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. Particular 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 (Mauschline, 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 mulli; 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 3-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 $\mu$Ci liter$^{-1}$) for bacteria and NaH$^{14}$CO$_3$ (50 $\mu$Ci liter$^{-1}$) for phytoplankton (Roman and Rublee, 1981). On these occasions, the incubation was for 1 h. This natural assemblage was, of course, a mixture of 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 Thalassiostra 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 nauplar Artemia, labeled by maintaining them for 2 days in labeled seawater. Of the cultured cells, Vibrio is the smallest relative to a 0.2-$\mu$m filter, a 0.6-$\mu$m filter retained >95% of labeled Isochrysis and Thalassiostra, and about 30% of labeled Vibrio, while a 5-$\mu$m filter retained <10% of Isochrysis and Vibrio, but 75% of the Thalassiostra. 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 algae, Spriydia 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-$\mu$m 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 from the water, filtered through a 5-$\mu$m filter, and resuspended in seawater. The <64-$\mu$m 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 $\mu$Ci 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). Replica 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 $\mu$m) 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$^{-1}$]•h$^{-1}$) on labeled particles were calculated as:

\[\text{Grazing rate} = \frac{(\text{dpm} \text{ mysid}^{-1})}{(\text{dpm} \text{ ml}^{-1} \text{ suspension h}^{-1} \text{ of incubation})}\]

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:

\[\text{Grazing rate} = \frac{(\text{dpm} \text{ mysid}^{-1})}{(\text{dpm} \text{ ml}^{-1} \text{ suspension h}^{-1} \text{ of incubation})}\]

Following Roman and Rublee (1981).

Biomasms of labeled sources of food, used in calculating specific activities, were determined as dry weights on pre-weighed filters or (for Thalassiostra) as extracted chlorophyll. These measures were corrected 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 $\mu$g C (mysid$^{-1}$) were calculated as:

\[\text{Ingestion rate} = \frac{(\text{dpm} \text{ mysid}^{-1})}{(\text{dpm} \text{ ml}^{-1} \text{ of food h}^{-1} \text{ of incubation})}\]

values for filter blanks were determined from filters which had been placed during filtration at the primary filter concentrating the particulate matter (Banoub and Williams, 1972). particulate matter was also collected in the lagoon behind the reef flat using water bottles, filter glass fiber filters, and analyzed for particulate organic carbon with the Perkin-Elmer Elemental Analyzer.

RESULTS

We found labeled fecal pellets in each of the seven experiments in which we tested them, implying that the incubation period was long enough for labeled food to be fecated. This would cause the true grazing rate to be estimated from the radioactivity retained by the mysids at the end of the degree of underestimation would probably increase with increased ingestion of food, since the gut passage time is likely to decrease nonlinearly increased rate of ingestion. There is, however, some ambiguity concerning the source of radioactivity in the fecal pellets. In most experiments, we fed embryos and young which were probably released from the marsupia of when the mysids were concentrated and killed at the end of the incubation. In the two experiments where we removed these aborted young, we found that the mysids contained significant radioactivity. These young could not feed; their radioactivity is therefore adsorbed. Because of this ambiguity, we have made no corrections in the comparison with the value estimated from uptake of the assemblage labeled bacteria) were somewhat higher (0.1–4.0 ml [mysid$^{-1}$]), median (mysid$^{-1}$). In most experiments, algae detritus was grazed at similar rates (1–12 ml [mysid$^{-1}$]•h$^{-1}$), though one experiment resulted in rates of 12–16 ml [mysid$^{-1}$]•h$^{-1}$ (Table 1). This may reflect the availability of some moderately large food particle detrital suspension. Concentrations >100 $\mu$C C$^{-1}$ appeared to depress grazing rate somewhat (Fig. 1B), but the very high ingestion rates when provided as food (see below) make it unlikely that satiation occurred ingestion of mucus and detritus were >0.6 $\mu$g C (mysid$^{-1}$)•h$^{-1}$.

The median concentration (20 samples) of POC in the water around this school was 26 $\mu$g C$^{-1}$•l$^{-1}$, the highest concentrations of added food augmented this value considerably. However, the concentrations of suspended, particulate organic carbon in the lagoon were 80–200 $\mu$g C$^{-1}$•l$^{-1}$ (median 97 $\mu$g C$^{-1}$•l$^{-1}$). We do not know whether this is a real difference between locations or is attributable to the different analytical methods employed for samples from the two locations.

