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Population biology and reproduction of the hermit crab *Clibanarius vittatus* (Decapoda: Anomura) in an estuarine region of southern Brazil

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The population dynamics and reproduction of the hermit crab Clibanarius vittatus *were evaluated on Pescadores Beach, located on the estuarine channel of São Vicente (São Paulo), Brazil. The hermit crabs were captured by hand during low tide, from May 2001 to April 2003. A total of 2554 hermit crabs were captured, of which 701 were males, 1741 non-ovigerous females, 48 ovigerous females and 64 intersex individuals. The size–frequency distribution of the males was represented by a platykurtic bell-shaped curve, which differed from the leptokurtic bell-shaped curve of the females. The smaller and intermediate classes were composed mainly of females (modal size 6.5–7.5 mm carapace shield length (CSL)), and the larger classes only by males (modal size 9.5–10.5 mm CSL). The overall sex-ratio was skewed toward females (0.39:1/M:F), differing significantly from the expected 1:1. A seasonal reproductive pattern was recorded for* C. vittatus *in this location, with more intensive reproductive activity in the warmer months. The absence of juveniles suggests that their recruitment area is different than the area inhabited by adults, possibly another area with more protection and specialized or different resources for young.*

Keywords: hermit crab, *Clibanarius vittatus*, reproduction, population biology

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INTRODUCTION

Studies of animal populations are essential to understand the dynamics of ecosystems. Generally, population analyses have focused on descriptions of density, size-structure, sex-ratio and breeding periods that can be compared to other populations of the same species, genus or other taxonomic levels (Litulo, 2005a). Although hermit crabs are not likely to be of commercial importance, they contribute to the mass of planktonic organisms in coastal waters that help to feed the young of commercial species (Squires *et al.*, 2001), and they are an important part of the trophic chain, mainly where their populations are largest.

In crustaceans, the reproductive cycle is influenced by biotic and abiotic factors that rule the larval, gonadal and embryonic development (Mantelatto & Garcia, 1999; Bertini *et al.*, 2004). The breeding season may vary between populations in response to the influence of environmental factors in a given area (Litulo, 2005b). Sastry (1983) proposed two reproductive patterns for crustaceans: (1) continuous reproduction, when ovigerous females occur uniformly throughout the year; or (2) seasonal reproduction, with peaks in some months, with ovigerous females occurring only in some months of the year.

In hermit crabs, four aspects of reproduction have been studied: (1) frequency of ovigerous females by months or seasons (Manjón-Cabeza & Garcia-Raso, 1995; Martinelli *et al.*, 2002; Litulo 2005 a, b); (2) analysis of fecundity (Mantelatto & Garcia, 1999; Turra & Leite, 1999; Negreiros-Fransozo *et al.*, 1992; Litulo, 2005c); (3) macroscopic analysis of the gonads (only by Bertini *et al.*, 2004); and (4) histology of gonads (Manjón-Cabeza & García-Raso, 2000a, b).

The hermit crab *Clibanarius vittatus* (Bosc, 1802) is the most abundant in the intertidal zone of the São Vicente Estuary. According to Melo (1999), this species lives in estuarine areas, coral reefs and sandy substrates, in shallow waters up to 22 m deep. Studies have treated its population biology and reproduction (Kicher, 1967); larval and juvenile development (Young & Hazlett, 1978; Brossi-Garcia, 1988, respectively); and other reproduction and population analysis (Fotheringham, 1975; Lowery & Nelson, 1988; Reigada & Santos, 1997; Turra & Leite, 2000, 2001; and Hazlett *et al.*, 2005). In these studies, the reproductive period was determined by the frequency of ovigerous females during the year, a common method used to study the reproduction of pleocyemata crustaceans.

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This study aimed to analyse the population structure (sizes of sexes, seasonal size–frequency distribution and sex-ratio) of the hermit crab *C. vittatus* in the estuarine region of São Vicente, state of São Paulo, Brazil, and the reproductive period based on the occurrence of ovigerous females during the seasons, compared to the frequency of gonad maturation stages.

