

Reproductive biology of the sandy shore crab *Matuta lunaris* (Brachyura: Calappidae)

O. S. Perez

Department of Marine Biology, James Cook University of North Queensland, Townsville, Queensland 4811, Australia

ABSTRACT: Reproduction of an intertidal calappid crab, *Matuta lunaris*, was studied histologically based on monthly gonad samples from a Queensland, Australia, population between April 1984 and May 1985. Males and females became sexually mature at carapace widths of 43 and 37 mm respectively. Reproductive activity, as determined from gamete production, mating behaviour and brood incubation, is continuous throughout the year. There was marked asynchrony between individual crabs and no apparent seasonality. Adult females could produce more than one egg batch following the single copulatory event; each egg batch comprised about 65 000 eggs.

INTRODUCTION

The reproductive biology of decapod crustaceans is well documented, particularly for brachyurans (reviewed by Sastry 1983). Despite the abundance of literature, however, very little is known of the reproductive biology of the Matutinae (Brachyura: Calappidae), including *Matuta lunaris*. Previous studies of *M. lunaris* have been limited to observations on reproductive behaviour (Perez & Bellwood 1989), the incidence of ovigerous females (Pillay & Nair 1976), and notes on larval development (Rajabai 1959), the latter two being based on populations in India.

Matuta lunaris is a common inhabitant of the surf zone of tropical sandy shores. It has a widespread distribution which extends from the Red Sea to South Africa, Asia and Australia (Chhapgar 1957, Sankarankutty 1962, Guinot 1966, Vannini 1976). In the Great Barrier Reef region, Australia, *M. lunaris* is commonly found in the surf zone of sandy shore beaches on the mainland and some inshore islands (Perez 1986).

Recent studies on the Great Barrier Reef have reported strong seasonal periodicities in the reproductive activity of many invertebrate groups including sponges (Fromont 1988), corals (Harrison et al. 1984, Babcock et al. 1986), polychaetes (Hutchings & Howitt 1988) and molluscs (Braley 1988, Shelley & Southgate 1988). Whether the shore invertebrate species in this region show a similar pattern, however, has not been well documented. The aim of this study therefore was to investigate the reproductive biology of *Matuta*

lunaris, a dominant sandy shore species, and to assess whether a similar pattern of seasonality exists. *M. lunaris* is particularly suitable for such a study as it is abundant and easy to obtain, with most size classes present in the surf zone throughout the year. Three aspects of its reproductive biology were investigated: (1) size at sexual maturity, (2) the annual reproductive cycle, and (3) brood size and egg number.

MATERIALS AND METHODS

Specimens of *Matuta lunaris* (Forskål) were collected from Pallarenda Beach, Townsville, Australia (19° 11.8' S, 146° 46.6' E) between April 1984 and May 1985. All specimens were collected during the mid-falling tide, using a 25 mm mesh, 10 m × 1 m seine net dragged along the substratum of the surf zone parallel to the shore. Each drag sampled an area of ca 250 m². All crabs were brought alive to the laboratory for analyses. Each crab was weighed to the nearest 0.1 g and the carapace width measured to the nearest 0.1 mm. Carapace width is defined as the maximum width of the carapace including the lateral spines. All crabs were dissected within 3 d of capture.

A preliminary study of the size at sexual maturity based on gonad states was undertaken. In both sexes, a minimum of 5 individuals from each 5 mm carapace width size class were dissected. The gonads were removed and fixed in Bouin's fluid for 1 wk. Fixed gonads were washed in 70 % ethanol, dehydrated and

cleared in an alcohol-xylene series, embedded in paraffin wax and sectioned at 6 μm . Sections were stained in Harris haematoxylin and eosin and mounted in synthetic mounting medium (DPX; B.D.H. Chemicals). The histological criterium for sexual maturity in males was defined as the presence of mature sperms in the spermatid ducts of the testis, whilst in females, it was the presence of mature ova in the ovary. Mature gametes were identified following the histological descriptions of other brachyurans (e.g. *Portunus sanguinolentus* [Ryan 1967a,b] and *Chionoecetes opilio* [Kon & Honma 1970a,b]). The size at sexual maturity based on gonad states was expressed as the minimum size at which mature gametes were observed in the gonads.

