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SEXUAL MATURITY, REPRODUCTIVE CYCLES, AND JUVENILE RECRUITMENT OF *PERISESARMA GUTTATUM* (BRACHYURA, SESARMIDAE) AT PONTA RASA MANGROVE SWAMP, INHACA ISLAND, MOZAMBIQUE

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A B S T R A C T

The sesarmid *Perisarma guttatum* is the most abundant crab species inhabiting the lower mangrove areas at Inhaca Island, and presumably an ecologically important species in this habitat. Among the scarce available information on its population ecology, this species is known to follow a semilunar rhythm of larval release, with breeding probably extended year-round. In this study, a population of *P. guttatum* was examined, from which estimates of sexual maturity were carried out for both sexes, and breeding activity was monitored to describe short-term variation of reproductive intensity. In an attempt to relate reproductive cycles with recruitment patterns of young, a systematic random sampling design was used to quantify and describe the juvenile population. Reproductive parameters in adults and density estimates for juveniles were obtained from samples taken at 4-d intervals over a 3-mo period. Reproductive activity increased over the study period. Females released larvae around the new and full moon, but lunar variation of the ovigerous ratio with peaks preceding full moon periods indicated that different breeding groups may account unevenly for the reproductive output of the population. Very young recruits made up the larger fraction of the juvenile population, and their density increased from the beginning to the end of the sampling season. Density variation pattern of first-crab stages followed fortnight cycles, but slow growth prevented recruitment pulses to be tracked in size-frequency distributions. Polymodal distributions corresponded to recent recruits and older juveniles originating from previous settlement seasons. Growth rates of identified age groups suggest that sexual maturity in females is likely to be achieved after 2 years or more.

Recent research has demonstrated that sesarmid crabs play an important ecological role in mangrove ecosystems. These organisms recycle large quantities of organic matter, affect species composition of the mangrove vegetation by selective seed predation, and cause deep physical changes of the substratum because of burrowing activity (see Lee, 1998, for review). Grapsoid crabs are usually distributed according to vertical zonation patterns in estuarine systems (Snelling, 1959; Hartnoll, 1975; Willason, 1981; Frusher *et al.,* 1994). This is also the case at Ponta Rasa Mangrove, where *Perisesarma guttatum* (Milne Edwards, 1869) is the most abundant sesarmid in the lower intertidal, usually associated with the root system of *Rhizophora mucronata* Lamarck, 1804. However, little is known of this species' biology and ecology.

Gove and Mambonhe (2000) described semilunar rhythms of larval release in this species, as described for several estuarine crabs. Such timing is thought to enhance larval survivorship by minimising predation risk and avoiding lethal conditions of salinity and temperature (see Forward, 1987, for review). In order to achieve precise synchrony of larval hatching, preceding gonad development and egg extrusion should also be under control. In contrast to the large amount of available information on the seasonal reproductive patterns of estuarine crabs (e.g., Seiple, 1979; Jones, 1980; Fukui and Wada, 1986; Emmerson, 1994), short-term changes are largely unknown. Taking samples at shorter intervals has provided new insight regarding some reproductive processes. In this sense, a closer view of reproductive behaviour, ovarian development, stage of attached embryos, and frequency of ovigerous females has allowed quantification of multiple brooding and egg-incubation periods in brachyuran species of *Sesarma* Say, 1817, and *Uca* Leach, 1814, apart from revealing new temporal variation trends still to be adequately interpreted (Pillay and Ono, 1978; Salmon and Hyatt, 1983; Zimmerman and Felder, 1991).

Early juvenile recruitment may depend on a

number of factors, such as habitat complexity (McMillan *et al.,* 1995; Stevens and Kittaka, 1998; Loher and Armstrong, 2000), predation (Dittel *et al.,* 1996; Fernández, 1999; Banks and Dinnel, 2000), and the presence of adult conspecifics (O'Connor, 1993; Gebauer *et al.,* 1998). Yet, contrasts in postlarval supply between areas exposed to different hydrologic dynamics were indicated to account for recruitment contrasts in the American lobster (Wahle and Incze, 1997). Larval availability is ultimately dependent on the reproductive output of parental stocks. Such cause-effect relationship may be eventually evidenced in closer systems, such as sheltered small estuaries, where regressing postlarvae may be correlated to past reproductive activity of the parental population.

Understanding the settlement and juvenile recruitment mechanisms of a given population would shed some light on the actual adaptive features of reproductive strategy. Sampling for juvenile stages is, however, a difficult task, involving the identification of settlement grounds and subsequent nursery areas. Ontogenetic habitat shift leading to spatial segregation of adult and young has been often documented in intertidal brachyurans (e.g., Heck and Hambrook, 1991; Spivak *et al.,* 1994; Flores and Negreiros-Fransozo, 1999), with young recruits densely aggregated within structurally complex microhabitats. Therefore, standard collecting techniques are likely to produce biased samples against smaller individuals (Hartnoll and Bryant, 1990). Specific sampling designs along adequate temporal scales and framed within recognised recruiting areas should thus be employed for studies on the juvenile ecology of most species. In the specific case of mangrove crabs undergoing predicted rhythms of larval release, it would be particularly interesting to verify whether density of first-crab stages follows equivalent temporal patterns. Because of extended year-round breeding (Sastry, 1983) and shorter molt-reproduction cycles (Conan, 1985) taking place in tropical mangrove species, commonly used long-term sampling protocols based on monthly observations are likely to fail to identify age groups. Taking advantage of short-term variation patterns may be thus an alternative to gather important information on the population dynamics of these organisms.

The present study focuses the reproductive ecology and juvenile recruitment patterns in *Perisesarma guttatum*. Sexual maturity is estimated and short-term reproductive cycles are described. Density of juveniles and their size structure were followed with the aim to relate temporal variations of reproductive intensity and recruitment of young. Size-frequency distributions were further analysed in an attempt to distinguish different pulses of incoming juveniles. Considering this particular case study, such analyses were thought to render useful information concerning early juvenile growth and recruitment dynamics into the studied population.

