Population biology of the hermit crab *Paguristes tortugae* Schmitt, 1933 (Anomura, Diogenidae) from Anchieta Island, Ubatuba, Brazil

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Abstract

The population of the infralittoral hermit crab *Paguristes tortugae* Schmitt, 1933 from Anchieta Island was studied with emphasis on its seasonal abundance, seasonal size-frequency distribution, sex ratio, recruitment and reproductive period based on juveniles and ovigerous female ratios, respectively. The animals were collected monthly by Scuba diving from January to December 1998 on the infralittoral rocky shores and sandy areas of South, East, Small Beaches and/or Wind Bay of Anchieta Island. Total mean hermit crab size, measured as shield length, was 4.20 ± 1.18 mm for males, 3.16 ± 0.98 mm for non-ovigerous females, and 3.72 ± 1.07 mm for ovigerous females. This island population differed in size-frequency distribution (bimodal) when compared to populations of the same species from other localities. Continuity in recruitment and reproduction was observed, with a high incidence from November to March (spring to autumn). The species *P. tortugae* presented sexual dimorphism in size, with a higher growth rate observed in males. Three individuals exhibited an abnormal gonopore position. The sex ratio pattern (anomalous) changed seasonally.

Key words: Anomura, hermit crab, *Paguristes*, population biology

Introduction

Decapod crustaceans present a high number of living species that inhabit a wide variety of biotopes. Consequently, this group represents promising study because the establishment of these animals in such environments derives from the evolution of adaptative population strategies. Thus, the Anomura represent a highly significant group among marine crustaceans, comprising more than 800 species of the hermit crabs of the world and have undergone considerable revision (Ingle, 1993). Hermit crabs represent an important portion of the many intertidal and moderately deep benthic communities, where they play an important role in the marine food chain (Fransozo and Mantelatto, 1998). Despite of this situation, the population aspects of hermit crabs have been poorly studied.

Of 46 hermit crab species recorded in Brazilian waters, 21 were recorded on the northern coast of São Paulo State, 14 of them belonging to the family Diogenidae and 7 to the family Paguridae (Melo, 1999; Mantelatto *et al.*, 2001). The genus *Paguristes* is represented by more than 100 species distributed in all tropical and subtropical oceans, occurring from the intertidal zones to moderate depths (Provenzano, 1978).

Paguristes tortugae Schmitt, 1933 is a relatively common species distributed in the Western Atlantic from Florida to Brazil (as far south as Santa Catarina State) (Rieger and Giraldi, 1997; Melo, 1999). This species has been studied concerning to systematic descriptions (Forest and Saint Laurent, 1967; Tommasi, 1967), post-embryonic development (Hebling and Negreiros-Fransozo, 1983), population structure and shell occupation (Negreiros-Fransozo and Fransozo, 1992), fecundity (Negreiros-Fransozo *et al.*, 1992; Mantelatto *et al.*, 2002), shell utilization pattern, and reproductive aspects (Gandolfi, 1996; Mantelatto and Dominciano *in press*).

Despite the reports about Brazilian shore populations of this species, they represent promising

material for study on comparative population biology and ecology with specimens from different areas. In addition, three groups of hermit crabs in particular (*i.e.*, the genera *Pagurus* and *Paguristes*, and the "*Pylopagurus*-like" species), have been a difficult group to study because there are many still-undescribed species and considerable identification problems among specialist and nonspecialists alike (Hendrickx and Harvey, 1999).

Hermit crabs have also been included in numerous reports of decapods from Central and South America (see Haig and Harvey, 1991 in review). However, few species have received more than brief attention. In Brazil, several studies on the population structure of hermit crabs were carried out in the Ubatuba region (São Paulo State) for *Pagurus criniticornis* (Dana, 1852), *Pagurus brevidactylus* (Stimpson, 1879), *Clibanarius antillensis* Stimpson, 1859 and *Clibanarius vittatus* (Bosc, 1802) by Negreiros-Fransozo *et al.* (1991), *Dardanus insignis* (de Saussure, 1858) by Fernandes-Góes (1997), *Calcinus tibicen* (Herbst, 1791) by Fransozo and Mantelatto (1998), *Loxopagurus loxochelis* (Moreira, 1901) by Martinelli *et al.* (*in press*), *Petrochirus diogenes* (Linnaeus, 1758) by Bertini and Fransozo (2000), and *Paguristes erythrops* by Garcia and Mantelatto (2001).

