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# Stratified settlement and moulting competency of brachyuran megalopae in Ponta Rasa mangrove swamp, Inhaca Island (Mozambique)

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**Abstract**

Information on recruitment processes of mangrove crustaceans is very limited, in spite of the great importance of these environments for the coastal zone. This study describes the settlement patterns of brachyuran crabs at Ponta Rasa mangrove swamp, Inhaca Island, in order to assess if settlement patterns reflect adult distribution. Hoghair filter collectors were deployed at different strata within the mangrove, and at the adjacent intertidal flat as control. Sampling was conducted daily for a period of 82 days. The collected megalopae were reared in the laboratory to assess their moulting competency and to enable identification. Settlement intensity was tested for association with wind stress, from different directions and averaged over time lags up to 6 days. A total of 960 megalopae settled during this study. Only 8% of the megalopae that settled at the control site belonged to mangrove dwelling species. Settlers inside Ponta Rasa swamp were exclusively mangrove species. *Ilyograpsus paludicola* settled mainly among *Rhizophora mucronata* and the mixed area of *Ceriops tagal* and *Bruguiera gymnorrhiza*, where adults occur, and *Perisesarma guttatum*, the most abundant sesarmid at Ponta Rasa, settled mainly at the creek. *Neosarmatium meinerti* settled among *Avicennia marina* pneumatophores, very close to the adult populations. Megalopae of mangrove *taxa* that settled outside the mangrove took longer to moult than the ones settling inside the swamp. In the intertidal areas of the mangrove, settlers took in average 1–2 days to moult, whereas in subtidal areas time to moult was in average 3–5 days. Thus, both distribution of settlers and moulting competency suggest that settling follows adult distribution. Tides have a strong influence on settlement at Ponta Rasa, with the effect that, due to the high sill at the entrance, neap tides do not penetrate the mangrove. The analysis of settlement data suggested a significant effect of wind-driven transport on onshore migration. There is however no obvious interpretation for the pattern observed. Probably, the distribution of different larval patches and the complex dynamic structure of currents within Maputo Bay and adjacent areas influence the settlement pattern.

*Keywords:* Settlement; Moulting competency; Mangrove; Brachyuran crabs; Megalopae; Inhaca Island

## 1. Introduction

Recruitment to the adult population involves larval transport to a suitable substrate, settlement, as the transition from a planktonic to a benthic existence, and survival after achieving the juvenile stage (Keough & Downes, 1982). Apart from exceptional cases in which density-dependent mortality due to predation largely determines recruitment success (Eggleston & Armstrong, 1995; Fernandez, Iribarne, & Armstrong, 1993; Lovrich & Sainte Marie, 1997), larval supply is often a factor restraining population density in a variety of marine invertebrates (e.g. Johnson, Bostford, Methot, & Wainwright, 1986; Roughgarden, Gaines, & Possingham, 1988; Wahle & Incze, 1997; Yoshioka, 1982). For crabs that inhabit coastal habitats such as mangroves and estuaries, it might be advantageous for larvae to have mechanisms of retention within the parental habitat, in order to avoid larval loss by advection to offshore areas and facing the problem of

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migrating back to a suitable adult habitat (Johnson, 1985). A number of brachyuran larvae exhibit behavioural mechanisms that favour their retention within the estuarine environment (Cronin & Forward, 1986; Lambert & Epifanio, 1982; McConaugha, 1988), but evidence has been provided for extensive offshore emigration during larval development in other species (e.g. Jamieson & Philips, 1988; Queiroga, 1996; Queiroga, Costlow, & Moreira, 1994; Abelló & Guerao, 1999). Although commonly considered a major event affecting benthic populations, the information obtained on the settlement process of estuarine invertebrates is still very unbalanced, much less documented in tropical than in temperate areas.

Environmental conditions affect larval development duration and mortality, which may hide the effect of seasonal breeding and shorter-term hatching cycles on the temporal variation of megalopal supply (Moloney, Botsford, & Largier, 1994). In addition, temporal settlement patterns are also dependent on both cross-shelf and estuarine transport (Shanks, 1998). This author has proposed tidally-driven mechanisms along with wind-driven surface flows, as transport mechanisms explored by intertidal species such as *Uca* spp. and *Callinectes sapidus*, and near bottom currents related to upwelling events by subtidal species such as *Libinia* spp. Zeng and Naylor (1996) also found tidal swimming rhythms that would ensure the use of tidal currents for onshore migration by *Carcinus maenas* megalopae. Once in estuaries, megalopae of several species also undertake vertical migrations related to the tidal rhythm, which prevent them from being flushed back to the sea and enhance their up-estuary transport (Christy & Morgan, 1998; Little & Epifanio, 1991; Olmi, 1994). These vertical migrations may be triggered by environmental cues of chemical (Forward & Rittschof, 1994) or physical nature, such as pressure, current speed, salinity and light (De Vries, Tankersley, Forward, Kirby-Smith, & Luettich, 1994; Forward & Rittschof, 1994; Tankersley, McKelvey, & Forward, 1995). As a result, settlement of brachyuran megalopae may be highly episodic, often associated with tidal range, wind direction, diel cycles and variations in salinity or temperature (Jones & Epifanio, 1995; Little & Epifanio, 1991; Mense, Posey, West, & Kincheloe, 1995; van Montfrans et al., 1995; Perry, Eleuterius, Trigg, & Warren, 1995; Rabalais et al., 1995; Wrona, Wiegert, & Bishop, 1995).

It is not clear at what stage megalopae achieve settling competency. There is evidence that timing of the juvenile moult is largely controlled by environmental cues. In *Uca pugilator*, moulting to the juvenile stage may be considerably delayed in the absence of adequate stimuli, namely the availability of sediment from the parental habitat (Christy, 1989) or the presence of adults (O'Connor, 1991). Similar results were obtained for porcelain crabs, which settle preferentially in the presence of conspecifics (Jensen, 1989). Moulting to the juvenile stage in *Callinectes sapidus* megalopae is induced by exposure to estuarine water or contact to the seagrass *Zostera marina*, rather than by the presence of adult crabs (Forward, Frankel, & Rittschof, 1994). Depending on the nature of cues inducing the metamorphic moult, competency may be attained at quite different distances from settlement grounds. Thigmotactic response is usually recognised as a property of competent larvae (Goodrich, van Montfrans, & Orth, 1989). Rearing collected megalopae until moulting may be used alternatively as a tool to assess competency.

