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Diet and feeding of *Gastrosaccus psammodytes* (Crustacea, Mysidacea) with special reference to the surf diatom *Anaulus birostratus*

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ABSTRACT: Laboratory studies were run on the beach mysid *Gastrosaccus psammodytes* Tattersal feeding on the surf diatom *Anaulus birostratus* to determine (a) ingestion rates in various food concentrations, and (b) possible differences between rates of ingestion on settled and homogeneous diatom suspensions, as well as between adult and juvenile day/night feeding. Increasing food supply was accompanied by a linear ingestion response during the first 3 h of feeding. Data suggest a lower threshold concentration below which the mysids will not feed but there was no clear evidence of an upper threshold. Ingestion curves over 12 h showed minimal ingestion after an initial period of active feeding. Field gut-content analysis indicated a change in diet from detritus during the day to diatoms and zooplankton after dark. Change in diet, and an offshore migration to behind the breaker line by part of *G. psammodytes* population, was probably associated with the daily change in life mode and distribution of *A. birostratus*.

INTRODUCTION

The bentho-pelagic mysid *Gastrosaccus psammodytes* is distributed along sandy shores in southern Africa from Namibia to Transkei (Brown & Talbot 1972, Wooldridge 1978). In Algoa Bay it is the only mysid represented in any number in the surf and swash zones where as many as 55 ind. m^{-2} have been recorded (Wooldridge 1981, 1983). *G. psammodytes* shows well-defined patterns of intraspecific zonation in which brooding females burrow in the inner shore area of the surfzone, while adult males, immatures and juveniles are found in greatest abundance in the water column a considerable distance from shore (Wooldridge 1983). During the day mysids remain confined to the intertidal and surfzone, but after dark migration occurs and part of the population is found behind the breaker line (Wooldridge 1981). Wooldridge (1983) also suggested that diel variation in distribution is related to feeding activity.

Persistent accumulations of the surf diatom *Anaulus birostratus* occur in the surfzone during the day, disappearing from the water column in the late afternoon. According to Talbot & Bate (1986) the main feature of this day/night vertical migration of cells is the alteration of their life mode from epipsammic at night to planktonic by day, interrupted by periodic breaks in this cycle by dispersive offshore transport. Talbot & Bate proposed that air bubbles and foam formed by toppling wave crests are the physical forcing functions responsible for the observed vertical stratification of *A. birostratus* during the day with physiological changes (clay coat formation) causing precipitation at night. During the day/night change between surface and epipsammic habitats cells may be transported out of the surfzone by rip currents and deposited behind the breaker line when these currents dissipate. Detritus is also transported out of the surfzone and deposited in this manner (Clutter 1966).

Nocturnal, seaward movement of *Gastrosaccus psammodytes* occurs in conjunction with an onshore migration by *Mesopodopsis slabberi*. This mysid also feeds actively on *Anaulus birostratus* in the laboratory, and Webb et al. (1987) suggested that its onshore movement is also influenced by offshore transport of phytoplankton and detritus by rip currents to behind the breaker line. Accumulations of surf diatoms in

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Algoa Bay represent a rich primary food source. Our investigation of field and laboratory feeding by *G. psammodytes* has clarified the foraging behaviour of this mysid in relation to diel changes in food availability.

MATERIALS AND METHODS

Field collection. *Gastrosaccus psammodytes* Tattersal were collected in both summer and winter from the upper 1.5 cm sand layer of the swash zone of the Sundays River beach, Algoa Bay, South Africa, using a 0.5 m wide benthic sledge with serrated, leading edge and 200 μm mesh cod end. Although mysids are patchily distributed in the swash zone (Brown & Talbot 1972), most sledge trawls yielded a rich supply of adults and some juveniles. Mysids were transported to the laboratory in 20 l buckets, kept at ambient temperature, and experiments performed within 24 h of capture. Diatoms *Anaulus birostratus* were collected from foam generated by wave action in the surfzone of the Sundays River beach.

