BULLETIN OF MARINE SCIENCE, 39(3): 623–629, 1986

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_2O_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 filtratic 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 radic 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 ass 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· 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

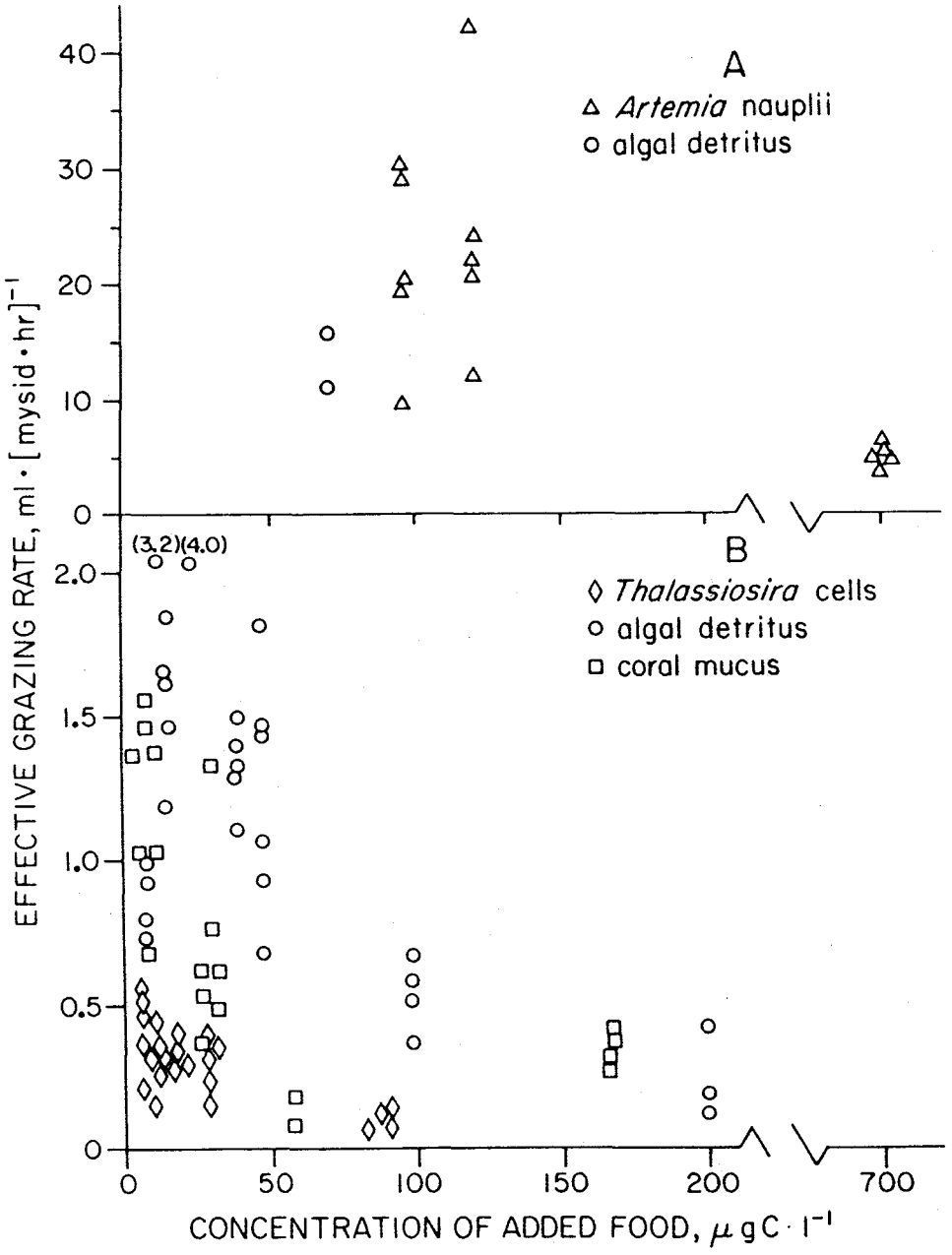

Figure 1. Grazing rates of *Anisomysis* on various types of food, as a function of the amount of food added to in situ containers. A. *Artemia* nauplii or algal detritus as food. B. *Thalassiosira* cells, algal detritus, or coral mucus as food.

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 ingestic 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 part 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* sp prey sometimes being preferred. (However, differences between prey sp aggregative and 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; t nificance must be as scavengers of large detrital particles and as preda smaller zooplankters. Several other species of mysids swarm at various t year in the lagoon behind the reef flat, including other *Anisomysis* sp Carleton, pers. comm.), and what appeared to be another species of mysid o just over the sand bottom in the same pocket where our *Anisomysis* hover 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 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 × 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 *Anisomysis* mean 2 × 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 i 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 upstrea

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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Literature Cited

Banoub, M. W. and P. J. LeB. Williams. 1972. Measurements of microbial activity and organic matter in the western Mediterranean Sea. Deep-Sea Res. 19: 433–444.

Blaxter, J. H. S. and J. R. Hunter. 1982. The biology of the clupeoid fishes. Adv. Mar. Biol. 20: 3–223.

Bowers, J. A. and H. A. Vanderploeg. 1982. *In situ* predatory behavior of *Mysis relicta* in Lake Michigan. Hydrobiol. 93: 121–131.

Coles, S. L. and R. Strathmann. 1973. Observations on coral mucus "flocs" and their potential trophic significance. Limnol. Oceanogr. 18: 673–678.

Ducklow, H. W. and R. Mitchell. 1979. Bacterial populations and adaptations in the mucus layers on living corals. Limnol. Oceanogr. 24: 715–725.

Emery, A. R. 1968. Preliminary observations on coral reef plankton. Limnol. Oceanogr. 13: 293–303.

Fox, D. L., J. D. Isaacs and E. F. Corcoran. 1952. Marine leptopel, its recovery, measurement, and distribution. J. Mar. Res. 11: 29–46.

