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Interaction of offshore and inshore processes controlling settlement of brachyuran megalopae in Saco mangrove creek, Inhaca Island (South Mozambique)

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ABSTRACT: It is usually considered that reinvasion of the estuarine habitat by crab larvae that develop in the sea involves 2 different steps, which are controlled by different factors: transport of larvae from the shelf towards the coast and upstream movement until appropriate settlement habitats are found. In order to investigate reinvasion of the Saco mangrove creek (Inhaca Island, Mozambique) by crab megalopae, the timing and spatial distribution of settlement were related to major environmental forcing factors. Several sets of experiments were performed, with different specific objectives, using megalopal collectors. The total supply of brachyuran megalopae to the mangrove creek over a 2 mo period responded to 2 forcing factors, the first related to cycles of tidal amplitude and the second to offshore wind stress. The response of settlement on the collectors to the tidal amplitude cycle was reflected by clear maxima recorded on every spring tide. This contrasts with the results of previous studies analysing single species recruitment processes, which found a much more irregular pattern. This result was interpreted as a consequence of 2 factors: (1) the use of a cumulative number of total Brachyura, which increases the probability of detecting supply pulses, and (2) a larger tidal range at Inhaca than at the locations where most previous studies took place. The results of this experiment suggest interaction of the stochastic effect of offshore wind stress, which maximises transport to the coastal area, with the deterministic effect of the tide and spring-neap cycles, which operate at the nearshore level to carry megalopae to specific mangrove areas. Settlement was also studied by deploying collectors in 3 different strata of the mangroves, and the results showed a differential settlement distribution in favour of lower areas in the vicinity of the mangroves. This suggests subsequent juvenile migration to suitable areas following first moult. Different settlement stimuli were also tested in the field by enclosing in the collectors a mixture of mangrove crabs and mangrove vegetal material. The results were inconclusive, as no significant differences were found; this was attributed to the effects of interference of stimuli between adjacent collectors and of proximity to mangroves.

KEY WORDS: Settlement · Megalopae · Larval transport · Mangrove · Inhaca island · Mozambique

INTRODUCTION

Many invertebrate and fish species that live in coastal and estuarine systems have a larval phase that is exported to the sea. Such species face the practical problem of returning to the systems where adult populations occur. Active directional swimming is not thought to be a general mechanism, because of its energetic cost and the small size of these organisms. It is generally considered (Boehlert & Mundy 1988,

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Shanks 1995) that the return migration, normally by a late-stage larva or a juvenile, involves 2 separate steps which are constrained by different environmental factors: (1) transport of the larvae from the shelf towards the coast, and (2) passage through inlets and upstream movement until an appropriate environment is found. In each of these steps, environmental forcing interacts with larval behaviour to produce marine biologists call a 'recruitment mechanism'. However, because different environmental processes dominate neritic waters and inshore waters, different behavioural traits are required of the larvae during each phase.

Advection and mixing processes on the shelf are responsible for the dispersal of eggs and larvae from the locations where they originated and for shoreward transport. Among others, the following processes for onshore transport have been identified (reviewed by Shanks 1995): (1) wind-generated superficial currents, including sea breezes and Langmuir circulation; (2) wind-drift currents and Ekman transport; (3) onshore convergence following relaxation of upwelling favourable winds; (4) residual tidal currents; (5) internal waves; (6) density-driven flow. Several of these processes remain speculative because of difficulties in measuring the actual rates at which they do indeed transport planktonic larvae. At best, our understanding is mostly based on correlations between larval settlement or supply, and time and space variations of the processes.

However, convincing evidence has been gathered in support of a number of these processes, namely: wind-generated superficial currents (Willis & Oliver 1990); Ekman transport (Goodrich et al. 1989, Little & Epifanio 1991, McConnaughey et al. 1992); onshore convergence following relaxation of upwelling winds (Farrell et al. 1991); and internal waves (Shanks 1983, 1985). In all these cases, the vertical position of the larvae, which interacts with vertical structure of the flow field, plays a crucial role. For instance, surface distribution is required for entrainment by internal waves, and upwelling and downwelling-favourable winds may transport larvae on- or offshore, depending on their depth distribution (Blanton et al. 1995). Other oceanographic features such as coastal fronts (Blanton 1991, 1996) or eddies (Perry et al. 1998) may influence larval drift, either by preventing offshore dispersal or by acting as a barrier to onshore flow. Due to spawning seasonality and high-frequency variability of most of these processes, mainly in regard to wind events, these onshore transport mechanisms are stochastic by nature (van Montfrans et al. 1995). Nevertheless, on a seasonal and longer-term basis, they can provide some degree of predictability, especially when some sort of retention process on the shelf prevents loss of larvae from the geographical area where they were produced (Epifanio 1995).