Brachyuran crabs are dominant in most mangrove habitats (Jones, 1984; Lee, 1998; Smith, 1991), thus adequate for modelling settlement in these systems. Surprisingly, information on megalopal settlement patterns in this ecosystem is very limited. Dittel and Epifanio (1990) and Dittel, Epifanio, and Lizano (1991) have studied the seasonal and tidal abundance of larvae in a mangrove tidal creek, Paula, Dray, and Queiroga (2001) evaluated the role of offshore and inshore processes in determining temporal settlement patterns in a tidal embayment, Moser and Macintosh (2001) have addressed the diel and fortnightly cycles of brachyuran settlement in a mangrove estuary and Wehrtmann and Dittel (1990) reported clinging to drifting leaves as a particular transport mechanism. The mangrove ecosystem often presents a clear habitat stratification, with mangrove assemblages usually distributed according to their tolerance to flooding among other factors. Many crabs are strongly dependent on propagules and leaf litter for feeding (Cannicci, Fratini, & Vannini, 1999; Dahdou-Guebas, Verneirt, Tack, Speybroeck, & Koedam, 1998; Fratini, Cannicci, Abincha, & Vannini, 2000) and sediment texture for burrowing (Lee, 1998). These factors are probably involved in the clear vertical zonation of crab species across mangrove forests (Hartnoll, 1975). How are such zonation patterns established across the mangrove area is still far from understood.

In this study, daily estimates of megalopal settlement were obtained over 82 days in different mangrove zones, from an adjacent tidal platform through the mangrove strata up to the higher *Avicennia marina* belt. The role of tidal amplitude and wind stress on the temporal settlement pattern of most important taxa was examined and the zonation of settlers assessed. Moulting competency of sampled megalopae, measured as time to the juvenile moult, was analysed.

## 2. Study site

This study took place at Ponta Rasa mangrove, Inhaca Island (26°S, 33°E). Inhaca is a 12.5-km long, 7-km wide island, 32 km off Maputo, Mozambique. The east coast is exposed to the Indian Ocean, whereas the western and southern coasts face Maputo Bay. In spite of the island's subtropical location, the warm Mozambique current to which it is exposed, and the shallow waters of Maputo Bay, induce the tropical character of the island (Kalk, 1995). Inhaca is composed of several habitats including forest and bushland, agricultural areas, rocky shores, sandy beaches, coral reefs, freshwater swamps and mangroves (Kalk, 1995).

Ponta Rasa is the smallest mangrove at Inhaca (Fig. 1), occupying an area of approximately 0.2 km$^2$, and is composed of four clearly different areas in terms of both fauna and flora, according to a zonation pattern caused by different tidal flooding (Guerreiro, Freitas, Pereira, Paula, & Macia, 1996). The lower area (Creek site) is a 500-m-long, 3-m-wide, and 1-m-deep creek at low tide, which drains into a sandy tidal flat (Hoguane, Hill, Simpson, & Bowers, 1999). A sill prevents both total drainage of the creek, though the creek is 0.6 m above sea level, and tidal flooding of the mangrove on the 3 days around neap tides (Hoguane et al., 1999). Bordering the creek (*Rhizophora* site) there is an area densely covered by *Rhizophora mucronata*. From this site landwards the mangrove is drained out of water during low tide, apart from some small pools. Higher in the mangrove (Mixed site) the vegetation is sparser, mainly composed of *Ceriops tagal* and *Bruguiera gymnorrhiza*. The uppermost zone is a sandier area dominated by the tree *Avicennia marina* (*Avicennia* site). This mangrove has no freshwater supply apart from diffused groundwater flow and rainfall. Tides are semidiurnal ranging 2 m at spring tides at the entrance of the creek, but only 0.8 m further inside the mangrove.

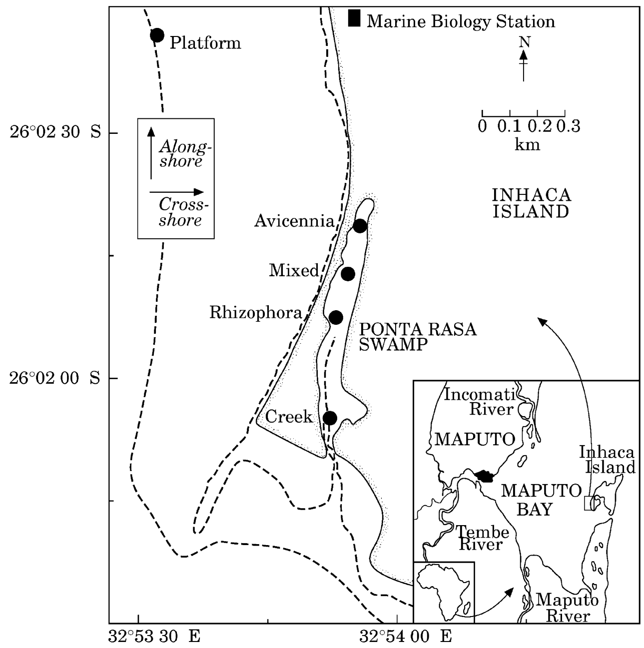

Fig. 1. Map of Ponta Rasa swamp, Inhaca Island, showing the position of sampling sites.

## 3. Materials and methods

### 3.1. Field sampling

Daily samples were taken for a period of 82 days, between 6 November 1999 and 25 January 2000. Four sites were selected for sampling, to represent habitat variability at Ponta Rasa (Kalk, 1995) (Fig. 1). Study sites are referred hereafter as Creek, *Rhizophora*, mixed and *Avicennia*. Control sampling took place at the tidal platform facing the Marine Biological Station (Platform site), where interspersed patches of coral debris and *Thalassodendrum ciliatum* are found over the sand flat. Groups of two replicate passive artificial collectors, as used by van Montfrans, Peery, & Orth (1990), were used at each site. Hoghair filter pieces of 1.5 cm × 40 cm × 40 cm were used as settling surfaces. At the Creek and Platform sites these surfaces coated a 40 cm long, 11 cm diameter PVC pipe and were suspended vertically, 1.5 m apart, from a long stick attached to a fixed location. The collectors were maintained at sub-surface by a buoy each. At the *Rhizophora*, mixed and *Avicennia* sites, the collectors were modified, because these areas are intertidal and only flooded during spring high tides. In order to assure a similar 'useful' settlement area and maintain humidity similar to the natural settlement habitat, the collector surface was deployed flat on the substrate, with the corners attached to roots and the edges covered with sediment. Settlement in artificial substrates of cylindrical and flat shape does not differ significantly, provided the settlement areas are equivalent (Metcalf, van Montfrans, Lipcius, & Orth, 1995).

