First appraisal on releasing and reinvasion of decapod larvae in a subtropical estuary from Brazil.

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ABSTRACT: First appraisal on releasing and reinvasion of decapod larvae in a subtropical estuary from Brazil. Releasing and reinvasion of decapod larvae, with emphasis on Brachyura, in a subtropical estuary were analyzed to a better understanding the early life cycle strategies of these crustaceans. This study was carried out at the confluence of the rivers Esco and Comprido, Bay of Fortaleza (23°20'00"S, 45°09'53"W), Ubatuba, Brazil, during the month of February, when most decapod species are breeding. The sampling region is characterized by semidiurnal tides. Three replicate samples were taken during ebb and flood periods for spring (1.1 m tidal range) and neap tides (0.35 m tidal range), at day and night. Samples were obtained using a plankton net (250 μm of mesh pore) which was placed at 10 cm under the water surface. After, the plankton net was towed against the current through a distance of 80 m. Mean filtered volume per sample was $11.75 \pm 2.12 \text{ m}^3$ ($N=12$) during ebb tides and $9.78 \pm 3.32 \text{ m}^3$ ($N=12$) in flood tides. Only penaeidean, caridean and brachyuran larvae were found in the samples during ebb tide periods. Caridean and brachyuran larvae were more abundant at night, the former prevailing during neap tides and the latter during spring tides. Within brachyuran, two patterns could be identified: a) larvae mainly released during spring tides (ocypodid, gracipid and pinnotherid); b) larvae mainly released in neap tides (xanthid zoaeae). Flood tide periods were more diverse in comparison to ebb tide periods, when penaeidean, caridean, thalassinidean, anomuran and brachyuran decapods larvae were obtained. Decapod larvae return to the estuary mainly at night. Carideans and ocypodid larvae were more abundant and reinvaide during neap tide, while penaeidean, thalassinidean, and xanthid larvae prevailed during spring tide. These patterns may be related to differences regarding resource requirements for larval development in each family, since some crab species complete their larval development in coastal marine waters while others do it in the estuary.

Key-Words: Decapod, Brachyura, larvae, dispersal, estuary, tide, South America.

RESUMO: Avaliação preliminar sobre a liberação e a reinvasão de larvas de decápodos num estuário subtropical do Brasil. Analisou-se a liberação e a reinvasão das larvas de decápodos com ênfase nos Brachyura num estuário subtropical como subsídio à compreensão das estratégias da fase inicial do ciclo de vida desses crustáceos. Este estudo foi realizado na confluência dos rios Esco e Comprido, Enseada da Fortaleza (23°20'00"S, 45°09'53"W), Ubatuba, Brasil, durante o mês de fevereiro, quando muitas espécies de decápodos estão se reproduzindo. A região de estudo é caracterizada por marés semidiurnas. As amostras foram coletadas no período diurno e noturno, com três repetições, durante a vazante e a enchente, em maré de sínquia (1.1 m de amplitude) e em maré de quadratura (0.35 m de amplitude). As amostras foram obtidas com uma rede de plancton (250 μm de diâmetro de malha), a qual foi arrastada a 10 cm abaixo da superfície da água e contra a corrente, por uma distância de 80 m. O volume médio filtrado por amostra foi de $11.75 \pm 2.12 \text{ m}^3$ ($N=12$) durante as marés vazantes e $9.78 \pm 3.32 \text{ m}^3$ ($N=12$) durante as marés enchentes. Nas amostras dos períodos de maré vazante foram encontradas somente larvas de penedéoces, carídeos e braquiúros. Larvas de carídeos e braquiúros foram mais abun-
Introduction

A considerable number of studies has been done on strategies of dispersal and recruitment of decapod crustaceans (Littie & Epifanio, 1991; Werhmann & Dittel, 1990; O'Connor, 1993; Boylan & Wener, 1993; Christy & Morgan, 1998). However, these studies have focused mainly on estuarine decapods of temperate regions. Thus, few studies have considered tropical and subtropical communities, of which most of the existing research was carried out in the Central American coast (Epifanio & Dittel, 1984; Dittel et al., 1991).