In the two experiments where dissolved isotopes rather than particulate were added to the chambers, the rate of grazing by the mysids on the orange, taking up NaH$^{14}$CO$_3$ (primarily phytoplankton) was always less than 1 ml (h$^{-1}$), while the grazing rate on thymidine-labeled particles (bacteria and p through bactiory, protozoans) was 0.5–7.3 ml (mysid$^{-1}$)•h$^{-1}$•h$^{-1}$. Given the high preference of the mysids for large particles, it is likely that much of the b ion was associated with relatively large detrital particles, rather than a cell.

We supplied naupliar Artemia at concentrations from 100 to 1000
A

\[ \triangle \text{Artemia nauplii} \]
\[ \circ \text{algal detritus} \]

B

\[ \triangle \text{Thalassiosira cells} \]
\[ \circ \text{algal detritus} \]
\[ \square \text{coral mucus} \]

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.

If the "grazing rate" is analogous to a "rate of effective search"; the latter term may be more apt 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 its 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 course, that a mysid would in reality be satiated for an hour or longer by one naupli during the actual 20 min incubation, though the calculated hourly inges be 3 h^{-1}.

*Artemia* nauplii are an unnatural prey, both more visible and less rap 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 part suggested by some high rates on algal detritus. In retrospect, we should hav e more homogeneous, large detrital particles. Results of Fulton (1982) for c mysid suggest rather complex selective behavior among natural animal mysids, even species whose gut contents indicate detritivory, *smaller* prey sometimes being preferred. (However, differences between prey sp aggregative escape behavior may have affected Fulton's results.) H.lective carnivory, in addition to macrophagous detritivory, is certainly p

**DISCUSSION**

In the context of the microbial ecology of Davies Reef, the *Anisomysis* we studied are of negligible importance in removing free-living cells; ti nicance must be as scavengers of large detrital particles and as predi smaller zooplankters. Several other species of mysids swarm at various 1 year in the lagoon behind the reef flat, including other *Anisomysis* sp Carleton, pers. comm.), and what appeared to be another species of mysid e over the sand bottom in the same pocket where our *Anisomysis* hover the dark coral patches. Whether any of these other species has a m impact on finely divided detritus, phytoplankton, and bacteria remain determined.

Even the grazing (or effective search) rates we measured using *Artemia* 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 p each of several daytime visits between 12 and 30 August. This school o 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 $67 \times 10^3$ mysids. J. Carleton (pers. comm.) ha mined the spacing between individuals in schools of other species of my Davies Reef to be about 9 body lengths, which, if applicable to *Anisomy mean $2 \times 10^3$ mysids in the school.

Enclosing mysids in the experimental chambers removed them from c though conditions of light, temperature, and water chemistry were natu schools maintained position over the dark patches, generally orienting c current; oscillatory motions due to waves were usually dominant, especially high tides, and net (i.e., long-period) currents on the reef flat during Aug less than 10 cm/sec^{-1} (G. Pickard, pers. comm.). We estimated the a 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 gra rate of 20 ml-(mysid-h)^{-1} would only be reduced by 3% of the water.

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"...
centration by $67 \times 10^3$ 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 too 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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LITERATURE CITED


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 taxonomically uniform, but formed characteristic seasonal and diel groupings. The dominant epibenthic species were Erythropus sp., Anomanyctis pulex, Desoynysia bidarvii, A. laternae, Pygodonotys stevei, A. anfibfluca, 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 absent from shallow and mid-water depths during the day, but were distributed horizontally at all depths in the water column at night. The dominant species in the water column at night were Pseudamphithoe inermis, A. laternae and Gasteropontes lineolatus, in descending order of abundance. Lagoonal mysids contribute little to the food of small reef planktivores, as all 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 (Ensmey 1968). Their aggregations occur in a variety of reef habitats (Ensmey 1968, Bicetcu 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, Reen 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 mysid's active 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
concentrated and subsampled using a Falcoam type splitter (Van Guelpen et al. 1982). A Bögrö ray and stereoscopic microscope were used for counting. Samples were analyzed for species composition and abundance, and the proportion of ovigerous 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 from density data by assuming isodonic packing and using the formula:

\[
\text{average nearest neighbour distance (cm)} = \frac{\ln(x)}{0.589 - 0.0233}
\]

