Diel horizontal migration of *Mesopodopsis slabberi* (Crustacea: Mysidacea) in Algoa Bay, southern Africa

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ABSTRACT· The mysid shrimp *Mesopodopsis slabberi* (van Beneden), exhibited a diel pattern of onshore-offshore movement off Sundays River beach, South Africa. Shoreward migration at sunset resulted in the presence of relatively high numbers of mysids after dark behind the breaker line (ca 6 m water depth) compared to further offshore. At first light, *M. slabberi* migrated back to deeper water (> 15 m) where it remained during daylight. The nocturnal presence of mysids behind the breakers is interpreted as a response to increased concentration of phytoplankton, principally *Anaulus australis* Drebes and Schulz, which outwelled from the inner surfzone through rip current activity. Consumption by *M. slabberi* was estimated to be 51 g C d^{-1}. On an annual basis, this approximated to 70 % of total available carbon consumed by the macrofaunal trophic assemblage in the Sundays River surfzone.

INTRODUCTION

Studies on the migration of zooplankton usually focus on stimuli inducing vertical migration and the adaptive significance of such movements (Enright 1977, Enright & Honegger 1977, Ringelberg 1980, Angel 1985). Other types of directed movement, i.e. movements resulting in patchy, non-random horizontal patterns (Hutchinson 1967), shore avoidance (Siebeck & Ringelberg 1969), daytime swarming followed by nocturnal dispersal (Hamner & Carleton 1979), and long distance horizontal migrations (Hamner & Hauri 1981), have received comparatively less attention.

In mysids, horizontal migration has been recorded for *Mysis relicta* in Lake Tahoe, Donner Lake and Fallen Leaf Lake in California/Nevada, USA (Morgan & Threlkeld 1982). Size dependent movements in these mysids were related to dietary changes during ontogenetic development. Williams & Collins (1984) investigated the seasonal distribution and variability in abundance of *Schistomysis spiritus* in the Bristol Channel, UK, and proposed that the horizontal movements of these mysids were affected by a number of biotic and physical variables acting in concert. Clutter (1967) investigated the possible causes and functions of the

zonation of the numerically dominant mysid species in La Jolla Bight, California, USA, and suggested that zonation may have developed in response to food availability patterns imposed by nearshore circulation systems.

Circulation patterns determine the distribution of detritus and phytoplankton off sandy beaches in Algoa Bay, South Africa (Talbot & Bate 1986). The diatom *Anaulus australis* Drebes & Schulz (formerly identified as *A. birostratus*), accumulates in surfzone surface waters during daylight, but begins to disperse in the late afternoon. Surface accumulation of cells is due to their positive buoyancy, presumably by adherence to air bubbles and subsequent concentration by waves advecting shorewards. After dark, the concentration of *A. australis* in the water column decreases significantly as cells change their life mode from planktonic to epipsammic (Talbot & Bate 1988a). Part of the inshore accumulation of cells, as well as surfzone detritus, is transported seawards by rip currents, depositing suspended material behind the breaker line as current velocities decrease and dissipate (Clutter 1967, Talbot & Bate 1988b). These currents thus distribute food produced in the inner surfzone and make it available to grazers beyond the breaker line.

Wooldridge (1983) recorded large numbers of *Mesopodopsis slabberi* (Van Beneden), at night, only

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behind the breaker line in Algoa Bay, and suggested that the nocturnal appearance of mysids is a reflection of a general onshore movement to exploit a rich food supply in the form of outwelling diatoms. This study investigates the nature of the diel horizontal migration of *M. slabberi* and attempts to explain changes in distribution in terms of food availability and predator avoidance. An attempt is also made to quantify the possible effect of mysid grazing pressure on *Anaulus australis*, which accounts for over 95 % of total annual primary production in the Sundays River surfzone system (Campbell & Bate 1988).

MATERIALS AND METHODS

Diel variation in distribution of *Mesopodopsis slabberi* was investigated off Sundays River beach in waters directly influenced by surf circulation cells (Fig. 1). This corresponds to the zone extending from the breaker line to the 10 m depth contour (McLachlan 1983).

Stations were positioned in water of 6, 10, 15 and 20 m depth using marker buoys (Fig. 1). Two separate 24 h sessions (February and March 1985) were completed at the 6 and 10 m stations. Replicate samples were collected every 3 h at each station and on each occasion. Two further sets of samples were collected in late afternoon and after dark at each of the 4 depth

zones in April and September 1986. A fifth set of samples was obtained at 3 to 5 h intervals between 14:00 h on 22 November and 09:00 h on 24 November 1985 at the 6 m station. Nocturnal longshore distribution was determined on 2 occasions (April and September 1986). Eight and 7 stations, respectively, were sampled along the 6 m depth contour over a distance of 2.5 km. Sampling was continuous on each occasion with tow distances monitored from the beach using a vehicle odometer.

