

closely resemble the sediment deposits we have been studying in the northern GBR (Figure 7 A,B).

Why do we know so much about the ancient phylloid algal bioherms, and why have geologists laboured long and hard to understand just how and why they were formed? These deposits are porous, just like *Halimeda* gravel, because of all the small spaces retained within the skeletal fragments. And because of this porosity, they have come to form major oil reservoirs in many parts of the world. However, the *Halimeda* deposits of the Great Barrier Reef will not attract exploration for some time. The GBR is so young geologically that, even if its *Halimeda* banks do have the composition, texture and appearance of potential bioherms, none of them will become commercially interesting for millions of years.

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*Dr E.A.(Ed) Drew's address is the Australian Institute of Marine Science, PMB No 3, Townsville MC, Queensland, 4810, Australia.*

## ZOOPLANKTON AND CORAL REEFS: AN OVERVIEW

J.H.Carleton

### Abstract

Early studies concerned with the role of zooplankton within coral reef ecosystems suffered from a poor understanding of fine-scale hydrodynamics near reefs and the inadequacy of traditional plankton sampling procedures in the reef environment. As a result, the quantity of zooplankton entering reefs from the surrounding sea and residing within various reef habitats, was severely underestimated. The introduction of scuba as a research tool enabled reef ecologists to make direct observations on the behaviour and distribution of zooplankton near reefs and to develop innovative sampling procedures appropriate for their capture. A plethora of information presently exists on the abundance and distribution of reef associated, demersal plankton. In future we must concentrate our investigations on the behaviour, life histories and physiological requirements of specific taxa, if we are to assess correctly the true role of zooplankton within coral reef ecosystems.

### Introduction

In a discussion on conditions favouring the growth of coral reefs, Charles Darwin concluded that "the relations which determine the formation of reefs on any shore, by the vigorous growth of the efficient kinds of coral must be very complex, and with our imperfect knowledge quite inexplicable". Since that time reef ecologists have attempted to resolve the apparent dilemma of the existence of such enormously diverse and dense assemblages of organisms in oceans poor in nutrients and plankton.<sup>2-8</sup> Coral reefs were initially viewed as highly efficient, self-sustaining entities isolated from the surrounding seas. This view was based on rates of primary production by reef benthos several times higher than in the surrounding seas<sup>4</sup> and the belief that extremely small quantities of plankton were imported to reef systems across the windward face.<sup>5,6</sup>

Recent studies suggest that these initial beliefs were incorrect and that plankton does play a significant role in reef trophodynamic processes. The development of a better understanding of fine scale hydrodynamics on and around coral reefs<sup>9</sup> has changed the view of reefs as "closed sys-

tems". It is now realised that close links to the surrounding seas exist in terms of water exchange,<sup>10-14</sup> nutrients,<sup>15-17</sup> planktonic egg and larval stages of reef animals<sup>18-20</sup> and the input of oceanic plankton.<sup>8,21-24</sup>

In addition to the input of oceanic plankton, reefs also harbour an abundant, diverse community of resident plankton which differs both qualitatively and quantitatively from those in the surrounding sea. These unique resident zooplankton assemblages are found throughout the water column within lagoons,<sup>21,24-28</sup> residing near the lagoon floor,<sup>29,30</sup> adjacent to coral outcrops<sup>24,31,32</sup> or within the reef substrate itself.<sup>33</sup>

In this paper I discuss the findings of a few selected papers from the more recent literature which have, through the application of innovative sampling procedures, significantly extended our knowledge of the role of zooplankton on coral reefs.

