*J. Mar. Biol. Ass. U.K.* (2001), **81**, 955–960
Printed in the United Kingdom

# Population dynamics of the hermit crab *Paguristes erythrops* (Diogenidae) from Anchieta Island, southern Brazil

Renata B. Garcia and Fernando L.M. Mantelatto*

Departamento de Biologia, FFCLRP, Universidade de São Paulo (USP), Brazil, Avenida Bandeirantes, 3900 Cep. 14040-901, Ribeirão Preto (SP), Brazil. *Present address: Department of Biology, Laboratory for Crustacean Research, University of Louisiana, Lafayette, PO Box 42451 Lafayette, LA 70504-2451, USA. E-mail: flmantel@usp.br

The population of *Paguristes erythrops* (Crustacea: Anomura) was studied based on seasonal abundance, size–frequency distribution, sex ratio and reproductive period (percentage of ovigerous females). Specimens were collected monthly by SCUBA diving in the infralittoral area of Anchieta Island, Ubatuba. A total of 543 individuals was analysed. Animal size (minimum and maximum shield length, respectively) was 1.7 and 11.8 mm for males, 1.7 and 10.3 mm for non-ovigerous females, and 3.2 and 7.8 mm for ovigerous females. The sex ratio was 0.91:1. Sexual dimorphism was recorded by the presence of males in the largest size-classes. The absence of ovigerous females during winter months (June to August) and their high incidence from January to March indicated discontinuity in the reproductive cycle, suggesting that females become ovigerous and breed in the summer, with the spawning period lasting from spring to autumn. This strategy of reproduction probably was based on competition with other coexisting species in this area.

## INTRODUCTION

Hermit crabs represent an important portion of the many intertidal and moderately deep tropical benthic communities, where they play an important role in the marine food chain (Fransozo & Mantelatto, 1998). Consequently, hermit crabs represent promising material for study because the establishment of these animals in such environments derives from the evolution of adaptive population strategies.

However, many species are known from only one or a few localities and many still remain undescribed. Three main groups in particular, i.e. the genera *Paguristes* and *Pagurus* and the 'Pylopagurus-like' species, have caused considerable identification problems among specialists (Hendrickx & Harvey, 1999). On the other hand, the important question about the underlying phylogenetic relationships among these mostly sympatric species has never been resolved. According to Goshima et al. (1996), there is a considerable time lag between the morphological description of new species and subsequent reports on their biology and ecology, which may cause insufficient understanding of the species.

In Brazil, several studies on the population structure of hermit crabs were carried out in the Ubatuba region, an important zone of faunal transition between Patagonia and tropical regions (Mantelatto & Garcia, 2000). However, few species have received more than brief attention, such as *Pagurus criniticornis* (Dana, 1852), *Pagurus brevidactylus* (Stimpson, 1858), *Clibanarius antillensis* (Stimpson, 1859) and *Clibanarius vittatus* (Bosc, 1802) studied by Negreiros-Fransozo et al. (1991), *Paguristes tortugae* Schmitt, 1933 studied by Negreiros-Fransozo & Fransozo (1992) and recently by Mantelatto & Sousa (unpublished results), *Calcinus tibicen* (Herbst, 1791) studied by Fransozo & Mantelatto (1998), and *Petrochirus diogenes* (Linnaeus, 1758) studied by Bertini & Fransozo (1999).

Despite the large number of studies that reported the species of the present study, *Paguristes erythrops* Holthuis, 1959 (see Melo, 1999 for review), no ecological or biological aspects have been studied previously, except for the postembryonic development reported by Hebling & Fransozo (1982). In this respect, the objective of the present study was to characterize the population structure and reproductive period of the hermit crab *P. erythrops* inhabiting the infralittoral area of Anchieta Island, which is an ecological reserve of São Paulo State, Brazil.

## MATERIALS AND METHODS

### *Study area*

Anchieta Island (23°33′S 45°05′W) has a total area of about 10 km$^2$ and was recently declared an ecological reserve of São Paulo State. This island is located landwards, separated from the coast by a 300 m long and 35 m deep canal. However, scientific information about the crustacean fauna from this area is scanty.

### *Sampling and analysis*

*Paguristes erythrops* were obtained monthly from January to December 1999 on the infralittoral rocky shores and sandy areas of East Beach in Anchieta Island. Specimens were captured during daytime by two persons using SCUBA diving methods over a period of 20 min over an area of about 850 m$^2$.