The collector surfaces were changed daily at low tide, which has a daily delay of around 50 min. The surfaces were stored in plastic bags and immediately transported to the laboratory. Another control experiment was performed between 15 December and 14 January to test for the effect of the timing of surface change on temporal variability of settlement. In this experiment, a pair of collectors was placed at the Platform site and changed daily at 15.00 h, irrespective of tidal condition. Measurements of temperature and salinity were taken daily with a conductivity probe at all sites where water was present.

### 3.2. Laboratory procedures

Megalopae were removed from the collector surfaces in the laboratory. Each surface was first rinsed and then immersed in abundant fresh water to remove the megalopae (van Montfrans et al., 1990). This water was then sieved, and placed in trays where megalopae were sorted out with a magnifying lens.

A maximum of nine megalopae per site per day and *taxon* were reared until the juvenile moult, to compare moulting competency of megalopae (determined as the time to moult) at the different sampling sites. Obtaining first crab stages also provided information for identification of settlers. Larvae were cultured in daily changed sea water taken from the platform outside the Marine Biological Station. Megalopae were kept in individual trays and fed with recently hatched *Artemia* sp. nauplii. Cultures were checked for moults twice a day (morning and night), and exuviae were preserved in 1:1 glycerin and 70% ethanol. Excess megalopae were preserved in 70% ethanol.

Cultured megalopal exuviae, first crab, and dead megalopae were primarily sorted into different morphotypes under a dissecting microscope and identification to species or family was performed whenever possible. Identification was based both on juvenile (Barnard, 1950; Crosnier, 1965) and larval characters (Krishnan & Kannupandi, 1990; Pereyra Lago, 1987, 1989, 1993; Chen, pers. comm.). The scarcity of descriptions of these two life stages of brachyurans from the Indo-Pacific region, rendered complete identification impossible in some cases. Still, even when morphotypes could not be identified, these were treated as a separate group in data analysis.

### 3.3. Data analysis

Data from the mixed and *Avicennia* sites were not used in the tests for significance in differences on salinity and temperature, because only data for the highest of high tides were available. Temperature and salinity from the *Rhizophora*, Creek and Platform sites were tested for homoscedasticity with Hartley's Fmax test (Sokal & Rolf, 1995). Temperature differences among sites were tested with a one-way ANOVA, followed by a Student Newman-Keuls test (Sokal & Rolf, 1995). Heterogeneous variances in salinity samples prevented parametric tests to be used. A one-way ANOVA by ranks (Zar, 1996) was used in this case.

The daily number of settling megalopae was mean subtracted, detrended, and subjected to spectral analysis (Rayner, 1971). The distribution of periodogram values was tested against the expected exponential distribution with the Bartlett Kolmogorov-Smirnov one sample test (Sokal & Rolf, 1995). This analysis was performed for the total brachyuran community, and for the two most abundant forms separately.

Daily tidal ranges were estimated as the average difference between high and low tides predicted by tide charts for the Maputo harbour (Instituto Hidrográfico de Portugal, 1999), as these data are not available for Inhaca Island. These are consistent predictions according to Hoguane et al. (1999). Three daily records (at 9.00, 15.00 and 21.00) of wind direction (in °) and velocity (km $\mathrm{h}^{-1}$) were obtained from the meteorological station of Maputo. Wind stress ($\tau_d$) (Pa) was calculated for directions ($d$) 0° (along-shore), 90° (cross-shore), for every measure, as:

$$\tau_d = \rho_a C|(\vec{v})|v_d$$

where $\rho_a$ is the air density (1.12 kg $\mathrm{m}^{-3}$), $C$ is the stress coefficient (0.0012), \vert(\vec \nu)\vert is the wind velocity and $v_d$ the wind velocity for direction $d$ (Silva, 1992). Daily average wind stress was calculated for each direction as the average of the three daily measures. Averages of the previous 0–6 days (lags 0–6) were calculated to account for cumulative effects of the wind transport. The variables tidal range, wind stress and settlement were graphically analysed, and data was then linearly grouped. Tidal range was classified into spring (>2.7), neap (<1.5) and intermediate tides. Wind stress was classified into strong ($|\tau_d| > 0.02$) and weak ($|\tau_d| < 0.02$), positive and negative. Settlement was classified as null ($=0$), low (<5), high (<30) and very high (>30). Frequencies were then calculated for these categories and three way contingency tables (with settlement, tidal range and wind stress as variables) were elaborated for each windstress averaged over lags of 0–6 days, for along-shore and cross-shore. These variables were tested for association with a log-likelihood ratio test (*G*-test) (Sokal & Rolf, 1995). Null hypothesis of independence for two and three factor interactions were tested at the 95% significance level. The influence of wind stress and tidal range was only tested at the Platform and Creek sites, because at the other sites, settlement is only possible when the tidal range is at maximum. At the Creek site, only intermediate and spring tide days were used in the analysis since there is no flooding during neap tide days. When significant, or almost significant interactions were found the test was decomposed to identify contrasting factor levels.

The moulting competency of larvae collected at the different sites was measured as the time they took to moult after being collected. Since different forms were caught at different sites, specific constraints might bias a general analysis. The competency of settlers at the sites was, therefore, compared using the two most abundant *taxa* in this study separately. Heteroscedasticity was found using Hartley's Fmax test for both species, and no transformations were found appropriate. Significance of differences was tested with a one-way ANOVA by ranks, followed by a Dunn test for multiple comparisons of mean ranks for unequal sample sizes with tied ranks (Zar, 1996). The daily pattern of moults (night time vs. daytime) was compared with a *G*-test.

## 4. Results

### 4.1. Temperature and salinity

There was water in all sampling days at the Platform and Creek sites, but only on 90% of the days at the *Rhizophora*, 54% at the Mixed and 28% at the *Avicennia* sites. The Platform and Creek sites showed similar ranges of temperature, though the average temperature was lower at the Creek than at the Platform site [Fig. 2(a)]. Both the range and average temperatures increased from the *Rhizophora*, to the Mixed and the *Avicennia* sites, though the number of sampled days decreased in this order. The differences between the *Rhizophora*, Creek and Platform sites were significant ($F = 27.4$; $P < 0.001$). These differences were significant between the Creek and the Platform sites ($P < 0.001$), the Creek and the *Rhizophora* sites ($P < 0.001$), but not between the *Rhizophora* and the Platform sites ($P = 0.07$).

