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Population biology and growth of three sympatric species of intertidal hermit crabs in south-eastern Brazil

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Hermit crab populations have been described in different habitats and latitudes but few studies focused on coexisting populations. Such information is especially important to evaluate the effect of coexistence in the population biology of such organisms. This study was done in the intertidal region of Pernambuco Islet, São Sebastião Channel, south-eastern Brazil. Random samples of crabs were taken monthly during one year to evaluate their size and sex. The three coexisting *Clibanarius* populations (*C. antillensis*, *C. sclopetarius*, and *C. vittatus*) showed similar patterns of sex ratio (skewed for females), sexual dimorphism (males larger than females), recruitment (February to June) and population growth but differed in size structure ($Cs > Cv > Ca$) and reproductive activity over the year. Population growth was estimated using the von Bertalanffy growth function (VBGF) and revealed that the growth of these three populations was strongly reduced from August to January and that longevity varied from 42 to 48 months. *Clibanarius antillensis* showed continuous reproduction with high frequency of ovigerous females over the year while *C. sclopetarius* and *C. vittatus* had a reproductive peak in April and absence of ovigerous females in August/September. Coexistence seemed to influence population biology of these hermit crabs, given the relationship of their reproductive periods and growth patterns to the shell adequacy to the crabs. The overlap in reproductive peaks and recruitment periods may strengthen competition for shells. Comparisons of the reproductive patterns of the hermit crab populations recorded to date emphasize that reproduction and, consequently, life strategies of hermit crabs are not directly dependent on taxonomic or geographical proximity, but on their evolutionary histories and on local processes acting on each assemblage or population.

INTRODUCTION

Populations are generally subjected to specific environmental pressures that lead them to evolve independently of each other and to exhibit particular gene frequencies maintained by geographical isolation. Populations, thus, reflect the constraints of the environments to which they are subjected. Studies that enable comparisons among such populations are conducted to understand how different environments influence them.

Studies on populations have been generally focused on their description. Questions related to distribution, density, sex ratio, sexual dimorphism, reproductive periods and recruitment are frequently addressed. Coexisting species may respond similarly to environmental pressures, although coexistence and, consequently, competitive exclusion may act in an opposite manner (Bach et al., 1976). The plasticity in population biology was described by Bertness (1981a) for hermit crabs subjected to different shell supplies.

The population biology of many hermit crabs has been well described, e.g. see Markham (1968); Ameyaw-Akumfi (1975); Fotheringham (1975); Bertness (1981b); Gherardi (1991); Negreiros-Fransozo & Fransozo (1992); Gandolfi (1996); and Turra & Leite (1999). In general, males are larger than females, a fact that makes sex ratio at high size-classes skewed for males, as well as for other crustacean groups (Wenner, 1972). Population growth of hermit crabs in nature has been described in a few studies (Manjón-Cabeza & García-Raso, 1994, 1998) and some information is available from laboratory rearing experiments (Markham, 1968; Fotheringham, 1976a; Bertness, 1981c; Asakura, 1992).

Reproductive periods of hermit crabs have been frequently described and reveal continuous to seasonal patterns (see Asakura & Kikuchi, 1984; Bertini & Fransozo, 2000). Reproductive activity was shown to be influenced by the adequacy of shells used by the crabs (Bertness, 1981b; Carlon & Ebersole, 1995). Moreover, reproductive peaks may vary between populations in response to species coexistence and competition for shells (Reese, 1968; Ameyaw-Akumfi, 1975; Fotheringham, 1976b).

Sympatric hermit crab populations have been investigated and their coexistence is associated with habitat and shell partitioning (Vance, 1972; Gherardi & Nardone, 1997). Coexistence exposes the crabs to competitive interactions, which, through resource partitioning, influence their reproduction (Bach et al., 1976) and growth (Bertness, 1981a). Three populations of hermit crabs of the genus *Clibanarius* coexist in the intertidal region of Pernambuco Islet: *C. antillensis* Stimpson, 1859, *C. sclopetarius* (Herbst, 1796) and *C. vittatus* (Bosc, 1802). These are very common species in intertidal and shallow subtidal habitats from eastern USA to south-eastern Brazil.

This study describes the population biology of three sympatric intertidal species of hermit crabs in south-eastern

Brazil. Population growth was evaluated in the field. Reproductive periods were described and compared with other populations in different latitudes. This study also discusses the influence of sympatry on the population biology of coexisting species of hermit crabs.

MATERIALS AND METHODS

This study was undertaken in the intertidal region of Pernambuco Islet, Araçá Region (23°49′S 45°24′W), São Sebastião, São Paulo, Brazil. This is a low slope area composed of different substrata (mud to boulders and rocky shore) all occupied by hermit crabs (Turra et al., 2000).

