POPULATION FEATURES OF THE WESTERN ATLANTIC HERMIT CRAB *Pagurus exilis* (ANOMURA, PAGURIDAE) IN BRAZIL

FERNANDO L. MANTELATTO, DANILLO L. A. ESPÓSITO, MARIANA TEROSSEI, RENATA BIAGI, AND ANDREA L. MEIRELES
Laboratory of Bioecology and Crustacean Systematics, Department of Biology, FFCLRP, University of São Paulo (USP), Av. Bandeirantes - 3900, CEP 14040-901, Ribeirão Preto (SP), Brazil. E-mail: flmantel@usp.br

1Programa de Pós Graduação em Biologia Comparada – FFCLRP/USP.

RESUMO

Aspectos populacionais do ermitão do Atlântico oeste *Pagurus exilis* (Anomura, Paguridae) no Brasil

A estrutura populacional do ermitão *Pagurus exilis* foi estudada, na região de Caraguatatuba (23° 34’ e 23° 51’S; 45° 10’ e 45° 26’O), litoral norte de São Paulo, Brasil, pela primeira vez quanto à distribuição de frequência de tamanho total e sazonal, razão sexual e período reprodutivo. Os animais foram coletados mensalmente durante dois anos consecutivos (2001/2003) com um barco de pesca equipado com redes “double rig”. No laboratório, os espécimes foram identificados, contados, pesados e medidos. Um total de 1963 animais foi capturado, sendo 1372 machos e 591 fêmeas (311 fêmeas não ovígeras e 280 fêmeas ovígeras). O tamanho dos animais (comprimento do escudo cefalotorácico) variou de 2,4 a 8,3 mm, e os machos foram significativamente maiores, demonstrando um dimorfismo sexual. A distribuição de frequência de tamanho demonstrou um padrão unimodal com distribuição não-normal. A razão sexual total foi significativamente diferente do esperado, em favor dos machos (1:0,43). A maioria das fêmeas ovígeras apresentou ovos no estágio inicial de desenvolvimento, com uma pequena porcentagem em estágios intermediário e final. O perfil encontrado apresenta uma população abundante com reprodução contínua (fêmeas ovígeras ocorrendo ao longo do ano).

PALAVRAS-CHAVE: estrutura populacional, período reprodutivo, razão sexual

ABSTRACT

The population structure of the hermit crab *Pagurus exilis* has been studied in Caraguatatuba region (23° 34’ and 23° 51’S; 45° 10’ and 45° 26’W), northern coast of São Paulo, Brazil for the first time in terms of total and seasonal size frequency distribution, sex ratio and reproductive season. The animals were monthly collected during two consecutive years (2001/2003) with a fishery boat equipped with “double rig” nets. At the laboratory, the specimens were identified, counted, weighed and measured. A total of 1,963 animals was captured, which 1,372 were males and 591 females (311 female non-ovigerous and 280 ovigerous ones). The size of animal (Cephalothoracic Shield Length) ranged from 2.4 to 8.3 mm, and males were significantly larger, showing a sexual dimorphism. The size frequency distribution showed an unimodal pattern with non-normal distribution. The total sex ratio was significantly different from the expected, biased towards males (1:0.43). Most ovigerous females presented eggs in initial developmental stage, with a few percentages in intermediary and final stages. The profile found an abundant population with a continuous reproduction (ovigerous females occurring along the year).

KEY WORDS: population structure, reproductive period, sex ratio

INTRODUCTION

The hermit crabs from Brazil constitute an outstanding component, with 48 species distributed in three families, e.g., Diogenidae, Paguridae, and Parapaguridae. Information on population structure of hermit crabs by systematized collections have been conducted for diogenid and pagurid species along the shallow waters areas of northern coast of São Paulo State during the last few years comprising studies by trawling (Negreiros-Fransozo and Fransozo 1992, Negreiros-Fransozo et al. 1997, Fransozo and Mantelatto 1998, Fransozo et al. 1998, Bertini and Fransozo 2000, Martinelli et al. 2002) and by scuba diving collections (Mantelatto and Sousa 2000, Garcia and Mantelatto 2001, Mantelatto et al. 2005, Biagi et al. 2006).

Despite the considerable number of studies that reported the biogeographic occurrence of the present species, *Pagurus exilis* (Benedict 1892) (see Melo 1999 for review), few works have been published on ecological or biological aspects, except for the post-embryonic development in laboratory conditions reported by Scelzo and Boschi (1969), the shell occupation reported by Terossi et al. (2006) and the spatial and seasonal distribution reported by Meireles et al. (2006).