MATERIALS AND METHODS

The study was conducted in the intertidal zone of Pescadores Beach (23°58′21″S–46°23′35″W: Figure 1), located on the estuarine channel of São Vicente (São Paulo), Brazil, which shelters a diverse marine fauna, including intertidal molluscs, macroalgae and benthic crustaceans (Sant'Anna *et al.*, 2006).

The hermit crabs were captured by hand during low tide, from May 2001 to April 2003. Monthly captures were made by two people, with a standard capture effort of 10 minutes. Water temperature (°C) was measured monthly. The hermit crabs were stored frozen. For analysis, the specimens were defrosted and removed from their gastropod shells, for identification according to Melo (1999). The carapace shield length (CSL) was recorded from the tip of the rostrum to the midpoint of the cervical groove, using a Vernier caliper (0.01 mm). For the size–frequency distribution analysis, size-class intervals of 1 mm of CSL were used. The size intervals of each class were determined according to the mathematical formula of Sturges (1926). After identification and biometric analysis, the sex of each individual was determined from the position of the gonopores and the presence of eggs, and four population categories were established: (1) males, with gonopores on the basis of the fifth pereopods; (2) non-ovigerous females, with gonopores on the basis of the third pereopods; (3) intersex individuals, with gonopores on the bases of both the third and fifth pereopods; and (4) ovigerous females. Individuals of uncertain sex and intersex individuals were not included in the statistical analyses of population and reproduction.

All the individuals were dissected to observe the stage of gonad maturation, and were classified according to three gonad stages determined for males (immature or rudimentary gonads, which are undifferentiated or thin and translucent with two small white ducts; developing, with an initial winding, pale or white filament; and developed, with a strongly coiled testis with the dominant visible organ pale white and a white vas deferens), and females (immature or rudimentary, with ovaries as two fine, wine-coloured filaments; developing, with ovarian maturation beginning and represented by two wine-coloured filaments, occupying a large volume in the abdomen; and developed, when ovaries are dark-wine-coloured and fill the abdomen). The reproductive period was determined by the percentage of individuals of the same sex with developed gonads and the monthly incidence of ovigerous females during the course of the sampling period.

The normality of the size–frequency distribution was tested by the Kolmogorov–Smirnov (KS) test for each population category, and the size of individuals was compared by the Kruskal–Wallis test. The monthly and overall sex ratios (M:F) were tested with the Chi-square test (χ^2). The relationship of sex-ratio to size-class was fitted only for classes with more than ten individuals, as recommended by Wenner (1972). The correlation of water temperature (°C) and the incidence of individuals with developed gonads were tested by Spearman's correlation. A significance level of 5% was adopted for all statistical analyses (Sokal & Rohlf, 1995).

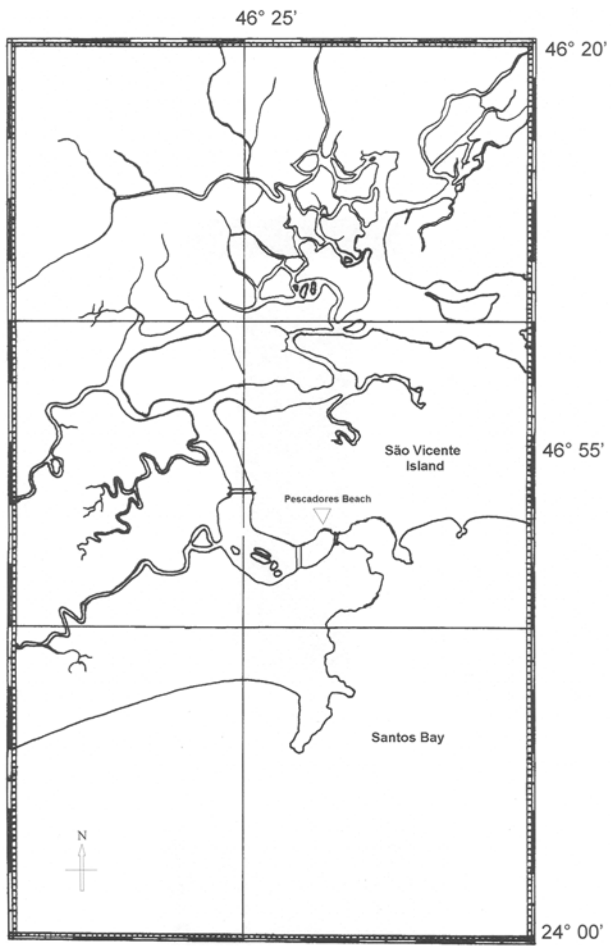

Fig. 1. Estuary of São Vicente (São Paulo), Brazil, showing the location of Pescadores Beach (setae).