Animals were frozen and transported to the laboratory where they were carefully removed from their shells,



https://doi.org/10.1017/S0025315401004891 Published online by Cambridge University Press

**Table 1.** Paguristes erythrops. *Total number of individuals collected monthly in the infralittoral area of East Beach, Anchieta Island, in 1999 (*, months with significant deviation from the expected 1:1 ratio).*

| Months | Males | % | Non ovigerous females | % | Ovigerous females | % | Total | % |
|---|---|---|---|---|---|---|---|---|
| January | 26 | 4.79 | 6 | 1.10 | 22 | 4.05 | 54 | 9.95 |
| February * | 32 | 5.89 | 8 | 1.47 | 44 | 8.10 | 84 | 15.47 |
| March | 18 | 3.31 | 2 | 0.38 | 25 | 4.60 | 45 | 8.29 |
| April * | 13 | 2.39 | 23 | 4.24 | 4 | 0.74 | 40 | 7.37 |
| May | 34 | 6.26 | 22 | 4.05 | 4 | 0.74 | 60 | 11.05 |
| June * | 35 | 6.45 | 18 | 3.31 | – | – | 53 | 9.76 |
| July | 30 | 5.52 | 40 | 7.37 | – | – | 70 | 12.89 |
| August | 7 | 1.29 | 3 | 0.55 | – | – | 10 | 1.84 |
| September | 28 | 5.16 | 15 | 2.76 | 8 | 1.47 | 51 | 9.39 |
| October | 9 | 1.66 | 12 | 2.21 | 1 | 0.19 | 22 | 4.05 |
| November | 5 | 0.92 | 1 | 0.19 | – | – | 6 | 1.10 |
| December | 22 | 4.05 | 18 | 3.31 | 8 | 1.47 | 48 | 8.84 |
| Total | 259 | 47.70 | 168 | 30.94 | 116 | 21.36 | 543 | |

measured for shield length (SL), and weighed (W). Sex was determined from the gonopore position. Measurements were made with a caliper rule (0.1 mm) and the small individuals were measured under a compound light microscope with a camera lucida.

The population structure was analysed as a function of the size–frequency distribution of the individuals and the sex ratio. The $\chi^2$-test was used to evaluate the sex ratio and to compare male and female percentage per month and the distribution frequency was tested by the Kolmogorov–Smirnov normality test (KS). The median size of individuals of both sexes was compared by the Mann–Whitney test (Zar, 1996). Pearson coefficient was used to check relationships between the absolute values of temperature and the number of individuals.

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. The occurrence of the juveniles (individuals of both sexes smaller than the smallest ovigerous female captured) characterized the recruitment in the population. To better visualize the results in terms of seasonal occurrence the monthly samples were grouped into summer (December, January and February), autumn (March, April and May), winter (June, July and August) and spring (September, October and November) samples.

## RESULTS

A total of 543 individuals was collected: 259 males (47.70%), 168 non-ovigerous females (30.94%), and 116 ovigerous females (21.36%) (Table 1).

The median size of males was significantly larger than the median size of non-ovigerous and ovigerous females ($P<0.05$). There was a unimodal size distribution for each sex, with non-normal distribution (KS=0.095; $P<0.05$) (Figure 1). Seasonally SL values were unimodal for the female group and slightly bimodal for the males