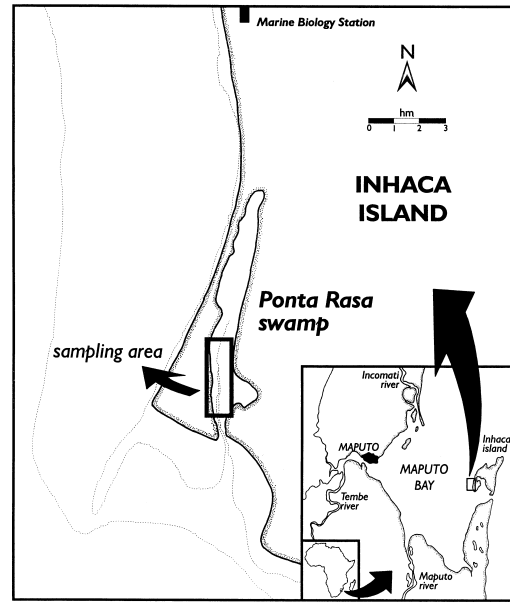

Fig. 1. The study region, highlighting the sampling area.

Materials and Methods

Study Site

Field work took place at Ponta Rasa mangrove, Inhaca island, Mozambique (Fig. 1). Although located in a subtropical latitude (26°S), the climate at Inhaca is considered to be tropical (McNae and Kalk, 1969), and its biota includes species found along the Eastern African coast, for what the region is regarded as transitional between the Northern tropical and Southern temperate biogeographic provinces.

The mangrove area where this study was conducted borders the Ponta Rasa creek, which is maintained by rainfall and fresh ground water, without any riverine input into the system. At low tide level, this creek is 500-m long and on average 3-m wide and 1-m deep. Direct effect of evaporation after flooding and rainfall may cause high oscillations of temperature and salinity. Other characteristics of this area are described by Hoguane *et al.,* 1999.

Collections of Adults and Larger Juveniles

Adult and subadult crabs were obtained at 4-d intervals, from 12 November 1999 to 19 January 2000, along

Table 1. Description of gonad developmental stages in *Perisesarma guttatum*.

Stage	Description	
	Females	Males
1	Not visible	Not visible
2	Very thin, filamentous; yellow with no visible oocytes	Vas deferens very thin, visible only under magnification; translucent
3	Ovaries still reduced; bright orange with visible oocytes	Vas deferens clearly visible
4	Ovaries occupying a relatively large space; orange	Testes partially convoluted; whitish
5	Ovaries larger; red with distinct oocytes	Testes convoluted; white
6	Ovaries occupying most available space; dark red to brown with clearly visible eggs	Testes enlarged; bright white

the margins of Ponta Rasa mangrove creek. Collections were carried out by two people over 2-h periods at low tide while crabs were foraging in the sediment surface or within the *Rhizophora mucronata* root system. This catch effort was designed to obtain about 50 individuals at each sampling date. In order to increase the size range for allometric analyses, a collection of juveniles ($n = 169$) was also obtained by carefully scanning the sediment surface near the root system. Captured crabs were placed inside plastic bags in the field and frozen immediately upon arrival at the Marine Biology Station.

Morphometric Analyses

Larger crabs were sexed according to abdominal shape while smaller ones were observed under a stereomicroscope to examine the morphology of pleopods. The dimensions chosen for morphometric analyses were carapace width (CW), distance between frontmost spines of carapace; chela height (ChH), distance between uppermost point of dactyl insertion and lowermost region of propodus; chela length (ChL), maximum length measured from tip of propodus; gonopod length (GL), distance between the lowermost point of protopod insertion and the curve just before distal tip; and abdomen width (AW), taken between the third and fourth somite both in males and females. Measurements of larger dimensions were carried out with vernier calipers while smaller ones (< 10 mm) were performed under a stereomicroscope provided with a micrometric eyepiece. All measurements were recorded to the nearest 0.1 mm. Allometric growth of all dimensions referring to carapace width was estimated using the allometric equation $Y = aX^b$ (Huxley, 1950). These relationships were log-linearized (base 10), and the computer program Mature II (Somerton, 1983) was used to define growth phases in cases where fitting more than one regression line resulted in a significant decrease of total residual sum of squares. The puberty molt is assumed to occur at the size where inflection points delimiting young and adult growth phases were located.

Table 2. Density estimates, standard deviations and coefficients of variation for the tested sampling methods. Densities are expressed in crabs·m^{-2}.

Method	Density	SD	CV
Corer (10 cm deep)	11.32	11.79	104.19
Quadrat (3 cm deep)	10.40	7.61	73.19
Quadrat (visual)	15.73	11.37	72.25

Analyses of Reproductive Parameters

Adult and subadult crabs obtained were also dissected for macroscopic examination of gonads. According to shape, colour, and size, gonads were classified into six different stages (Table 1). Individuals with gonads in stages 3–6 were considered mature. At this stage, bright orange ovaries had already started the vitellogenic development phase (Sastry, 1983) and spermatophore density becomes much higher (Campbell and Eagles, 1983). The logistic equation, $Y = 1/(1 + A \cdot e^{Bx})$, was used to describe the relationship between mature proportion (Y) and size (X), standing as the midpoint of examined 3-mm CW class intervals. A linear regression model was used to fit the data after transformation (Somerton, 1980; appendix 1). The size at 50% maturity was then calculated and regarded as a second estimate of size at the onset of sexual maturity. The development stage of embryos in captured ovigerous females was assessed following Boolootian *et al*. (1959). In order to better assess temporal variation patterns of the studied parameters, 95% confidence intervals were calculated for the proportion of ovigerous females, and interquartile range for the ranked variables gonad condition and development stage of embryos.

