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Population structure and reproductive biology of the fiddler crab *Uca urvillei* (Brachyura: Ocypodidae) in Maputo Bay (south Mozambique)

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Population structure and reproductive biology of the fiddler crab *Uca urvillei* (Brachyura: Ocypodidae) in Maputo Bay (south Mozambique)

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Abstract

Although fiddler crabs are among the main faunal components in mangrove habitats, few studies have described the population structure and reproduction of tropical species. Such information is important for understanding their life cycle and ecology. In this study, the population structure and reproduction of *Uca urvillei* were studied at Costa do Sol, a tropical mangrove forest in Maputo Bay, southern Mozambique. Ten 1.0-m² squares were sampled during low tide periods, between January and December 2003. The population is characterized by normal size distributions, which are slightly skewed to the left. Males on average are larger than females. Males were more abundant than females and the monthly sex ratios were male-biased. Juveniles were found year-round but were less common in June and December. Both gonadosomatic index and frequency of ovigerous females showed that *Uca urvillei* breeds continuously with peaks in summer and a strong decrease in winter. Egg number was proportional to female size.

Keywords: *Breeding season, fecundity, mangrove forests, Mozambique, population structure, Uca urvillei*

Introduction

Breeding patterns in crustaceans are a result of a trade-off between environmental factors and reproductive processes (Flores and Paula 2002). Gonad maturation is influenced by temperature in general, but other factors such as light, food availability, salinity, and tidal periodicity seem to be the most prominent factors controlling reproduction in crustaceans (Sastry 1983; Morgan and Christy 1995).

In brachyuran crabs, breeding may take place year-round or be restricted to a few months. It is assumed that in subtropical and tropical environments, breeding is a continuous process because environmental conditions are favourable for gonad development, feeding and larval release. In temperate regions it is often restricted to a few months

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due to resource limitations (Sastry 1983; Ituarte et al. 2004). Predation is perhaps the most important factor causing short-term periodicities in reproductive activities among temperate crabs, because gametes and early life history stages of many crabs are vulnerable to predators (Morgan and Christy 1995).

Brachyuran crabs follow diverse reproductive strategies. For example, the reproductive activity of a female begins before the maturity moult: the initial growth and development of oocytes is based on autochthonous material (primary vitellogenesis) (Giese and Kanatani 1987; Ituarte et al. 2004). After this moult, the oocyte growth involves the contribution of allochthonous material (secondary vitellogenesis), which takes place during the intermoult period of mature females (Meusy and Payen 1988; Ramirez Llodra 2002). In addition, mature oocytes are fecundated and extruded, eggs are attached to the long pleopodal setae and embryonic development takes place. Ovarian maturation usually resumes while females are still incubating eggs (Yamaguchi 2001b; Flores and Paula 2002).

Fiddler crabs live in the intertidal zones of mud-sandy sediments in estuarine and sheltered areas (Colby and Fonseca 1984; Mouton and Felder 1995; Nobbs and McGuinness 1999; Costa and Negreiros-Fransozo 2003; Johnson 2003). During their burrowing activity, a large amount of sediment is removed and changed. This increases water and organic matter content as well as aeration of the sediment (Hartnoll et al. 2002; Colpo and Negreiros-Fransozo 2004). Fiddler crabs are also important consumers of detritus, bacteria, fungi, and benthic macroalgae (Weis and Weis 2004). They release billions of their larvae into the planktonic community where they can be both prey and predators to other invertebrates and fish (Christy and Salmon 1984; Litulo 2004a, 2004b).

Fiddler crabs can be separated into two groups by the morphology of their carapace front (Crane 1975). Wide-front crabs include Central, South and North American species, while narrow-front crabs are found in the Indo-Pacific region (Crane 1975; Christy and Salmon 1984). Such differences are a consequence of variations of ecological pressures that promote alternatives, but with similarly adaptive strategies (Christy and Salmon 1984).

The characterization of natural populations is important for understanding their ecological stability (Costa and Negreiros-Fransozo 2003). In fiddler crabs, this has been mostly accomplished through the analysis of density, spatial dispersion; size structure, sex ratio; frequency of ovigerous females and juvenile recruitment (e.g. Salmon and Hyatt 1983; Colby and Fonseca 1984; Thurman 1985; Spivak et al. 1991; Colpo and Negreiros-Fransozo 2004). Few authors have included the gonad analysis as a tool to assess reproductive activity in fiddler crabs (e.g. Mouton and Felder 1995; Rodriguez et al. 1997; Yamaguchi 2001a). This is probably related to difficulties in dissecting and identifying the reproductive structures due to their relative small size.