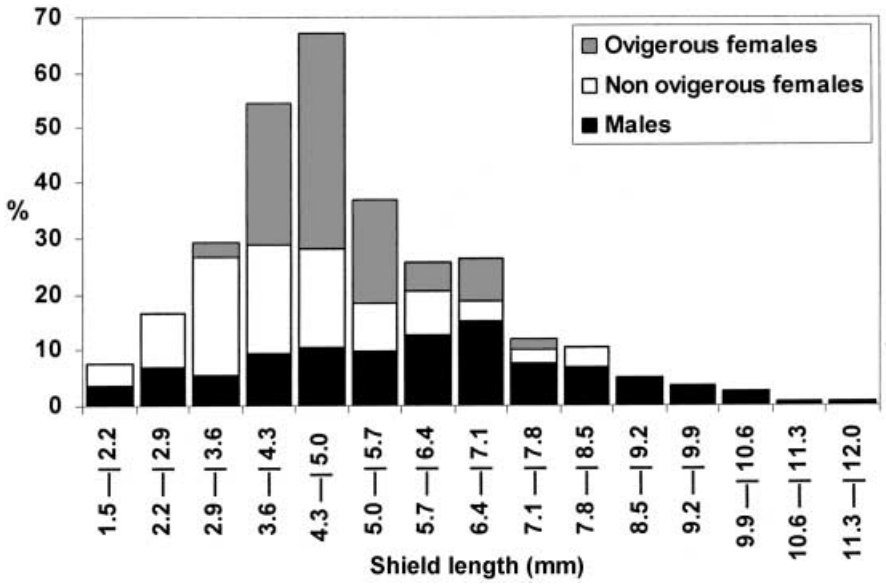


**Figure 1.** *Paguristes erythrops*. Size–frequency distribution for the total individuals collected.



https://doi.org/10.1017/S0025315401004891 Published online by Cambridge University Press

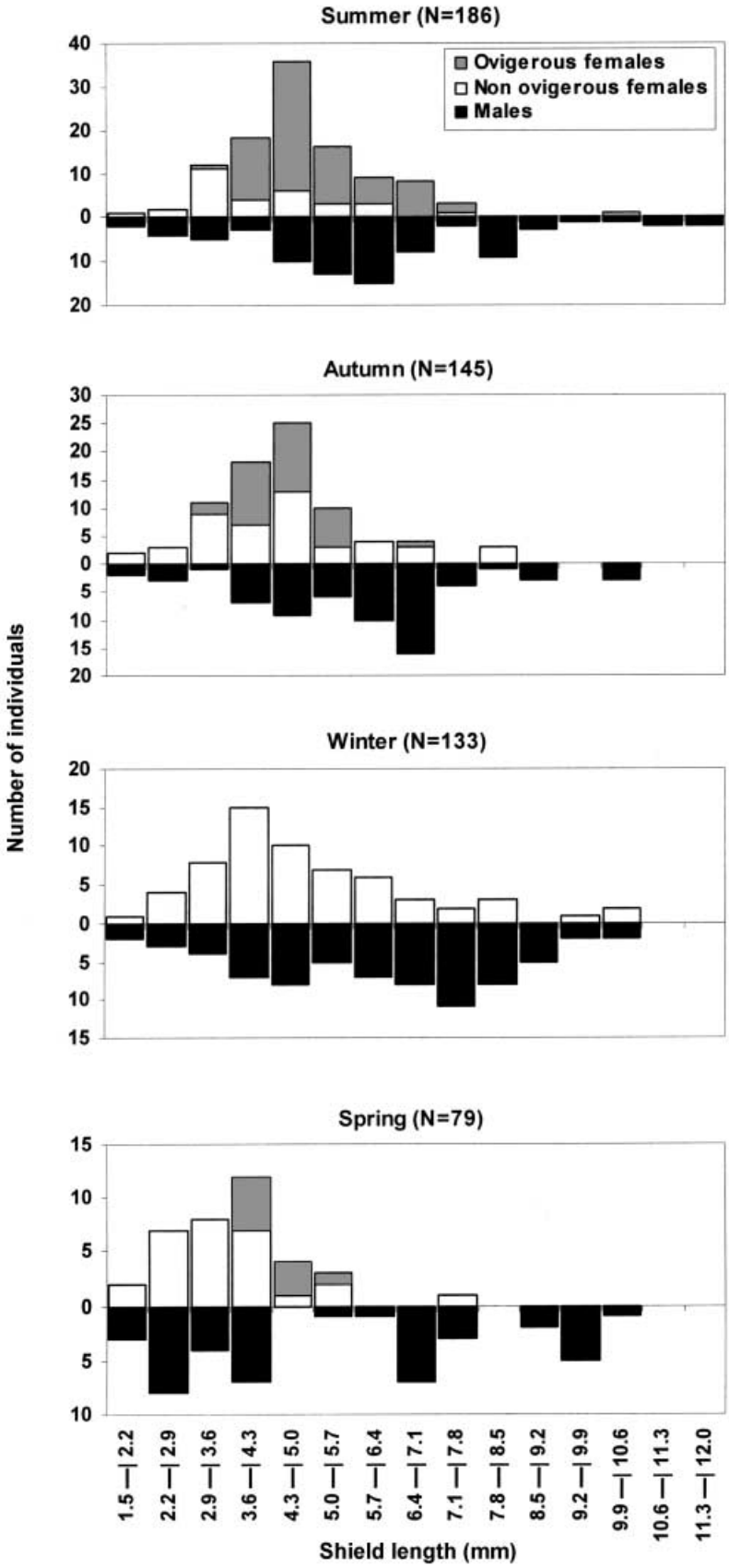


**Figure 2.** *Paguristes erythrops*. Seasonal size-class frequency distribution of individuals.

(Figure 2). The size–frequency histograms show a clear prevalence of specimens measuring 2.9–7.1 mm SL, with highest modal size ranging from 6.4 to 7.1 mm in SL for males, from 2.9 to 3.6 in SL for non-ovigerous females, and from 4.3 to 5.0 mm in SL for ovigerous females.