Sub-surface and near-bottom samples were collected at every station using 500 μm mesh WP 2 plankton nets (57 cm diam.) fitted with Kahlsico 005 WA130 flowmeters. Nets were also attached to separate surface floats to allow for depth regulation. Nets were towed at ca 1.5 m s^{-1} behind a 6 m skiboat fitted with an echo sounder. On occasions, a small quantity of sand was present in the bottom net and attested to the general proximity of the net to the substrate. During each 3 min tow, ca 70 m^3 of water was filtered.

Daylight sampling along the shore-normal transect line and within 1.5 m of the substrate was carried out on 2 occasions (August and September 1986) by SCUBA divers using hand nets. Sheltered areas under overhangs and in gullies of rocky reefs located in water of 15 and 20 m depth were sampled, as well as the sandy floor up to 50 m distant from reef outcrops.

In the laboratory, samples were resuspended in known volumes of water and subsamples taken from the middle depth of the suspension in order to facilitate counts of adult and juvenile mysids under 40 × magnification. Five subsamples were taken in each case and an average number of animals in each size class obtained. This number was used to calculate the number of mysids present per cubic metre of water at the time of sampling.

Offshore transect data were analysed using BMDP (Biomedical Data Processing) univariate (1V) and multivariate (2V) statistical packages and by Tukey multiple comparison procedure. Longshore data were subjected to Kolmogorov-Smirnov analysis.
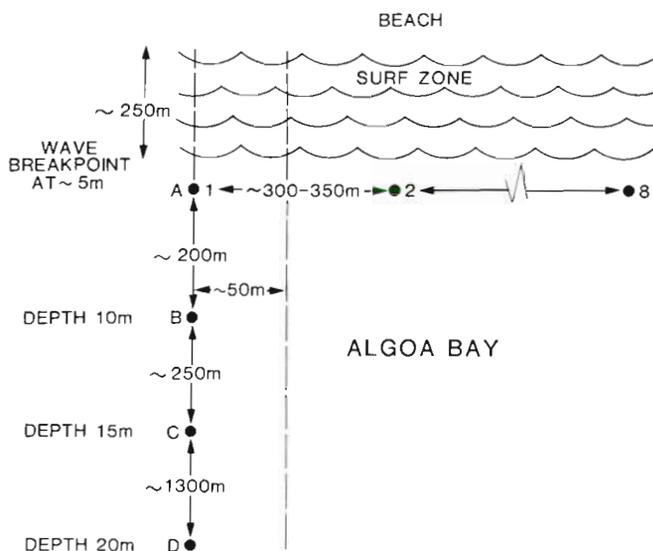

Fig. 1 Diagrammatic representation of shore-normal and shore-parallel sampling stations off Sundays River beach, Algoa Bay, southern Africa. A to D indicate the relative position of stations at the 6, 10, 15 and 20 m depth zones. Replicate samples were collected 50 m to the east of this transect line. 1 to 8 indicate the locality of the series of stations sampled continuously over 2.5 km

RESULTS

Pooled offshore data indicated a statistically significant difference in the number of mysids present during daylight, sunset, dark and sunrise (F = 3.42; p < 0.05). Although the data suggested an increase in the number of mysids after dark, Tukey analysis of similarities and differences between groups indicated no significant difference between the number of animals taken in sunset, dark and sunrise samples. No mysids were taken during daylight in WP 2 plankton nets.

Shortly before sunset, few or no mysids were recorded at the shallowest station behind the breaker line. At this time, mysids were usually present in surface and near-bottom samples at the 10 m station. This contrasted to the pattern of horizontal distribution recorded after dark. Analysis of pooled data from nocturnal samples indicated significant differences ($F = 5.5$; $p < 0.05$) between numbers of mysids taken at different depths, with the greatest number of animals taken at the 6 m depth station (immediately behind the breaker line and ca 250 m offshore from the beach). Fewer animals were caught at 10 m depth (ca 200 m beyond the breakers) and no mysids were netted at the 15 and 20 m stations, i.e. further than 500 m offshore of the breaker line. The number of mysids varied greatly between sampling sessions, but time averaged values of 337 mysids m^{-3} water at the 6 m depth contour throughout the night, compared to 42 m^{-3} at the 10 m depth contour, illustrate the trend. At sunrise, mysids were more abundant at the 10 m station and by full light, no mysids were taken in the water column out to the deepest station sampled. This pattern is clearly evident in Table 1 which presents data for one of the 24 h series.

