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IN SITU FEEDING OF A SCHOOLING MYSID, *ANISOMYSIS* SP., ON DAVIES REEF—MECOR #4

M. M. Mullin and M. R. Roman

ABSTRACT

Mysids enclosed in situ and incubated with various radioisotopically labeled types of food had highest grazing or searching rates for relatively large animal prey (*Artemia* nauplii), generally lower rates for algal detritus and coral mucus, and ecologically trivial rates for single-celled phytoplankton and bacteria. These mysids are therefore most important as macrophages and carnivores in the organic budget of the reef.

We conducted this study in August 1984, on Davies Reef (18°51′S, 147°39′E), 77 km east of Cape Cleveland, N. Queensland, Australia, on the Great Barrier Reef, as part of a general study (Microbial Ecology on a Coral Reef—MECOR) of the organic budget of this reef with emphasis on detritus and bacteria. Particulate organic matter occurs in the water column in many forms, and in sizes ranging from free-living bacterial cells (0.2–0.5 μm) to macroalgal fragments and mucilaginous aggregates several mm in size and containing complex assemblages of bacteria and protozoa. Coral reefs have long been known to produce relatively large amounts of detritus and bacterial-detrital aggregates (Johannes, 1967; Coles and Strathmann, 1973; Sorokin, 1974; Moriarty, 1979; Hatcher, 1983), and at least some of the crustacean zooplankton of the reef ingest these materials (Sorokin et al., 1970; Gerber and Marshall, 1974; Richman et al., 1975; Gerber and Gerber, 1979).

We chose to investigate the feeding of mysids because their behavior made them convenient for in situ measurements and because Gottfried and Roman (1983) reported that *Mysidium integrum* W. Tattersall could ingest and assimilate coral mucus and associated bacteria, and could be maintained on this source of food up to 2 months. Therefore mysids are potential consumers in the microbial budget of the reef. Mysids as a group range from filter-feeders on phytoplankton to carnivores, with detritus being a major component of the gut contents of many species (Mauchline, 1980). Predatory feeding by freshwater *Mysis relicta* Lovén was studied by Bowers and Vanderploeg (1982) using an in situ method in which the mysids were removed from the environment and then returned to it.

METHODS

The mysids (*Anisomysis mullini*; Murano, in press) were observed during the daytime swarming above dark coral rock patches within and around a sandy depression (1.5–3 m deep, depending on stage of tide) near the seaward edge of the reef flat. As described by Steven (1961), Emery (1968) and others for other mysids (see Mauchline, 1980, for review), these swarms had several attributes of true schools—parallel orientation and approximately uniform separation between similar-sized individuals of both sexes, and concerted behavior of many individuals in response to variations in water flow or to approach by a swimmer. Many females carried young in the marsupium. The average dry weight per mysid was 280 μg; eye-to-telson length was 5 mm for both sexes.

We entrapped groups of animals in situ in the 5-liter, clear lucite (perspex) chamber described by Mullin (1983) or by hand nets. In the latter case, we transferred the animals under water to 2.5-liter glass jars or to the 5-liter, transparent lucite grazing chamber described by Roman and Rublee (1981). We then placed the containers on the sandy bottom near a coral patch. The entrapped mysids (20–100 per container, visibly no more concentrated than those in natural schools) usually resumed cruising inside the container several minutes after enclosure, sometimes as a small school, though there was no current within the chamber.

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Five to 30 min after enclosing the mysids, we injected radioisotopes into each container under water, mixed the contents, withdrew a sample for analysis of particulate radioactivity, and positioned the chamber on the bottom to incubate. In 29 experiments, the radioisotopes were in the form of labeled particles, but on two occasions the unconcentrated, ambient particulate matter was labeled by injection of [methyl-^{3}H]-thymidine (20 μCi·liter^{-1}) for bacteria and NaH^{14}CO$_3$ (50 μCi·liter^{-1}) for phytoplankton (Roman and Rublee, 1981); on these occasions, the incubation was for 1 h. This natural assemblage was, of course, present as unlabeled particulate matter in all experiments. Most incubations with labeled particles were for 0.5 h, based on gut passage time reported for *Mysidium* by Gottfried and Roman (1983), but evidence that the mysids produced some labeled feces prompted us to shorten the incubation to 0.3 h for measurements with naupliar brine shrimp, *Artemia salina* L., as the source of food.

Homogeneous sources of food were cultures of unicellular phytoplankton, *Isochrysis galbana* Parke or *Thalassiosira pseudonana* Hasle and Heimdal, labeled by uptake of NaH^{14}CO$_3$ through photosynthesis; suspensions of the bacterium, *Vibrio alginolyticus* Sakazaki, labeled by heterotrophic uptake of [methyl-^{3}H]-thymidine or ^{3}H-acetate; and naupliar *Artemia*, labeled by maintaining them for 2 days in ^{14}C-labeled *Isochrysis*. Of the cultured cells, *Vibrio* is the smallest and *Thalassiosira* the largest; relative to a 0.2-μm filter, a 0.6-μm filter retained >95% of labeled *Isochrysis* and *Thalassiosira*, and about 50% of labeled *Vibrio*, while a 5-μm filter retained <10% of *Isochrysis* and *Vibrio*, but 75% of the *Thalassiosira*. *V. alginolyticus* is commonly found in the mucus of living coral (Ducklow and Mitchell, 1979).