In this report, we describe the population structure of *P. tortugae* in the infralittoral region of Anchieta Island (Ubatuba), São Paulo State, Brazil, with respect to seasonal abundance, seasonal size-frequency distribution based on shield length as a measure of animal size, recruitment and reproductive period based on juveniles and ovigerous female ratios, respectively.

Material and Methods

Study Area

Anchieta Island (23º 33'S and 45º 05'W) was recently declared an ecological reserve of São Paulo State. The island has a total area of about 10 km^2, located landwards, and separated from the coast by a 300 m long and 35 m deep canal. There are six small beaches, and almost the entire shore area is rocky, with an irregular surface and areas with large boulders. This area is important in view of the significant anthropogenic activity, which has led to the expansion of the tourist center (Mantelatto and Garcia, 2002). The physical and chemical features of this area have been described by Medeiros (1992), however scientific information about the crustacean fauna from this location is scanty.

Sampling

Hermit crabs were obtained monthly from January to December 1998 on the infralittoral rocky shores and sandy areas of South, East, Small Beaches and/or Wind Bay of Anchieta Island. Except for January and July (with one site sampled), at least two of these sites were sampled monthly as a function of ocean conditions permitting access and diving activities. Specimens were captured during the daytime by three people using SCUBA diving methods over a period of 20 min over the same area of about 850 m^2. This methodology provided large amounts of material from this area and thus was considered efficient for the hermit crab population study (Mantelatto and Garcia, 2002).

Analysis

Animals were frozen and transported to the laboratory where they were carefully removed from their shells and measured for cephalothoracic shield length (CSL = from the tip of the rostrum to the V-shaped groove at the posterior edge). Sex was determined from the gonopore position (on the basis of the 3rd and 5th pair of pereopods for females and males, respectively). Measurements were made with a caliper rule (0.1 mm) or with a camera lucida. The specimens were grouped into 0.5 mm size class intervals from 1.0 to 8.0 mm.

The reproductive condition of the population was expressed as the percentage of females carrying eggs relative to the total number of females collected (Fransozo and Mantelatto, 1998). The chi-square

test (χ^2) was used to evaluate the sex ratio and to compare male and female percentage per month. The size distribution frequency was analyzed by the Kolmogorov-Smirnov Normality test (KS). The mean size of individuals of both sexes was compared by the Mann-Whitney Sum test. All used tests are in accordance with the methods described by Zar (1996).

Results

There were no significant differences between number and size of the specimens from the four sampled areas on Anchieta Island and therefore the data were pooled for analysis. A total of 2429 individuals (mean, and minimum to maximum shield length) of *P. tortugae* were obtained, represented by 1092 males (4.20 ± 1.18 mm, 1.0 to 7.8 mm), 495 non-ovigerous females (3.16 ± 0.98 mm, 1.1 to 6.2 mm), and 842 ovigerous females (3.72 ± 1.07 mm, 1.8 to 6.7 mm). The mean size of males was significantly larger than the mean size of females ($P < 0.0001$). Three males presented anomalous characteristics in gonopore position. Two of them with a normal pair of gonopores on 5th pereiopod and one gonopore on the left 4th pereiopod, and the third abnormal male presented a pair of gonopores on the 5th pereiopod, one gonopore on the 4th and another on the 3rd pereiopod. These abnormal individuals were included in the male category because they presented a pair of pleopods on the first two abdominal segments.

The KS test indicated that female data ($KS = 0.120$; $P < 0.0001$) and male data matches ($KS = 0.058$; $P < 0.0001$) varied significantly from the pattern expected for a population of normal distribution.

There was a conspicuous bimodal size distribution for males and ovigerous females and an unimodal distribution for non-ovigerous females (Table I and Figure 1). Male modal size ranged from 3.0 to 3.5 and from 4.5 to 5.0 mm of CSL. Non-ovigerous females showed a modal size ranging from 2.5 to 3.0 mm and ovigerous females a modal size ranging from 2.5 to 3.0 mm and from 4.0 to 5.0 mm of CSL. Males reached a larger size than females since only males occurred in the largest two size classes. Monthly CSL values were, in general, bimodal and slightly asymmetrical. Recruitment into the zone studied (by specimens which belong to the previously defined size class < 1.8 mm CSL, based on the smallest ovigerous females size) occurred in all months (Figure 2).

