

# Patterns of temporal occurrence of brachyuran crab larvae at Saco mangrove creek, Inhaca Island (South Mozambique): implications for flux and recruitment

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*Temporal patterns of larval occurrence of brachyuran taxa were described from Saco mangrove creek, Mozambique, based on plankton samples. Brachyuran larvae were collected hourly in four 24 h cycles during neap and spring tidal periods at a fixed station, in November 1997 and February 1998. Results indicate a semilunar cycle of larval release activity for most species. Newly-hatched stages of sesarmids showed a peak occurrence in post-crepuscular ebbing tides, *Macrophthalmus* spp. and *Uca* spp. showed highest densities during ebbing tides at night. *Dotilla fenestrata* and *Pinnotheridae*, in spite of showing a semilunar pattern, did not display significant differences between day and night. Most mangrove taxa showed thus a clear larval exportation behaviour during ebb tides, with little return during the following floods, with varying degrees of dependence on the diel period. *Megalopae* were restricted to the night period, and highest values were obtained during spring tidal periods. However, maximum values of megalopae were obtained both during flood and ebb periods, contrary to most previous studies. This is interpreted as a bi-directional transport of non-competent megalopae into and from the mangrove area.*

## INTRODUCTION

Evidence has been provided for extensive emigration during larval development of estuarine decapod crustaceans [(Queiroga *et al.*, 1994) and references therein]. Irrespective of timing of larval release by the ovigerous female populations, effective exportation from parental areas is accomplished through the use of tidal currents by the larvae (Christy and Stancyk, 1982; Brookins and Epifanio, 1985; Levin, 1986; Geyer and Signell, 1992; Morgan, 1996b; Queiroga *et al.*, 1997; Garrison, 1999). The magnitude and local characteristics of these current patterns will ultimately determine the magnitude of larval fluxes between the estuary and adjacent shelf areas.

Studies on the distribution of larval stages of several estuarine species, such as *Uca* spp. by Lambert and Epifanio (Lambert and Epifanio, 1982), *Carcinus maenas* by Queiroga (Queiroga, 1996) and *Upogebia africana* by Wooldridge and Loubser (Wooldridge and Loubser, 1996), among others, indicate a spatial distribution pattern in which first zoeae and megalopae are found inside the estuaries whereas intermediate stages are found offshore. The lower exposure to predation, stability of salinity and temperature, increased species dispersal and genetic exchange between isolated habitats, have been recognized as selective advantages for export of larvae (Strathmann, 1982; Sulkin and Van Heukelem, 1982; Bilton *et al.*, 2002). However, the synchrony of

larval emission induces larval aggregation, which putatively increases the survival due to saturation of predators, and concentration of larval release in specific periods can be related to separation of larval patches of different ages, to avoid cannibalistic behaviour that is common in larvae with different predation capabilities (Paula, 1989, 1998). Morgan and Christy (Morgan and Christy, 1997) further suggest that planktivorous fishes constitute selective agents for reproductive synchrony and larval export, and that larvae released during the day or retained inside areas with large densities of predator fishes must have protections against the predators.

Release of decapod crustacean larvae thus does not occur randomly, but rather is precisely timed with respect to cycles in environmental factors (Saigusa and Hidaka, 1978; Christy and Stancyk, 1982; Forward, 1987). The timing of larval release can be related to lunar phase, time of day and/or phase of tide (Christy, 1978, 1982; Forward *et al.*, 1982). The timing of tidally timed activities may vary along coastlines, because species may range through several tidal environments (Morgan, 1996a). The periodicity, phasing and range of tides differ geographically, which necessarily causes the timing of tidally timed activities to change relative to light–dark and lunar cycles (Paula, 1989; Morgan and Christy, 1994). Rhythmicity of larval release is recognized as a phenomenon that strongly affects the transport and dispersion of larvae of coastal and estuarine decapods (Christy and Stancyk, 1982) and produces clear fluxes matching precisely the environmental cycles (Dittel and Epifanio, 1990; Pereira *et al.*, 2000). Rhythmicity of larval release not only has a direct influence on larval mortality, it ultimately affects recruitment of the larvae to parental populations (Queiroga *et al.*, 1994).

Larval release frequently shows a lunar or semi-lunar rhythm (Forward, 1987). The littoral and supralittoral species usually have semi-lunar rhythms in larval release. The most frequently described pattern is hatching during spring tides, at new and full moons (Wheeler, 1978; Christy, 1982; Forward, 1987). Species with larval emission synchronized with the quarter or intermediate phases of the moon have also been described (Christy, 1986; Paula, 1989; Queiroga *et al.*, 1994; Gove and Paula, 2000), demonstrating the determinant effects of different timing of tidal phases in different geographical areas. There are exceptions, however, with some intertidal species showing no relation to a particular cycle (Forward, 1987; Gove and Paula, 2000).

Larval release always occurs around the time of high tide (Saigusa and Hidaka, 1978; Christy, 1986; Forward *et al.*, 1982, 1986), but the particular timing of release within species is variable and can present fluctuations around the time of high tide (Forward, 1987; Gove and Paula,

2000). For decapods which display a diel rhythm in larval release, this event often occurs mainly in the first half of the night phase of the 24 h period (Saigusa and Hidaka, 1978; Forward *et al.*, 1982; Christy, 1986; Anger *et al.*, 1994).