Experimental procedure. Foam samples were filtered through a 200 μm mesh sieve to remove large zooplankters and stored in a large tank (50 to 80 l). After the cells had settled overnight, excess water was removed and experimental concentrations of *Anaulus birostratus* were obtained by dilution of this stock with seawater. Diatom concentrations ranged from 2×10^4 to 4.5×10^5. These values represent a range of cell concentrations from the lowest reproducible counts obtainable with our counting method to the highest concentrations recorded in the surfzone. *A. birostratus* divides most actively in the early morning (Talbot & Bate 1986). To minimise changes in cell concentrations in control beakers, experiments were not undertaken during this time.

The relationship between phytoplankton cell concentration and rate of mysid ingestion – using *Anaulus birostratus* at winter temperatures of 16 and 19°C and at a summer temperature of 23°C – was investigated. At each concentration of *A. birostratus*, 4 replicate 1 l jars, each containing 5 mysids (sexes separate), were prepared. Experiments were run for 3 h. Effects of temporal changes on ingestion rates were investigated at 2 different concentrations of *A. birostratus* (8.55×10^4 and 3.7×10^5 cells ml^{-1}), experimental sets being analysed every 2 h for 12 h. Effects of stirring and diel feeding patterns in adult (14 mm total length) and juvenile (7 mm) mysids were also investigated. Mysids were excluded from a control jar for each experimental series.

Sub-samples were taken at the beginning and end of each run to determine changes in phytoplankton concentration in experimental and control jars. Jar contents were poured through a 200 μm sieve at the end of each run to thoroughly mix the suspension and to remove the mysids before analysis. Random sub-samples (5 ml) were taken using a 0.5 cm^2 diameter glass tube which sampled all levels of the suspension, thus limiting possible error due to vertical stratification. Sub-samples were preserved immediately using 5 drops of Lugol's solution. Cell counts were made using the haemocytometer technique described by Lund et al. (1958). A 0.1 mm deep haemocytometer with improved Neubauer Ruling was employed. At least 8 counts per sub-sample were taken and if the total number of cells counted was less than 300, further counts were made. The coefficient of variation associated with the counting procedure was kept below 10 %.

Ingestion rates were derived from the difference between final concentrations in experimental and control containers. This procedure provides reasonable estimates as long as the difference between initial and final control concentrations is kept to a minimum (Paffenhöfer 1971). Initial and final algal concentrations in feeding experiments were never more than 10 % above or below the average food concentration, which is less than the value (25 %) quoted by Paffenhöfer (1971).

Gut content analyses were performed on freshly caught adult *Gastrosaccus psammodytes* sampled in the swash zone over 23 h. Mysids sampled were immediately taken to a mobile field laboratory, sacrificed, guts removed and their contents examined under 400× magnification.

Experiments were also designed to investigate the ability of *Gastrosaccus psammodytes* to feed on diatoms within and on sand-surface layers. Beach sand was introduced into 3 tanks (A, B, C) to a depth of 5 cm. A dense concentration of *Anaulus birostratus* was carefully poured onto the sand of all 3 tanks without disturbing the substratum and allowed to drain. After draining and settlement, the sand surfaces of Tanks B and C were covered with 1 mm and 5 mm fresh sea sand respectively. All 3 tanks were then carefully filled with sea water to a depth of 20 cm. A plastic sheet covered the substratum to prevent disturbance of sand and diatoms while pouring water. Once filled, the plastic sheet was removed and 10 *G. psammodytes* introduced. Mysids were removed after 3 h and their guts examined under 10× magnification.

The time course of gut filling was studied using starved *Gastrosaccus psammodytes* in a suspension of *Anaulus birostratus* (concentration = 3.11×10^4 cells ml^{-1}). At intervals, 10 mysids were removed and examined under a dissecting microscope at 10× magnification over 3 h. Filling of proventriculus, gut, gastric glands and the colour of the gut contents was recorded.

Observation on gut clearance rates was made after mysids had been fed *Anaulus birostratus* for 24 h. Proventriculus, gut and gastric glands of 10 mysids per sample were examined under a dissecting microscope at 10× magnification and the number of mysids with empty sections of gut noted.