Samples were taken monthly during one year, from October 1995 to September 1996, in low-tide periods. An intertidal area (50 m long and 8 m wide) was selected and divided into one hundred 0.5 m wide transects perpendicular to the water line. Five randomized transects were sorted and sampled each month using 0.25 m^2 subjacent squares from the water line to the supralittoral fringe. The number of hermit crabs was counted in each square. Complementary samples were obtained in an adjacent area using search effort when the number of crabs was too low in transects (<30 ind per month).

Hermit crabs were transported to the laboratory of the Centro de Biologia Marinha of Universidade de São Paulo (CEBIMar-USP) where they were removed from their shells, measured (shield length, mm), and sexed (males, ovigerous females, non-ovigerous females, and intersex). Intersex individuals were those with gonopores in the basis of both third and fifth pereopods (Wenner, 1972). Reproductive activity was estimated using data on frequency of ovigerous females over the year.

The comparison of shield length among the three species and evaluation of the population sex ratio (proportion of males in the entire population) were done using only the data from transects. Data from complementary samples were included in the analysis to evaluate population growth, the relation between sex ratio and crab size, and the reproductive period of the three species. The relationship between sex ratio and crab size was analysed by grouping the hermit crabs in size-classes of 0.50 mm and calculating sex ratio for each one. Data were plotted and a model was fitted using the method of distance weighted least squares (DWLS). Extreme size classes were generally represented by few individuals (<9 ind) and were not considered in this analysis.

The log-likelihood *G*-test (Zar, 1984) was used to compare the reproductive activity pattern of each population. Size comparisons were done using one-way ANOVA followed by Scheffé's test for pair-wise comparisons (Zar, 1984). Statistical analyses were performed at the 0.05 significance level. Standard deviation is presented through the text.

The estimates of the parameters of the von Bertalanffy growth function (VBGF) were based on the size–frequency distribution over time of each hermit crab population using the software FISAT (Gayanilo & Pauly, 1997). A growth function with temporal oscillation suggested by Gayanilo & Pauly (1997) was used:

$$L_t = L_\infty[1 - e^{-K(t-t_0)-(CK/2_\pi)[\sin 2_\pi(t-WP+0.5)-\sin 2_\pi(t_0-WP+0.5)]}]$$

where L_t is the length at a given time t, L_∞ the asymptotic length (mm), K the growth constant or curvature parameter (rate at which L_∞ is approached), t_0 the starting sample and size-class through which the growth curve passes, C the amplitude of seasonal growth (0, minimum; 1, maximum) and WP (winter point) the proportion of the year when growth rate is slowest. The goodness-of-fit of the VBGF was accessed by the calculation of Rn (0, minimum; 1, maximum) of the ELEFAN I routine (Gayanilo & Pauly, 1997). L_∞ was estimated using the Powell–Wetherall method using temporal weighting for the data of all samples transformed to the percentage of total sample. First estimate of K was done with the *scan of K values* routine of ELEFAN I. These two parameters (L_∞ and K) were entered in an *automatic search* routine to calculate C and WP and to fit the best set of parameter's values of the VBGF, i.e. the values that lead to the best value of Rn. The index of Munro & Pauly (1983) modified by Sparre (1987) ($\phi' = \text{LnK} + 2\text{LnL}_\infty$) was calculated to compare growth parameters among hermit crab populations.

RESULTS

Population structure

A total of 724, 391 and 536 individuals of *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus* respectively, were collected both in the random and complementary samples over the studied period (Figure 1). Size distribution (Figure 2) differed among the three populations (ANOVA, F=796.322; df=2; P<0.001). Individuals of *C. antillensis* (3.76 ±0.92 mm) were, on average, smaller than those of *C. vittatus* (6.98 ±1.04 mm; Scheffé's test, P<0.001) and *C. sclopetarius* (7.77 ±1.34 mm, P<0.001). Individuals of *C. vittatus* were also smaller than those of *C. sclopetarius* (P<0.001). Size distribution of *C. antillensis* showed a more pronounced peak (leptokurtic bell shaped curve) in comparison with the two other populations.

