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REPRODUCTION OF THE SPECKLED SWIMMING CRAB *ARENAEUS CRIBRARIUS* (BRACHYURA: PORTUNIDAE) ON THE BRAZILIAN COAST NEAR 23°30′S

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ABSTRACT

The reproductive biology of *Arenaeus cribrarius* from Ubatuba, São Paulo State, Brazil, was studied. Swimming crabs were sampled monthly for two years with otter trawls in two bays. A total of 941 males and 1,012 females were examined. Mating took place mainly in autumn involving postmolt females and intermolt males. At that time, gonad regression was verified in adult males, due to spermatophore transfer, and the molting of adult females. Ovigerous females or females with mature gonads were present year-round but more frequently captured during spring and summer. We found that 1% of all adult females were premolt, which indicated the occurrence of another mature instar and thus the absence of a well-defined terminal molt after puberty. Intermolt males were captured throughout the whole study period.

Arenaeus cribrarius (Lamarck, 1818) is a portunid crab that prefers sandy beach surf zones, where it remains buried most of the time. In the shallow soft bottoms of the northern coast of São Paulo State, Brazil, this is the third most abundant Brachyuran and the second ranking portunid (Fransozo *et al.*, 1992). During recent years, the biology of this swimming crab has been extensively studied (Pinheiro and Fransozo, 1993a, b; Pinheiro *et al.*, 1996, 1997), because it is a large edible crab with some commercial importance. However, little is still known about its reproduction, excepting its larval development (Stuck and Truesdale, 1988), sexual maturity (Pinheiro and Fransozo, 1998), reproductive behavior (Pinheiro and Fransozo, 1999), and fecundity (Pinheiro and Terceiro, 2000).

According to Hartnoll and Gould (1988), the reproduction and growth of brachyuran crabs is extremely diversified. Portunids, majids and cancrids are often studied because they are eaten (Haefner, 1985). A great deal of research has been undertaken to estimate abundance and judge their potential for culture by estimating their reproductive season (Armstrong, 1988; Ingles and Braum, 1989; Sumpton, 1990), spawning season (Paul, 1982; Heasman *et al.*, 1985), fecundity (Costa and Negreiros-Fransozo, 1996; Santos and Negreiros-Fransozo, 1997; Mantelatto and Fransozo, 1997), and reproductive cycle (González-Gurriarán, 1985; Choy, 1988; Pinheiro and Fransozo, 1997).

In Decapoda breeding may take place year-round (continuous pattern) or be restricted to a few months (discontinuous pattern) due to thermal conditions in winter (Sastry, 1983). The breeding cycle periodicity is affected by endogenous and environmental factors (Wenner *et al.*, 1974; Batoy *et al.*, 1987), like temperature (Heasman *et al.*, 1985; Campbell and Fielder, 1986) and photoperiod (Knudsen, 1964; Little, 1968; Saigusa, 1992; Flores and Negreiros-Fransozo, 1998). They work as metabolic, biochemical, and hormonal modulators, triggering the processes of ecdysis, mating, and gonad development (Sastry, 1983).

In the present study, the reproduction of *A. cribrarius* was examined by assessing the temporal and seasonal status of gonad maturation, molting, development of eggs, spermathecae repletion, and percentage of ovigerous females at population, to characterize a reproductive pattern.

MATERIALS AND METHODS

Specimens of *A. cribrarius* were collected monthly during two consecutive years (May/1991 to April/1993),

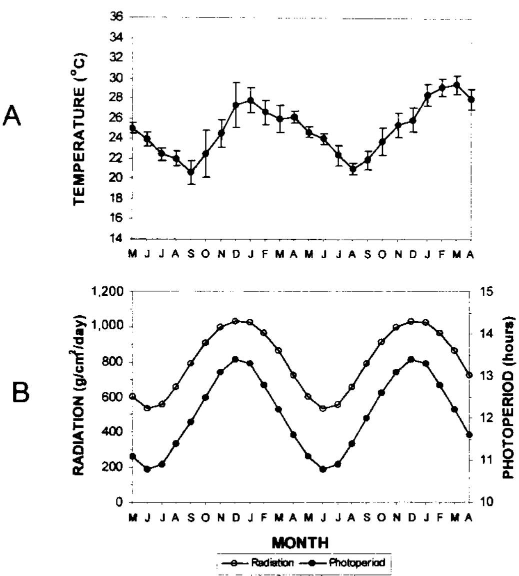

Fig. 1. Average monthly values of water temperature (A), solar radiation and photoperiod (B) recorded in the sampling area over the 2-year study period.

in the North coast of São Paulo State, Brazil (23°25′–23°35′S; 45°00′–45°12′W). Samples were obtained from Fortaleza Bay (first year) and Ubatuba Bay (second year), using trawler supplied with a double-rig (15-mm mesh size, 10-mm in the cod end). During each sampled month two trawls were pulled for 90 min, increased to four 90-min trawls during September to December when the abundance of this species is known to be relatively low (Pinheiro *et al.,* 1996).

After trawling, *A. cribrarius* specimens were sorted from the sediment and other organisms, packaged in plastic bags and frozen (−5°C) until analyses, when they were defrosted and sexed. Females with triangular and suboval-shaped abdomens were considered juvenile and adult crabs, respectively. In males, both juvenile and adult specimens have inverted "T"-shaped abdomens, but in juvenile crabs the abdomen adheres to the thoracic sternites (Pinheiro and Fransozo, 1993b). The presence of ovigerous females was recorded. The determination of the reproductive season was obtained by analyzing the monthly proportion of ovigerous females in relation to total adult females and comparing that with percentage of females with mature gonads, registered each month.