Overall sex ratio was 0.91:1 in favour of females and was not different from the expected 1:1 ($\chi^2$=1.15; $P$<0.05).



https://doi.org/10.1017/S0025315401004891 Published online by Cambridge University Press

Monthly sex ratios (percentage of males) ranged from 32.50 to 83.33%. Monthly, the proportion of females (non-ovigerous and ovigerous) was almost higher than that of males, except in May, June, August, September and November (Table 1). In almost all larger size-classes (5.7–12.0 mm SL) the proportion of males increased, reaching values of 100%. The sex ratio favoured females in size-classes of 2.9–5.0 mm (Figure 3).

Analysis of reproductive activity, indicated by the presence of ovigerous females, revealed a discontinuity in the period from June to August (winter) and in November. Their highest incidence was verified during the summer, indicating the peak of the reproductive period (Table 1 and Figure 4). The first spawn occurred among females belonging to the 2.9–3.6 mm size-classes, whereas approximately 50% or more of the females were ovigerous in size-classes from 3.6 to 5.7 mm.

Recruitment in the studied area, represented by the individuals of both sexes belonging to the size-classes 1 and 2 (1.5–2.9 mm SL) occurred in almost all months, except January and August. A moderate recruitment was observed from April to June, about two summer months after the period of maximum spawning. A high incidence of juveniles was noted from September to December (Figure 4), at least six months after the last peak of ovigerous female occurrence. No significant correlation

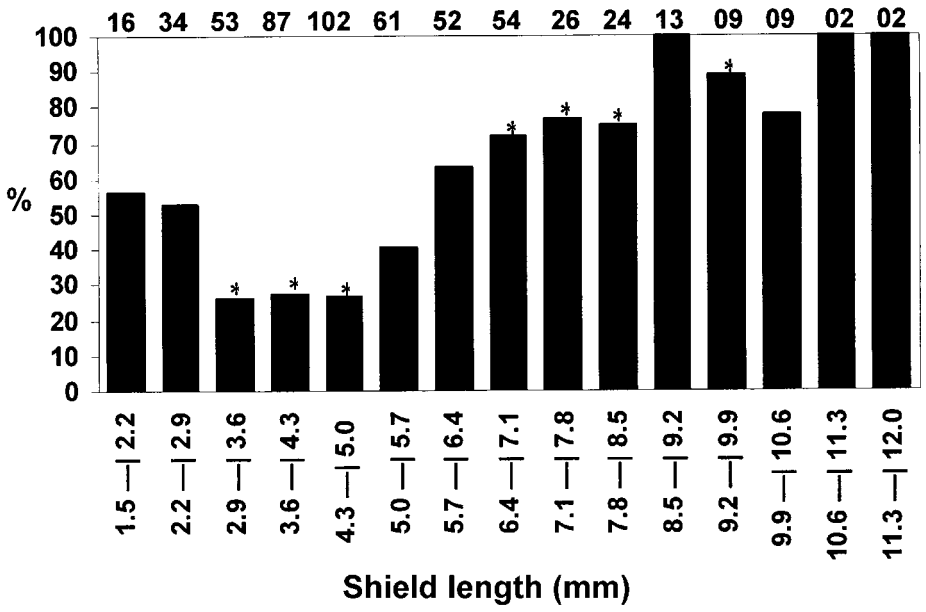


**Figure 3.** *Paguristes erythrops*. Sex ratio as a percentage of males in relation to size, with indication of those values showing significant (*) deviation from the expected 1:1 sex ratio (values above columns correspond to the total number of individuals in each size-class).