A high proportion of ovigerous females was recorded for *C. antillensis* (73.59%), which occurred almost exclusively in two size-classes (Figure 2). *Clibanarius sclopetarius* (34.54%) and *C. vittatus* (39.51%) showed lower frequencies of ovigerous females, which occurred in more size-classes than those of *C. antillensis*. The smallest ovigerous female of *C. antillensis*, *C. sclopetarius* and *C. vittatus* were

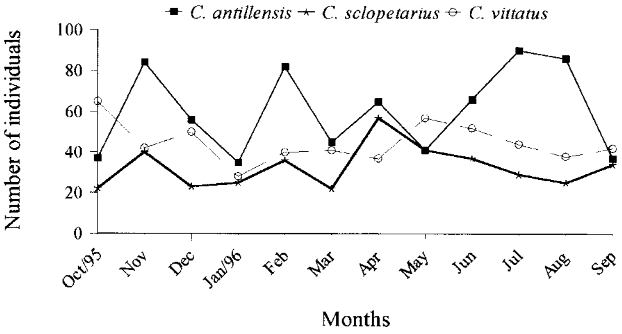

Figure 1. Number of individuals of *Clibanarius antillensis*, *C. sclopetarius*, and *C. vittatus* collected in the monthly samples over the studied period at Pernambuco Islet, São Sebastião, Brazil. Data from both transects and complementary samples.

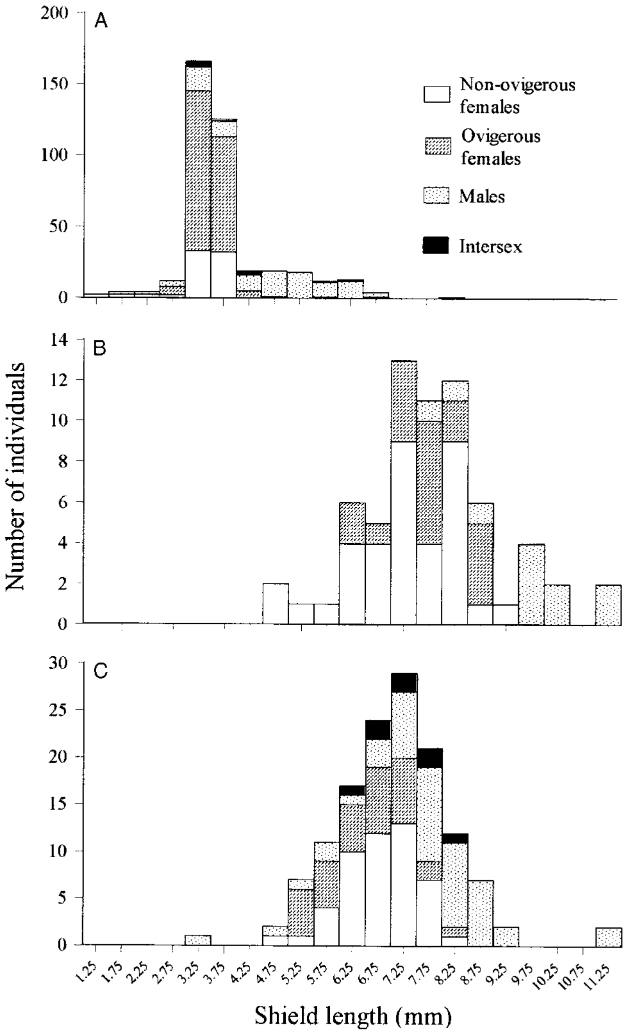

Figure 2. Size–frequency distribution (shield length, mm) of males, ovigerous females, non-ovigerous females and intersex individuals of (A) *Clibanarius antillensis*, (B) *C. sclopetarius* and (C) *C. vittatus*, Pernambuco Islet, São Sebastião, Brazil. Data from transects.

2.55 mm, 5.69 mm and 5.07 mm shield length, respectively.

The three populations presented particular proportions of males and females (Log-likelihood *G*-test, $G=7.72$; df=2; $P<0.05$) but all were skewed for females (Table 1). *Clibanarius sclopetarius* presented proportionally more females than *C. vittatus* and *C. antillensis*. Intersex individuals occurred in low frequencies in the three populations (~2–7%). Sex ratio was related to the size of hermit crabs (Figure 3). Males were frequent at smaller size-classes but were less abundant than females. Females became extremely abundant in intermediate size-classes, with males outnumbering females only in the larger ones.