A comparison between surface and near-bottom samples collected after dark at 6 and 10 m stations indicate significantly greater numbers of mysids nearer the substrate (Students t-test $= 2.21$; $p < 0.05$; $n = 43$). On one occasion, the ratio increased to 1:18 (surface:bottom) at the shallow station. These data suggest a generally demersal distribution of the visiting population after dark.

Size class composition of mysids varied; in February and March 1985, juveniles (< 8.0 mm length) were mainly represented. Juveniles were relatively less abundant on the other occasions. Although abundance of juveniles in samples may reflect general size composition at the time of sampling for the population generally, size selective swarming of mysids is noted in the literature (Clutter 1969, Wittman 1977, Mauchline 1980). Differences in size class composition between swarms is attributed to differential swimming speed between large and small individuals.

Continuous sampling along the 2.5 km transect behind the breaker line did not establish discrete patterns in adult and juvenile distribution (Table 2). Combined numbers m^{-3} revealed a continuous distribution of *Mesopodopsis slabberi* ($D_{0.05, 8.985} = 143$; $p < 0.05$), with mysids absent from this zone during daylight.

Sampling of water in gullies and under overhangs of ca 2 m high reef at 15 m depth, using SCUBA and a hand net, yielded rich concentrations of *Mesopodopsis slabberi*. Ten sweeps of the 15 cm diam net, in both gullies and under overhangs, yielded an average of 1777 mysids of both sexes and all size classes. Sampling at a similar reef in water 20 m deep yielded an average of only 20 mysids 10^{-1} sweeps of the net. Samples taken as close as possible to the sandy substrate in the area immediately surrounding each reef, and the sandy bay floor 50 m shorewards of each reef, seldom yielded mysids, except on rare occasions when individual animals were taken.

DISCUSSION

Mesopodopsis slabberi is abundant in inshore waters of Algoa Bay, South Africa, where concentrations exceeding 15 000 m^{-3} have been recorded (Wooldridge 1983). During the day, mysids were absent in shallow areas behind the breaker line. In the late afternoon,

Table 1. *Mesopodopsis slabberi*. Offshore distribution (no. m^{-3}) sampled over 24 h during March 1985 behind the breaker line at 5 and 10 m depth stations. Data refer to samples collected along each shore-normal transect line illustrated in Fig. 1

Time	Sample depth	5 m	10 m
Daylight	Surface	0	0
		0	0
	Near bottom	0	0
		0	0
Sunset	Surface	0	60
		0	8
	Near bottom	0	94
		1	12
Night	Surface	127	51
		43	2
	Near bottom	374	109
		113	38
Sunrise	Surface	31	130
		0	123
	Near bottom	214	463
		2	248
Daylight	Surface	0	0
		0	0
	Near bottom	0	0
		0	0

Table 2. *Mesopodopsis slabberi*. Longshore distribution (no. m^{-3}) sampled at night on 2 occasions behind the breaker line in water of 6 m depth. Relative position of stations illustrated in Fig. 1

Sample depth	Station							
	1	2	3	4	5	6	7	8
Surface	70	49	99	126	46	38	30	33
Near bottom	99	45	117	113	94	37	33	36
Surface	48	49	31	69	88	21	146	—
Near bottom	110	259	178	205	183	121	170	—

they migrated onshore from deeper bay waters (> 15 m), covering a horizontal distance of ca 500 m. After dark, *M. slabberi* was present in water 6 to 10 m deep, with significantly greater numbers immediately behind the breakers than further out in the 10 m depth zone. Mysids were also more abundant nearer the substrate than in near-surface waters. At first light, *M. slabberi* migrated back offshore.

The nocturnal zonation of *Mesopodopsis slabberi* may be interpreted as a response to the pattern of food availability. A distinctive feature of the dominant surfzone diatom *Anaulus australis* is its neustonic mode of life, presumably as a result of cell adherence to air bubbles during the day (Talbot and Bate 1988a). Concentrations of *A. australis* accumulate in close proximity to rip systems which may also transport cells entrained in the water column further offshore (Talbot & Bate 1987). When rips discharge into relatively calm water, *A. australis* cells sink due to a reduction in air bubble formation (Talbot & Bate 1988b). Talbot & Bate (1989) also describe the shift in the spatial distribution of *A. australis* during a 10-d storm-calm-storm cycle. During this study, 51 % of the inshore population was temporally transported behind the breaker line. Accumulation of material behind the breakers is thus a potentially rich source of food to mysids foraging in this zone.