Salinity range at the Platform site was much lower than at the mangrove sampling sites, but average salinity was similar at this site and the Creek [Fig. 2(b)]. The other sampling sites had lower average salinities. The range of salinity was maximum at the *Avicennia*, followed by the *Rhizophora*, then the Mixed, and finally the Creek site, though the number of sampled days increased in this order. The differences among *Rhizophora*, Creek, and Platform sites were non-significant ($H = 1.6$; $P = 0.459$).

### 4.2. Megalopal settlement

*Spatial distribution of settling taxa.* During this study, a total of 960 megalopae were collected. Of these, 672 settled at the mangrove Creek (Fig. 3). Among these 64% were *Perisesarma guttatum*. *Ilyograpsus paludicola* comprised 15% and the rest of the forms consisted of unidentified damaged megalopae (16%), and a group of species (5%) consisting of *Dotilla fenestrata*, Portunidae sp.1, Grapsidae sp.1 and sp.2, *Scylla serrata*, *Metopograpsus* sp., and Xanthidae sp.1 and sp.2. At the *Rhizophora* site, 63 megalopae settled, 48% were *Ilyograpsus paludicola*, 24% were *Perisesarma guttatum*, and 28% belonged either to other forms (Portunidae sp.1, Xanthidae sp.1, Grapsidae sp.3 and sp.1) or were unidentifiable. At the Mixed site, of the 73 megalopae collected, 45% were *Ilyograpsus paludicola*, 21% were *Perisesarma guttatum* and 34% belonged to other species (Grapsidae sp.1, Grapsidae sp.3 and sp.1) or were unidentifiable. At the *Avicennia* site, only 13 megalopae were collected, 7 belonging to *Perisesarma guttatum*, 3 to *Neosarmatium meinerti* and 3 were unidentifiable. At the Platform site, 139 megalopae settled, only 5% belonged to *Ilyograpsus paludicola* and 3% to *Perisesarma guttatum* (the most abundant *taxon* at the mangrove sites), and the rest 92% were distributed by Xanthidae

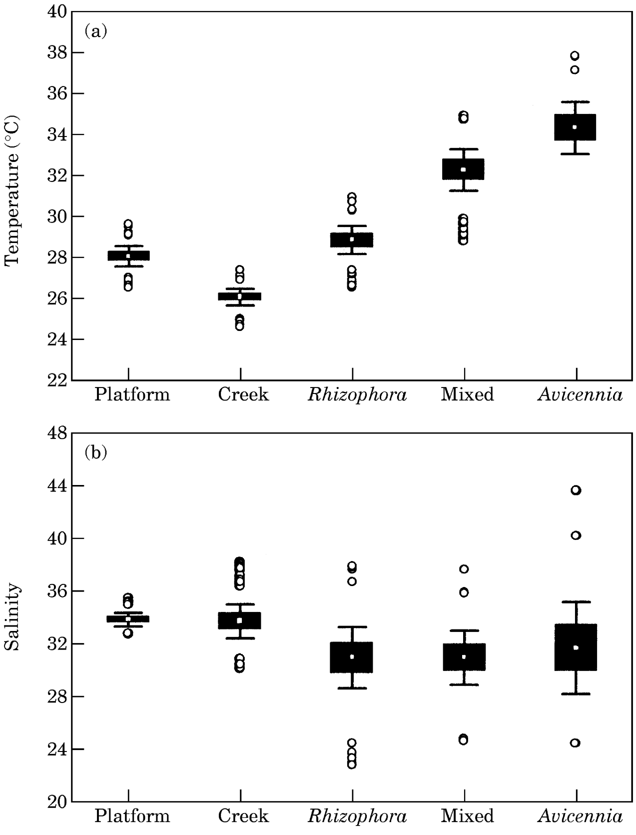

Fig. 2. Box plots of (a) temperature (°C) and (b) salinity at the Platform, Creek, *Rhizophora*, Mixed and *Avicennia* sites. Average, standard error, 95% confidence interval and outliers are indicated.

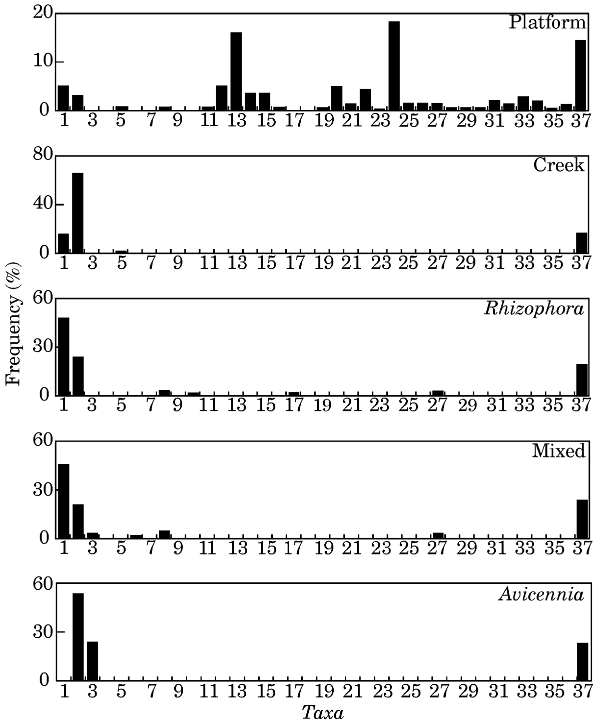

Fig. 3. *Taxa* composition of megalopae settling at the Platform, Creek, *Rhizophora*, mixed and *Avicennia* sites. 1. *Ilyograpsus Paludicola*; 2. *Perisesarma guttatum*; 3. *Neosarmatium meinerti*; 4. *Dotilla fenestrata*; 5. *Metopograpsus* sp.; 6. Grapsidae sp.1; 7. Grapsidae sp.2; 8. Grapsidae sp.3; 9. *Scylla serrata*; 10. Portunidae sp.1; 11. Portunidae sp.2; 12. Portunidae sp.3; 13. Portunidae sp.4; 14. Portunidae sp.5; 15. Portunidae sp.6; 16. Portunidae sp.7; 17. Xanthidae sp.1; 18. Xanthidae sp.2; 19. Xanthidae sp.3; 20. Xanthidae sp.4; 21. Xanthidae sp.5; 22. Xanthidae sp.6; 23. Xanthidae sp.7; 24. Majidae sp.1; 25. Majidae sp.2; 26. Majidae sp.3; 27. sp.1; 28. sp.2; 29. sp.3; 30. sp.4; 31. sp.5; 32. sp.6; 33. sp.7; 34. sp.8; 35. sp.9; 36. sp.10; 37. not identified.

forms 3 to 4, Portunidae forms 2 to 7, Majidae forms 1 to 3, and 9 other forms, all absent from the mangrove sites. *Metopograpsus* sp., Grapsidae sp.1 and sp.3 and unidentifiable megalopae also settled in low numbers on these collectors. The most abundant forms here were Portunidae sp.1 and Majidae sp.1.