In the present study, the population biology of the hermit crab *P. exilis* is assessed with emphasis on size structure, sex ratio, and breeding period in the infralittoral area of Caraguatatuba region, Southern Atlantic, Brazil. This information is important to understand the biology of this endemic southwestern hermit crab with distribution along the coast of Brazil, Uruguay and Argentina.
MATERIAL AND METHODS

Specimens were collected from Caraguatatuba region (23° 34’ and 23° 51’S; 45° 10’ and 45° 26’W), state of São Paulo, during daytime with double-rig trawl nets (20 mm mesh size in the net body and 15 mm in the cod end). The trawls were standardized parallel to the beach along transects of 18 Km² performed on depths from 5 to 35 m. Bottom water was collected with a Nansen bottle in order to obtain the measures of temperature (ºC) and the salinity (p.s.u.).

The hermit crabs were obtained monthly over a two-year period (July/2001-June/2003) and identified according to Melo (1999). After capture the animals were frozen and transported to the laboratory. Processing started by careful removal of hermit crabs from their shells in an anticlockwise fashion, counted, weighed and measured for the cephalothoracic shield length (SL). Measurements were carried out using Vernier calipers (± 0.1 mm accuracy). Sex was checked by the gonopore position.

The population structure was analyzed as a function of the size frequency distribution of the individuals and the sex ratio. The breeding period of the population was expressed as the percentage of females carrying eggs (ovigerous females) relative to the total number of females collected each month (Mantelatto and Souza 2000). The ovigerous females’ eggs were classified in accordance to the methodology of Mantelatto and Garcia (1999) modified from Boolootian et al. (1959): Initial Stage (stages 1-4), Intermediate Stage (stages 5-8) and Final Stage (stages 9 and 10). Specimens smaller than the smallest egg-bearing female captured (i.e. SL < 3.1 mm) were considered juveniles.

The chi-square test ($\chi^2$) was used to compare total and monthly percentage of males and females and 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).

RESULTS

A total of 1,963 individuals were collected: 1,372 males, 311 non-ovigerous females, and 280 ovigerous females (Table 1). There was a clear unimodal size frequency distribution for each sex, with non-normal distribution (KS = 0.041; $P < 0.05$) (Figure 1).

Size range within each demographic category was 2.4 – 8.3 mm SL (mean 5.42 ± 0.88 SD) for males, 2.7 – 6.8 mm (4.65 ± 0.74) for non-ovigerous females and 3.1 – 6.6 mm (4.65 ± 0.65) for ovigerous females. The mean size of males was significantly larger than the mean size of females (U = 192164.5; $P < 0.01$). The size-frequency histograms show a clear prevalence of specimens measuring 4.0 – 6.5 mm SL (Figure 1). Modal sizes ranged from 4.5 to 6.5 in SL for males, 3.5 to 5.0 for non-ovigerous females, and 4.0 to 5.5 for ovigerous females. Young juveniles (SL < 3.1 mm) were found only in the first year of study and in a low number (N = 13).

Overall sex ratio was 1:0.43 in favor of males and differed significant from the 1:1 ratio ($\chi^2 = 310.11$; $P < 0.05$). Monthly sex ratios ranged from 1:0.04 to 1:1.22. The proportion of females (non-ovigerous and ovigerous ones) was higher than that of males only in October/2001. In the smallest size class (2.0 to 2.5 mm SL) and at all larger size classes (7.0 to 8.5 mm SL) the proportion of males reached values of 100%, characterizing the anomalous pattern of Wenner (1972) (Figure 2).

Analysis of reproductive activity, indicated by the presence of breeding females, revealed a discontinuity in October/2001 and December/2002. Furthermore, in November/2002 no individual of P. exilis was collected. Ovigerous females occurred in high proportion in relation to total females captured from July to September/2001, November and December/2001, January and March/2002, August to October/2002, February to April/2003. Thus, we may characterize a continuous reproductive period (ovigerous females occurring along the year) with peaks in different seasons along the two years studied (Figure 3).
TABLE 1 – *Pagurus exilis*. Number of individuals collected monthly during the studied period.