To investigate the annual reproductive cycle, sampling was carried out at monthly intervals. To avoid any variability in the reproductive states as a result of lunar cycles, all samples were collected within 2 d of the full moon of each month. The temporal pattern of reproductive activity was determined using a combination of the gonad index method, histological analysis of the testis and ovaries and the incidence of ovigerous females, mating pairs and females with ripe ovaries. A minimum of 10 mature males and 12 mature females were dissected each month, following Boolootian et al. (1959). The gonads were removed and processed following the procedure described above. In addition, the female ovaries were weighed to the nearest 0.001 g using an electric analytical balance and the gonad index determined following Giese & Pearse (1974) and Grant & Tyler (1983a).

In testis sections, the cells within 50 randomly selected lobes in each crab were classified based on the 4 stages of spermatogenic development: spermatogonia, spermatocytes, spermatids and spermatozoa. The percentage of lobes containing a particular cell type were calculated for each individual and the mean frequency calculated for 10 to 12 individuals each month.

In ovarian sections, the sizes of oocytes/ova were measured using an eyepiece graticule calibrated against a stage micrometer. Only those oocytes or ova sectioned through the nucleus were measured. One hundred oocytes and ova were measured in each crab and grouped into 4 size classes based on cell diameter, following the methods of Grant & Tyler (1983b). The percentage of oocytes in each size class was then calculated for each individual and the mean frequency calculated for 12 individuals each month. As there was a recognizable spent stage in the gonads of female *Matuta lunaris*, sections of spent ovaries were classified as such, without attempting to measure the oocytes.

Ovigerous females were dissected within 1 d of capture. The ovaries were removed, weighed and processed following the procedure described above. The egg

mass was removed from the abdomen, weighed to the nearest 0.001 g and its colour noted. Three subsamples were taken, weighed to the nearest 0.001 g and the number of eggs counted. The mean number of eggs per egg mass was calculated following Fielding & Haley (1976) and Du Preez & McLachlan (1984).

Statistical comparisons between months were undertaken using 1-way ANOVAs, following Zar (1974). All percentages were log-transformed prior to testing.

RESULTS

Size at sexual maturity

Results are summarized in Table 1. The smallest sexually mature male was 43.5 mm carapace width, whilst the smallest sexually mature female was 41 mm carapace width.

Annual reproductive cycle

There appears to be no distinct seasonality in the male reproductive cycle. Spermatogonia, spermatocytes, spermatids and mature spermatozoa were consistently found in the lobes of the testis throughout the study period (Fig. 1). Although there was a significant difference between months in the mean number of lobes containing spermatogonia ($F = 4.793$, $df = 13,119$, $p < 0.01$) and spermatids ($F = 2.365$, $df = 13,119$, $p < 0.05$), there was no significant difference between months in the mean number of lobes containing spermatocytes ($F = 1.340$, $df = 13,119$, $p > 0.05$) or mature spermatozoa ($F = 1.944$, $df = 13,119$, $p > 0.05$). The frequency of mature males with testes containing mature spermatozoa was relatively high throughout

Table 1 *Matuta lunaris*. Sizes at sexual maturity based on relative frequency (%) of individuals dissected with mature gametes in the gonads

Carapace width (5 mm size classes)	Male		Female	
	No.	Mature (%)	No.	Mature (%)
25.0–29.9	7	0	5	0
30.0–34.9	5	0	6	0
35.0–39.9	10	0	6	0
40.0–44.9	9	40	15	100
45.0–49.9	8	47	7	100
50.0–54.9	10	83	7	100
55.0–59.9	10	100	6	100
60.0–64.9	5	100	5	100
65.0–69.9	5	100	no individuals	