### *4.3. Temporal pattern*

The temporal pattern of settlement at the Platform site was continuous (Fig. 4) with a significant period of 8 days. Settlement was significantly associated to the along-shore wind stress with no time lag ($P = 0.0275$). The effect of north and south winds was shown to be significantly different ($P < 0.01$), with a higher settlement rate associated to south winds.

At the mangrove sites, settlement occurred in discrete peaks with significant periods of 16 to 20 days. At the Creek site, the first three spring tides had the greatest peaks, increasing in intensity, and no significant settlement took place in the second half of the experiment. The highest periodogram value corresponded to a 20 day period. Here, settlement was significantly associated with cross-shore wind stress ($P < 0.05$), with a lag of 3–5 days ($P = 0.0335, 0.0135, 0.0441$, respectively). Eastern winds were extremely rare, and strong western winds were shown to enhance settlement ($P < 0.01$ for lag 3, $P < 0.01$ for lag 4 and $P < 0.01$ for lag 5). At the *Rhizophora* site, settlement occurred in six discrete peaks, lower and narrower than at the Creek, usually starting 1 or 2 days after the peak at the Creek. There was a significant period of 16 days. At the Mixed site, the

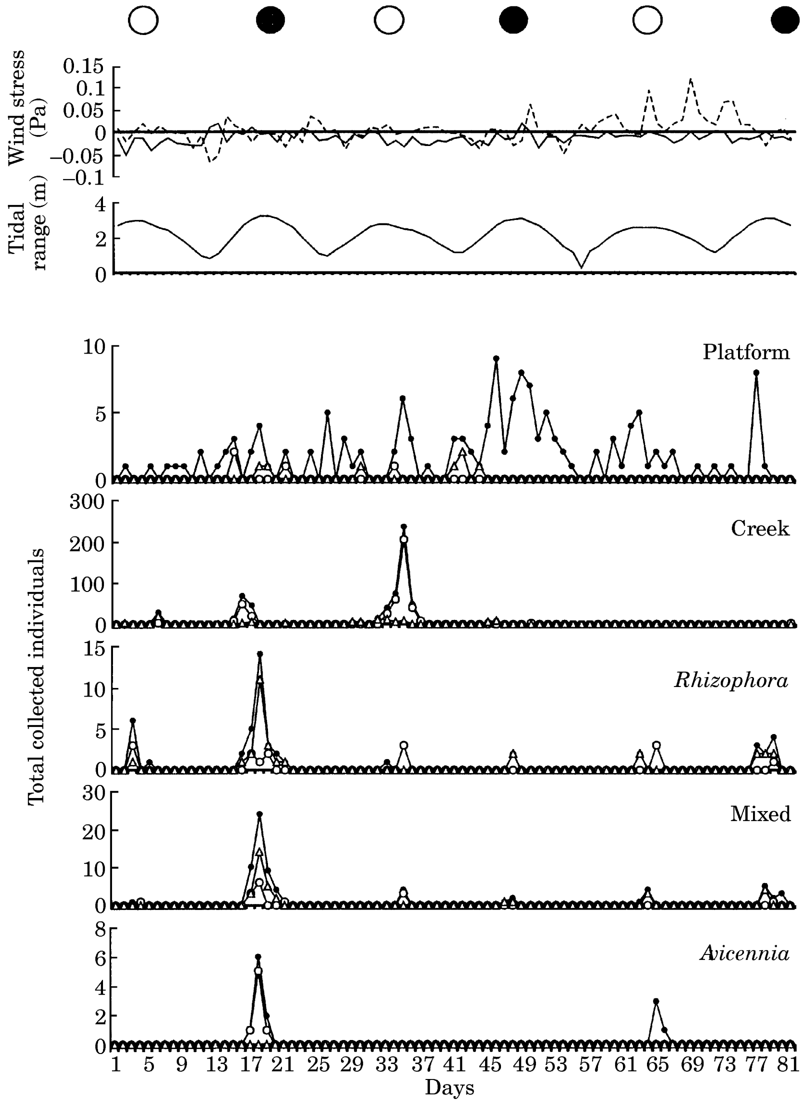

Fig. 4. Daily variation of wind stress components along-shore (u) and cross-shore (v); average tidal range; total number of megalopae, total number of *Ilyograpsus paludicola* and total number of *Perisesarma guttatum* megalopae settling at the Platform, Creek, *Rhizophora*, Mixed and *Avicennia* sites. Shaded bars indicate intervals without tidal flooding. ●, Total megalopae; ○, *P. guttatum*; △, *I. paludicola*.

pattern was similar to *Rhizophora*, with a significant period of 16 days. The peaks were also narrower than the ones at the Creek and *Rhizophora*. At the *Avicennia* site only two 'one-day' peaks were observed, and the periodogram highest value was obtained for the 16 day period.

The data from the control experiment comparing the collectors removed at low tide with the collectors removed at a constant time (Fig. 5) showed that both time-series are correlated ($P < 0.01$).

### 4.4. *Ilyograpsus paludicola*

Settlement of *Ilyograpsus paludicola* occurred during discrete peaks of *c*. 4 days and no settlement occurred between these maxima. This species was only present at the Creek during five peaks (Fig. 4), with a significant period of 13.3 days. Settlement was not significantly associated with wind stress ($P > 0.05$), but for lags 2–4, $P$-values were close to significance ($P = 0.0752, 0.0506, 0.0773$, respectively). Decomposition into two-way tables showed that strong western winds significantly enhance settlement of this species ($P < 0.01$). *I. paludicola* settled in five peaks at the *Rhizophora* site, with a significant period of 20 days. At the Mixed site, four settlement events were recorded with a significant period of 26.7 days. The few megalopae that settled at the Platform were also recorded during three discrete peaks with a significant period of 11 days.

