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Rhythms of larval release of decapod crustaceans in the Mira Estuary, Portugal

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Abstract

Rhythms of larval release of the most abundant decapod crustaceans in the Mira Estuary, Portugal, were observed based on plankton samples made over consecutive ebbing tides during one lunar cycle in June 1986. Most species showed a semi-lunar rhythm of larval release, centered on crepuscular high tides around the quarter moons. The study suggests that the larval-releasing activity is connected to the hour of the high tide rather than to tidal amplitude.

Introduction

In the past few years, a considerable number of papers on the rhythms of larval release of decapod crustaceans have been published (see reviews by De Coursey 1983, Forward 1987). In sublittoral species, which apparently experience no tidal influence, the rhythm is primarily related to the light-dark cycle (e.g. *Homarus gammarus:* Ennis 1973, Branford 1978; *Nephrops norvegicus:* Moller & Branford 1979).

Littoral and supralittoral species have tidally related rhythms. These species also frequently have semi-lunar rhythms in larval release, with release occurring at a particular tidal condition that cycles with a semi-lunar period. With few exceptions, larval-release occurs consistently between sunset and 24.00 (local time), when the high tide is within this period during the lunar month (e.g. *Aratus pisoni:* Warner 1967; *Cardisoma guanhumi:* Gifford 1962; *Sesarma intermedium* and *S. haematocheir:* Saigusa and Hidaka 1978, Saigusa, 1981; *Panopeus herbstii, Pinnixa chaetoperana, S. cinereum, S. reticulatum* and *Uca* spp.: Christy and Stancyk 1982; *Uca pugilator, U. minax* and *U. pugnax:* De Coursey 1979, Christy 1978, 1982; *U. pugilator:* Bergin 1981, Salmon and Hyatt 1983; *U. pugnax:* Wheeler 1978 and others).

Most of these studies suggest that the combination of release in the early evening and during highest amplitude high tides would have a determinant adaptive value (e.g. Saigusa 1981, Christy 1982, Christy and Stancyk 1982). However, this combination is not universal. Christy (1986) found that intertidal crabs on an exposed shore of the western Pacific release their larvae over the neap high tides, which are crepuscular in that area. Christy (1986) suggested that it would not be necessary for these crabs to synchronize with spring high tides, as they would not need higher amplitude tidal currents to disperse their larvae. Salmon et al. (1986) suggested that sublittoral estuarine species could be also less dependent on the amplitude of tides than the littoral ones.

In spite of the conclusions of the above-mentioned studies, the question remains to be answered: what is the pattern of larval release in estuaries with crepuscular neap high tides? Are the larvae released late in the evening, when spring ebbing tides will maximize seaward transport, or will they be released in neap ebbing tides, when these are only crepuscular, which seems to be the general pattern? What then is the adaptive value of such behaviour?

An attempt has been made to answer these questions using a plankton sampling program in the Mira Estuary, southwestern Portugal, where neap high tides occur early in the evening. The study assumes that abundance of first zoeal stage in the plankton reflects the magnitude of larval release by females.

Materials and methods

The Mira Estuary is a small estuary on the southwestern Portuguese coast (Fig. 1). Water varies from vertically homogeneous in spring tides, which occur at new and full moons, to slightly stratified in neap tides during quarter phases of the moon (Andrade 1986). Tidal penetration ranges from 2.5 km in neap tide to 7.5 km in spring tide, in average.

A fixed station was sampled consecutively over 55 ebbing tides, 2 h after high tide, during June, 1986. A plankton net with circular mouth aperture, 40 cm in diameter and

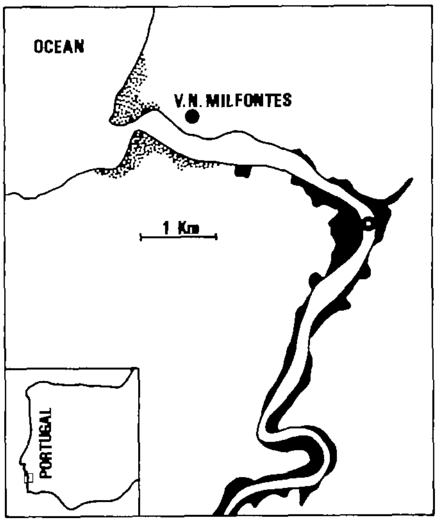

Fig. 1. Map of Mira Estuary showing collection station (✪) June 1986. ■ Salt-marshes, ▒ sandy shores

150 cm long was used, with a mesh of 500 μm, and equipped with a Hidrobios flowmeter. Tows were made horizontally, at a depth of 1 m, for 10 min at a speed of about 1 knot ($0.5\ \mathrm{m\,s^{-1}}$).