Six species of fiddler crabs are known from the East African region: *Uca annulipes* (H. Milne Edwards, 1837), *U. chlorophthalmus* (H. Milne Edwards, 1837), *U. inversa* (Hoffman, 1874), *U. vocans hesperiae* (Crane, 1975), *U. tetragonon* (Herbst, 1790), and *U. urvillei* (H. Milne Edwards, 1852) (Skov and Hartnoll 2001). They have been studied in great detail particularly regarding ecology and distribution (Skov and Hartnoll 2001; Hartnoll et al. 2002; Skov et al. 2002). Few studies have been conducted on their reproduction. Emmerson (1994, 1999) addressed questions related to their breeding season, sex ratios and fecundity, in Mgazana, South Africa. More recently, Litulo (2004a, 2004b) investigated some external factors regulating breeding season and fecundity of *Uca annulipes* at Costa do Sol mangrove, Maputo Bay, southern Mozambique.

Uca urvillei (H. Milne Edwards, 1852) is one of the largest (max CW=35 mm) and most abundant species in the Mozambican mangrove forests. It is commonly found in the centre

of forests mainly dominated by *Rizophora mucronata* (Lamarck, 1804). No data on size structure and breeding season in Mozambican waters have been available for this species.

This study aimed to analyse the population structure and reproduction of *U. urvillei*, namely size structure, sex ratio, breeding season, and fecundity at Costa do Sol mangrove, Maputo Bay, southern Mozambique.

Materials and methods

Field sampling and laboratory analysis

Costa do Sol mangrove lies in Maputo Bay, southern Mozambique (25°51'S, 26°18'E). The mangrove vegetation of this area is dominated by *Avicennia marina* (Forskål, 1907) and small patches of *Rizophora mucronata* (Lamarck, 1804) (Litulo 2004a). This region is characterized by two seasons: rainy (from October to March) and dry (from April to September). The mean annual rainfall is about 1000 mm per year. The mean diurnal temperature ranges from 32°C in summer to 22°C in winter. Tides are semi-diurnal, with a maximum spring tidal range of 3.9 m. Most decapod crustaceans inhabiting Maputo Bay mainly use it as an adult habitat and spawning ground, while larval and juvenile development occur in the deeper channels of mangrove forests (Litulo 2004a).

Samples were taken monthly (at full moon and during low tide periods) from January to December 2003. Specimens were collected by hand during the day-time by two people over a period of approximately 1 h over the same area of about 500 m².

On each sampling occasion, a total of 20 1.0-m² (1.0 m × 1.0 m) squares were set out in the area. Ten were randomly chosen for sampling. Each of the 10 squares was excavated with a corer to a depth of 50 cm. Collected crabs were bagged, labelled and preserved in 70% ethanol for analysis. In the laboratory, specimens were sexed and checked for egg masses. Crab carapace width (CW) was measured using Vernier callipers (± 0.05 mm accuracy) or with the aid of a stereomicroscope (CW < 6.1 mm). Crabs in which pleopods could not be distinguished (CW < 6.1 mm) were recorded as juveniles.

Adult males and females were dissected under a stereomicroscope and their gonads were removed, identified and stored with their respective females and males. Afterwards, both females and gonads were weighed using an analytical balance (0.0001 g accuracy) after drying at 70°C for 12 h (Yamaguchi 2001a).

Ten to 15 eggs were removed from the females' pleopods and were classified into three developmental stages (modified from Rabalais 1991; Rodriguez et al. 1997; Yamaguchi 2001b; Flores and Paula 2002): Stage I—freshly extruded egg mass sponge with an orange colour due to a large quantity of yolk, no signs of segmentation and the egg appears as a ball of cells; Stage II—incubation at its halfway period, the sponge has a light brown colour tending to grey, the compound eyes of the larvae are visible and the embryo occupies one-third of the volume of the egg; Stage III—the larvae are a few days from eclosion and are totally formed, the sponge is dark brown tending to black and little quantity of yolk is left.