### 4.5. *Perisesarma guttatum*

At the Creek, *Perisesarma guttatum* was present only during three periods, but this species was responsible for the highest peaks including one on December 10th, that reached a maximum of 192 megalopae on one single collector (Fig. 4). The highest periodogram value corresponded to a 20-day period. Settlement was not found to be significantly associated to any factor tested. However decomposition of the almost significant 2–4 days lags of cross-shore wind stress ($P = 0.0956, 0.1004, 0.0670$, respectively), showed that the high settlement events of *Perisesarma guttatum* were significantly associated with the extremely rare East winds.

At the *Rhizophora* collectors, settlement of this species occurred during five peaks without a significant periodogram peak. At the Mixed site, the five settlement events had a significant period of 20 days (Fig. 4). At the *Avicennia* site, this species settled on only one occasion. At the Platform, *Perisesarma guttatum* settled during three distinct peaks without a significant period.

### 4.6. *Moulting competency*

At the Platform, mangrove *taxa* took longer to moult than those that were exclusively found at the Platform (Fig. 6). A total of 134 *Ilyograpsus paludicola* megalopae were reared (5 from the Platform, 76 from the Creek, 29 from the *Rhizophora*, and 24 from the Mixed site). The average time to moult was 1 day at the Mixed site, 1.3 days at the *Rhizophora* site, 3.5 days at the Creek and 11.3 days at the Platform. The frequency distribution of the time to moult was bimodal at the Creek. Ninety-one percent of the megalopae took between 1 and 5 days to moult, but 9% took between 8 and 18 (Fig. 7). Only seven megalopae were distributed in the second modal peak. These cases were not used for comparison with the other sites because they may be related to different phenomena. The differences between sites were found to be highly significant ($H = 53.6$; $P < 0.001$), in all pairwise comparisons.

A total of 104 *Perisesarma guttatum* megalopae were reared (69 from the Creek, 13 from the *Rhizophora*, 15 from the Mixed and 6 from the *Avicennia* site). The average time to moult was of 3.5 days at the *Avicennia* site, 2.3 days at the Mixed site, 1.9 days at the

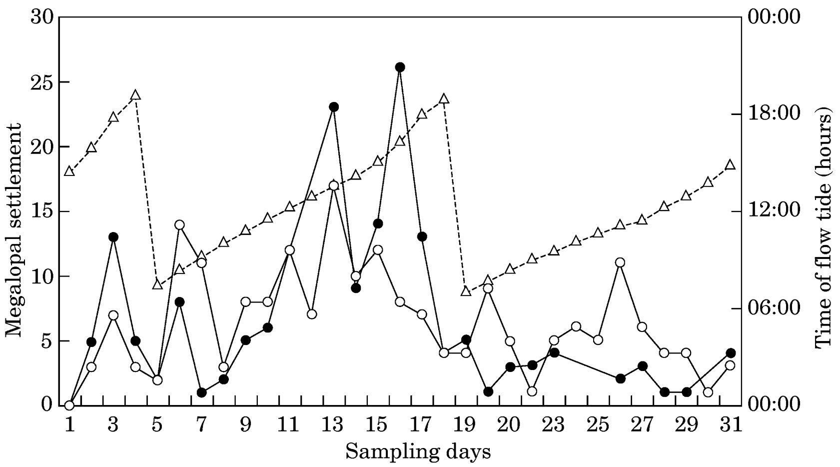

Fig. 5. Total number of megalopae settling at the Platform site, on collectors changed at 15.00 and at low tide. ●, 15.00 sampling; ○, low tide sampling; △, time of low tide.

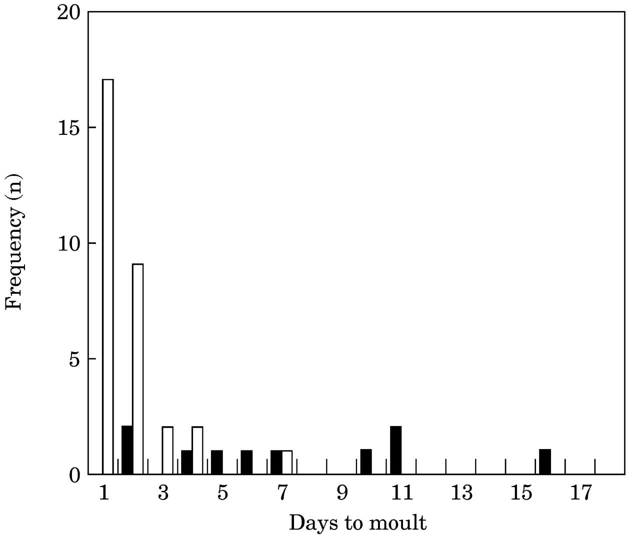

Fig. 6. Frequency distribution of days to moult of megalopae of mangrove and Platform *taxa* settling at the Platform. ■, Mangrove settlers; □, platform settlers.

*Rhizophora* site and 5.4 days at the Creek (Fig. 7). Only one megalopa of this species settled at the Platform, so this site was not used for comparisons. A trend similar to what was found for *Ilyograpsus paludicola* was observed for the distribution of frequencies of time to moult at the Creek. A similar procedure was thus followed. The differences between sites were also significant ($H = 19.5$; $P < 0.01$), but only between the Creek and *Rhizophora* ($Q = 3.098$; $P < 0.05$) and mixed sites ($Q = 2.563$; $P < 0.05$). Differences between diurnal and nocturnal moulting were also highly significant both for *Ilyograpsus paludicola* ($G$ test = 23.0; $P < 0.0001$) and *Perisesarma guttatum* ($G$ test = 83.7; $P < 0.0001$).

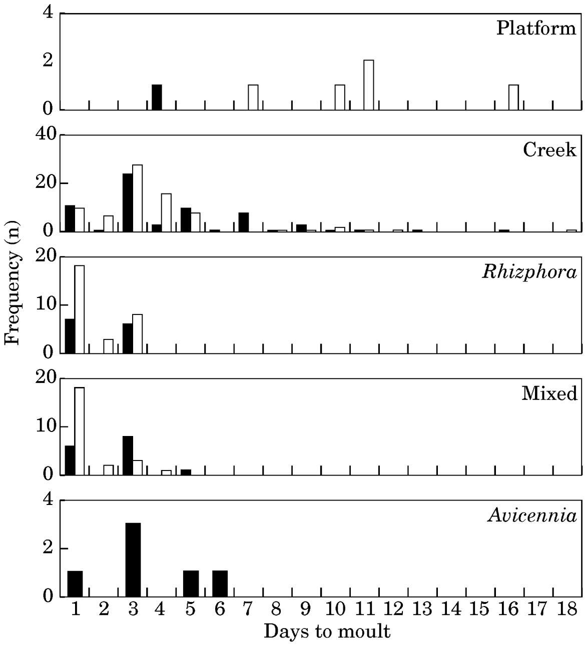

Fig. 7. Frequency distribution of days to moult of *Ilyograpsus paludicola* and *Perisesarma guttatum* megalopae settling at the Platform, Creek, *Rhizophora*, Mixed and *Avicennia* sites. ■, *P. guttatum*; □, *I. paludicola*.