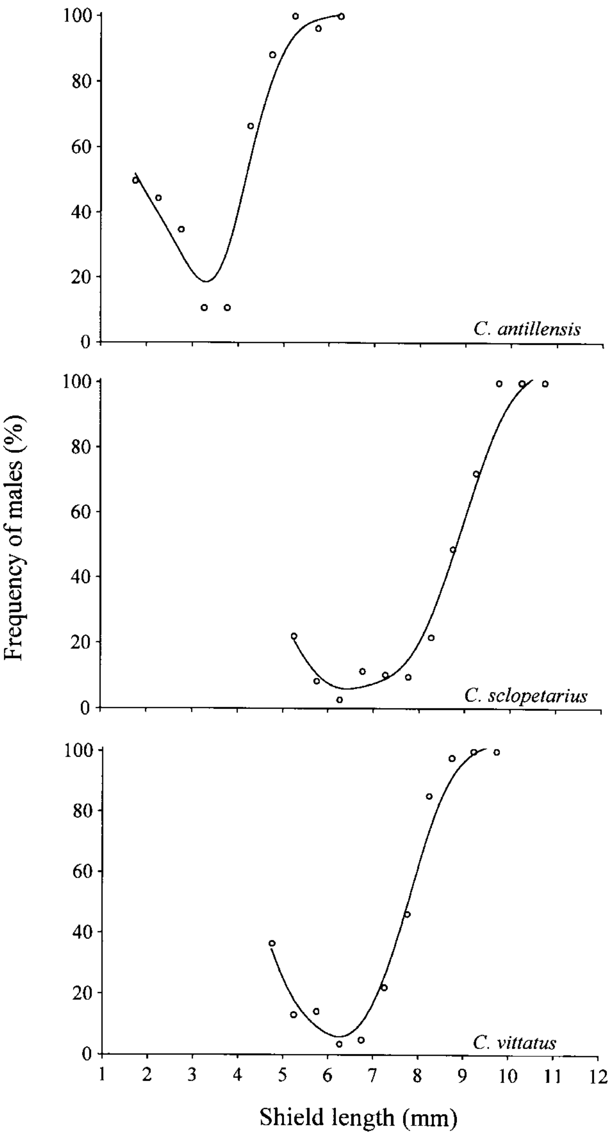

Figure 3. Relationship between sex ratio and crab size for *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus*, Pernambuco Islet, São Sebastião, Brazil. Data from both transects and complementary samples. Lines fitted using the method of distance weighted least squares.

Table 1. *Frequency of males, females, and intersex individuals of* Clibanarius antillensis, C. sclopetarius *and* C. vittatus *collected in transects in the intertidal region on Pernambuco Islet. The log-likelihood* G*-test compared the proportion of males and females for each population.*

Species	Females	Males	Intersex	M:F	*G*	df	*P*
C. antillensis	284	109	10	1:2.6	80.74	1	<0.001
C. sclopetarius	55	11	0*	1:5	32.02	1	<0.001
C. vittatus	81	44	8	1:1.84	11.10	1	<0.001

df, degrees of freedom; M:F, proportion of males and females; * *Clibanarius sclopetarius* presented only two intersex individuals in the complementary samples.

Table 2. *Analysis of variance for the shield length (mm) among males, ovigerous females, non-ovigerous females and intersex individuals of* Clibanarius antillensis, C. sclopetarius *and* C. vittatus, *collected in the intertidal region of Pernambuco Islet. Data from both transects and complementary samples.*

	Non-ovigerous females			Ovigerous females			Intersex			Males					
Species	N	$\bar{X}$	±SD	N	$\bar{X}$	±SD	N	$\bar{X}$	±SD	N	$\bar{X}$	±SD	*F*	df	*P*
C. antillensis	75	3.34^{a}	0.62	209	3.48^{a}	0.35	10	4.15^{b}	1.02	109	4.57^{b}	1.18	57.783	3	<0.001
C. sclopetarius	36	7.24^{a}	1.09	19	7.69^{a}	0.74				11	9.66^{b}	1.19	23.780	2	<0.001
C. vittatus	49	6.76^{a}	0.70	32	6.47^{a}	0.79	8	$7.25^{a,b}$	0.73	44	7.59^{b}	1.23	10.594	3	<0.001

N, number of observations; $\bar{X}$, mean; SD, standard deviation; df, degrees of freedom; ^{a,b}, superscript figures show the result of pair-wise comparisons by Scheffé's test ($P<0.05$).

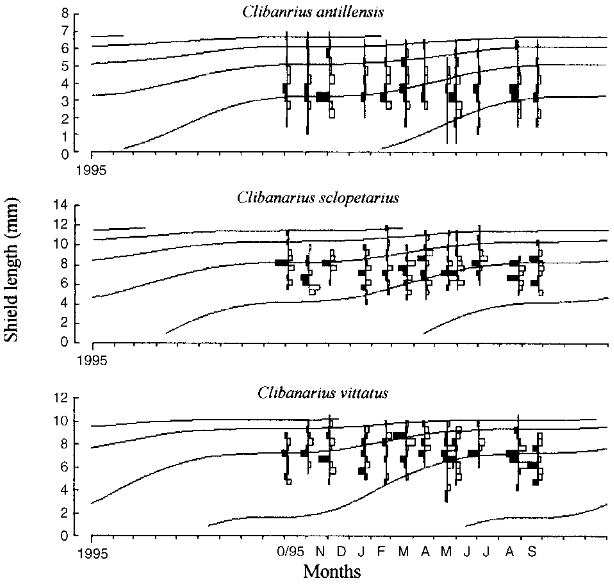

Figure 4. Size–frequency histograms for *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus* over the studied period and the fitted von Bertalanffy growth functions (VBGF). Data from both transects and complementary samples. Parameters of VBGF in Table 4.