Closer inshore, most often in estuaries and enclosed bays, deterministic processes dominate. Here, because of geomorphological constraints, currents and other factors associated with the tidal cycle are predictable environmental forcing agents. Experimental and field studies have demonstrated that decapod late-stage larvae, in which reinvasion of estuarine systems has been better studied, use selective tidal stream transport (Harden Jones et al. 1984) to travel upstream against the net seaward flow of estuarine waters. In these species, selective tidal stream transport is accomplished by synchronous vertical migration of the megalopa stage from the bottom to the overlying water during flood-tide, and settlement to the bottom during the following ebb-tide. Vertical migration can be controlled by endogenous activity cycles (*Uca* spp., Tankersley et al. 1995) or by exogenous factors associated with the tidal cycle (*Carcinus maenas*, Zeng & Naylor 1996, Queiroga 1998; *Callinectes sapidus*, de Vries et al. 1994, Forward et al. 1995, Tankersley et al. 1995). Moreover, it was demonstrated in the case of *Uca* spp. and *C. sapidus* megalopae that chemical cues present in estuarine waters inhibit swimming during the day, causing concurrent sinking to the bottom (Forward & Rittschof 1994). These 2 patterns of behaviour are responsible for the concentration maxima of megalopae that several authors found in the water column of estuaries during nocturnal flood-tides (e.g. Little & Epifanio 1991, Olmi 1994, Queiroga et al. 1994, Queiroga 1998).

On coasts with a semidiurnal tidal regime, the phase relationship (beat) between the tidal and the diel cycles is ca 15 d. Accordingly, it would be expected that recruitment events occur in these species with a semilunar periodicity. An extensive study on *Callinectes sapidus*, conducted simultaneously in several western Atlantic estuaries with semidiurnal tides (van Montfrans et al. 1995), found evidence that the lunar cycle may indeed synchronise recruitment events across estuaries, although local and mesoscale oceanographic conditions, as well as larval release periodicity, may obscure the basic semilunar pattern. Interestingly, in another study in the Gulf of Mexico coast using the same methodology, no semilunar periodicity was observed (Rabalais et al. 1995). Here, the tides are diurnal or mixed, and the phasing of the tides relative to the light-dark cycle varies temporally over the year.

Once in shallow habitats, settlement of the megalopae depends on the recognition of environmental cues at the appropriate areas (Epifanio et al. 1988, Luckenbach & Orth 1992, Eggleston & Armstrong 1995, Welch et al. 1997). Competent megalopae show plasticity in the duration of the stage in response to sediment type or the presence of adults of the same or other species. This suggests that crab megalopae can shorten or delay settlement and metamorphosis until appropriate environmental conditions are encountered (Sulkin & van Heukelem 1986, O'Connor 1991, Wolcott & de Vries 1994, Forward et al. 1996).

Inhaca island is located at the entrance of Maputo bay, southern Mozambique. Maputo bay is characterised by shallow bottoms and extensive intertidal flats, and receives the discharges of 3 rivers. The waters around Inhaca island are influenced by the tide, and also to some degree by fluvial discharges. Plankton productivity around the island follows the seasonality of rainfall in the area (Paula et al. 1998). Tides are semidiurnal, with more than 3 m tidal amplitude during the spring-tide period. Mangroves are widely distributed on Inhaca shores (Guerreiro et al. 1996), and brachyuran populations are diverse and abundant (Kalk 1995).

The present paper describes a sampling experiment conducted at Inhaca Island, Mozambique, which provided the opportunity of using megalopal collectors in a different environmental setting from that in previous works. Specifically, we examine the dependence of megalopal supply to a mangrove on wind-forcing and the lunar cycle. We also use this technique to quantify settlement rates among different mangrove habitats and to test, in the field, the influence of different stimuli on settlement magnitude.

MATERIALS AND METHODS

The technique of artificial settlement substrates, or megalopae collectors, was developed to describe high-frequency (>1 d) supply of crab megalopae, and has been extensively used during the last decade in western Atlantic and Gulf of Mexico estuaries (e.g. van Montfrans et al. 1990, 1995, Olmi et al. 1990, Metcalf et al. 1995, Rabalais et al. 1995). In the present study we used similar collectors, made of a cylindrical PVC core, 40 cm in length and 11 cm in diameter, coated with a hogshair filter (4 cm thick). The total settlement area of each collector was 0.144 m^2. The collectors were usually deployed in modules of 3, suspended from a long stick anchored to the bottom by a line and a heavy weight. A set of buoys maintained the collectors afloat immediately below the water surface. The collectors were placed approximately 1 m apart in order to minimise interference between experimental treatments. One single attachment to the bottom held each module of collectors parallel to the tidal current. Each day, all collector surfaces were changed during the diurnal low tide. In the laboratory, the collectors were washed in fresh water to extract megalopae from the dense hogshair filter surface. Megalopae were then preserved in buffered 4% formaldehyde for subsequent counting.

