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THE SPATIAL AND TEMPORAL DISTRIBUTION OF MYSID SHRIMPS AND PHYTOPLANKTON ACCUMULATIONS IN A HIGH ENERGY SURFZONE

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ABSTRACT — Rich concentrations of the diatom, *Anaulus australis* (Drebes and Schulz) are regularly recorded in high-energy surfzones along the south coast, southern Africa. Diatom accumulations exhibit well defined patterns of formation and dissolution which are closely linked to the morphodynamic state of the beach and the diel cycle. The tichoplanktonic mysid shrimp, *Gastrosaccus psammodytes* O. Tattersall, is endemic to the surfzone and feeds extensively on this diatom. Evidence is presented which supports the hypothesis that the mysid responds to spatial and temporal variations in distribution of the primary food source. During the day, significantly greater numbers of mysids are regularly associated with diatom patches which are located in close proximity to rip systems adjacent to the beach. While lateral currents feeding into rip channels are probably the main forcing function in dictating mysid distribution patterns, relatively low energy surf conditions would permit mysids, particularly adults, to respond to a concentration gradient and exploit the rich food supply. At night, *A. australis* becomes endopsammic and is not available to mysids foraging in the water column. Previous studies have shown that at this time, the brooding component of the population remains inshore becoming more carnivorous in their feeding behaviour. Other classes (non-brooding component) disperse more widely, ranging beyond the breaker line where then exploit an alternate food supply available to them.
INTRODUCTION

The tichoplanktonic mysid shrimp *Gastrosaccus psammodytes* O. Tattersall, is abundant along sandy shores in southern Africa (Wooldridge, 1983). It contributes significantly to the surf zone macrofaunal food web along the Sundays river beach (McLachlan and Bate, 1985), where it feeds extensively on the diatom *Anaulus australis* (Dredes and Schulz; Webb et al., 1988). This diatom (formally *A. birostratus*) accounts for over 95% of total annual primary production in the system and this has been estimated to be 480 g C m⁻² yr⁻¹ or 120 kg C per running meter of surf zone per year (Campbell and Bate, 1988).

A distinctive feature of *Anaulus australis* is the regular occurrence of visible accumulations (McLachlan and Lewin, 1981) which are generally associated with rip-current activity in the surf (Talbot and Bate, 1987a). Clear patterns of diel periodicity are evident, the concentration of cells in the water column decreasing significantly after dark (Talbot and Bate, 1986, 1987a).

During the day, the concentration of cells is also greater near the water surface compared to the water column. This surface accumulation of cells is due to their positive buoyancy by cell adherence to air bubbles. A neustonic mode of life aids retention within the surf zone and is effected through onshore shear stress of wave bores which impart a net shoreward vector of surface water layers (Talbot and Bate, 1988a). Cells entrained in the water column are advected seawards through rip systems, the seaward shift of entrained cells extending to the limit of rip-head activity. When rips discharge into relatively calm water, *A. australis* cells sink due to a reduction in air bubble formation as waves cease to overtop.

*Anaulus australis* also exhibits a well defined pattern of temporal variability. In the late afternoon cells become psammophytic, adhering to sediment particles as a consequence of anatomical changes at the surface of the cell's frustule (Talbot and Bate, 1988a). As a result, cells disappear from the water column and are not available to foraging mysids.

Both *Anaulus australis* and *Gastrosaccus psammodytes* are primarily associated with the breaker zone, becoming quantitatively unimportant further offshore (McLachlan and Bate, 1985; Talbot and Bate 1988b; Wooldridge, 1983). This degree of endemism and the distinctive pattern in the distribution of *Anaulus australis* led to the hypothesis that *G. psammodytes* may itself respond to temporal and spatial variations in the distribution of the primary food source (Wooldridge, 1983). This possibility prompted the following questions: 1) does *G. psammodytes* occur in greater numbers in association with the phytoplankton accumulations than in areas of relatively low diatom concentrations ?, and 2) if so, is this association a response to physical and/or biological influences ?