Thirty-four ovigerous females with eggs at stage I were selected randomly for egg counting. Pleopods were removed from females, placed in petri dishes filled with seawater, and eggs detached by the gradual addition of a solution of sodium hypochlorite (7%). Bare pleopods were then discarded by gently stirring in a beaker filled with 200 ml of seawater. Three 1.5-ml sub-samples were taken using a pipette, with eggs counted under a dissecting microscope. The average value obtained was then extrapolated for the whole suspension to

estimate the number of eggs (Diaz et al. 1983; Flores and Paula 2002; Ramirez Llodra 2002).

Data analysis

The population size structure was analysed as a function of the size frequency distribution of the individuals. Specimens were grouped in 3.0-mm size-class intervals, from 3.5 to 34.5 mm CW. The period of time when ovigerous females were found in the population is referred to as the breeding season and the monthly occurrence of ovigerous females was assessed through one-way ANOVA followed by Scheffe's test for multiple comparisons.

The chi-square test (χ^2) was used to evaluate sex ratio and the size frequency distribution was tested for normality by the Kolmogorov–Smirnov Normality test (KS) (Underwood 1997). The mean size of males and females was compared using the Student's *t* test (Underwood 1997).

The gonadosomatic index (GSI) was calculated as follows: $GSI = GDW / CDW \times 100$, where GDW is the gonad dry weight and CDW is the crab dry weight.

Linear regression was employed to relate egg number (EN) (ln transformed) to carapace width (CW) (ln transformed). Student's *t* test was employed to verify whether the slope of the regression equation (*b*) differed from 3 ($H_0: b=3$) (Underwood 1997).

Results

Population structure

A total of 1325 crabs, 636 females and 689 males, was obtained throughout the study period. Males (mean=19.67, SD=3.52, range=4.5–35.5 mm CW) were, on average, larger than females (mean=17.81, SD=2.36, range=4–32.5 mm CW) ($t=10.65$, $P<0.05$).

Figure 1 shows the overall size frequency distribution of all crabs obtained during the study period. There was a conspicuous unimodal size distribution, with normal distribution

Figure 1. *Uca urvillei* (H. Milne Edwards, 1852). Size frequency distributions of all individuals sampled during the study period.

for males (Kolmogorov–Smirnov test, $KS=0.048$, $P>0.05$) and females ($KS=0.063$, $P>0.05$). The size histograms show a clear dominance of individuals measuring from 13.5 to 28.5 mm CW. The modal size of males lies between 20.5 and 22.5 mm while in females it lies between 23.5 and 25.5 mm CW.

Monthly size frequency distributions were in general uni- or bimodal and slightly skewed to the left (Figure 2). In this study, the smallest ovigerous female captured was 6.1 mm CW. On this basis, all crabs of both sexes of smaller size were considered juveniles. Recruitment into the study area was almost continuous, except in June and December, when a small number of juveniles was recorded in the population (Figure 2).

The monthly number of crabs, percentages and sex ratios examined during the study period are listed in Table I. Males ($n=689$) were slightly more abundant than females ($n=636$), but the overall sex ratio (1:0.92) was not significantly different from the 1:1 ratio (χ^2 test, $P>0.05$). In general, monthly sex ratios were male-biased, except in May, August, and November.

Reproductive biology

Figure 3 shows the temporal variation of the GSI in females (A) and males (B) of adult crabs sampled at Costa do Sol mangrove during the study period. In females, higher gonad activity was recorded from August to December and a strong decrease from March to July. In males, gonad activity peaked in March and September and decreased from April to July.

The monthly frequencies of ovigerous females obtained during the study period are shown in Figure 4. From these, it can be seen that *Uca urvillei* breeds continuously with two peaks of spawning in September and December. Oviposition decreased in winter (April to July).

Egg number varied widely, from 5000 (CW=10.0 mm) to 30,000 (CW=30.1 mm CW) (mean=17,196.47, SD=8727) and increased in accordance with female size. The slope of the logarithmic regression ($b=1.706$) was lower than 3.0 ($t=1.565$, $P>0.05$) (Figure 5).