Supply of megalopae to mangrove and non-mangrove habitats. Two groups of 3 collectors were deployed for studying settlement over time, 1 at the Saco mangrove main channel and 1 in the channel near the Marine Biology Station (EBM), outside the mangrove area, at Inhaca island (Fig. 1: A, B). This experiment was started on November 15, 1997, and lasted for 25 d. In order to analyse the effects of sampling station and date on megalopal supply, a 2-way ANOVA was used. However, according to Cochran's test, variances were highly heterogeneous, a feature that was impossible to correct by any of the usual transformations. Accordingly, a non-parametric ANOVA of the ranks of the numbers of megalopae in the collectors was employed, following the procedure described by Zar (1984).

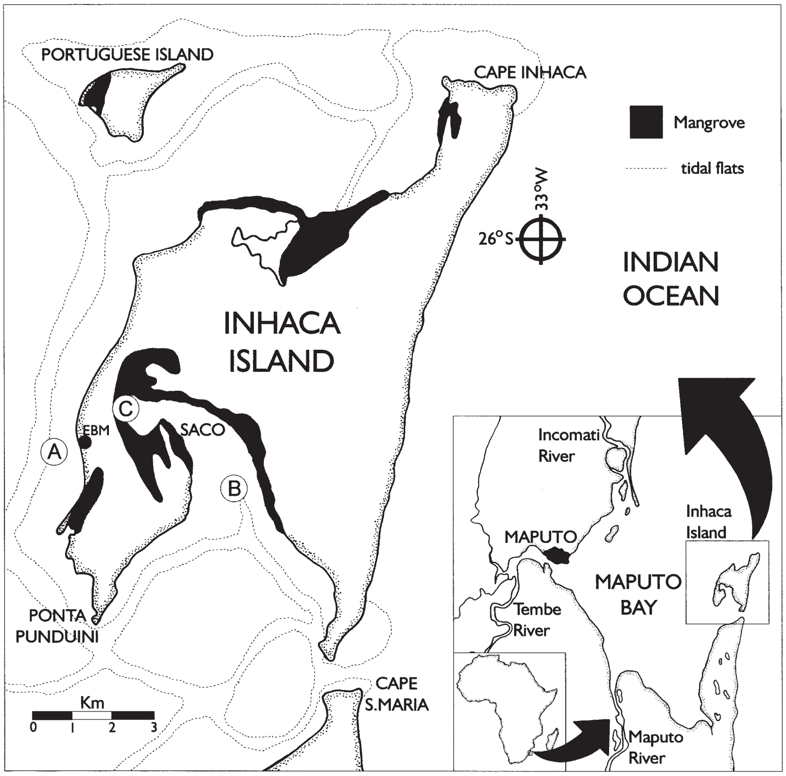

Fig. 1. Map of Inhaca island showing position of megalopae collecting sites. A: flats near Marine Biology Station (EBM); B:Saco mangrove creek, used for longer time-series and for study of settlement cues; C: mangrove transect used to study settlement as function of mangrove strata

Influence of tidal amplitude and wind stress on supply of megalopae to mangrove habitat. One group of 3 collectors was deployed in the Saco mangrove main channel (Fig. 1: B) for a period of 8 wk, starting on January 15, 1998. The time-series of the accumulated number of megalopae caught daily in the 3 collectors was detrended and the mean subtracted, and the series then subjected to spectral analysis. To investigate the relationship between tidal amplitude, wind stress and megalopae supply, multiple regression analysis was employed, using average daily tidal range and average daily wind stress as independent variables. It is assumed that once megalopae are within reach of the mangroves, tidal currents carry them immediately to the sampling station. However, because wind stress is a vector, its influence on onshore transport will depend on its direction. Moreover, a wind stress effect on inshore recruitment may occur with a lag of several days, corresponding to advection velocities and distances of coastal water masses. To identify both the direction and time lag of the wind effects on supply to the mangroves (settlement on the collectors), several multiple regression models were fitted to the data, using tidal range and wind stress for predetermined directions and time lags as independent variables. For this purpose, wind-stress components along directions separated by 15° intervals were calculated, starting with 0° and ending with 165°. We then calculated regression surfaces using all possible combinations of wind stresses along the above directions and time lags of 0 to 5 d.

Since no tidal gauge exists at Inhaca Island, estimated tidal ranges were obtained from the tide tables for the harbour of Maputo, published by the Instituto Hidrográfico of Portugal. Wind data were obtained from the weather station at Maputo. Observations during the period of interest were made daily at 09:00, 15:00 and 21:00 h, wind direction being recorded in octants. Each octant was converted to degrees, and wind stresses (τ) for each observation time and direction (d, in 15° intervals) were calculated using the equation:

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

where ρ_a is air density (1.12 kg m^{-3}), C is the stress coefficient (0.0012), $\vec{v}$ is wind velocity, and v_d is the wind velocity component for direction d. The 3 daily wind-stress values for each direction were then averaged to produce 1 daily mean stress value for each component. For graphical comparisons, u (positive to West) and v (positive to North) components of wind stress were plotted with megalopal abundance on the collectors over time.