The fact that some newly-hatched larvae show diel vertical migration may lead to an underestimation of the diurnal abundance with 1 m deep horizontal tows. However, total depth of the estuary in the sampled area has a maximum of 3 m with little or no stratification. On the other hand, most studies refer to first-stage larvae as being photopositive, and hatching occurring mainly during the night. Therefore, we assume that diel differences in mid-water densities of first zoeal stages reflect magnitude of larval release by females.

Samples were fixed and preserved in buffered 5% formaldehyde. Sub-sampling was made using a Folsom plankton splitter, and the fraction counted had at least 500 larvae. Larvae were counted and identified under a binocular microscope. Identification was based on published descriptions.

Results

The first zoeal stage of 31 decapod crustaceans were identified and counted in the samples. In this study only the eight most abundant species in the plankton are considered.

Figs. 2 to 4 show the abundance of the first zoeal stages throughout the lunar cycle. Most species exhibited a semi-lunar rhythm of larval release, centered on neap tides around quarter moons. This rhythm was marked in all species but *Xantho pilipes* and *Carcinus maenas* (Figs. 3c and 4b), including the subtidal ones, the shrimps *Palaemon* spp. and *Crangon crangon* (Fig. 2 a, b). This may indicate the advantage for estuarine species, including the subtidal, to have semi-lunar rhythmicity in reproduction.

Crangon crangon was not in its reproductive annual maxima, and this may be the reason why, although present,

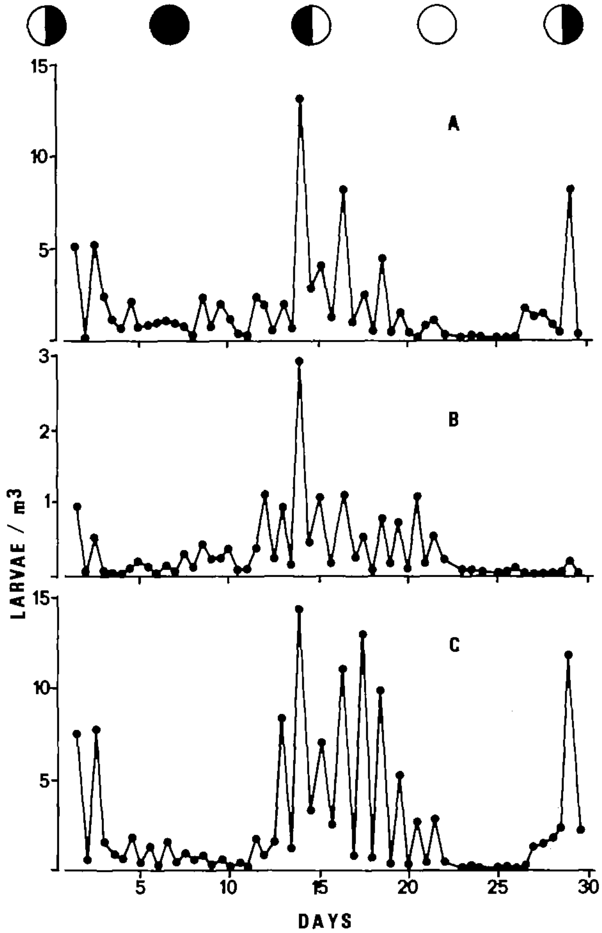

Fig. 2. Variation in the densities of stage I zoeae in the plankton. (A) *Palaemon* spp.; (B) *Crangon crangon*; (C) *Upogebia pusilla*. Full moon, new moon and quarters are indicated by open, closed and half-filled circles, respectively

it did not show a strong rhythm (Fig. 2b). Several authors have reported aperiodic larval release in crabs, when observations were made early in their breeding seasons (Wheeler 1978, Christy and Stancyk 1982). It seems that for some species the releasing activity gradually synchronizes with the semi-lunar period in the beginning of the breeding season.

Although June is in the maximum period of reproduction for *Xantho pilipes*, no obvious semi-lunar rhythm of larval-release was evident (Fig. 3c). Late larval stages of this crab are abundant in the upper estuary, suggesting that a retention process is involved (own unpublished observations). This species may have a pattern of larval release similar to *Rhithropanopeus harrisii* on the American coasts, with an essentially tidally related rhythm (Forward et al. 1982). *X. pilipes*, as *R. harrisii*, inhabits oyster beds of the upper estuary.

Palaemon spp. includes *P. adspersus* and *P. elegans*, both abundant on the *Zostera* spp. belts in the median parts of the estuary. Mid-June neap tides were the first period in the larval-releasing activity for *Uca tangeri*, because its zoeae begin to occur in the plankton during June (own unpublished observations).