Fulton, R. S., III. 1982. Predatory feeding of two marine mysids. Mar. Biol. 72: 183–191.

Gerber, R. P. and M. B. Gerber. 1979. Ingestion of natural particulate organic matter and subsequent assimilation, respiration, and growth by tropical lagoon zooplankton. Mar. Biol. 52: 33–44.

——— and N. Marshall. 1974. Ingestion of detritus by the lagoon pelagic community at Enewetok Atoll. Limnol. Oceanogr. 19: 815–824.

Gottfried, M. and M. R. Roman. 1983. Ingestion and incorporation of coral-mucus by reef zooplankton. Mar. Biol. 72: 211–218.

Hatcher, B. G. 1983. The role of detritus in the metabolism and secondary production of coral reef ecosystems. Pages 317–325 *in* J. T. Baker, R. M. Carter, P. W. Sammarco and K. P. Stark, Proc. Inaugural Great Barrier Reef Conf. James Cook Univ. Press.

Hollibaugh, J. T., J. A. Fuhrman and F. Azam. 1980. Radioactively labeling of natural assemblages of bacterioplankton for use in trophic studies. Limnol. Oceanogr. 25: 172–181.

Johannes, R. E. 1967. Ecology of organic aggregates in the vicinity of a coral reef. Limnol. Oceanogr. 12: 189–195.

Mauchline, J. 1980. The biology of mysids and euphausiids. Adv. Mar. Biol. 18: 1–677.

Moriarty, D. J. W. 1979. Biomass of suspended bacteria over coral reefs. Mar. Biol. 53: 193–200.

Mullin, M. M. 1983. *In situ* measurement of filtering rates of the salp, *Thalia democra* phytoplankton and bacteria. J. Plank. Res. 5: 279–288.

Murano, M. In Press. A new species of the genus *Anisomysis* from the Great Barrier Reef. Crus

Richman, S., Y. Loya and L. B. Slobodkin. 1975. The rate of mucus production by corals assimilation by the coral reef copepod *Acartia negligens*. Limnol. Oceanogr. 20: 918–92

Roman, M. R. and P. A. Rublee. 1981. A method to determine *in situ* zooplankton grazi on natural particle assemblages. Mar. Biol. 65: 303–309.

Sorokin, Y. I. 1974. Bacteria as a component of the coral reef community. Pages 3–10 *i* Cameron et al., Proc. Second Intern. Symp. Coral Reefs, Vol. 1. Great Barrier Reef Cor

———, T. S. Petipa and Y. V. Pavlova. 1970. Quantitative estimate of marine bacterioplar a source of food. Okeanol. 10: 332–340 (Eng. trans.)

Steven, D. M. 1961. Shoaling behaviour in a mysid. Nature 192: 280–281.

Strickland, J. D. H. and T. R. Parsons. 1972. A practical handbook of seawater analysis, Bull. Fish. Res. Bd., Canada 167: 1–310.

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Addresses: *(M.M.M.) Institute of Marine Resources, A-018, Scripps Institution of Oceanc University of California, San Diego, La Jolla, California 92093; (M.R.R.) Horn Point Labo University of Maryland, Box 775, Cambridge, Maryland 21613.*

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Marine Biology

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

J. H. Carleton and W. M. Hamner**

Australian Institute of Marine Science, Townsville, Queensland 4810, Australia

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 absent 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

* A.I.M.S. Contribution No. 477

** Present address: Department of Biology, University of California, Los Angeles, California 90024, USA

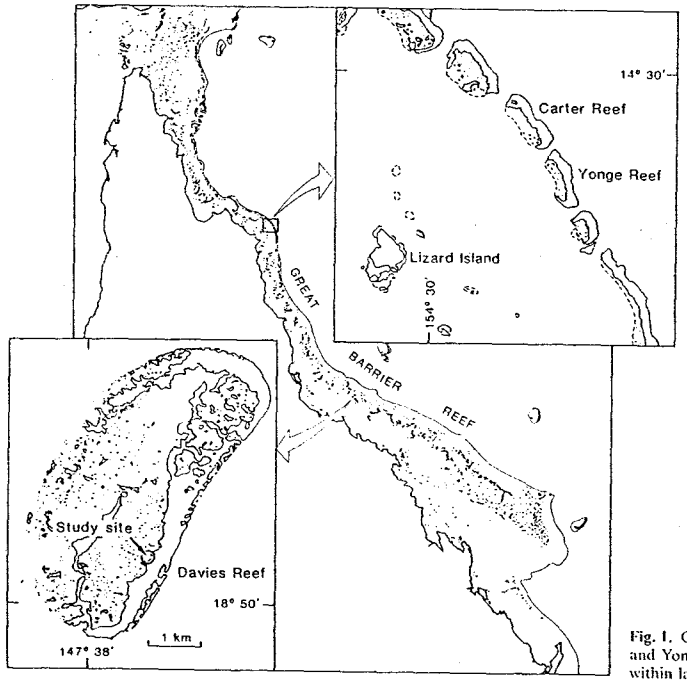

Fig. 1. Geographic location of Davies, Carter and Yonge Reefs, Great Barrier Reef. Study site within lagoon at Davies Reef is also shown

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	Pelagic species
Family Mysidae	Family Mysidae
Subfamily Siriellinae	Subfamily Siriellinae
Hemisiriella parva Hansen	Genus *Sirella* Dana
Subfamily Gastrosaccinae	(*Thompsoni* group)
Gastrosaccus indicus Hansen	(*Thompsoni* subgroup)
Anchialina grossa Hansen	*Siriella thompsoni* H. M. Edwards
Pseudanchialina inermis Illig*	*Siriella gracilis* Dana
Subfamily Mysinae	*Siricila nodosa* Hansen
Tribe Erythropini	*Siriella affinis* Hansen
Erythrops sp.	*Siriella quadrispinosa* Hansen
Tribe Leptomysini	*Siriella vulgaris* Hansen
Doxomysis littoralis Tattersall	*Siriella* sp. a
Prionomysis stenolepis Tattersall*	*Siriella* sp. b
Tribe Mysini	(*Inornata* group)
Anisomysis pelewensis li*	*Siriella inornata* Hansen
Anisomysis laticauda Hansen	*Siriella media* Hansen
Anisomysis australis Zimmer*	(*Acquiremis* group)
Anisomysis lamellicauda Hansen*	*Siriella acquiremis* Hansen
Anisomysis bifurcata Tattersall*	*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, *Prionomysis 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