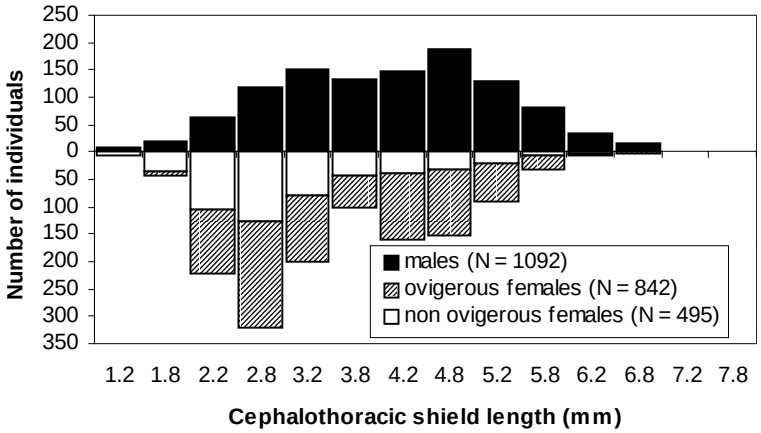

Figure 1: *P. tortugae*: Size frequency distribution of individuals collected from Anchieta Island during January to December 1998.

Overall sex ratio (proportion of males = 0.82 : 1.0) was significantly different from the expected 1:1 sex ratio ($\chi^2 = 24.7$; $P < 0.05$), and the proportion of males clearly increased with larger sizes in *P. tortugae*.

Analysis of reproductive activity indicated by the presence of ovigerous females, revealed that spawning period extended along all months, with a high occurrence of ovigerous females (more than 50 % of mature females) that peaked throughout summer, except for October (41.6 %). This condition was a strong indicator of high reproductive activity (Figure 3). The first spawn occurred among females belonging to the 1.5–2.0 mm CSL size class, whereas the proportion (50.0 % or more) of ovigerous females was clearly increased with larger sizes in *P. tortugae* (Figure 4).