Density Estimates and Size Structure of the Juvenile Population

During initial field observations, it was observed that the bulk of juvenile crabs does not shelter in specific microhabitats. Instead, they are mainly found over the mudflats within a close distance from the creek margin. Three different sampling techniques were initially tested in order to obtain adequate density estimates of juveniles. As a pilot study, twenty sampling units were randomly assigned for each method over both margins of the mangrove creek. The sampling frame was established from the creek low-tide water level to the upper limit of the *Rhizophora mucronata* root system, covering a 4–5-m wide belt. Mean count values, coefficients of variation (Table 2) and sampling effort were compared as to establish the best sampling method. Corer sampling (∅ 15 cm, 10 cm deep) was the most time-consuming method due to the great amount of sediment that needed to be sieved, and provided the less precise estimates. Further field observations suggested that *Perisesarma guttatum* juveniles do not shelter in the deep grounds of fiddler crabs' burrows, but indistinctly used any available shelter within the first sediment layer. Therefore, two different techniques using 50 × 50 cm quadrats were also tested. For both methods, a 6-cm high square frame enclosed

Table 3. Results of studied allometric relationships. ChH = chelar height; ChL = chelar length; AW = abdomen width; GL = gonopod length; M = males; F = females; Y = young; A = adult; + = positive allometry; – = negative allometry; 0 = isometry; log indicates base 10 logarithms.

Dimension		*n*	Linearized equation log Y = log a + b log X	r^2	Allometric level[1]	Somerton's *F* test	
						Value[2]	Cut point (mm)[3]
Ch H	M	505	log CW = –1.27 + 1.63 log ChH	0.980	+		
	F	252	log CW = –1.04 + 1.35 log ChH	0.980	+		
Ch L	YM	9	log CW = –0.56 + 1.24 log ChL	0.981	+	18.4	9.3
	AM	495	log CW = –0.86 + 1.53 log ChL	0.980	+		
	F	244	log CW = –0.56 + 1.22 log ChL	0.993	+		
AW	M	569	log CW = –0.48 + 0.91 log AW	0.981	–		
	YF	85	log CW = –1.02 + 1.70 log AW	0.958	+	152.2	15.3
	AF	268	log CW = –0.22 + 1.05 log AW	0.906	+		
GL	YM	9	log CW = –3.63 + 4.26 log GL	0.922	+	>1,000.0	9.4
	AM	533	log CW = –0.56 + 1.00 log GL	0.957	0		

[1] *t*-test for H_0: $\beta = 1$ are all significant at $P = 0.000$ except GL in AM.
[2] All *F*-ratios correspond to $P < 0.0001$.
[3] Inflection point estimated in Mature II analyses.

the sampling plot to prevent the evasion of crabs. In the first one, the 3-cm upper layer within the quadrat was removed, and crabs were sorted out using a sieve with a 0.5-mm mesh size. This method showed better results, but it still required thorough sieving. In the second quadrat technique, all juveniles visually spotted inside each quadrat were collected within a period of 2 min. This method required even less sampling effort, rendered higher efficiency and provided similar precision as achieved in the first quadrat method (Table 2), and it was chosen for further sampling.

The number of sampling units to be used was established taking into account the gains in precision, calculated as the standard error divided by the mean, against sampling effort (Andrew and Mapstone, 1987). Density estimates of these organisms show a very high variance due to a clearly aggregated distribution over the sampling area; therefore, a large sample size would be needed to reach a precision of 0.1. The sample size chosen was thirty sampling units, which rendered average precision of 0.09 ± 0.02 over the study period. For sampling, a systematic random design was chosen, in which quadrats were haphazardly placed and examined at an approximately 4–5-m interval, covering the whole sampling area. Estimates of average density and crab size were obtained from the population at 4-d intervals, from November 14th to January 17th. Collected crabs were placed in small labelled vials and immediately frozen upon arrival at the Marine Biology Station. Variability of density estimates in temporal analyses was assessed by calculating 95% confidence intervals.

At the laboratory, individuals were sorted out from other crab species, namely *Sarmatium* Dana, 1851, *Neosarmatium* Serène and Soh, 1970, and *Ilyograpsus* Barnard, 1851, and their carapace width (CW) and length (CL) were measured to the nearest 0.1 mm under a binocular microscope supplied with a micrometric ocular. Size frequency distributions were carried out in intervals of 0.4-mm CW, and modal progression analyses were calculated after separating polymodal distributions in their normal components following Bhattacharya (1967). The developing degree of abdominal appendages was also verified under a microscope. As in estimating 50% maturity regarding developmental stage of gonads, size at which sexual differentiation takes place was assessed by plotting and regressing the relationship between carapace width and proportion of individuals with developing pleopods. In this case, 0.5-mm class intervals were used.

In order to obtain information on the duration and size of first crab instars, megalopae obtained from artificial collectors (Paula *et al.,* 2000) were reared separately under laboratory conditions. Individual compartments (20 ml) were partially filled with 34‰ sea water, which was changed daily. Recently hatched *Artemia* nauplii were used as food. Rearing boxes were checked daily for the presence of exuviae, and sizes of both crabs and exuviae were measured as stated above.

Results

Sexual Maturity and Reproductive Cycles

A total of 578 males (from 3.6- to 30.4-mm CW) and 370 females (3.5–26.0-mm CW) were collected. From those females, 84 individuals were ovigerous (ranging from 14.1 to 23.7 mm).

Sexual Dimorphism and Morphometric Maturity.—Linearized allometric expressions, determination coefficients, *t*-tests for departures from isometry, and outcomes of Somerton's analyses are given for each relationship and sex in Table 3. Positive allometric growth was found in all cases, except from the negative allometric growth of the abdomen in males and the isometric growth of gonopods in adult males. Relatively higher allometric growth of chelae in males during the adult phase accounts for a clear sexual dimorphism which can be verified in Fig. 2A.