STUDY SITE

Surveys were carried out 2 km from the mouth of the Sundays estuary in the eastern sector of Algoa Bay (Fig. 1). The beach is uninterrupted for 42 km and although occasionally dissipative, its modal morphodynamic state is classified as Intermediate (Short and Wright, 1983). In this state the beach is characterized by active rip systems separated by welded bars occurring at a frequency of two per running kilometer of beach (Talbot and Bate, 1987b). Surf zone width is generally 300 m and median sand particle size ca 260 μm (McLachlan and Hanekom, 1979). Wave height at the breakpoint ranges from 1 to 6 m (McLachlan and Bate, 1985). Intertidal width is 50 - 60 m (McLachlan, 1980b). Tides are semi-diurnal subequal with a maximum spring range of 2.1 m (McLachlan and Bate, 1985).

![Fig. 1. — Map illustrating the locality of the Sundays river beach in Algoa Bay, South Africa.](image)

METHODS

Microtopography of the study area was surveyed on each of nine visits spanning a period of 18 m (Table I). These visits cover a range of morphodynamic states. On each occasion, up to ten transect lines were established at 25 m intervals perpendicular to the shoreline. Transects were marked by a series of poles beginning at spring high water and extending into the surf to a depth of ca 1.5 m. Surveys were done using a dumpy level and stadia rod. Isobaths were drawn by eye.

Mysids were sampled using a sled 50 cm wide towed for a distance of 20 m along each transect line. Sampling commenced about 1 h before low water of spring tide (10h00) on each occasion, beginning at Station 1. A sampling session was completed in about 3 h. Tows were undertaken by a single operator wading in the surf. The bottom leading edge of the sled was inverted and serrated, removing the top cm of substrate when towed. Sand and organisms present were swept towards the back.
of the sled, the sand filtering through an inclined stainless-steel mesh floor (1 mm aperture). Mysids were retained in a plankton net attached behind the sled.

Replicate samples were taken at all stations, the sled held at arms-length and to the side of the worker so that the advancing sled sampled untrampled substrate during the course of a tow. Maximum depth to which the sampler could be handled was about 1.5 m. In the laboratory entire samples were enumerated. Mysids were separated into adult and immature classes, based on the form of the female brood pouch or male third pleopod.

Longshore distribution of mysids was statistically tested using one-way Analysis of Variance (ANOVA). Data from individual transect lines were pooled into three sets, depending on locality relative to rip systems. Variance homogeneity was tested using Bartlett's test. In the absence of rips (Dissection of the beach, Talbot and Bate, 1987b), while others may operate on a larger scale across the outer boundary into the nearshore.

In an intensive investigation of the dynamics of Anaulus australis along the Sundays river beach, Campbell (1988) recorded average chlorophyll $a$ concentrations of 14 - 15 mg m$^{-3}$ in areas outside the phytoplankton patches. Patches first become visible at 40 - 100 mg chlorophyll m$^{-3}$. Concentration is maximal in surface foam (adherence to air bubbles), but regular redispersion into the water column occurs as a result of wave turbulence. During her study, Campbell (1988) visually rated the intensity of patches on a scale of 1 to 10 and regressed these values against chlorophyll $a$ concentration. On this scale a patch intensity of 10 related to a concentration of 15 000 mg m$^{-3}$. The relationship was exponential and was expressed as $y = 341.1 \times \exp (0.348 \times x)$, $F$ statistic = 0.410, d.f. = 31 and $p = 0.75$ for phytoplankton patches. Patches first become visible at 40 - 100 mg chlorophyll m$^{-3}$.

RESULTS AND DISCUSSION

During the day, visible phytoplankton accumulations were present in the surfzone on five of the nine visits and all were closely associated with active rips during the duration of sampling (ca 3 h). On the first occasion (Fig. 2, Table I), a mean of 76 (95% confidence level $\pm 12$, $n = 4$) adult mysids per 10 m$^2$ was present in association with the A. australis patch. This was significantly higher than mean abundance on the adjacent beach terrace where no phytoplankton was visible ($21 \pm 7$, $n = 12$).
Corresponding numbers of immature mysids averaged 36 and 26 respectively with no significant difference between locations. At the eastern end of the terrace, an active rip was also evident, but no *A. australis* accumulation was present. Along this rip edge, abundance of immature mysids averaged 118 (+ 20, n = 2). This was significantly higher than their abundance on the adjacent terrace. Adults averaged 20 (+ 12, n = 2) along this transect line (T10) and this was significantly lower than their abundance in the phytoplankton patch near the western rip. Along T10, adult numbers did not differ significantly from that recorded on the beach terrace.