### Oceanic plankton

Early studies concerned with the abundance, diversity, flux and fate of zooplankton as it approaches and crosses a windward coral reef face suffered from the limitations of traditional sampling procedures in reef environments<sup>31,32,34</sup> and a poor understanding of fine scale physical oceanographic processes near reefs.<sup>9</sup> Odum and Odum,<sup>5</sup> investigating trophic processes on coral reefs, measured both primary production and flux in plankton biomass as the water flowed unidirectionally downwind across the reef flat from the reef crest to the lagoon. They were unable to sample on the reef face at Eniwetok Atoll due to the enormous turbulence generated by wind and breaking waves and their most seaward station was located just behind the breaker zone. Plankton samples from this station contained a mixture of algal fragments, fecal material and even sand, but no zooplankton. Subsequent studies employing a similar upstream/downstream sampling regime corroborated these findings<sup>6,8,35</sup> and it was generally concluded that there was little input of open ocean zooplankton to coral reef ecosystems.

Hamner et al.<sup>22</sup> hypothesized that planktivorous fish on the windward reef face form a "wall of mouths" which removes most zooplankton from the water near the reef face before that water physically impinges upon the reef surface. To test this hypothesis they simultaneously collected zooplankton and representative specimens of plankton eating fish for gut analysis, visually estimated the abundance of these planktivores and measured small-scale water movement over the windward reef face. Davies Reef, a platform reef in the central region of the Great Barrier Reef, was chosen for the study as it lies downwind of several other reefs which considerably reduce the fetch and wave height, allowing scuba divers easy access to the windward face.

Zooplankton samples were collected over the outer reef slope at surface, 5 and 10 m depths, just in front of the breaker zone, just behind the breaker zone, and over the reef flat. At the deep sampling stations on the outer reef slope a diver propulsion vehicle was used to manoeuvre the plankton nets close to the reef substrate. Zooplankton densities were highest in deep water away from the reef and decreased steadily towards the reef. As in earlier studies, plankton sample taken over the reef flat behind the breaker zone contained little zooplankton.

Fluorescein dye released by divers at various depths near the reef face indicated that the oceanic water that crosses the reef top is not simply from the surface layer as previously believed, but comes primarily from deeper layers. Thus the denser assemblages of zooplankton found in the deeper water off the reef are carried upwards across the outer reef slope and over the reef crest. Water flowing from a depth of 25 m to the surface over a 1 m wide swath of reef is inspected by some 500 individual fish of 13 different species. By analysing the contents of fish guts and measuring zooplankton flux from deep water to the reef crest, they estimated this assemblage of fish to consume 1,180,000 food items per day. This would translate to 0.5 metric tons of plankton per linear kilometre of reef front per day.

These important findings, in contrast to earlier studies, demonstrate the importance of oceanic zooplankton as a source of nutrient for coral reef ecosystems, albeit in a rather indirect manner. It appears that most zooplankton approaching coral reefs is eaten by planktivorous fish which in turn defecate onto the reef surface, a process which enhances the growth of corals and benthic algae. Breaking waves tear fragments of benthic algae off the reef crest which together with fecal material, flows onto the reef flat. It is the nutrients within this mixture of by-products from secondary production on the reef front, and not the zooplankton itself, which enter the reef trophic economy.

Reef ecologists now appreciate the importance of having a good understanding of water movement around and over coral reefs if they are to have any hope of explaining biological processes within these systems.<sup>9</sup> The traditional view that all material imported to reefs enters across the windward face is now known to be too simplistic. Reefs with exposed back reef slopes or lagoons which are open to the surrounding sea on their leeward side are subjected to tidal flushing.<sup>9,12,14,36</sup> Ocean material is carried onto back reef slopes or into leeward lagoons by the flooding tide<sup>23,36</sup> and reef products are dispersed by the ebbing tide.<sup>18,20</sup>

Roman et al.<sup>23</sup> investigating abundance and grazing rates of zooplankton on coral reefs noted that within the reef lagoon, maximum daytime densities of oceanic copepods occurred during high water, indicating an input of external plankton during flood tide. These copepods are not only a source of food for larger reef predators, but also recycle nutrients within the reef lagoon through their grazing activ-

ity. The greatest abundance of zooplankton biomass occurred during high water at night. However, on these occasions the oceanic copepods comprised a much smaller proportion of total zooplankton numbers. The nocturnal samples were dominated by mysids, ostracods and decapod shrimps, animals which reside on or near the lagoon floor during the day, entering the water column only at night.