Influence of external stimuli as cues for settlement. This experiment attempted to assess the influence of the presence of adult mangrove crabs (genera *Sesarma* and *Uca*) and of mangrove plants (*Avicennia marina* and *Rhizophora mucronata*) as cues for settlement. Modified collectors were used in this experiment, in which the internal PVC core was replaced by a cylindrical sleeve made of flexible, large-pore iron mesh, supported by a PVC frame. A coarse-mesh bag containing the crabs or leaves was placed inside the inner core which, because of its perforated wall, allowed the chemical cues to flow through the hogshair filter. At the entrance of the Saco mangrove channel (Fig. 1: B) 3 modules of 3 collectors each were deployed. Each module had 1 collector with a mixture of about 20 crabs of both genera in equal proportions, and another with a mixture of leaves and branches of the mangrove trees, also in equal proportions. The third collector was left empty as a blank control. Each module of 3 collectors was anchored to the bottom by a line and a weight. Consequently, the collectors were aligned with the tidal current. In order to prevent the same stimulus from always facing the current, the position of the stimuli within each module of collectors was randomised. This experiment lasted for 27 d and began on January 15, 1998. The effects of chemical cues on the settlement of megalopae on the collectors was analysed with a 1-way ANOVA. It was not considered necessary to transform the data,because variances were only slightly heterogeneous according to Cochran's test.

Settlement of megalopae as a function of mangrove strata. This experiment measured the settlement of megalopae along a transect defined across the Saco mangrove belt (Site C: Fig. 1). Three strata were considered within this transect: a bare mud platform on the lower shore, the bottom under the *Avicennia marina* canopy at mid-shore, and the bottom under the *Rhizophora mucronata* canopy on the upper shore. Three collectors were laid on the bottom in each stratum and secured with sticks; the trapping surface was changed while the collectors were still submersed. The duration of this experiment was 11 d and it started on February 25, 1998. The difference in settlement intensity on collectors placed in *A. marina*, *R. mucronata* and bare mud strata was studied by a 1-way ANOVA followed by *post hoc* multiple-comparison Bonferroni tests to identify pair-wise differences between group means. Again, heterogeneous variances of the original data were impossible to correct, and so the analysis was performed on ranks of the numbers of megalopae.

RESULTS

Supply of megalopae to mangrove and non-mangrove habitats

A comparison between the collectors deployed near the flats of the Marine Biological Station (EBM) and those at Saco creek channel (Sites A and B: Fig. 1) shows that differences were statistically significant (Fig. 2; $p < 0.001$), but only during the peak period of abundance. During this period, the collectors deployed at Saco collected more megalopae than the replicates at EBM.

Influence of tidal amplitude and wind stress on supply of megalopae to the mangrove habitat. Fig. 3B shows the daily evolution of settlement from January to March 1998, measured by the collectors located in Saco mangrove channel. The occurrence of megalopae in the collectors clearly reflects the semilunar cycle of tidal amplitude, with peaks over the spring tides around full and new moon. The highest number of megalopae collected on a single collector was 62, and the highest daily average in all collectors was 50.3. Spectral analysis for this series showed a major spectral density peak for a frequency of 0.0667 (corresponding to a period of 14.99 d, Kolmogorov-Smirnov test, $d = 0.3780$, $p < 0.01$). Although the cyclic pattern is clearly discernible from the data, considerable differences between the magnitude of consecutive peaks are also evident.

As expected from the graphical analysis in Fig. 3, regression coefficients for the variable tidal range were always significant ($p < 0.001$; Table 1). However, significant ($p < 0.05$) regression coefficients for the variable wind stress were only obtained for a time lag of 3 d and wind directions of 0°, 150° and 165°. Coefficients were positive for 0° and negative for the other 2 directions. The result obtained for 0° can be transposed to a direction of 180° by simply changing the sign of the regression coefficient, thus obtaining significant negative effects of wind stress on megalopae settlement for a time lag of 3 d and directions between 150° and 180°, the best fit being for a direction of 165°. Therefore, as wind stress towards 165° increases, the number of megalopae settling on collectors deployed at Saco decreases.

Influence of external stimuli as cues for settlement. No significant differences were found between collectors with different stimuli (Fig. 4; $p < 0.10$). Over the period of the experiment, fluctuations in captures were related to cycles of tidal amplitude.