The stage of gonad maturity was verified by macroscopic inspection of gonads (Pinheiro and Fransozo, 1998). Three stages were considered: immature, developing, and mature. Molt stages were identified following the characteristics used by Drach and Tchernigovtzeff (1967) and Yamaoka and Scheer (1970). Three categories were recognized: postmolt (A_1–B_2), intermolt (C_1–C_4), and premolt (D_0–D_4). The spermathecae of each female were removed and classified as empty (± 5-mm spermathecal length and limp aspect) or full (± 15-mm spermathecal length and swollen appearance as sperm plugs). For each ovigerous female 20 eggs were removed, and the stage of embryonic development was recorded according to Boolootian *et al.* (1959). For analysis, stages 1–4 were grouped and regarded as "initial," stages 5–8 as "intermediate," and stages 9–10 as "final."

Table 1. Mean values of water temperature, rainfall, photoperiod, and solar radiation in each season in the Ubatuba region (SP). Values summarize readings obtained from May/1991 to April/1993.

Season	Temperature (°C)	Rainfall (mm)	Photoperiod (h)	Solar radiation (cal/cm²/d)
Summer	27.9 c*	250.4 a	12.8 b	952.0 b
Autumn	25.3 b	171.4 a	11.2 a	621.2 a
Winter	21.7 a	124.5 a	11.4 a	690.3 a
Spring	24.9 b	116.0 a	13.0 b	982.0 b

*Mean values with the same letter in a given column do not differ statistically ($P > 0.05$).

The monthly dynamics of the above parameters were analyzed through graphic examination of the respective percentage occurrence of relevant stages. High intensity was designated to months when percentage occurrence was higher than 25%, according to Jensen and Armstrong (1989), Abelló (1989), and Sardá (1991). The repetition of high intensity months between sampled years determined fixed patterns of occurrence (FP).

In order to check seasonal breeding patterns the data were grouped in the four seasons using contingency tables and analyzed by Goodman's test (Goodman, 1964, 1965) that compare multinomial proportions. The same test was used to analyze the association between the biological parameters studied (molt stages vs. gonad maturation, embryonic development vs. gonad maturation, spermathecae replenishment vs. molt stages) for a total sample of 1,815 adult specimens (821 males and 994 females). This data set includes biological analyses obtained from 263 specimens (143 males and 120 females) sampled previously by Pinheiro (1991) in the same region. In all statistical analyses the 5% significance level was chosen for decisions.

Daily records of water temperature were obtained at the Oceanographic Institute of the University of São Paulo (IO/USP) North Station. Photoperiod and solar radiation theoretical data were calculated each month for the latitude at the study area (23°30′30″S), according to Sellers (1965) and Varejão-Silva and Ceballos (1982), respectively. Seasonal contrasts of environmental variables were tested with ANOVA, and differences among average values were then tested by the Tukey test ($\alpha = 0.05$). Visual interpretation of graphs was the means to analyze the association between temperature and photoperiod with the process of gonad maturation (of both males and females) and frequency of ovigerous females.

Results

Environmental Factors

Water temperature averaged 24.9 ± 1.7°C, showing small variations during the study (20.6° to 29.4°C). Lower mean monthly values were recorded during austral winter months, while higher ones characterized summer season (Fig. 1A). Seasons show differences in temperature, photoperiod, and solar radiation (Table 1). Photoperiod was longer from October to March (spring and summer), compared to the period from April to Sep-

Table 2. *Arenaeus cribrarius* (Lamarck, 1818). Number of individuals of each category collected monthly from May/1991 to April/1993 in Ubatuba region (SP).

Month/Year	Males		Females			Total
	Juvenile	Adult	Juvenile	Adult (without eggs)	Ovigerous	
May/1991	10	31	1	6	3	51
June	12	58	4	31	8	113
July	27	62	10	16	7	122
August	12	9	4	10	5	40
September	16	30	5	25	20	96
October	6	23	–	13	13	55
November	12	45	4	33	5	99
December	1	4	–	1	1	7
January/1992	2	10	1	8	5	26
February	2	23	–	11	42	78
March	17	14	9	14	10	64
April	20	18	12	28	2	80
May	1	31	1	10	–	43
June	13	38	5	68	3	127
July	4	16	1	40	13	74
August	8	32	5	60	7	112
September	3	27	–	76	4	110
October	3	27	–	51	4	85
November	3	41	–	44	3	91
December	6	18	2	39	3	68
January/1993	32	28	19	21	14	114
February	23	28	9	25	3	88
March	15	38	8	52	2	115
April	5	37	–	49	4	95
Total	253	688	100	731	181	1,953

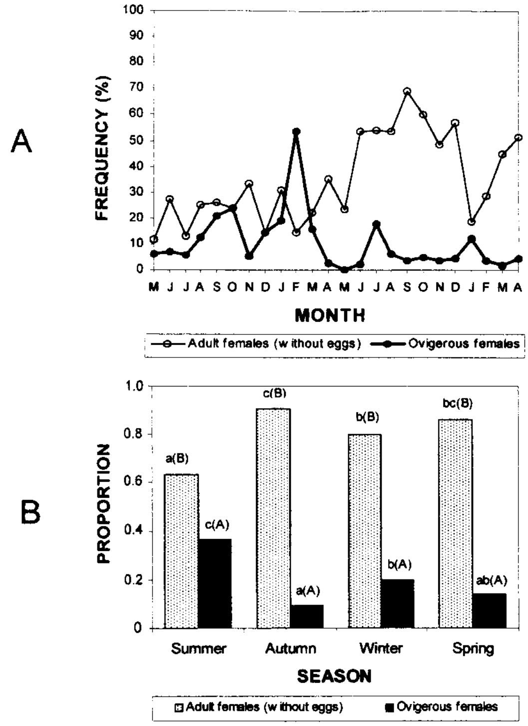

Fig. 2. *Arenaeus cribrarius* (Lamarck, 1818). A) Monthly frequency, and B) proportion of both ovigerous and nonovigerous adult females in each season over the study period (bars filled with the same pattern and sharing at least one small letter are not significantly different; bars filled with a different pattern within a given season and sharing at least one capital letter are not significantly different).

tember (autumn and winter) (Fig. 1B). Solar radiation followed a similar pattern.