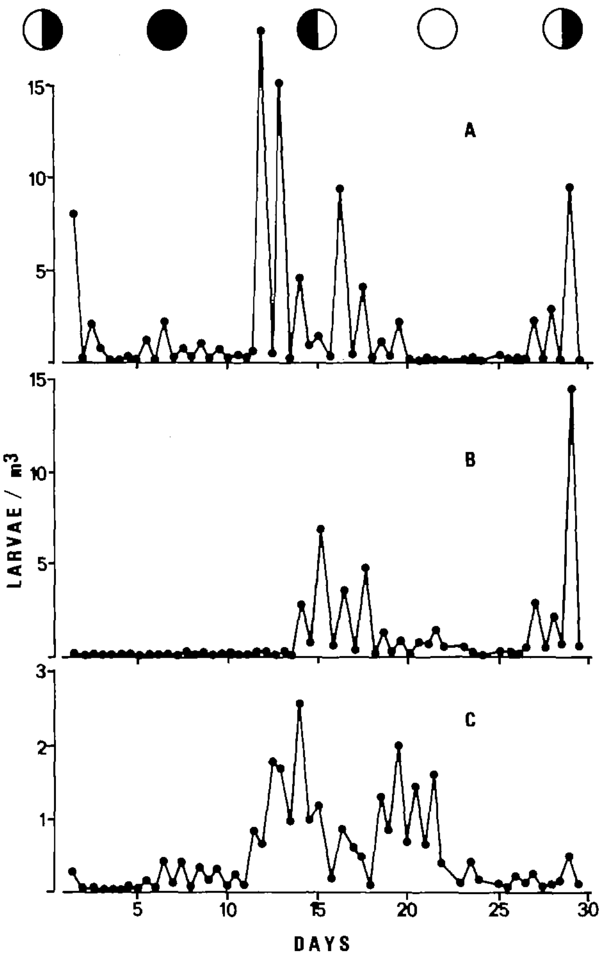

Fig. 3. Variation in the densities of stage I zoeae in the plankton. (A) *Anapagurus* sp.; (B) *Uca tangeri;* (C) *Xantho pilipes.* Moon phases are indicated as in Fig. 2

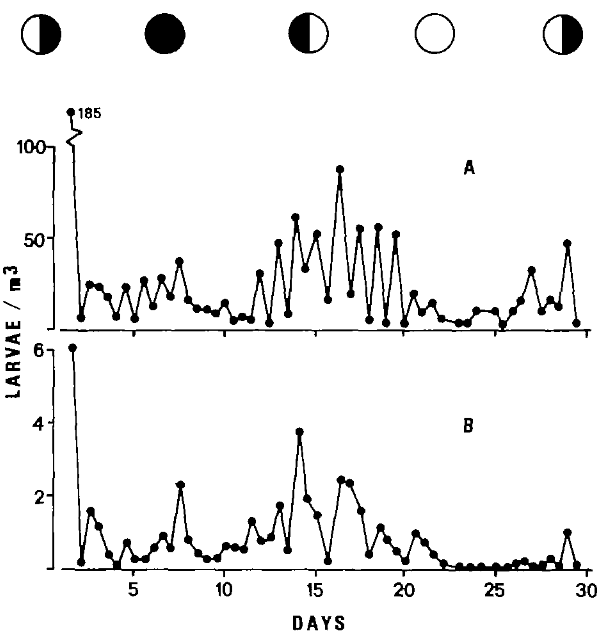

Fig. 4. Variation in the densities of stage I zoeae in the plankton. (A) *Pachygrapsus marmoratus;* (B) *Carcinus maenas.* Moon phases are indicated as in Fig. 2

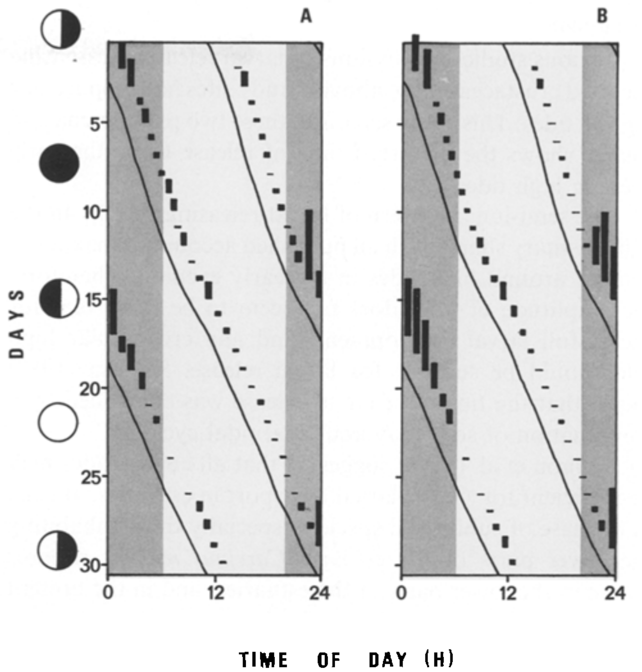

Fig. 5. Variation in the densities of stage I zoeae in the plankton, in relation to time of day and high tide. (A) *Palaemon* spp.; (B) *Upogebia pusilla.* Bars represent percentage lunar maximum of larval abundance. Continuous lines represent hour of high tide. Moon phases are indicated as in Fig. 2