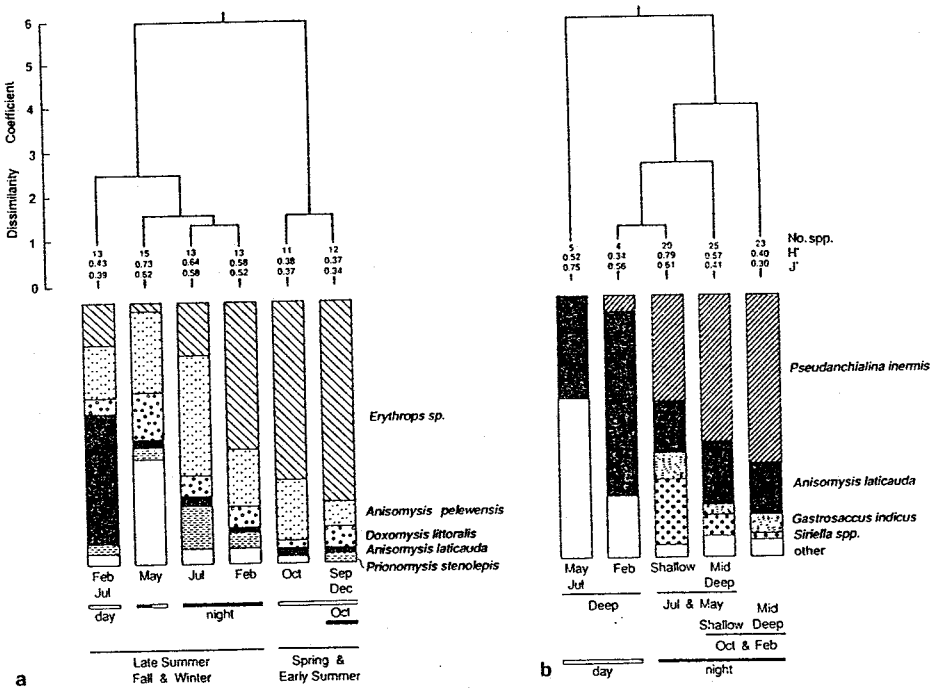

Fig. 2. Dendrograms summarizing classification analyses on all 25 mysid species encountered during study. Number of species (No. spp.), Shannon-Wiener diversity index (H'), Pielou's evenness index (J') and relative abundances of dominant species given for each significant ($p<0.05$) group. (a) Dendrogram 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

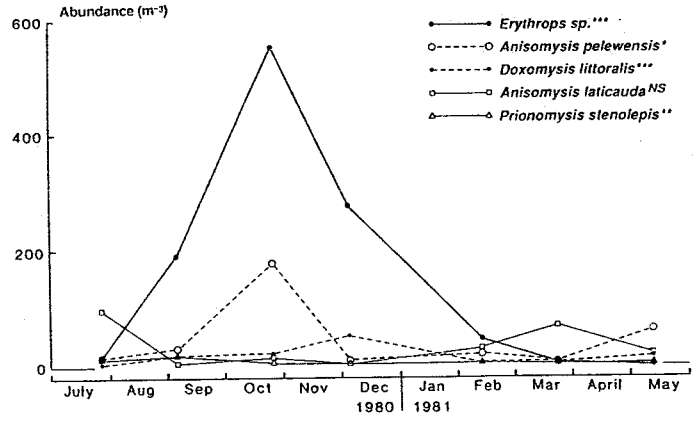

Fig. 3. Diurnal abundances of five most abundant epibenthic mysid species. *$p<0.05$; **$p<0.01$; ***$p<0.001$

Table 2. Seasonal and diel abundances in benthic trap of seven most abundant mysid species. The two-factor analyses compared diurnal and nocturnal abundances for months July (J), October (O), February (F), and May (Ma); the one-factor analyses compared only diurnal abundances for all 7 mo. ANOVA: analysis of variance; SNK: Student-Newman-Keuls multiple-range procedure for comparing means; JD: July day; JN: July night; OD: October day; ON: October night; FD: February day; FN: February night; MaD: May day; MaN: May night; S: September; D: December; Mr: March

Species	Abundance (cm^{-3})											Two-factor analyses				One-factor analyses	
	July		Sep.	Oct.		Dec.	Feb.		Mar.	May		ANOVA			SNK	ANOVA seasonal	SNK
	day	night		day	night		day	night		day	night	inter-action	sea-sonal	diel			
Erythrops sp.	17.1	5.6	191.3	553.2	229.3	276.2	44.7	18.7	6.1	1.2	1.1	***	***	***	OD>ON>FD>FN, JD>JN, MaD, MaN	***	O>D,S>F>J>Mr>Ma
Anisomysis pelewensis[a]	15.4	9.2	31.1	176.1	62.7	9.5	19.6	7.2	5.4	61.7	14.1	**	***	**	OD> all others	*	O>Mr,D
Doxomysis littoralis	3.9	1.2	18.0	22.0	8.4	52.1	3.4	1.7	1.3	15.6	2.3	*	***	***	OD,MaD> all others	***	D>O,S,Ma>F,J>Mr
Anisomysis laticauda[a]	97.5	0.1	4.9	14.2	0.6	3.4	30.8	0.1	68.2	21.0	0.3	NS	NS	***	NS	NS	–
Prionomysis stenolepis[a]	13.0	4.6	18.8	4.9	1.8	2.4	1.5	2.0	2.3	3.7	1.8	*	***	**	JD> all others	**	J,S>D, F,Mr,Ma
Anisomysis lamellicauda[a]	6.4	0.0	2.5	10.2	0.0	0.3	4.5	0.2	1.3	2.8	0.1	NS	NS	**	NS	NS	–
Anisomysis australis[a]	0.5	0.1	0.1	2.7	0.2	0.3	2.2	0.1	1 069.3	1.7	0.1	NS	NS	**	NS	NS[b]	–
Total	157.7	2.12	268.5	786.3	303.4	346.2	109.2	31.5	1 155.5	116.1	32.3	**	***	***	OD>ON> all others	***[c]	O>all others