As representative sources of detritus for Davies Reef, we chose the alga, *Spyridia filamentosa* Harvey, and coral mucus derived from colonies of *Porites* sp. We collected detached *S. filamentosa* that had accumulated in sand channels, ground it in a tissue grinder and incubated the <64-μm fraction in seawater on shipboard for 48 h prior to feeding studies. *Porites* colonies were collected from the reef flat and maintained in seawater on shipboard. Mucus aggregates were collected by pipette from colony surfaces and ground in a tissue grinder, and the <64-μm fraction was incubated in seawater for 48 h before use. The natural epiphytic bacterial communities of the algal detritus and coral mucus were labeled with 50 μCi·liter^{-1} [methyl-^{3}H]-thymidine (Hollibaugh et al., 1980; Gottfried and Roman, 1983) for 24 h. This technique of labeling the epiphytic bacteria had been shown to give estimates of ingestion by the copepod, *Acartia tonsa*, and mysid, *Mysidium integrum*, feeding on mucus, comparable to measurements in which the substrate itself had been isotopically labeled (Gottfried and Roman, 1983). Replicate non-labeled suspensions of algal detritus and coral mucus were used to determine the concentration (as dry weight and carbon) of detrital particles in suspension.

Following the in situ incubation, we withdrew a second sample from the chamber for analysis of radioactivity of the food particles and removed and treated the mysids as described for salps in Mullin (1983). Two to seven batches of 5–12 mysids each were analyzed per experiment.

Radioactivities of filters (0.2 or 0.6 μm) containing particulate matter, mysids, fecal pellets, and aborted embryos were determined in Aquasol II® in a Beckman 2800® liquid scintillation counter after digestion in Protosol®. For the mysids, a few drops of H$_2$O$_2$ were necessary to bleach the pigment extracted by the digestion.

Grazing rates (=rates of effective clearance of particles from the water, ml·[mysid·h]$^{-1}$) on labeled particles were calculated as:

$$(\text{dpm}\cdot\text{mysid}^{-1})/(\text{dpm}\cdot\text{ml}^{-1}\text{ food suspension}\cdot\text{h of incubation}).$$

Adsorption of radioactivity by heat-killed mysids from one suspension each of labeled *Isochrysis* and *Vibrio* was measured, and calculated grazing rates of living mysids on ^{14}C- or ^{3}H-labeled particles were corrected for the appropriate adsorption, assuming that such adsorption was a linear function of the concentration of labeled particles. The grazing rates on assemblages of natural particles were calculated as:

$$2(\text{dpm}\cdot\text{mysid}^{-1})/(\text{dpm}\cdot\text{ml}^{-1}\text{ suspension}\cdot\text{h of incubation})$$

following Roman and Rublee (1981).

Biomasses of labeled sources of food, used in calculating specific activities, were determined as dry weights on pre-weighed filters or (for *Thalassiosira*) as extracted chlorophyll. These measures were converted to particulate organic carbon (POC) through measured POC/dry weight or POC/chlorophyll ratios of unlabeled material, the POC being determined with a Perkin-Elmer Elemental Analyzer. Ingestion rates as μg C·(mysid·h)$^{-1}$ were calculated as:

$$(\text{dpm}\cdot\text{mysid}^{-1})/(\text{dpm}\cdot\mu\text{g C}^{-1}\text{ of food}\cdot\text{h of incubation}).$$

On three successive days, we took water samples in the vicinity of a school of *Anisomysis*. Particulate matter was concentrated on heat-cleaned glass fiber filters, and POC was determined by wet oxidation in dichromic acid (Strickland and Parsons, 1972) followed by back-titration with 0.1 N acidic ferrous ammonium sulfate (Fox et al., 1952). To account for possible adsorption of dissolved organic matter, values for filter blanks were determined from filters which had been placed during filtrati
the primary filters concentrating the particulate matter (Banoub and Williams, 1972).
particulate matter was also collected in the lagoon behind the reef flat using water bottles, fil
glass fiber filters, and analyzed for particulate organic carbon with the Perkin-Elmer Elem
lyzer.

RESULTS

We found labeled fecal pellets in each of the seven experiments in w
tested for them, implying that the incubation period was long enough f
labeled food to be defecated. This would cause the true grazing rate to b
estimated from the radioactivity retained by the mysids at the end of inc
the degree of underestimation would probably increase with increased
ingestion of food, since the gut passage time is likely to decrease nonlinea
increased rate of ingestion. There is, however, some ambiguity concer
source of radioactivity in the fecal pellets. In most experiments, we fo
embryos and young which were probably released from the marsupia of
when the mysids were concentrated and killed at the end of the incuba
the two experiments where we removed these aborted young, we found
contain significant radioactivity. These young could not feed; their radi
suggests adsorption and thus it is possible that the radioactivity of the f
also adsorptive. Because of this ambiguity, we have made no corrections
loss.

The mysids grazed the cultured phytoplankton and bacteria at such l
(<0.6 ml·[mysid·h]$^{-1}$) that we conclude that the schools are unlikely to r
significant sources of mortality for free-living bacteria cells and small phyt
ton. Results for *Thalassiosira* are included in Figure 1B. In all cases
ingestion of the added food were <0.01 μg C·(mysid·h)$^{-1}$, or <0.01%
C·h^{-1}.