Selective tidal stream transport is a mechanism by which planktonic larvae and other organisms use vertical differences of water velocity in a shear current system to promote transport in an ‘appropriate’ way or direction (Chen *et al.*, 1997; Queiroga *et al.*, 1997; Forward and Tankersley, 2001). This is a typical situation for species that have an exportation strategy in their dispersive phase of life cycle [e.g. (Oishi and Saigusa, 1997)]. The timing of larval release, typically on nocturnal ebb tides [e.g. (Paula, 1989; Morgan and Christy, 1995)], and vertical migration mechanisms that position the newly-hatched larvae in strong near-surface ebb currents [e.g. (Zeng and Naylor, 1996; Duchêne and Queiroga, 2001)], promote rapid seaward transport [e.g. (Christy, 1982; Christy and Stancyk, 1982; Brookins and Epifanio, 1985; Salmon *et al.*, 1986; Epifanio *et al.*, 1988; Dittel *et al.*, 1991; Queiroga *et al.*, 1994)]. However, retention mechanisms do not involve particular behaviour of newly-hatched stages, yet being more dependent on initial collocation of the larval population in relation to the hydrological estuarine gradient (Paula, 1998; Bilton *et al.*, 2002).

Mechanisms of recruitment of larvae to parental populations have also been intensively investigated [(Dittel and Epifanio, 1982; Johnson and Gonor, 1982; Brookins and Epifanio, 1985; Epifanio *et al.*, 1988; Boylan and Wenner, 1993; van Montfrans *et al.*, 1995; Forward *et al.*, 1997; Christy and Morgan, 1998; Eggleston *et al.*, 1998; Paula *et al.*, 2001, 2003) among others]. Reinvasion of estuaries by megalopae is also accomplished by tidal stream transport. In this case the larvae settle on the bottom during ebb and swim to the water column during flood, thereby progressing upstream into the estuary (Little and Epifanio, 1991; Olmi, 1994; Christy and Morgan, 1998; Queiroga, 1998).

Patterns of larval fluxes (emigrating larvae and immigrating post-larvae) have been extensively studied in temperate estuaries, but are not as well known for tropical systems, including mangroves. Few studies on larval fluxes were carried out in tropical estuaries (Epifanio and Dittel, 1982; Dittel and Epifanio, 1990; Dittel *et al.*, 1991), but the described processes for an estuarine mangrove of Costa Rica were similar to temperate estuaries (Christy and Stancyk, 1982; Pereira *et al.*, 2000). Paula *et al.* (Paula *et al.*, 2001, 2003) have also found similar determinants for settlement timing in Mozambican mangroves.

This work aimed to describe the patterns of brachyuran larval fluxes between Saco mangrove and adjacent waters, using plankton sampling at a fixed station. The description of emigration and immigration temporal patterns of early

and late-stage larvae was the specific objective. The study targeted mainly the more abundant taxa in the mangroves of the area, such as the Ocypodidae (genera *Uca* and *Macrophthalmus*) and the Sesamidae, but other abundant brachyuran taxa present in the plankton of the mangrove creek, such as *Dotilla fenestrata*, Grapsoidea non determined and the families Pinnotheridae and Leucosiidae, were also investigated.

## METHOD

### Study site

The sampling program was conducted at Saco mangrove creek, Inhaca Island (26°S; 33°E). Inhaca Island (Figure 1) is 12.5 km long and 7 km wide, and lies 32 km due east of Maputo (Kalk, 1995). The east coast facing the Indian Ocean contrasts with the western and southern coasts facing Maputo bay (Kalk, 1995). The interaction between the freshwater discharge from three rivers (Incomati River in the north, Maputo River in the south and Tembe River in the west) and the tide of the Indian Ocean originate complex circulation patterns inside the bay (Gove, 1997).

The more extensive mangrove area at Inhaca is located at the upper end of the south bay, expanded

into a bilobed ‘sac’, known as the Saco da Inhaca. This bay resembles a large triangular lagoon, having a length of 10 km from north to south, and a width of 6 km at the mouth, between Ponta Punduine (which separates the western shore from the south bay) and Ponta Torres (the south-east point). The triangular part of the bay is dominated by the ocean current that surges at Ponta Torres; a branch of this ocean current enters the southern bay of the island, flowing up the channel (De Boer *et al.*, 2000). In the middle reaches of the bay the channel described divides into two: one branch travelling northwards to the mangrove and another branch leading south-west towards Ponta Punduine and the Maputo bay.

At the study site the tides are semi-diurnal, with an average spring and neap tidal range of 2.2 and 0.7 m respectively. The water from Maputo bay starts to fill the southern bay 2 h after low tide, in contrast to the current at Ponta Torres, which starts to flood the bay immediately after low tide. The bulk of the water filling the bay comes from the Indian Ocean, and the water from Maputo bay enters the area south of Inhaca on a basin-wide scale; this implies relatively efficient mixing with oceanic water (De Boer *et al.*, 2000). According to Mavume (Mavume, 2000) the tidal range decreases from the Ponta Torres Strait to the inner bay (5–20%). Depending on the tidal amplitude the residence time driven by tides is between 1 and 2 days

