pattern similar to that described for a northern population (Stephenson, 1934) where summer sea temperatures are on average 2–3°C warmer than at One Tree Island (Done *et al.*, 2003; AIMS, 2008). This suggests that the environmental factors controlling reproduction such as day length, sea temperatures and lunar cycle exert a similar influence on the reproductive periodicity of this chiton along its range in eastern tropical Australia. The predicted 1–2°C rise in sea temperature over the next century (Polaczanska *et al.*, 2007) may not adversely affect the reproduction of *A. gemmata* populations located at their southern limit, as local populations of this species may have an inbuilt capacity for reproduction at higher temperatures or may be sustained by propagules originally from northern areas. However, it is not known how low latitude populations near the equator will fare. The future of high intertidal species, such as *A. gemmata*, remains uncertain as it is unlikely that the physical processes that created its beachrock habitat currently at sea level (see Barbosa *et al.*, 2008) would keep pace with rising sea levels associated with global warming (Polaczanska *et al.*, 2007).

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Correspondence should be addressed to:

S.S. Barbosa
Anatomy and Histology
Bosch Institute, F13
University of Sydney
New South Wales 2006
Australia
email: sergio@anatomy.usyd.edu.au

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