Grazing rates on coral mucus (as determined from uptake of the as
labeled bacteria) were somewhat higher (0.1–4.0 ml·[mysid·h]$^{-1}$, median
[mysid·h]$^{-1}$). In most experiments, algal detritus was grazed at similar ra
1B), though one experiment resulted in rates of 12–16 ml·[mysid·h]$^{-1}$ (F
This may reflect the availability of some moderately large food particle
detrital suspension. Concentrations >100 μg C·liter^{-1} appeared to dep
grazing rate somewhat (Fig. 1B), but the very high ingestion rates when
were provided as food (see below) make it unlikely that satiation occurre
of ingestion of mucus and detritus were ≤0.6 μg C·(mysid·h)$^{-1}$.

The median concentration (20 samples) of POC in the water around th
school was 26 μg C·liter^{-1}; the highest concentrations of added food aug
this value considerably. However, the concentrations of suspended, par
organic carbon in the lagoon were 80–200 μg C·liter^{-1} (median 97 μg C·l
we do not know whether this is a real difference between locations or is attri
to the different analytical methods employed for samples from the two lo

In the two experiments where dissolved isotopes rather than particula
were added to the chambers, the rate of grazing by the mysids on the org
taking up NaHCO$_3$ (primarily phytoplankton) was always less than 1 ml·(
h)$^{-1}$, while the grazing rate on thymidine-labeled particles (bacteria and p
through bactivory, protozoans) was 0.5–7.3 ml·(mysid·h)$^{-1}$. Given the a
preference of the mysids for large particles, it is likely that much of the b
biomass was associated with relatively large detrital particles, rather than a
cells.

We supplied naupliar *Artemia* at concentrations from 100 to 1,000

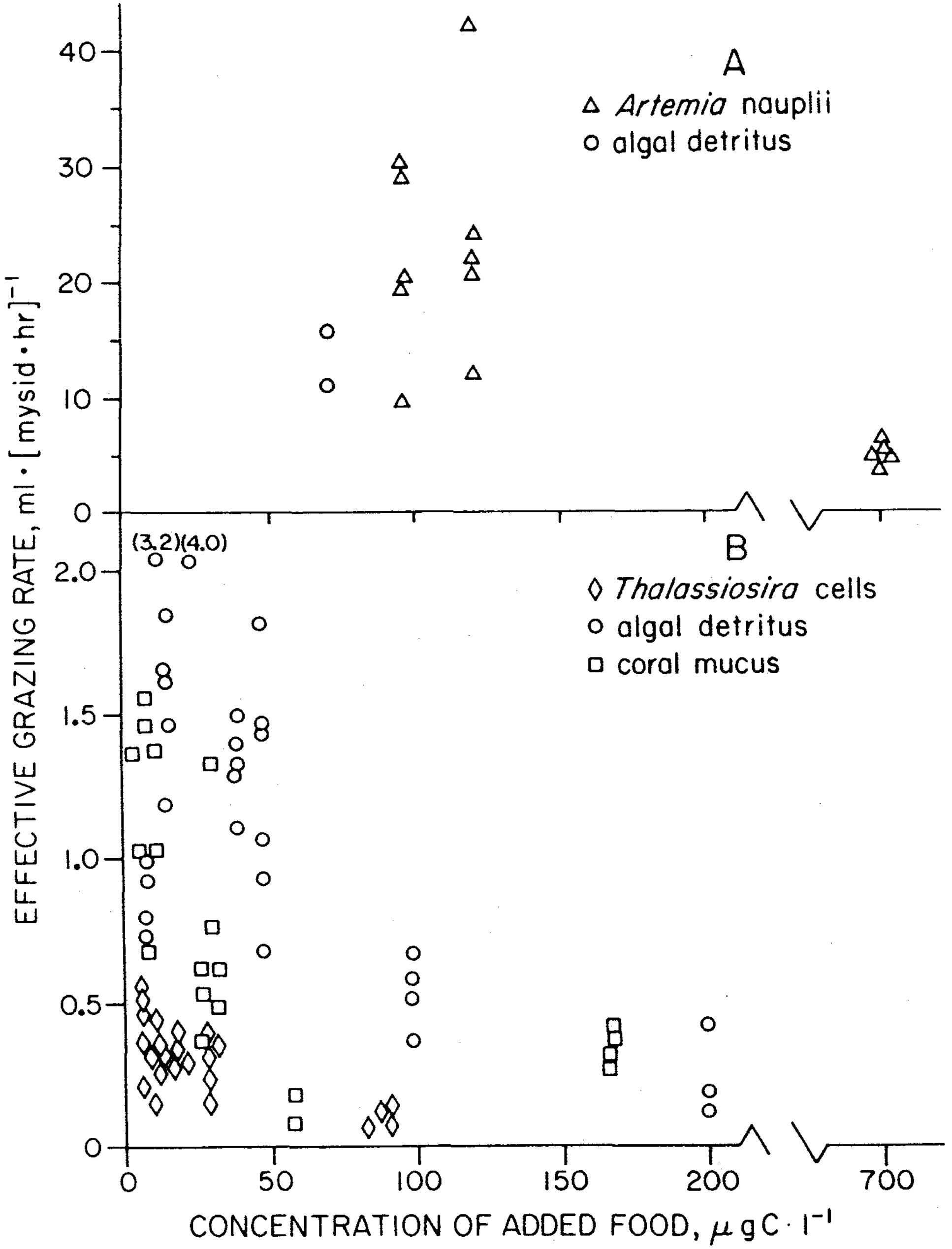

Figure 1. Grazing rates of *Anisomysis* on various types of food, as a function of the amount of food added to in situ containers. A. *Artemia* nauplii or algal detritus as food. B. *Thalassiosira* cells, algal detritus, or coral mucus as food.