During a further exercise (Fig. 3, Table I), adult numbers were significantly higher in the patch area (80 ± 16, n = 2) than on the beach terrace (44 ± 10, n = 4). No phytoplankton was visible on the opposite side of the rip and here mean adult abundance was lower relative to the patch area, but the difference was not significant at the 95% level (51 ± 16, n = 2). The distribution of immature mysids followed the pattern described in Fig. 2, with significantly greater numbers present in the patch (51 ± 25, n = 2) than on the beach platform where no phytoplankton was visible (18 ± 17, n = 4). Again numbers were higher on the edge of the rip (96 ± 25, n = 2) than in the phytoplankton patch, but the difference was not statistically significant.

Results for the remaining exercises are not illustrated, but are fully discussed with a summary presented in Table I. On the third occasion when phytoplankton was visible in the surf, adult patterns of distribution mirrored that illustrated in Fig. 2. Significantly greater numbers were recorded in association with the patch (174 ± 41, n = 2) than along the rip-edge (28 ± 32, n = 3), or on the beach terrace (20 ± 40, n = 2); effectively the latter two groups of samples had few or no mysids present. Immature mysids occurred in significantly greater numbers in association with the patch (31 ± 14, n = 2) and along the rip edge (29 ± 14, n = 2) than on beach terrace (8 ± 10, n = 3).

Adult mysids were homogeneously distributed along the beach on a single occasion when *Anaulus australis* patches were visible (59 ± 20, n = 5 and

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50 ± 13, n = 11 for the patch and beach terrace respectively). Abundance was significantly less along the edge of the rip (2 ± 33, n = 2). Immature mysids were similarly distributed, with no significant difference between locations (163 ± 107, n = 5 in the locality of the patch and 234 ± 73, n = 11 on the beach terrace). Numbers were less along the edge of the rip for both adults and immatures, but mean densities did not differ significantly from other areas sampled.

On the following day, the same locality was sampled for *Gastrosaccus psammodytes*. The phytoplankton patch was relatively small and only visible at a single transect site. Here, adult abundance was significantly greater (92 ± 17, n = 2) than at the other seven transects where abundance was statistically homogeneous with the mean not exceeding 33 at any site. Immature *G. psammodytes* followed the same pattern, with significantly greater numbers associated with the *Anaulus* patch (116 ± 24, n = 2). Mean abundance at the other localities did not exceed 56.

No phytoplankton was visible in the surfzone on a further two occasions. Neither visit reflected any significant difference in longshore distribution of adult mysids, but immatures on one occasion were significantly more abundant on the edge of the rip (181 ± 32, n = 2) than on the beach terrace (41 ± 30, n = 2). On the second visit, longshore abundance of immature mysids was not statistically different.

The remaining two sampling sessions were undertaken shortly after storm waves resulted in a dissipative surfzone state. The visits were separated by two weeks during which time no rips were present. On both occasions the longshore distribution of adult and immature mysids was statistically homogeneous.

The occurrence of increased mysid abundance in association with phytoplankton accumulations may be due to longshore transport of animals by water currents as they flow into rip channels, or mysids may actively seek out increased concentrations of the food source. Both would result in greater numbers of mysids adjacent to active rips. However, the degree to which each influences redistribution probably fluctuates, the latter becoming more important when current velocity is relatively low. Current velocity may vary on a spatial and temporal scale; increasing towards rip channels, as well as responding to short-term oscillations between waves. Maximum velocity, however, is associated with rip channels where they may average up to 1 m sec⁻¹, but velocities exceeding 2 m sec⁻¹ have been recorded (Talbot and Bate, 1987c).

The potential redistribution of mysids by currents will be determined by a number of factors, including water velocity, the spatial distribution of the population, the degree of pelagic activity displayed by different size-classes as well as swimming ability of individuals. Smaller mysids would be more vulnerable to translocation compared to their adult counterparts since their swimming ability would be less effective in holding station against relatively strong...
currents. Although *Gastrosaccus psammodytes* has not undergone specific morphological change to facilitate survival in such a physically harsh environment, behavioural adaptations are well developed. These are linked to intraspecific zonation of the population (Wooldridge, 1983). Adult females are closest inshore where they remain buried in the sand below the swashline. Other classes are further distant from the beach. By remaining in a band higher up on the shore where much of the wave energy has dissipated, adult females will be less frequently disturbed from the substrate. Conversely, the greater proportion of immature mysids nearer the wave breakpoint would result in increased disturbance from the substrate as wave turbulence reworks the sediment. Increased pelagic activity of immature mysids would render them more susceptible to relocation by water transport compared to their brooding counterparts closer inshore.