* $p<0.05$; ** $p<0.01$; *** $p<0.001$
[a] Schooling species
[b] Non-parametric tests used for analysis
[c] March data excluded from analysis

Table 3. Abundance data from nocturnal net 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

Species	Abundance (m^3)												ANOVA			SNK
	July			October			February			May			inter-action	location in water column	time of year	
	shal-low	mid	deep	shal-low	mid	deep	shal-low	mid	deep	shal-low	mid	deep				
Pseudanchialina inermis	0.50	5.70	7.00	2.30	9.70	17.60	4.60	22.00	25.50	1.60	3.60	6.60	NS	***	***	FD>JS
Anisomysis laticauda[a]	0.58	1.20	0.33	2.40	6.50	12.60	3.00	3.00	4.00	0.60	1.60	1.40	**	**	***	OD>all others
Gastrosaccus indicus	0.23	0.05	0.16	0.25	2.10	4.10	0.10	0.30	0.25	0.47	0.10	0.15	***	NS	***	OD,OM>all others
Total	2.46	7.17	8.12	6.01	19.79	37.72	10.42	29.25	29.95	3.25	5.92	8.85	NS	**	***	OD,FM,FD>JS,MS

** $p<0.01$; *** $p<0.001$
[a] Schooling species

three species dominated nocturnal plankton net samples and accounted for approximately 90% of all mysids (Table 3). The greatest concentrations usually occurred in the mid and deep layers, especially during October and February (Fig. 4). The main exception to this distribution pattern was the case of *P. inermis* in May. On that occasion, the abundance of *P. inermis* increased steadily from the surface towards the bottom (Fig. 4). Individuals belonging to the primarily pelagic genus *Siriella* were often present, but their abundance was low (<1 m^{-3}) and, with the exception of February, they were confined to the surface layer.

Reproductive effort

With the exception on *Doxomysis littoralis*, the proportion of oviparous females varied throughout the year (Fig. 5). *Anisomysis pelewensis* and *A. laticauda* had the greatest proportion of gravid females in May, *Prionomysis stenolepis* the greatest proportion in October, and *Erythrops* sp. the greatest proportion in December. Fecundity was very constant throughout the year in most species. Only *A. laticauda* varied significantly, having a greater number of embryos per female in May than July (Fig. 5).

School data

Although densities within and between schools were highly variable (10 500 to 501 500 mysids m^{-3}; Table 4), average spacing between individuals, when expressed in terms of body lengths, did not differ significantly among species ($p>0.05$; analysis of variance). Generally, length-frequency distributions were normal and those that were skewed tended towards greater numbers of smaller individuals.

Schools were generally monospecific, and comprised of individuals from a single age class (juvenile, immature or mature). Only two out of the twelve *Anisomysis australis* schools sampled contained large numbers of individuals of another mysid species (*A. lamellicauda*). On one occasion larval fish were also present in a school of *A. australis*. Only one school of mature *A. australis* contained a large number of immatures (ratio of 1 immature to 2 matures). Sex ratios for the most part did not differ significantly from 1:1 ($p>0.05$; χ^2). None of the females collected from schools, regardless of species, carried eggs or larvae.

Discussion

Intensive sampling of zooplankton undertaken by the Great Barrier Reef Expedition (Tattersall 1936) collected only 10 of the 25 species encountered during the present study. The majority of those species described by Tattersall were captured by standard net tows at night and belonged to the genus *Siriella*, which is primarily pelagic. The sampling gear and procedures employed by the Great Barrier Reef Expedition did not effectively capture epibenthic species.

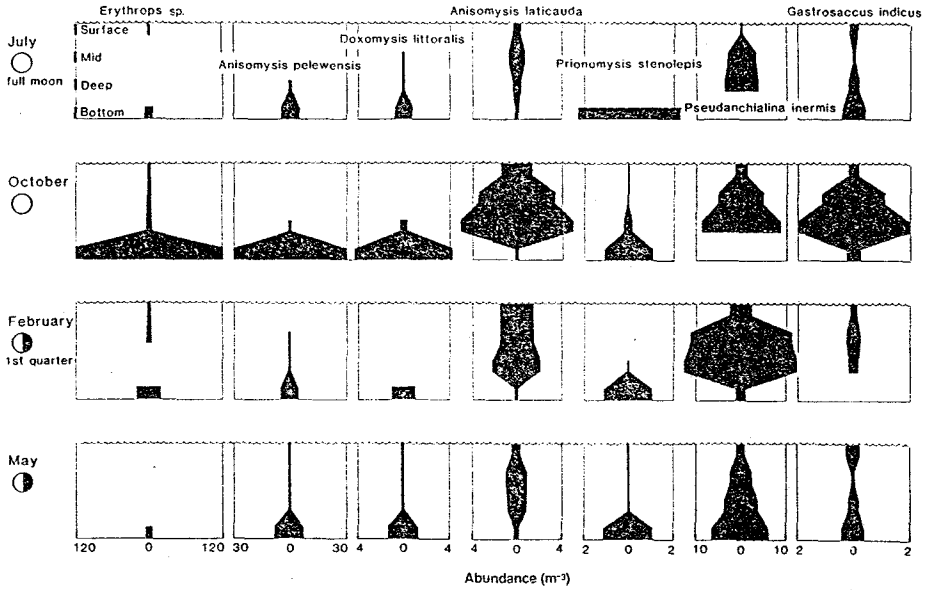

Fig. 4. Nocturnal, vertical distributions and abundances of five most abundant epibenthic species and three most abundant species in water column at night. *Anisomysis laticauda* was only epibenthic species which was consistently present in water column at night throughout year

