

Larval release rhythms and tidal exchange in the estuarine mudprawn, *Upogebia africana*

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Received 16 February 1996; in revised form 9 July 1996; accepted 14 August 1996

Key words: estuary, tidal exchange, mudprawn larvae, semi-lunar, recruitment, behaviour

Abstract

The mudprawn, *Upogebia africana* is common in intertidal regions of many South African estuaries. The life cycle is complex, incorporating a marine phase of development during the larval stages. Breeding peaks are in summer and first-stage larvae are released into the plankton at night. Maximum release activity and export to the marine environment follow a semi-lunar cycle synchronized to the time when high water in the estuary is crepuscular. This occurs after peak spring tidal amplitude. Estuarine reinvasion by postlarvae is also nocturnal, and maximum return occurs after neap's when low water at sea occurs around sunset. Rhythmic cycles of larval export and postlarval estuarine reinvasion are therefore asynchronous during the lunar cycle and are best explained by the timing of the change in light intensity relative to high and low water respectively. If maximum activity rhythms of Stage 1 and postlarvae are independent of tidal amplitude, then timing of maximum release and reinvasion during the lunar cycle would alter as the time of sunset shifts between solstices. Much of southern Africa experiences a semi-arid type climate and most estuaries close off from the sea for varying periods owing to sandbar development across tidal inlets. Larvae do not metamorphose if trapped in estuaries and recruitment ceases. Thus, mudprawn populations are directly affected by tidal inlet dynamics. In extreme cases populations become locally extinct if inlets remain closed for extended periods.

Introduction

Active exchange of specific larval stages between estuaries and the marine nearshore is well-documented for littoral and supralittoral decapods, particularly brachyurans (Sandifer, 1975; Christy & Stancyk, 1982; Johnson & Gonor, 1982; DeCoursey, 1983; Epifanio et al., 1984; Epifanio, 1988; McConaugha, 1988; Dittel et al., 1991; Little & Epifanio, 1991; Queiroga et al., 1994). Newly hatched larvae released in estuaries are exported to adjacent coastal waters where they undergo further development before reinvasion of the adult habitat by megalopae and juveniles. Larval release patterns are rhythmic, usually in relation to tidal, diel and lunar cycles. Rhythms relating to the lunar phase are mostly semilunar, with releases mostly linked to the time of spring tides (Forward, 1987). If tidal and diel rhythms are also important, then most commonly larvae are released at the new and full moon, in the first

few hours after sunset and around the time of high tide (Forward, 1987).

A strategy of synchronized larval release linked to the spring tide cycle was commonly associated with increased potential for larval export, but as pointed out by Paula (1989), previous studies on the timing of larval release did not separate the effect of the change in light intensity from the effect of tidal amplitude. In the Mira estuary, larval release of most decapod species investigated followed a semi-lunar rhythm linked to crepuscular neap high tides (Paula, 1989). This suggested that larval release was connected to the hour of high tide, rather than to tidal amplitude (Paula, 1989). Observations by Queiroga et al. (1994) showed a similar larval release pattern for *Carcinus maenas* in the Ria de Aveiro, with highest peaks during nocturnal neap ebb tides. Peaks of abundance occurred any time during the night, but consistently followed high water. These observations supported Paula's conclusion that

it was the time of high tide during the day-night cycle rather than tidal amplitude that was important in promoting synchrony with the lunar cycle (Queiroga et al., 1994).

The timing of larval reinvasion of estuaries is poorly documented compared to the export phase. These mostly deal with brachyurans. Evidence suggests that movement into and up estuaries is by selective tidal transport, usually at night around spring tides (Epifanio et al., 1984; Dittel & Epifanio, 1990; Little & Epifanio, 1991). In other studies no clear difference in megalopal abundance between spring and neap tide phases was evident (De Vries et al., 1994; Queiroga et al., 1994).