Although longshore currents feeding into rip channels are probably the main forcing function in observed spatial patterns of mysid distribution, larger individuals may to some degree, actively seek out phytoplankton accumulations. This would only be possible under relatively low energy surf conditions. Once present in a foodpatch, greater swimming ability would aid them in maintaining station during forays to the surface to exploit a rich food supply. Prevailing water velocities would be a critical factor and would imply that larger individuals are less transient than immature mysids.

Phytoplankton accumulations and adult mysid females generally occur in overlapping depth bands along the beach. Reproductive activity is a continuous process in *Gastrosaccus psammodytes*, with individual females producing multiple broods of up to 80 young per brood (Wooldridge, 1983). These are released at intervals of 10 days under summer conditions, the interval between brood release and extrusion of a further batch of eggs being about 24 h. Reproductive demands are therefore high, and it would be advantageous for adult females to conserve energy by maintaining a proportionally greater benthic existence as well as exploiting a concentrated food source. In this respect, brooding females were always well represented in samples collected in the vicinity of the *Anaulus australis* accumulations (Fig. 2 and 3).

Two active rips were present during the exercise illustrated in Fig. 2, but only the rip system at the western end of the beach terrace has an associated phytoplankton patch. Although numbers of immature mysids were significantly higher along the margins of each rip, increased numbers of adults were only present in association with the phytoplankton patch at the western end. These data support the hypothesis that although current velocity might have been the principal forcing function in determining distribution of smaller mysids, they were sufficiently weak across the beach terrace to enable adults to maintain station and respond to a biological gradient and exploit the concentrated food supply. This pattern of differential distribution of adult and immature mysids relative to the presence or absence of phytoplankton along the beach terrace was also recorded on other sampling occasions (Table I). But beyond a threshold velocity, currents would become the principal forcing function in dictating mysid distribution.

In the late afternoon, *Anaulus australis* disappears from the water column and cells become psammophilic (*Gastrosaccus psammodytes*). These diel changes in phytoplankton behaviour also coincide with mysid redistribution patterns. In contrast to diurnal patterns of spatial distribution, night sampling indicates that part of any mysid population becomes planktonic, animals moving offshore behind the breaker line (Wooldridge 1981, 1983). Differential pelagic activity is evident between population size classes, with immature mysids being most active (McLachlan *et al.*, 1979; Wooldridge, 1983). This change in the diel pattern of behaviour is also associated with changes in diet (Webb *et al.*, 1988). Mysids do not feed on psammophilic *Anaulus australis* and the absence of this diatom in the water column at night (Webb and Bate, 1986), results in a marked change towards a carnivorous diet in that component of the population which remains in the inner surfzone at this time (Webb *et al.*, 1988). The continued presence of mysids inshore is largely due to the brooding component of the population (Wooldridge, 1983), and this general benthic existence would again conserve energy otherwise spent in pelagic activity.

Diurnal entrainment of particles in rip currents would result in offshore transport (Webb and Bate, 1988b). Since *Anaulus australis* remains in the inner surfzone because of its association with airbubbles, cells periodically lost to the inner zone and transported behind the breaker line would begin to settle out in this calmer area due to the lack of airbubble formation. Consequently, increased concentrations of *A. australis* may accumulate near the bottom behind the breakers where they remain until stirred up and advected shorewards by an increase in wave energy (Webb and Bate, 1986c). Accumulations of these cells behind the breakers in hypothesized for the nocturnal offshore migration of *Gastrosaccus psammodytes*. In the absence of the availability of *A. australis* in the inner surfzone at night, pelagic mysids can continue to exploit accumulations of food through migration. Conversely, mysids generally located offshore during the day, could migrate onshore and also exploit the same foodresource. This has been shown for the gregarious species, *Mesopodopsis slabberi* which occurs in high numbers (up to 15,000 m⁻³) just above the substrate and immediately behind the breaker line at this time (Webb *et al.*, 1987).
The distribution and behaviour of these two mysid species is thus closely associated with the spatial and temporal periodicities of the primary foodsource along the Sundays river beach. This association is particularly evident for the diatom *Anaulus australis* and *Gastrosaccus psammodytes*, both of which are endemic to the surfzone ecosystem.

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