RESULTS

A total of 2554 hermit crabs were captured in the intertidal zone of Pescadores Beach: 701 males, 1741 non-ovigerous females, 48 ovigerous females and 64 intersex individuals. Male individuals were significantly larger than females ($P < 0.05$), but intersex individuals were the same size as males (Table 1).

The overall size–frequency distribution of the population differed from normality (KS = 0.0755; $P < 0.01$), with a unimodal distribution. The size–frequency distribution of the males was represented by a platykurtic bell-shaped curve that differed from the leptokurtic bell-shaped curve for females (Figure 2). Although the size–frequency distribution of the population did not show a normal distribution, this was not true for all sexes; the size–frequency distribution for males differed from normality (KS = 0.0791; $P < 0.01$), but the size–frequency distributions of non-ovigerous females and ovigerous females showed significant normal distributions (KS = 0.03; $P > 0.05$ and KS = 0.1079; $P > 0.05$).

Table 1. Number of individuals and size-range (carapace shield length) of the hermit crabs captured on Pescadores Beach. N, number of individuals; Min, minimum; Max, maximum; x mean; SD, standard deviation; M, males; F, non-ovigerous females; OF, ovigerous females; INT, intersex individuals.

Sex	N	Min	Max	x ± SD
M	701	2.7	13.8	8.93 ± 1.81 a
F	1741	2.6	11.7	6.61 ± 1.14 b
OF	48	4.9	9.4	6.71 ± 1.07 b
INT	64	5.4	12.3	9.37 ± 1.43 a
Total	2554	2.6	13.8	7.32 ± 1.74

Means followed by the same lower-case letter did not show significant differences ($P > 0.05$).

In the same figure, we can observe that the smaller and intermediate classes were composed mainly of females (modal size 6.5–7.5 mm CSL), and the larger classes only of males (modal size 9.5–10.5 mm CSL).

The seasonal size–frequency distribution of the population (Figure 3) showed unimodal and bimodal distributions during the seasons. Few juveniles were recorded in this location, and females were more abundant than males during the two years of the study. Ovigerous females occurred in all seasons of the year, but in lower frequency in the winter. The abundance of females by month is shown in Table 2. The sex ratio (M:F), was nearly always skewed toward females, except in two months of the study period, the overall sex-ratio (0.39:1; M:F) differed significantly from 1:1 ($\chi^2 = 475.399$; $P < 0.001$). The sex-ratio related to size, showed an anomalous curve (Figure 4), with females extremely abundant in intermediate size-classes, and males numerically superior in the larger ones.

The percentage of individuals with developed gonads was larger in the warmer months of the year (Figure 5). The percentage of ovigerous females (Figure 6) evidenced a seasonal

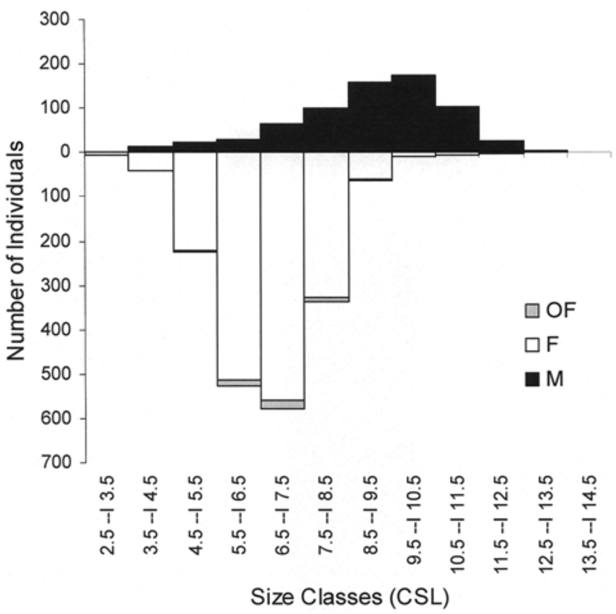

Fig. 2. Size–frequency distribution of individuals of *Clibanarius vittatus* caught on Pescadores Beach, São Vicente Estuary (São Paulo), Brazil. CSL, carapace shield length.

