Population and reproductive features of the western Atlantic hermit crab *Pagurus criniticornis* (Anomura, Paguridae) from Anchieta Island, southeastern Brazil

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ABSTRACT. The population of the hermit crab *Pagurus criniticornis* (Dana, 1852) was studied based on seasonal abundance, size frequency distribution, sex ratio, reproductive period, fecundity and shell relationship. Specimens were collected monthly by SCUBA diving in the infralittoral area of Anchieta Island, Ubatuba. A total of 1,017 individuals was analyzed. Animal size (minimum and maximum shield length, respectively) was 0.7 and 2.9 mm for males, 0.6 and 2.8 mm for non-ovigerous females, and 1.0 and 2.5 mm for ovigerous females. The sex ratio was 1:1.29. Sexual dimorphism was recorded by the presence of males in the largest size classes. Ovigerous females were captured during all months along the year, with percentages varying from 8% (July) to 84.3% (February) in relation to the total females collected. Mean ± SD fecundity was 168 ± 125 eggs and tended to increase with increasing hermit size. Shells of four gastropod species [*Cerithium atratum* (Born, 1778), *Morula nodulosa* (Adams, 1845), *Anachis lyrata* (Sowerby, 1832) and *Modulus modulus* (Linnaeus, 1758)] were occupied by ovigerous females of *P. criniticornis* but fecundity was not significantly different in relation to the different shell types. The profile showed continuous and intense reproduction of *P. criniticornis* probably related to strategies developed to compensate for interspecific competition in the studied insular area.

KEYWORDS. Crustacea, hermit crab, populational biology, fecundity.

RESUMO. Caracterização populacional e reprodutiva do ermitão do Atlântico Ocidental *Pagurus criniticornis* (Anomura, Paguridae) da Ilha Anchieta, sudeste do Brasil. A população do ermitão *Pagurus criniticornis* (Dana, 1872) foi avaliada com base na abundância sazonal, distribuição da freqüência de tamanho, razão sexual, período reprodutivo, fecundidade e relação com a concha ocupada. Os espécimes foram coletados mensalmente por meio de mergulho autônomo no infralitoral da Ilha Anchieta, Ubatuba. Um total de 1.017 indivíduos foi analisado. O tamanho dos animais (comprimento mínimo e máximo do escudo cefalotorácico, respectivamente) foi de 0,7 e 2,9 mm para os machos, 0,6 e 2,8 mm para as fêmeas não ovígeras e 1,0 e 2,5 mm para as fêmeas ovígeras. A razão sexual foi de 1:1,29. Foi observado dimorfismo sexual em função da presença de machos nas maiores classes de tamanho. Fêmeas ovígeras foram capturadas em todos os meses do ano, com a porcentagem variando de 8% (Julho) a 84,3% (Fevereiro) em relação ao total de fêmeas coletadas. A fecundidade média foi de 168 ± 125 ovos e tendeu a ser maior com o aumento do tamanho do ermitão. Fêmeas ovígeras de *P. criniticornis* foram encontradas ocupando quatro espécies de conchas de gastrópodes [*Cerithium atratum* (Born, 1778), *Morula nodulosa* (Adams, 1845), *Anachis lyrata* (Sowerby, 1832) e *Modulus modulus* (Linnaeus, 1758)] no entanto, a fecundidade não foi significativamente diferente em relação aos diferentes tipos de conchas. A população de *P. criniticornis* apresentou um perfil reprodutivo contínuo e intenso, possivelmente relacionado a estratégias de desenvolvimento que compensam a competição interespecífica existente na área de estudo.

PALAVRAS-CHAVE. Crustacea, ermitão, biologia populacional, fecundidade.

Hermit crabs represent an important portion of many intertidal and moderately deep tropical benthic communities (Fransozo & Mantelatto, 1998). Consequently, this group of decapods provides promising material for study because the establishment of these animals in such environments derives from the evolution of adaptive population strategies. Nevertheless, there is relatively little information on the life history or reproductive ecology of hermit crabs if compared to other decapods (F. L. Mantelatto, pers. comm.).

Aspects of reproduction, such as egg production and the estimate of the fecundity, are important facets that have been used to assess the reproductive biology and are essential for the understanding and to assure the natural renewal of the decapod populations, as well as to develop an adequate handling of the species (Caddy, 1989). Furthermore, the highly diverse and plastic reproductive characteristics of crustaceans may provide a good opportunity to study the fitness consequences of different reproductive strategies (Goshima *et al.*, 1996). The intriguing hermit crabs in particular, distinctive for sheltering their fragile and uncalcified abdomen in gastropod shell, afford an opportunity to study the interaction between resource (Garcia & Mantelatto, 2000) and reproductive strategy (Mantelatto *et al.*, 2002; Miranda *et al.*, 2006).