liter^{-1} in 3 experiments; densities of nauplii resident on Davies Reef at the time of the study were 1–4 liter^{-1} (Roman, unpubl.). *Artemia* nauplii were grazed at rates of 3.9–41.6 ml·(mysid·h)$^{-1}$ (median = 19 ml·[mysid·h]$^{-1}$), which represented rates of ingestion of 1–6 nauplii·(mysid·h)$^{-1}$. Note that the "grazing rate"

is analogous to a "rate of effective search"; the latter term may be more ap
for the case of feeding on *Artemia* or other nauplii. Depression of the gra
at the highest concentration of nauplii (Fig. 1A) suggests saturation of f
a mean ingestion of about 4 nauplii·(mysid·h)$^{-1}$ which is equivalent t
C·(mysid·h)$^{-1}$, or 3% of mysid bodily C·h^{-1}. It is possible, of cours
mysid would in reality be satiated for an hour or longer by one naupli
during the actual 20 min incubation, though the calculated hourly ingesti
be 3 h^{-1}.

Artemia nauplii are an unnatural prey, both more visible and less rapi
mers than most copepod nauplii. Hence, we cannot at present determine
the relatively high grazing rates by *Anisomysis* on naupliar *Artemia*
predilection for carnivory or simply an efficient removal of large par
suggested by some high rates on algal detritus. In retrospect, we should ha
more homogeneous, large detrital particles. Results of Fulton (1982) for c
mysids suggest rather complex selective behavior among natural animal
mysids, even species whose gut contents indicate detritivory, *smaller* s
prey sometimes being preferred. (However, differences between prey s
aggregative and escape behavior may have affected Fulton's results.) H
lective carnivory, in addition to macrophagous detritivory, is certainly

DISCUSSION

In the context of the microbial ecology of Davies Reef, the *Anisomysis*
we studied are of negligible importance in removing free-living cells; t
nificance must be as scavengers of large detrital particles and as pred
smaller zooplankters. Several other species of mysids swarm at various
year in the lagoon behind the reef flat, including other *Anisomysis* sp
Carleton, pers. comm.), and what appeared to be another species of mysid
just over the sand bottom in the same pocket where our *Anisomysis* hove
the dark coral patches. Whether any of these other species has a mor
impact on finely divided detritus, phytoplankton, and bacteria remain
determined.

Even the grazing (or effective search) rates we measured using *Artemi*
prove that an individual school has a marked effect on large particles at a
We found a school of *Anisomysis* hovering over a particular dark coral
each of several daytime visits between 12 and 30 August. This school
an estimated volume of 100 liters and, assuming a spacing between m
two body lengths (as is typical of clupeoid fishes; Blaxter and Hunter
contained approximately 67 × 10^3 mysids. J. Carleton (pers. comm.) ha
mined the spacing between individuals in schools of other species of m
Davies Reef to be about 9 body lengths, which, if applicable to *Anisomysis*
mean 2 × 10^3 mysids in the school.

Enclosing mysids in the experimental chambers removed them from
though conditions of light, temperature, and water chemistry were natu
schools maintained position over the dark patches, generally orienting
current; oscillatory motions due to waves were usually dominant, especiall
high tides, and net (i.e., long-period) currents on the reef flat during Augu
less than 10 cm·sec^{-1} (G. Pickard, pers. comm.). We estimated the axi
school parallel to the current to be 50 cm (though quite variable), so a p
water moving with the net current would take at least 5 sec to pass thro
hovering school. In this minimal time, particles large enough to be graz
rate of 20 ml·(mysid·h)$^{-1}$ would only be reduced by 2% of the

centration by 67 × 10^3 mysids. However, since sustained swimming speeds of most mysids are on the order of 10 body lengths·sec^{-1} (Mauchline, 1980), or 5 cm·sec^{-1} for *Anisomysis,* it is doubtful that *Anisomysis* would be hovering and feeding in the water column in a long-lasting 10 cm·sec^{-1} current.

To reduce particles to 50% of their upstream concentration, either each mysid would have to search 420 ml·h^{-1} in a 5 cm·sec^{-1} current (i.e., at maximal sustained swimming), or, at 20 ml·$(mysid·h)^{-1}$, a parcel of water would have to take about 3.5 min to pass through the school. The latter situation would require a swimming speed of only 0.5 body lengths·sec^{-1}. Hence, either our estimate of the grazing rate per mysid is much to low (due, perhaps, to satiation, or to the fact that food particles were not moving by the enclosed mysids in a current), or this particular school has a major impact on suspended matter only in periods of slack water when maximal sustained swimming is not required. It would now be useful to calculate a rate of effective search for these mysids based on measurements of their perceptive distances and successes of attack for different types of detrital particles and zooplankton, and to make feeding measurements in a chamber permitting water motion.