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 (5°40'S) (Fig. 1). The same mysid species sampled at both locations and the sites 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 of strategy (Burr 1970) were used, and the results were summarized by dendrograms (Bohlen 1987). The sample groupings produced by the hierarchical classification were validated by the method of Sandiland and Young (1979a, 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 (\(I'\)) and Pietsch's evenness index (\(J\)) (Pietsch 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 variance was heterogeneous, abundances (no. individuals m⁻²) were transformed to \(\log_2(x+1)\) (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 (Underwater 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 experimental 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 heterogeneous, 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 15 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 (Sandiland 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 twoCC components. The number of spe-
Species in the epibenthic community was fairly constant (11 to 13) throughout the year in both day and night samples. Erythrops sp., Anisomysis pelverens, Diosamysis littoralis, A. laticuda, Prionomyys steinolus, 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. pelverens dominated the nocturnal July community (H' = 0.58), and A. laticuda dominated the July and February diurnal samples (H' = 0.39). The highest diversity index (H' = 0.73) was in May, due primarily to even approximating of individuals among the 15 species present (H' = 0.62). As determined by the methods of Abe et al. (1985), the two most abundant epibenthic species, Erythrops sp. and A. pelverens, contributed most to the differences between myid 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 myid concentrations were five times lower than those at night. Diurnal deep samples contained only 1 to 5 species, belonging primarily to the genus Anisomysis. These samples were dominated by A. laticuda (H' = 0.56 to 0.73). Nocturnal samples were dominated by Pseudanchialina inermis. This was especially true for those samples from the mid and deep layers in October and February (H' = 0.79). The highest species diversity (H' = 0.79) occurred in shallow nocturnal samples from July and May due to a high H' (0.61) caused by relatively even abundances of the 12 species belonging to the genus Sirella.

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 x diet) 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 pelverens and Diosamysis 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, Prionomyys steinolus 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 laticeps, 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, χ²).

In addition to Anisomysis laticeps, individuals of Pseudanchialina inermis and Diosamysis littoralis were consistently dispersed through the water column at night. These species contributed significantly (p < 0.01) to the differences between day and night samples (Table 2). This was especially true for those species that were present at night but absent during the day (p < 0.01).
Table 2. Abundance and diel abundances in benthic trap of seven most abundant mysid species. The two-factor analysis compared diurnal and nocturnal abundances for months July (J), October (O), February (F), and May (M); the one-factor analyses compared only diurnal abundances for all 3 mo. ANOVA analysis of variance; SNK: Student-Newman-Keuls multiple-range procedure for comparing means; J: July; O: October; D: December; M: March

<table>
<thead>
<tr>
<th>Species</th>
<th>July (%)</th>
<th>Oct (%)</th>
<th>Dec (%)</th>
<th>Feb (%)</th>
<th>Mar (%)</th>
<th>May (%)</th>
<th>ANOVA (inter-</th>
<th>SNK</th>
<th>ANOVA (seasonal)</th>
<th>SNK</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Kroylophora</em> sp.</td>
<td>17.1</td>
<td>3.6</td>
<td>191.3</td>
<td>553.2</td>
<td>229.3</td>
<td>276.2</td>
<td>44.7</td>
<td>18.7</td>
<td>6.1</td>
<td>1.2</td>
</tr>
<tr>
<td><em>Antoniopsis</em> pelorideus*</td>
<td>15.4</td>
<td>9.2</td>
<td>31.1</td>
<td>176.1</td>
<td>62.7</td>
<td>9.5</td>
<td>19.6</td>
<td>7.2</td>
<td>5.4</td>
<td>16.7</td>
</tr>
<tr>
<td><em>Decomys</em>* littoralis*</td>
<td>3.9</td>
<td>1.2</td>
<td>18.0</td>
<td>22.0</td>
<td>8.4</td>
<td>52.1</td>
<td>3.4</td>
<td>1.7</td>
<td>13.5</td>
<td>15.6</td>
</tr>
<tr>
<td><em>Antoniopsis</em> lacteolus*</td>
<td>97.5</td>
<td>0.3</td>
<td>4.9</td>
<td>142.0</td>
<td>0.6</td>
<td>3.4</td>
<td>30.8</td>
<td>0.1</td>
<td>66.2</td>
<td>21.0</td>
</tr>
<tr>
<td><em>Pseudocalanus</em> listeri*</td>
<td>13.0</td>
<td>4.6</td>
<td>19.8</td>
<td>4.9</td>
<td>1.9</td>
<td>2.4</td>
<td>1.5</td>
<td>1.5</td>
<td>2.0</td>
<td>3.7</td>
</tr>
<tr>
<td><em>Antoniopsis</em> maculata*</td>
<td>6.4</td>
<td>0.0</td>
<td>2.5</td>
<td>10.2</td>
<td>0.0</td>
<td>0.3</td>
<td>4.5</td>
<td>0.2</td>
<td>1.3</td>
<td>2.8</td>
</tr>
<tr>
<td><em>Antoniopsis</em> mexicana*</td>
<td>0.5</td>
<td>0.1</td>
<td>0.2</td>
<td>2.7</td>
<td>0.2</td>
<td>0.3</td>
<td>2.2</td>
<td>0.1</td>
<td>166.9</td>
<td>1.7</td>
</tr>
<tr>
<td>Total</td>
<td>137.7</td>
<td>2.12</td>
<td>266.5</td>
<td>766.3</td>
<td>303.4</td>
<td>346.2</td>
<td>109.2</td>
<td>31.5</td>
<td>1155.5</td>
<td>156.1</td>
</tr>
</tbody>
</table>