### Reef associated plankton

The existence of unique assemblages of zooplankton within the lagoons of reef atolls was noted by early researchers.<sup>25,26,37</sup> These communities differed from those in the surrounding seas, both in terms of species composition<sup>21,27,28,38</sup> and in terms of numbers of individuals.<sup>21,25,26,37</sup> However, the presence of resident communities of zooplankton in close proximity to coral was not realised until the introduction of scuba as a research tool. Scientists could then make direct observations on the behaviour and distribution of zooplankton near reefs and sample in areas previously inaccessible to traditional sampling methodologies.

Emery<sup>31</sup> while scuba diving on reefs in the Florida Keys, observed swarms and schools of zooplankton which were capable of maintaining their position on the reef through active swimming and by utilizing crevices, caves and coral heads as protection from predators and currents. He also noted that large numbers of resident plankton appeared only at night and apparently spent the day within the reef substrate. Porter<sup>39</sup> defined this assemblage of animals which burrow or hide within the reef substrate during the day, rise up into the water column at dusk and return before dawn, as demersal plankton. He also suggested that most of the zooplankton ingested by corals was nocturnal, coming from the reef itself. Subsequent researchers referred to the presence of demersal plankton on reefs,<sup>40,41</sup> although their actual existence was based primarily on inferential evidence from net tows and gut-content analysis of nocturnal feeding fish and corals.

Allredge and King<sup>42</sup> were the first scientists to actually sample demersal plankton as it moved into the water column from the reef substrate at night. By using "emergence traps" (transparent perspex boxes open to the bottom and containing an internal, inverted perspex funnel) they collected quantitative data on the abundance, distribution and substrate preference of these animals. Six substrate types and five reef zones were sampled over a 3-week period at Lizard Island, in the northern section of the Great Barrier Reef.

They discovered that the abundance of demersal plankton varied significantly with substrate types and reef zones. The highest mean density of zooplankton emerged from coral ( $11,264/m^2$ ) and the lowest from reef rock ( $840/m^2$ ). The density of demersal zooplankton was 6 times

greater on the face than in any other zones, averaging  $7,900/m^2$ . They suggested these differences were due to the availability of physical niches in which demersal plankton could hide. Living coral had the greatest level of 3-dimensional relief whereas reef rock had the least. The significantly higher densities of emerging plankton on the reef face was most likely due to a greater variety of substrate types.

Their estimate of demersal plankton biomass emerging into the reef waters at night was very much higher than the biomass of the total plankton (both oceanic and demersal) obtained at night over coral reef by previous investigators. Their estimate from Lizard Island of  $79.5 \text{ mg dry weight}/m^3$  was 1.5 times higher than those from the Caribbean,<sup>8</sup> 2.7 to 5.3 times higher than atolls in the Indian Ocean,<sup>21</sup> and  $9.0^{43}$  to almost  $100^6$  times greater than Bermuda. Allredge and King<sup>42</sup> argue that plankton nets and water sampling devices (Niskin or Nansen bottles) are ineffective at capturing plankton in the immediate vicinity of coral and that previous studies using standard sampling techniques had greatly underestimated the abundance, and therefore importance, of plankton over coral reefs.

The study of Allredge and King<sup>42</sup> initiated a plethora of similar investigations<sup>33</sup> employing a great variety of emergence traps to study spatial and temporal variability in these organisms. In spite of increased interest into reef associated plankton, little attention was paid to those organisms which form visible aggregations over reefs.<sup>31</sup> These zooplankters do not enter the reef substrate and are not, therefore, sampled effectively by emergence traps.