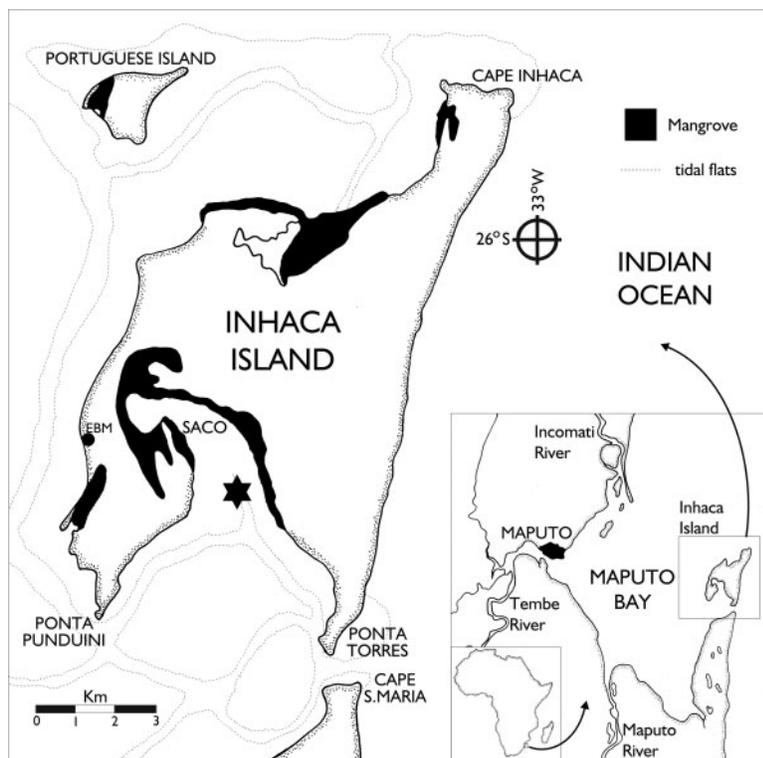


Fig. 1. Map of Inhaca Island, showing position of sampling station.

(Manhique, 2000). Salinity varies from 30 to 35.5 p.p.t. (Kalk, 1995; Gove and Mambonhe, 2000). Saco mangrove swamp represents a typical habitat of tropical estuaries on east African coasts (Kalk, 1995; Guerreiro *et al.*, 1996).

### 24 h sampling cycles

The study was conducted at a fixed station in Saco main channel (Figure 1). Temperature and salinity were registered with a probe, in the sub-superficial layer of the water column. Depth was also measured. Sub-surface horizontal zooplankton hauls were made using a net with mouth aperture 25 cm, mesh pore size 330  $\mu\text{m}$ , equipped with a flowmeter. Trawls took 10 min at  $\sim 1$  knot. Samples were fixed and preserved in buffered 4% formaldehyde. Sampling interval was 1 h and lasted for at least 24 h. Sampling was conducted in November 1997 (15–16 and 22–23) and February 1998 (13–14 and 20–21), encompassing one neap and one spring tide in each month.

### Laboratory methods

Subsamples were obtained as necessary using a Folsom Plankton Splitter. In the laboratory the subsamples were transferred to 70% ethanol. A minimum of 400 larvae were identified and counted using a stereo microscope, and when necessary an optical Olympus BH2 compound microscope. Identification of newly-hatched stages was mainly based on descriptions of Rice (Rice, 1980), Ingle (Ingle, 1991), Paula *et al.* (Paula *et al.*, 2000), and especially through reference to larval collections obtained *in situ* from ovigerous females, and which, due to their dimension, are currently being published separately [e.g. (Clark and Paula, 2003; Dornelas *et al.*, 2003; Flores *et al.*, 2003)]. The identification of brachyuran megalopae was based on descriptions by Dornelas *et al.* (Dornelas *et al.*, 2000), Quintana (Quintana, 1986), and Yatsuzuka and Iwasaki (Yatsuzuka and Iwasaki, 1982). For this study, typical mangrove taxa were treated at the lowest possible taxonomic level.

### Data analysis

Abundance was expressed as number of larvae per  $\text{m}^3$  of water. The overall effects of the phases of tide and day on the abundance of larvae were investigated through a 3-way analysis of variance (ANOVA), in which phase of tide (ebb, flood), phase of day (day, night) and tidal amplitude period (spring, neap) constituted the three factors in the analysis, each with two levels (Underwood, 1997). In order to discriminate better between the different phases of the tide and day cycles, all the samples that were collected immediately before and after the high/low tide and sunset/sunrise predicted times were not considered. The data were subjected to a logarithmic