The genus *Pagurus* Fabricius, 1775 is a heterogeneous pagurid group consisting of more than 170 species worldwide (Lemaitre & Cruz Castaño, 2004). It is one of the most species-rich genera in Anomura and is distributed in shallow waters such as littoral, subtidal and intertidal areas. However, ecological information such as reproduction and life history is still scarce for the genus (Goshima *et al.*, 1996).

Pagurus criniticornis (Dana, 1852) is a tropical small species with geographic distribution restricted to the Western Atlantic (Melo, 1999). It constitutes an abundant population in the hermit crab community of

São Paulo coast (MANTELATTO & GARCIA, 2002) representing promising material for study on comparative population biology and ecology with specimens from different areas. As far as we know, the specific knowledge on the population biology of *P. criniticornis* is retricted to the data available for one sample collection carried out at continental intertidal area of São Sebastião region (NEGREIROS-FRANSOZO *et al.*, 1991). The present investigation analyzed the population biology of *P. criniticornis* from systematic samplings performed in the infralittoral area of Anchieta Island, southeastern Brazil, in terms of sex ratio, size frequency distribution, breeding season, fecundity and shell relationship.

MATERIAL AND METHODS

Specimens of *P. criniticornis* were obtained monthly from January to December 1999 from the infralittoral area of East Beach in Anchieta Island (23°33'S, 45°05'W), northern coast of São Paulo. The hermit crabs were captured during daylight by two SCUBA divers over a period of 30 min over an area of about 800 m^2. After collection, the animals were frozen and transported to the laboratory where they were carefully removed from their shells by hand. If necessary the shells were broken. The animals were counted, measured for shield length (SL) and weighed (WW). Sex was checked from the gonopore position. Measurements were taken under a compound light microscope with a camera lucida. The voucher crabs were deposited in the Crustacean Collection of the Biology Department of FFCLRP (CCDB), University of São Paulo (Catalogue number: 1,476 to 1,484 and 1,741 to 1,745).

The population structure was analyzed as a function of the size frequency distribution of the individuals and the sex ratio. The chi-square test (χ^2) was used to evaluate the sex ratio and to compare male and female percentage per month. The distribution frequency was tested by the Kolmogorov-Smirnov normality test (KS). The mean size of individuals of both sexes was compared by the Mann-Whitney test (ZAR, 1996). The reproductive period of the population was expressed as the percentage of females carrying eggs (ovigerous females) relative to the total number of females collected.

Shell species were identified according to RIOS (1994) and confirmed by Dr. Osmar Domaneschi from Instituto de Biociências da Universidade de São Paulo. The following measurements were taken: Shell Dry Weight (SDW), Shell Aperture Width (SAW), and Shell Aperture Length (SAL). Shell internal volume (SIV) was measured according to MANTELATTO & GARCIA (2000).

From a total of 306 ovigerous females captured, only 44 were used for fecundity analysis. We selected individuals with embryos in stages from late blastula to early gastrula (MANTELATTO & GARCIA, 1999 modified from BOOLOOTIAN *et al.*, 1959; Initial Stage: stages 1 to 4; Intermediate Stage: stages 5 to 8, and Final Stage: stages 9 and 10). This procedure was adopted in order to avoid confounding effects of embryonic diameter swelling during the late stages of development and because of egg loss from the brood during incubation. The eggs were carefully removed from the pleopods and counted under a light stereomicroscope. Frequency distributions of SL and fecundity were calculated for the females whose eggs were quantified. After frequency tabulation, mean egg number of brooded egg mass was determined for each size class. The average volume (mm^3) of eggs was calculated according to JONES & SIMONS (1983) from the formula $1/6\ \pi\ I^3$ (where I is the mean of two diameters, including the chorionic membrane tightly adhering to the embryonic surface) of a sub-sample of 15 eggs per female. The longest and shortest diameters of each egg (the eggs tended to be oval) were measured under a compound light microscope with a camera lucida. Data were analyzed statistically by regression of dimensions plots ($Y = ax + b$).

To determine correlations between fecundity and shell variables, regressions and correlation coefficients were computed. The ANOVA on Ranks test was used to compare the fecundity between the occupied shell species. The level of significance was $p<0.05$.

RESULTS

Population structure. A total of 1,017 individuals were collected, represented by 445 (43.76%) males, 266 (26.16%) non-ovigerous females and 306 (30.08%) ovigerous females. The highest number of *P. criniticornis* was recorded in February, and the lowest number was found in September (Tab. I).

The mean size of the population was 1.89 ± 0.39 mm SL; females (1.86 ± 0.36 mm SL) were significantly smaller than males (1.93 ± 0.41 mm SL), characterizing sexual dimorphism.

The size frequency histograms presented non-normal distribution (KS = 0.076) of individuals and clear prevalence of specimens measuring 1.4 to 2.4 mm SL (Fig. 1).

Ovigerous females (1.97 ± 0.30 mm SL) were present throughout the year, with highest occurrence in summer (Tab. I). The first spawn occurred among females belonging to the 1.0 —|1.2 mm SL size class (Fig. 1).