RESULTS

Significant changes in *Anaulus birostratus* cell concentrations were not observed in control beakers over the experimental periods (3 to 12 h). Statistical comparison of feeding-rate data of *Gastrosaccus psammodytes* at 16, 19 and 23°C showed no significant difference at the 95 % level (slope: $p > 0.5$; y-intercept: $p > 0.5$). A linear regression was fitted for the pooled 16, 19 and 23°C experimental data ($r = 0.93$, $N = 53$; Fig. 1). Michaelis-Menten and Ivlev expressions were also fitted to the pooled data (Michaelis-Menten: MSE = 1.94; Ivlev without threshold: MSE = 3.21; Ivlev with threshold: MSE = 2.40). Mean square error (MSE) values for these expressions indicate that the Michaelis-Menten equation with a feeding threshold of 9.3×10^3 cells ml^{-1} provided the best fit, but there is no statistically significant difference between models. The linear expression also indicates that a low concentration threshold (3×10^4 cells ml^{-1}) may exist. Ingestion increased steadily from 2×10^5 cells $mysid^{-1}$ at a food concentration of 2.5×10^4 cells ml^{-1}, to 1.2×10^7 cells $mysid^{-1}$ at a food concentration of 4.25×10^5 cells ml^{-1} (Fig. 1).

The relationship between rates of ingestion per mysid in 2 concentrations of *Anaulus birostratus* is illustrated in Fig. 2. Curves were fitted to the data by least-squares criteria and extrapolated by hand from the first reading (after 2 h) to time zero, based on observations of gut filling. Ingestion was rapid during the first 2 h, reaching 0.9×10^6 cells $mysid^{-1}$ at a food concentration of 8.55×10^4 cells ml^{-1} and 4.35×10^6 cells $mysid^{-1}$ at a food concentration of 3.70×10^5 cells ml^{-1}. Thereafter the number of cells ingested remained relatively unchanged, increasing only slightly over time. No difference in feeding rate was found between stirred experimental jars and those in which phytoplankton cells were allowed to settle (Table 1). There was no statistically significant difference between day and night feeding of adult female or juvenile *Gastrosaccus psammodytes*, but the difference between adult and juvenile feeding rates was significant ($p < 0.01$).

The stomachs of mysids removed from the tank with a layer of settled *Anaulus birostratus* on the surface of the sandy bottom (Tank A), were filled after 3 h, but no diatoms were found in the guts of mysids in tanks with buried cells indicating that the mysids can feed on epipsammic *A. birostratus* but not on diatoms trapped interstitially.

Stomach contents of *Gastrosaccus psammodytes* collected and analysed in the field indicated a change in diet over 23 h (Table 2). Unidentifiable amorphous detrital material filled the gut during the day while unfragmented diatoms (*Chaetoceros* sp. and centric species) were first noted just before sunset. Diatom fragments became abundant between 23.00 h and 03:00 h and remained present, although in reduced numbers, until the last observation was made at 08:30 h the next morning. Copepod fragments and centric diatoms were present in the stomach contents of

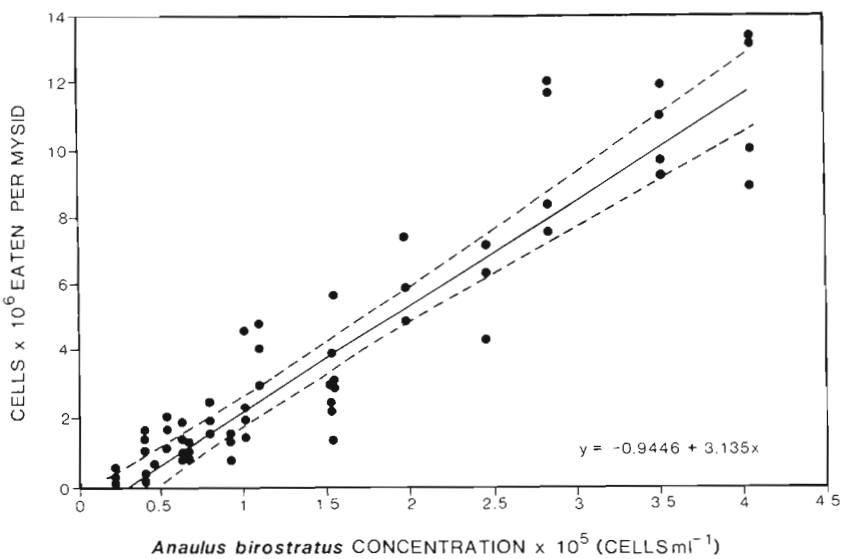

Fig. 1. *Gastrosaccus psammodytes*. Feeding rate. Linear regression for the pooled 16, 19 and 23°C data ($r = 0.93$, $N = 53$)