## 5. Discussion

Mangroves have characteristic vertical zonation patterns defined by dominant vegetation. This vegetation distribution is a consequence of the physico-chemical gradient that arises from different exposure to tidal flooding (Roy, 1989). The abiotic parameters measured in this study reveal contrasting environmental conditions among the sampled strata. Adult brachyuran populations also follow the vertical zonation of the mangroves (Hartnoll, 1975). This study suggests that such a pattern of distribution may already be present in settlement.

The Sesarmidae is one of the most abundant crab families in the southern East African mangroves. *Neosarmatium smithi* is usually found in the *Rhizophora* and Mixed areas. *Neosarmatium meinerti* inhabits the *Avicennia* zone and sand flats of the upper mangrove. *Perisesarma guttatum* is distributed from the *Rhizophora* to the *Avicennia* zones. *Sesarma leptosoma* is found at the *Rhizophora* zone. *Sesarma eulimene* and *Sesarma orthmanni* are found at the *Avicennia* zone and sand flats of the upper mangrove (Hartnoll, 1975). Additionally, studies on the breeding cycles of *Neosarmatium meinerti*, *Sesarma eulimene*, *Sesarma catenata* in a Transkei mangrove (South Africa) (Emmerson, 1994) and *Perisesarma guttatum* at Saco mangrove (Inhaca Island) (Gove & Mambonhe, 2000) have shown that these species were releasing larvae since before and through the experimental period of our study. Flores, Saraiva, & Paula (in press) have additionally found early juvenile size classes to be present at this mangrove during the present study, which further indicates settlement of this species to be occurring.

Ocypodids are represented at Ponta Rasa mangrove by five *Uca* species (*U. annulipes*, *U. inversa*, *U. chlorophthalmus*, *U. urvillei* and *U. hesperiae*), and *Macrophthalmus depressus*. Settling megalopae of these species were not observed in the collectors. It is possible that during the study period (November to January) no ocypodid megalopae were available to settle. The most abundant species, *U. annulipes*, breeds from March to April (Emmerson, 1994). On the other hand, selectivity of hoghair surfaces is not entirely assessed, and it may be that most ocypodids ‘avoid’ such substrates. In fact, most sesarmids live associated with complex structural substrates even when burrowing, such as mangrove and marsh plant roots. Most ocypodids, on the contrary, burrow in open regular sediment areas, structurally very homogeneous, and thus could be adapted to settle in the absence of refuges. The grapsid *Ilyograpsus paludicola*, the second most abundant species settling at the mangrove sites, is apparently not one of Ponta Rasa's most abundant crabs. Adults were however consistently collected in the *Rhizophora* zone throughout the study. Furthermore its small dimension makes it hard to distinguish among the complex substrate structures and sesarmid juveniles, and therefore its abundance may often be underestimated.

Moulting competency is thought to be a good indicator of settlement. Assuming a constant mortality rate, probability of successful recruitment increases with decreasing delay between settlement and the juvenile moult. Further, brachyuran megalopae are known to rely on environmental cues to regulate the moulting time (Christy, 1989; Forward et al., 1994; O'Connor, 1991; O'Connor & Ludge, 1999; Strasser & Felder, 1999). *Uca minax* and *U. pugnax* have different competency timing and different mortality when exposed to salinity typical of each species habitat (Epifanio, Little, & Rowe, 1988). Whether this was used as a mechanism of selection of settlement site, or as a post-settlement regulator of distribution was not clear. O'Connor (1993) found that *Uca pugilator* and *U. pugnax* settled at different intertidal areas, similar to each species adult distribution. Selection of settlement site has also been documented for *Callinectes sapidus* (Morgan, Zimmer-Faust, Heck, & Coen, 1996; Welch, Rittschof, Bullock, & Forward, 1997). Delaying juvenile moult may negatively affect survival and growth of later stages (Gebauer, Paschke, & Anger, 1999).

At the Platform site, mangrove *taxa* were rare, and megalopae were mainly flat and reef species. At the mangrove sites, only mangrove species settled, showing the effectiveness of cues in guiding megalopae to suitable specific habitats. *Ilyograpsus paludicola* settled mainly from the Creek to the Mixed zones, where adults occur, while *Perisesarma guttatum* settlement was mostly confined to the Creek area. Adults and juveniles of this species are in fact most abundant on the creek margins. *Neosarmatium meinerti* settled mainly at the upper *Avicennia* zone, where adults burrow. The few collected *Scylla serrata* megalopae occurred at the Creek site. Moulting competency further corroborates this hypothesis. Mangrove *taxa*, when collected in the non-mangrove habitat, took longer to moult in the laboratory. At the Platform site, the rare settling *Perisesarma guttatum* megalopae took at least 4 days to moult, and *Ilyograpsus paludicola* at least 7 days.

At the Creek site *P. guttatum* and *I. paludicola* only settled during the flooding events, which showed that no megalopae remained in the water column to settle later. Although most megalopae moulted in the laboratory in the first few days from collection, some individuals took longer to moult. As rearing in the laboratory involved no inclusion of settlement cues, as sediment or biotic mangrove stimuli, the reasons for the delay in moulting could not be properly assessed. At the intertidal mangrove sites, moulting was usually faster. In the higher mangrove areas, namely those experiencing the environmental extremes caused by evaporation, desiccation and thermo-haline fluctuations, it is crucial that megalopae moult rapidly, to acquire tolerance mechanisms and juvenile behaviour that minimises stress. Juveniles of *Neosarmatium meinerti*, the main settler at the *Avicennia* site, are known to share the adult burrows where environmental conditions are not as harsh as at the surface (Emmerson, 2001). It could also be that most of the early planktonic megalopae are flushed back with the receding tide, to avoid being trapped in retained pools. Paula et al. (2000) have shown megalopae to be present outside the Saco mangrove (Inhaca Island) in both flood and ebb periods in similar abundance, suggesting continuous advection of megalopae to the area and settlement of the competent fraction only. Goodrich et al. (1989) suggest that sampling using collectors selects competent megalopae within the available larvae present in the water column.

