Population structure and breeding biology of the hairy crab *Pilumnus vespertilio* (Fabricius, 1793) (Crustacea: Brachyura: Pilumnidae) in southern Mozambique

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**Abstract**

The population structure and reproduction of *Pilumnus vespertilio* were studied for the first time in Mozambique. Random samples of crabs were taken monthly from January to December 2002 from a pebble area of Inhaca Island, southern Mozambique. A clear sexual dimorphism was observed in the present population with males reaching greater sizes than females. Sex ratio was female-biased, and the monthly size–frequency distributions were often bimodal. The annual reproductive cycle of *Pilumnus vespertilio* was continuous with peaks of breeding in summer. Results suggest that embryonic development may be synchronized within the population as a result of the very high reproductive activity observed in summer. Juveniles are recruited mostly in winter in the study area.

**Keywords:** Breeding biology, Inhaca Island, Mozambique, Pilumnus vespertilio, population structure, sex ratio

**Introduction**

Reproduction is the main mechanism to maintain species proliferation and continuity and, in brachyuran crabs is extremely diversified, ultimately shaped to maximize egg production and offspring survivorship (Hartnoll and Gould 1988). The determination of breeding periods is governed by a complex interaction of endogenous and exogenous factors, allowing both intra- and inter-specific variations regarding the duration of the reproductive season (Sastry 1983). Generally, peaks of higher breeding activity may be associated with variations of temperature, salinity, oxygen, food availability, photoperiod, rainfall, among others (Meusy and Payen 1988; Costa and Negreiros-Franzo 2003; Litulo 2004).

Reproductive periods of brachyuran crabs have been frequently described and vary from seasonal to continuous patterns (Pinheiro and Fransozo 2002). It is assumed that the variations verified in the breeding patterns are often related to fluctuations observed in the
environmental conditions, latitudinal position and intertidal distribution of species which varies from region to region (Emmerson 1994; Yamaguchi 2001a, 2001b), or to biotic factors such as seasonal planktonic food, which is essential for larval development (Paula et al. 1998; Litulo 2004).

Despite the abundance of published literature on the reproductive biology of many brachyurans (e.g. Meusy and Payen 1988; Perez 1990; Emmerson 1994, Rodriguez et al. 1997), very little is known about the reproductive biology of tropical brachyurans (Emmerson 1994; Leme and Negreiros-Fransozo 1998; Oshiro 1999).

_Pilumnus vespertilio_ (Fabricius, 1793) is one of the most abundant crabs in the tidal areas of Inhaca Island, southern Mozambique. The first account on the ecology of _Pilumnus vespertilio_ (Fabricius, 1793) was given by Clark and Paula (2003) who analysed its larval development. There are no published studies on the population biology and reproduction of _P. vespertilio_ in East Africa. This paper describes the population structure and breeding biology of _Pilumnus vespertilio _from Inhaca Island, southern Mozambique, with emphasis on its size structure, sex ratio, breeding season and juvenile recruitment.

**Materials and methods**

**Field sampling and laboratory analysis**

This study was conducted from January to December 2002 during low tide in the exposed pebble area in front of the Marine Biological Station of Inhaca, Inhaca Island, southern Mozambique (26°00' S, 33°00' E). The climate at this location is a mixture of tropical and subtropical, partly influenced by the south-eastern trade wind, and a northerly monsoon, but also occasionally by strong and cold south-west winds or cyclones from the north-east. The winter (April to September) is usually cold and dry, while summer (October to March) is warm and rainy (Guerreiro et al. 1996; Paula et al. 1998). Guerreiro et al. (1996) and Paula et al. (1998) give detailed descriptions regarding the ecology, fauna and flora of the island.

Each month (during full moon), crabs were randomly collected through a catch-per-unit-effort performed by two people during a period of 1 h covering the same area of 300 m². Collected crabs were preserved in 70% ethanol until further analysis. In the laboratory, crabs were identified, sexed and measured for carapace width (CW) using a vernier calliper (± 0.05 mm) or with the aid of a compound microscope equipped with a calibrated ocular micrometer.