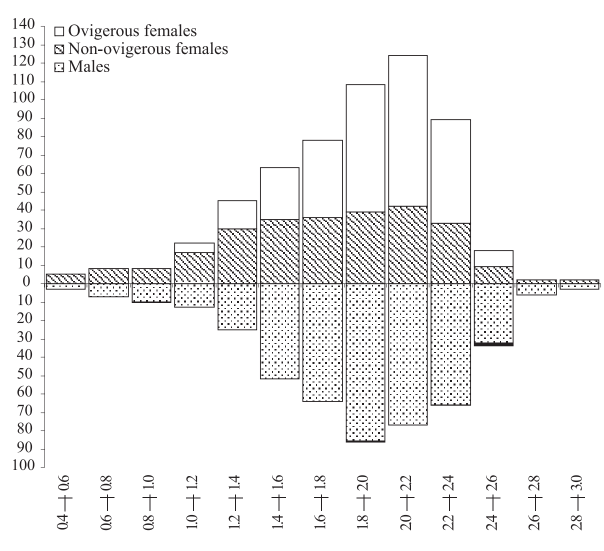

Fig. 1. Size frequency distribution of individuals of *Pagurus criniticornis* (Dana, 1852) collected during 1999 on Anchieta Island, southeastern Brazil.

The overall sex ratio 1:1.29 was significantly different from the expected 1:1 (χ^2 = 15.84; $p<0.05$). Significant difference in favour of males was obtained only in the largest size classes (2.4 —| 2.8 mm) (Fig. 2).

Fecundity. The mean fecundity of the 44 ovigerous females analyzed was 168 ± 125 eggs. Individual fecundity ranged from 6 (SL = 2.1 mm) to 538 (SL = 2.3 mm) eggs. The general egg shape of *P. criniticornis* is slightly oval with mean diameter of 0.360 ± 0.046 mm and mean volume of 0.026 ± 0.011 mm^3.

Ovigerous females with eggs in the initial stage of development were found at high frequency (more than 50%) along the months (Fig. 3). This pattern demonstrates an annual reproductive cycle with rapid embryonic development.

The egg number (FE) increased in accordance with female size (r = 0.44) (Fig. 4), with a variation in mean number of eggs for each size class studied, in agreement with the pattern of fecundity described for other decapods.

Fecundity *versus* shell type. Shells of four gastropod species were occupied by ovigerous females of *P. criniticornis*. *Cerithium atratum* (Born, 1778) was the most occupied one (90.57%) followed by *Morula nodulosa* (Adams, 1845) (7.07%), *Anachis lyrata* (Sowerby, 1832) (0.67%) and *Modulus modulus* (Linnaeus, 1758) (0.67%). Three individuals (1.02%) were found in too damaged shells that were impossible to identify (non-identified).

Fecundity analysis carried out in relation to shell dimensions demonstrated positive but not all significant correlations (Tab. II). Regression analysis in relation to the shell types were evaluated only to *C. atratum* and *M. nodulosa* shells because of the low number (< 1%) of occurrence of the others.

Table I. Total number of individuals of *Pagurus criniticornis* (Dana, 1852) collected monthly in 1999 in the infralittoral area of East Beach, Anchieta Island, Southeastern Brazil.

Months	Males	%	Non ovigerous females	%	Ovigerous females	%	Total	%
January	32	56.14	7	12.28	18	31.58	57	5.60
February	62	33.88	19	10.38	102	55.74	183	17.99
March	17	37.78	8	17.78	20	44.44	45	4.42
April	45	52.94	17	20.00	23	27.06	85	8.36
May	59	45.98	29	22.31	42	32.31	130	12.78
June	81	51.59	68	43.31	8	5.10	157	15.44
July	23	47.91	23	47.91	2	4.17	48	4.72
August	38	50.67	25	33.33	12	16.00	75	7.37
September	9	64.28	3	21.43	2	14.29	14	1.38
October	31	57.41	18	33.33	5	9.26	54	5.31
November	16	64.00	7	28.00	2	8.00	25	2.46
December	32	22.22	42	29.17	70	48.61	144	14.16
Total	445	43.76	266	26.15	306	30.09	1,017	100.00

Table II. Regression analysis of fecundity *versus* the most occupied shells by *Pagurus criniticornis* (Dana, 1852) (r, correlation coefficient; SL, shield length; FWW, female wet weight; SAW, shell aperture width; SAL, shell aperture length; SDW, shell dry weight; SIV, shell internal volume; FE, fecundity; *, significant correlation p<0.05).