In order to obtain realistic estimates of copepod densities within swarms on coral reefs in the central region of the Great Barrier Reef, Hammer and Carleton<sup>32</sup> employed four independent sampling methodologies. Quantitative data on copepod densities were first obtained by divers swimming nets through swarms. Swarms were next sampled with a plankton pump. The third method required divers to rapidly open a large plastic bag, in a manner similar to a pelican's pouch, to engulf discrete portions of swarms. Finally, swarm densities were directly recorded photographically.

The density estimates they obtained were quite variable as each sampling methodology had a distinctive bias. Mean density from net tows was  $166,800 m^3$ , equivalent to  $570 \text{ mg dry weight } m^3$ . Plastic bag sampling produced a mean swarm density of  $210,000 m^3$  a figure 20% higher than that obtained with nets, and photographic sampling produced the highest estimates ( $325,000 - 586,000 m^3$ ). The plankton pump was a dismal failure. The copepods reacted immediately to the suction generated by this device and avoided capture.

These values for local densities of zooplankton on reefs were 3 to 15 times higher than previous estimates and emphasized the importance of using imprecise but distinc-

tive sampling techniques to obtain credible results, rather than relying on a single methodology, no matter how precise the replicates.

At night the swarms disperse throughout the water column, wash over the reef top, and presumably become available as food to the many nocturnal planktivores. Plankton net samples taken over the reef top at night contained mostly demersal plankton and swarming species of copepods. At midnight, 63% of the zooplankton captured were species of copepods which form swarms by day.

Swarming appears to be widespread among tropical copepods. At least seven species and probably more have been noted to engage in swarming behaviour in three of the world's oceans.<sup>32</sup> The reasons for swarming are numerous but protection from predators is undoubtedly very important. Large schools of mysids (small shrimp like crustaceans) which are potential predators on copepods<sup>44</sup> blanket the floor of coral reef lagoons in the immediate vicinity of swarms. To minimize predation by mysids, copepods always aggregate in close proximity to coral outcrops. The swarms are sufficiently far enough away from the coral as to be out of the foraging range of the smallest fish yet close enough to be afforded protection against mysids predation by the larger fish. The larger planktivorous fish (10 cm and longer) swim through the swarms oblivious to their presence, but readily devour any mysids which venture too near.

Mysids are a highly visible component of resident coral reef plankton.<sup>31</sup> Their aggregations occur in many reef habitats<sup>31,32,45</sup> and they function as macrophages, carnivores and detritivores within coral reef ecosystems.<sup>44,46</sup> They dominate the epibenthic community within coral reef lagoons forming large, patchily distributed shoals which vary in length (5 to 7 m), width (1 to 3 m) and depth (0.3 to 0.9 m). They are strong swimmers with well developed eyesight and easily avoid capture by standard sampling devices such as plankton nets, plankton sleds and diver swum nets.<sup>34</sup>

In order to collect detailed information on seasonal, daily and small-scale spatial variations in the species composition and abundance of epibenthic lagoon mysids Carleton and Hammer<sup>34</sup> developed a unique sampling device which made use of the mysids' escape response to effect their capture. Lagoon mysids, along with many other epibenthic taxa, do not burrow into the sediment when disturbed but move horizontally away from the source of aggregation without rising more than a few centimetres above the substrate. This behaviour pattern enables a large portion of the lagoon epibenthic community to be herded. The device they developed is similar to pound or Fyke nets<sup>47</sup> used to capture fish. The epibenthic trap consisted of two sets of components: a horizontal perspex funnel with a detachable collection box fitted to its apex and a variable air lift attached to the posterior end of the collection box, and a set of plastic curtains (two clear plastic side curtains and an

opaque "driving" curtain). The open side of the funnel, driving curtain and side curtains, which were supported by fence pickets driven into the substrate, enclosed a 10 m<sup>2</sup> 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. 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. They also used standard plankton nets to collect samples from discrete depths through the water column both day and night, and the same photographic techniques used in the study on copepod swarms to estimate densities within schools.