**Data analysis**

The population size structure was analysed as a function of the size–frequency distribution of all individuals collected during the study period. Specimens were grouped in 3.0-mm size class intervals from 5.0 to 36.0 mm CW. The period of time when ovigerous females were found in the population was referred to as the breeding season (Diaz and Conde 1989; Costa and Negreiros-Fransozo 2003). Assessment of recruitment was based on the proportion of juveniles in the samples (individuals of both sexes smaller than the smallest ovigerous female collected). The chi-square test ($\chi^2$) was used to evaluate the sex ratio and the overall size–frequency distributions were tested for normality using the Kolmogorov–Smirnov (Lilliefors) ($D$) test (Underwood 1997). The mean size of males and females was compared using the Mann–Whitney Sum test. Monthly estimates of the proportions of
juveniles were tested for correlation with temperature using Pearson’s correlation (Underwood 1997). Average values of temperature were obtained at the local meteorological station (INAM, Instituto Nacional de Meteorologia). Mean ± standard error is presented through the text.

Results

A total of 930 individuals was collected during the study period: 375 males (40.3%), 359 non-ovigerous females (38.6%) and 196 ovigerous females (21.1%) (Table I). Males ranged from 5.0 to 31.2 mm CW (18.31 ± 5.67) and females from 5.67 to 28.9 mm CW (16.28 ± 7.43). Males were on average larger than females (Mann–Whitney Sum test, \(P < 0.001\)).

Figure 1 shows the size–frequency distributions for all sampled crabs. In both males and females, size–frequency distributions differed from normality (Kolmogorov–Smirnov Lilliefors test, \(D_{\text{males}} = 0.09984, P < 0.05; D_{\text{females}} = 0.06598, P < 0.05\)) as well as from asymmetry (\(t\)-test for \(H_0: \gamma = 0; g_{\text{males}} = -0.496, t = 4.41; g_{\text{females}} = -0.182, t = 3.65, P < 0.05\)) (Figure 1). Males had a bimodal distribution with prevalence of specimens (modal size) measuring 5.0–10.0 mm CW and 17.0–25.0 mm CW whereas females had a unimodal size–frequency distribution (20.0–25.0 mm CW), respectively.

Monthly size–frequency distributions were generally uni- or bimodal (Figure 2) and juveniles were found year-round, with higher incidence in winter. Pearson’s correlation analyses indicate that the relative frequency of juveniles was negatively correlated with mean air temperature (\(r = -0.61, P < 0.05\)) (Figure 3).

The overall sex ratio (1:1.48) was significantly different from the expected 1:1 proportion (\(\chi^2\)-test, \(P < 0.05\)) and was female biased during most parts of the study (Table I).

Ovigerous females were recorded during all months throughout the year, showing continuous reproduction with high percentages of occurrence in January, March, October, November, and December (Table I). The size of the smallest ovigerous female collected

Table I. Total number of Pilumnus vespertilio (Fabricius, 1793) specimens collected at Inhaca Island, southern Mozambique.

| Month   | Males | Non-ovigerous females | Ovigerous females | Total n | Sex ratio (M:F) |
|---------|-------|-----------------------|-------------------|---------|----------------|
| January | 33    | 43.42                 | 20                | 23      | 76             | 1:1.31 |
| February| 20    | 35.08                 | 19                | 18      | 57             | 1:1.85 |
| March   | 15    | 29.41                 | 16                | 20      | 51             | 1:2.4  |
| April   | 19    | 35.18                 | 21                | 14      | 54             | 1:1.84 |
| May     | 30    | 42.86                 | 30                | 10      | 70             | 1:1.33 |
| June    | 57    | 50.89                 | 48                | 7       | 112            | 1:0.96 |
| July    | 48    | 45.28                 | 53                | 5       | 106            | 1:1.21 |
| August  | 17    | 18.28                 | 72                | 4       | 93             | 1:4.47 |
| September| 29   | 33.72                 | 40                | 17      | 86             | 1:1.96 |
| October | 52    | 60.46                 | 13                | 21      | 86             | 1:0.65 |
| November| 39    | 48.15                 | 15                | 27      | 81             | 1:1.10 |
| December| 375   | 40.32                 | 359               | 196     | 930            | 1:1.48 |

\(n\), number of individuals. *Significant difference from the expected 1:1 ratio (\(\chi^2\)-test, \(P < 0.05\)).
was 15.1 mm CW. All individuals of a smaller size than this were considered to be juveniles.