Settlement of megalopae according to mangrove strata. Fig. 5 shows the settlement of megalopae along the mangrove transect (Fig. 1: C). Intensity of settlement varied significantly across treatments ($p < 0.01$). Settlement was stronger in the mud flat than in the other 2 strata, but no significant differences (probability level of 0.05) were detected between collec-

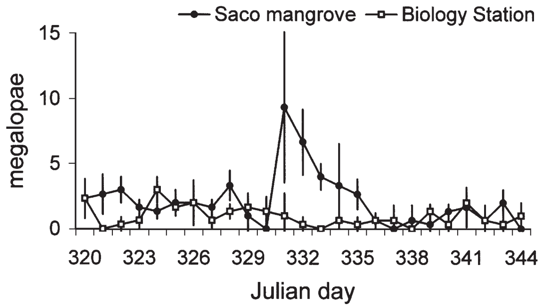

Fig. 2. Mean (±1 SE) daily number of megalopae per collector, over 25 d at Saco mangrove creek and Marine Biology Station

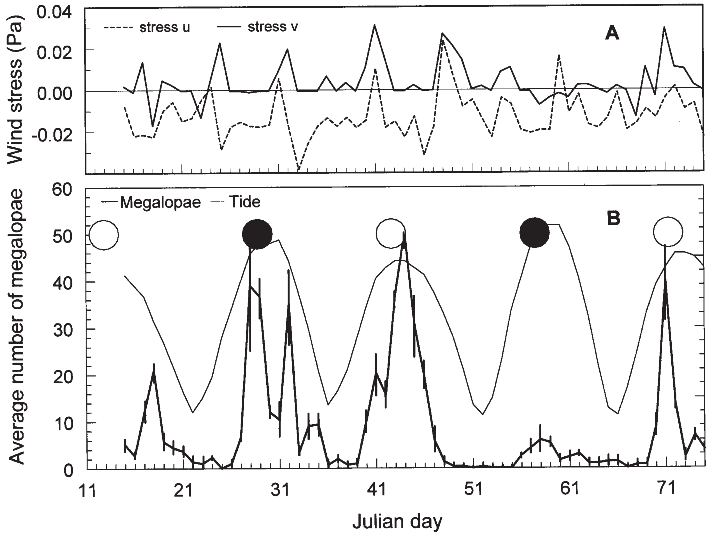

Fig. 3. (A) Average daily wind stress at Maputo along *u* (positive to West) and *v* (positive to North) components; (B) average (±1 SE) daily number of megalopae per collector at Saco mangrove creek, and average daily expected tidal range. (●) new moon; (○) full moon

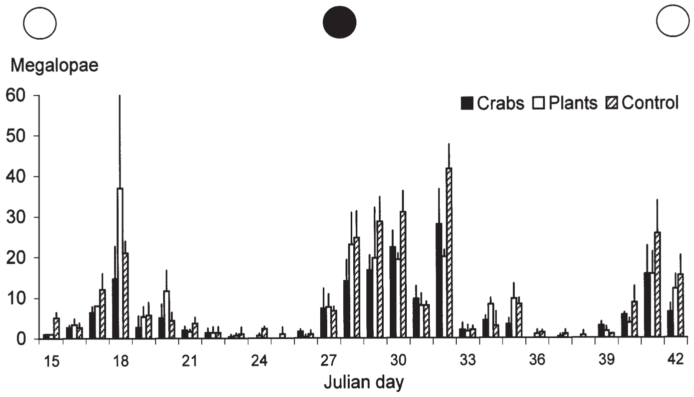

Fig. 4. Average (+SE) daily number of megalopae that settled on collectors containing mangrove crabs, mangrove plants, or a blank control, during 1 lunar period. Moon symbols as in Fig. 3. (●) new moon; (○) full moon

tors located under the *Avicenia marina* and *Rhizophora mucronata* canopies. The collectors deployed on the bare mud flat showed a maximum daily average of 31 megalopae per collector, with a maximum of 44 in a single collector.

Table 1. Results of multiple regression analysis of megalopae settlement in collectors at Saco creek, Inhaca Island, on tidal range and wind stress. Direction in degrees, lag in days. Dir = direction; p = probability values; r^2 = coefficient of determination. Bold-face indicates significant regression