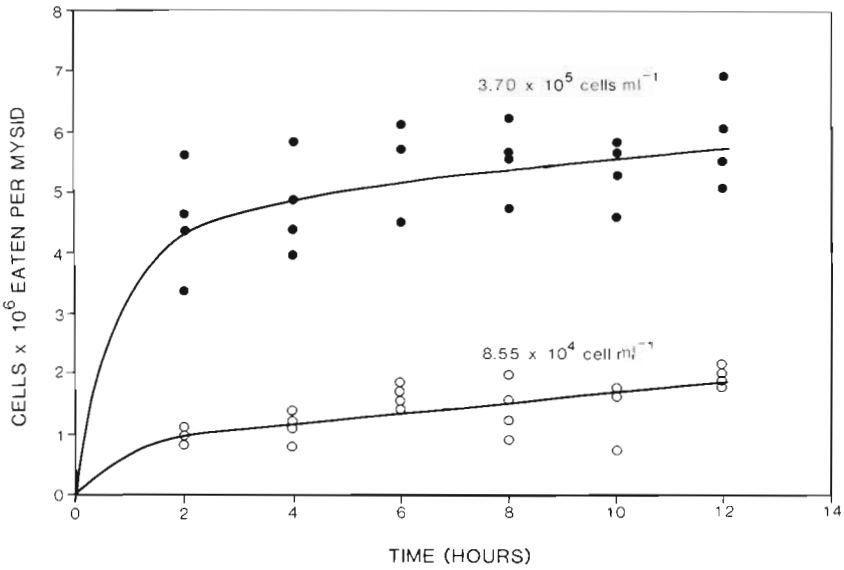

Fig. 2. *Gastrosaccus psammodytes*. Rate of ingestion per individual mysid in 2 concentrations of diatoms *Anaulus birostratus*

Table 1. *Gastrosaccus psammodytes*. *t*-test analysis of mysids grazing on *Anaulus birostratus*. No. of cells (mean of experimental replicates) eaten during 3 h experiments

Experimental condition	Mean no. of cells eaten ($\times 10^7$)	*t*	*n*
Adult female	$\bar{x} = 2.755 \pm 0.684$	10.86••	20
Juvenile	$\bar{x} = 1.250 \pm 0.339$		
Day (adult)	$\bar{x} = 2.942 \pm 0.697$	0.17 ns	10
Night (adult)	$\bar{x} = 2.539 \pm 0.677$		
Day (juvenile)	$\bar{x} = 1.231 \pm 0.427$	0.06 ns	10
Night (juvenile)	$\bar{x} = 1.270 \pm 0.252$		
Stirred algae	$\bar{x} = 1.97 \pm 0.326$	1.43 ns	20
Unstirred algae	$\bar{x} = 2.10 \pm 0.273$		

ns: not significant
•• Significant at 99% level

Table 2. *Gastrosaccus psammodytes*. Field observation of gut contents over 23 h

Sample times	Detritus	Diatom fragments	Centric diatoms	Copepod fragments	*Chaetoceras*
09:30 h	•••••				
12:00 h	•••••				
14:00 h	•••••				
16:00 h	•••••				
18:00 h	••••		••		•
20:00 h	NM	NM	NM	NM	NM
23:00 h	••	••••	•••	•	
03:00 h	••	••••	•••	•••	
05:00 h	•••	•••	•••	•••	
07:00 h	•••	•••	•••	•••	
08:30 h	••••	•			•

••••• Comprises 100% of gut content
•••• Predominant
••• Abundant but not predominant
•• Few cells/fragments, but immediately obvious
• One or two cells/fragments
NM: No mysids in sample

all mysids sampled at night, but not in mysids taken in daylight.