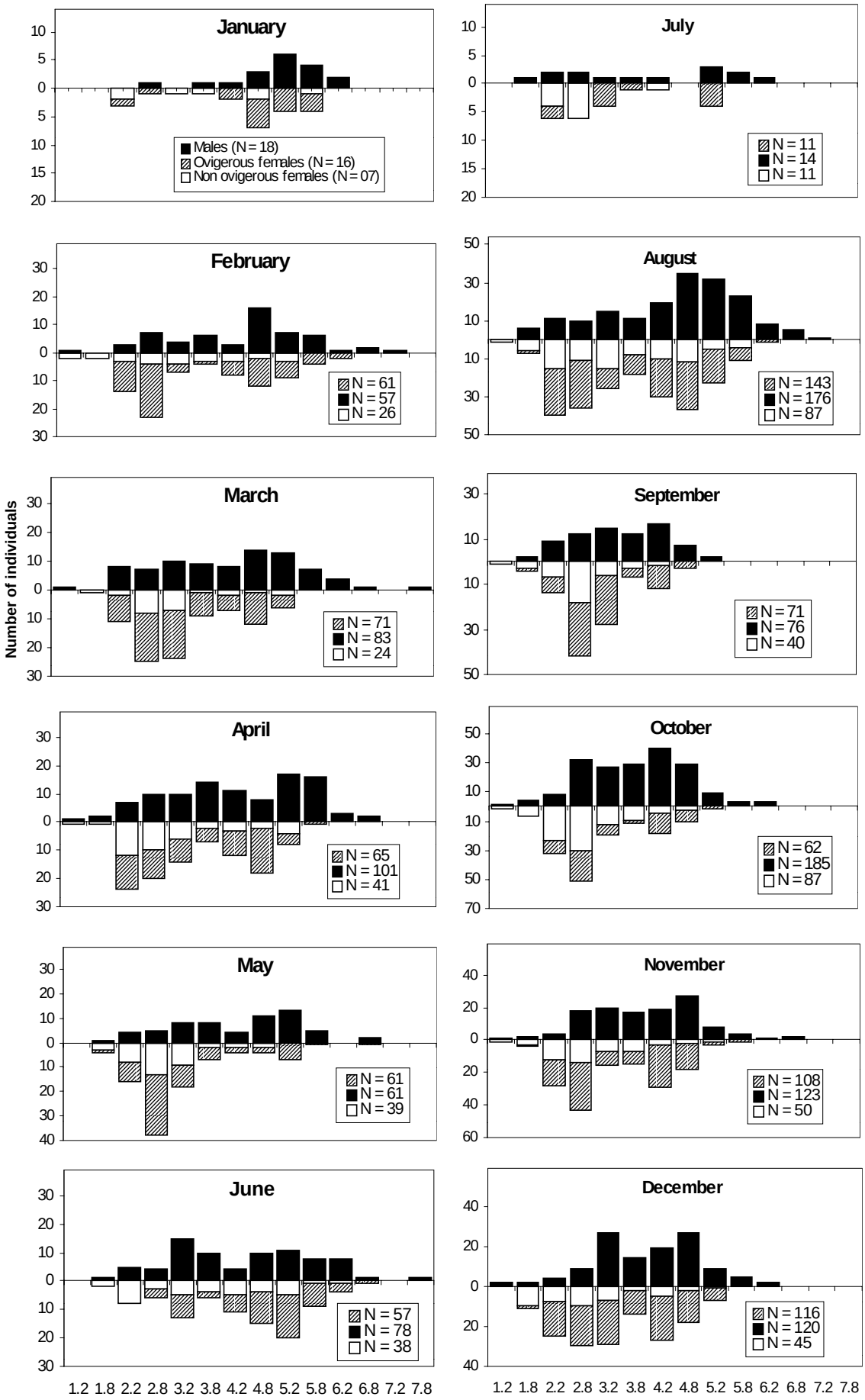

Figure 2: *P. tortugae*: Monthly size class frequency distributions.

Table I: *P. tortugae*: Size frequency distribution of hermit crabs collected on Anchieta Island from January to December 1998. The values indicate the number of individuals and the percentage in relation to the total specimens captured.

Size classes (mm)	Males	%	Non ovigerous females	%	Ovigerous females	%	Total	%
1.0 ⊣ 1.5	7	0.29	7	0.29	0	0	14	0.58
1.5 ⊣ 2.0	21	0.86	37	1.52	5	0.20	63	2.60
2.0 ⊣ 2.5	65	2.68	104	4.30	117	4.81	286	11.80
2.5 ⊣ 3.0	117	4.82	127	5.23	194	7.98	438	18.03
3.0 ⊣ 3.5	152	6.26	79	3.25	120	4.94	351	14.40
3.5 ⊣ 4.0	132	5.43	42	1.73	58	2.37	232	9.60
4.0 ⊣ 4.5	146	6.01	40	1.65	121	4.98	307	12.60
4.5 ⊣ 5.0	187	7.72	31	1.28	123	5.06	341	14.04
5.0 ⊣ 5.5	130	5.36	21	0.86	71	2.90	222	9.14
5.5 ⊣ 6.0	83	3.43	6	0.25	25	1.03	114	4.70
6.0 ⊣ 6.5	33	1.36	1	0.04	6	0.25	40	1.65
6.5 ⊣ 7.0	15	0.62	0	0	2	0.08	17	0.70
7.0 ⊣ 7.5	2	0.08	0	0	0	0	2	0.08
7.5 ⊣ 8.0	2	0.08	0	0	0	0	2	0.08
Total	1092	45	495	20.4	842	34.6	2429	100