<table>
<thead>
<tr>
<th>Months</th>
<th>Males</th>
<th>%</th>
<th>Non-Ovigerous Females</th>
<th>%</th>
<th>Ovigerous Females</th>
<th>%</th>
<th>Total</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jul/01</td>
<td>153</td>
<td>7.79</td>
<td>47</td>
<td>2.39</td>
<td>47</td>
<td>2.39</td>
<td>247</td>
<td>12.58</td>
</tr>
<tr>
<td>Aug/01</td>
<td>114</td>
<td>5.81</td>
<td>31</td>
<td>1.58</td>
<td>63</td>
<td>3.21</td>
<td>208</td>
<td>10.60</td>
</tr>
<tr>
<td>Sep/01</td>
<td>21</td>
<td>1.07</td>
<td>2</td>
<td>0.10</td>
<td>2</td>
<td>0.10</td>
<td>25</td>
<td>1.27</td>
</tr>
<tr>
<td>Oct/01</td>
<td>9</td>
<td>0.46</td>
<td>11</td>
<td>0.56</td>
<td>0</td>
<td>0.00</td>
<td>20</td>
<td>1.02</td>
</tr>
<tr>
<td>Nov/01</td>
<td>5</td>
<td>0.25</td>
<td>1</td>
<td>0.05</td>
<td>1</td>
<td>0.05</td>
<td>7</td>
<td>0.36</td>
</tr>
<tr>
<td>Dec/01</td>
<td>28</td>
<td>1.43</td>
<td>2</td>
<td>0.10</td>
<td>10</td>
<td>0.51</td>
<td>40</td>
<td>2.04</td>
</tr>
<tr>
<td>Jan/02</td>
<td>290</td>
<td>14.77</td>
<td>41</td>
<td>2.09</td>
<td>46</td>
<td>2.34</td>
<td>377</td>
<td>19.21</td>
</tr>
<tr>
<td>Feb/02</td>
<td>21</td>
<td>1.07</td>
<td>7</td>
<td>0.36</td>
<td>2</td>
<td>0.10</td>
<td>30</td>
<td>1.53</td>
</tr>
<tr>
<td>Mar/02</td>
<td>66</td>
<td>3.36</td>
<td>10</td>
<td>0.51</td>
<td>11</td>
<td>0.56</td>
<td>87</td>
<td>4.43</td>
</tr>
<tr>
<td>Apr/02</td>
<td>52</td>
<td>2.65</td>
<td>5</td>
<td>0.25</td>
<td>3</td>
<td>0.15</td>
<td>60</td>
<td>3.06</td>
</tr>
<tr>
<td>May/02</td>
<td>33</td>
<td>1.68</td>
<td>19</td>
<td>0.97</td>
<td>3</td>
<td>0.15</td>
<td>55</td>
<td>2.80</td>
</tr>
<tr>
<td>Jun/02</td>
<td>29</td>
<td>1.48</td>
<td>9</td>
<td>0.46</td>
<td>3</td>
<td>0.15</td>
<td>41</td>
<td>2.09</td>
</tr>
<tr>
<td>Jul/02</td>
<td>84</td>
<td>4.28</td>
<td>40</td>
<td>2.04</td>
<td>28</td>
<td>1.43</td>
<td>152</td>
<td>7.74</td>
</tr>
<tr>
<td>Aug/02</td>
<td>9</td>
<td>0.46</td>
<td>3</td>
<td>0.15</td>
<td>5</td>
<td>0.25</td>
<td>17</td>
<td>0.87</td>
</tr>
<tr>
<td>Sep/02</td>
<td>19</td>
<td>0.97</td>
<td>0</td>
<td>0.00</td>
<td>5</td>
<td>0.25</td>
<td>24</td>
<td>1.22</td>
</tr>
<tr>
<td>Oct/02</td>
<td>4</td>
<td>0.20</td>
<td>0</td>
<td>0.00</td>
<td>1</td>
<td>0.05</td>
<td>5</td>
<td>0.25</td>
</tr>
<tr>
<td>Nov/02</td>
<td>0</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
<td>0</td>
<td>0.00</td>
</tr>
<tr>
<td>Dec/02</td>
<td>9</td>
<td>0.46</td>
<td>3</td>
<td>0.15</td>
<td>0</td>
<td>0.00</td>
<td>12</td>
<td>0.61</td>
</tr>
<tr>
<td>Jan/03</td>
<td>28</td>
<td>1.43</td>
<td>3</td>
<td>0.15</td>
<td>2</td>
<td>0.10</td>
<td>33</td>
<td>1.68</td>
</tr>
<tr>
<td>Feb/03</td>
<td>47</td>
<td>2.39</td>
<td>1</td>
<td>0.05</td>
<td>1</td>
<td>0.05</td>
<td>49</td>
<td>2.50</td>
</tr>
<tr>
<td>Mar/03</td>
<td>60</td>
<td>3.06</td>
<td>7</td>
<td>0.36</td>
<td>12</td>
<td>0.61</td>
<td>79</td>
<td>4.02</td>
</tr>
<tr>
<td>Apr/03</td>
<td>109</td>
<td>5.55</td>
<td>10</td>
<td>0.51</td>
<td>15</td>
<td>0.76</td>
<td>134</td>
<td>6.83</td>
</tr>
<tr>
<td>May/03</td>
<td>102</td>
<td>5.20</td>
<td>17</td>
<td>0.87</td>
<td>5</td>
<td>0.25</td>
<td>124</td>
<td>6.32</td>
</tr>
<tr>
<td>Jun/03</td>
<td>80</td>
<td>4.08</td>
<td>42</td>
<td>2.14</td>
<td>15</td>
<td>0.76</td>
<td>137</td>
<td>6.98</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>1372</td>
<td>69.89</td>
<td>311</td>
<td>15.84</td>
<td>280</td>
<td>14.26</td>
<td>1963</td>
<td>100</td>
</tr>
</tbody>
</table>