In males, changes of the relative growth rates of both chelae and gonopods are significant (Fig. 2A, B; Somerton's *F*-tests in Table 3), providing almost identical estimates of size

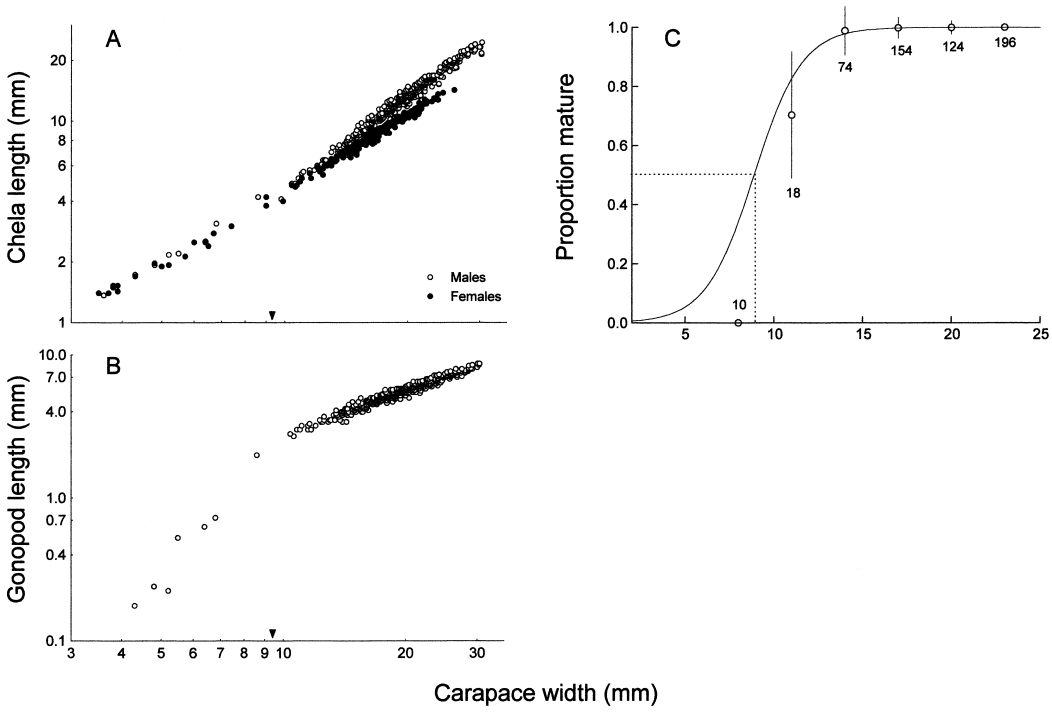

Fig. 2. Estimates of size at the onset of sexual maturity for males. Allometric relationships between log carapace width and both log chela length (A) and log gonopod length (B). Relative growth of female chela length is also represented to depict sexual dimorphism. Down arrows indicate size at the onset of sexual maturity as obtained using the Somerton's Mature II computer technique. C: Fitted logistic equation to the relationship between proportion of individuals with developed gonads vs. carapace width. Number of examined individuals within each size class is shown. Bars represent 95% confidence intervals, and dotted line indicates the size of 50% maturity.

at the onset of sexual maturity (9.3–9.4-mm CW). Differentiation of juvenile developing pleopods into functional gonopods explains the very high relative growth rate of gonopods in young males. In the case of females, the same analysis for the allometric growth of the abdomen indicated that the puberty molt should take place in considerably larger individuals around 15.3-mm CW (Fig. 3A, Table 3).

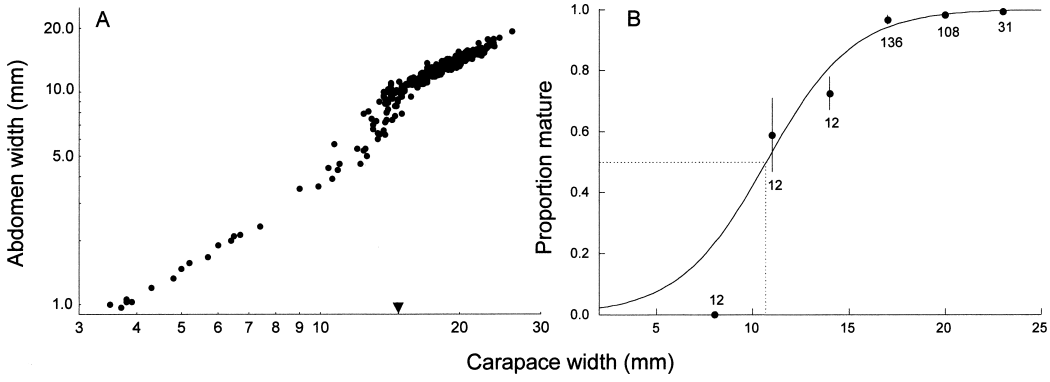

Fig. 3. Estimates of size at the onset of sexual maturity for females. A: Allometric relationships between log carapace width and log abdomen width. Down arrow indicates size at the onset of sexual maturity as obtained using the Somerton's Mature II computer technique. B: Fitted logistic equation to the relationship between proportion of individuals with developed gonads vs. carapace width. Number of examined individuals within each size class is shown. Bars represent 95% confidence intervals, and dotted line indicates the size of 50% maturity.

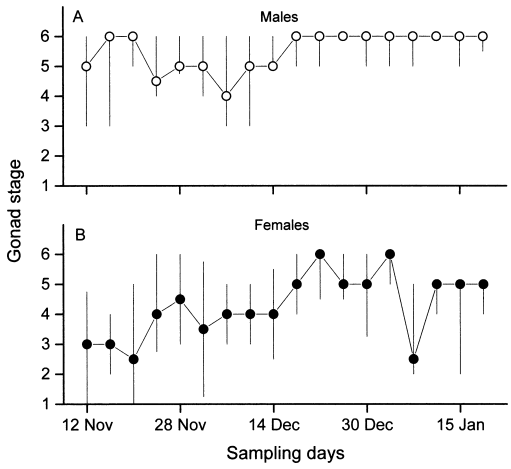

Fig. 4. Short-term temporal variation of median gonad development in males (A) and females (B). Above and below bars indicate third and first quartiles when different from median values. Sample size ranged from 25 to 41 individuals in males and 10 to 30 individuals in females.