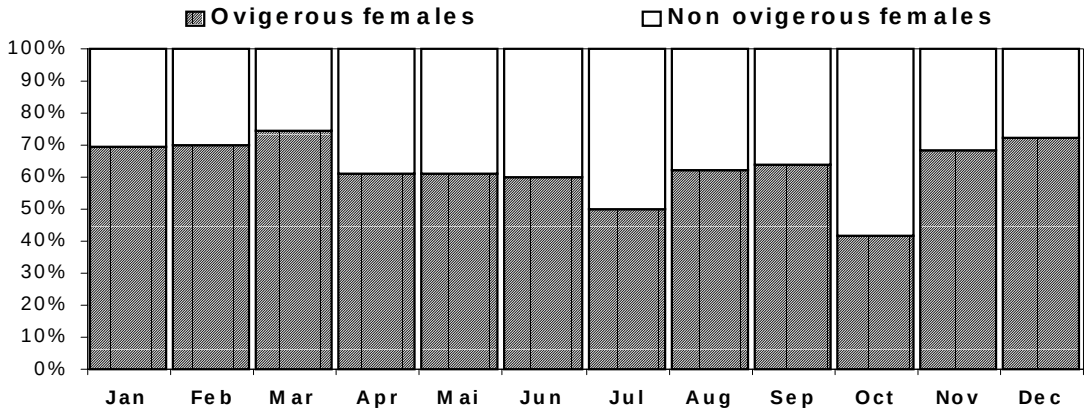

Figure 3: *P. tortugae*: Percentage of non-ovigerous and ovigerous females during the study period (1998).

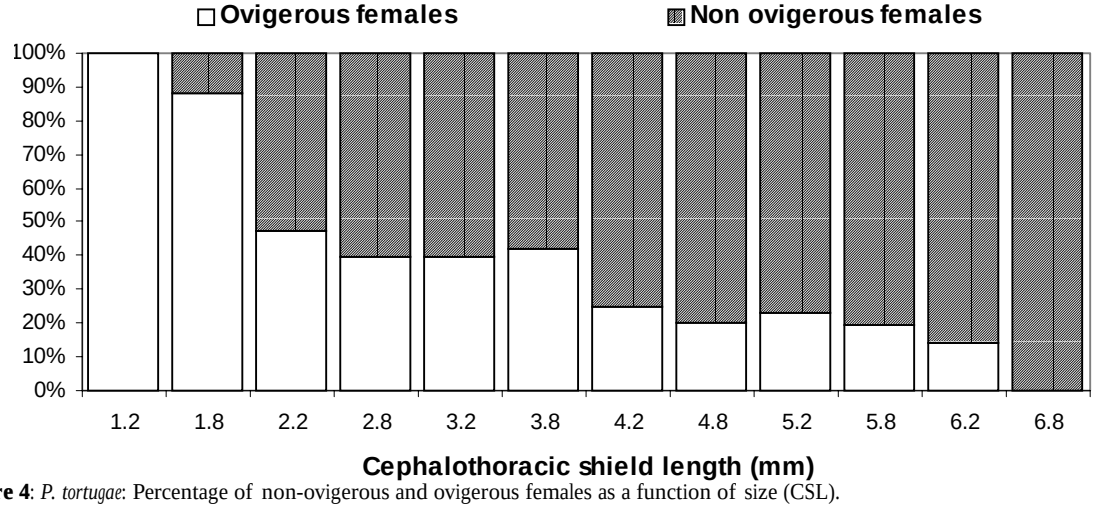

Figure 4: *P. tortugae*: Percentage of non-ovigerous and ovigerous females as a function of size (CSL).

Discussion

The sampling methodology used in this study, that provided large amount of specimens from irregular surfaces, revealed an abundant population of *P. tortugae* in the region of Anchieta Island. This population consisted of specimens of different sizes, with high potentiality for reproduction and growth on a large scale.

Paguristes tortugae is sexually dimorphic in relation to size, with males reaching larger cephalothoracic shield lengths than females, corroborating the pattern reported for this species from other sites (see Negreiros-Fransozo and Fransozo, 1992 and Gandolfi, 1996). This condition was well documented for other hermit crab species (Ameyaw-Akunfi, 1975; Bertness, 1980; Blackstone, 1985; Lowery and Nelson, 1988; Asakura, 1992; Martinelli *et al.*, *in press*; Fransozo and Mantelatto, 1998; Manjón-Cabeza and García-Raso, 1998). According to Abrams (1988), three factors can interfere in the sexual dimorphism of hermit crabs: 1) the difference in energy available for growth, with males growing more because they do not expend energy in egg production, but use their full energy for structural metabolism; 2) the larger reproductive effort exhibited by males may be due to their ability to fertilize more than one female; 3) males of larger dimensions have a greater chance on obtaining females for copulation as a function of intraspecific fights. All these factors can interfere in the size of *P. tortugae* males.