reproductive pattern at this location, with more intensive reproductive activity in the warmer months. This is supported by a positive correlation between water temperature and females with developed gonads ($rs = 0.61$; $P = 0.0017$). Dissections of the intersex individuals revealed male gonads, with one paired coiled whitish duct.

DISCUSSION

The sexual dimorphism in relation to size observed in the present study is a common aspect of hermit-crab biology, as suggested by several previous reports (Fransozo & Mantelatto, 1998; Manjón-Cabeza & García-Razo, 1998; Turra & Leite, 2000; Mantelatto & Martinelli, 2001; Branco *et al.*, 2002; Bertini *et al.*, 2004; Macpherson & Raventos, 2004; Litulo, 2005a, c; Litulo & Tudge, 2005; Mantelatto *et al.*, 2005). According to Abrams (1988), three factors may influence sexual dimorphism in hermit crabs: (1) the difference of energy available for growth, with less somatic growth in females due to greater expenditure of energy in egg production; (2) the larger reproductive effort exhibited by males, which are able to copulate with more than one female; and (3) the larger dimensions of males, to optimize fertilization of the females and win intraspecific fights.

In this population of *C. vittatus* in São Vicente Estuary, the differential growth rate between the sexes (as proposed by Abrams, 1988) suggests an important factor for the sexual dimorphism. According to the growth analysis of this same population by Sant'Anna *et al.* (2008), males have a larger constant growth than do females (males, $K = 0.51$; and females, $K = 0.40$), and the different growth periods of the sexes reduce intraspecific competition for gastropod shells. A slower growth rate of females would be a consequence of utilization of relatively small shells in nature, as suggested by Litulo (2005 a, c) for *Dardanus deformis* (H. Milne-Edwards, 1836) and *Clibanarius longitarsus* (De Haan, 1849), respectively.

A few ovigerous females and juveniles were captured during the present study, a result similar to that obtained by Litulo (2005a) for *D. deformis* in Maputo Bay, Mozambique. The lower abundance of juveniles suggests that the recruitment area is different from the area inhabited by adults, possibly another area with more protection and specialized or different resources for the juveniles. Although there is a good supply of smaller shells of *Littorina* sp., suitable for juveniles, at Pescadores Beach (personal observation), it is possible that *C. vittatus* ovigerous females migrate to the entrance of the estuary, where their larvae have access to optimum salinities for the first juveniles (25 to 35‰, according to Young & Hazlett, 1978), avoiding the wide salinity variations in the study area (20 to 35‰, according to Sant'Anna *et al.*, 2006). Thus, when the juvenile hermit crabs return inside the estuary they already measure several millimetres in size. A similar absence of juvenile individuals was noted by Turra & Leite (2000), who studied three sympatric species of hermit crabs of the genus *Clibanarius*, on another part of the Brazilian coast. As estimated by these authors, the recruitment period (December to March, according to Sant'Anna *et al.*, 2008) was equivalent to those months when greater reproductive activity was observed in this population.

The sex-ratio of the *C. vittatus* population in the present study was skewed toward females, with a difference from