There were differences in the size of individuals among reproductive classes (males, non-ovigerous females, ovigerous females and intersex individuals) in the three studied populations (Table 2). In general, males were larger than ovigerous and non-ovigerous females, which showed similar sizes. Intersex individuals showed a tendency to present intermediate sizes between males and females.

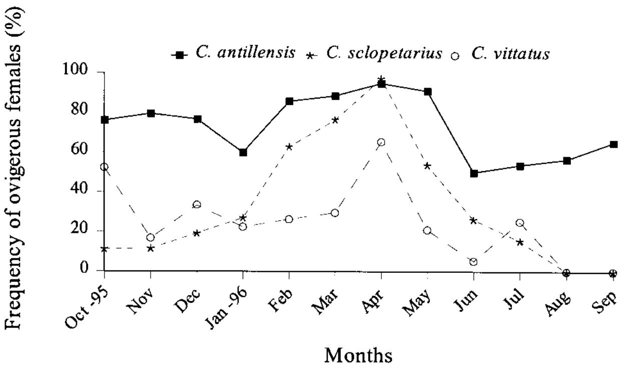

Figure 5. Reproductive activity (ovigerous females/all females) of *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus* over the studied period, Pernambuco Islet, São Sebastião, Brazil. Data from both transects and complementary samples. First sample taken in October 1995.

Population growth

The analyses of the size–frequency distributions over the year (Figure 4) revealed that the shield length of the three studied populations was different (ANOVA, *Clibanarius antillensis*: $F=2.419$; df=11; $P=0.006$; *C. sclopetarius*: $F=3.973$; df=11; $P<0.001$; *C. vittatus*: $F=3.158$; df=11; $P<0.001$). The parameters of the von Bertalanffy growth curve fitted for the studied populations are shown in Table 3. The von Bertalanffy growth curve was fitted for each population and showed that they produced only one cohort per year, with three to four cohorts coexisting at the same time, and with similar recruitment periods (Figure 4). They also presented similar degrees of seasonal oscillation in growth through the year (C), with a marked reduction between August and January

Table 3. *Parameters of the von Bertalanffy growth curves fitted for the data on size–frequency distribution of* Clibanarius antillensis, C. sclopetarius, *and* C. vittatus *over the studied period.*

Species	L_{∞}	K	C	WP	Rn	Life Span (months)	Recruitment (estimates)	ϕ'
C. antillensis	7.39	0.60	1.0	0.9	0.228	48	Feb–Jun	3.49
C. sclopetarius	12.70	0.65	0.9	0.78	0.208	47	Apr	4.65
C. vittatus	10.67	0.96	1.0	0.7	0.232	42	May–Jun	4.69

L_{∞}, asymptotic length (mm); K, growth constant; C, amplitude of seasonal growth (0, minimum; 1, maximum); WP (winter point), the proportion of the year when growth rate is slowest; Rn, goodness-of-fit index (0, minimum; 1, maximum) of the ELEFAN I routine (Gayanilo & Pauly, 1997); $\phi'=\text{LnK} + 2\text{LnL}_{\infty}$, index of Munro & Pauly (1983) after Sparre (1987).

Table 4. *Reproductive patterns of some hermit crab populations. [Updated from Asakura & Kikuchi (1984) and Bertini & Fransozo (2000)].*