Relative Abundance

A total of 1,953 specimens of *A. cribrarius,* 941 males (253 juvenile and 688 adult) and 1,012 females (100 juvenile, 912 adult, of which 181 ovigerous), were obtained (Table 2). Nonovigerous females (80.2%) outnumbered ovigerous females (19.8%).

Ovigerous females were present throughout the study period (Fig. 2A), with higher percentage during the first year, showing variation from 3.7% to 79.3%. A fixed pattern (FP) was verified in January and July (Fig. 7), corresponding to a higher intensity during summer, which contrasts with a secondary peak in winter ($P > 0.05$) (Fig. 2B). The percentage during winter was significantly different when compared to summer and autumn values, but not different from those in spring ($P > 0.05$).

Molting

Adult postmolt males were recorded during the whole sampling period (Fig. 3A), and an FP was observed for July, September, and December (Fig. 7). Intermolt individuals showed a continuous FP, with monthly frequencies ranging between 28.6% and 89.2%. Proportions of each molt stage did not differ significantly among seasons ($P > 0.05$) (Fig. 3B).

Adult postmolt females were more frequent from June to August 1991, in May 1992, and April 1993 (Fig. 3C). No FP was detected after interannual comparisons for data grouped monthly (Fig. 7). When data were sorted by seasons, no significant differences were found for the occurrence of adult premolt females. In contrast, postmolt females peaked in autumn and differed significantly with their occurrence in summer ($P < 0.05$). Regarding the intermolt stage, this trend was inverted (Fig. 3D).

Gonads

Generally, the percentage of adult males with mature gonads was higher than 27%

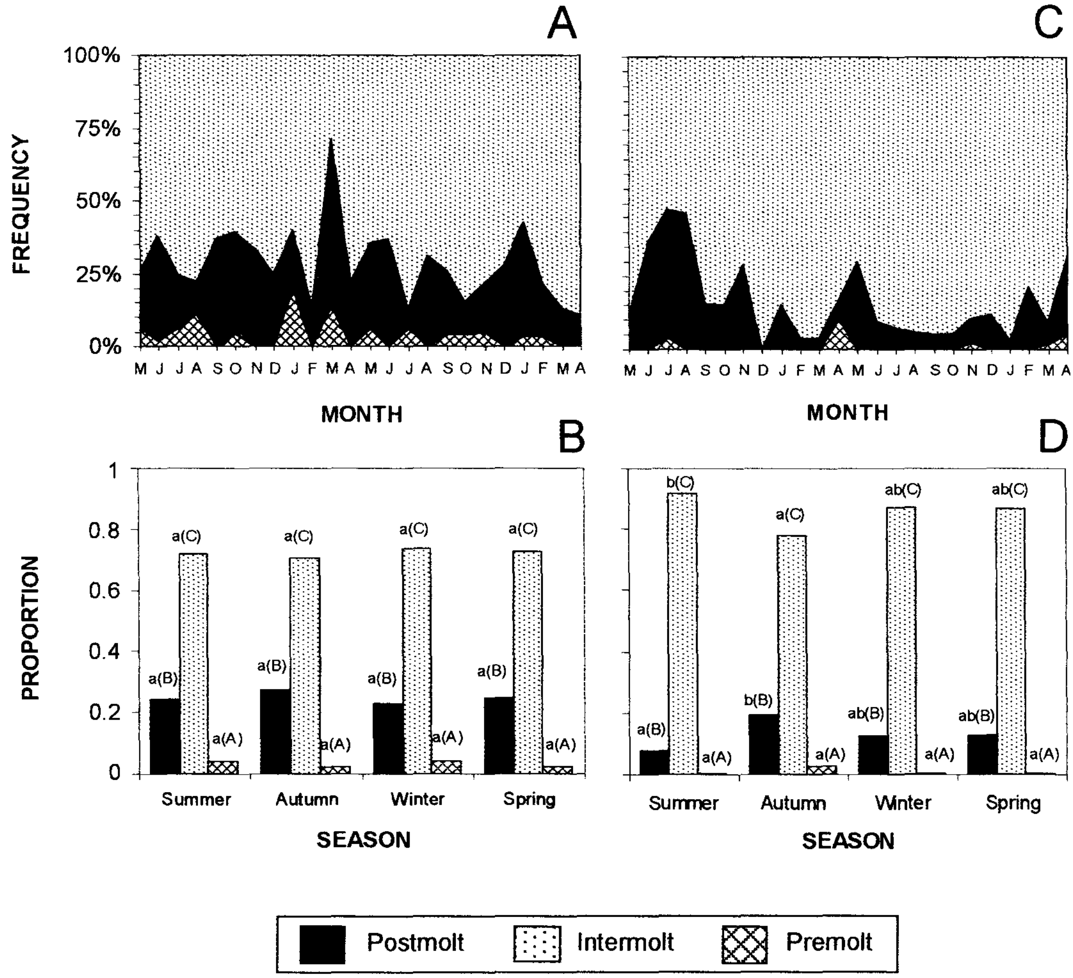

Fig. 3. *Arenaeus cribrarius* (Lamarck, 1818). Molt stages of adult specimens by month (A = males; C = females) and season (B = males; D = females) over the study period (bars filled with the same pattern and sharing at least one small letter are not significantly different; bars filled with a different pattern within a given season and sharing at least one capital letter are not significantly different).

throughout the study (Fig. 4A), showing a long FP (Fig. 7). During autumn, no significant difference was found between frequencies of males with developing and mature gonads ($P > 0.05$). In the remaining seasons, males with mature gonads outnumbered males with developing and immature gonads (Fig. 4B).