Information on anomuran larval life history strategies and involving selective tidal transport is limited. Johnson & Gonor (1982) described the life history pattern of *Callinassa californiensis*, with Zoea 1 larvae flushed into the ocean on ebb tides. Megalopae entered the estuary on the flood. In their study all sampling occurred during daylight and no rhythms in the exchange process were investigated. *Upogebia pusilla* released larvae around crepuscular neap's (Paula, 1989), but no data on reinvasion by later stage larvae are available. Emmerson (1983) investigated larval movements in the mudprawn *U. africana*. Greater numbers of Stage 1 larvae were exported at night from the estuary during a spring compared to a neap tide. Although not specifically identified, late stage thalassinid larvae were collected on nocturnal flood tides, with no reported difference in abundance between spring and neap phases (Emmerson, 1983). Wooldridge (1991, 1994), subsequently concluded that the marine phase of development was obligatory for this species. The present study focuses on the timing of larval exchange in *U. africana* and reports on: (a) the timing of larval release in relation to diel, tidal and lunar cycles, (b) the timing of estuarine reinvasion by late-stage larvae and, (c) stage specificity with respect to observed larval distribution patterns.

Distribution of *Upogebia africana*

Upogebia africana is common in muddy substrata of many estuaries around southern Africa. It is endemic to the region (Day, 1981), with distribution up the east coast of Africa probably curtailed by high water temperatures (Hill & Allanson, 1971). It is often a dominant macrobenthic organism in intertidal regions; for example, in the Swartkops estuary it contributes

> 80% to total macrofaunal biomass on the mudflats (Hanekom et al., 1988). By contrast, Day (1981) observed that mudprawns were absent in estuaries that had 'closed for some time'. This species has a wide salinity tolerance range, molting successfully in 3.4 PSU (Hill, 1981).

Reproductive biology

Upogebia africana is reproductively active during most months of the year, with the onset of the breeding cycle coinciding with increasing water temperature after midwinter (Hill, 1977; Hanekom & Erasmus, 1989). Fecundity differs considerably between populations, although specific studies reflect a positive correlation between the size of *U. africana* and the number of eggs produced per brood (Hill, 1977; Hanekom & Erasmus, 1989). Prawns of 18.0 mm carapace length in the Swartkops estuary produced a brood size of about 1620 eggs (Hanekom & Erasmus, 1989). Prawns of the same size in the Kowie produced only about 1070 eggs (Hill, 1977). In the former estuary, the authors concluded that up to three broods were produced per annum. Maximum brood number was calculated for prawns in the Knysna system, with brood number increasing to seven in a sector of the estuary heated by effluent from a power generating plant (Hill, 1977). However, Hanekom & Erasmus (1989) reworked Hill's data and concluded that up to four broods of eggs were produced per female per annum.

The incubation time for eggs of *Upogebia africana* determined experimentally is given by $\log y = 4.037 - 1.881 \log x$, where y is the estimated development time in days and x the water temperature in °C (Hill, 1977). Thus at 25°C, development was complete in 25 days, at 21°C development was complete in 36 days, and at 15°C, eggs hatched after 67 days (Hill, 1977).

Materials and methods

Early life history of *Upogebia africana* are undescribed in the literature, but larvae collected in the field were identified after comparison with laboratory-reared animals. Four larval and a postlarval stage are produced, the first four stages exhibiting similar characteristics to those described for *U. affinis* (Sandifer, 1973).

Selective tidal transport of *Upogebia africana* larvae was investigated in the Swartvlei (diel and tidal cycles) and Gamtoos (lunar cycle) estuaries (Figure 1).

Swartvlei is an estuarine coastal lake 8.8 km² in area that connects to the sea by a meandering shallow channel 7.2 km in length. While the lake has a maximum depth of about 17 m, the channel does not exceed 4 m in depth (Whitfield, 1988). The estuary is only open to the sea in summer; during the remainder of the year alongshore transport of sand results in the mouth channel closing off from the sea.