FIGURE 1 – *Pagurus exilis*. Size frequency distribution (SL) for the total of males and females (non-ovigerous and ovigerous) sampled.
FIGURE 2 – *Pagurus exilis*. Percentage of males in relation to the total number of individuals by size class (* = no significant difference in the proportion 1:1).

FIGURE 3 – *Pagurus exilis*. Percentage of ovigerous females (in relation to the total females collected) during the study period.

The occurrence of each of the three egg stages is shown in Figure 4. Ovigerous females with a high frequency (more than 50%) of the initial egg stage were found in almost all months excepting April, June, August and October/2002. The tendency to decrease the occurrence of females with initial egg stage with increasing intermediary and final stages was detected along the period studied, which demonstrates an annual reproductive cycle.
**FIGURE 4** – *Pagurus exilis*. Percentage of ovigerous females with different embryos in developmental stages from Caraguatatuba region.

**DISCUSSION**

*Pagurus exilis* presented an unimodal pattern of size frequency distribution. This condition is a well-known pattern present in many tropical and subtropical hermit crabs and was reported to other pagurids as *Pagurus criniticornis* (Dana 1852) (Faria 2004, Mantelatto et al. in press), *Pagurus brevidactylus* (Stimpson 1858) (Mantelatto et al. 2005) and *Anapagurus alboranensis* Garcia-Gomez 1994 (Macpherson and Raventos 2004). According to Diaz and Conde (1989) such pattern of size frequency distribution is generally observed in stable structured populations, with continuous recruitment and constant indexes of mortality. Nevertheless, based on the low number of juveniles captured and the absence of data on specimens’ survival, it was not possible to make recruitment and mortality statements about this studied population.

The population pattern of monthly distribution was heterogeneous, varying from 0 to 377 individuals. Such variation might be related to non-biotic factors or even to some natural life cycle aspects (reproduction, natality) and/or migration as result of competition with other hermit crab sympatric species.

The larger size reached by the males allow us to infer that they present a higher growth rate in relation to the females. This may be interpreted as a reproductive strategy, with the females deviating greater amount of energy for reproduction, while the males canalizes it for growth (Bertness 1981, Abrams 1988). Another explanation for this difference of sizes between males and females is the advantage that having a larger size provides to males during intra-specific fights to obtain a partner for reproduction (Abrams 1988). Other *Pagurus* species also presented the sexual dimorphism pattern as *P. criniticornis* (Faria 2004, Mantelatto et al. in press), *P. brevidactylus* (Mantelatto et al. 2005), *P. excavatus* (Herbst 1791) (Macpherson and Raventos 2004) and *P. filholi* (De Man 1887) (Goshima et al. 1998). However, *P. lanuginosus* De Haan 1849 and *P. geminus* McLaughlin 1976 presented a differential pattern from *P. exilis*, where males showed an intermediate size among non-ovigerous and ovigerous females (Imazu and Asakura 1994).

*Pagurus exilis* presented an anomalous pattern of sex ratio which is, according to Wenner (1972), is common among the marine crustaceans decapods and may be resultant of distinguishing indexes of growth and mortality, reproductive migration or sexual reversion, this last discarded for *P. exilis*.

The constant presence of ovigerous females along the year, excepting October/01, November and
December/02, allows us to classify the reproductive period of this species as continuous according to Sastry (1983). The absence of ovigerous females in these months may be resultant of reproductive migration or samples collection particularities.