* p < 0.05; ** p < 0.01; *** p < 0.001
1 Schooling species
2 Non-parametric tests used for analysis
3 Mann-Whitney test excluded from analysis

Discussion

Although species within and between schools varied significantly, having a greater number of eggs per female in May than July (Fig. 5). The eggs of species such as P. pelorideus and A. lacteolus were found mainly in the mid and deep layers, especially during October and February. In addition, the abundance of P. pelorideus increased sharply from the surface to the deep layers, especially during October and February. In contrast, the abundance of A. lacteolus decreased sharply from the surface to the deep layers. The percentage of gravid females in May was significantly lower than in July (Fig. 4). The percentage of gravid females in May was significantly higher than in July (Fig. 5).

Table 3. Abundance data from nocturnal set samples of three most abundant species. JS: July; surface; OM: October; mid-depth; OD: October; deep; FM: February; mid-depth; FD: February; deep; MS: May; surface; MD: May; deep. Other abbreviations as in Table 2

<table>
<thead>
<tr>
<th>Species</th>
<th>July</th>
<th>October</th>
<th>February</th>
<th>May</th>
<th>ANOVA (inter-</th>
<th>location in water column</th>
<th>time of year</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pseudocalanus</em> listeri*</td>
<td>0.50</td>
<td>5.70</td>
<td>7.00</td>
<td>2.30</td>
<td>9.70</td>
<td>17.60</td>
<td>4.60</td>
</tr>
<tr>
<td><em>Antoniopsis</em> lacteolus*</td>
<td>0.38</td>
<td>1.20</td>
<td>0.33</td>
<td>2.50</td>
<td>12.90</td>
<td>12.60</td>
<td>4.00</td>
</tr>
<tr>
<td><em>Antoniopsis</em> maculata*</td>
<td>0.23</td>
<td>0.03</td>
<td>0.16</td>
<td>0.23</td>
<td>2.10</td>
<td>4.10</td>
<td>0.10</td>
</tr>
<tr>
<td>Total</td>
<td>2.46</td>
<td>7.17</td>
<td>8.12</td>
<td>6.01</td>
<td>19.79</td>
<td>37.72</td>
<td>10.42</td>
</tr>
</tbody>
</table>

* p < 0.001
1 Schooling species

Although species within and between schools showed highly significant differences (p < 0.001), the species richness of the sample was not significantly different (p > 0.05). The species richness of the sample was not significantly different (p > 0.05). The species richness of the sample was not significantly different (p > 0.05).
The density of mysids on the lagoon floor, when converted to numbers per unit area (109.2 to 876.3 m$^{-2}$), is one to three orders of magnitude greater than those for more temperate marine species (0.1 m$^{-2}$). Didawell 1975; 2.6 to 21.6 m$^{-2}$, Maahelie 1980). Only the freshwater mysid Mytilus reticulatus occurs in abundance approaching those reported here (300 m$^{-2}$, Morgan and Becton 1976). Nocturnal mysid densities found in this study (2.5 to 10.4 m$^{-2}$) are similar to those (11 m$^{-2}$) captured by Tranter and George (1972) in the lagoon surface waters at Kavarati Atoll, using nets similar to ours (no bridles; 200 um mesh). The significant seasonal variations in abundances, with greatest densities occurring during the spring and summer, are consistent with observations on general zooplankton abundances for specific reefs within the Great Barrier Reef province (Salle et al. 1976, 1978, Hamner and Carlton 1979, McWilliam et al. 1981, Jacoby and Greenwood 1988) and for the Great Barrier Reef lagoon (Rumel 1934, Ikeda et al. 1982).