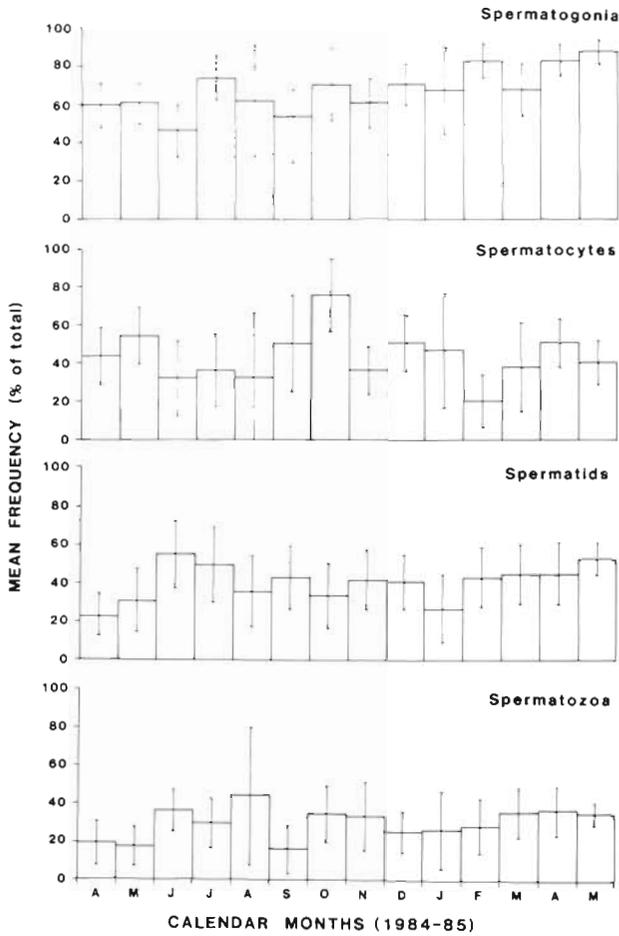


Fig. 1 *Matuta lunaris*. Summary of relative frequency of male gametogenic cell types each month, expressed as mean percentage of lobes containing each cell type. NB. Lobes often contain more than one cell type. Vertical bars: 95% CI, n = 12 in all months except September where n = 10

the study period, ranging from 62.5 to 100% with a mean of 94.4% ($\pm 2.45\%$, 95% CI).

As in male *Matuta lunaris*, there is no strong seasonality in the female reproductive cycle. Marked ovarian activity was observed in most months of the year, with the single exception of December 1984 where the mean gonad index was relatively low and no mature ova nor females with ripe ovaries were recorded (Figs. 2 and 3). The frequency of ovarian cells measuring 1 to 50 μm varied significantly between months ($F = 2.240$, $df = 13,157$, $p < 0.02$) but the frequencies of oocytes measuring 51 to 100 μm and 101 to 150 μm did not ($F = 0.915$, $df = 13,157$, $p > 0.25$, and $F = 0.722$, $df = 13,157$, $p > 0.25$, respectively). Although there was a significant difference between months in the mean gonad indices ($F = 2.239$, $df = 13,157$, $p < 0.02$) and in the frequency of mature ova in ovarian sections ($F = 1.883$, $df = 13,157$, $p < 0.05$), this appeared to be a result of the atypical data in December 1984, as there was no

significant difference between the other months (Student-Newman-Keuls, $p > 0.05$). The percentage of mature females with ripe ovaries varied only slightly throughout the year, with an increase in May and September 1984 and no females with ripe ovaries in December 1984. Ovigerous females were only recorded between August 1984 and March 1985, whilst mating pairs were found in most months of the year. However, no distinct patterns were apparent in either parameter.

In addition, there was no apparent relationship between the mean monthly gonad indices, the frequency of ovigerous females and the frequency of mating pairs. These observations and the large degree of within-sample variability in the individual gonad indices and ovarian cell frequencies each month suggest a lack of reproductive synchrony among individuals in the population.

Biology of ovigerous females

A total of 26 ovigerous females were collected from the study area between August 1984 and March 1985. The smallest egg-bearing female was 40.7 mm