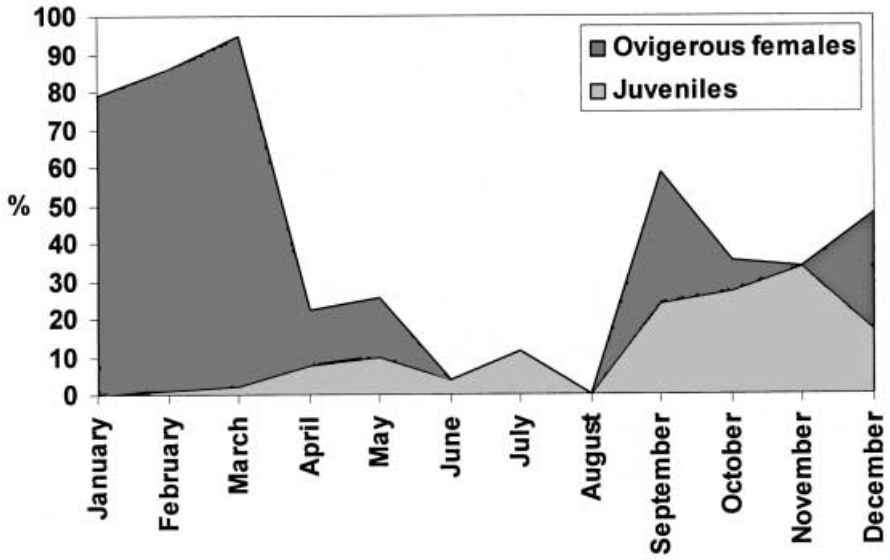


**Figure 4.** *Paguristes erythrops*. Percentage of ovigerous females (in relation to the total females collected) and of juveniles (N=50) during the study period.



https://doi.org/10.1017/S0025315401004891 Published online by Cambridge University Press

($P < 0.05$) was observed between the temperature and number of individuals captured.

## DISCUSSION

*Paguristes erythrops* presented unimodality in the size–frequency distribution for the total individuals analysed. However, seasonally, bimodal and trimodal distributions were observed for males. According to Díaz & Conde (1989), bimodality and/or polymodality generally reflects recruitment pulses, different mortality rates between sexes and/or behavioural differences (e.g. cryptic habit, migration) without any interruption in size-classes. We believe that these factors in association with differential life times and migration for resources (shells) may have influenced and contributed to the pattern found for the males in the present study.

Different patterns of size distribution were found for males and females. Females presented a non normal distribution with a peak of occurrence in an intermediate class while the distribution of males was skewed toward larger size-classes. This and the unequal sex ratio probably can be attributed to such factors 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. However, 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 (see Mantelatto & Garcia, 2000 for 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 0.91:1 proportion obtained did not differ from the expected value (1:1). In this sense, *P. erythrops* is an exception, in agreement with the Fisher Theory (Fisher, 1930). According to this author, natural selection favours an equal proportion between the sexes. Thus, we may infer that in general aspects, the population studied in the infralittoral area of East Beach on Anchieta Island is well-established and stable mainly in terms of incorporation and mortality rates of individuals. Also, it is important to consider that the search for and utilization of shells is the major adaptation of the hermits, influencing population size, with one sex (generally the males) being more successful in obtaining shells (Bertness, 1981).

The sex ratio analysis by size-classes revealed a sexual proportion tending to deviate from the expected 1:1 in favour of males in the larger specimens. In the intermediate classes the sex ratio tended to females, not differing from 1:1 in the first two classes (juveniles). 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) for hermit crab populations inhabiting both the intertidal and infralittoral areas.

The females presented higher and significant occurrence than the males in the summer season, which may be related to the recruitment of females involved in reproductive activity during this period (January–March). The absence of ovigerous females in the winter characterized a discontinuous reproductive cycle. This pattern was similar to that of *Calcinus tibicen* (Fransozo & Mantelatto, 1998) and *Petrochirus diogenes* (Bertini & Fransozo, 1999) in the Ubatuba region, and other hermit crab species worldwide such as *Clibanarius vittatus* (Lowery & Nelson, 1988), *Pagurus bernhardus* (Linnaeus, 1758) (Lancaster, 1990), *Clibanarius virescens* (Krauss, 1843) (Imazu & Asakura, 1994), *Pagurus middendorffi* Brandt, 1851 (Wada et al., 1995), *Pagurus nigrofascia* Komai, 1996 (Goshima et al., 1996), *Pagurus filholi* (De Man, 1887) (Goshima et al., 1998), *Pagurus lanuginosus* De Haan, 1849 (Wada et al., 2000), and *Calcinus tubularis* (Linnaeus, 1767) (Pessani et al., 2000).