Hermit crab	Reproductive pattern	Reproductive peak	Area	Study
Diogenidae				
Calcinus laevimanus	Continuous	May–Aug	Kaneoho, Hawaii (21°N)	Reese (1968)
Calcinus latens	Continuous	Feb–Mar	Kaneoho, Hawaii (21°N)	Reese (1968)
Calcinus obscurus	Seasonal	Dec–Feb	Flamenco Island, Panama (8°N)	Bertness (1981b)
Calcinus tibicen	Seasonal	Apr–Jun	Barbados, India (13°N)	Lewis (1960)
Calcinus tibicen	Seasonal	Nov–Mar	Ubatuba, Brazil (23°S)	Fransozo & Mantelatto (1998)
Calcinus tubularis	Seasonal	Aug	Almería, Spain (37°N)	Manjón-Cabeza & García-Raso (1995)
Calcinus tubularis	Seasonal	Aug	Ligurian Sea, Mediterranean (43°N)	Pessani et al. (2000)
Clibanarius albidigitus	Seasonal	Dec–Feb	Flamenco Island, Panama (8°N)	Bertness (1981b)
Clibanarius antillensis	Continuous	Feb–May	São Sebastião, Brazil (23°S)	Present study
Clibanarius antillensis	Continuous	Nov–Mar	São Sebastião, Brazil (23°S)	Turra & Leite (1999)
Clibanarius chapini	Continuous	Jan–Oct	Tengpobo, Ghana (6°N)	Ameyaw-Akumfi (1975)
Clibanarius erythropus	Seasonal	Jul	Gulf of Tunis, Tunisia (36°N)	Reed & Manning (2000)
Clibanarius sclopetarius	Seasonal	Feb–May	São Sebastião, Brazil (23°S)	Present study
Clibanarius senegalensis	Continuous	Sep–Dec	Tengpobo, Ghana (6°N)	Ameyaw-Akumfi (1975)
Clibanarius tricolor	Seasonal	Apr–Jun	Barbados, India (13°N)	Lewis (1960)
Clibanarius virescens	Seasonal	May–Jun	Tokara, Japan (29°N)	Miyake (1956)
Clibanarius virescens	Seasonal	Jul–Sep	Kominato, Japan (35°N)	Imazu & Asakura (1994)
Clibanarius vittatus	Seasonal	May–Aug	Texas, USA (29°N)	Fotheringham (1975)
Clibanarius vittatus	Seasonal	Apr, Oct	São Sebastião, Brazil (23°S)	Present study
Clibanarius vittatus	Seasonal	Apr–Sep	Florida, USA (27°N)	Lowery & Nelson (1988)
Clibanarius zebra	Continuous	Feb, Apr	Kaneoho, Hawaii (21°N)	Reese (1968)
Diogenes nitidimanus	Seasonal	Apr–Nov	Amakuse, Japan (32°N)	Asakura & Kikuchi (1984)
Diogenes pugilator	Continuous	Apr, Jul	Cadiz, Spain (36°N)	Manjón-Cabeza & García-Raso (1998)
Paguristes tortugae	Continuous	Over the year	São Sebastião, Brazil (23°S)	Gandolfi (1996)
Petrochirus diogenes	Seasonal	Feb–Apr	Ubatuba, Brazil (23°S)	Bertini & Fransozo (2000)
Paguridae				
Pagurus bernhardus	Seasonal	Nov–May	Penzance, England (50°N)	Lancaster (1990)
Pagurus brevidactylus	Continuous	Over the year	São Sebastião, Brazil (23°S)	Gandolfi (1996)
Pagurus dubius	Seasonal	Oct–Mar	Amakuse, Japan (32°N)	Kikuchi (1962)
Pagurus filholi	Continuous	Apr–Jul	Hakodate Bay, Hokkaido, Japan (42°N)	Goshima et al. (1998)
Pagurus geminus	Seasonal	Jan–Apr	Sagami Bay, Japan (35°N)	Kurata (1968)
Pagurus geminus	Seasonal	Jan–Jun	Kominato, Japan (35°N)	Imazu & Asakura (1994)
Pagurus lanuginosus	Seasonal	Nov–Mar	Sagami Bay, Japan (35°N)	Miyake (1978)
Pagurus lanuginosus	Seasonal	Jan–Apr	Kominato, Japan (35°N)	Imazu & Asakura (1994)
Pagurus lanuginosus	Seasonal	Oct–Nov, Feb–Jun	Hokkaido, Japan (44°N)	Wada et al. (2000)
Pagurus longicarpus	Seasonal	Oct–Apr	Florida, USA (28°N)	Wilber (1989)
Pagurus maclaughlinae	Continuous	Autumn–Spring	Florida, USA (27°N)	Tunberg et al. (1994)
Pagurus middendorffii	Seasonal	Nov–Feb	Hakodate Bay, Hokkaido, Japan (42°N)	Wada et al. (1995)
Pagurus nigrofasciata	Seasonal	May–Feb	Hakodate Bay, Hokkaido, Japan (42°N)	Goshima et al. (1996)
Pagurus sp.	Continuous	Over the year	Flamenco Island, Panama (8°N)	Bertness (1981b)
Discorsopagurus schmitti	Seasonal	Jan–Apr	Washington, USA (38°N)	Gherardi & Cassidy (1995)
Cestopagurus timidus	Seasonal	Apr–Nov	Almería, Spain (37°N)	ManjónCabeza & García-Raso (1994)

(indicated by WP values in Table 3). The asymptotic length differed between species and was proportional to the mean size of the individuals in each population. Growth rates were inferior to unit and varied from 0.60 to 0.96. The estimated longevity ranged from 42 to 48 months.

Reproductive activity

The reproductive activity of *C. antillensis* was different from that of *C. sclopetarius* (Log-likelihood *G*-test, $G=65.95$; df=11; $P<0.001$) and of *C. vittatus* ($G=40.638$; df=11; $P<0.001$). *Clibanarius sclopetarius* and *C. vittatus* also differed in reproductive activity ($G=29.736$; df=9; $P=<0.001$), but showed a reproductive peak in April and absence of ovigerous females in August and September (Figure 5). The reproductive activity of these two species may be considered discontinuous or seasonal, while *C. antillensis* showed a heterogeneously continuous reproduction due to their variable high frequency of ovigerous females over the whole studied period (Figure 5).