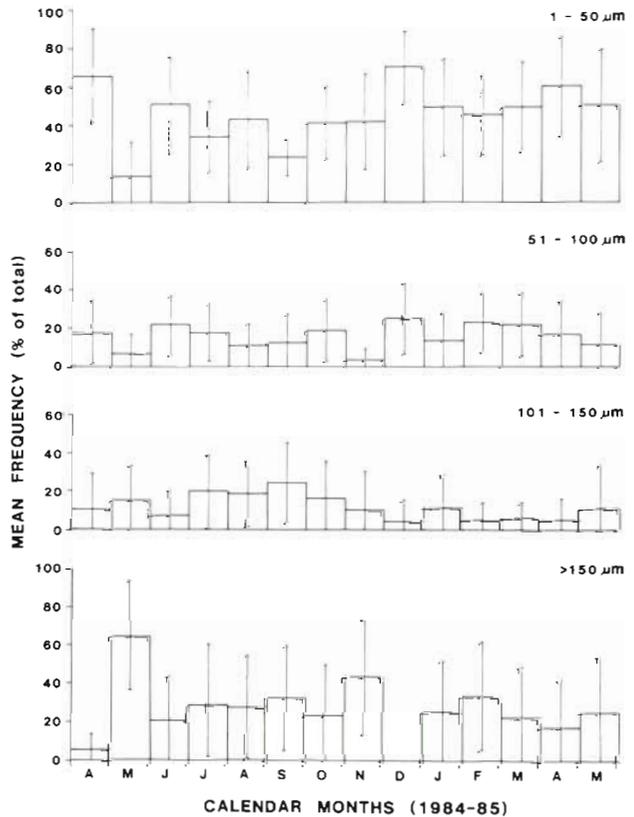


Fig. 2 *Matuta lunaris*. Summary of relative frequency of ovarian cell sizes each month, expressed as mean percentage of the total number of cells examined in each size class. Vertical bars: 95% CI, n = 12 in all months

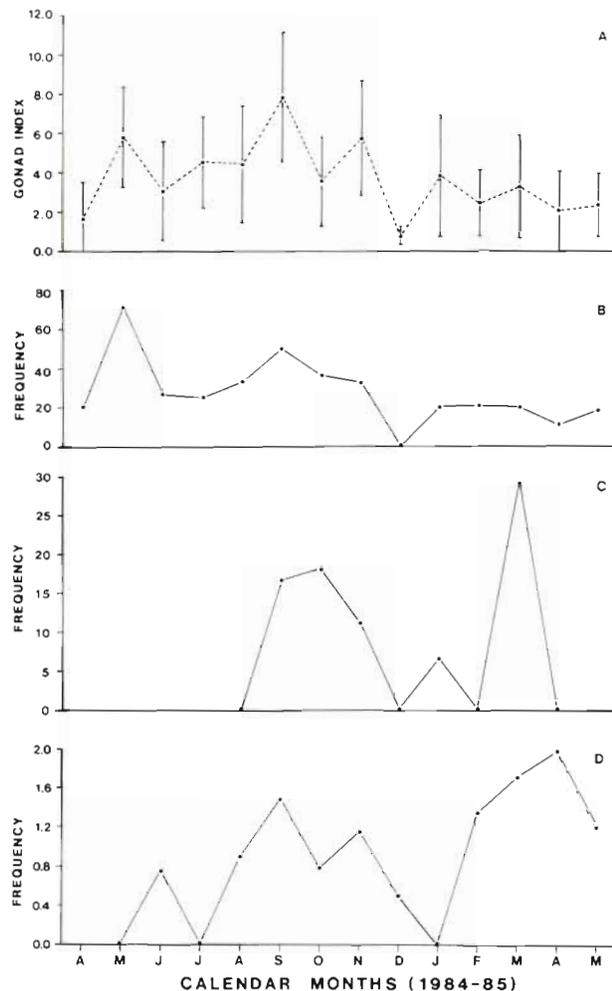


Fig. 3. *Matuta lunaris*. Annual reproductive activity expressed in terms of: (A) mean monthly female gonad index \pm 95% CI ($n = 12$); (B) relative frequency of adult females with ripe ovaries, expressed as a percentage of the total number of adult females collected per month; (C) relative frequency of ovigerous females, expressed as a percentage of the total number of adult females collected per month; and (D) relative frequency of mating pairs, expressed as a percentage of the total number of crabs collected per month

carapace width. Three stages of brood development were recognized. Stage I, newly laid, Stage II, developing; and Stage III, mature. There was no detectable trend in the occurrence of these brood stages. The results of this study, expressed separately for each of these stages, are summarized in Table 2.

Histologically, it appears that mature females can produce more than one brood. Marked ovarian activity was observed in most ovigerous females with the exception of those with ovaries in the spent phase. In all individuals, oogonia were present in considerable numbers. All the females with Stage II egg masses and 83.3% of females with Stage III egg masses had ovaries exhibiting advanced stages of vitellogenesis (Table 2).

In addition, all the ovigerous females had spermathecae filled with spermatozoa.