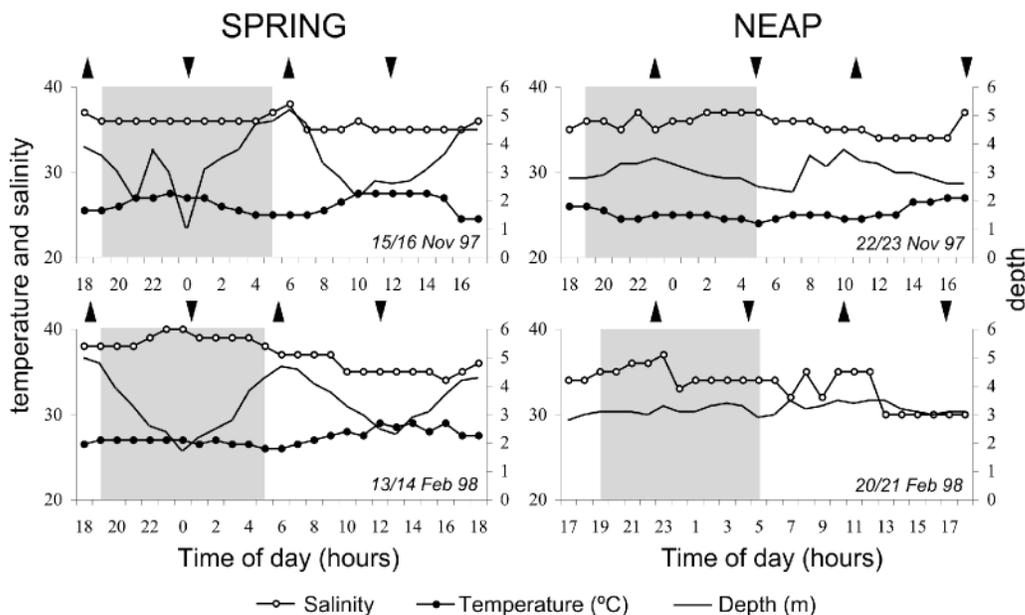
transformation:  $\text{LN}(x + 1)$ . The transformation applied to the data did not prevent heterocedasticity in all cases, but several authorities refer that the analysis of variance is robust enough to perform well even if the data deviate somewhat from the requirements of normality and homocedasticity (Sokal and Rohlf, 1981; Zar, 1996; Underwood, 1997). This analysis was performed for newly-hatched zoeae of species of *Sesarma sensu lato* (*Perisesarma guttatum*, *Parasesarma catenata*, *Sesarma leptosoma*, *Chiromantes eulimene*, and *Neosarmatium meinerti*) and *Uca* (*U. vocans*, *U. chlorophthalmus*, *U. annulipes* and *U. urvillei*), for *Macrophthalmus* spp. (the larvae of the three species present in the area, *M. grandidieri*, *M. depressus* and *M. boscii*, are undistinguishable and were thus treated as a whole), and for *Dotilla fenestrata*. Most abundant megalopae were, due to limited available descriptive information, treated as Sesarmidae n.d., Pinnotheridae n.d. and Grapsidae sp.2.

## RESULTS

Depth fluctuations reflect generally the tidal cycles, with higher values around the high tide time as expected, and lower values during low tide (Figure 2). This is particularly evident during the spring tidal periods, and during the neap tides the pattern is not so evident. This is due to the fact that Saco mangrove channel is narrow and that during the night, with a total lack of reference points inland, it becomes difficult to follow. To avoid this problem, during the February sampling period a buoy with flashing light was used for positioning during hydrological data measurements.

Maximum range of salinity during the 24 h was not  $>5$  and maximum range of temperature did not exceed  $5^\circ\text{C}$ . During the November spring tides there was an increase of temperature around both high tides. Salinity fluctuations were small and this parameter tended to decrease more during the day low tide as opposed to the night period (night period from 19 30 h until 5 00 h).

A high diversity of decapod larvae was present in the samples. Considering the newly-hatched stages, in the family Sesarmidae were identified: *Perisesarma guttatum*, *Parasesarma catenata*, *Chiromantes eulimene*, *Sesarma leptosoma*, *Neosarmatium meinerti* and Sesarmidae n.d.; in the Grapsidae: *Metopograpsus* spp.; in the Hymenosomatidae: *Hymenosoma orbiculare* and two other non-described forms; in the Leucosiidae: *Philyra plathykira* and at least one non-described form; in the Ocypodidae: *Uca vocans*, *U. chlorophthalmus*, *U. urvillei*, *U. annulipes*, *Dotilla fenestrata* and *Macrophthalmus* spp.; in the family Pinnotheridae: at least three different forms; and other taxa such as Alpheidae (three different forms), Hyppolitidae (a single species), *Calcinus latens*, *Clibanarius virescens*, *Coenobita cavipes*,



**Fig. 2.** Hydrological parameters over the four sampled 24 h cycles. Dark boxes indicate night period, up arrows high tide time and down arrows low tide time.

*Dardanus deformis* and *Lucifer* spp. The megalopae were separated into Pinnotheridae, Leucosiidae, Portunidae sp1, *Scylla serrata*, *Ilyograpsus paludicola*, *Dotilla fenestrata*, Sesamidae, Grapsidae sp1 and sp2, *Thalamita* sp., Xanthidae sp1 and sp2, Paguridae, and 10 undescribed forms. The results obtained for the most abundant brachyuran larvae are as follows.

### Mangrove taxa

As a general rule, first-stage zoeae from all species were more abundant during ebb tides, particularly at night, reflecting hatching activity around high tide or during the ebb (Figures 3–5); first stage zoeae of the Sesamidae showed this pattern (see Figure 3). At a specific level *Perisesarma guttatum* was the most abundant form, and in the spring tidal period of November 1997 provided the maximum observed density for any larval crustacean during the sampled period. In this period concentration reached almost 8000 ind. m<sup>-3</sup> during the nocturnal ebb tide, indicating a strong larval release activity by the female population in the mangrove; the same pattern was observed for the other Sesamidae species, but with lower densities. Hatching during the spring tidal period of February 1998 was of lower magnitude, but still densities reached 80 larvae m<sup>-3</sup>, and showed a very similar temporal pattern. During neap tidal periods there was a consistent increase in numbers around nocturnal high tide time, but density was very low, not reaching 3 ind. m<sup>-3</sup>.

*Uca vocans* was the most abundant species of genus *Uca* (Figure 4), and during spring tides newly-hatched larvae

reached a maximum of ~20 ind. m<sup>-3</sup>. During the neap tides density was residual for all newly-hatched stages of this genus, with generally <1 larva m<sup>-3</sup>. During spring tides diurnal occurrence was shorter and restricted to one sampling interval, while during the night larvae were consistently present for 4–6 h.