Discussion

Population structure

The global size–frequency distributions for both sexes of *Pilumnus vespertilio* at Inhaca Island were found to be different, with males having a bimodal and females a unimodal distribution, and both skewed to the left. This type of distribution has been reported by several authors (Diaz and Conde 1989; Spivak et al. 1996; Flores and Paula 2002). As stated by Thurman (1985), the size–frequency distribution of a population is a dynamic characteristic that can change throughout the year as a result of reproduction and rapid recruitment from larvae. Poisson-like size–frequency distributions can be found in certain situations due to seasonal mortality pulses and behavioural differences in harsh environmental conditions (Thurman 1985; Underwood 1997).

Sexual dimorphism was observed in the present population, with males reaching larger sizes than females. Lopez Greco et al. (2000) and Mantelatto et al. (2003) suggest that females may have lower somatic growth than males because they concentrate their energetic budget for gonad development, a fact that may lead them to have a lower somatic growth than observed in males. Moreover, males reach larger sizes due to copulation with more than one female, since larger males have greater chances of obtaining females for copulation, and win intra-specific fights (Wada et al. 2000).

Monthly size–frequency distributions were either uni- or bimodal throughout the study period. This pattern has been attributed to migration (Leme and Negreiros-Fransozo 1998; Flores and Negreiros-Fransozo 1999), differential mortality (Diaz and Conde 1989) and
Figure 2. *Pilumnus vespertilio* (Fabricius, 1793). Monthly size–frequency distributions. White bars, males; grey bars, non-ovigerous females; black bars, ovigerous females.
growth rates (Costa and Negreiros-Fransozo 2003). According to Zimmerman and Felder (1991), differences in the monthly size–frequency distributions are typically found in species that produce several clutches per season.

In this study, the overall and monthly sex ratios were female-biased. Deviations from the 1:1 ratio might result from sexual differences in the spatio-temporal distribution and mortality of organisms (Lardies et al. 1998; Wada et al. 2000), sex reversal, differential life span, migration, longevity of each sex, food restriction, utilization of different habitats, and growth rates (Wenner 1972). Emmerson (1994) and Lardies et al. (2004) suggest that deviations from the 1:1 ratio can internally regulate the size of a population by affecting its reproductive potential. Additionally, lunar phases and intertidal zonation are known to be determinants for sex ratio variation in brachyuran crabs (Emmerson 1994).

Breeding biology

The study of breeding in Crustacea can facilitate the understanding of the adaptive strategies and reproductive potential of a species and its relationship with the environment and other species. In the case of brachyurans, the breeding patterns are a result of a trade-off between growth and reproductive processes.

The annual reproductive cycle of *P. vespertilio* at Inhaca Island was continuous throughout the year, with peaks of occurrence of ovigerous females in the warmer months. This condition has been reported in several brachyurans (e.g. Thurman 1985; Diaz and Conde 1989; Perez 1990; Zimmerman and Felder 1991; Negreiros-Fransozo et al. 2002). It is generally suggested that near the tropics reproduction occurs year-round because environmental conditions are generally favourable for feeding, gonad development and larval release (Cobo 2002; Pinheiro and Fransozo 2002).

Females of *Pilumnus vespertilio* showed a strong reproductive activity with high percentages of egg-bearing females occurring in summer. This suggests that the present
species has a rapid embryonic cycle with an incubation period of less than a month (between 20–25 days) and settlement takes place immediately after the hatching of the larvae in the area. This ensures constant larval supply in the area, which may determine some aspects of population dynamics such as settlement of megalopae, and juvenile recruitment, which may contribute to the maintenance of population size.

Juvenile recruitment was constant throughout the year as a result of the high reproductive activity observed in the population. Looking at Figure 3, it can be seen that juveniles recruit to the adult population during the colder months, a period when reproductive activity is decreasing. Fransozo et al. (1999) reported the same pattern. According to these authors, timing is the ultimate factor affecting breeding, allowing larvae to encounter adequate food supplies for development. Furthermore, breeding in summer, when temperatures are higher and phytoplankton more abundant, would shorten development time and reduce larval predation (Emmerson 1994). This seems to apply for the population of *P. vespertilio* from Inhaca Island since according to Paula et al. (1998), the favourable period for phyto- and zooplankton abundance in the island occurs from September to November and March due to nutrient accumulation in Maputo Bay along the rainy season.

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