Of the 912 adult females analyzed, 61.1% contained developing gonads while 38.9% had mature gonads. Developing females were more frequent from May to September 1991, May 1992, and from March to April 1993, showing an FP from April to June (autumn). Mature specimens were particularly common from October 1991 to April 1992 and from June 1992 to March 1993 (Fig. 4C), with an FP observed between October and March (Fig. 7). Higher proportions of females with mature gonads occurred during months when photoperiod was also higher (spring and summer). During spring most adult females had mature gonads. Higher proportion of individuals with mature gonads in spring contrasts with both values during summer/winter and autumn. The pattern was inverted for developing individuals, which were predominant in autumn but less frequent in spring (Fig. 4D).

Condition of Spermathecae

Adult females with full spermathecae were recorded throughout the study period (Fig. 5A), but an FP was evident for May, June, and November (Fig. 7). Individuals with full

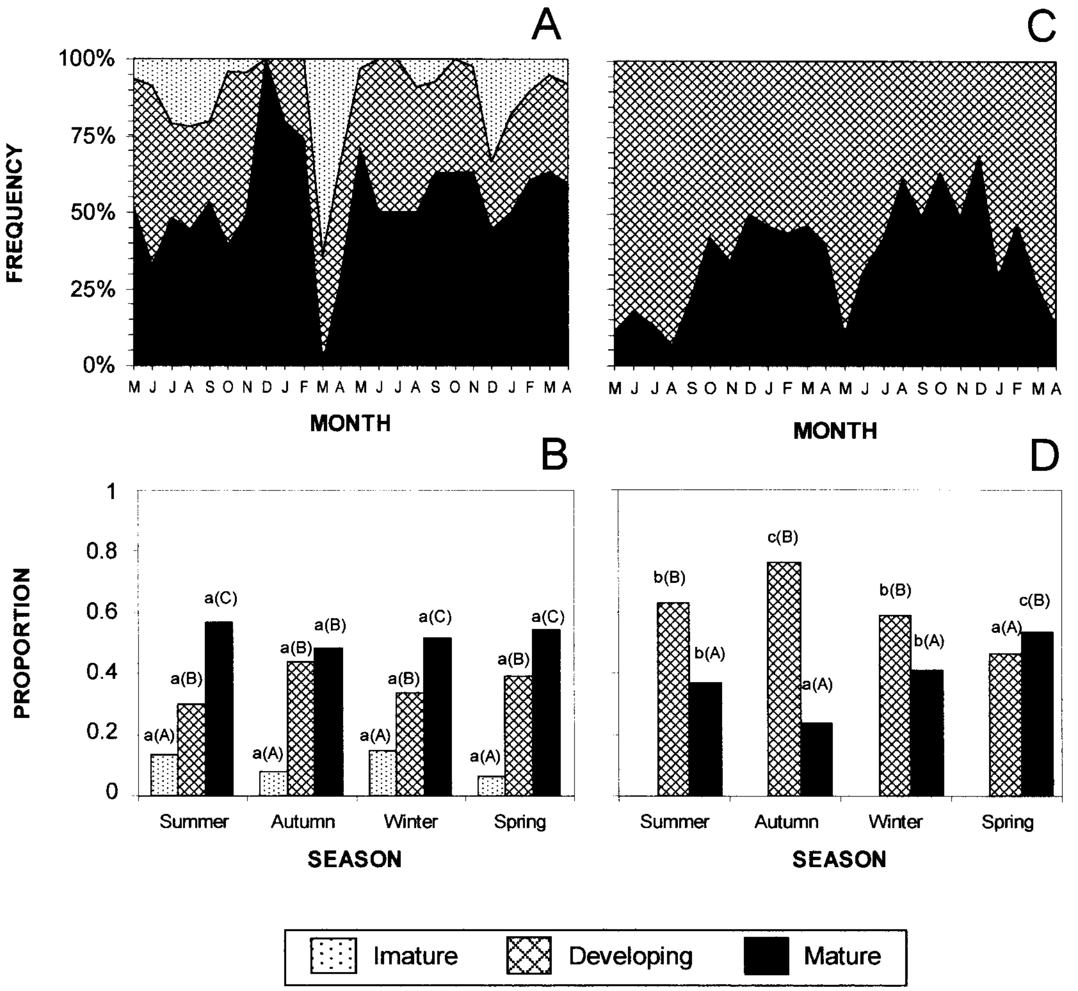

Fig. 4. *Arenaeus cribrarius* (Lamarck, 1818). Gonad stages of adult specimens by month (A = males; C = females) and season (B = males; D = females) over the study period (bars filled with the same pattern and sharing at least one small letter are not significantly different; bars filled with a different pattern within a given season and sharing at least one capital letter are not significantly different).

spermathecae were more frequent during autumn, contrasting with the remaining seasons. The inverted trend was observed for crabs bearing empty spermathecae (Fig. 5B).