Observation of packing and colouration of gut contents of mysids fed *Anaulus birostratus* at a concentration of 3.11×10^4 cells ml^{-1} is illustrated in Table 3. The foregut was filled within 5 min and the gastric glands of all mysids began to fill within 10 min, followed by a colour change from green to yellow of contents of some mysids after 15 min. After 1 h the gastric-gland contents of all mysids sampled were completely yellow. Faeces were observed in the hindgut after 75 min. After being fed *A. birostratus* for 24 h, the foreguts of all mysids sampled cleared within 1 h. The hindguts of all mysids had emptied within 2 h, while it took 22.5 h for the gastric glands of all mysids to clear (Table 4).

DISCUSSION

Three types of response curves relating zooplankton ingestion rates to various concentrations of food particles have been observed: (a) increased ingestion rate in direct proportion to increased food concentration up to a saturation point (Frost 1972); (b) weak evidence for saturation levels (Deason 1980); (c) proportional ingestion rates without any transition of feeding behaviour (Reeve & Walter 1977, Mayzaud & Poulet 1978, Huntley 1981). These response curves are based on copepod

Table 3. *Gastrosaccus psammodytes*. Gut filling when feeding on *Anaulus birostratus* through time (diatom concentration 3.11×10^4 cells ml^{-1}). Numbers are no. of mysids out of 10 with food in the gastric gland of the colouration indicated and the presence of faeces in the hindgut of individuals sampled

Time	Foregut	Gastric gland				Hindgut (faecal pellets)
		Tinged green	Green/yellow	Yellow	Brown	
0	Empty	Empty	Empty	Empty	Empty	Empty
5 min	Full	6				Empty
15 min	Full	5	5			Empty
30 min	Full		2	8		Empty
45 min	Full		1	9		Empty
1 h	Full			7	3	Empty
1 h 15 min	Full			1	9	Faeces
3 h	Full				10	Faeces

Table 4. *Gastrosaccus psammodytes*. Gut clearing after being fed *Anaulus birostratus* (concentration 2.22×10^4 cells ml^{-1}). Percentages of mysids sampled having empty sections of gut; 10 mysids were examined per sample

Time period	Proventriculus	Gut	Gastric gland
Start	Full	Full	Full
30 min	90 % Empty	60 % Empty	Full
1 h	100 % Empty	75 % Empty	Full
1 h 30 min	100 % Empty	90 % Empty	Full
2 h	100 % Empty	100 % Empty	6 % Empty
2 h 30 min	100 % Empty	100 % Empty	19 % Empty
3 h 30 min	100 % Empty	100 % Empty	20 % Empty
4 h 30 min	100 % Empty	100 % Empty	25 % Empty
5 h 30 min	100 % Empty	100 % Empty	25 % Empty
7 h 30 min	100 % Empty	100 % Empty	30 % Empty
8 h 30 min	100 % Empty	100 % Empty	35 % Empty
9 h 30 min	100 % Empty	100 % Empty	50 % Empty
14 h 30 min	100 % Empty	100 % Empty	86 % Empty
22 h 30 min	100 % Empty	100 % Empty	100 % Empty

feeding and any comparison with mysid feeding data should be viewed cautiously. However, the paucity of quantitative data on mysid ingestion and filtration rates requires, at least initially, that results be considered in the light of the behaviour of other pelagic filter feeders.

A maximum ingestion rate for *Gastrosaccus psammodytes* was not found by increasing phytoplankton cell concentrations up to 4×10^5 cells ml^{-1} (Fig. 1). Observations indicate that ingestion is in proportion to diatom concentration over a maximum of 3 h, even in concentrated suspensions from dense phytoplankton accumulations. Fitting of functional response curves to the data shows no significant difference between a linear regression and various curvilinear relations. Lehman (1976) notes that theories separating Ivlev, Michaelis-Menten and rectilinear equations are insufficiently supported and no one model has statistically proven to be better than another. Present data (Fig. 1) suggest the possibility of a threshold concentration below which *G. psammodytes* will not feed. If the cost in energy for searching and capturing food is high relative to the nonfeeder's metabolic rate, it may be advantageous to cease feeding behaviour when food concentration is very low (Mullin et al. 1974).