DISCUSSION

Population structure

The studied hermit crab populations exhibited different mean sizes, but there was a greater overlap in the sizes of *Clibanarius sclopetarius* and *C. vittatus* than between them and *C. antillensis*. Only the largest individuals of *C. antillensis* overlapped in size with the smallest individuals of the two other species (Figure 2). This overlap in size among individuals of the three studied species was evidence that they need shells with similar sizes or architecture and, when scarce, these shells may force them to undergo competitive interactions. Shell (Turra, 1998) and habitat partitioning (differences in microhabitat use) (Turra et al., 2000) among these populations may also be enabling species coexistence in this area as also pointed out by Vance (1972a) and Gherardi & Nardone (1997) for other hermit crab assemblages.

These three hermit crab populations were sexually dimorphic with males being larger than both ovigerous and non-ovigerous females. This situation is generally attributed to differential growth between males and females (Markham, 1968; Bertness, 1981c; Asakura, 1992). Asakura (1992) suggested that smaller growth rates of females would be a consequence of the utilization of relatively small shells and of the higher energy allocation to reproduction in relation to males. In this way, shell partitioning between sexes may cause size differences between males and females, as demonstrated by Wada (1999), and, consequently, a reduction in intraspecific competition. This situation is probably taking place at Pernambuco Islet since the partitioning of shell types and sizes between males and females of these three populations was documented by Turra (1998). Sexual dimorphism in hermit crabs has also been related to the theory of sexual selection (Bertness, 1981b; Harvey, 1990). Larger males present higher fitness due to their higher success in copulating females than the smaller ones (Harvey, 1990), except when in low adequacy shells (Hazlett & Baron, 1989).

Despite juveniles of these populations not occurring in the sampled area, the fitted von Bertalanffy growth functions (VBGF) suggested recruitment from February to June. In fact, such periods were equivalent to the peaks of reproductive activity of these populations. Habitat partitioning between adults and juveniles may be taking place as also recorded by Reese (1968) and Asakura & Kikuchi (1984) for populations of other species. Recruitment of the three species at the same period may cause competition among juveniles for first shells, which may enhance mortality of subordinate species. Moreover, such habitat segregation is also supposed to be associated with higher supplies of small sized gastropod shells in nursery areas (Reese, 1968).

According to Wenner (1972), sex ratios differing from 1:1 are widespread among crustaceans. Among hermit crabs, females are likely to be more abundant than males (Ameyaw-Akumfi, 1975; Gherardi, 1991; Asakura, 1992; Negreiros-Fransozo & Fransozo, 1992; Imazu & Asakura, 1994; Gandolfi, 1996; Turra & Leite, 1999). This may be explained by higher mortality acting on males (Leigh, 1970) or by habitat partitioning, differential feeding restriction, or differential spatial dispersion patterns between sexes (Darnell, 1962). However, reasonable explanations should consider the sex determination system acting on each population, i.e. if the actual sex of the individuals is determined genetically or environmentally.

Wenner (1972) described four patterns for the relationship between sex ratio and crustacean size: standard, reversal, intermediate, and anomalous. The three sympatric *Clibanarius* populations at Pernambuco Islet exhibited the anomalous pattern (Figure 1), which predominates among hermit crabs (see Bertini & Fransozo, 2000 for a recent review). Wenner's study pointed out some explanations for this pattern: (1) differences between sexes in longevity and in the time spent for growing; (2) differential migration; (3) differential mortality; (4) differential growth rates; (5) sex reversal. Sex reversal (sequential hermaphroditism) is very common among animals (Warner, 1975) but its occurrence and, consequently, its sequence in hermit crabs still remains uncertain.

Population growth

Population growth in the field was estimated using the VBGF and showed a clear pattern for the three populations. Growth rates (K) were smaller than unit (<1) and varied among the studied populations. These values were higher than those of the temperate small sized hermit crabs *Cestopagurus timidus* (K=0.041, Manjón-Cabeza & García-Raso, 1994) and *Diogenes pugilator* (K=0.14–0.27, Manjón-Cabeza & García-Raso, 1998). Longevity was very similar among these three studied populations (42 to 48 months) and revealed overlap of generations. Moreover, the longevity and the index of Munro & Pauly (1983) of the studied populations were higher than those of *C. timidus* (21 months and -0.84) and *D. pugilator* (24 to 27 months and 1.15–1.53). This index revealed that the three *Clibanarius* populations have proportionally higher growth rates (K) and maximum length than the two other hermit crab species studied to date. Such differences in growth between tropical and temperate populations may be attributed to differences in their maximum length (L_∞) or in food availability (seasonality), although the role of shells should also be considered. The relatively low values of Rn (goodness-of-fit parameter) for the fitted VBGF were probably related to the wide reproductive periods of these populations, which made cohort identification difficult.