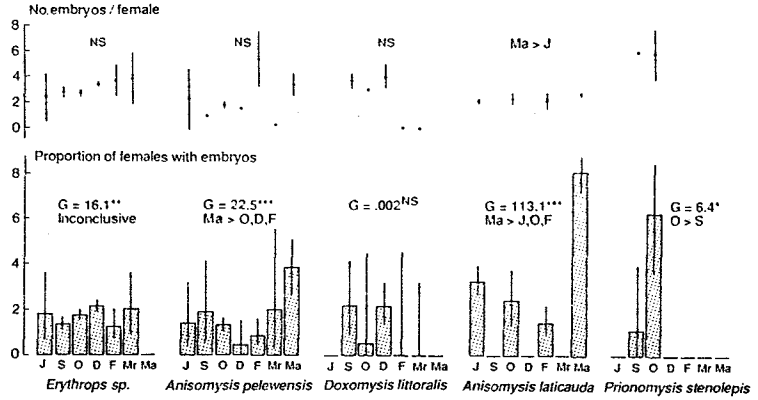

Fig. 5. Seasonal reproductive effort of five most abundant epibenthic mysid species. J: July; S: September; O: October; D; December; F: February; Mr: March; Ma: May. * $p<0.05$; ** $p<0.01$; *** $p<0.001$

The density of mysids on the lagoon floor, when converted to numbers per unit area (109.2 to 786.3 m^{-2}), is one to three orders of magnitude greater than those for more temperate marine species (0.1 m^{-2}, Dadswell 1975; 2.6 to 21.6 m^{-2}, Mauchline 1980). Only the freshwater mysid *Mysis relicta* occurs in abundances approaching those reported here (200 m^{-2}, Morgan and Beeton 1978). Nocturnal mysid densities found in this study (2.5 to 10.4 m^{-3}) are similar to those (11 m^{-3}) captured by Tranter and George (1972) in the lagoon surface waters at Kavaratti Atoll, using nets similar to ours (no bridles; 200 μm mesh). The significant seasonal variations in abundances, with greatest densities

Table 4. School density and composition data for four species of epibenthic mysids. CV: coefficient of variation; J: juvenile; I: immature; M: mature individuals; g_1: measure of skewness; g_2: measure of kurtosis

Species	Photographic data				Hand-net sample data						
	(*n*)	Density (nos. m^{-3}) $\bar{x}$ (CV)	Nearest neighbour distance in:		Nos. of:			Sex ratio	Length frequency		
			cm $\bar{x}$ (CV)	Body lengths	J	I	M	♂:♀	$\bar{x}$ (CV)	g_1	g_2
Anisomysis pelewenis	(4)	291 100 (0.70)	1.9 (0.21)	6.4		1	86	51:36	3.0 (0.07)	0.40	0.70
Prionomysis stenolepis	(5)	24 800 (0.35)	4.2 (0.18)	7.8		13	11	14:10	5.4 (0.16)	−0.90	0.73
	(2)	10 500 (0.46)	5.6 (0.16)	11.2		8	1	6:3	4.9 (0.08)	0.96	1.36
		$\bar{x}$=17 700 (0.57)		$\bar{x}$=9.5 (0.25)							
Anisomysis lamellicauda	(8)	30 600 (0.59)	4.2 (0.25)	10.0		26		17:9	4.2 (0.15)	−0.28	−0.27
	(4)	52 200 (0.61)	3.4 (0.15)	7.7		7		4:3	4.3 (0.18)	−0.25	−1.21
	(6)	37 100 (0.43)	3.8 (0.20)	7.0		10	5	8:7	5.3 (0.07)	−1.12	0.58
		$\bar{x}$=40 000 (0.28)		$\bar{x}$=8.24 (0.19)		20	1	4:17***	5.1 (0.08)	−0.19	−0.52
Anisomysis australis	(10)	35 700 (0.43)	3.8 (0.15)	7.4		7	56	43:20**	5.1 (0.13)	−0.72*	0.04
	(6)	36 500 (0.50)	3.8 (0.15)	7.0		1	67	24:4*	5.4 (0.08)	−0.25	0.65
	(6)	198 700 (0.31)	2.1 (0.11)	6.7		50	1	28:23	3.1 (0.17)	2.08***	8.10***
	(8)	30 600 (0.59)	4.2 (0.25)	10.0		42	7	25:4***	4.2 (0.15)	−0.28	−0.27
	(9)	48 500 (0.57)	3.4 (0.16)	8.8		32	2	23:11	3.9 (0.09)	0.21	0.83
	(10)	49 200 (0.47)	3.4 (0.17)	14.5		97		66:31***	2.4 (0.18)	0.09	−0.08
	(6)	87 500 (1.18)	3.2 (0.28)	11.6		88		39:49	2.8 (0.16)		
	(11)	30 900 (0.44)	4.0 (0.19)	9.0		38	84	48:74*	4.5 (0.18)	−0.87***	1.04*
	(6)	93 300 (0.46)	2.8 (0.18)	15.6	119	1	10		1.8 (0.57)	2.50***	5.09***
	(2)	501 500 (0.66)	1.6 (0.23)	3.5		22	49	38:33	4.5 (0.15)	−0.83**	0.35
	(6)	37 100 (0.43)	3.8 (0.20)	7.0			13	5:8	5.4 (0.06)	−1.12	0.58
	(13)	62 500 (0.33)	3.1 (0.12)								
		$\bar{x}$=101 000 (1.33)		$\bar{x}$=9.2 (0.32)							

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

occurring during the spring and summer, are consistent with observations on general zooplankton abundances for specific reefs within the Great Barrier Reef province (Sale et al. 1976, 1978, Hamner and Carleton 1979, McWilliam et al. 1981, Jacoby and Greenwood 1988) and for the Great Barrier Reef lagoon (Russel 1934, Ikeda et al. 1982).