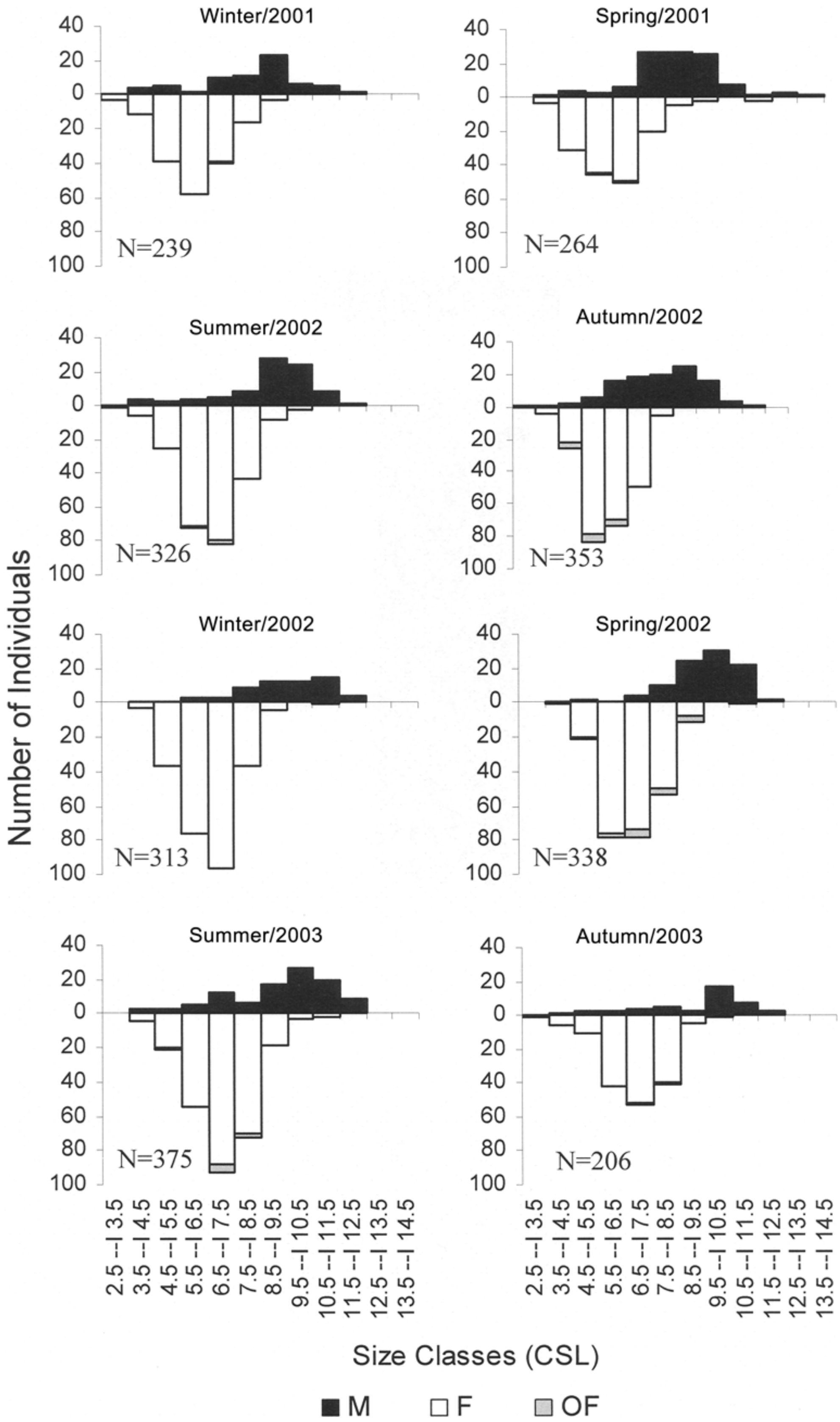

Fig. 3. Seasonal size – frequency distribution of individuals of *Clibanarius vittatus* captured on Pescadores Beach, São Vicente Estuary, Brazil. CSL, carapace shield length.

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Table 2. Sex-ratio by month obtained for the population of hermit crabs *Clibanarius vittatus* on Pescadores Beach, São Vicente (São Paulo), Brazil.