The number of eggs per brood ranged from 40 000 to 100 000 with a mean of ca 65 000. Although both the number of eggs per brood and the brood weight did not vary significantly with carapace width ($r = 0.0036$, $F = 0.0310$, $p > 0.05$, and $r = 0.0064$, $F = 0.0548$, $p > 0.05$, respectively), a significant difference was found between the mean number of eggs per brood and the stage of development (1-way ANOVA, $F = 9.542$, $df = 2,7$, $p < 0.05$) with an apparent decrease in the mean number of eggs per brood in Stages II and III egg masses. This may, however, be a result of the limited number of ovigerous females available ($n = 10$). The mean brood weight and egg diameter did not change markedly with development.

DISCUSSION

Size at sexual maturity

Results indicate that sexual maturity in *Matuta lunaris* occurs after the puberty moult. Histologically, the onset of sexual maturity is characterised by the development of gametes in the gonads. In males, this occurs between 40.0 and 50.0 mm carapace width, whereas in females, it is between 35.0 and 40.0 mm carapace width. These sizes correspond with sizes at which the puberty moult occurs for each sex (Bellwood & Perez 1989) and at which sex-related changes in the relative growth of several morphological characters have been observed (e.g. abdomen width; Perez 1986b). It is interesting to note that, for females, the single copulatory event also occurs at this size (Perez & Bellwood 1989).

Biology of ovigerous females

There is evidence to suggest that *Matuta lunaris* females can produce more than one batch of eggs from the single copulatory event. Firstly, the spermathecae of all ovigerous females examined were full of spermatozoa. Sperm storage has been reported in other brachyuran species including *Chionoecetes bairdii* (Adams & Paul 1983), *Halicarcinus australis* (Lucas & Hodgkin 1970) and *Portunus sanguinolentus* (Ryan 1967b). In all cases, the females were observed to produce multiple egg batches within the breeding period without subsequent copulation.

Secondly, marked ovarian activity characterized by high gonad indices and advanced states of vitellogenesis was observed in most ovigerous females. In addition, there was a characteristic proliferation of oogonia and newly formed oocytes into the empty

Table 2. *Matuta lunaris*. Observations on the biology of ovigerous females. Mean values are expressed as mean \pm 95% CI

	Stage ^a		
	I	II	III
A. Reproductive state			
Individuals examined	5	3	18
Minimum carapace width (mm)	43.5	41.9	40.7
Mean carapace width (mm)	46.1 \pm 3.8	43.4 \pm 3.9	46.5 \pm 1.3
Mean body weight (g)	1.55 \pm 1.4	3.42 \pm 2.8	3.46 \pm 0.9
Mean % of ovarian cell stages			
1–50 μ m	55.2 \pm 29.2	22.0 \pm 15.5	36.3 \pm 11.1
51–100 μ m	28.8 \pm 29.2	8.3 \pm 18.3	5.4 \pm 6.8
101–150 μ m	14.6 \pm 40.5	69.7 \pm 29.6	56.9 \pm 14.3
> 150 μ m	2.0 \pm 5.6	0.0 \pm 0.0	1.4 \pm 2.6
Full spermatheca	100 %	100 %	100 %
Spent ovaries	60 %	0 %	17 %
Advanced vitellogenesis	20 %	100 %	83 %
B. Reproductive effort			
Individuals examined	4	2	4
Mean brood weight (g)	1.66 \pm 0.42	1.21 \pm 0.36	1.26 \pm 0.47
Mean egg size (μ m)	291 \pm 2.08	279 \pm 0.93	274 \pm 3.19
Mean egg number	86990 \pm 30837	44450 \pm 41763	49270 \pm 13756
^a Stage I: newly laid, no cleavage, clear, bright orange yolk; II: developing, eye pigment visible in some embryos, orange-brown or tan egg mass; III: mature, zoea larvae visible with distinct pigmentation, black-brown egg mass			

spaces previously occupied by ova in the ovaries of those individuals in the 'spent' phase. The occurrence of ripening ovaries simultaneous with brooded eggs has been reported in other brachyuran species (Ryan 1967b, Pillay & Nair 1971) and several anomuran species (Ameyaw-Akumfi 1975, Varadarajan & Subramoniam 1982). This has been interpreted as an indication of the potential to produce a second brood during the same breeding season (Pillay & Nair 1971).