Hermit crabs may display continuous (with or without peaks) or seasonal reproductive patterns regardless of the family and geographical region (see Litulo 2004 for review). According to Sastry (1983) tropical and subtropical species present such tendency to reproduce all over the year as it was observed to P. criniticornis (Faria 2004, Mantelatto et al. in press) and P. brevidactylus (Mantelatto et al. 2005) in Brazilian waters. However, most hermit crabs display a discontinuous reproductive cycle as it was observed to Calcinus tibicen (Herbst, 1791) (Fransozo and Mantelatto 1998) and Petrochirus diogenes (Linnaeus, 1758) (Bertini and Fransozo 2000) in the Ubatuba region, and other hermit crab species worldwide such as Calcinus tubularis (Linnaeus 1767) (Pessani et al. 2000), Clibanarius vittatus (Bosc, 1802) (Lowery and Nelson 1988), Clibanarius virescens (Krauss 1843) (Imazu and Asakura 1994), Pagurus bernhardus (Linnaeus 1758) (Lancaster 1990), 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), and Pagurus lanuginosus De Haan 1849 (Wada et al. 2000).

Tropical species breed for longer periods probably due the favorable non-biotic conditions which are important for reproduction (Litulo 2004). According to Negreiros-Fransozo and Fransozo (1992), the hermit crabs from tropical and subtropical regions generally concentrate their reproductive period in the hottest months of the year, when the food resources for the larvae are abundant and the high temperatures sped up the metamorphosis process.

According to Giese (1959), among marine invertebrates larval hatching occurs during favorable 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 and Bagnall 1976). This hypothesis is likely to be true for P. exilis because this population coexist in this studied area with other seven hermit crab species (Meireles et al. in press). Peaks of ovigerous females were detected in different seasons, i.e., summer 2001, winter 2001/2002, spring and autumn 2002, spring 2003. Thus, we may not infer that P. exilis concentrates its reproduction in determined periods.

Analyzing the stage of eggs development, we found a great amount of eggs in the initial stage and a small percentage of eggs in the intermediate and final stages. Specimens that present this pattern demonstrate a great reproductive potential and a fast embryonic development (less than 30 days), typical of species from tropical regions (Mantelatto et al. 2002). The large amount of eggs in the initial stage of development may indicate that the spawning process occurs in every month of the year and ensures a continuous larval supply. Furthermore, observations under laboratory conditions revealed that spawning and hatching occurred in a short period of time (less than 45 days).

Scelzo and Boschi (1969) observed, in laboratory, that P. exilis took approximately 45 days at 18°C to complete its larval development. Since in almost all months we found ovigerous females with eggs in intermediate and/or final stage of development we may expect that juveniles are being recruited to the population all over the year. However, a low number (N = 13) of juveniles (SL <$3.1mm) had been found in the studied period, and thus we infer that settlement may occur in a different habitat other than the usual one for the adults, due to the fragility of these organisms and necessity of a specific food and shell supplies.

According to the results presented here we may conclude that this studied species is relatively abundant when compared with other pagurid populations living closed by; also it is well adapted to the environment where it lives, which offers the necessary conditions to adults for its growth and reproduction. Nevertheless, the coexistence with seven other hermit crab species (Meireles et al. in press) might promote some interference in population features (e.g. monthly distribution, reproductive period), aiming to minimize inter-specific competition, and therefore influencing the life history of this population. This study constitutes the first account on the population biology to better understand the life cycle of P. exilis in the study area. However, more work need to be done in terms of comparative studies with populations farther to the south in order to understand the dynamic of this species.
ACKNOWLEDGEMENTS

This work was part of a bachelor thesis by MT and DLAE and was supported by a Scientific Initiation Fellowships from FAPESP and PIBIC/CNPq, respectively. ALM is grateful to FAPESP (Proc. 02/01646-7) for Ph.D. fellowship and RB to CNPq (Proc. 150581/2003-3) for Post Doctoral fellowship. FLM is also indebted to CNPq for an ongoing research fellowship. Special thanks to those who collaborated during the course of this study, especially to Dr. Adilson Fransozo for support and facilities during sampling collections provided by FAPESP – Biota Program (Proc. 98/07090-3), to all NEBECC colleagues and to members of the Laboratory of Bioecology and Crustacean Systematics of FFCLRP/USP for their help during field and laboratory work. We thank Rogério Costa and Ronaldo Zucchi for commenting on an earlier version of the manuscript during bachelor thesis defense. We wish to express our gratitude to the anonymous reviewers for critical reading and suggestions on the earlier version of this manuscript. All experimental work was conducted in Brazil and complied with its existing laws.

LITERATURE CITED


Data de recebimento: 05/03/2007
Data de aceitação: 12/06/2007