Dir	Lag	Regression coefficients		Significance of regression coefficients (p<)		r^2
		Tidal range	Wind stress	Tidal range	Wind stress	
0	0	6.96	114.83	0.00012	0.4395	0.2140
	1	7.13	−34.53	0.00010	0.8045	0.2066
	2	7.03	109.92	0.00010	0.4234	0.2146
	3	**7.08**	**301.99**	**0.00005**	**0.0250**	**0.2722**
	4	7.17	261.38	0.00005	0.0547	0.2551
	5	7.06	−58.74	0.00010	0.6873	0.2080
15	0	7.04	48.83	0.00011	0.7113	0.2076
	1	7.16	−61.71	0.00009	0.6087	0.2094
	2	7.06	51.88	0.00010	0.6624	0.2084
	3	7.15	223.644	0.00005	0.0551	0.2550
	4	7.25	217.72	0.00005	0.0640	0.2517
	5	7.07	−15.71	0.00010	0.8996	0.2060
30	0	7.08	120.25	0.00010	0.9771	0.2058
	1	7.18	−75.99	0.00008	0.4842	0.2125
	2	7.08	14.86	0.00010	0.8899	0.2060
	3	7.18	168.37	0.00006	0.1096	0.2403
	4	7.19	183.23	0.00005	0.0841	0.2459
	5	7.09	9.82	0.00010	0.9294	0.2059
45	0	7.10	−31.02	0.00009	0.7874	0.2068
	1	7.18	−86.44	0.00008	0.3997	0.2155
	2	7.08	−12.17	0.00010	0.9047	0.2060
	3	7.19	128.78	0.00006	0.1961	0.2285
	4	7.31	158.34	0.00005	0.1149	0.2394
	5	7.11	27.47	0.00009	0.7910	0.2068
60	0	7.10	−62.34	0.00009	0.5853	0.2099
	1	7.17	−97.51	0.00007	0.3381	0.2183
	2	7.08	−36.42	0.00010	0.7185	0.2076
	3	7.19	97.11	0.00007	0.3263	0.2190
	4	7.31	139.91	0.00005	0.1610	0.2324
	5	7.13	42.94	0.00009	0.6731	0.2082
75	0	7.09	−96.58	0.00009	0.4143	0.2149
	1	7.12	−111.91	0.00007	0.2906	0.2210
	2	7.06	−63.54	0.00010	0.5464	0.2108
	3	7.16	66.29	0.00008	0.5202	0.2115
	4	7.29	124.07	0.00006	0.2332	0.2251
	5	7.16	60.10	0.00008	0.5669	0.2103
90	0	7.05	−139.64	0.00009	0.2737	0.2221
	1	7.13	−131.84	0.00008	0.2540	0.2235
	2	7.04	−99.74	0.00010	0.3868	0.2160
	3	7.11	27.56	0.00009	0.8068	0.2066
	4	7.26	105.20	0.00007	0.3556	0.2175
	5	7.18	82.74	0.00008	0.4668	0.2130
105	0	6.99	−196.89	0.00009	0.1670	0.2317
	1	7.08	−158.22	0.00008	0.2307	0.2254
	2	7.00	−153.17	0.00010	0.2454	0.2242
	3	7.04	−33.70	0.00011	0.7938	0.2067
	4	7.19	72.30	0.00008	0.5794	0.2100
	5	7.21	115.52	0.00007	0.3715	0.2167
120	0	6.90	−266.41	0.00010	0.0996	0.2423
	1	7.02	−184.78	0.00009	0.2342	0.2251
	2	6.94	−229.74	0.00010	0.1387	0.2355
	3	6.94	−141.23	0.00012	0.3522	0.2176
	4	7.09	3.19	0.00011	0.9835	0.2058
	5	7.23	162.00	0.00007	0.2882	0.2212

DISCUSSION

A higher number of megalopae settled on the collectors located in the vicinity of Saco mangroves, than in the zone near the Marine Biology Station. This result was expected, as Saco bay is a diverse and rich complex of intertidal habitats, where brachyuran populations are more abundant than on the control flats (see Kalk 1995). It thus seems obvious that the megalopal stages do not settle indiscriminately in nearshore habitats, but find appropriate areas and settle near their respective adult populations. This implies specific and differential transport and the recognition of appropriate chemical or other environmental cues for settlement behaviour.

That the deterministic component of the settlement pattern has semilunar periodicity is obvious from the data in Figs. 3 to 5, and statistical tests merely confirm this. It reflects cycles of tidal amplitude, and the arrival of megalopae in the mangrove area occurs when flood-tides are post-crepuscular, as during the spring-tide period in the area. Therefore, the major factor affecting periodicity of settlement on the collectors in at the Saco mangroves is the semilunar cycle. This process operates at the local nearshore level, where tidal currents are the main factor accounting for larval transport. Most studies describing the return migration of megalopae to nearshore areas refer to transport mainly during nocturnal flood-tides (e.g. de Vries et al. 1994, Olmi 1994, Tankersley & Forward 1994, Hovel & Morgan 1997, Queiroga 1998). The high synchronisation of settlement with cycles of tidal amplitude in this experiment may be due to the larger tidal amplitude and semilunar range at Maputo bay compared to those areas where most of the above investigators

Table 1 (continued)