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Marine Biology

Resident mysids: community structure, abundance and small-scale distributions in a coral reef lagoon*

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Abstract

Seasonal and diel variations in community structure and abundance of coral-reef lagoon mysids were examined at Davies Reef in the central region of the Great Barrier Reef (GBR) between June 1980 and May 1981. Twenty-five mysid species belonging to three subfamilies of the family Mysidae were captured during the study, with six new records for the GBR. The epibenthic mysid community differed from that in the overlying water, was faunistically uniform, but formed characteristic seasonal and diel groupings. The dominant epibenthic species were *Erythrops* sp., *Anisomysis pelewensis*, *Doxomysis littoralis*, *A. laticauda*, *Prionomysis stenolepis*, *A. lamellicauda*, and *A. australis*, five of which formed schools. Total mysid abundances ranged between 110 and 790 m^{-3} with peak abundance in October. Schooling species occurred at local densities of up to 500 000 m^{-3}. Mysids were a~~bsent~~ from shallow and mid-water depths during the day, but were distributed throughout all depths at night with peak abundances in mid-water and deep layers. The dominant species in the water column at night were *Pseudanchialina inermis*, *A. laticauda* and *Gastrosaccus indicus*, in descending order of abundance. Lagoonal mysids contribute little to the food of sessile reef planktivores, as all but three species remain concentrated near or on the lagoon floor both day and night. The contribution of resident lagoon mysids to reef trophodynamics is probably through remineralization of lagoon detritus. Given the vast reef areas comprised of sandy lagoons, the large populations and relatively large size of lagoon mysids, this trophodynamic role may be of considerable importance.

Introduction

Mysids form a highly visible component of resident coral reef plankton (Emery 1968). Their aggregations occur in a variety of reef habitats (Emery 1968, Băcescu 1975, Hamner and Carleton 1979) and they play an important role as macrophages, carnivores and detritivores in reef trophodynamics (Gottfried and Roman 1983, Mullin and Roman 1986). Mysids are also one of the characteristic taxa which comprise the unique zooplankton assemblages contained in coral reef lagoons (Tranter and George 1972). These zooplankton communities differ from those of the surrounding sea, both in terms of species composition (Gerber and Marshall 1974, Renon 1977, 1978), and in terms of numbers of individuals (Motoda 1940, Johnson 1949, 1954).

The majority of studies concerned with reefal lagoon zooplankton has concentrated on demersal organisms, those forms which burrow or hide within the reef substrate during the day, rise up into the water column at dusk and return before dawn (Porter 1974). A great variety of emergence and re-entry traps has been designed to study spatial and temporal variability in these zooplankters (see Jacoby and Greenwood 1988 for review), yet mysids usually constitute a very small portion of the samples collected by these devices. In contrast, the use of an epibenthic trap designed specifically to make use of the ~~mysids'~~ escape response to effect their capture (Carleton and Hamner 1987), produces abundance estimates that are very much higher.

In this ~~study, quantitative~~ data were collected on seasonal, diel and small-scale spatial variations in the species composition and abundance of epibenthic mysids in the lagoon of Davies Reef on the Great Barrier Reef, using the epibenthic trap and plankton nets. These data, therefore, provide the first quantitative detailed information on the sources of variation in the distribution, species composition and abundance of this unique resident community and are an essential prerequisite for further studies on the role of mysids in the trophodynamics of coral reef lagoons.

Materials and methods

Sampling

Samples were collected between June 1980 and May 1981 in the lagoon at Davies Reef (Fig. 1). The sites were just behind

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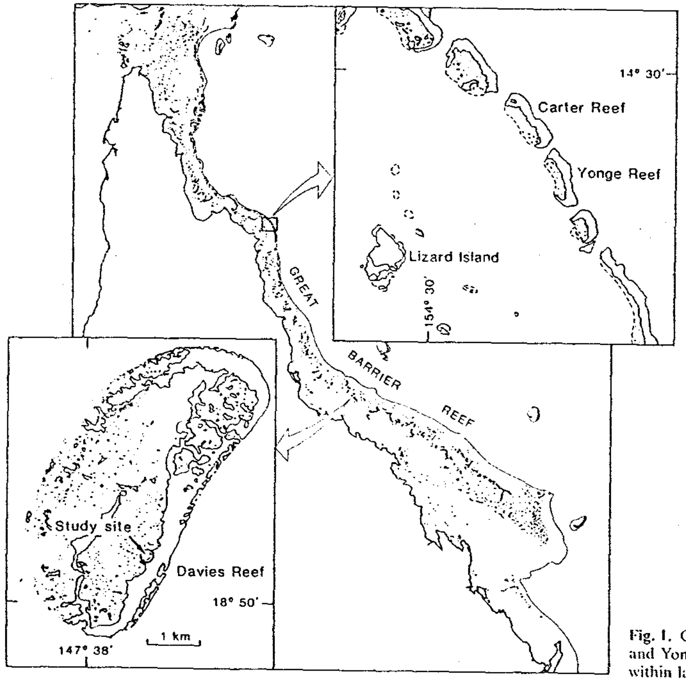

Fig. 1. Geographic location of Davies, Carter and Yonge Reefs, Great Barrier Reef. Study site within lagoon at Davies Reef is also shown

the fore-reef flat over a white carbonate sand bottom (Tudhope 1983) well away from any coral outcrops. Water depth varied between 8 and 11 m.