Months	Males	Females	Sex-ratio (M:F)	χ^2	*P*
May 2001	27	50	0.54*	6.87	0.0122
June	24	62	0.39*	16.79	0.0001
July	18	53	0.34*	17.25	0.0001
August	26	55	0.47*	10.38	0.0019
September	67	81	0.83^{ns}	1.32	0.2853
October	18	25	0.72^{ns}	1.14	0.3602
November	19	54	0.35*	16.78	0.0001
December	30	101	0.30*	38.48	0.0000
January 2002	30	49	0.61*	4.57	0.0429
February	27	89	0.30*	33.14	0.0000
March	46	84	0.55*	8.34	0.0054
April	32	97	0.33*	32.75	0.0000
May	33	61	0.54*	8.34	0.0054
June	13	63	0.21*	32.89	0.0000
July	20	71	0.28*	28.58	0.0000
August	26	120	0.22*	60.52	0.0000
September	12	32	0.37*	9.09	0.0042
October	42	125	0.34*	41.25	0.0000
November	40	87	0.46*	17.39	0.0000
December	33	117	0.28*	47.04	0.0000
January 2003	38	73	0.52*	11.04	0.0013
February	34	80	0.42*	18.56	0.0000
March	11	71	0.15*	43.90	0.0000
April	35	89	0.39*	23.52	0.0000

^{ns}, non-significant; $^{*}P < 0.05$.

the expected proportion (1:1). The same has been recorded for various populations of different hermit-crab species around the world (Manjón-Cabeza & García-Raso, 1998; Benvenuto & Gherardi, 2001; Macpherson & Raventos, 2004; Litulo, 2005c; Litulo & Tudge, 2005) and in two other populations of *C. vittatus* (Lowery & Nelson, 1988; Turra & Leite, 2000). The same pattern was obtained for overall sex-ratio, and as a function of size, showed an anomalous curve pattern according to the classification proposed by Wenner (1972). This author suggested four explanations for this pattern of the

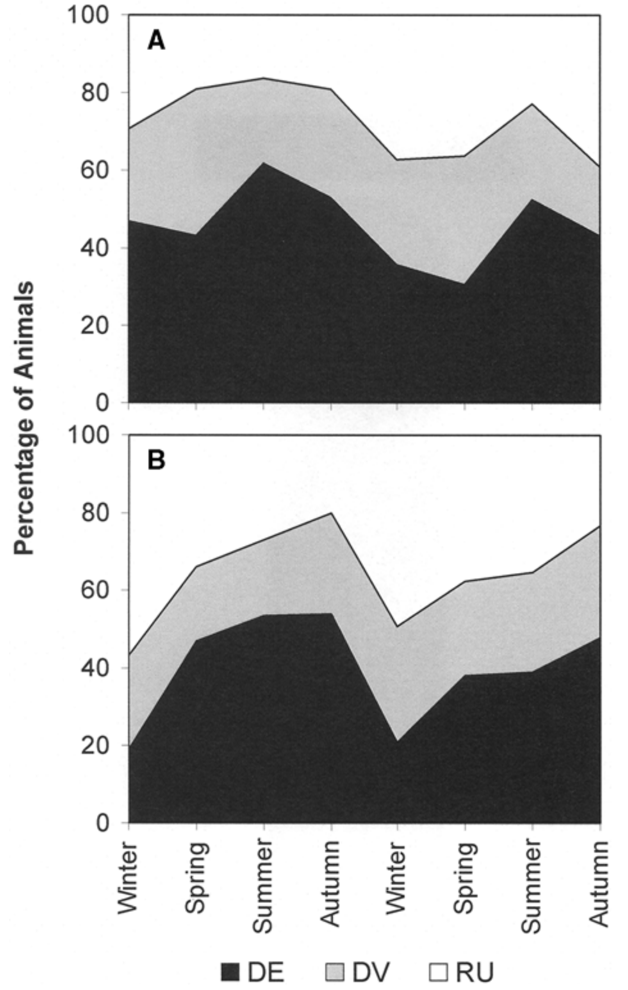

Fig. 5. Seasonal percentage of males (**A**) and females (**B**) of *Clibanarius vittatus*, with rudimentary (RU), developing (DV) and developed (DE) gonads during the study period on Pescadores Beach, São Vicente Estuary, Brazil.

sex-ratio: (1) differences between the sexes in longevity and time for growth; (2) differential migration; (3) different mortality or growth rates between sexes; and (4) sex reversal. In *C. vittatus*, the most probable causes are the difference in the