Dir	Lag	Regression coefficients		Significance of regression coefficients (p<)		r^2
		Tidal range	Wind stress	Tidal range	Wind stress	
135	0	6.81	–318.31	0.00012	0.0754	0.2485
	1	6.96	–182.00	0.00011	0.3085	0.2200
	2	6.88	–304.30	0.00010	0.0871	0.2452
	3	6.83	–303.19	0.00012	0.0879	0.2465
	4	6.96	–124.97	0.00012	0.4799	0.2126
	5	7.23	209.00	0.00006	0.2427	0.2244
150	0	6.85	–255.58	0.00014	0.2288	0.2255
	1	6.98	–112.99	0.00012	0.5381	0.2110
	2	6.89	–294.57	0.00011	0.1044	0.2414
	3	**6.84**	**–422.20**	**0.00008**	**0.0177**	**0.2798**
	4	6.94	–259.38	0.00010	0.1508	0.2338
	5	7.15	202.47	0.00007	0.2858	0.2213
165	0	6.87	–206.58	0.00013	0.2197	0.2263
	1	7.06	–21.97	0.00011	0.8937	0.2060
	2	6.96	–199.57	0.00010	0.2172	0.2262
	3	**6.96**	**–393.59**	**0.00006**	**0.0131**	**0.2863**
	4	7.05	–295.57	0.00007	0.0658	0.2512
	5	7.09	129.10	0.00009	0.4546	0.2134

carried out their experiments. Specific mechanisms of megalopal transport to mangrove areas, such as utilisation of floating mangrove leaves, have been described by Wehrtmann & Dittel (1990).

Our results suggest, however, that a coupling of offshore and inshore physical processes are involved in controlling the magnitude and periodicity of megalopae settlement in Inhaca mangroves. There are large fluctuations of settlement magnitude among the consecutive peak periods of megalopal abundance which cannot be easily explained unless we assume that inshore larval availability may be significantly influenced by other phenomena besides tides. The results of a regression of megalopal abundance on offshore wind stress from particular directions seem to provide at least part of the answer. A significant correlation was found between abundance and wind regimes that run northwards almost parallel to the coast. According to Ekman theory these conditions produce coastal convergence currents, thereby inducing effective transport of megalopae to nearshore coastal areas (Goodrich et al. 1989, Little & Epifanio 1991, McConnaughey et al. 1992).

The hydrography of Maputo Bay and adjacent neritic waters is not well known, but Lutjeharms & Jorge da Silva (1988) have shown the complex dynamics of mesoscale features, including countercurrents and eddies, that derive from the Mozambique Current. This current system runs southwards along the Mozambique coast, following isobaths of the slope. North of Maputo Bay (roughly at 24°30′ S), an indentation of the coastline associated with abrupt downstream broadening of the continental shelf engenders topographically-trapped lee eddies. Interpretation of thermal configurations derived from satellite imagery shows that the centres of the eddies may lie between 35 and 70 km from Inhaca Island. These eddies, northward inshore countercurrents, and associated shear structures, may contribute to the retention of larvae in areas adjacent to Maputo Bay and restrict offshore dispersal, as shown for *Callinectes sapidus* in other areas (Perry et al. 1998). Retention of larvae could make wind stress more effective for inshore larval transport (Epifanio 1995). Willis & Oliver (1990) have also described wind-stress-dependent transport for coral larvae.

Wind-induced currents must maximise larval onshore transport to the entrance of the bay, as most larvae will be carried out from Maputo Bay to neritic waters. The lag of 3 d in the supply of megalopae to the mangroves could be explained by the distance from shore of the water mass carrying the larvae, and other delays may also operate on a range of other factors (e.g. larval origin, prevailing winds and currents previous to megalopal competence, etc). Thus the stochastic effect of the wind regime seems to significantly influence megalopal availability in nearshore water bodies, superimposing its effects on the deterministic nature of tidal cycles. As larvae reach the nearshore area, they are presumed to be transported to appropriate areas by subsequent flood-tides. Tidal amplitude is highly correlated with megalopal settlement magnitude, and this is clearly the factor accounting for the major cyclic component of the settlement process.

A major constraint that precludes detailed analysis of megalopal time-series in the Western Indian Ocean is the lack of information regarding morphology of crus-