Three replicate sets of diurnal and nocturnal samples were taken from the lagoon floor and from surface, mid and deep strata in July and October 1980 and in February and May 1981 with an epibenthic trap and plankton nets. Variation in seasonal abundances and reproductive effort was studied using additional samples taken in September and December 1980 and in March 1981.

The trap captured both benthic and epibenthic organisms (Carleton and Hamner 1987). It consisted of two sets of components: a perspex funnel with a detachable collection box and variable air lift, and a set of plastic curtains (two clear plastic side curtains and an opaque "driving" curtain). The funnel, driving curtain and side curtains, which were supported by fence pickets hammered into the substrate, were placed so as to enclose a 10 m^2 area of the bottom. Two divers, by pushing the driving curtain slowly along the lagoon floor, herded all entrapped organisms living on or up to 1 m above the bottom into the funnel. A volume of 10 m^3 was thus sampled. The animals were moved through the funnel and into the collection box by activating the air lift and by continued motion of the driving curtain. Once the organisms had entered the box, the sliding door at its mouth was closed. The box was detached from the funnel and taken to the surface, where its contents were concentrated. Samples were fixed with 10% buffered formalin. This procedure was repeated and ~~the~~ two sweeps combined to form one representative sample. Replicate benthic samples were taken sequentially with three separate traps placed 4 to 6 m apart.

Water-column samples (surface, mid and deep strata) were collected sequentially with a single, horizontally towed, plankton net. The order in which the three depth strata were sampled within each replicate set was determined with a random numbers table. The plankton net, towed from the bow of a dinghy and without a bridle so as to minimize avoidance (Clutter and Anraku 1968, Birkeland 1984), had a 0.5 m diam opening, 235 μm mesh, and carried a General Oceanics flowmeter placed eccentrically within the mouth (Fraser 1968). Tows were for 5 min at approximately 60 cm s^{-1}.

In the laboratory, animals from the lagoon floor were separated from sand by swirling the samples in a large, shallow pan and decanting the supernatant through a series of sieves (Birkett and McIntyre 1971). This procedure was repeated until the wash was free of plankton. Large or rare organisms were removed from the various fractions and counted. The more homogenous remaining residues were

concentrated and subsampled using a Folsom type splitter (Van Guelpen et al. 1982). A Bogorov tray and stereoscopic microscope were used for counting. Samples were analysed for species composition and abundance, and the proportion of oviparous females and the mean number of embryos per female were determined.

For species with complex schooling behaviours (Carleton 1986), school density and composition were determined using photographs and hand-net samples. The photographic techniques employed were similar to those described by Hamner and Carleton (1979) with nearest-neighbour distances calculated from density data by assuming isahedronic packing and using the formula:

$$\text{average nearest neighbour distance (cm)} = (\text{no. mysids cm}^{-3} \times 0.589)^{-0.3333}$$

Samples from schools were processed for species composition, age-class structure, sex ratios, and size-frequency distributions. These data were collected in another study of lagoon mysids during January 1977 on Carter and Yonge Reefs (15°40'S) (Fig. 1). The same mysid species schooled at both locations and the sizes and distributions of schools were very similar (Carleton 1986). It was assumed that the internal characteristics of the schools were also very similar.

Data analysis

All data derived from individual replicate samples ($n = 105$) taken during the study were subjected to agglomerative, hierarchical classification techniques to discriminate associations among the 25 mysid species encountered during the study. Bray-Curtis similarity coefficients (Bray and Curtis 1957) and Burr's incremental sum of squares strategy (Burr 1970) were used, and the results were summarized by dendrograms (Belbin 1987). The sample groupings produced by the hierarchical classification were validated by the method of Sandland and Young (1979 a, b), and the species contributing most to the differences between the various groupings were determined by the methods of Abel et al. (1985). Shannon-Wiener diversity index (H') and Pielou's evenness index (J') (Pielou 1969, 1975) were calculated for each group.

Abundance data for each epibenthic species captured more than once were analysed by univariate procedures. Data from the benthic trap and standard plankton nets were analysed separately due to the differences in their sampling efficiency (Carleton and Hamner 1987). Seasonal and diel differences in benthic abundances were tested using fixed two-factor ANOVA with four levels (July, October, February and May) in the first factor and two levels (diurnal and nocturnal) in the second factor. Differences in abundances at the shorter time scale (six weekly intervals) were tested by single-factor analyses with seven levels (July, September, October, December, February, March and May).

Nocturnal differences in distribution and abundance throughout the water column were tested using fixed two-factor (depth and season) ANOVA with three levels (surface, mid and deep) in the first factor and four levels (July, October, February and May) in the second.

Prior to running the analyses, Cochran's C-test was used to test for homogeneity of variance. Where variances were heterogeneous, abundances (no. individuals m^{-3}) were transformed to $\log_{10}(x+1)$ (Sokal and Rohlf 1981). In the single-factor analyses, due to heteroscedastic variance, it was necessary to use non-parametric procedures for two of the species (Kruskal-Wallis test; Sokal and Rohlf 1981).

Means from significant parametric tests were compared using the Student-Newman-Keuls procedure (Unterwood 1981) and those from significant non-parametric tests were compared using the Games and Howell method (Sokal and Rohlf 1981).