Shell Species	n	Relation	Linear Equation Y = aX + b	r
Total	44	FE x SL	(Y = 170.58x - 173.83)	0.44*
	44	FE x FWW	(Y = 2011.3x + 48.359)	0.40*
	44	FE x SAW	(Y = 39.223x + 42.07)	0.32*
	44	FE x SAL	(Y = 4.0739x + 146.47)	0.70
	44	FE x SDW	(Y = 103.01x + 119.64)	0.14
	20	FE x SIV	(Y = 595.93x+ 128.89)	0.23
C. atratum	38	FE x SL	(Y = 150.81x - 128.76)	0.35*
	38	FE x FWW	(Y = 1791.6x + 69.208)	0.33*
	38	FE x SAW	(Y = 28.0055x + 86.024)	0.21
	38	FE x SAL	(Y = 8.2974x + 138.89)	0.12
	38	FE x SDW	(Y = 75.965x + 144.89)	0.10
	16	FE x SIV	(Y = 88.065x - 0.2989)	0.12
M. nodulosa	6	FE x SL	(Y = 179.38x - 216.72)	0.70*
	6	FE x FWW	(Y = 1634.6x + 18.813)	0.64
	6	FE x SAW	(Y = 82.794x - 83.894)	0.73*
	6	FE x SAL	(Y = 25.118x - 87.902)	0.69
	6	FE x SDW	(Y = 116.73x + 36.031)	0.32
	6	FE x SIV	(Y = 1579.1x - 16.383)	0.63

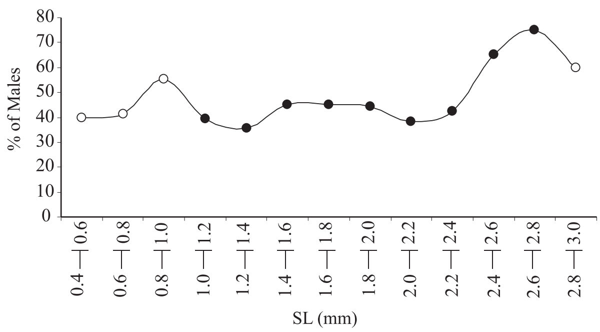

Fig. 2. Percentage of males regarding the total of individuals of *Pagurus criniticornis* (Dana, 1852) collected during 1999 on Anchieta Island, southeastern Brazil, in each size class (● = significant difference of 1:1; p<0.05).

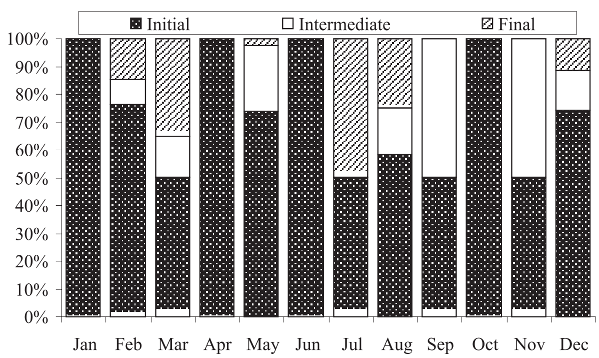

Fig. 3. Percentage of ovigerous females of *Pagurus criniticornis* (Dana, 1852) with embryos in different developmental stages from Anchieta Island, southeastern Brazil, in 1999.

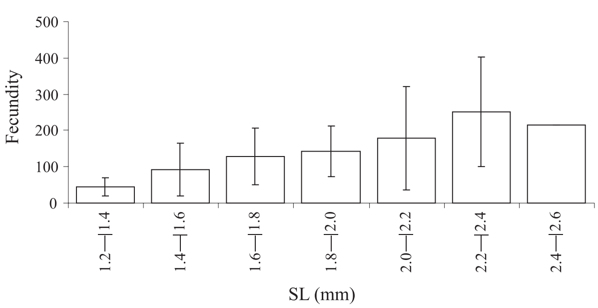

Fig. 4. Mean fecundity and standard deviation per size class of *Pagurus criniticornis* (Dana, 1852) from Anchieta Island, southeastern Brazil (n= 44; SL, Standard Length).

It was verified that the fecundity of the ovigerous females in *C. atratum* shells was not significantly higher than that of the ovigerous females occupying *M. nodulosa* shells, indicating that egg number was not influenced by this factor.

DISCUSSION

In carcinology, the populational information has been assessed in several ways. Size frequency distribution is the most used parameter to characterize the population structure since it changes throughout the year as a result of reproduction, recruitment from larvae and death (Thurman, 1985). In the present study, the population presented an unimodal pattern of distribution which usually characterizes the occurrence of slight monthly variations. It may usually result from the balance between continuous recruitment without class disruption and mortality rates. This is a common pattern observed in other decapod crustaceans as the brachyuran fiddler crabs *Uca longisignalis* (Salmon & Atsaides, 1968) and *Uca thayeri* (Rathbun, 1900) [studied respectively by Mouton & Felder (1995) and Costa & Negreiros-Fransozo (2002)], and other hermit crabs as *Paguristes erythrops* Holthuis, 1959 and *Pagurus brevidactylus* (Stimpson, 1879) [Garcia & Mantelatto (2001) and Mantelatto *et al*. (2005), respectively].