The importance of studying estuarine zooplankton relies on the assumption that estuaries are a nursery ground for larval and juvenile stages of many species, including crustaceans and fishes. However, the mechanisms which determine the patterns of distribution of zooplankton in this community are poorly understood. Grindley (1984) suggested that the patterns of distribution of zooplankton frequently bear little relation to the distribution of the physical and chemical parameters conventionally investigated, such as salinity, temperature, dissolved oxygen and the concentrations of various nutrients. According to Grindley (1984), tidal exchange appears to be the single and the most important factor controlling distribution of plankton. McConaugha (1988 and 1992), on the other hand, postulated a scenario suggesting that the tradeoff between predation and food availability determines patterns of distribution of zooplankton. He suggested further that, although offshore development may reduce predation on larvae, a possible disadvantage could be the low density of prey items available to larvae.

Brachyuran larvae are an excellent model system for studying larval transport mechanisms as they have a definitive number of stages whose duration is known for ecologically relevant conditions (McConaugha, 1988).

For the area under consideration, the crab species composition (Cobo et al., 1993), the reproductive biology of some brachyurans (Leme & Negreiros-Francozo, 1998; Cobo & Francozo, 1999), and the larval development of most brachyuran species (Costlou & Bookhout, 1968a; Warner, 1968; Díaz & Ewald, 1968; Kurata et al., 1981; Francozo & Hebling, 1986 and Francozo et al., 1998; Bross-Garcia & Rodrigues, 1993; Rodrigues & Hebling, 1996; Rieger, 1996, 1997 and 1998) have been intensively studied. Additionally, some studies on influence of salinity on larval development of mangrove crabs from South American coast were conducted by Costlou & Bookhout (1968b), Francozo & Negreiros-Francozo (1986), Díaz & Bevilacqua (1986), Montu et al. (1990), and Messerknecht et al. (1991).

Within this context, the area and the organisms considered in the present study can potentially enhance our understanding of the mechanisms that determine patterns of dispersal and recruitment of mangrove organisms, mainly brachyurans.
Material and Methods

According to Negreiros-Franoso et al. (1991), the annual variation of local temperature of the seawater near the sampling site was 24.4 ± 2.7°C, the salinity 33.3 ± 1.5‰, and the oxygen 5.86 ± 1.38 mg/l; the bottom was predominantly composed of very fine sand and silt-clay and the organic content of the sediment was 1.8 ± 1.3%.

During February of 1997, plankton samples were obtained from a single site at the confluence of the rivers Comprido and Esquiro, which discharge their waters in the Bay of Fortaleza (23°29'00"S, 45°00'53"W), Ubatuba, Brazil. Samples were taken using a plankton net (250 µm of mesh width) in ebb and flood tides, with three replicates during both spring and neap tides, at day and night light conditions. The plankton net was placed at 10 cm under the water surface and it was towed against the current through a distance of 80 m. Water volume was measured with a flowmeter attached to the net.

Each plankton sample was preserved with 4% formalin. In the laboratory, samples were examined to exclude gelatinous animals and allochthonous material. Then each sample was divided into subsamples using a Motoda's Plankton sampler splitter. The total number of larvae (N) in each sample was computed by: N = n × 2^m, where N = total number of larvae, n = partial number of larvae in each subsample, and m = number of divisions in Motoda equipment. After, the total number of larvae was expressed in m³ of filtered water.

All decapod larvae were sorted from the subsamples, staged and identified based on Boschi (1981) and Pohle et al. (1999).

Zoeal stages were identified by the number of terminal process on telson and setae on antenna for penaeideans and carideans (Gore, 1985 and Calazans, 1994), and plumose setae on maxilliped exopod for brachyurans (Pohle et al., 1999).

A logarithmic transformation [ln(x+1)] of concentrations was used to stabilize the variance, and the mean value was computed from the replicates for each tide and light conditions. A F-test (Zar, 1996) validated the log-transformation. A two-way ANOVA (day/night and ebb/flood being the factors) was performed (Sokal & Rohlf, 1995). In addition, a Tukey HSD test was used to compare the means (p<0.05), a posteriori.