Heterogeneity in the proportion of females carrying embryos was tested by two-way contingency tables using the G-test, a test for independence (Sokal and Rohlf 1981), and homogeneous subsets were extracted by simultaneous test procedures employing an experimentwise error rate (Sokal and Rohlf 1981). Multiple-range procedures were used to compare seasonal differences in the mean number of embryos carried by females. Where the variances for the set of means being compared were heteroscedastic, as determined by Bartlett's test for homogeneity of variances, the Games and Howell method was employed, otherwise the GT2-method was used (Sokal and Rohlf 1981).

For the length-frequency distributions obtained from schools the two descriptive statistics, g_1 and g_2, were calculated and their significance tested (Sokal and Rohlf 1981). Class structure and sex ratio data were compared using two-way contingency tables (Sokal and Rohlf 1981).

The critical probability level for significance testing was set at 5% for all analyses.

Results

Community composition

A total of 25 species belonging to three subfamilies of the family Mysidae (Table 1) and comprising 136 253 individuals were collected. Six of the epibenthic species are new records for the Great Barrier Reef.

Classification of all replicate samples ($n = 105$) produced 12 significantly different groups (Sandland and Young 1979a, b). The majority of shallow and mid-water diurnal net samples separated from all other samples at a high level of dissimilarity. This group was devoid of mysids and is not considered further. The next split in this initial classification segregated all of the trap samples from the remaining net samples. These two data sets (trap and remaining net samples) were then subjected to separate cluster analyses (Fig. 2).

Classification of the trap samples produced six significantly different groups (Fig. 2a). Samples clustered into seasonal groupings (spring and early summer, and late summer, autumn and winter) which disassociated at lower levels of dissimilarity into the diel components. The number of spe-

Table 1. List of mysid species encountered during present study between June 1980 and May 1981 on Davies Reef, Great Barrier Reef. Resident species are those captured by benthic trap, pelagic species those captured primarily by plankton nets towed through surface waters at night. Asterisk indicates new record for Great Barrier Reef

Resident species

- Family Mysidae
  - Subfamily Siriellinae
    - *Hemisiriella parva* Hansen
  - Subfamily Gastrosaccinae
    - *Gastrosaccus indicus* Hansen
    - *Anchialina grossa* Hansen
    - *Pseudanchialina inermis* Illig*
  - Subfamily Mysinae
- Tribe Erythropini
  - *Erythrops* sp.
- Tribe Leptomysini
  - *Doxomysis littoralis* Tattersall
  - *Prionomysis stenolepis* Tattersall*
- Tribe Mysini
  - *Anisomysis pelewensis* Ii*
  - *Anisomysis laticauda* Hansen
  - *Anisomysis australis* Zimmer*
  - *Anisomysis lamellicauda* Hansen*
  - *Anisomysis bifurcata* Tattersall*

Pelagic species

- Family Mysidae
  - Subfamily Siriellinae
  - Genus *Sirella* Dana
  - (*Thompsoni* group)
  - (*Thompsoni* subgroup)
    - *Siriella thompsoni* H. M. Edwards
    - *Siriella gracilis* Dana
    - *Siriella nodosa* Hansen
    - *Siriella affinis* Hansen
    - *Siriella quadrispinosa* Hansen
    - *Siriella vulgaris* Hansen
    - *Siriella* sp. a
    - *Siriella* sp. b
  - (*Inornata* group)
    - *Siriella inornata* Hansen
    - *Siriella media* Hansen
  - (*Aequiremis* group)
    - *Siriella aequiremis* Hansen
    - *Siriella distinguenda* Hansen
    - *Siriella conformalis* Hansen

cies in the epibenthic community was fairly constant (11 to 15) throughout the year in both day and night samples. *Erythrops* sp., *Anisomysis pelewensis, Doxomysis littoralis, A. laticauda, Prionomysis stenolepis, A. lamellicauda* and *A. australis* were usually present throughout the year (Table 2). However, the species diversity index (H') was quite variable due primarily to differences in relative abundances of a number of species (Fig. 2a). *Erythrops* sp. dominated the species associations during the spring and early summer, producing the lowest diversity indices ($H'=0.37$ to 0.38). *A. pelewensis* dominated the nocturnal July community ($J'=0.58$), and *A. laticauda* dominated the July and February diurnal samples ($J'=0.39$). The highest diversity index ($H'=0.73$) was in May, due primarily to even apportioning of individuals among the 15 species present ($J'=0.62$). As determined by the methods of Abel et al. (1985), the two most abundant epibenthic species, *Erythrops* sp. and *A. pelewensis*, contributed most to the differences between mysid associations.

Classification of the remaining net samples produced five significantly different groups (Fig. 2b). There was no obvious pattern associated with season, depth or time of day. However, diurnal mysid concentrations were five times lower than those at night. Diurnal deep samples contained only 4 to 5 species, belonging primarily to the genus *Anisomysis*. These samples were dominated by *A. laticauda* ($J'=0.56$ to 0.75). Nocturnal samples were dominated by *Pseudanchialina inermis*. This was especially true for those samples from the mid and deep layers in October and February ($J'=0.30$). The highest species diversity ($H'=0.79$) occurred in shallow nocturnal samples from July and May due to a high J' (0.61) caused by relatively even abundances of the 12 species belonging to the genus *Siriella*.