The seasonal component (C and WP) of the growth functions fitted for the three hermit crab populations showed a marked relationship with the periods of low shell adequacy to the crabs (periods when crabs were using proportionally heavier shells than the preferred ones) (Turra, 1998). In contrast, growth was faster when shell adequacy became better or when shells were proportionally lighter in relation to optimal shells. Moreover, reduction in crab growth (August to January) preceded the reproductive peaks (April) of these populations, suggesting a trade-off between growth and reproductive investments as also pointed out by Bertness (1981a,c).

The limitation of crab growth by shells was demonstrated for other hermit crabs species under laboratory conditions only (Markham, 1968; Fotheringham, 1976a; Bertness, 1981c; Asakura, 1992). *Clibanarius sclopetarius* occupied optimal shells in almost all months suggesting the competitive dominance of this population (Turra, 1998). The use of sub-optimal and proportionally heavier shells by *C. antillensis* can be associated with its low growth rate and with its high reproductive activity (see below), as demonstrated by Bertness (1981a,c) for other populations. The higher values of the growth constant (K=0.96) of *C. vittatus* in comparison to the two other populations were probably associated with the variations in shell adequacy over the year. This species used inadequate and relatively heavier shells frequently (June to February, see Turra, 1998). The use of optimal to relatively lighter shells only from March to May probably lead the crabs to grow asymptotically with high growth rates. This was the unique possibility of growth without (or with reduced) shell restriction experienced by this species in the studied period.

Reproductive activity

Hermit crab populations show continuous (with or without peaks) or seasonal reproductive patterns (Asakura & Kikuchi, 1984; Bertini & Fransozo, 2000; Table 4), without any clear relationship with taxa as also pointed out by Asakura & Kikuchi (1984). This was also evidenced since the coexisting *Clibanarius* populations described in the present study show marked differences in their reproductive activity. In general, populations of the same species did not show these two extreme patterns, i.e. continuous and seasonal, despite the possibility of such plasticity due to arguments on the influence of shell adequacy in hermit crab reproductive activity (Bertness, 1981a). In fact, such a switch in the reproductive pattern is known only for *Pagurus geminus* [Table 4, synonym of *P. filholi*, Sandberg & McLaughlin (1993)], with two populations displaying seasonal reproduction and one reproducing over the year despite an extremely low frequency of ovigerous females in February. Variation in the period of the reproductive peaks occurred between different populations of *Pagurus geminus*, *P. lanuginosus*, *Clibanarius virescens*, *C. antillensis* and *C. vittatus* (see Table 4). These small differences between such populations may be associated with geographical and local conditions according to Giese (1959). Populations of a given species at different latitudes subjected to particular climatic and oceanographic conditions may have different reproductive patterns. In contrast, the influence of local processes on the reproduction of *C. antillensis* was evidenced given that the two studied populations of this species are situated about 700 m apart and are subjected to similar climatic and oceanographic conditions. Continuous or wide reproductive periods shown by many hermit crab populations (Table 4) may reveal successive breeding (Lancaster, 1990; Asakura, 1992) or asynchronous reproduction (Giese, 1959). This, associated with the data on longevity of the three populations focused in the present study, suggests that they are likely to be iteroparous instead of semelparous.

The reproductive activity of the studied hermit crab populations was demonstrated to be inversely correlated to the adequacy of shells (see Turra, 1998) as also suggested by Reese (1968), Bertness (1981a), Lancaster (1990), and Carlon & Ebersole (1995). Such shell inadequacy was probably associated with the abilities of the crabs of these populations to find, use and hold gastropod shells as also pointed out by Reese (1968) and Bertness (1981b). Moreover, competition for shells between mature and newly settled hermit crabs (Reese, 1968) may influence reproductive activity and cause displacement of reproductive peaks and recruitment periods in coexisting populations.

Seasonal reproduction is associated with environments with high variation in temperature or food availability (Giese, 1959). Seasonal reproductive periods are more frequent (28 populations) among hermit crabs than the continuous ones (13). The number of populations studied to date in tropical areas (18 populations) was slightly smaller than in temperate ones (23). Both continuous and seasonal reproductive patterns were frequent in the tropics (55% and 45%, respectively), but seasonal patterns (87%) outnumbered the continuous (13%) in temperate waters. Hypothesis to explain 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, such as competition and shell use, should also be considered.

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