During the course of the study twelve species of resident epibenthic mysids were collected. Six of these were new records for the Great Barrier Reef and one was new to science. These results again emphasize the need to develop specific sampling procedures for studying resident reef plankton. The mysids community comprised of these species differed from that in the overlying water, was faunistically uniform, but formed characteristic seasonal and diel groupings. Total mysids abundances ranged between 100 and 790 m<sup>3</sup> (31 to 220 mg dry weight m<sup>3</sup>) with peak abundances occurring during the Austral spring (October). Of the seven dominant species, five engaged in schooling behaviour. Schooling species occurred at local densities ranging between 10,500 m<sup>3</sup> for the larger species and over 500,000 m<sup>3</sup> for the smaller species. The biomass equivalent would be 2,940 to 140,000 mg dry weight m<sup>3</sup>. The upper estimate is 1.5 to 80 times greater than the biomass estimate for swarming copepods. However, unlike the copepods, only one of the schooling species moved into the surface waters at night, the rest remaining on or near the lagoon floor. For this reason lagoonal mysids contribute little to the food of sessile reef planktivores such as corals.

Lagoon mysids may play an important role in nutrient regeneration. Coral reef lagoons are considered zones of net heterotrophy requiring a continuous input of organic material (algal fragments, coral mucus, fecal material, etc.) from areas of high primary production<sup>48,49</sup> to sustain a complex of secondary, detritus-based food webs.<sup>50</sup> Most coastal and littoral mysids utilize organic detritus to a considerable extent<sup>51</sup> and it is possible that the epibenthic mysids community is responsible for the remineralization of 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 and relatively large size of lagoon mysids, their trophodynamic contribution to the reef as a whole may be considerable.

## Conclusions

The initial view that zooplankton plays an inconsequential role in coral reef trophodynamics is now known to

be incorrect. A better understanding of small-scale hydrodynamic processes near reefs had led to a revised estimate in the quantity of ocean material entering reef ecosystems. At the same time the development of unique procedures for sampling zooplankton in the reef environment has produced realistic estimates for the abundance and variability of resident zooplankton.

Reef associated zooplankton have evolved complex behavioural adaptations to ensure their survival within coral reef systems. To treat them as behaviourally inept, passive particles, existing solely as a food supply for larger reef animals, is not only ecologically naive, but also perpetrates a great disservice to an interesting, highly evolved group of reef organisms. We must extend our research efforts beyond studies concerned simply with distribution and abundance, and concentrate on investigations into the behaviour, life histories and physiological requirements of specific taxa, if we are to correctly assess the true contributions of zooplankton to coral reef ecosystems.

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*John H. Carleton, MSc, is an experimental scientist at the Australian Institute of Marine Science. The Institute's address is PMB No. 3, Townsville Mail Centre, Queensland, 4810, Australia.*

## THE AMAZING NEMATOCYST

Jacque Rifkin

### Summary

Granular electron-dense material is contained both within the tubule and the capsule. The matrices contained within each compartment are different chemically from one another. During discharge, the cnidocil apparatus on the nematocyte is triggered. Polymerisation of the capsular matrix occurs, water rushes into the capsule and discharge of the tubule takes place. As the tubule everts, granular matrix contained within it emerges progressively as discharge occurs. As tubules transfix capillaries in the dermis, tubular matrix (venom) passes into them. The capsular matrix emerges once the entire tubule everts. Venom obtained by disruption of nematocysts of *Chironex fleckeri* was injected into mice by the intravenous, intraperitoneal and subcutaneous routes. Mice survived injections delivered by the intraperitoneal and subcutaneous routes. This suggests that only material delivered by the intravenous route is responsible for the rapid systemic effects manifested after a serious sting.

The implications of this mode of envenomation for the first aid treatment of *C fleckeri* are discussed.