Embryonic Stages

Ovigerous females were obtained in all monthly samples (Fig. 6A), with an FP verified for January and July (Fig. 7). Females carrying early-extruded eggs were obtained in samples taken throughout the study period, with an FP occurring from January to April and June to October (Fig. 7). No FPs were distinguished in the case of females bearing late-staged embryos; however, their frequency was relatively high during spring and summer. From a total of 181 ovigerous females, 55.8% carried early embryos, 24.9% intermediate embryos, and 19.3% late embryos. No seasonal differences were found in the occurrence of any of these developmental stages (Fig. 6B).

Association Between the Parameters Examined

Within the postmolt condition, males with developing gonads (56.6%) were more frequent than those bearing immature (32.8%) or mature (10.6%) gonads. Differences between the two latter categories are not significant ($P > 0.05$). Most of the intermolt males had mature gonads (65.3%), contrast-

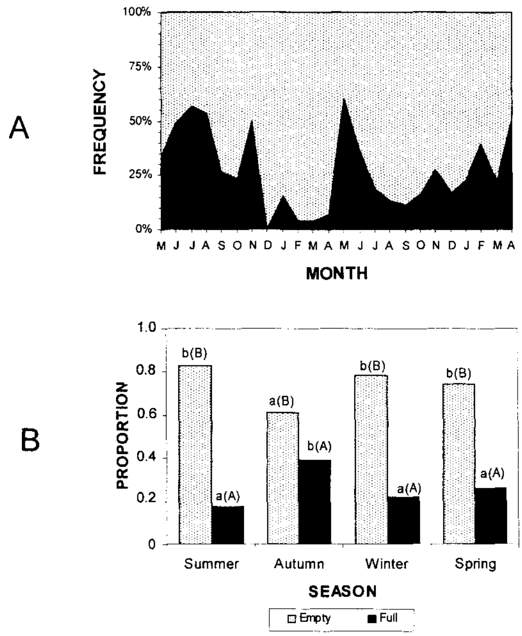

Fig. 5. *Arenaeus cribrarius* (Lamarck, 1818). Spermathecal replenishment stage of adult females by month (A) and season (B) over the study period (bars filled with the same pattern and sharing at least one small letter are not significantly different; bars filled with a different pattern within a given season and sharing at least one capital letter are not significantly different).

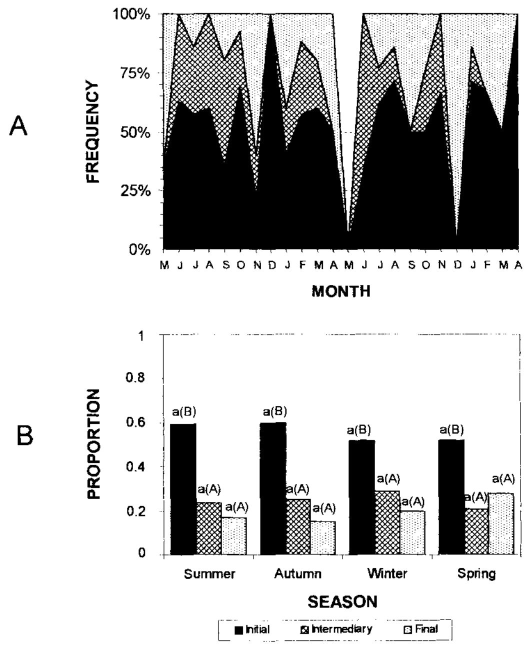

Fig. 6. *Arenaeus cribrarius* (Lamarck, 1818). Embryonic developmental stages of ovigerous females by month (A) and season (B) over the study period (bars filled with the same pattern and sharing at least one small letter are not significantly different; bars filled with a different pattern within a given season and sharing at least one capital letter are not significantly different).

ing with the proportion of developing (27.7%) and immature (7.0%) individuals. In premolt crabs no such differences were observed.

In postmolt adult females, 93.6% had developing gonads, which significantly differed from the percentage of crabs with mature (0.7%) or immature (5.7%) gonads ($P < 0.05$). Considering intermolt females, the occurrence of developing gonads (52.6%) prevailed over mature (47.2%) and immature (0.2%) ($P < 0.05$). In the case of premolt crabs, the high frequency of individuals with developing gonads (90.9%) contrasts with the much lower frequency of crabs with mature and immature gonads, which were not statistically significant ($P > 0.05$).

Full spermathecae were found in 252 of the 994 females analyzed. Both postmolt (53.2%) and intermolt crabs (46.8%) were found in the condition. No premolt females were found with full spermathecae. In general, higher occurrence of full spermathecae was found in individuals with developing gonads (96.4%). Crabs with gonads in other developmental stages and with full spermathecae were not found. Similar results were obtained for each molt stage, with 96.3% for postmolt and 96.6% for intermolt crabs.

From the 219 ovigerous females analyzed, 56.6% carried early eggs, whereas intermediate and final eggs accounted for 22.4% and 21.0%, respectively. The ovigerous females were found with either mature (22.4%) or developing (77.6%) gonads. No ovigerous females with immature gonads were recorded. Within females carrying early embryos, 90.3% had mature gonads, contrasting with the small percentages of crabs with immature and mature gonads, which did not differ significantly ($P > 0.05$). A very similar trend was observed for females with intermediate eggs. The only difference was a reduction of the frequency of females with developing gonads (71.4%). For females with late embryos, the percentage of females with developing and mature gonads was the same (50%).