Results

Tides at the sampling site are semi-diurnal. During the sampling period, tidal range was 1.1 m in spring and 0.35 m in neap tides.

Mean filtered volume per sample was 11.75 ± 2.12 m³ during ebb tides and 9.78 ± 3.32 m³ during flood tide which does not differ statistically (N = 12; p > 0.10).

All the larvae obtained during ebb tide are early zoeal stages (I or II). Only penaeidean, caridean and brachyuran larvae were collected during ebb tide. Both caridean and brachyuran larvae were more abundant at night, with the former prevailing during neap tides and the latter during spring tides. For brachyuran larvae, two patterns could be clearly identified: members of the families Ocypodidae, Grapsidae and Pinnothriidae released their larvae chiefly during spring tides, while Xanthidae zoeae release took place mainly during neap tides.

The zoeae identification was feasible only for brachyurans as many of them have already been described concerning to their larval morphology. Thus it could be identified the larvae of Ucides cordatus and Uca sp (Ocypodidae); Cardisoma guanumi (Gecarcinidae); Sesarma rectum, Aratus pisonii, Goniopsis cruentata, Armases angustipes and Armases rubripes (Grapsidae); Zaops ostreum (Pinnothriidae); Eurytium limosum and Panopeus occidentalis (Xanthidae) and Callinectes danae (Portunidae).
Table 1: Mean number of larvae m$^{-3}$ sampled and obtained during ebb tide period in each collection schedule.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Neap Tide</th>
<th>EBB</th>
<th>Spring Tide</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day</td>
<td>Night</td>
<td>Day</td>
</tr>
<tr>
<td>Penaeidea</td>
<td>17.0 ± 9.7 c</td>
<td>515.4 ± 65.8 a</td>
<td>18.50 ± 9.8 c</td>
</tr>
<tr>
<td>Caridea</td>
<td></td>
<td></td>
<td>60.5 ± 26.3 b</td>
</tr>
<tr>
<td>Gecarcinidae</td>
<td>2.53 ± 0.6 c</td>
<td>2.03 ± 1.1 c</td>
<td>16.7 ± 11.4 b</td>
</tr>
<tr>
<td>Grapsidae</td>
<td>5.53 ± 3.8 b</td>
<td>7.33 ± 2.5 b</td>
<td>45.3 ± 21.4 a</td>
</tr>
<tr>
<td>Ocypodidae</td>
<td></td>
<td></td>
<td>0.8 ± 0.9 b</td>
</tr>
<tr>
<td>Pinnotheridae</td>
<td>1.1 ± 1.0 ns</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Portunidae</td>
<td>0.27 ± 0.5 b</td>
<td>3.1 ± 0.9 a</td>
<td>0.6 ± 0.6 b</td>
</tr>
</tbody>
</table>

Comparisons were made among mean number of individuals within each taxa by means of a two-way ANOVA. Tukey HSD test. Values with at least one same letter in the line did not differ statistically (p<0.05). ns, means no difference from zero.

**Figure 1:** Density of decapod larvae during ebb tide in the estuary of Comprido and Escurso rivers, Ubatuba, São Paulo, Brazil. (Car = Caridea; Ocy = Ocypodidae; Gra = Grapsidae; Xan = Xanthidae. Pen = Penaeidea; Pin = Pinnotheridae; Por = Portunidae; Gec = Gecarcinidae; Ln = neperian logarithm; x = number of larvae).
Table II: Mean number of larvae m⁻³ sampled and obtained during flood tide period in each collection schedule.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Neap Tide</th>
<th>Spring Tide</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day</td>
<td>Night</td>
</tr>
<tr>
<td>Penaeideae</td>
<td>1.6 ± 0.6 b</td>
<td>248.9 ± 51.9 a</td>
</tr>
<tr>
<td>Caridea</td>
<td>0.2 ± 0.2 c</td>
<td>29.7 ± 12.9 a</td>
</tr>
<tr>
<td>Hippiidae</td>
<td>0.03 ± 0.05 b</td>
<td>0.5 ± 0.9 ab</td>
</tr>
<tr>
<td>Thalassinida</td>
<td>7.7 ± 7.8</td>
<td>2.7 ± 2.8</td>
</tr>
<tr>
<td>Grapsidae</td>
<td>0.3 ± 0.5 b</td>
<td>0.3 ± 0.38 ns</td>
</tr>
</tbody>
</table>