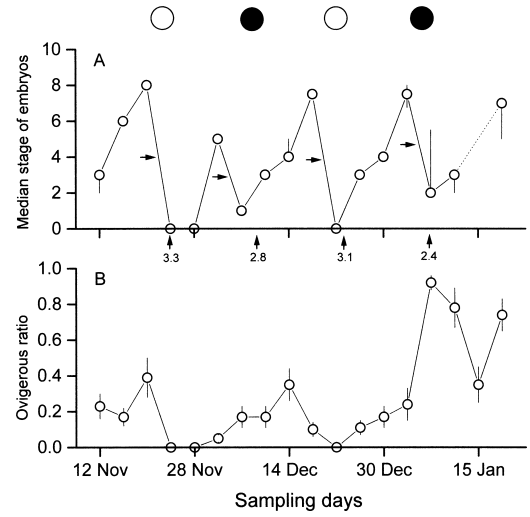

Fig. 5. Short-term temporal variation of median stage of incubated embryos (A) and proportion of ovigerous females (B). In the upper plot, third and first quartiles are represented as bars when different from median values; horizontal arrows indicate estimated dates of peak larval release, and up arrows with numbers below indicate dates of tide range maxima and respective height in meters. In the lower plot, bars indicate 95% confidence intervals. Full and new moons are represented as white and black circles, respectively.

Gonadal Maturity.—The relationship between proportion of individuals with developed gonads and size is illustrated in Figs. 2C and 3B for males and females, respectively. Fitting the logistic equation to data provided predictive models in both cases (males: r^2 = 0.94; $P < 0.05$; logistic parameters, A = 725.21, B = –0.74; females: r^2 = 0.96; $P <$ 0.01; logistic parameters, A = 74.97, B = –0.42). Estimates for size at 50% maturity are 8.9-mm CW for males and 10.4-mm CW in the case of females.

Reproductive Cycles.—Figure 4 represents the variation of median development stage of gonads for individuals larger than the size at 50% maturity. The pattern shown suggests that reproductive activity increased from the beginning to the end of the sampling period. In males, these values present some variation until December 14th but remained constant thereafter, with median development stage of gonads always at its maximum (Fig. 4A). In females, there is a wider variation of median gonad stage, most probably reflecting oogenetic cycles taking place during this period (Fig. 4B). Peaks of median gonad stage are not significant due to high interquartile range of median values. Furthermore, highest values are not separated by similar time intervals, thus providing no evidence of breeding rhythms. The lowest value, recorded on January 7th, corresponds to a large proportion of ovigerous females carrying early embryos (Fig. 5A, B) and thus just resuming oogenesis.

Temporal variation of median stage of brooded embryos shows a clear semilunar pattern (Fig. 5A). At each sampling date, variation was minimal, except on January 7th when individuals with recently extruded egg batches were sampled together with females that had not released larvae yet. Estimated as the mid-date between sampling days separated by a decrease of median stage of embryos, events of maximum larval release precede spring tides of maximum tide range by two to four days.

The ovigerous ratio seems to follow a lunar cycle variation, with peaks preceding larval release during the full moon (Fig. 5B). Breeding intensity increased throughout the sampling period with the percentage of ovigerous females almost reaching 100 percent of all potentially mature females during the last peak.

Juvenile Recruitment

Within the target microhabitat, juvenile density varied from 15.7 to 30.5 crabs · m^{-2}. Density increased from the beginning to the

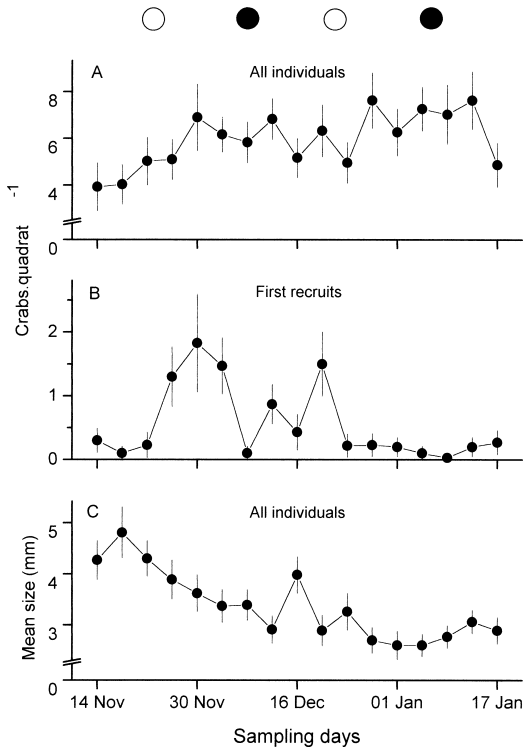

Fig. 6. Short-term temporal variation of density (A, B) and size (C) of juveniles. In all cases, bars indicate 95% confidence intervals.

end of the sampling period but not steadily (Fig. 6A). Crabs measuring from 0.9- to 1.1-mm CW, which correspond to 1st stages as observed in the laboratory, do not ingress into the mangrove habitat continuously. Instead, a higher discrete recruitment pulse was detected around November 30th and a lower one centered on December 16th (Fig. 6B). Such pulses are separated by a semilunar period (16 d) with effective recruitment decreasing 63%, as considering the areas below these pulses in Fig. 6B. A third pulse would be expected with maximum around January 1st, but no significant recruitment of first stages was recorded. The average size of sampled crabs decreased consistently over the sampling period (Fig. 6C) due to the increasing proportion of very small crabs in the sampled area.

Changes of the juvenile population structure were also evident in size-frequency distributions (Fig. 7). Histograms clearly indicate the presence of three different age groups, with the older one missing in some sampling dates. Relative frequency of the age group comprising newly settled crabs, increases through the sampling period. Figure 8 shows the growth pattern of tracked age groups after decomposition of size-frequency distributions. Modal groups 2 and 3 were identified in all sampling dates, but there was no statistical support for separation of the older group in some samples. Apart from some noise, probably due to sampling error and procedural constraints, growth of the younger age groups is regular within this time interval. As expected, growth increment, in terms of percentage, decreases markedly but growth rates do not differ considerably (Table 4).