Although the benthic trap used in this study was designed to make use of the mysids' escape response to effect their capture (Carleton 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. *Anisomysis pelewensis* and *Prionomysis stenolepis* form small (5 to 30 cm diam) quiescent schools which are evenly 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. lamellicauda* and *A. australis* often formed large, patchily distributed shoals 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 shoals 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^{-3}), 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 Carleton 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. Mauchline (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 capture by benthic fishes (Gobioidei), 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 aggregation as schools often contained more than one species; there were often sexually immature individuals within schools of mature animals, and there were schools comprised solely of juveniles.

The lack of brooding females in samples collected directly from schools is probably due to 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 through the use of hand nets and subsequent handling of samples underwater most probably results in the loss of eggs and larvae from brood chambers.

With the exception of *Doxomysis littoralis*, a small percentage of females were oviparous at each of the sampling dates. This percentage varied significantly, the lowest being 5% for *Anisomysis pelewensis* in December and the highest being 80% for *A. laticauda* in May. This ubiquity of oviparous females coupled with the prevalence of juveniles throughout the year (8 to 100%), is indicative of continuous breeding (Goodbody 1965). The fecundity estimates in this study are probably low, as embryos maybe shed from the brood pouch during capture and subsequent handling. If it is assumed that a constant proportion was always lost, then only the fecundity of *A. laticauda* varied seasonally ($p > 0.05$; Fig. 5).

There was no obvious correlation between breeding effort, as measured by both proportion of females with embryos and the 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 life span of individuals was shorter than 6 wk, then whole generations may have gone unsampled. Alternatively, seasonal fluctuations in abundance maybe due to factors other than reproduction. Survivorship may change greatly throughout the year as a result of fluctuations in food availability or changes in predator abundance.

The numerical classification analyses highlighted the uniformity in species composition of the epibenthic mysid community throughout the year. The same six species were always present (Table 2) and species associations were characterized primarily by changes in relative abundance of the more dominant mysids (Fig. 2). Seasonal uniformity in species composition is consistent with previous work on resident and demersal zooplankton communities in reef lagoon (Sale et al. 1978, McWilliams et al. 1981). In this study, it may have been due in part to the mysids' nocturnal distribution patterns. Loss of zooplankton from the sheltered waters of the reef lagoon usually occurs when individuals enter the wind-generated surface currents at night. The majority of reefal lagoon mysids remained concentrated on or near the lagoon floor during the night and, with one exception (*Anisomysis laticauda*) did not migrate into the surface waters. This would result in few individuals being swept away from the reef.

The nocturnal preference of reef lagoon mysids for positions near or on the bottom is common among shelf and littoral mysids (Mauchline 1980) and many coral reef epibenthic and demersal organisms (Emery 1968, Sale et al. 1976, 1978, Alldredge and King 1980, 1985). Only in May did individuals from the majority of epibenthic mysids migrate into the surface layer. Also, *Pseudanchialina inermis*, usually found at greatest densities in the mid and deep layers, occurred on that occasion in greatest density on the lagoon floor. Decreased light level is a major cue in stimulating emergence and subsequent vertical migrations in the majority of demersal and epibenthic zooplankton (Alldredge and King 1980, Jacoby and Greenwood 1988). In May, heavy cloud cover combined with early setting of the moon produced the lowest light levels experienced during the study. These darkened conditions may account for the anomalous nocturnal distribution patterns demonstrated by most mysid species on that occasion.

Resident demersal plankton are of nutritional value to reef planktivores because of their nocturnal migrations into the water column (Alldredge and King 1977, Porter and Porter 1977, Porter et al. 1977, Hobson and Chess 1979, Grimm and Clayshulte 1981, McWilliam et al. 1981, Walter et al. 1981, Robichaux et al. 1981, Ohlhorts 1982). However, at Davies Reef, only three reef-associated mysid species, *Pseudanchialina inermis*, *Anisomysis laticauda*, and *Gastrosaccus indicus*, were consistently present in the surface waters at night, with most epibenthic species remaining concentrated near the lagoon floor. The epibenthic lagoon mysids, therefore, probably contribute little to the available food supply of sessile reef planktivores such as corals. Lagoon mysids may, however, play an important role in nutrient regeneration. There is a continuous input of detrital material into coral reef lagoons from areas of high primary production, resulting in a complex of secondary, detritus-based food webs (Hatcher 1983). Most coastal and littoral mysids utilize organic detritus to a considerable extent (Mauchline 1980), and it is possible that the epibenthic mysid community of coral reefs may also be responsible for the remineralization of a substantial proportion of lagoon detritus. Large areas of Indo-Pacific reefs are either sandy lagoons or back-reef slopes and, given the extremely high density per m^2 and the relatively large size of lagoon mysids, their trophodynamic contribution to the reef as a whole may be considerable.