The 21 km long Gamtoos estuary (Figure 1) is incised into a well-developed floodplain. The channel-like nature of the estuary results in a narrow intertidal zone that is generally < 10 m in width. A blind tidal arm 1.4 km from the mouth represents a former channel when the estuary opened to the sea 4 km to the east of the present inlet. Flooding in 1971 breached the barrier dune complex, creating a more direct channel to the sea. This blind extension of the estuary presently supports a large mudprawn population. Maximum estuarine width of 275 m occurs just inside the narrow inlet channel (50 m at MSL) and spans a well-developed flood tidal delta. The estuary narrows rapidly to 75 m in mid-estuarine regions, decreasing further to 25 m at the limit of tidal influence. Water depth in the main channel does not exceed 5 m, but is generally < 2 m. Maximum width and depth in the lagoon is 250 and 1.8 m respectively.

In the lake area of Swartvlei estuary, sampling for *U. africana* larvae was conducted monthly over 17 months at four stations. Near-surface samples were collected after dusk using a 75 cm diameter net of 500 μ m mesh. At each station about 70 m³ of water was filtered. Diel and tidal rhythms of larval release and postlarval return were also investigated in the Swartvlei system. These were done in summer during five 24 h sessions. On each occasion a single station in the tidal inlet (width 20 m, maximum water depth 1.9 m) was sampled hourly using the 75 cm diameter net, beginning at 08h00. Flood and ebb tide water volumes were computed hourly for all 25 h sessions, using a one-dimensional hydrodynamic model (Huizinga, 1987).

Zooplankton samples were collected monthly over 26 months at eight stations along the Gamtoos estuary. At each station, sub-surface and near-bottom samples were collected using two slightly modified WP2 plankton nets (57 cm diameter, 200 μ m mesh). Each net was attached to boom fixed on either side of the bow of a flat-bottomed boat (4.5 m length). This ensured that nets sampled in water undisturbed by propeller action. Shallow water at Stations 1, 5 and 7 (< 1.5 m depth) precluded near-bottom sampling at these sites. All sampling was done at night around new moon,

commencing on the ebb tide. Approximately 20 m³ of water was filtered on each occasion.

Larval release rhythms in relation to the lunar cycle were investigated during two extended field exercises in the Gamtoos estuary (August–September 1989; January–February 1990). The same sampling procedures were followed during the two exercises. The WP2 nets were deployed at a fixed station in the inlet channel (maximum water depth 1.5 m) along the eastern bank of the estuary. Four replicate samples were collected every 1.5 h, beginning at 17h00 and terminating at 08h00 the following morning. During the first exercise, the 15 h sessions were conducted weekly for five weeks over alternate spring and neap tides. A final sampling session was undertaken in the seventh week. This resulted in a series of samples representing three neap's and four spring tide periods. Sampling during the second exercise (January–February 1990) was undertaken over 16 days, sampling every second night beginning at 17h00 and terminating at 08h00 the following morning. The exercise commenced during a neap tide phase (Last quarter) and ending the following neap.

Tides are semidiurnal, with high water of spring tides occurring around 16h00 on the coast. Thus one of the two daily high waters centred around sunset follows after maximum tidal range.

Results

Upogebia africana larvae were not present in Swartvlei lake samples. Only first-stage larvae were recorded in the Gamtoos (Figure 2). Single peaks in larval abundance occurred relatively late during the summer of 1990 at Station 2 (near-surface abundance, > 2800 ind m⁻³; below midwater, 191 ind m⁻³). In the following summer, maximum larval abundance was recorded in December at Station 4 (near-surface abundance, > 5000 ind m⁻³; below midwater, 950 ind m⁻³). The relative distribution of larvae in the water column was consistent, with significantly more larvae nearer the surface compared to deeper waters (Wilcoxon sign test, $Z = 7.212$, $N = 54$).