In most tropical and subtropical regions the reproductive season occurs during the warmer months, a period when the food sources are abundant in the plankton (Negreiros-Fransozo & Fransozo, 1992). According to Giese (1959), among marine invertebrates larval hatching occurs during favourable periods, maximizing survival. However, temporal variations in the occurrence of ovigerous females and larval stages may contribute to the reduction of interspecific megalopa competition for food and for the gastropod shells (Fotheringham & Bagnall, 1976). This hypothesis is likely to be true for *P. erythrops*, mainly because five other hermit crab species are coexistent in the same area (Mantelatto & Garcia, in press).

Alternatively, Fotheringham & Bagnall (1976) mentioned that the occurrence of larval settlement during the winter may be advantageous because of an increase of small gastropod shell availability due to the mortality of the juvenile gastropods during this season. Studies on megalopa and juvenile settlement are in progress to elucidate this aspect of the population studied.

It can be seen that hermit crabs have high plasticity in their reproductive activity, marked by different strategies adopted by populations of the same species in different localities, as well as by different species inhabiting the same area. According to Reese (1968), the reproductive variations are the result of local ecological adaptations, and the temporal hatching pattern may not be generalized when considering just one environmental factor. In this sense, studies on the fecundity, gonadal development and coexistence with other hermit crab species may contribute to a better understanding of the reproductive cycle of *P. erythrops* on Anchieta Island.

Despite the discontinuity in the presence of ovigerous females, a large number of juveniles was observed during the study period. The occurrence of these individuals in almost all months reflected the continuous recruitment in the population with a peak of incidence from six to nine months after the peak of ovigerous females. According to Hebling & Fransozo (1982), *P. erythrops* attains the megalopa phase 15 days after larval hatching in laboratory conditions. This fast postembryonic development associated with the short number of zoea stages and the reduced time to reach the megalopa phase is characteristic of the genus *Paguristes* (Povenzano, 1978).

Considering that in one month the *P. erythrops* larvae reach the first juvenile stage, we may infer that after six months they reach the size (SL) of the individuals captured in the present study, corroborating the data obtained for the peak of the reproductive and juvenile



https://doi.org/10.1017/S0025315401004891 Published online by Cambridge University Press

recruitment period. In this sense, the equal proportion of the two sexes and the continuous and effective juvenile recruitment in the population lead us to infer that the *P. erythrops* population in the studied area is equilibrated and well-adapted with respect to the intra- and inter-relationships that determined its presence on Anchieta Island.

The authors are grateful to FAPESP for financial support during the sampling work (Proc. 98/07454-5) and for a Doctoral Fellowship to R.B.G. (Proc. 00/02554-3). 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, and to all colleagues of the Crustacean Bioecology Laboratory for their help during field and laboratory work. F.L.M.M. is grateful to Dr Darryl L. Felder and Department of Biology—University of Louisiana at Lafayette for facilities during the early preparation of this manuscript. All experiments conducted in this study comply with current applicable state and federal laws.

## REFERENCES

Abrams, P.A., 1988. Sexual difference in resource use in hermit crabs; consequences and causes. In *Behavioral adaptations to intertidal life* (ed. G. Chelazzi and M. Vannini), pp. 283–296. New York: Plenum Press.

Bertini, G. & Fransozo, A., 1999. Population dynamics of *Petrochirus diogenes* (Crustacea, Anomura, Diogenidae) in the Ubatuba region, São Paulo, Brazil. *Crustacean Issues*, **12**, 331–342.

Bertness, M.D., 1981. Competitive dynamics of a tropical hermit crab assemblage. *Ecology*, **62**, 751–761.

Díaz, H. & Conde, J.E., 1989. Population dynamics and life history of the mangrove crab *Aratus pisonii* (Brachyura, Grapsidae) in a marine environment. *Bulletin of Marine Science*, **45**, 148–163.

Fisher, R.A., ed., 1930. *The genetical theory of natural selection*, 2nd rev. New York: Dover.

Fotheringham, N. & Bagnall, R.A., 1976. Seasonal variation in the occurrence of planktonic larvae of sympatric hermit crabs. *Journal of Experimental Marine Biology and Ecology*, **21**, 279–287.

Fransozo, A. & Mantelatto, F.L.M., 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**, 738–745.