Comparisons were made among mean number of individuals within each taxa by means of a two-way ANOVA, Tukey HSD test. Values with at least one same letter in the line did not differ statistically (p>0.05); ns, means no difference from zero.

Figure 2: Density of decapod larvae during flood tide in the estuary of Comprido and Escuro rivers, Ubatuba, São Paulo, Brazil. (Car = Caridea; Ocy = Ocypodidae; Gra = Grapsidae; Xan = Xanthidae; Pen = Penaeideae; Pin = Pinnotheridae; Por = Portunidae; Gec = Gecarcinidae; Hip = Hippiidae; Tha = Thalassinidae; Ln = neperian logarithm; x = number of larvae).
Penaeidean, caridean, thalassinidean, anomuran and brachyuran decapods larvae were collected during flood tide. Decapod larvae seem to return to the estuary mainly at night, those of carideans, and ocypodid being more abundant during neap tide; whereas, those of penaeideans, thalassinideans, and xanthid crabs during spring tide. There was no difference in abundance of pinnotherid larvae concerning neap and spring tides.

Mysis and megalops of the following decapod groups were found only at night in the spring tide: penaeideans (n=112) and xanthids (n=16); and in the neap tide: ocypodids (n=4) and xanthids (n=4).

Discussion

In general, the data strongly suggest a preference of decapod larvae releasing during nocturnal spring ebb tides. This indicates that a large component of the larval community is being expelled from the estuary and that there ought to exist different mechanisms acting upon the recruitment of these species back to the estuary.

According to McConaughy (1988), nocturnal hatching does not appear to be directly related to estuarine retention or advection, because species with retained larvae and those with expelled larvae both display this behavior. However, maximum larval release during ebb tide could facilitate larval advection from the estuary.

Nocturnal releasing of decapod larvae is probably related to the reduction of predation by visual predators. As already mentioned by Christy & Morgan (1998), there is considerable support for the hypothesis that predation, primarily by daytime-active planktivorous fish (Lazzaro, 1987 and Johnson et al., 1990), selects for larval release on large amplitude, nocturnal ebb tides; such timing promotes rapid nocturnal emigration of newly hatched crab larvae from shallow estuarine and coastal.

These observed patterns may be associated to differences regarding resource requirements for larval development in each family, since some crab species complete larval development in coastal marine waters while others do it in the estuary. There are at least two distinct brachyuran larval release strategies at the estuary mouth: one associated probably to larval dispersal to marine waters (the majority of Grapsidae, Ocypodidae and Pinnotheridae species, during the spring tide) and the other related to larval retention inside or in adjacent waters of the estuary (the majority of Xanthidae species, during neap tide). In both cases, maintenance of viable populations within the adult estuarine habitat depends on reinvasion by late-stage larvae or juveniles.

The present study did not achieve which zoae have adopted the retention mechanism, but it can be supposed that species which tolerate a wide range of salinity could complete their metamorphosis inside or near the estuary. Thus, the mangrove crabs Cardisoma guanhumi, Sesarma rectum and Eurythium limosum, whose larval salinity tolerances have been studied by Costlow & Bookhout (1968), Frasozo & Negreiros-Franoso (1986) and Messerknecht et al. (1991), respectively, could present such mechanism as they attain the first juvenile stages within a good survival rates at different salinities.

Some authors have asserted that reinvasion mechanisms could be due to other environmental (Little & Epifanio, 1991) or biotic factors (Werthmann & Dittler, 1990). Thus, more detailed studies are needed on zooplankton of estuarine subtropical and tropical areas before an accurate assessment on this aspect can be discussed.

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