The release of Stage 1 larvae by *U. africana* and the return of postlarvae collected in the inlet of the Swartvlei estuary indicated diel and tidal rhythms of activity. Patterns were repetitive for the five 25 h sessions and only two data sets are presented (Figures 3A & 3B). Sampling sessions were separated by one week; collected approximately three days after the peak of

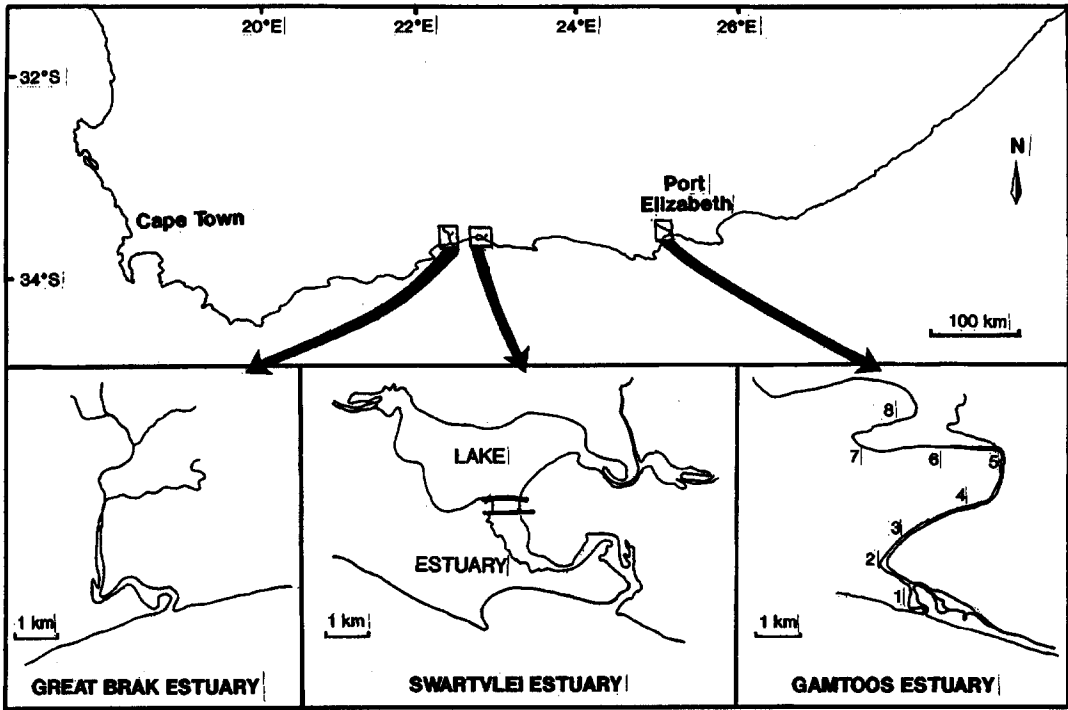


Figure 1. Map of southern Africa showing the locality of estuaries mentioned in the text. Physical aspects of estuary are also shown.