Similar patterns of size distribution were found for males and females. Both presented non-normal distribution with a peak of occurrence in intermediate classes whereas the distribution of males skewed toward larger size classes. This and the unequal sex-ratio probably can be attributed to factors such as differential mortality and growth rates between sexes and migrations (Wenner, 1972; Hartnoll, 1982), with males reaching larger sizes in less time than females but being influenced by shell limitation. On the other hand, natural selection may favour large males if they have an advantage over small males either in competition for receptive females and/or more frequent successful copulation (Abrams, 1988). The larger size of the males reflecting sexual size dimorphism has been a common pattern among hermit crabs and especially for *Pagurus* and *Clibanarius* (see McLay, 1985 and Mantelatto & Garcia, 2000 for a review), a fact that may represent an advantage in competition for resources.

Crustacean populations, in almost all cases, have sex ratios differing from 1:1 (Wenner, 1972). In the present study the proportion obtained (1:1.3) differed statistically from the expected value (1:1), which is not in agreement with the Fisher Theory (Fisher, 1930). According to that author, natural selection favours an equal proportion between the sexes. However, differences in the sex ratio can be related to differences in life cycle, growth rate and behavior of males and females (Wenner, 1972).

The sex-ratio analysis by size classes revealed an anomalous pattern (see Wenner, 1972 for review) which is characterized by a decrease in the males/females ratio in the intermediary classes and subsequent increase in the largest size classes. Probably, the deviation of proportion males/females found in the present study (females more abundant in the middle-size classes) may be attributed to a faster growth of males, to sexual selection and to smaller longevity of females (Bertness, 1981; Abrams, 1988; Benvenuto & Gherardi, 2001). This pattern has been the most common one reported in the literature (Wenner, 1972; Manjón-Cabeza & García Raso, 1995; Gherardi & Nardone, 1997; Fransozo & Mantelatto, 1998; Garcia & Mantelatto, 2001) for hermit crab populations inhabiting both the intertidal and infralittoral areas. Unfortunately, we are not able to compare the present results with those of Negreiros-Fransozo *et al*. (1991) which were obtained from one punctual collection.

Ovigerous females with eggs in the early developmental stages were collected round all year indicating that reproduction is not interrupted at any time of the reproductive cycle. Considering the occurrence of small sized ovigerous females (from 1.0 —| 1.2 mm range), the low number of juveniles (n=16) and the continuous reproductive pattern observed in the population studied, we may infer that sexual maturity occurs early in the life cycle of *P. criniticornis* in Anchieta Island. Based on the small size of ovigerous females captured (1.0 mm of SL), we may also infer that sexual maturity may occur at approximately 2 and 3.5 months in the life cycle of this species in this area.

According to LANCASTER (1990), early sexual maturity seems to be a tendency among hermit crabs, which may be determined by interespecific competition and shell availability. Similar pattern of sexual maturity was observed to *Pagurus annulipes* (Stimpson, 1862) (CARLON & EBERSOLE, 1995), *Diogenes pugilator* (Roux, 1829) (MANJÓN-CABEZA & GARCÍA-RASO, 1999), *Paguristes tortugae* Schmitt, 1933 (MANTELATTO & SOUSA, 2000) and *Pagurus brevidactylus* (Stimpson, 1859) (MANTELATTO *et al*., 2005). Furthermore, high adult mortality leads to small size at maturation, whereas high juvenile mortality leads to large size at maturation (STEARNS, 1989). This implies that future reproduction prospects determine the timing for reproduction of each individual: individuals with higher chances of survival would invest more energy into growth instead of reproduction, whereas individuals with poorer prospects for survival would invest more energy into reproduction (YOSHINO *et al*., 2002).

The fecundity recorded for *P. criniticornis* from Anchieta Island was lower than that reported for *Pagurus pollicaris* Say, 1817 (FOTHERINGHAM, 1976) and *Pagurus longicarpus* Say, 1817 (FOTHERINGHAM, 1976), and similar to *P. brevidactylus* (IOSSI *et al*., 2005). Variations in fecundity for species of the same genus can be related to environmental adaptations, variations in animal size and geographic location (FOTHERINGHAM, 1976; SASTRY, 1983; CARLON & EBERSOLE, 1995; MANTELATTO & FRANSOZO, 1997). In this case we agree with IOSSI *et al*. (2005) who proposed that not only these factors can influence the fecundity of a species but also the interspecific competition (especially in terms of competition for resources).

The low fecundity observed in some individuals may occur as a function of the presence of very young ovigerous females assumed to be spawning for the first time. According to SOMERTON & MEYERS (1983), these primiparous females produce a lower number of eggs than multiparous ones. A variation in number of eggs was observed within the same size class, probably indicating a process of multiple spawning within the same reproductive season (AMEYAW-AKUMFI, 1975; MANTELATTO & GARCIA, 1999; MANTELATTO *et al*., 2002; IOSSI *et al*., 2005). This variation in fecundity by size class is influenced either by the number of spawns in the same reproductive cycle or by inadequate shell occupancy.