*Macrophthalmus* spp. larvae were very abundant (Figure 5), reaching >100 ind. m<sup>-3</sup> during the spring tidal periods. During neap tides maximum first stage density was <10 ind. m<sup>-3</sup>. The magnitude of larval concentration is very similar in day and night ebbing tides.

As expected, most taxa showed strong interactions between the factors considered (see Table I). Results corroborate the patterns perceived by graphical analysis, and further highlight some differences between taxa and developmental stage (newly-hatched zoeae and megalopae). However, results from the megalopal stage have to be analysed with caution, as addressed taxa represent groups of species, which potentially may have individually different patterns.

Significant interactions between amplitude period and tidal phase were common among mangrove newly-hatched stages, such as the most abundant sesamids (*Perisesarma guttatum* and *Parasesarma catenata*), the genus *Uca* (except *U. annulipes*) and *Macrophthalmus* spp.). Interaction between amplitude and day periods was significant only in *P. guttatum* and *Neosarmatium meinerti*. Significant effects of single factors were shown by *Chiramantes eulimene* (amplitude period), *Sesarma leptosoma* (amplitude and day periods) and *Uca annulipes* (amplitude period).

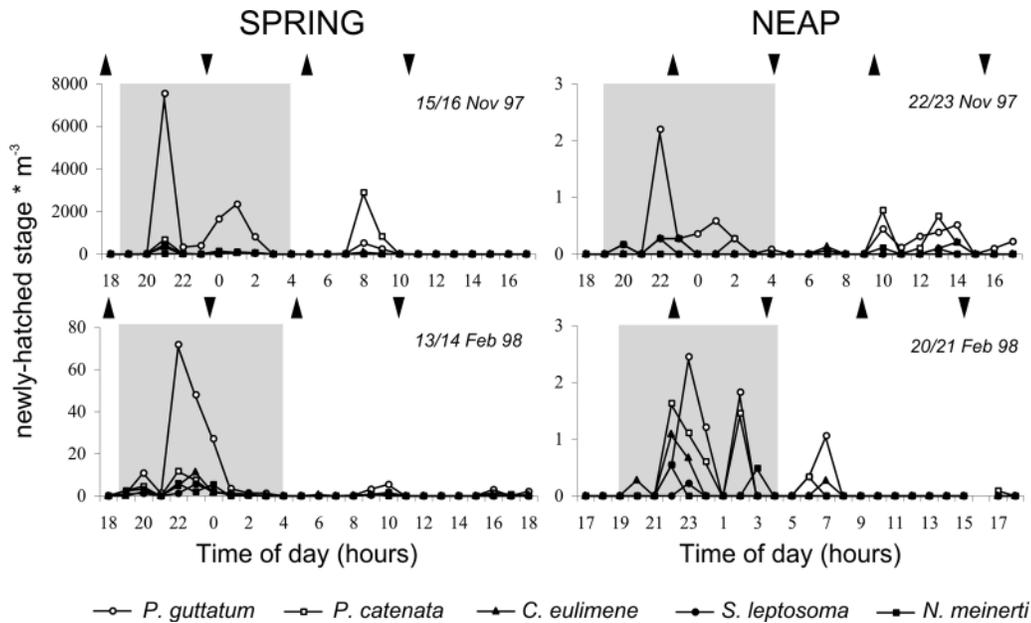


Fig. 3. Density of newly-hatched stages of Sesarmidae over the four sampled 24 h cycles. Symbols as in Figure 2.

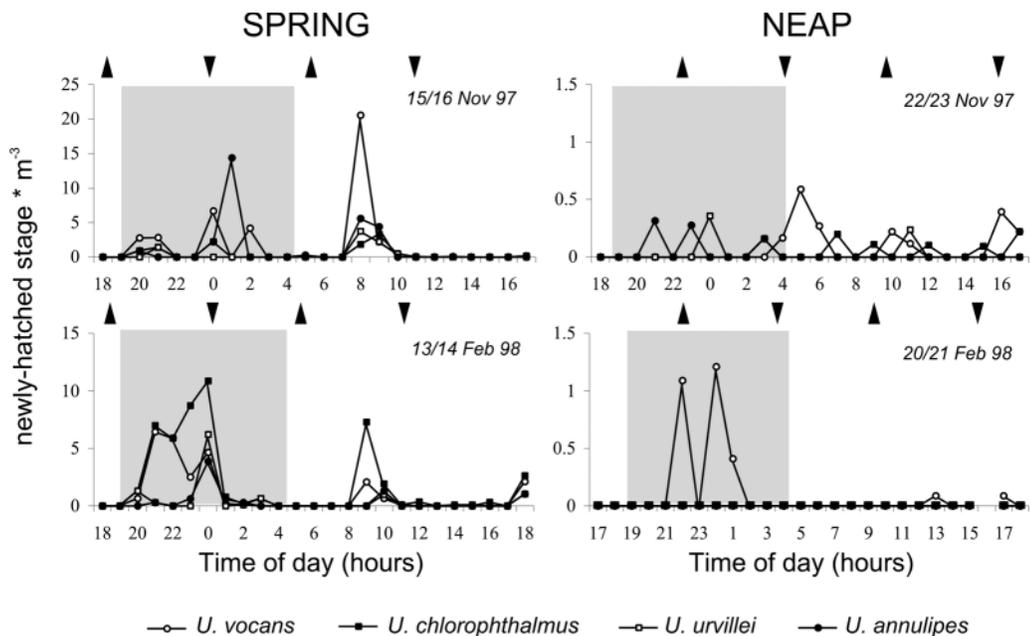


Fig. 4. Density of newly-hatched stages of the genus *Uca* over the four sampled 24 h cycles. Symbols as in Figure 2.