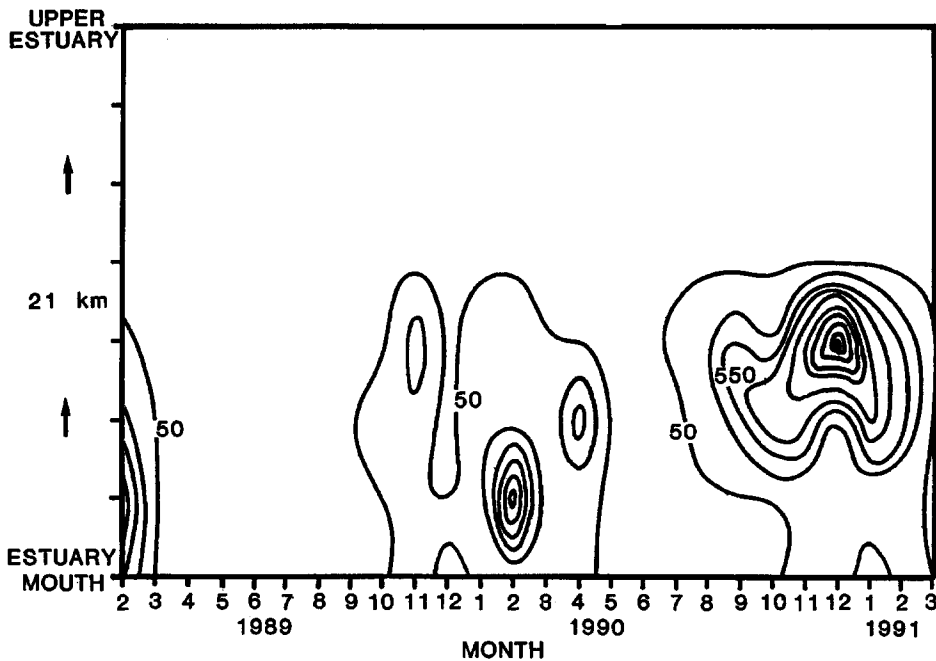


Figure 2. Distribution of Stage 1 *Upogebia africana* larvae in the Gamtoos estuary. Sampling was undertaken on the ebbing tide on each occasion. No other larval stages were present in zooplankton samples. Minimum density shown in 50 larvae m^{-3} of water. Interval is 500 larvae m^{-3} . Maximum recorded exceeded 5000 m^{-3} in December 1990.

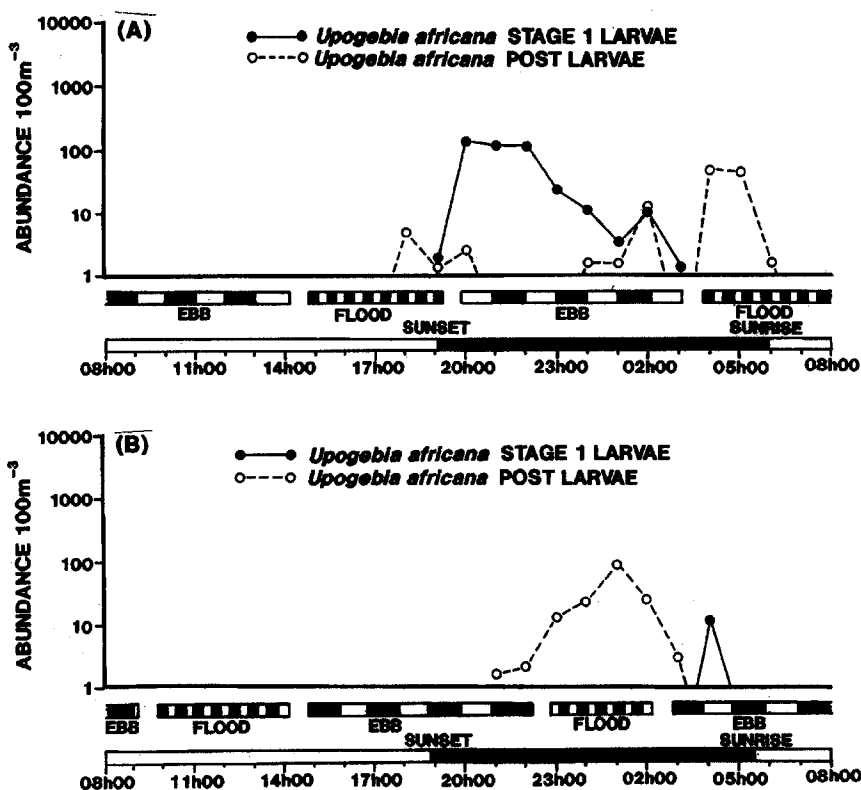


Figure 3. Diel and tidal rhythms of *Upogebia africana* stage 1 and postlarvae. Zooplankton samples were collected in the tidal inlet of Swartvlei estuary on the 22–23rd October 1986 (3A) and 29–30th October 1986 (3B).

spring and neap tides respectively. Larvae were present at night only, with larvae showing stage-specific relationships to the state of the tide. During spring tide sampling (Figure 3A), maximum abundance of Stage 1 larvae was recorded shortly after sunset (200 ind 100 m⁻³). Abundance levels remained relatively high over the first two hours, but declined during the remainder of the protracted ebb tide (> 7 h). *U. africana* postlarvae appeared briefly towards the end of the flood in the late afternoon, and again in the latter part of the ebb. Numbers however, were generally low (< 10 ind 100 m⁻³). Postlarvae were again present during the pre-dawn phase of the flood tide, leaving the plankton at sunrise.