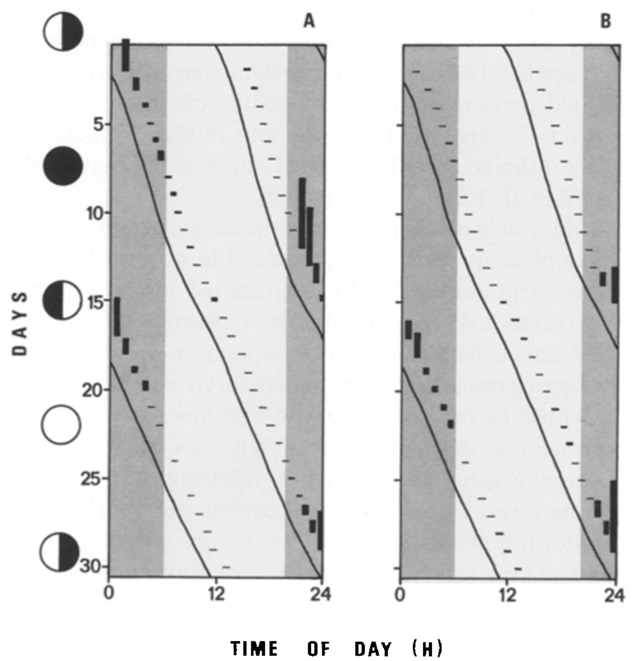

Fig. 6. Variation in the densities of stage I zoeae in the plankton, in relation to time of day and high tide. (A) *Anapagurus* sp.; (B) *Uca tangeri.* Larval abundance and hour of high tides are indicated as in Fig. 5. Moon phases are indicated as in Fig. 2

Figs. 5 and 6 summarize the abundance of the first zoeal stages of *Palaemon* spp., *Upogebia pusilla, Anapagurus* sp. and *Uca tangeri* over the lunar period in relation to the times of high tides and the light-dark cycle. Higher densities are consistently in the first half of the evening, when high tides prevail from sunset to around 24.00 (local time).

Discussion

In previous studies on rhythms of larval release of estuarine decapod crustaceans (see above), study sites had crepuscular highest tides. This study separates these two phenomena and clearly shows the preferred time of release to be the early evening high tides.

The semi-lunar pattern of larval-releasing activity in the Mira Estuary shares with all published accounts a maximum activity around high tides in the early evening. Therefore, the amplitude of tides does not seem to be important for successfull larval development, and any crepuscular high tide should be suitable for larval release. Saigusa (1982) found that the timing of larval release was controlled by a combination of solar day and local tidal cycle.

Salmon et al. (1986) suggested that all ebbing tides may be sufficient for "safe" larval transport in estuaries, at least in the case of sublittoral species, especially those inhabiting the lower parts of the estuary. *Carcinus maenas* releases larvae in the lower parts of the estuaries, and in the present study no apparent semi-lunar rhythm emerged.

There is no published study showing that differences in dispersion caused by neap or spring tides could significantly affect survival and recruitment. Differences between estuaries, namely the period of residence of the water mass and the average local amplitude of tides could be much stronger.

Release at night minimizes visual predation of both adult females and larvae (Ennis 1975, Branford 1978, De Coursey 1979, Bergin 1981, Christy 1982, Forward et al. 1982, Forward 1987). On the other hand, release during high tide could prevent larvae from reaching the upper parts of the estuary, where lethal combinations of high temperature and low salinity can affect larval survival (Christy 1982, Forward et al. 1982, Forward 1987).

At this point one may ask why the releasing activities do not take place on all night high tides, but only in the early evenings. The answer is probably related to the "swamp effect" (Lobel 1978) over predators. Synchrony in the emission of larvae by the releasing population would induce larval aggregation, increasing larval survival. The onset of night would be the only perceptible phenomena to induce synchrony, and the crepuscular high tide could perhaps act as entraining agent, inducing larval-releasing activity on the following days. Christy (1986) observed emission also on high tides following sunrise in *Petrolisthes armatus*, which could also be a synchronizing agent for some species.

As pointed out by Forward (1987) the time the females lay their eggs determines when in the lunar month they will hatch; thus, in order to fully understand the patterns of larval-release activity, the rhythmicity of oviposition and its entraining agents should be investigated. The semi-lunar rhythm of larval release could be a combination of a cycle of oviposition timing, incubation time, and tidal/diel rhythmicity of larval release activity.

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