Although the benthic trap used in this study was designed to make use of the mysids' escape response to their capture (Carlton and Hamner 1987), the densities obtained for schooling species were very much lower than those estimated from photographic techniques (Table 4). The discrepancy between the two procedures is due to the spatial distribution of the schools. Anomysis perelegnus and Prionomysis semileptus form small (3 to 30 cm diam) quiescent schools which are very dispersed across the lagoon floor. Sampling these species with the trap in effect computes a final density of individuals which normally occur in small discrete aggregations over the 10 m$^{-2}$ sampling area. On the other hand, A. lancilbilis and A. australis often formed large, patchily distributed schools which varied in length (5 to 7 m), width (1 to 3 m) and depth (0.3 to 0.9 m). The area sampled by the trap was too small to capture these huge schools and thus produced unrealistic estimates of their true abundance. Only in March were large numbers of A. australis captured by the trap (1 070 m$^{-2}$), although schools of this species were always present. The discrepancy between the two techniques used in this study again emphasizes the importance of using more than one sampling procedure to obtain realistic abundance estimates for individual species (Hamner and Carlton 1979).

Schooling appears to be advantageous in terms of population size. Five of the seven most abundant species that occurred in Davies Reef lagoon engaged in schooling behaviour. Maahelie (1980) suggests a number of advantages associated with schooling behaviour, including protection of individuals and populations against predators and facilitation of breeding. Epibenthic lagoon mysids probably school for protection from predation. Most mysid schools were located high enough above the lagoon substrate to avoid being by benthic fishes (Gobioides), which were present in densities as high as 18 m$^{-2}$. Although the sex ratios within most schools did not differ significantly from 1:1, it is doubtful that the schools functioned primarily as breeding aggregations as schools most often contained more than one species; there were often sexually immature individuals within schools of mature animals, and there were schools composed solely of juveniles.

The lack of brooding females in samples collected directly from schools is probably due to the sampling technique rather than any biological reason. Intuitively, an advantage would
be gained by the presence of gravid females in schools through the maintenance of population numbers by the immediate recruitment to the school of young released from the marsupium (Mauchline 1980). Rough treatment of specimens and consequent handling of samples underwater most probably results in the loss of eggs and larvae from broad channels.

With the exception of _Dunedinia australis_, a small percent of the fecundity of males is lost during capture and subsequent handling. If it is assumed that a constant proportion was always lost, then only the fecundity of _A. latitarda_ varied seasonally (r = 0.05; Fig. 9).

There was an obvious correlation between breeding ef-

fort, as measured by both proportion of females with en-

bryos and number of embryos carried, and peaks in seasonal abundance. This may have been because the sampling frequency (approximately 6 wk between collections) was too long to note true patterns in seasonal reproduction. If the breeding season was shorter than 6 wk, then whole generations may have gone unsampled. Alternatively, seasonal fluctuations in abundance may be due to factors other than reproduction. Survivorship may change greatly throughout the life cycle of a species, and the reproductive success of individuals captured at different times of the year may be very different.


Spatial variability in lipid composition of calanoid copepods from Fram Strait, the Arctic

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Abstract
The calanoid copepods Calanus hyperboreus and C. finmarchicus were investigated in view of their lipid and wax ester content and their fatty acid and alcohol composition. Analyses were performed in females and copepodid stages V and IV from the Fram Strait region between Greenland and Spitsbergen in 1984. This region offers different food conditions like diatom blooms in the North East Water Polynya. Food shortage in areas with very close ice cover, high phytoplankton biomass in the marginal ice zone and lower biomass in the open Atlantic water. Lipids contained generally more than 70% wax esters. Highest levels were found in C. hyperboreus with more than 90%. This percentage was not very variable, in spite of large differences in dry weight and lipid content. Copepods with particularly high weight and lipid content were found in the North East Water Polynya. The lightest individuals were found under the pack ice. Lipid proportions per unit dry weight were higher in C. hyperboreus than in C. finmarchicus, whose lowest values were found in the open Atlantic water. Spatial variability in fatty acid composition was much higher than in alcohol composition. The principle alcohols, 20:1 and 22:1, generally accounting for more than 80% of total alcohols. In C. hyperboreus the predominant monounsaturated fatty acid was 16:1, while under the ice 20:1 and 22:1 dominated. In the marginal ice zone and in the open water, the 18:4 acid reached percentages up to 30% of total fatty acids. These changes were related to the different food conditions. C. hyperboreus appears to be best adapted to the cold water and unfavourable conditions of polar regions because of its high lipid and wax ester store with long-chain wax esters of high calorific value.

Introduction
The life of herbivorous copepods in high latitudes is determined by the extreme seasonality of food availability.

References
[Insert list of references here]