Discussion

Population structure

The size frequency distribution of a population is a characteristic that changes throughout the year as a result of reproduction, rapid recruitment from larvae, and death (Thurman 1985). The yearly size frequency distributions in the present species were normally distributed over the year. Such a pattern has been reported in several fiddler crabs: *Uca spinicarpa* (Rathbun, 1901) and *U. longisignalis* (Salmon and Atsides, 1968) (Mouton and Felder 1995), *U. thayeri* (Rathbun, 1900) (Costa and Negreiros-Fransozo 2003), *U. vocator* (Herbst, 1804) (Colpo and Negreiros-Fransozo 2003), and *U. pugilator* (Bosc, 1802) (Johnson 2003). According to Thurman (1985), Poisson distributions in size-class can be observed in fiddler crabs due to seasonal mortality pulses in harsh environmental conditions.

The mean size of males was larger than that of females. This seems to be a common trend in brachyurans: females have a large decline in somatic growth because energy is channelled into gonad development and egg production (Hartnoll and Gould 1988). On the other hand, males reach larger sizes due to the requirement to fertilize more than one female and, at the same time, males with larger dimensions have greater chances of obtaining females

Table I. *Uca urvillei* (H. Milne Edwards, 1852): total number, percentages, and sex ratios of crabs sampled during the study period at Costa do Sol mangrove, Maputo Bay, southern Mozambique.

Month	Males	%	Females	%	Total	Sex ratio
January	49	64.47	27	35.53	76	1:0.55*
February	40	54.79	33	45.21	73	1:0.82 ns
March	60	57.14	45	42.86	105	1:0.75*
April	78	57.35	58	42.65	136	1:0.74*
May	29	32.58	60	67.42	89	1:2.07*
June	78	58.65	55	41.35	133	1:0.71*
July	85	56.29	66	43.71	151	1:0.78*
August	41	31.30	90	68.70	131	1:2.20*
September	65	55.08	53	44.92	118	1:0.81 ns
October	59	54.63	49	45.37	108	1:0.83 ns
November	65	48.15	70	51.85	135	1:1.07 ns
December	40	57.14	30	42.86	70	1:0.75*
Total	689	52.00	636	48.00	1325	1:0.92 ns

*Significant deviations from 1:1 (χ^2 , $P < 0.05$); ns, not significant.

for copulation and to win intra-specific fights (Johnson 2003). In the present population, this assertion is supported by the larger size attained by males.

Monthly size frequency distributions indicate that *Uca urvillei* presents uni- and bimodal distributions over the year. This kind of distribution is seen in species that produce several clutches per individual (Mouton and Felder 1995; Costa and Negreiros-Fransozo 2003). Additionally, the lack of larger individuals in the present population was evidenced by the monthly left-skewed size frequency distributions. Generally, left-skewed size frequency distributions indicate high mortality in larger size-classes (Underwood 1997). On the other hand, sampling agile organisms in complex habitats is often a difficult task because they may retreat to inaccessible refuges, causing an extra source of sampling bias. This situation may be responsible for the present results as difficulties in sampling fiddler crabs are often related to burrowing behaviour and to the complexity of the habitat (presence of pneumatophores).

The overall sex ratio did not differ significantly from the expected 1:1 ratio. However, significant deviations were observed in most months. This agrees with previous findings of Emmerson (1994), Skov and Hartnoll (2001), Skov et al. (2002), and Johnson (2003) who found that monthly sex ratios differed significantly from the 1:1 ratio in other fiddler crabs. There can be several reasons why such different sex ratios are recorded for populations of fiddler crabs: differential life span, temporal utilization of habitats, migration patterns, growth, and death (Wenner 1972; Johnson 2003).

Most tropical mangrove forests are inhabited by brachyuran crabs that show an exportation life-cycle strategy. Soon after hatching, the larvae of many mangrove crabs migrate from estuaries to coastal waters, where larval development is completed before post-larval stages recruit to mangrove forests to settle (Papadopoulos et al. 2002). At the same time, most mangrove crabs time their hatching to be coincident with periods of high phytoplankton productivity, which is essential for larval feeding and growth. Vannini et al. (2003) suggest that if juveniles are not observed in a population, the possible explanations

Figure 2. *Uca urvillei* (H. Milne Edwards, 1852). Monthly size frequency distributions of crabs sampled at Costa do Sol mangrove, Maputo Bay, southern Mozambique. White bars, males; grey bars, non-ovigerous females; black bars, ovigerous females.