Under laboratory conditions, crabs attain the fourth juvenile instar in 44 d with an average size of 1.9-mm CW (Table 5). These results agree with growth estimates from modal progression analyses. Yet, neither intermolt periods increase nor growth factors decrease through the instar sequence as expected. Instar duration varied from 11.2 to 17.3 days (Table 5), and growth factor, as percentage increment at molt, varied from 20.0% to 31.9% with no trend according to size. Initial pleopod differentiation takes place at an average size of 4.65-mm CW (Fig 9; parameters of the logistic function, $A = 725.21$, $B = -0.74$ males: $r^2 = 0.94$; $P < 0.0001$).

Discussion

In brachyuran crabs, estimating size at the onset of sexual maturity using a single criterion may lead to unrealistic conclusions regarding actual size at which these organisms are functionally mature. Results from allometric data and gonad analyses are often compared in the case of economically exploited species because of the need to accurately estimate size at maturity in such cases (e.g., Watson, 1970; Fielding and Haley, 1976; Campbell and Eagles, 1983). A comparative analysis should be also applied in species performing a key role in their habitats as carried out by Haefner (1990) and López Greco and Rodríguez (2000).

The latter authors have evidenced great contrasts among different estimates in the closely related species *Chasmagnathus granulatus* Dana, 1851. This is the case of *P. guttatum* females, in which gonadal maturity is also achieved much earlier. However, the size of the smallest ovigerous female is surprisingly high, closer to the size of allometric maturity. This may be due to a longer primary vittelogenesis in younger primiparous females

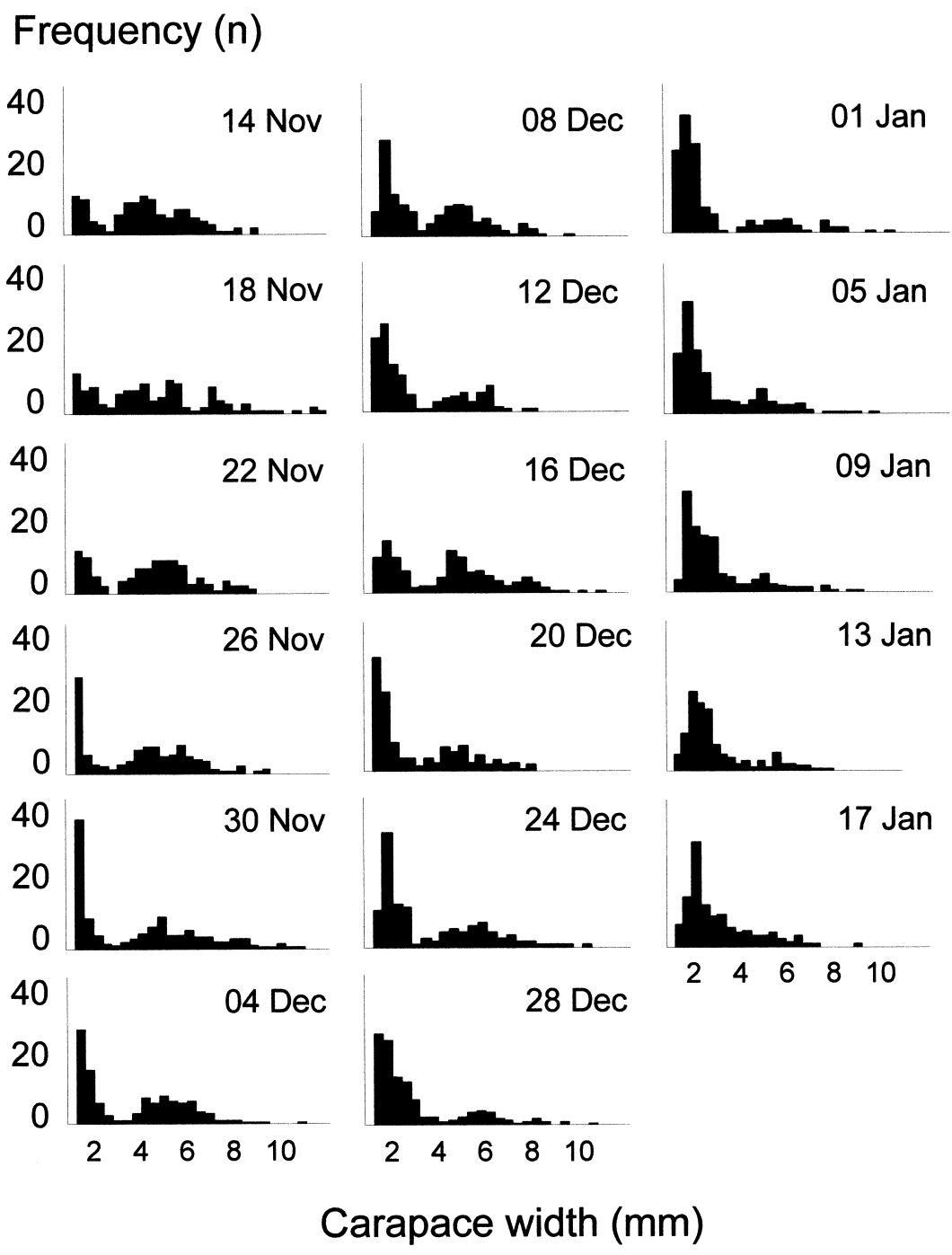

Fig. 7. Size-frequency distributions of juveniles throughout the sampling period.

as observed by Jensen and Armstrong (1989) for king crabs. In males, the allometric growth of sexually dimorphic chelae and gonopods points to the same size estimate, which is only slightly higher than the estimate obtained from the analysis of gonads. In majid crabs, there is evidence that adolescent pre-pubertal males may only succesfully mate under conditions of low abundance of larger, post-pubertal competitors (Sainte Marie *et al.*,