Discussion

Mate recognition and copulation are considered ethological characters triggering the

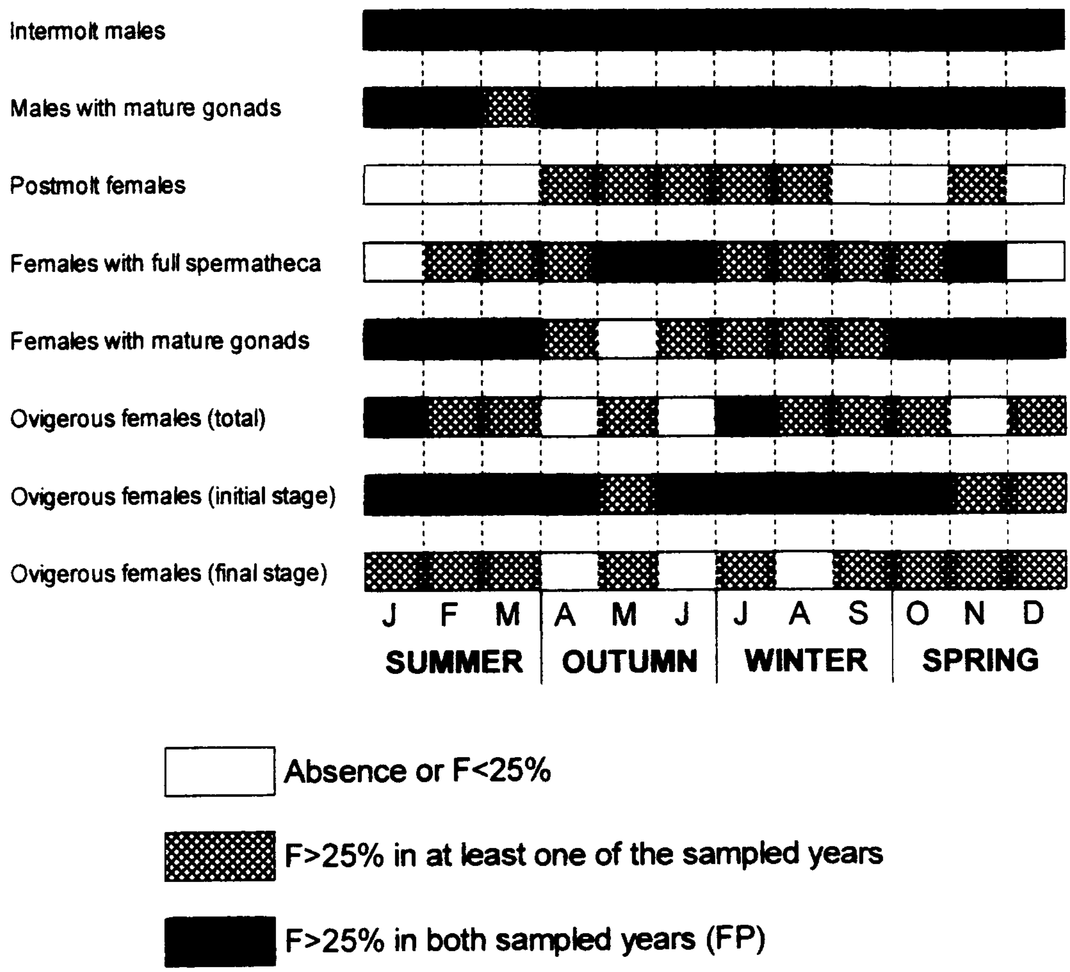

Fig. 7. *Arenaeus cribrarius* (Lamarck, 1818). Monthly and seasonal occurrence of fixed patterns (FP) verified for the main reproductive features during the period encompassed from May/1991 to April/1993 (F = means frequency of occurrence; FP = fixed patterns of occurrence).

reproductive cycle of crustaceans, showing great importance in the determination of the onset of reproduction (Mori, 1987). During mating, brachyuran males transfer their spermatophores to the females' spermathecae where they are stored until fecundation. In the beginning, the consistency of spermatophores is gelatinous, as sperm plugs, and they persist for a period that varies among species. Within the Portunidae, this period may be extremely short (Spalding, 1942; Abelló, 1989) or relatively long, lasting for about one month (Ryan, 1967b; Choy, 1988). The high percentage of intermolt *A. cribrarius* females with full spermathecae indicates that this species follows the latter pattern. In portunids, the mating period can be detected by means of analyzing the monthly frequency of adult postmolt females throughout the year (Bawab and El-Sherief, 1988) and confirmed by analyses of spermathecal condition. This is particularly important in species with long storage periods such as *A. cribrarius* females that mate during the postmolt stage (Pinheiro and Fransozo, 1999). Mating is more likely to occur during autumn, although females with full spermathecae were sampled nearly year-round. Also in autumn, there was a higher incidence of postmolt females and a regression of gonads in males and females, presumably as a result of sperm transfer and energetic allocation for the molting process, respectively. The high breeding intensity in spring and summer is the more common pattern in portunid crabs, but there are some portunids that breed mainly during the coldest

Table 3. Review of reproductive period of some portunid species (D = discontinuous; SC = seasonal-continuous; C = continuous) estimated from the temporal occurrence of ovigerous females and/or adult females with mature gonads.