Neap ebb tide commenced at ca 14h45 the following week and persisted well beyond sunset (Figure 3B). No Stage 1 larvae were present in the plankton during this time. Postlarvae appeared towards the end of the ebb, attaining peak abundance (ca 100 ind 100 m⁻³) after midnight on the flood tide. Stage 1 appeared in low numbers just before dawn and after the change of the tide (9 ind 100 m⁻³).

Flood and ebb tide water volumes (Huizinga, 1987) integrated with larval abundance per hour (Figures 3A & 3B), provided information on net flux across the Swartvlei mouth for the two 24-h series (Table 1). Both series showed a net export of Stage 1 larvae on the ebb tide and a postlarvae gain to the estuary on the flood tide. Greater numbers of Stage 1 larvae were exported around spring tide, while postlarvae returned to the estuary in greater numbers around the neap sampling period.

The greater abundance of Stage 1 around spring tides was also evident during the two field exercises undertaken in the Gamtoos estuary. Weekly sampling during the first exercise showed that average ebb tide abundance of Stage 1 larvae was significantly greater at spring tides compared to neap's ($p < 0.05$, Kruskal-Wallis test). There was no statistical difference in larval abundance between new and full moon spring tides ($p > 0.05$, Kruskal-Wallis test). Postlarval numbers were consistently low during the first exercise, and it was not possible to determine whether differences existed between spring and neap periods.

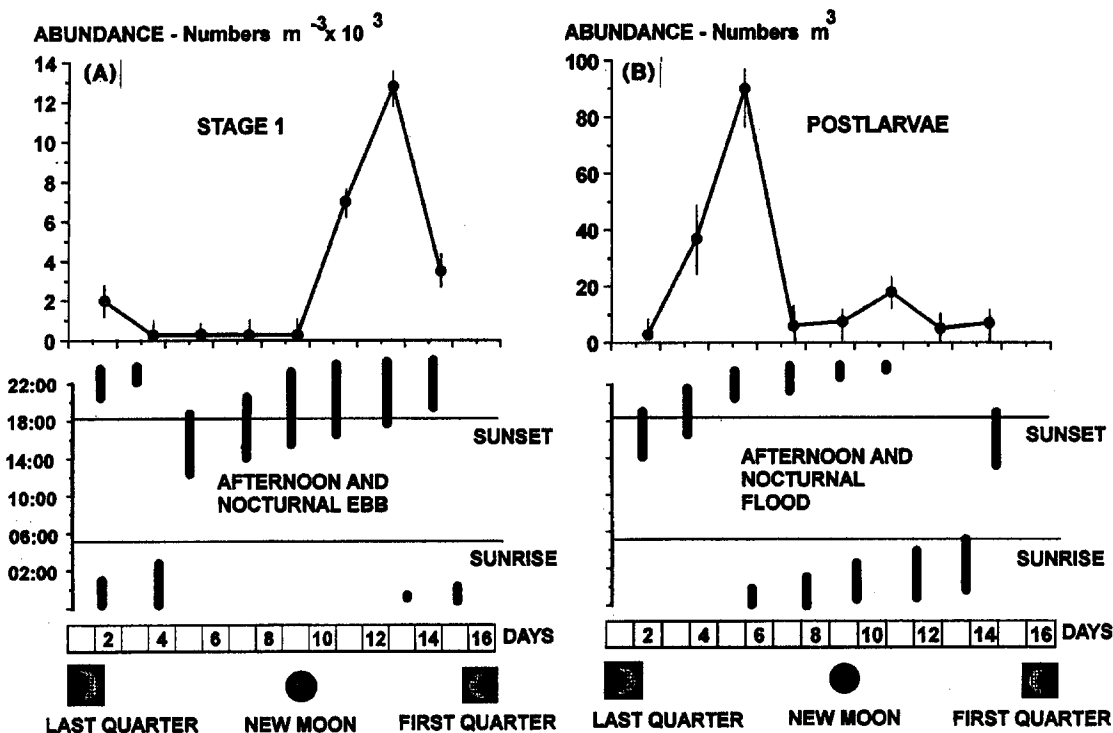


Figure 4. Stage 1 larval export (4A) and postlarval import (4B) of *Upogebia africana* in the Gamtoos estuary. Sampling undertaken on alternate nights beginning 17:00 and terminating 08:00 the following morning. Four replicate samples collected every 1.5 h. Data points indicate mean abundance (± 1 SD) over the ebb (4A) or flood (4B) phase for each sampling date. Data points represent between 20 and 28 samples, depending on the duration of the flood or ebb tide.