Distribution and abundance

Throughout the year, there were more mysids captured on the lagoon floor during the day than at night. However, total abundances and relative differences between day and night abundances varied with season (interactions) in over half of the species (Table 2). Variations in seasonal abundances were indicated by both the two-factor (season × diel) and single-factor (season) analyses. However, the period of peak abundance was not the same for every species (Fig. 3). The three dominant epibenthic species, *Erythrops* sp., *Anisomysis pelewensis* and *Doxomysis littoralis*, were most abundant during the Austral spring and early summer from September through to December (Fig. 3, Table 2). During the winter and spring months of July and September, *Prionomysix stenolepis* was most abundant. Five of the seven most abundant epibenthic species engaged in schooling behaviour (Table 2).

The majority of epibenthic species remained on or near the lagoon floor at night. For example, *Erythrops* sp. in October had benthic abundances which were two orders of magnitude greater than in the overlying water (Fig. 4). Only one resident lagoonal mysid, *Anisomysis laticauda*, a species which schooled above the bottom during the day and was relatively abundant in diurnal trap samples (up to 62%; Table 2), consistently migrated into the water column at night (Table 3; Fig. 4). Juvenile, immature and mature individuals of this species were found in the water column, and the proportion of each stage did not differ significantly from the population as a whole (all samples pooled: $p>0.05$; χ^2).

In addition to *Anisomysis laticauda*, individuals of *Pseudanchialina inermis* and *Gastrosaccus indicus* were consistently dispersed through the water column at night. These

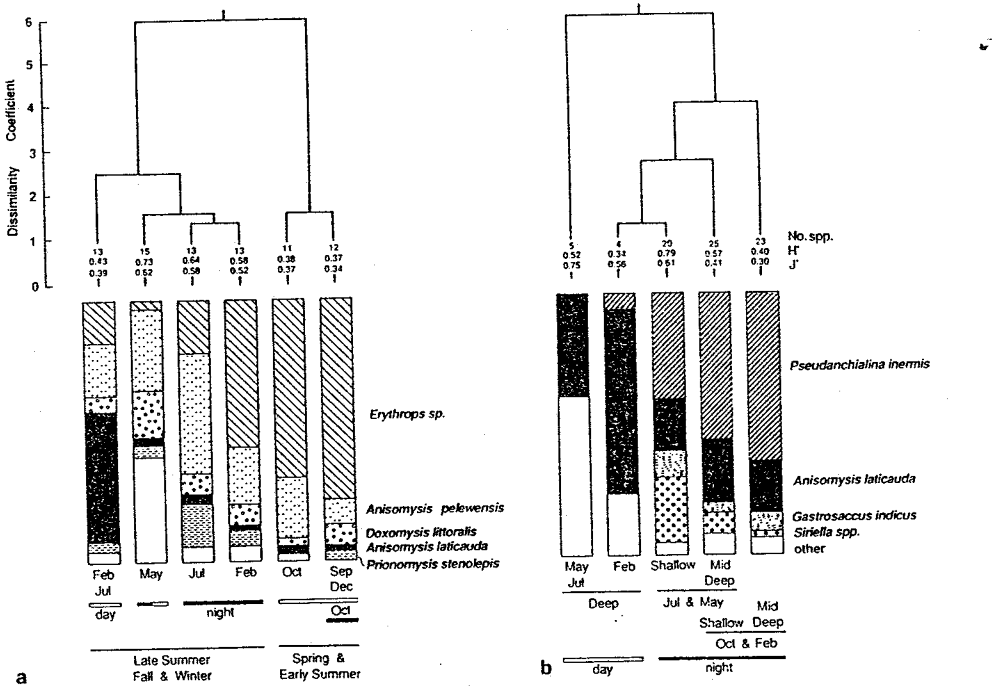

Fig. 2. Dendrograms summarizing classification analyses on all 25 mysid species encountered during study. Number of species (No. spp.), Shannon-Wiener diversity index (H'), Pielou's evenness index (J') and relative abundances of dominant species given for each significant ($p<0.05$) group. (a) Dendrogram produced from all replicate trap samples ($n=33$); bar chart showing proportions of five most abundant epibenthic species. (b) Dendrogram produced from majority of replicate net samples ($n=48$; shallow and mid-water diurnal samples excluded); bar chart showing proportions of genus *Siriella* and three most abundant species in water column at night. *Anisomysis laticauda* was abundant in both diurnal trap samples and nocturnal net samples

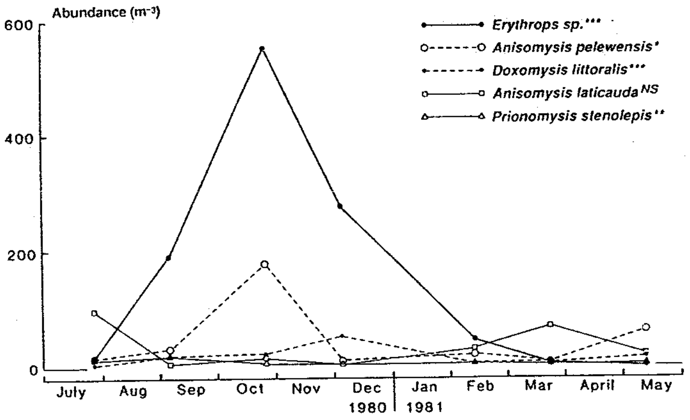

Fig. 3. Diurnal abundances of five most abundant epibenthic mysid species. $^*p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$