The number of eggs produced per egg batch by *Matuta lunaris* varied widely, ranging from 40 000 to 100 000 eggs with a mean of about 65 000 eggs. This is notably higher than the estimated number of eggs per brood recorded from *M. lunaris* in India (1100 to 2580 eggs; Pillay & Nair 1976). Mean egg diameter, however, was comparable with those recorded by Rajabai (1959) and Pillay & Nair (1976). The size and number of eggs in *M. lunaris* are consistent with the general observations of Bliss (1968) that swimming crabs and lower intertidal crabs produce a relatively large number of small eggs when compared to other brachyuran species.

Annual reproductive cycle

The annual reproductive cycle of *Matuta lunaris* on Pallarenda Beach was continuous, with uninterrupted breeding throughout the year. In males, this was indicated by: (1) the consistent presence of spermatogonia, spermatocytes, spermatids and mature spermatozoa in

the lobes of the testes throughout the study period, with no significant difference between months in the mean number of lobes containing spermatocytes or spermatozoa, and (2) the relatively high frequency (> 62 %) of mature males with testes containing mature spermatozoa in each month of the year. In females, continuous reproduction was indicated by: (1) marked ovarian activity in most months of the year with no apparent patterns of seasonality in the fluctuations of the gonad indices, (2) the presence of mature females with ripe ovaries in 13 mo of the 14 mo study period, and (3) the presence of mating pairs in most months of the year, with no distinct pattern of seasonality in their occurrence.

Although in the past it was generally believed that tropical invertebrate species breed continuously throughout the year (Semper 1881 in: Pillay & Nair 1971, Stephenson 1934, Giese & Pearse 1974), recent studies have reported seasonal periodicities in the reproductive cycles of many tropical groups such as sponges (e.g. Fromont 1988, Ilan & Loya 1988), corals (e.g. Harrison et al. 1984, Babcock et al. 1986), polychaetes (e.g. Caspers 1984, Hutchings & Howitt 1988) and molluscs (e.g. Nagabhushanam & Deshpande 1982, Braley 1982, 1988). Among the crustaceans, several tropical species have also been reported to demonstrate seasonal reproduction, for example *Panulirus argus* (Kanciruk & Herrnkind 1976), *Cryptodormia hilgendorfi* (McLay 1982), *Scylla serrata* (Hill 1975) and *Portunus pelagicus* (Potter et al. 1983). The majority of tropical crustacean species, however, continue to be reported to breed for

an extended period or even continuously throughout the year. This includes most species of anomurans (Ameyaw-Akumfi 1975, Subramoniam 1979, Varadarajan & Subramoniam 1982) and many brachyurans (Ryan 1967a,b, Pillay & Nair 1976, Du Preez & McLachlan 1984, Gotelli et al. 1985, reviewed by Sastry 1983). *Matuta lunaris* therefore appears to be a typical tropical brachyuran species in that it demonstrates a continuous reproductive pattern.

It is interesting to note, however, that upon close examination, the reproductive activities of most continuously breeding tropical species often fluctuate to some extent throughout the year. Examples of such species include the hermit crab *Clibanarius clibanarius* (Varadarajan & Subramoniam 1982) and the brachyurans *Portunus sanguinolentus* (Ryan 1967a,b) and *Ovalipes punctatus* (Du Preez & McLachlan 1984). In this respect, *Matuta lunaris* is unusual in that the fluctuations in its reproductive intensity are slight, showing no significant differences between months. This degree of continuity, with no significant differences, has not been demonstrated previously in other brachyuran species.

Finally, it must be noted that whilst the population of *Matuta lunaris* from Pallarenda Beach reproduces continuously throughout the year, the breeding pattern of populations of *M. lunaris* in India was reported by Pillay & Nair (1976) to be seasonal. Such intraspecific variability in the reproductive patterns of geographically separate populations of a single species has been observed in other brachyurans, such as *Portunus pelagicus* (Rahaman 1967, Ryan 1967a,b, Pillay & Nair 1971) and *Helice crassa* (Nye 1977, Jones 1980). These differences have been explained in terms of geographic differences in temperature, salinity and food availability. A study of the environmental factors which determine the reproductive pattern of *M. lunaris*, therefore, would be of considerable interest.

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