The pattern of maximum larval release around tides was confirmed during the 16-day Gamtoos exercise (Figure 4A). However, peak larval abundance in the plankton did not coincide with predicted maximum tidal amplitude (1.78 m for Port Elizabeth on Day 11; Hydrographer, 1990), but on the following sampling occasion when sunset coincided with high water in the estuary. This occurred on Day 13 when predicted tidal amplitude at sea was 1.67 m (Hydrographer, 1990). The association between larval abundance and crepuscular high water is further shown by comparing Day 9 with Day 15 (Figure 4A). On Day 9, relatively low numbers of Stage 1 larvae coincided with a tidal amplitude of 1.55 m (Hydrographer, 1990); larval abundance on Day 15 was an order of magnitude higher, but predicted tidal amplitude was only 1.14 m. On the latter occasion high tide in the estuary occurred shortly after sunset (Figure 4A).

Maximum abundance of postlarvae entering the estuary was recorded when low slack water at sea occurred around sunset (Figure 4B), and when tidal amplitude had just passed its lowest predicted val-

ue (0.26 m for Port Elizabeth on Day 3; Hydrographer, 1990). These peaks in Stage 1 and Postlarval abundance therefore follow the pattern described for Swartvlei (Table 1). In both estuaries maximum numbers of Stage 1 occurred around spring tides, while postlarvae were more abundant around neap's.

Discussion

Semi-lunar, diel and tidal rhythms of larval release widely described for estuarine invertebrates (e.g. De Coursey, 1983; Epifanio, 1988; Forward, 1987; Paula, 1989 among others) are also entrained in *Upogebia africana*. Although the timing of maximum release in *U. africana* was linked to the spring tide phase of the lunar cycle, consecutive sampling at two-day intervals showed that peak larval abundance in the plankton centred on crepuscular highwater. This occurred after the timing of maximum tidal amplitude (Figure 4A). Paula (1989) concluded that tidal amplitude was less important than the timing of high tide and that any crepuscu-

Table 1. Flux of *Upogebia africana* larvae across the mouth of the Swartvlei estuary during two 24 h sampling series (22–23rd October and 29–30th October 1986). Water volumes were computed using the 1-dimensional hydrodynamic model of Huizinga (1987). Hourly flow volumes were integrated with larval abundance shown in Figures 3A and 3B. (+) indicates net flood tide import and (–) net ebb tide export for the specific larval stages (after Wooldridge, 1994)

	Stage 1		Postlarvae	
	Day	Night	Day	Night
Post-spring (3 days)				
Flood tide	0	817	7613	88367
Ebb tide	0	540528	0	0
Net export (–) or import (+)	–539711		+95980	
Post-neap (3 days)				
Flood tide	0	0	0	202455
Ebb tide	0	9843	0	2175
Net export (–) or import (+)	–9843		+200280	

lar high tide should be suitable for larval release. Previous studies mostly centred on a comparison of samples collected at spring and neap tides, without considering shorter-term temporal patterns associated with a particular tidal phase. In regions where highest tidal amplitude and sunset clearly do not coincide, the association between larval abundance and crepuscular high tide support Paula's conclusion that larval-releasing activity is connected to the hour of high tide rather than to tidal amplitude (e.g. Christy, 1986; Queiroga et al., 1994).