Gherardi, F. & Nardone, F., 1997. The question of coexistence in hermit crabs: population ecology of a tropical intertidal assemblage. *Crustaceana*, **70**, 608–629.

Giese, A.C., 1959. Comparative physiology: annual reproductive cycles of marine invertebrates. *Annual Review of Physiology*, **21**, 547–576.

Goshima, S., Kawashima, T. & Wada, S., 1998. Mate choice by males of the hermit crab *Pagurus filholi*: do males assess ripeness and/or fecundity of females? *Ecology Resource*, **13**, 151–161.

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 *The biology of Crustacea, embryology, morphology, and genetics*, vol. 2 (ed. D.E. Bliss), pp. 11–196. New York: Academic Press.

Hebling, N.J. & Fransozo, A., 1982. Desenvolvimento pós-embrionário de *Paguristes erythrops* Holthuis, 1959 (Decapoda, Diogenidae), em laboratório. *Revista Brasileira de Biologia*, **42**, 117–128.

Hendrickx, M.E. & Harvey, A., 1999. Checklist of Anomuran crabs (Crustacea, Decapoda) from the eastern tropical pacific. *Belgium Journal of Zoology*, **129**, 363–389.

Imazu, M. & Asakura, A., 1994. Distribution, reproduction and shell utilization patterns in three species of intertidal hermit crabs on a rocky shore on the Pacific coast of Japan. *Journal of Experimental Marine Biology and Ecology*, **184**, 41–65.

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

Lowery, W.A. & Nelson, W.G., 1988. Population ecology of the hermit crab *Clibanarius vittatus* (Decapoda, Diogenidae) at Sebastian Inlet, Florida. *Journal of Crustacean Biology*, **8**, 548–556.

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.

Mantelatto, F.L.M. & Garcia, R.B., 2000. Shell utilization pattern of the hermit crab *Calcinus tibicen* (Diogenidae) from southern Brazil. *Journal of Crustacean Biology*, **20**, 460–467.

Mantelatto, F.L.M. & Garcia, R.B., in press. Hermit crab fauna from the infralittoral area of Anchieta Island (Ubatuba, Brazil). In *Modern approaches to the study of Crustacea* (ed. E.E. Briones and F. Alvarez). Mexico.

Melo, G.A.S., 1999. *Manual de identificação dos Crustacea Decapoda do litoral brasileiro: Anomura, Thalassinidea, Palinuridea e Astacidea*. São Paulo: Editora Plêiade.

Negreiros-Fransozo, M.L. & Fransozo, A., 1992. Estrutura populacional e relação com a concha em *Paguristes tortugae* Schmitt, 1933 (Decapoda, Diogenidae), no litoral norte do Estado de São Paulo, Brasil. *Naturalia*, **17**, 31–42.

Negreiros-Fransozo, M.L., Fransozo, A. & Hebling, N.J., 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**, 135–148.

Pessani, D., Damiano, M.T., Maiorana, G. & Tirelli, T., 2000. The biology of the hermit crab *Calcinus tubularis* (Decapoda, Diogenidae) in nature and in the laboratory. *Crustacean Issues*, **12**, 377–383.

Provenzano, A.J. Jr, 1978. Larval development of the hermit crab *Paguristes spinipes* Milne Edwards, 1880 (Decapoda, Diogenidae) reared in the laboratory. *Bulletin of Marine Science*, **28**, 512–526.

Reese, E.S., 1968. Annual breeding seasons of three sympatric species of tropical hermit crabs with a discussion of factors controlling breeding. *Journal of Experimental Marine Biology and Ecology*, **2**, 308–318.

Wada, S., Goshima, S. & Nakao, S., 1995. Reproductive biology of the hermit crab *Pagurus middendorffii* Brandt (Decapoda, Anomura, Paguridae). *Crustacean Resource*, **24**, 23–32.

Wada, S., Kitaoka, H. & Goshima, S., 2000. Reproduction of the hermit crab *Pagurus lanuginosus* and comparison of reproductive traits among sympatric species. *Journal of Crustacean Biology*, **20**, 474–478.

Wenner, A.M., 1972. Sex ratio as a function of size in marine Crustacea. *American Naturalist*, **106**, 321–350.

Zar, J.H., 1996. *Biostatistical analysis*. Upper Saddle River: Prentice Hall.

*Submitted 12 June 2001. Accepted 26 September 2001.*



https://doi.org/10.1017/S0025315401004891 Published online by Cambridge University Press