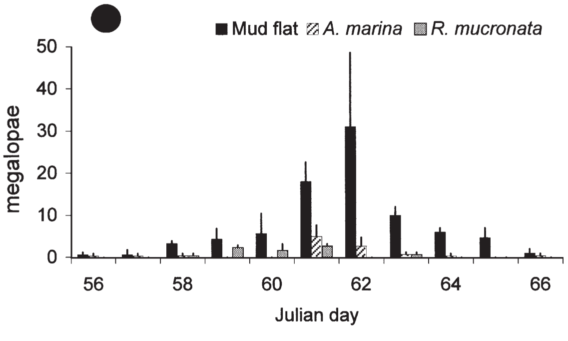

Fig. 5. Average (+SE) daily number of megalopae that settled on collectors during a new moon period in a transect along the vertical profile from the lower bare mud flat to below the canopies of *Avicennia marina* and *Rhizophora mucronata*

tacean larvae from the area, as for other planktonic larvae in general (see Paula et al. 1998). No taxonomic keys are available, and the high number of species does not permit accurate species assignment. This limitation obliges us at this stage to consider megalopae as a whole, Brachyura *sensu strictu*, and species patterns are thus masked by overall trends. The results obtained from our time-series at the Saco mangrove creek are striking because of the regularity of occurrence of settlement peaks over the full and new moons during the period of the experiment. In most, if not all extended studies of this kind (e.g. van Montfrans et al. 1995) many peaks are 'missing'. These studies were conducted on a single species, and the lack of recruitment events during some periods that seemed suitable for recruitment were attributed to variations in the temporal and spatial distribution of megalopae on the shelf. Even if the tide is right, and the wind blowing from the appropriate direction, if there are no megalopae in the region there will be no recruitment to the estuary. The existence of a monospecific pool of megalopae in such conditions that would be transported to tidal areas depends on the species' reproductive season or hatching periodicity and on the past history of the advective events. When one considers brachyuran megalopae as a whole; as in the present study, there is a greater probability of a constant supply of megalopae to be transported into the tidal area, and thence a more continuous settlement time-series can be observed. Most mangrove crab species have similar life cycles, including export strategy from parental areas, so the cyclic phenomenon described here may reflect identical recruitment mechanisms. Thus, taken in conjunction with previous reports on other crabs, the present study may help to establish a common mechanism of a 'universal' nature among the Brachyura and, possibly, among other groups whose late-stage larvae invade tidal areas.

In semidiurnal tidal regimes, as at Inhaca, a semilunar period of megalopae recruitment coincident with spring tides may arise from several non-exclusive factors. Firstly, spring tides carry a larger volume of water into the estuaries and, other things being equal, more larvae will be transported into the estuary. Secondly, a higher rate of increase of hydrostatic pressure and salinity with the rising tide will presumably trigger a swimming response of more megalopae to the water column, since it has been shown (Tankersley et al. 1995) that (1) there is a minimum threshold in the rate of increase of these 2 environmental factors capable of eliciting an upward response by a megalopa resting on the bottom, and (2) above that threshold the response increases with the absolute magnitude of the difference. Thirdly, since the beat period between the diel and the tidal cycles is 15 d, it can be expected that, in some locations, night flood-tides occur preferentially during a particular phase of the moon. At Inhaca Island, 1 of the 2 daily low tides consistently occurs around midnight during the new and full moons, and the flood that follows takes place before sunrise. The general rule is that crab megalopae are more abundant in estuarine waters during night flood-tides (preliminary data show that this is also the case at Inhaca: see Paula et al. 2000). Christy & Morgan (1998) showed that the proportion of crab megalopae found during the flood phase of the tidal cycle increases with the proportion of the flood that takes place during the night. Hence, the semilunar variation in the phase relationship between both cycles may constitute an additional factor promoting synchrony of megalopal recruitment to estuaries with semidiurnal tides. Moreover, this effect may change seasonally, because of the variable duration of the night during the year.

The above considerations are probably of little interest for interpreting results regarding spatial settlement, since different species may have different cues for finding or recognising appropriate substrates. Nevertheless, the differences in magnitude of settlement between the lower (bare mud flat) and the mid (below mangrove canopy) parts of the mangrove seem to indicate that megalopae preferentially settle lower in the mangroves, and subsequently migrate as juveniles up into the intertidal zone.

Further field studies of settlement cues are needed. Are the global effects of 'mangrove vicinity' sufficient to explain the differences in settlement found between mangrove areas and other adjacent coastal areas? Due to the complexity of mangrove areas and the mosaic structure of different habitats and potential cues, we feel that the nature and importance of cues for settlement behaviour can only be addressed properly in controlled experiments. The spatial interference and magnitude of stimuli also remain to be assessed. A number of studies refer to the importance of chemical cues for settlement-site selection (e.g. Epifanio et al. 1988, Luckenbach & Orth 1992, Eggleston & Armstrong 1995). Welch et al. (1997) described patterns of settlement related to avoidance of predators. However, there may be a number of different reasons for the absence in the present study of significant differences between experimental treatments. Firstly, the adult crabs that were used as stimuli belonged to only 2 species, not necessarily the same ones that were available as megalopae in the water column during the study period; thus, the chemical cue could have been the wrong one. Secondly, the proximity of the mangroves, with all their associated chemical signals, may mask the preferences of the megalopae. Thirdly, these preferences may also be concealed by interference of the different stimuli among the replicate collectors, which was not tested.

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