Maximum estuarine incursion by *Upogebia africana* postlarvae was synchronized to the timing of crepuscular low tide at sea. Respective peaks in Stage 1 efflux and postlarval influx are therefore asynchronous. Whereas maximum release of first-stage larvae occurred after highest tidal amplitude, postlarval return peaked after lowest tidal amplitude. These data support the conclusion that change in light intensity and timing of the early evening tide is also the more important trigger for *U. africana* postlarval return, rather than tidal amplitude. These data also suggest a semilunar cycle of larval reinvasion. Although postlarval density may be lower around spring tides, the larger water volume moving through the inlet may mask the net gain to

the estuarine population. Despite differences in water volume exchanged between spring and neap tide periods, Table 1 still reflected a greater gain of postlarvae around neap's in the Swartvlei system.

Larval release patterns in *U. africana* peaked after highest tidal amplitude. Although the potential for successful seaward transport on the larger water volume is reduced, export is promoted by rapid larval release close to high tide as well as larval behaviour rhythms. In *U. africana* the nocturnal appearance of Stage 1 in the plankton was abrupt (Figure 3A), with peak numbers present at the beginning of the ebb tide. Integration of ebb tide water volumes (Huizinga, 1987) and larval abundance illustrated in Figure 3A, showed that > 90% of larvae left the estuary during the initial 3 h of the protracted (7 h) ebb tide. Export from the estuary was further promoted by near-surface aggregation of larvae where water velocities are maximal.

If activity rhythms of Stage 1 and Postlarvae are independent of tidal amplitude, then timing of maximum larval release and estuarine reinvasion by postlarvae would alter during the lunar cycle as the time of sunset shifts between the solstices. At the beginning of the breeding season in winter, maximum release of larvae would occur nearer spring tides (local sunset occurs around 17h15 in mid-June) compared to 19h30 in mid-December (see Figure 4A). Similarly, maximum postlarval reinvasion would shift nearer neap's in winter compared to December. This would be necessary for rhythms of optimal activity to maintain synchrony with crepuscular high and low water respectively.

Upogebia africana is absent in closed estuaries (Day, 1981) and two hypotheses have been put forward in an attempt to explain their absence in these systems. Day (1981) suggested that since *U. africana* is a suspension feeder, detrital transport would cease in non-tidal estuaries and this would account for its disappearance. Alternatively, Wooldridge (1991, 1994) concluded that the marine phase of larval development in *U. africana* is obligatory. First-stage larvae do not metamorphose if trapped in closed systems. Thus, survival of estuarine populations is dependent on the temporal relationship between open and closed phases of the inlet. This was shown for the population in the Great Brak estuary (Wooldridge, 1994). Although the inlet opened twelve times between April 1990 and September 1992, recruitment occurred once only when the inlet remained open to the sea for one month. The net effect was a discontinuity in size-class distribution that manifested itself in clumped cohorts that shifted

in accordance with described growth rates (Hanekom & Baird, 1992).

Most South African estuaries do not maintain a permanently open channel to the sea (Reddering & Rust, 1990) leading to temporary curtailment in larval exchange. Generally, tidal inlets become constricted or periodically blocked by sandbars (Reddering, 1988). Of the 289 river mouths along the southern African coast, only 37 or 12.8% maintain a permanent connection with the sea. Most of these estuaries are also small, having tidal prisms of 10^6 m³ or less (Reddering & Rust, 1990). Climatic characteristics of the region, coupled to a growing demand for freshwater, have led to an increasing requirement for irrigation and storage reservoir schemes. Major dams now have a total capacity greater than 50% of the total mean annual runoff in the region (Department of Water Affairs, 1986). Reduced freshwater discharge into estuaries, particularly during flood events, has resulted in less effective scour and removal of accumulated sediment (Reddering & Esterhuysen, 1987; Reddering, 1988; Whitfield & Bruton, 1989). Smaller floods may even be filtered out of the discharge spectrum (Reddering & Esterhuysen, 1987). Because of changing river flow patterns, natural cycles of opening and closing of tidal inlets are being artificially modified and many estuaries close more frequently and remain so for extended periods. These anthropogenic perturbations have significant and negative implications for estuarine organisms that incorporate a marine phase of development during their life cycle.

Acknowledgements

The FRD Estuarine Joint Programme, Department of Environmental Affairs and University of Port Elizabeth are acknowledged for financial support.

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