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Literature cited

Abel, D. J., Williams, W. T., Williams, D. McB. (1985). A fast classificatory algorithm for large problems under the Bray-Curtis measure. J. exp. mar Biol. Ecol. 89: 237–245

Alldredge, A. L., King, J. M. (1977). Distribution, abundance and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. 41: 317–333

Alldredge, A. L., King, J. M. (1980). Effects of moonlight on the vertical migration patterns of demersal zooplankton. J. exp. mar. Biol. Ecol. 44: 133–156

Alldredge, A. L., King, J. M. (1985). The distance demersal zooplankton migrate above the benthos: implications for predation. Mar. Biol. 84: 253–260

Băcescu, M. (1975). Contributions to the knowledge of the mysid (Crustacea) from the Tanzanian waters. Univ. Sci. J. Univ., Dar es Salaam 1: 39–61

Belbin, L. (1987). PATN: pattern analysis package. Reference manual. Part 1. CSIRO Division of Wildlife and Rangelands Research, Melbourne

Birkeland, C. (1984). A contrast in methodologies between surveying and testing. UNESCO Rep. mar. Sci. 21: 11–26

Birkett, L., McIntyre, A. D. (1971). Treatment and sorting of samples. In: Holme, N. A., McIntyre, A. D. (eds.) Methods for the study of marine benthos. Blackwell, Oxford, p. 156–168

Bray, J. R., Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325–349

Burr, E. J. (1970). Cluster sorting with mixed character types. II. Fusion strategies. Aust. Comput. J. 1: 98–103

Carleton, J. H. (1986). The mysid community: distribution, abundance and composition, Davies Reef lagoon, Great Barrier Reef. MSc. Thesis, James Cook University of North Queensland

Carleton, J. H., Hamner, W. M. (1987). A diver operated device for the capture of mobile epibenthic organisms. Limnol. Oceanogr. 32: 503–510

Clutter, R. I., Anraku, M. (1968). Avoidance of samplers. Monogr. oceanogr. Methodol. (UNESCO) 2: 57–76

Dadswell, M. J. (1975). Some notes on shoaling behaviour and growth of *Mysis gaspensis* (Mysidacea) in a small Newfoundland estuary. Can. J. Zool. 53: 374–377

Emery, A. R. (1968). Preliminary observations on coral reef plankton. Limnol. Oceanogr. 13: 293–303

Fraser, J. H. (1968). Standardization of zooplankton sampling methods at sea. Monogr. oceanogr. Methodol. (UNESCO) 2: 145–169

Gerber, R., Marshall, N. (1974). Reef pseudoplankton in lagoon trophic systems. Proc. 2nd int. Symp. coral Reefs 2: 105–107 [Cameron, A. M. et al. (eds.) Great Barrier Reef Committee, Brisbane]

Goodbody, I. (1965). Continuous breeding in populations of two tropical crustaceans, *Mysidium columbiae* (Zimmer) and *Emerita portoricensis* (Schmidt). Ecology 46: 195–197

Gottfried, M., Roman, M. R. (1983). Ingestion and incorporation of coral-mucus detritus by reef zooplankton. Mar. Biol. 72: 211–218

Grimm, G. R., Clayshulte, R. N. (1981). Demersal plankton from Western Shoals, Apra Harbor, Guam (Abstract). Proc. 4th int. Symp. coral Reefs 2: p. 454. [Gomez, E. D. et al. (eds.) Marine Sciences Center, University of the Philippines, Quezon City, Philippines]

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

Hatcher, B. G. (1983). The role of detritus in the metabolism and secondary production of coral reef ecosystems. In: Baker, J. T. et al. (eds.) Proceedings of the Inaugural Great Barrier Reef Conference; August 29–September 2 1983, Townsville, Australia. James Cook University Press, Townsville, p. 317–325

Hobson, B. G., Chess, J. R. (1979). Zooplankters that emerge from the lagoon floor at night at Kure and Midway Atolls, Hawaii. Fish. Bull. U.S. 77: 275–280

Ikeda, T., Carleton, J. H., Mitchell, A. W., Dixon, P. (1982). Ammonia and phosphate excretion by zooplankton from the inshore waters of the Great Barrier Reef. II. Their *in situ* contributions to nutrient regeneration. Aust. J. mar. Freshwat. Res. 33: 683–698

Jacoby, C. A., Greenwood, J. G. (1988). Spatial, temporal, and behavioral patterns in emergence of zooplankton in the lagoon of Heron Reef, Great Barrier Reef, Australia. Mar. Biol. 97: 309–328

Johnson, M. W. (1949). Zooplankton as an index of water exchange between Bikini Lagoon and the open sea. Trans. Am. geophys. Un. 30: 238–244

Johnson, M. W. (1954). Plankton of northern Marshall Islands: Bikini and nearby atolls, Marshall Islands. Prof. Pap. U.S. geol. Surv. 260-F: 300–314

Mauchline, J. (1980). The biology of mysids. Adv. mar. Biol. 18: 1–369

McWilliam, P. S., Sale, P. F., Anderson, D. T. (1981). Seasonal changes in resident zooplankton sampled by emergence traps in One Tree Lagoon, Great Barrier Reef. J. exp. mar. Biol. Ecol. 52: 185–203

Morgan, M. D., Beeton, A. M. (1978). Life history and abundance of *Mysis relicta* in Lake Michigan. J. Fish. Res. Bd Can. 35: 1165–1170

Motoda, S. (1940). Comparison of the condition of water in bay, lagoon and open sea in Palao. Palao trop. biol. Stn Stud. 2: 41–48

Mullin, M. M., Roman, M. R. (1986). *In situ* feeding of a schooling mysid, *Anisomysis* sp., on Davies Reef-MECOR 4. Bull. mar. Sci. 39: 623–629

Ohlhorst, S. L. (1982). Diel migration patterns of demersal reef zooplankton. J. exp. mar. Biol. Ecol. 60: 1–15

Pielou, E. C. (1969). An introduction to mathematical ecology. John Wiley & Sons, Inc., New York

Pielou, E. C. (1975). Ecological diversity. John Wiley & Sons, Inc., New York

Porter, J. W. (1974). Zooplankton feeding by the Caribbean reef-building coral *Montastrea cavernosa*. Proc. 2nd int. Symp. coral Reefs 2: 111–115. [Cameron, A. M. et al. (eds.) Great Barrier Reef Committee, Brisbane]

Porter, J. W., Porter, K. G. (1977). Quantitative sampling of demersal plankton migrating from different coral reef substrates. Limnol. Oceanogr. 22: 553–556