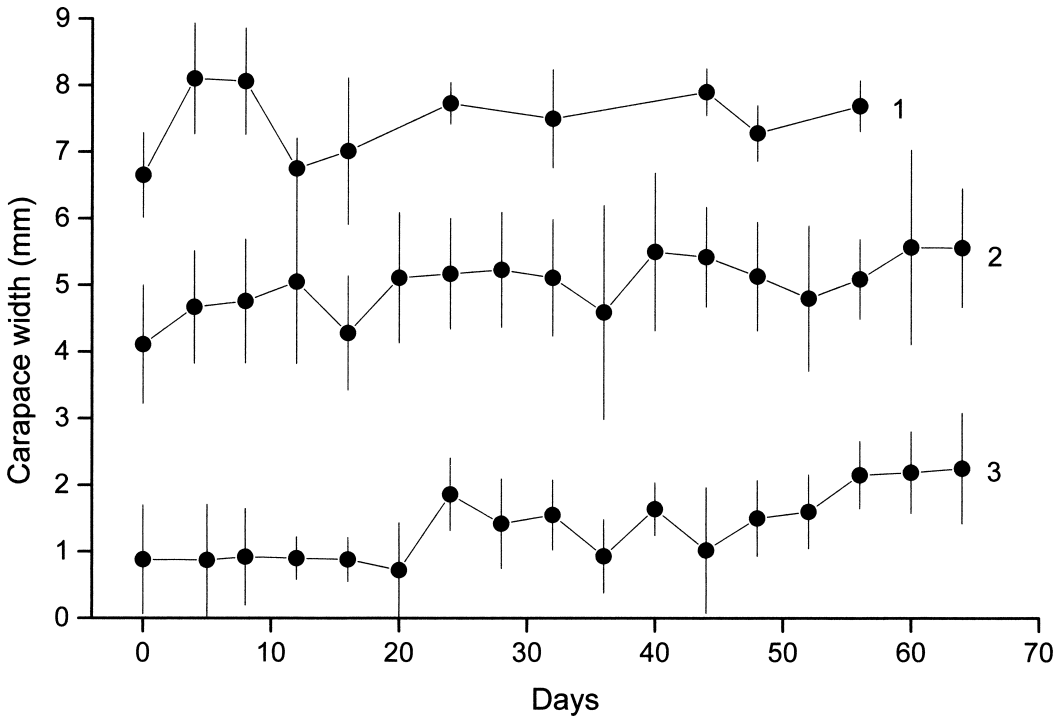

Fig. 8. Average size of distinguished juvenile cohorts over the sampling period. Bars indicate standard deviations; 1, 2, and 3 are age-group identifiers.

1995), for what functional sexual maturity is regarded to take place only after the puberty molt (Sampedro *et al.*, 1999). In grapsoids, growth is not ceased once matrurity is achieved but continues through an indefinite stage sequence. Therefore, size differences between potentially mature males may be quite high and exlcusion of younger crabs during agonistic interactions expected. Moreover, small males attempting to mate may face the risk of being predated by the female (López Greco and Rodríguez, 1999). It should be pointed out, however, that *in situ* mating experiments controlling for habitat complexity and crab density are needed to adequately assess the actual mating chances of crabs within the size range of sexual maturity estimates.

After mating and evacuating spermatophores, males may spend several days to be ready to copulate again (Sastry, 1983). Short-term cycles of testicular activity were not detected in *P. guttatum* males. There was some variation during the first half of the sampling period, but testes of most of the males were fully developed thereafter. Otherwise, cycles of ovarian development are evident for females. Variation of median gonad developmental stage along the sampling days was too wide to be only accounted as sampling error.

The observed irregular temporal variation of median developmental stage of ovaries is probably due to reproductive activity of co-

Table 4. Growth estimates for juveniles; CW_i and CW_f stand for average carapace width of age groups at t_0 and at the last date in which a given group was detected.

	Modal groups		
	1	2	3
CW_i–CW_f (mm)	6.65–7.69	4.11–5.56	0.90–2.25
Growth rate (mm·month^{-1})	0.56	0.68	0.63
Growth increment (%)	15.64	35.28	150.00

Table 5. Size and duration of juvenile instars reared under laboratory conditions.

	Carapace width (mm)			Duration (d)		
Instar	Mean	SD	*n*	Mean	SD	*n*
1	0.92	0.04	21	17.3	6.6	15
2	1.20	0.10	14	11.2	3.5	9
3	1.44	0.14	7	15.2	6.7	5
4	1.90	—	1	—	—	—

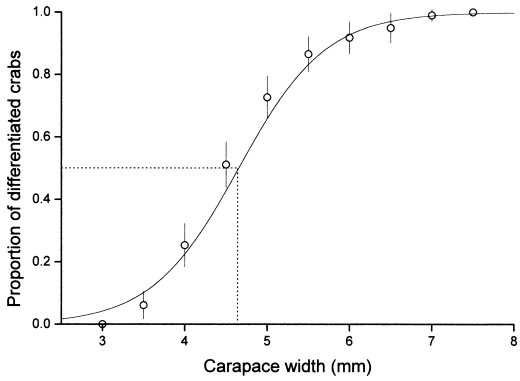

Fig. 9. Fitted logistic equation to the relationship between proportion of sampled crabs with differentiated pleopods and carapace width. Bars show 95% confidence intervals, and the dotted line indicates the size at which 50% of crabs show developing pleopods.

occurring breeding groups releasing larvae in alternate spring-tide periods. Our observations on females held at natural temperature conditions evidenced that stage 3 embryos (according to Boolootian *et al.,* 1959) took 15 days to hatch (unpubl. data); therefore, a given breeding female cannot release larvae in two successive spring tides. Highly synchronized semilunar larval release, as indicated by the temporal variation of median stage of incubated embryos obtained herein and rhythms of larval release in the laboratory observed by Gove and Mambonhe (2000), suggests that there are two separate breeding groups releasing larvae around the new and full moon, respectively. Yet, the reproductive output of the full-moon group seems to be markedly higher as indicated by the variation pattern of the proportion of ovigerous females in which discrete peaks preceding full moon periods are evident. Similar differences were already reported by Saigusa and Hidaka (1978). It is interesting to note that during the study period, highest tide ranges were also recorded at full-moon spring tides (see Fig. 5A). For this low intertidal sesarmid, the main advantage of larval release during tides of maximum amplitude could be the fast transport from near-shore areas thus avoiding heavy predation by coastal fishes (see Morgan and Christy, 1995). However, it should be pointed out that this source of selective pressure might not be a driving force shaping larval release rhythms. For instance, larval release for most of the common decapod crustaceans at the Mira Estuary, Portugal, is centered on crepuscular high tides regularly taking place during neap-tide periods (Paula, 1989). At the study region, post-crepuscular ebbing tides coincide with highest tidal ranges during spring tides. Therefore, it is not possible to identify which entraining cycle is contributing the most for the observed pattern of larval release.