In both spring tides the Sesarmidae megalopal (the only megalopal taxa assigned definitively to mangrove fauna) densities were higher when compared with the neap tidal periods (Figure 6). The maximum values were around 12 ind. m<sup>-3</sup> during nocturnal flooding tides. The density fluctuations show that during the day a residual population was in synchrony

with the flooding tide. ANOVA results (Table I) revealed highly significant interaction effects ( $P < 0.001$ ) for amplitude and day periods, which are a consequence of the presence of Sesarmidae megalopae during the neap tidal period at night and during the neap tidal period at both diurnal and nocturnal flooding tides.

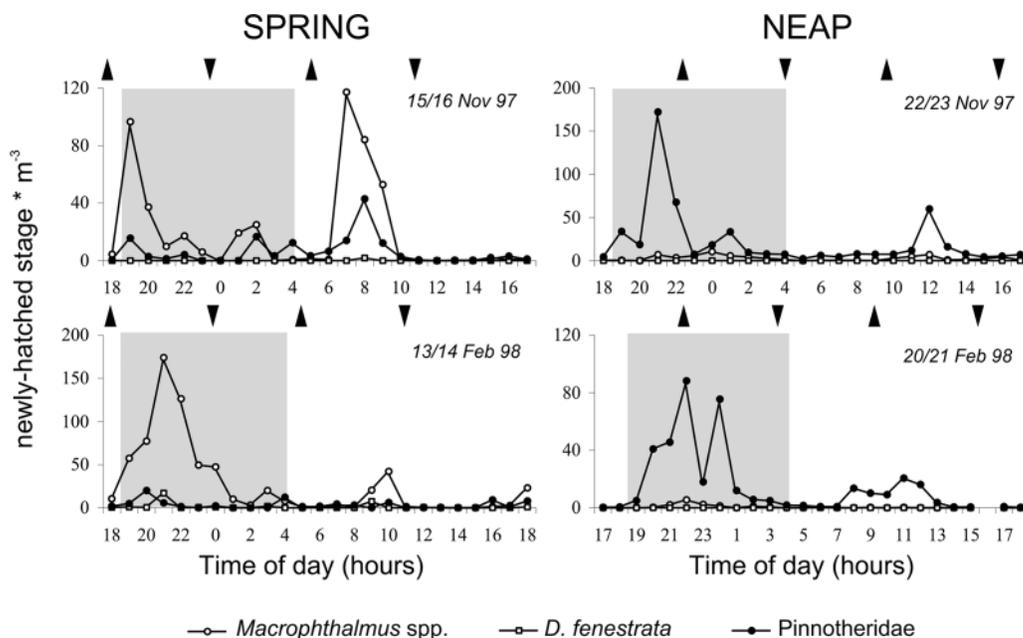


Fig. 5. Density of newly-hatched stages of *Macrophthalmus* spp., *D. fenestrata* and Pinnotheridae over the four sampled 24 h cycles. Symbols as in Figure 2.

Table I: 3-way ANOVA results for main effects and interactions of most abundant brachyuran taxa

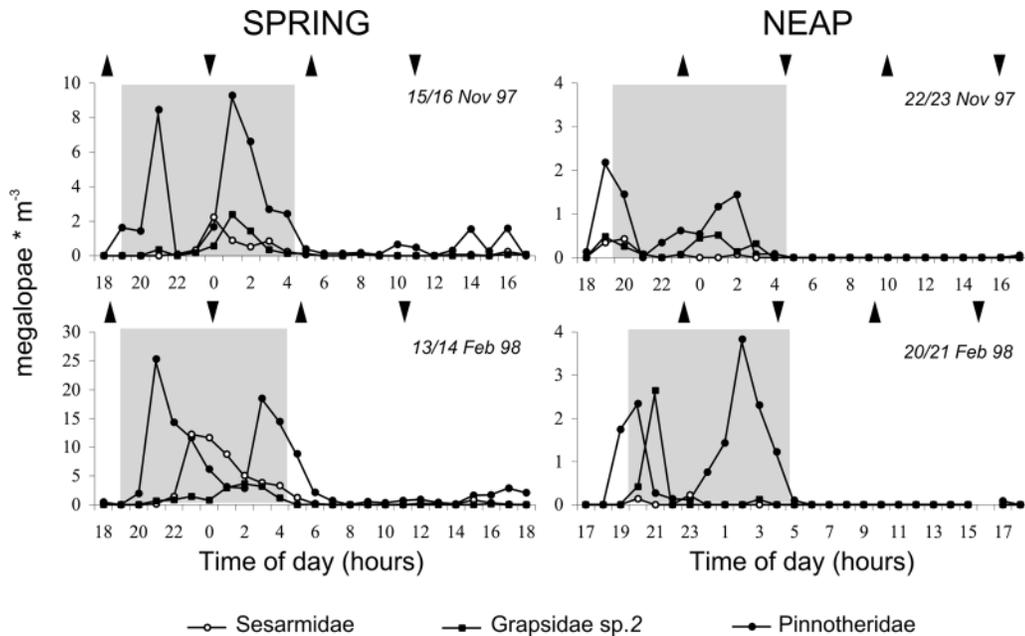
taxon	Factors			Interactions			
	(1) tidal range	(2) phase of tide	(3) time of day	12	13	23	123
<i>Parasesarma catenata</i>	***	*	ns	*	ns	ns	ns
<i>Perisesarma guttatum</i>	***	*	**	*	*	ns	ns
<i>Chiromantes eulimene</i>	***	0.0734	0.0784	0.0600	ns	ns	ns
<i>Sesarma leptosoma</i>	***	0.0811	*	0.0631	0.0522	ns	ns
Zoael stage I <i>Neosarmatium meinerti</i>	***	ns	***	ns	***	ns	ns
<i>Uca vocans</i>	***	**	ns	**	ns	ns	ns
<i>Uca chlorophthalmus</i>	***	***	ns	***	ns	ns	ns
<i>Uca urvillei</i>	**	*	ns	*	ns	ns	ns
<i>Uca annulipes</i>	*	ns	ns	ns	ns	0.0751	ns
<i>Macrophthalmus</i> spp.	***	***	***	**	ns	ns	ns
<i>Dotilla fenestrata</i>	*	ns	ns	ns	ns	ns	ns
Pinnotheridae	***	ns	***	ns	**	**	ns
Sesarmidae	***	*	***	0.0688	***	ns	ns
Megalopa Pinnotheridae	***	ns	***	ns	**	ns	ns
Grapsidae sp.2	**	***	***	ns	**	***	ns