Porter, J. W., Porter, K. G., Batac-Catalan, Z. (1977). Quantitative sampling of Indo-Pacific demersal reef plankton. Proc. 3rd int. Symp. coral Reefs 2: 105–112. [Taylor, D. L. (eds.) Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami, Fla]

Renon, J. P. (1977). Zooplancton du lagon de l'atoll de Takapoto (Polynésie Française). Annls Inst. océanogr., Paris (N.S.) 53: 217–236

Renon, J. P. (1978). Un cycle annuel du zooplancton dans un lagon de Tahiti. Cah. O.R.S.T.O.M. Sér. Océanogr. 16: 63–88

Robichaux, D. M., Cohen, A. C., Reaka, M. L., Allen, D. (1981). Experiments with zooplankton on coral reefs or, will the real demersal plankton please come up? Pubbl. Staz. zool. Napoli (I. Mar. Ecol.) 2: 77–94

Russel, F. S. (1934). The zooplankton. III. A comparison of the abundance of zooplankton in the Barrier Reef Lagoon with that of some regions in northern European waters. Scient. Rep. Gt Barrier Reef Exped. 2: 159–201

Sale, P. F., McWilliam, P. S., Anderson, D. T. (1976). Composition of the near-reef zooplankton at Heron Reef, Great Barrier Reef. Mar. Biol. 34: 59–66

Sale, P. F., McWilliam, P. S., Anderson, D. T. (1978). Faunal relationships among the near-reef zooplankton at three locations on Heron Reef, Great Barrier Reef, and seasonal changes in this fauna. Mar. Biol. 49: 133–145

Sandland, R. L., Young, P. C. (1979a). Probabilistic tests and stopping rules associated with hierarchical classification techniques. Aust. J. Ecol. 4: 399–406

Sandland, R. L., Young, P. C. (1979b). Tables of probabilities associated with the fission of replicate samples in classification. Rep. Div. Fish. Oceanogr. C.S.I.R.O. Aust. 108: 1–21

Sokal, R. R., Rohlf, F. J. (1981). Biometry. The principles and practice of statistics in biological research. 2nd ed. W. H. Freeman & Co., San Francisco

Tattersall, W. M. (1936). Mysidacea and Euphausiacea. Scient. Rep. Gt Barrier Reef Exped. 2: 143–176
Tranter, D. J., George, J. (1972). Zooplankton abundance at Kavaratti and Kalpeni Atolls in the Laccadaves. Proc. 1st int. Symp. coral reefs. 1: 239–256. [Mukundan, C., Gopinadha Pillai, C. S. (eds.) Marine Biological Association of India, Cochin]
Tudhope, A. W. (1983). Processes of lagoonal sedimentation and patch reef development, Davies Reef, Great Barrier Reef of Australia. Ph. D. thesis, University of Edinburgh
Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. mar. Biol. A. Rev. 19: 513–605
Van Guelpen, L., Markle, D. F., Duggan, D. J. (1982). An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. J. Cons. int. Explor. Mer 40: 226–236
Walter, C., Pasamonte, J. N., Talaue, L. L. (1981). A preliminary quantitative study on emergence of reef associated zooplankton from a Philippine coral reef. Proc. 4th int. Symp. coral Reefs 2: 443–452. [Gomez, E. D. et al. (eds.) Marine Sciences Center, University of the Philippines, Quezon City, Philippines]

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

G. Kattner[1], H. J. Hirche[1] and M. Krause[2]

[1] Alfred-Wegener-Institut für Polar- und Meeresforschung, Columbusstraße, D-2850 Bremerhaven, FRG
[2] Institut für Allgemeine Botanik der Universität Hamburg, Ohnhorststraße 18, D-200 Hamburg 52, FRG

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 the North East Water Polynya, 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. In the Greenland Sea in addition to seasonal gradients there are also sharp spatial gradients in food supply resulting from the hydrographic regime and ice cover. Thus, under the pack ice on the East Greenland Shelf, chlorophyll concentrations are very low during most of the year, while in polynyas phytoplankton blooms can develop much earlier. Highest chlorophyll concentrations were observed in the marginal ice zone of the Polar Front region where the Polar water meets Atlantic water (Smith et al. 1985, Smith et al. 1987, Spies 1987).

The life cycles of some calanoid copepod species are well adapted to this environment. They spend most of the year in a resting stage, metabolizing lipids stored in large oil sacs at a highly reduced rate (Hirche 1983). Lipids are also mobilised during gonadal maturation (Bamstedt 1979, Gatten et al. 1980) and are an essential component of copepod eggs (Sargent and Henderson 1986). Little is known on the lipid content of Arctic copepods. High concentrations were found, often consisting of a high proportion of wax esters (Lee 1974, 1975, Sargent et al. 1981, Tande and Henderson 1988; reviewed by Sargent et al. 1976, Clarke 1983, Sargent and Henderson 1986). The fatty acid component of wax esters is highly variable, reflecting the fatty acids of food organisms. Fatty alcohols are less variable, as are the principle alcohols, 20:1 and 22:1, which have to be synthesised de novo from precursors such as fatty acids, carbohydrates, and amino acids (Farkas et al. 1973, Sargent and McIntosh 1974).

During MIZEX (Marginal Ice Zone Experiment) 1984 in the Fram Strait region between East Greenland and Svalbard, samples were collected to study the lipid and wax ester content as well as the fatty acid and alcohol composition of the dominant calanoid copepods *Calanus finmarchicus* and *C. hyperboreus*. *C. hyperboreus* is at least a biennial (Harding 1966, Dawson 1978) Arctic species (Grainer 1963) while *C. finmarchicus* has one generation per year (Lie 1965) and is a boreal species inhabiting the North Atlantic (Marshall and Orr 1955). The distributions of the two species overlap in the Greenland Sea (Smith 1988). Reproduction in *C. finmar-*