According to HINES (1982), the egg size is the best reproductive variable to determinate if the spawn has numerous and small eggs or few and large eggs, resulting in large variation in fecundity between species. Larger eggs produce an offspring better adapted to the search for food and with greater competitive ability (BERTNESS, 1981). The eggs of *P. criniticornis* were smaller than eggs of the other species of Paguridae except *P. brevidactylus* (see IOSSI *et al*., 2005 for review). This fact may indicate that these species compensate the smaller eggs produced by releasing numerous, but less competitive planktonic larvae during their continuous reproductive cycle.

On Anchieta Island, ovigerous females of *P. criniticornis* presented a low plasticity of shell occupation, being *C. atratum* significantly more occupied than other species. This pattern may be associated with the preference of this hermit species for *C. atratum* shells in the natural habitat as well as to its availability in the area. MANTELATTO & MEIRELES (2004) found 32 species of gastropod shells available in this area where *C. atratum* was the most available (38.63% of the total). However, we may also speculate about the adaptation of the ovigerous females to a given shell species as a function of its availability in the enviromment and of the fact that these females do not change shells frequently as the others (males and non ovigerous females).

According to FOTHERINGHAM (1976), shell weight directly affects the amount of energy used in reproduction, shifting it to activities such as locomotion and the search of food, among others. REDDY & BISESWAR (1993) observed in *Clibanarius virescens* (Krauss, 1843) and *Calcinus laevimanus* (Randall, 1839) and ELWOOD *et al*. (1995) in *Pagurus bernhardus* (Linnaeus, 1758) that the number of eggs produced was larger among ovigerous females occupying lighter shells. In the present study we detected no significant difference in the mean weight of the shell species occupied.

Differences on the fecundity in relation to the shell species occupied were not registered and thus did not reflect a real influence of shell type on the number of eggs produced. However, the influence of the shell type and size on egg production of hermit crabs was reported: 1) *P. bernhardus* ovigerous females inhabitants of *Littorina obtusata* (Linnaeus, 1758) shells produced more eggs than those in *Gibbula* spp. shells (ELWOOD *et al*., 1995); 2) shell type influenced the fecundity of *P. tortugae* depending on the size of the ovigerous females (MANTELATTO *et al*., 2002); 3) the fecundity of *P. brevidactylus* in *M. nodulosa* shells was significantly higher than that of the ovigerous females occupying *C. atratum* shells (IOSSI *et al*., 2005). This later also postulated that although fecundity is an important tool used to estimate the reproductive potential of a hermit species, it should be seen as part of the strategy developed to guarantee survivorship, which is influenced by a number of factors including habitat resource, intra- and interspecific competition, and the intrinsic way of living of the species.

In this respect, the population and reproductive aspects of *P. criniticornis* were related to a strategy to compensate for interspecific competition, i.e., high and continuous reproductive effort with low fecundity and small eggs produced, continuous recruitment and early maturity.

Acknowledgements. This manuscript is part of Master Dissertation by FCRF and CLI. The major funding for this project was provided by a grant to FLM by FAPESP (Grant 98/07454-5) and for a Doctoral Fellowship to RB (Proc. 00/02554-3). FCRF, RB and FLM are grateful to CNPq for Ph.D., Post Doctoral and Research on-going fellowships, respectively. We thank Secretaria do Meio Ambiente do Estado de São Paulo, IBAMA and Parque Estadual da Ilha Anchieta for permission (Proc. 42358/98) and facilities during the sampling work. Special thanks are due to Dr. Osmar Domaneschi (Zoology Department, IB – USP) for assistance with shell identification, to members of the Laboratory of Bioecology and Crustacean Systematics of FFCLRP/USP for their help during the field and laboratory work, to the Programa de Pós-Graduação em Biologia Comparada – FFCLRP/USP for support, assistance and facilities and to two anonymous reviewers who provided helpful comments on the manuscript.

REFERENCES

ABRAMS, P. A. 1988. Sexual difference in resource use in hermit crabs: consequences and causes. *In*: CHELAZZI, G. & VANINI, M. eds. **Behavioral adaptations to intertidal life.** New York, Plenum. p. 283-296.

AMEYAW-AKUMFI, C. 1975. The breeding biology of sympatric species of tropical intertidal hermit crabs, *Clibanarius chapini* and *Clibanarius senegalensis*. **Marine Biology 29**(1):15-28.

BENVENUTO, C. & GHERARDI, F. 2001. Population structure and shell use in hermit crab, *Clibanarius erythrops*: a comparison between Mediterranean and Atlantic shores. **Journal of the Marine Biological Association of the United Kingdom 81**(1):77-84.