(1) Tidal range (spring/heap), (2) phase of tide (ebb/flood), (3) time of day (day/night). \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001, ns - non significant. When close to significance level (0.1 < p < 0.05) the probability value is indicated.

Other taxa

The first zoael stage of *D. fenestrata* occurred during spring tidal periods with low densities (Figure 5). The abundance peaks for this species occurred at ebbing tides. During the

neap tidal periods *D. fenestrata* was totally absent. During the neap tides the Pinnotheridae zoael concentration was higher, reaching almost 175 ind. m<sup>-3</sup>, at high tide time.



**Fig. 6.** Density of most abundant megalopae over the four sampled 24 h cycles. Symbols as in Figure 2.

The magnitude of larval abundance was higher during the night periods.

Abundance of Pinnotheridae megalopae reached a maximum of  $\sim 25 \text{ ind. m}^{-3}$ . During the day pinnotherid megalopae were completely absent, or if present their abundance was residual. Differences between abundance during ebbing or flooding tides were not evident. The differences between sampling tidal periods (Table I) were found to be highly significant ( $P < 0.001$ ), as well as the differences between the phase of day ( $P < 0.001$ ). The interaction between these two factors was significant ( $P < 0.001$ ), which confirms the megalopae presence during nocturnal neap tides.

Density of Grapsidae sp. 2 megalopae during nocturnal spring tides were  $< 5 \text{ ind. m}^{-3}$ . During the neap tides the densities were very low. The highest values were registered during the flooding tides. The differences between day and night (Table 1) were found to be highly significant ( $P < 0.001$ , megalopae presence in night samples); phase of tide also had a significant effect ( $P < 0.001$ ) on megalopae densities, with maximum values at flooding tides. The interaction between these two factors was statistically significant ( $P < 0.001$ ), which strongly suggests that abundance of Grapsidae sp. 2 megalopae was synchronized with the nocturnal flooding tides.

The other megalopal taxa referred to were analysed as a whole. The pattern of distribution was similar to the described for Grapsidae sp. 2. During nocturnal flooding tides, in the spring tidal period, the densities were higher and reached a maximum of  $5 \text{ ind. m}^{-3}$ . Due to the high

diversity of this group, statistical analysis was not considered, because the possible patterns could have no biological significance.

## DISCUSSION

Only small fluctuations occurred in the temperature and salinity data, which reflect the more or less homogeneous water masses around Inhaca Island during the sampling period (Paula *et al.*, 1998). The influence of estuarine hydrological gradients is reduced by the dimension and wide opening of Maputo bay to the adjacent shelf area. Temperature tends to increase slightly during the day, reflecting the importance of insolation during the hot months. The shallowness of the waters around western Inhaca induces anomalies derived from atmospheric conditions, as expected, with a cooling during nocturnal low tides and when the sky was cloudy, and a temperature (and salinity) increase when insolation was stronger.

In spite of differences in overall abundance that spanned 2–3 orders of magnitude among individual species, a consistent feature in the Sesarmidae was that abundance of the zoeae was high during spring tides and negligible during neap tides. During both tidal amplitude regimes zoeae of this group consistently occurred in the water column during ebb, especially when these occurred after sunset. Small numbers were detected during flood, indicating that zoeae were flushed out of the mangrove. This pattern of occurrence implies that larval emission by females takes place

during night ebbing tides that recur with a semilunar periodicity, and is similar to that described in other geographical areas for *Sesarma cinereum* (De Vries and Forward, 1989) and *S. haematocheir* (Saigusa, 2000). It is also consistent with results obtained in the laboratory and in the field for reproductive behaviour of *Perisesarma guttatum* (Flores *et al.*, 2002; Gove and Mambonhe, 2000). The night release is expected to minimize visual predation on both newly-hatched larvae and releasing females (De Coursey, 1979; Bergin, 1981; Forward, 1987), and concentration may lead to saturation effect over predators (Paula, 1989, 1998). The maximum amplitude ebbing tides disperse larvae and subsequent larval stages undergo development in neritic water masses. Late zoeal stages are thus very rare in the samples during all sampled 24 h, probably because of their vertical distribution and increased dispersal [e.g. (Sandifer, 1975; Paula, 1998)].