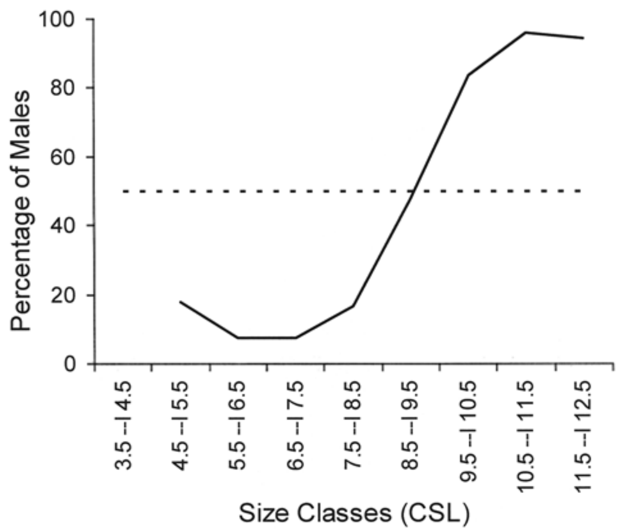

Fig. 4. Percentage (fitted with a mobile mean) of males by size-classes, of *Clibanarius vittatus* caught on Pescadores Beach, São Vicente Estuary, Brazil. CSL, carapace shield length; horizontal line (- - -) represents the expected sex-ratio (1:1).

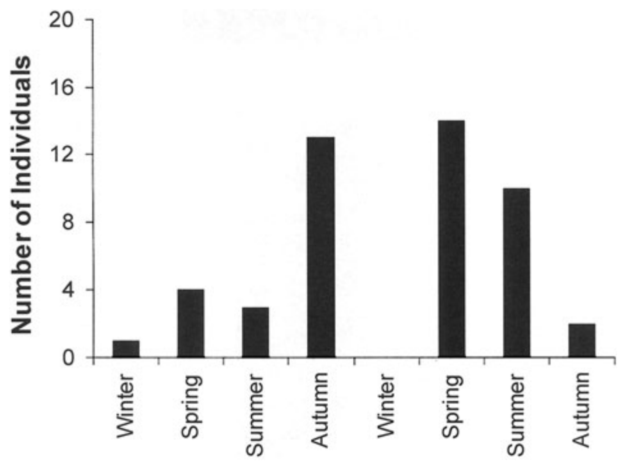

Fig. 6. Seasonal abundance of ovigerous females of *Clibanarius vittatus* caught during the study period on Pescadores Beach, São Vicente Estuary, Brazil.

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growth rates between the sexes, with an influence of longevity (Sant'Anna *et al.*, 2008) or habitat partitioning as suggested by Turra & Leite (2000). Sex reversal occurs in a low percentage of *C. vittatus* populations (see present study and Turra & Leite, 2000), representing a third and minor cause of the sex-ratio pattern observed, and there still is no explanation for the mechanism of sex reversal in hermit crabs (Turra & Leite, 2000; Turra, 2004).

Hermit crabs may have continuous or seasonal reproduction (Manjón-Cabeza & Garcia-Raso, 1998; Bertini & Fransozo, 2000; Turra & Leite, 2000). In this study, the *C. vittatus* population showed a seasonal reproductive pattern with some large peaks of individuals with developed gonads in some warmer months (seasonal–continuous pattern, according to Pinheiro & Fransozo, 2002). These data corroborate those obtained for another *C. vittatus* population by Turra & Leite (2000). Seasonal reproduction is associated with environments characterized by wide variations in temperature or food availability (Giese, 1959). Temperature may act as a metabolic, biochemical and hormonal modulator, triggering the mechanisms of ecdysis, mating and gonad development. However, the availability of and/or competition for shells may influence reproductive activity and cause displacement of reproductive peaks and recruitment periods in coexisting populations (Turra & Leite, 2000; Wada *et al.*, 2000).

Finally, Turra & Leite (2000) suggested that the occurrence of populations with seasonal reproductive patterns in the tropics and with continuous reproduction in temperate areas may be based on populations' evolutionary histories, although local factors should be considered. But a statistical analysis of a more exhaustive data set is required to elucidate any patterns in breeding peaks across latitudes (in both hemispheres), and comparative breeding records for congeners found over a wide range of latitudes should provide the best picture (Litulo & Tudge, 2005).

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