Figure 3. *Uca urvillei* (H. Milne Edwards, 1852). Monthly variation of gonadosomatic index (GSI) of adult females (A) and males (B) throughout the study period. Error bars represent standard deviation.

are that: (1) recruitment may occur irregularly over time, and one or more generations may be completely missing; (2) the young occupy a different habitat from adults; or (3) the young occupy the same habitat as the adults but remain concealed in refuges. In the species studied here, recruitment occurs more intensively in the first quarter of the year. Recently, Litulo (2004a), while working with a population of the fiddler crab *Uca annulipes* in the same area, found that the larvae of this crab are exported to the deeper channels where predation is lower. In keeping with putative affinities of the species with mangrove habitats, it is possible to suggest that juveniles of *Uca urvillei* may develop in different habitats than those occupied by adults, a fact that may lead to the lower apparent recruitment rate observed in the present study. In summary, it is possible to infer that for decapod crustaceans which complete their life cycles within estuaries, larval and juvenile retention in deeper channels may be the primary mechanism of recruitment to adult populations, whilst

Figure 4. Monthly percentages of ovigerous females in each month in *Uca urvillei* (H. Milne Edwards, 1852). The same letters above bars indicate no statistical differences among months through Scheffe's test for multiple comparisons.

for species whose larvae are flushed into the sea, immigration of megalopae and juvenile from coastal waters is the major mechanism by which the parental population is re-stocked.

Reproductive biology

The breeding patterns of brachyuran crabs are highly diversified. Such differences are reflected in the timing of the reproductive cycle, ovarian development and oviposition (Meusy and Payen 1988; Mouton and Felder 1995; Negreiros-Fransozo et al. 2002; Pinheiro and Fransozo 2002). While nearshore crabs adapted to temperate regions restrict ovarian development and egg laying to narrow temperature optima of spring and summer, tropical and subtropical species display continuous or more extended reproduction periods (Sastry 1983; Perez 1990), as a result of the available favourable conditions for gonad development (e.g. temperature, rainfall, phytoplankton, and photoperiod) and larval release.

Figure 5. *Uca urvillei* (H. Milne Edwards, 1852): ln egg number plotted against ln carapace width (mm).

In the present study, the temporal variation of gonadosomatic indexes and ovigerous females indicates that *U. urvillei* follows continuous reproduction. Looking at Figures 3 and 4, it is evident that both gonad activity and oviposition are synchronous processes. Both females and males have their maximum gonad activity during summer, followed by a strong decrease in winter probably because of decrease of temperature. Similar conclusions have been drawn for Tanzanian and Brazilian fiddler crabs by Skov (2001) and Colpo and Negreiros-Fransozo (2004).

Ovigerous females of *U. urvillei* often exceeded 50% in the study area. This may evidence a higher reproductive activity. Sastry (1983) and Giese and Kanatani (1987) state that the reproductive activity of a species or population may be related to the tidal level and external factors. While many nearshore crabs inhabiting temperate regions appear to restrict gonad development to relatively narrow temperature optima of spring and summer, tropical and subtropical crabs often have more extended periods of reproduction with well-defined trends.

It is well known that breeding activity varies along a latitudinal gradient as a function of environmental changes. The smallest ovigerous female captured at Costa do Sol mangrove (25°51'S, 26°18'E) was 6.1 mm CW compared to 14.4 mm CW for the smallest reproductive female captured by Emmerson (1994) at Mgazana, South Africa (31°47'S, 29°25'E). If we bear in mind the potential differences observed in maturation and reproductive activity related to geographical area (reviewed by Emmerson 1994; Litulo 2004a), it is possible to infer that *Uca urvillei* exhibits a latitudinal trend in reproduction in which smaller crabs inhabit lower latitudes and the larger ones higher latitudes. This is another piece of evidence of how latitudinal trends may influence reproduction in brachyuran crabs.

Fecundity is a species-specific factor, not only regarding the number of eggs extruded in a single batch but also the frequency of brood production during the breeding season (Pinheiro et al. 2003). Because the production of eggs is an energetically expensive process, reproductive traits related to egg production play important roles in the evolution of life-history strategies (Ramirez Llodra 2002). The fecundity of *U. urvillei* increased isometrically in accordance with female size as indicated by the slope of the logarithmic equation between egg number and female size. A close analysis of the scatterplot of this relation shows that egg number varied within the same size-class. Such variations are often related to multiple spawnings and parasitism.

With this study, part of the life history of *Uca urvillei* was partially described. However, future studies must address questions related to reproductive investment, larval ecology and spatial distribution for a better understanding of the biology of this crab in the study area.

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