Sampling for density estimates of juvenile crabs is usually a difficult task. A number of problems may arise depending on the conditions under which each specific study is conducted. In our case, identifying recruiting areas was not a problem, but sources of sampling bias should be taken into account. Juveniles of the closely related species *Sesarma longipes* Krauss, 1843, and *S. leptosoma* Hilgendorf, 1869, should also recruit into the low intertidal and may have been inadvertently counted in samples. However, overestimation due to misidentified juveniles should be minimum because these species are rare compared to *P. guttatum,* which is absolutely dominant in the study area. Another problem is the underestimation due to failure in visually detecting crabs. Deviations from real values are likely to be significant, and we find no obvious way to correct for such bias. Corer and quadrat methods involving sieving were less efficient than visual counts, probably because handling colloidal masses could damage part of the crabs. Perhaps a chemical treatment to disassemble colloid particles would provide a means to separate crabs more efficiently, but the cost of processing samples in that way make such a technique only feasible for calibration purposes.

Average precision of 0.09 in density estimates allows the detection of most significant temporal changes occurring in the juvenile population. During the sampling period, recruitment intensity increased as expected for a species with higher reproductive activity in summer. By the end of the sampling period, the structure of the juvenile population had changed markedly, with the percentage of recent settlers establishing around 90 percent from December 28th. It would be interesting to gather similar information on the structure of the juvenile population later during the recruitment season, but, considering the temporal trend obtained, the proportion of very young recruits would hardly exceed the maximum values reported herein. During periods

of very high settlement rates, increasing larval supply may no longer affect juvenile density in dungeness crab populations (Eggleston and Armstrong, 1995). Predation by older juveniles may be a major factor controlling the density of incoming recruits (Fernandez *et al.,* 1993; Lovrich and Saint-Marie, 1997), but other sources of mortality should be also significant because there is no evidence for a cannibalistic functional response of older crabs to variation of juvenile density in other mangrove sesarmids (Kneib *et al.,* 1999).

Cohort strength of young-of-the-year individuals obviously depends on settlement success during the recruitment season. Although ruled by a number of deterministic factors, namely the duration of larval development (e.g., Tsuchida and Watanabe, 1997; Flores and Negreiros-Fransozo, 1999) and inshore transport by tidal currents (e.g., van Montfrans *et al.,* 1990; DeVries *et al.,* 1994; Eggleston *et al.,* 1998), other stochastic events such as wind-driven surface transport (e.g., Goodrich *et al.,* 1989; Jones and Epifanio, 1995; Clancy and Cobb, 1997; Eggleston *et al.,* 1998; Paula *et al.,* in press) may either enhance or completely suppress settlement events. Virtual lack of incoming recruits after December 24th is certainly a result of previous hydrologic processes adverse to inshore transport, as evidenced by temporal analyses of megalopal settlement during the same period in this area (Paula *et al.,* 2000).

Different recruitment pulses cannot be independently tracked in size frequency distributions, probably due to slow growth of incoming recruits preventing the separation of these crabs into modal components. During a semilunar period, first-crab stages would only molt once at best (Table 5) prior to the next settlement event. By using 0.4-mm size class intervals, first- and second-crab stages will not be separated and thus distinguished in different modes. Therefore, settlement peaks originate a single modal group for a given recruitment season, and modal progression analysis should thus render average growth for all these juveniles. The growth results presented in Table 4 can be used to estimate the time elapsed between recruitment seasons. Based on the growth of the youngest age group, settlers take 2.13 mo to reach 2.25 mm. The time required for those juveniles to reach 4.11 mm, which is the size of the intermediate age group at t_0, may be obtained by dividing the growth increment (4.11–2.25 mm) by the average growth rate estimated for both groups (0.655 mm·mo^{-1}). This results in 2.84 months, which summed to the age of the youngest group at the end of the sampling period indicates that the interval between those recruitment seasons would be approximately 4.97 months. The seasonal variation of breeding activity is not known for this species, but breeding cycles were reported for eight mangrove species in South Africa (Emmerson, 1994). The main breeding period of closely related species *Sesarma eulimene* de Man, 1887, and *Parasesarma catenata* Ortmann, 1897, is centered in the summer with two clear reproductive peaks at the beginning and at the end of the season, from four to six months apart. In the case of following a similar trend in *P. guttatum,* the recruiting cohorts identified in the present study may be a result of equivalent early and late reproductive peaks.

Growth factors and intermolt periods of first juvenile instars do not follow the expected variation through the instar sequence (see Mauchline, 1977). Decreasing growth factors and increasing intermolt periods would be apparent in a longer instar sequence. Within the initial juvenile phase, growth components may not vary considerably. Using the average growth increment at molting (27.4%) obtained from laboratory rearing, and both the mean intermolt period of captive crabs (14.6 d) and growth rates from the field, it may be predicted that initial sexual differentiation would only take place at the 8th crab stage after 102–173 d, when juveniles attain the size at which 50 percent of crabs had undergone initial pleopod development. These are only rough estimates but comparable to the data available to *Sesarma rectum* Randall, 1840 (Fransozo and Hebling, 1986), in which pleopod differentiation starts at the 12th instar.

By combining the growth data from modal progression analyses and estimates of size at sexual maturity, it is suggested that reproducing females would be 2-yr old at least. An individual would achieve the size of the smallest ovigerous female in 24 months using the juvenile growth rates obtained. Subadults are expected to grow even slower. Long juvenile development and delayed sexual maturity seem to be characteristic features of the life-history of mangrove sesarmids when compared to other grapsoids (Flores *et*

al., 1998). There is a need to gather more information on the population ecology of mangrove sesarmids before addressing specific questions on eventual trade-offs related to this reproductive strategy.

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