Another abundant genus that showed consistent results along the different 24 h cycles, is *Macrophthalmus*. Three species are present in the area, of which *M. depressus* is the only true mangrove species. *Macrophthalmus depressus* and *M. boscii* occur on a variety of intertidal flats around the mangrove area. Since these habitats were also present upstream of the sampling site, the samples probably contain zoeal larvae of the three species. Densities of newly-hatched stages reflect again the semilunar period, as expected in view of the results obtained for the rhythmicity of *M. grandidieri* in the laboratory (Gove and Paula, 2000). The high density during day and night situations suggested that this taxon did not show any relation to the diel cycle. However, the statistical analysis showed a significant effect of time of day on the abundance of the genus, probably because of the magnitude of the difference measured during 13/14 February between night and day samples. An interesting feature of the temporal distribution of *Macrophthalmus* spp. larvae is evident when compared with Sesarmids, as larval release is not restricted to the night period, following results obtained in the laboratory for *M. grandidieri* (Gove and Paula, 2000). *Macrophthalmus grandidieri* released its larvae independently of diel cycle, probably because the larvae of this species are small, and thus difficult to detect by the predators, and according to Christy (Christy, 1986) species with inconspicuous larvae may hatch during day time.

*Uca* spp. zoeae showed similar magnitude between day and night ebbing tides. This may reflect heterogeneous strategies among the several species of *Uca* that inhabit East African mangroves. Most will release their larvae semilunarly, but in *U. vocans* that pattern was not so evident probably because this species inhabits the lower flats adjacent to the mangrove (Gove and Paula, 2000) and may not need to wait for high amplitude tides to safely release its

larvae. *Uca vocans* larvae also hatched both during the day and at night. This pattern could be an indication that their larvae do not suffer very much from visual predation, due to their small size (MacDiarmid, 1985; Gove and Paula, 2000) or pigmentation. The colour of this species is coincident with the spectral radiation of the coastal waters, which make the larvae difficult to be detected by visual predators (Gove and Mambonhe, 2000). *Uca annulipes*, *U. chlorophthalmus* and *U. urvillei* zoeae hatched at night, presumably to minimize visual predation of both releasing females and newly-hatched zoeae (Bergin, 1981; Forward, 1987). This is consistent with their pale pigmentation which contrasts greatly with the green–yellow spectral radiation of the coastal waters (Gove and Mambonhe, 2000), making them an easy target for visual predators (Christy, 1986).

*Dotilla fenestrata* zoeae were absent during neap tides, while Pinnotheridae zoeae were clearly more abundant during these periods. Both *Dotilla* and the Pinnotheridae are not mangrove species, inhabiting sandy and muddy flats around the west coast of Inhaca Island. Species living in lower intertidal and shallow subtidal areas often hatch their larvae during low amplitude tides, because populations are inundated every high tide (Pereira *et al.*, 2000).

Megalopae of all taxa were mostly restricted to the night period. This is the common pattern found in estuarine and mangrove systems [e.g. (Little and Epifanio, 1991; Olmi, 1994; Christy and Morgan, 1998; Paula *et al.*, 2001)] and results from inhibition of swimming during the day by chemical substances present in estuarine water, which result from the decomposition of organic matter (Forward and Rittschof, 1994; Forward *et al.*, 1997). Once in estuaries, megalopae of several species also undertake vertical migrations related to the tidal rhythm, enhancing their transport up the estuary and maintaining them inside the estuarine boundaries (Little and Epifanio, 1991; Olmi, 1994; Christy and Morgan, 1998; Queiroga, 1998; Paula *et al.*, 2001). This selective tidal stream transport mechanism (Forward and Tankersley, 2001) is accomplished by swimming from the bottom to the water column induced by reactions to the increase in hydrostatic pressure and salinity during the rising tide (De Vries *et al.*, 1993; Tankersley *et al.*, 1995). The higher densities of megalopae recorded in the present study during spring tides are consistent with behavioural reactions triggered by higher rates of pressure and salinity during large amplitude tides. However, the picture obtained in the present study is more complex, because megalopae were collected in significant numbers also during ebb tides, suggesting that megalopae were being transported in both directions in and out of the mangrove, without significant settlement. The megalopal stage has two different phases. In the non-competent phase

habits are mainly planktonic and the larva has not yet reached a physiological capacity for progressing to the juvenile moult. In the competent phase larvae will have to recognize cues for active selective transport to appropriate settlement areas, settle and metamorphose (Epifanio *et al.*, 1988). The densities of megalopae recorded in the present study may thus reflect pumping during flooding tides of a pool of nearshore megalopae in different physiological stages [e.g. (Little and Epifanio, 1991; Queiroga *et al.*, 1994; Queiroga, 1998)], from which some individuals will settle during the ebbing tides. The residual, which may form a significant fraction of the collected megalopae, could be the non-competent population that do not display settlement behaviour in spite of having developed selective transport mechanisms to the mangrove vicinity. Forward *et al.* (Forward *et al.*, 2003) found that megalopae with no response to cues from settlement substrates were in postmoult or intermoult conditions, while competent megalopae were in later stages (pre-moult). Pinnotheridae megalopae were the most abundant forms, and showed maxima both during ebb and flood periods in all sampling cycles. Grapsidae sp. 2 and Sesarmidae megalopae were rarer and also showed peaks during both phases of the tide. Further analysis of the trends would need discrimination between different species, which is not possible at present.

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