BERTNESS, M. D. 1981. Pattern and plasticity in tropical hermit crab growth and reproduction. **American Naturalist 117**(5):754-773.

BOOLOOTIAN, R. A.; GIESE, A. C.; FARMANFARMAIN, A. & TUCKER, J. 1959. Reproductive cycles of five West Coast crabs. **Physiological Zoology 32**(4):213-220.

CADDY, J. F. 1989. **Marine invertebrates fisheries. Their assessment and management**. New York, John Wiley & Sons. 752p.

CARLON, D. B. & EBERSOLE, J. P. 1995. Life-history variation among three temperate hermit crabs: the importance of size in reproductive strategies. **The Biological Bulletin 188**(3):329-337.

COSTA, T. M. & NEGREIROS-FRANSOZO, M. L. 2002. Population biology of *Uca thayeri* Rathbun 1900 (Brachyura: Ocypodidae) in a subtropical South American mangrove area: results from transect and catch-per-unit-effort techniques. **Crustaceana 75**(10):1201-1218.

ELWOOD, R. W.; MARKS, N. & DICK, J. T. A. 1995. Consequences of shell-species preferences for female reproductive success in the hermit crab *Pagurus bernhardus*. **Marine Biology 123**(3):431-434.

FISHER, R. A. 1930. **The genetical theory of natural selection**. New York, Doven. 219p.

FOTHERINGHAM, N. 1976. Population consequences of shell utilization by hermit crabs. **Ecology 57**(3):570-578.

FRANSOZO, A. & MANTELATTO, F. L. 1998. Population structure and reproductive period of the tropical hermit crab *Calcinus tibicen* (Decapoda: Diogenidae) in the region of Ubatuba, São Paulo, Brazil. **Journal of Crustacean Biology 18**(4):738-745.

GARCIA, R. B. & MANTELATTO, F. L. 2000. Variability of shell occupation by intertidal and infralittoral *Calcinus tibicen* (Anomura, Diogenidae) populations. **Nauplius 8**(1):99-105.

____. 2001. Population dynamics of the hermit crab *Paguristes erythrops* (Diogenidae) from Anchieta Island, Southern Brazil. **Journal of the Marine Biological Association of the United Kingdom 81**(6):955-960.

GHERARDI, F. & NARDONE, F. 1997. The question of coexistence in hermit crabs: population ecology of a tropical intertidal assemblage. **Crustaceana 70**(5):608-629.

GOSHIMA, S.; OHMORI, H. & WADA, S. 1996. Reproductive biology of the hermit crab *Pagurus nigrofascia* (Anomura, Paguridae). **Crustacean Research 25**:86-92.

HARTNOLL, R. G. 1982. Growth. *In*: BLISS, D. E. ed. **The Biology of Crustacea, Embryology, Morphology, and Genetics.** New York, Academic. v. 2, p.11-196.

HINES, A. H. 1982. Allometric constraints and variables of reproductive effort in brachyuran crabs. **Marine Biology 69**(3):309-320.

IOSSI, C. L.; BIAGI, R. & MANTELATTO, F. L. 2005. Egg production and shell relationship of the hermit crab *Pagurus brevidactylus* (Anomura: Paguridae) from southern Brazil. **Animal Biology 55**(2):111-121.

JONES, M. B. & SIMONS, M. J. 1983. Latitudinal variation in reproductive characteristics of a mud crab, *Helice crassa* (Grapsidae). **Bulletin of Marine Science 33**:656-670.

LANCASTER, I. 1990. Reproduction and life history strategy of the hermit crab *Pagurus bernhardus*. **Journal of Marine Biological Association of the United Kingdom 70**:129-142.

LEMAITRE, R. & CRUZ CASTAÑO, N. 2004. A new species of *Pagurus* Fabricius, 1775 from the Pacific coast of Colombia, with a checklist of eastern Pacific species of the genus. **Nauplius 12**(2):71-82.

MANJÓN-CABEZA, M. E. & GARCÍA RASO, J. E. 1995. Study of *Calcinus tubularis* (Crustacea, Diogenidae) from a shallow *Posidonia oceanica* meadow. **Cahiers de Biologie Marine 36**:277-284.

___. 1999. Shell utilization by the hermit crabs *Diogenes pugilator* (Roux, 1829), *Paguristes eremita* (Linnaeus, 1767) and *Pagurus forbesii* Bell, 1845 (Crustacea: Decapoda: Anomura), in a shallow water community from southern Spain. **Bulletin of Marine Science 65**(2):391-405.

MANTELATTO, F. L. & FRANSOZO, A. 1997. Fecundity of the crab *Callinectes ornatus* Ordway, 1863 (Decapoda, Brachyura, Portunidae) from the Ubatuba region, São Paulo, Brazil. **Crustaceana 70**(2):214-226.

MANTELATTO, F. L. & GARCIA, R. B. 1999. Reproductive potential of the hermit crab *Calcinus tibicen* (Crustacea, Anomura) from Ubatuba, São Paulo, Brazil. **Journal of Crustacean Biology 19**(2):268-275.