Species	Source (year)	Locality (country)	Latitude	Reproductive period	Year seasons (1)			
					SU	A	W	SP
Carcinus maenas (Linnaeus, 1758)	Broekhuysen (1936)	Den Helder (Holland)	52°54′N	D	–	*	****	*
Liocarcinus holsatus (Fabricius, 1798)	Choy (1988)	Gower Peninsula (England)	51°33′N	SC	*	*	****	****
Liocarcinus puber (Linnaeus, 1767)	Choy (1988)	Gower Peninsula (England)	51°33′N	D	*	–	****	*
Liocarcinus depurator (Linnaeus, 1758)	Mori and Zunino (1987)	Gulf of Genova (Italy)	44°18′N	SC	*	*	****	*
Macropipus tuberculatus (Roux, 1830)	Mori (1987)	Gulf of Genova (Italy)	44°18′N	D	–	****	****	–
Macropipus puber (Linnaeus, 1767)	González-Gurriarán (1985)	Ria de Arousa (Spain)	42°18′N	SC	*	*	****	****
Macropipus tuberculatus (Roux, 1830)	Abelló (1989)	Barcelona (Spain)	41°50′N	D	*	****	****	–
Liocarcinus depurator (Linnaeus, 1758)	Fernández *et al.* (1991)	Ria de Arousa (Spain)	41°28′N	SC	*	*	****	****
Callinectes sapidus Rathbun, 1869	Dudley and Judy (1971)	Beaufort Inlet (USA)	34°43′N	D	****	–	–	****
Callinectes arcuatus Ordway, 1863	Paul (1982)	Huizake-Caimanero Lagoon (Mexico)	22°48′N	SC	****	*	****	****
Callinectes toxotes (Ordway, 1863)	Paul (1982)	Huizake-Caimanero Lagoon (Mexico)	22°48′N	D	–	****	****	–
Scylla serrata (Forskål, 1775)	Prasad and Neelakantan (1989)	Karwar (India)	14°50′N	SC	*	****	****	*
Portunus pelagicus (Linnaeus, 1758)	Ingles and Braum (1989)	Ragay Gulf (Philippines)	13°30′N	SC	****	*	****	*
Portunus pelagicus (Linnaeus, 1758)	Batoy *et al.* (1987)	Ormoc (Philippines)	11°00′N	C	****	****	****	****
Portunus pelagicus (Linnaeus, 1758)	Pillay and Nair (1971)	Cochin Backwaters (India)	9°58′N	SC	*	****	****	*
Callinectes danae Smith, 1869	Pita *et al.* (1985)	Santos, SP (Brazil)	24°00′S	SC	*	*	*	****
Arenaeus cribrarius (Lamarck, 1818)	Pinheiro and Fransozo (1994)	Ubatuba, SP (Brazil)	23°29′S	SC	****	*	*	****
Portunus spinimanus Latreille, 1819	Santos (1994)	Ubatuba, SP (Brazil)	23°30′S	SC	*	*	****	****
Arenaeus cribrarius (Lamarck, 1818)	This study	Ubatuba, SP (Brazil)	23°30′S	SC	****	*	****	****
Charybdis natator (Herbst, 1789)	Sumpton (1990)	Moreton Bay (Australia)	27°00′S	SC	****	*	*	****
Portunus pelagicus (Linnaeus, 1758)	Campbell and Fielder (1986)	Moreton Bay (Australia)	27°00′S	SC	****	*	****	****
Portunus sanguinolentus (Herbst, 1783)	Campbell and Fielder (1986)	Moreton Bay (Australia)	27°00′S	D	****	–	****	****
Callinectes danae Smith, 1869	Branco *et al.* (1992)	Lagoa da Conceição, SC (Brazil)	27°35′S	SC	****	*	*	****
Ovalipes punctatus (De Haan, 1833)	Du Preez and McLachalan (1984)	Port Elizabeth (South Africa)	34°00′S	SC	*	****	****	*
Scylla serrata (Forskål, 1775)	Hill (1975)	Kleinmond Estuary (South Africa)	34°36′S	SC	****	*	*	****
Ovalipes catharus (White, 1843)	Armstrong (1988)	Blueskin Bay (New Zealand)	45°52′S	D	****	–	–	****

(1) Symbols representing reproductive intensity in each season (SU = summer; A = autumn; W = winter; SP = spring) are as follows: **** = high intensity; * = low intensity; – = absence of ovigerous females and/or adult females with mature gonads.

months (Table 3). *Arenaeus cribrarius* in this study shows summer and spring breeding that conforms to results of Branco *et al.* (1990) farther south in the Conceição Lagoon, Brazil (27°35′S). By examining the geographical locations of the portunid species cited in Table 3, it can be concluded that breeding mainly during the coldest months of the year is most frequent at higher latitudes.

According to Sather (1966), molting activity in crustaceans is higher during warmer months. However, the reduced temperature range verified in tropical regions favor the extension of the molting season (Churchill, 1919; Travis, 1954), contrary to what is observed in temperate regions where winter is more severe (Carlisle, 1957). As expected, molting activity was recorded throughout the study period in *A. cribrarius,* with a noticeable asynchrony between sexes, which is a characteristic feature of portunids (Hartnoll, 1969). Hartnoll mentioned that molting in males does not markedly affect the reproductive process of portunids, because of their specific mating system and lengthy intermolt period. For females, however, mating takes place during the postmolt phase, conditioning the reproductive timing in this species.

According Pinheiro and Fransozo (1999), *A. cribrarius* females are copulated before puberty molt during first postmolt adult instar. The number of adult instars differs among portunid species, ranging from two for *Portunus sanguinolentus* (Herbst, 1783) to five for *Charybdis (C.) feriatus* (Linnaeus, 1758), according Ryan (1967b) and Campbell and Fielder (1988), respectively. *Arenaeus cribrarius* may be at least a second mature instar, because 1% of adult females were observed in premolt condition. The females that are not copulated at puberty molt can be at another instar but with an observed shortening of mating behavior (Pinheiro and Fransozo, 1999).