This study suggests that, at least for some species of mangrove brachyurans, the adult zonation pattern is expressed already at the settlement phase. This contradicts the suggestion by Paula et al. (2001), that megalopae preferentially settle low on the mangrove with subsequent juvenile migration to higher levels. That study, carried out at Saco mangrove, had shown higher settlement in the adjacent mud flat than at mangrove strata. However, as precise identification of settling megalopae was not possible at that stage, the majority could belong to species inhabiting the flat, and not to true mangrove forest forms. For tropical systems such as the mangroves and adjacent coastal ecosystems at Inhaca Island, where a high diversity of fauna occurs, it is thus crucial to improve our knowledge on identification of megalopae.

Tides are an important mechanism of transport since they periodically move great masses of water in and out of the coastal habitat. Settlement of megalopae has been shown to be influenced by these periodic variations (Boylan & Wenner, 1993; Mense et al., 1995; Metcalf et al., 1995; van Montfrans et al., 1995; van Montfrans et al., 1990; Rabalais et al., 1995; Wrona et al., 1995). The effect of tides on megalopal settlement is particularly evident at Ponta Rasa mangrove, since spring tides are the only possible route for the incoming megalopae. In spite of this evidence, a great variability between spring tidal periods is apparent, undoubtedly related to larval availability and onshore transport mechanisms.

The present results concerning the relation of settlement intensity to wind stress are of complex interpretation. There is evidence for a significant wind-driven transport on onshore migration, but the complexity of Maputo bay precludes a clear understanding to be drawn. Apart from tidal currents, wind stress also strongly affects coastal currents, and is known to influence settlement of brachyurans (Epifanio, 1995; Goodrich et al., 1989; Johnson, 1995; Olmi, 1995). Wind stress was found to be the most important variable influencing recruitment, both positively and negatively, on the numerical model of simulation of dispersal and recruitment of *Callinectes sapidus* in Chesapeake Bay (Johnson & Hess, 1990). Influence of winds on settlement depends not only on the currents that are generated, but also in the vertical and horizontal distribution of megalopae which are to be transported (Blanton, Wenner, Wenner, & Knott, 1995). Further, different *taxa* may have behavioural traits that explore different transport mechanisms into a suitable settlement area.

The total megalopae settling at the Platform site was related to a south-wind induced stress of the same day. The platform site is directly flooded by the incoming tide from the Indian Ocean, entering Maputo bay (Saide, pers. comm.). To obtain a significant correlation with winds blowing on the settlement day, the responsible larval patches would have to be available very close to the coast. At the Saco mangrove, a similar result a significant effect was observed for the same wind stress direction, however for a lag period of 3 days (Paula et al., 2001). At Saco mangrove, the tide mainly floods directly from the Indian Ocean through the Machangulo inlet (de Boer, Rydberg, & Saide, 2000). Larval availability on the shelf seems to be determinant for the lag period required for onshore transport.

The total settlement at the Creek site showed a different pattern. Cross-shore wind stress significantly enhanced settlement with a lag period from 3 to 5 days. A different mechanism seems to be operating for the *taxa* settling within the mangrove, and probably regard to the complex structure of water masses and larval distribution in Maputo Bay. The larvae settling at the Platform site are diverse and mainly composed of *taxa* that occur in the lower part of the bay, within the flats and reefs. Since those species release larvae closer to the entrance of the bay, the larvae have more chances of dispersing to the shelf waters, and thus onshore transport is mostly dependent on shelf processes. On the contrary, mangroves are widespread along the bay margins and also within the Maputo, Espírito Santo and Incomati estuaries which discharge into the bay. The residence of water masses and patterns of circular and residual currents in the bay are not well known (Saide, pers. comm.). Due to the dimension of the bay, it may be that larval patches can maintain and develop through to megalopae within its boundaries. The residence time for the Maputo bay waters in relation to the ocean is approximately 2 weeks, with a weak clockwise circulation with outflow of lower salinities of river influence (Saide, pers. comm.). According to the author, at the eastern part of the bay, where Inhaca Island is located, the major component of the net flux is the flooding tide, but wind-generated velocities and flux may well exceed the residual fluxes. The bay is very shallow, and mixing processes homogenize the water column; the wind-driven transport vector must be close to the wind direction, if the tidal effect is not considered. Cross-shore western winds should therefore enhance settlement on the eastern part of the bay (where Inhaca is located). This effect could be traced in the settlement pattern of *Ilyograpsus paludicola* with a delay of 2–3 days, by decomposing the log-linear model. However, for *Perisesarma guttatum*, the most abundant species, the picture was not as clear. The wind responsible' for the major settlement peaks was the rare east blowing wind, which can only be interpreted as transport from the shelf through Machangulo inlet or from the bay main entrance, specially if larvae are very high in the water column.

It seems clear that a diversity of larval patches of different origins and dispersal within the bay and adjacent areas, as well as the complex dynamic structure of current patterns, preclude, at this stage, a clear understanding of the transport mechanism related to the wind forcing. Moreover, shelf processes transporting megalopae onshore can break larval aggregations and deliver them irregularly on the coastline (Shanks & Wright, 1987). Further complications also arise from complex near-shore small-scale currents (Aldredge & Hamner, 1980).

The effect of local factors, such as estuarine dimension and complexity, is not fully understood. In some examples, such as *Callinectes sapidus* in the east coast on North America, there seems to be a post-settlement planktonic dispersal by early juvenile instars (Etherington & Eggleston, 2000). These results are from large systems, and megalopae could be 'obliged' to settle when the physiological limit is reached for moulting. In other areas, where megalopae can reach more easily suitable habitats, this process could then be skipped. Scale factor thus remains to be properly assessed. In the present study, spatial settlement pattern seems to follow the adult distribution, however Ponta Rasa is a small mangrove area and is reached directly by the water mass entering Maputo Bay from the Indian Ocean. Nevertheless, different ecological processes may be acting, as portunids such as *C. sapidus* are highly mobile animals thus depending on large migratory movements, whereas most mangrove crabs are faithful to their burrow areas.

The conjunction of stochastic (winds) and deterministic (tides) factors with availability of offshore megalopal patches produces a variable supply of settling megalopae to the coastal ecosystems (Xie & Eggleston, 1999). The highly episodic recruitment events may in fact be the most important factor structuring crab populations in these systems (Johnson et al., 1986), as opposed to post-settlement control processes.

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