Although *Anaulus australis* forms high concentrations inside the breaker line, the gregarious *Mesopodopsis slabberi* is only rarely present in this inshore zone (Wooldridge 1983). Conditions are probably unfavourable due to turbulent surf, abrasion by suspended particles, mechanical dislodgement of larvae from the broodpouches of females, and suspension of sand particles which may interfere with feeding (Clutter 1967).

During daylight, *Mesopodopsis slabberi* occurred in gullies and under overhangs of reefs which were present in water of 15 to 20 m depth along the study transect. Few or no mysids were taken over the sandy bottom away from reef systems. The general absence of *M. slabberi* over the sandy floor of the bay may possibly be attributed to the distribution of predators such as juvenile *Argyrosomus hololepidotus* which were abundant throughout the year in the shallow waters of the bay (Smale 1984). This teleost is an epibenthic feeder foraging over sandy substrates, with *M. slabberi* forming a major prey item.

Berril (1968) recorded mysids hiding amongst shells, rocks, beds of algae and mangrove roots, while field studies by Glass (1971) and Stein (1977) have illustrated the strategic benefits of reefs and other protective structures to prey species. Reefs may thus form a relative sanctuary for *Mesopodopsis slabberi* providing consealment from major predators such as *Argyrosomus hololepidotus*.

Campbell & Bate (1988) have estimated primary production in the inner Sundays River surfzone as 120 000 g C m^{-1} yr^{-1}, while primary production between the breaker line the outer limit of riphead activity was estimated as 100 000 g C m^{-1} yr^{-1}. Other sources of carbon input into the Sundays River surfzone are relatively small, the total available pool of carbon being ca 230 000 g C m^{-1} yr^{-1} (McLachlan & Romer in press).

Mesopodopsis slabberi feed actively on both settled and suspended *Anaulus australis* cells in the laboratory and show an initial linear ingestion response to increasing food concentrations (Webb et al. 1987). Estimates of the effects of *M. slabberi* grazing on *A. australis* are restricted by the patchiness of both grazer and diatom, but the following possible scenario may be described. *M. slabberi* aggregate at night in the 200 m wide zone between the 6 and 10 m depth contours. A 1 m wide strip of this region has an approximate volume of 1600 m^3 and, at an average concentration of 65 adult and 510 juvenile *M. slabberi* m^{-3} (Wooldridge 1983), would theoretically contain 104 000 and 816 000 mysids respectively. Mean abundance was determined from 20 samples collected over 2 yr at 6 to 10 m depth off Sundays River beach. Ingestion rates of adult and juvenile mysids of 10 and 5 mm body length are taken from Webb et al. (1987) using the lowest experimental cell concentration (1.76 × 10^4 cells ml^{-1}). *A. australis* biomass is 2 000 000 cells mg^{-1} dry mass with carbon equal to 40 % dry mass (Campbell 1988). Using these values, *M. slabberi* could consume 51 g C d^{-1}, which on an annual basis, is ca 70 % of the total organic carbon consumption of the macrofaunal trophic assemblage in the Sundays River surfzone (McLachlan & Romer in press). Although macrofauna only account for 11 % of the total carbon budget (McLachlan and Romer in press), mysid shrimps clearly occupy a key position in the macrofaunal foodweb.

LITERATURE CITED

Angel, M. V. (1985). Vertical migrations in the oceanic realm: possible causes and probable effects. In: Rankin, M. A. (ed.) Migration: mechanisms and adaptive significance. Cont. Mar. Sci. Univ. Tex. (Supp.) 27: 45–70

Berril, M. (1968). The schooling and antipredatory behaviour of mysid shrimp. Ph.D thesis, Princeton University, Princetown

Campbell, E. E. (1988). The estimation of phytomass and primary production of a surfzone. Ph.D thesis, University of Port Elizabeth, Port Elizabeth

Campbell, E. E., Bate, G. C. (1988). The estimation of annual primary production in a high energy surfzone. Botanica Mar. 31: 337–343

Clutter, R. I. (1967). Zonation of nearshore mysids. Ecology 48: 200–208

Clutter, R. I. (1969). The microdistribution and social behaviour of some pelagic mysid shrimps. J. exp. mar. Biol. Ecol. 3: 125–155

Enright, J. T (1977). Diurnal vertical migration: Adaptive significance and timing. Part 1. Selective advantage: a metabolic model. Limnol. Oceanogr. 22 (5): 856–872

Enright, J. T., Honegger, H. W. (1977). Adaptive significance and timing. Part 2. Test of the model: details of timing. Limnol. Oceanogr. 22 (5): 873–886