___. 2000. Shell utilization pattern of the hermit crab *Calcinus tibicen* (Diogenidae) from Southern Brazil. **Journal of Crustacean Biology 20**(3):460-467.

___. 2002. Hermit crab fauna from the infralitoral area of Anchieta Island (Ubatuba, Brazil). *In*: BRIONES, E. E. & ALVAREZ, F. eds. **Modern Approaches to the Studies of Crustacean.** New York, Kluwer Academic/Plenum. p.137-145.

MANTELATTO, F. L. & SOUSA, L. M. 2000. Population biology of the Atlantic hermit crab *Paguristes tortugae* (Anomura, Diogenidae) from Anchieta Island, Ubatuba, Brazil. **Nauplius 8**(2):185-193.

MANTELATTO, F. L. & MEIRELES, A. L. 2004. The importance of shell occupation and shell availability in the hermit crab *Pagurus brevidactylus* (Stimpson, 1859) (Paguridae) population from Southern Atlantic. **Bulletin of Marine Science 75**(2):27-35.

MANTELATTO, F. L.; ALARCON, V. F. & GARCIA, R. B. 2002. Egg production strategies in the tropical ermit crab *Paguristes tortugae* from Brazil. **Journal of Crustacean Biology 22**(2):390-397.

MANTELATTO, F. L.; CHRISTOFOLETTI, R. A. & VALENTI, W. C. 2005. Population structure and growth of the hermit crab *Pagurus brevidactylus* (Anomura: Paguridae) from the northern coast of São Paulo, Brazil. **Journal of Marine Biological Association of the United Kingdom 85**(1):127-128.

MCLAY, C. L. 1985. Moulting and growth in *Pagurus traversi* and *P. novizealandiae* (Decapoda: Anomura: Paguridae): the effects of neighbours. **New Zealand Journal of Marine and Freshwather Research 19**(3):327-337.

MELO, G. A. S. 1999. **Manual de identificação dos Crustacea Decapoda do litoral brasileiro: Anomura, Thalassinidae, Palinuridae, Astacidae.** São Paulo, Plêiade. 551p.

MIRANDA, I.; MEIRELES, A. L.; BIAGI, R. & MANTELATTO, F. L. 2006. Is the abundance of the red brocade hermit crab *Dardanus insignis* (Decapoda: Anomura: Diogenidae) in the infralittoral region of southern Brazil determined by reproductive potential? **Crustacean Research 6**(special number):45-55.

MOUTON, E. C. & FELDER, D. L. 1995. Reproduction of the fiddler crabs *Uca longisignalis* and *Uca spinicarpa* in a Gulf of Mexico salt marsh. **Estuaries 18**(3):459-481.

NEGREIROS-FRANSOZO, M. L.; FRANSOZO, A. & HEBLING, N. L.. 1991. Estrutura populacional e determinação do tamanho da concha ocupada por 4 espécies de ermitões (Crustacea, Decapoda, Anomura) do litoral de São Paulo. **Biotemas 4**(2):135-148.

REDDY, T. & BISESWAR, R. 1993. Patterns of shell utilization in two sympatric species of hermit crabs from the Natal coast (Decapoda, Anomura, Diogenidae). **Crustaceana 65**(1):13-24.

RIOS, E. C. 1994. **Seashells of Brazil**. Rio Grande, Instituto Acqua, Museu Oceanográfico de Rio Grande, Universidade Federal do Rio Grande. 368p.

SASTRY, A. N. 1983. Ecological aspects of reproduction. *In:* Waterman, T. H. ed. **The biology of Crustacea. VIII. Environmental adaptations**. New York, Academic. p.179-270.

SOMERTON, D. A. & MEYERS, W. S. 1983. Fecundity differences between primiparous and multiparous female Alaskan tanner crab (*Chionoecetes bairdi*). **Journal of Crustacean Biology 3**(2):183-186.

STEARNS, S. C. 1989. Trade-offs in life history evolution. **Functional Ecology 3**(3):259-268.

THURMAN, C. L. 1985. Reproductive biology and population structure of the fiddler crab *Uca subcylindrica* (Stimpson). **The Biological Bulletin 169**(1):215-229.

WENNER, A. M. 1972. Sex ratio as a function of size in marine Crustacea. **The American Naturalist 106**(949):321-350.

YOSHINO, K.; GOSHIMA, S. & NAKAO, S. 2002. Temporal reproductive patterns within a breeding season of the hermit crab *Pagurus filholi*: effects of crab size and shell species. **Marine Biology 141**(6):1069-1075.

ZAR, J. H. 1996. **Biostatiscal analysis.** New Jersey, Prentice-Hall. 907p.

Recebido em agosto de 2006. Aceito em fevereiro de 2007. ISSN 0073-4721
Artigo disponível em: www.scielo.br/isz