The high number of individuals of *P. tortugae* in the study area was probably related to their high reproductive effort, corroborated by the number of ovigerous females (34 % of the total individuals captured) and by the sex ratio in favor of females. Also, based on the size of the smallest ovigerous females (1.8 mm of CSL) we may infer that the sexual maturity occurs in small-sized individuals in the life cycle of *P. tortugae* in the Anchieta region.

The smallest and the largest individuals captured (respectively 1.0 and 7.8 mm of CSL) were males. Negreiros-Fransozo and Fransozo (1992) found a smaller population (respectively 2.0 and 7.6 mm of CSL) of *P. tortugae* from the rocky coast of a nearby area (Lázaro Beach). However, the mean values (CSL) of males, non-ovigerous and ovigerous females were higher than those of specimens captured on Anchieta Island. It is possible that the differences were associated with the type of gastropod shell species occupied at both sites. On Lázaro Beach, individuals of *P. tortugae* were captured occupying *Stramonita haemastoma* (Linnaeus, 1767) shells, in opposite to the condition observed on Anchieta Island where the individuals captured were preferentially occupying *Pisania auritula* (Link, 1807), and *Morula nodulosa* (Adams, 1845) shells, with *S. haemastoma* being occupied at a low percentage (5.5%) (Mantelatto and Garcia, 2001). Considering that shell size can interfere on hermit size (Markham, 1968; Bertness, 1981), it is possible to infer that the larger sizes attained by *S. haemastoma* individuals can promote the greater growth of hermits from Lázaro Beach.

In our study there were few juveniles smaller than 1.0 mm in CSL. These observations and the maximum size attained by the specimens support the hypothesis that recruitment may occur in a habitat different from that occupied by adults probably due to the need for protection and/or food resources (Fransozo and Mantelatto, 1998). Alternately, the juveniles may prefer deeper sea-beds, as mentioned for *Calcinus tubularis* (Linnaeus, 1767) by Manjón-Cabeza and García-Raso (1995). Hazlett (1983) described the daily movement of *C. tibicen* in St. Thomas, US Virgin Island, which may be correlated to foraging for resources and shell acquisition.

The bimodality in size frequency distribution found in the present study was also reported by Gandolfi (1996), while Negreiros-Fransozo and Fransozo (1992) described a unimodal pattern for *P. tortugae* from Lázaro Beach. The unimodality of size frequency distributions is a common pattern observed in decapod crustaceans and usually characterizes the occurrence of slight monthly variations and may usually result from continuous recruitment without class disruption, and from mortality rates (Díaz and Conde, 1989). The pattern observed for *P. tortugae* in the present study, as well as in a study by Gandolfi (1996), is uncommon and may reflect recruitment pulses or behavioral differences (Díaz and Conde, *op. cit.*). A hypothesis to answer this question probably is defined by the life cycle of *P. tortugae* that occurs

over a period of 1.5 - 2 years. The second peak in size distribution frequency in the last size classes corresponds to a strong recruitment of a population of individuals in the second year of life, which belonged to the first peak in size frequency distribution in the previous year, and so on. The bimodality in monthly size frequency distribution is a strong factor eliminating the hypothesis of catastrophic mortality.

The sex ratio investigated in size classes of *P. tortugae* presented an anomalous pattern (see Wenner, 1972 for a review). This model was described for *Calcinus latens* (Randall, 1840) and *Calcinus laevimanus* (Randall, 1840) by Gherardi and McLaughlin (1994) and Wenner (*op. cit.*), respectively. Disparities in crustacean sex ratio can be related to differences in life cycle, growth rate for each sex, and sexual reversion (Wenner, *op. cit.*). For the studied species this pattern changed with the season, indicating that this phenomenon (sex ratio pattern) is more a function of season or habitat than of size. However, the presence of three individuals with anomalies (intersexes) needs further studies in order to clarify the questions about the reproductive cycle, the possibility of hermaphroditism, developmental abnormality and/or the "feminizing" of male crabs by parasites (i.e., crabs which would otherwise be males developing female characteristics) (O'Brien, 1999).

The sex ratio favoring females, taken together with a continuous reproductive period throughout the year and a relatively early sex maturity, favors the hypothesis of a trait associated with a considerable behavioral difference in development, as supported by the high population density detected in the study region.

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