Ingestion curves showed minimal ingestion after an initial 2 h period of active feeding regardless of food concentration offered (Fig. 2). Once the gastric glands were filled and the digestive processes began (contents yellow, see Table 3), filtering continues at a reduced level. Foraging theorists state that optimal filtering rates are reached at fairly low food concentrations and predict that once the gut of a filter feeder is filled, filtering would almost cease, with energy being expended only to maintain gut packing (McArthur 1972, Lehman 1976).

Present data support this prediction, but suggest that digestive processes also play a role in controlling filtering rate; once the content of the gastric glands have turned yellow (Table 3), the mysid reduces its filtering rate to a lower level. Within the range of food concentration used, this seems independent of amount ingested (Fig. 2); hence digestion may play a complementary role to gut packing as a determining factor controlling filtering rate in *Gastrosaccus psammodytes*. Reduced gut residence time with increased food concentration, as occurs in *Daphnia pularica* (Murtaugh 1985), is a mechanism which could facilitate density-dependent ingestion in *G. psammodytes*.

There is general agreement that mysids are omnivorous, eating detritus and small living organisms as well as feeding by filtration (Tattersal & Tattersal 1951, Brown & Talbot 1972, Nath & Pillai 1973, Mauchline 1980, Johnston & Lasenby 1982). *Gastrosaccus psammodytes* follows this pattern and exhibits a diel transition in feeding behaviour (Table 2), feeding more

actively at night in the field (Brown & Talbot 1972, McMurray unpubl.).

Mysids are said to completely macerate food (Mauchline 1980), but the gut contents of *Gastrosaccus psammodytes* fed *Anaulus birostratus* contained recognizable fragments of the diatom as distinct from amorphous detritus. More robust phytoplankters such as *Aulacodiscus kittonii* and *Chaetoceros* sp. take longer to macerate and can easily be identified amongst the gut contents.

Apart from filter feeding, *Gastrosaccus psammodytes* also feeds by swimming just above the surface of the sand with the cephalothorax and abdomen forming an obtuse angle to each other (Brown & Talbot 1972). This brings the antennae and antennules, as well as the uropods and telson, into contact with the sand and, as the mysid swims forward, food particles are ploughed up and swept by the thoracic endopodites into the mouth. The lack of significant difference in ingestion rates between mysids in stirred and unstirred experimental jars (Table 1) suggests that this is an effective mode of feeding.

In the laboratory no significant differences were found between day and night feeding (Table 1). Nath & Pillai (1973) also noted that *Gastrosaccus simulans* feeds continuously under laboratory conditions and that the intestine is always filled with food. Lack of significant differences between day and night feeding rate in the laboratory suggests that increased feeding at night in the field is related to changing environmental conditions, e.g. changes in available food type and abundance. Changes in gut content from amorphous detrital material during the day to fragmented diatoms at night were most noticeable.

Anaulus birostratus undergoes an alternation of life mode from planktonic during the day to epipsammic at night. Talbot (1986) postulates that this is effected by the change in adherence of diatoms from air bubbles during the day to sand grains at night. Sand ploughing by *Gastrosaccus psammodytes* enables utilization of epipsammic *A. birostratus* in the surfzone at night and may partially explain more active feeding after dark and the change in diet reflected by gut contents. Adult male, immature and juvenile *G. psammodytes* have been observed feeding on surfzone diatom accumulations during the day (McMurray unpubl.). Records of these mysids beyond the breaker line at night indicate a movement away from their daytime distribution within the surfzone (Wooldridge 1981) to a region where *A. birostratus* and detrital food material are deposited by dissipating rip currents (Talbot 1986).

Webb et al. (1987) have recorded *Mesopodopsis slabberi* feeding behind the breaker line at night, and Clutter (1966) suggests that the circulation of a large amount of detrital food material outside the breaker zone could be the major factor influencing the distribution of nearshore mysids such as *Metamysidopsis elongata*. Similarly, association between the distribution patterns of *Anaulus birostratus* and the intraspecific zonation of *Gastrosaccus psammodytes* may be postulated in the ecosystem of the Sundays River beach as the diatom becomes available as food both during the day and after dark: (a) when forming surface accumulations during the day; (b) when epipsammic in the surfzone at night; (c) when distributed by rip currents to behind the breaker line after dark.

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