Glass, N. R. (1971). Computer analysis of predation energetics in the largemouth bass. In: Patten, B. S. (ed.) Systems analysis and simulation in ecology, Vol. 1. Academic Press, New York, p. 325–363

Hamner, W. M., Carleton, J. H. (1979). Copepod swarms: attributes and role in coral reef ecosystems. Limnol. Oceanogr. 24: 1–14

Hamner, W. M., Hauri, I. R. (1981). Long-distance horizontal migration of zooplankton (Scyphomedusae, Mastigias). Limnol. Oceanogr. 26: 414–423

Hutchinson, G. E. (1967). A treatise on limnology, Vol. 2. John Wiley, New York

Mauchline, J. (1980). The biology of Mysids and Euphausids. In: Blaxter, J. H. S., Russell, F. S., Yonge, M. (eds.). Advances in marine biology, Vol. 18. Academic Press, New York

McLachlan, A. (1983). The ecology of sandy beaches in the Eastern Cape, South Africa. In: McLachlan, A., Erasmus, T (eds.) Sandy beaches as ecosystems. Junk, The Hague, p. 539–546

McLachlan, A., Romer, G. (in press). Trophic relationships in a high energy beach and surf zone ecosystem. In: Barnes, M., Gibson, R.(eds.) Trophic relationships in the marine environment. Aberdeen University Press, Aberdeen

Morgan, M. D., Threlkeld, S. T. (1982). Size dependent horizontal migration of *Mysis relicta*. Hydrobiologia 93: 63–68

Ringelberg, J. (1980). Introductory remarks: Causal and teleological aspects of diurnal vertical migration. In: Kerfoot, W C. (ed.) Evolution and ecology of zooplankton communities. University Press of New England, Hanover, p. 65–68

Siebeck, W., Ringelberg, J. (1969). Spatial orientation of planktonic crustaceans. 1. The swimming behaviour in a

horizontal plane. 2. The swimming behaviour in a vertical plane. Int. Verein. Theoret. Angew. Limnol. Verhandel. 17· 831–847

Smale, M. J. (1984). Inshore small mesh trawling survey of the Cape south coast. Part 3. The occurrence and feeding of *Argyrosomus hololepidotus, Potatomus saltatrix* and *Merluccius capensis*. S. Afr. J. Zool. 19: 170–179

Stein, R. A. (1977). Selective predation, optimal foraging and the predator-prey interaction between fish and crayfish. Ecology 58: 1237–1253

Talbot, M. M. B., Bate, G. C. (1986). Diel periodicities in cell characteristics of the surfzone diatom *Anaulus birostratus*: their role in the dynamics of cell patches. Mar. Ecol. Prog. Ser. 32: 81–89

Talbot, M. M. B., Bate, G. C. (1987). The spatial dynamics of surf diatom patches in a medium energy cuspate beach. Botanica Mar. 30: 459–465

Talbot, M. M. B., Bate, G. C. (1988a). The use of false buoyancies by the surf diatom *Anaulus birostratus* in the formation and decay of cell patches. Estuar. cstl Shelf Sci. 26: 155–167

Talbot, M. M. B., Bate, G. C. (1988b). Distribution patterns of the surf diatom *Anaulus birostratus* in an exposed surfzone. Estuar. cstl Shelf Sci. 26: 137–153

Talbot, M. M. B., Bate, G. C. (1989). Beach morphodynamics and surf-zone diatom populations. J. exp. mar. Biol. Ecol. 129: 231–241

Webb, P., Perissinotto, R., Wooldrige, T. H. (1987). Feeding of *Mesopodopsis slabberi* (Crustacea, Mysidacea) on naturally occurring phytoplankton. Mar Ecol. Prog. Ser. 38: 115–123

Williams, R., Collins, N. R. (1984). Distribution and variability in abundance of *Schistomysis spiritus* (Crustacea, Mysidacea) in the Bristol channel in relation to environmental variables, with comments on other mysids. Mar. Biol. 80: 197–206

Wittman, K. J. (1977). Modification of association and swarming in north Adriatic Mysidacea in relation to habitat and interacting species. In: Keegan, B. F., Ceidigh, P. E., Boaden, P. J. S. (eds.) Biology of benthic organisms. Pergamon Press, Oxford

Wooldridge, T H. (1983). Ecology of beach and surfzone mysid shrimps in the Eastern Cape, South Africa. In: McLachlan, A., Erasmus, T. (eds.) Sandy beaches as ecosystems. Junk, The Hague, p. 449–460