The delimitation of the reproductive season in pleocyemates has been obtained by estimating the period in which ovigerous females appear in the population. Despite Ryan's (1967a) statement suggesting the use of gonad development analyses to support such data, some authors verified that there is agreement between both methods (Batoy *et al.,* 1987). The association found between molting and gonadal development in *A. cribrarius* indicates that molting coincides with gonad regression. This is due to the energetic partitioning between somatic growth and reproduction (Adiyodi and Adiyodi, 1970), which are the biological processes that demand the most energy, more than all the remaining physiological activities together (Adiyodi, 1985). Many temperate brachyurans follow a seasonal breeding cycle, mainly breeding during spring and summer when environmental conditions are more favorable for survival of offspring and ceasing completely during winter (Warner, 1977). Tropical and deep-water crustaceans generally breed continuously year-round as a result of the low temperature variation in those regions (Sastry, 1983). This pattern may be easily recognized in Table 3, because there is a clear contrast between portunids from higher latitudes and those species distributed near the equator. The influence of environmental factors on the reproduction of crustaceans is often reported in the literature (Orton, 1920; Segerstrale, 1970; Steele *et al.,* 1977; Campbell and Fielder, 1986). Water temperature and photoperiod are the most relevant parameters affecting the reproductive cycle (Payen, 1980–81), but light intensity is the main factor triggering oogenesis. Photoperiod and temperature increase promote a higher metabolic rate and raise the neuroendocrinological sensibility, thus inducing gametogenesis (Laubier-Bonichon, 1978). Water temperature is negatively correlated with duration of embryonic and postembryonic development in crustaceans (Wear, 1974; Pinheiro *et al.,* 1994); therefore, summer breeding would favor survivorship (Giese, 1959). Anderson *et al.* (1977) and Stuck and Truesdale (1988) recorded high frequency of *A. cribrarius* ovigerous females during spring and summer, corroborating the present study. However, winter temperatures do not seasonally constrain reproduction in tropical populations of *A. cribrarius* because ovigerous specimens have been recorded when water temperature varied from 19° to 31°C. Yet, their occurrence during warmer months, when temperatures ranged from 28° to 31°C, is more frequent (Pinheiro *et al.,* 1996). Pinheiro and Terceiro (2000) explain the high frequency of ovigerous females during winter by the spawning of primiparous females, because mating occurs chiefly in autumn.

Several authors have shown that breeding portunid females migrate to specific areas where they incubate their eggs (Williams and Hill, 1982; Archambault *et al.*, 1990). Among the possible environmental conditions required for egg-carrying females, the granulometry of the sediment (Churchill, 1919; Broekhuysen, 1936; Pinheiro *et al.*, 1996), and temperature / salinity levels (Sandoz and Rogers, 1944; Costlow and Bookhout, 1959) are known to particularly favor brooding. According to Pinheiro *et al.* (1996), ovigerous females of *A. cribrarius* in Fortaleza Bay show significant association with sediment comprised of coarse (0.5–1.0 mm) and intermediate (0.25–0.5 mm) sand grains than with other environmental factors. Lower abundance of ovigerous females in Ubatuba Bay (second year of samples) is probably a result of migration of breeding females to other areas, because very fine sediments are found in the deeper bottoms of Ubatuba Bay (Nakagaki, 1994), contrasting with Fortaleza Bay (first year of samples).

The long breeding season verified for *A. cribrarius* can be due to the average high water temperature and reduced variation of both temperature and photoperiod, which characterize the intertropical region. The occurrence of multiple broods in portunids (Mori, 1987; Bawab and El-Sherief, 1988) was also attributed to *A. cribrarius* by Pinheiro and Fransozo (1999). According these authors *A. cribrarius* females may incubate six successive broods without molting and produce at least two successive broods in a single mature instar because 50% of the ovigerous females carrying late embryos also had mature gonads. This aspect explains continuous reproduction in this species.

Seasonal reproduction may be advantageous in the case of coexistence between species with similar trophic niche, behavior patterns, or environmental requirements. *Callinectes* spp. may show temporal partitioning of their environment (Paul, 1982; Negreiros-Fransozo and Fransozo, 1995). Asynchronous occurrence between ovigerous females of *C. ornatus* (summer) and *C. danae* (winter) observed by Negreiros-Fransozo and Fransozo (1995) is also suggested in Pinheiro *et al.* (1997), who showed a broad niche overlap (40.2%) between these species. According these authors, there is also a high niche overlap between *A. cribrarius* and those portunids (42.9% with *C. ornatus* and 59.5% with *C. danae*), which indicates that interspecific competition is likely to occur, exhorting direct pressure on reproduction.

The classification of the breeding season, as proposed by Sastry (1983) for crustaceans, addresses two different cases: continuous and discontinuous reproduction. However, if duration, occurrence, and intensity of breeding are taken into account, then a redefinition of such classification would be desirable in cases when a wider array of reproductive patterns is discernible, as it can be verified in the Portunidae (Table 3). In this way, continuous reproduction should be applied when ovigerous individuals and/or females bearing mature gonads are present year-round with similar monthly frequencies throughout. If breeding is still recorded over all the year, but monthly frequency of reproducing females varies with recognizable periods of higher reproductive activity, then seasonal-continuous reproduction would apply. Finally, if the presence of ovigerous specimens and/or females with mature gonads are restricted to a determined period, or season, then seasonal reproduction may be used.

Studies on the reproduction of portunids often show asynchronous molting between adult males and females. This is particularly common if restricted areas, e.g., small bays, are chosen for sampling (Pinheiro and Fransozo, 1994). Larger areas are, however, adequate if one intends to describe breeding seasons, mating events, and oviposition within a given population. Preferentially, an extensive sampling program should be also adopted, including monthly samples over a period of at least one year. This would prevent the absence of certain population categories in samples. Lacking ovigerous females during certain occasions, as obtained by Pinheiro *et al.* (1996), may be related to the sampling procedure in a single bay. In contrast, intense sampling over larger areas are likely to provide more representative samples, as illustrated in this study where ovigerous *A. cribrarius* females were found in all months.

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