PRODUCTION OF PARTICULATE ORGANIC MATTER BY THE REEF ON KAVARATTI ATOLL (LACCADIVES)

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ABSTRACT

The concentration of particulate organic carbon in the vicinity of Kavaratti Atoll is much greater than that of the surrounding sea. The particulate organic matter, which is largely produced by the coral reef, amounts to about 20% of the total gross production of the reef community. It is suggested that, in the absence of an adequate standing crop of phytoplankton, the particulate matter may form an important source of energy to zooplankton in coral reef waters.

INTRODUCTION

Coral reefs are highly productive communities in tropical waters of low phytoplankton and nutrient contents (Sargent and Austin 1954; Odum and Odum 1955). It has become apparent that organic aggregates and microscopic particles are abundant in association with them (Johannes 1967; Marshall 1965, 1968). The conclusion that coral reefs are among the most productive marine communities known has largely been drawn from a study of oxygen changes in waters flowing over the reef. In this study, conducted on one of the atolls of the Laccadive Archipelago during November and December 1968, the estimation of particulate organic carbon gave some useful information on its apparent release from a productive reef into the surrounding sea.

Kavaratti Atoll is located in the Arabian Sea, 10°33′ N lat and 72°36′ E long, about 200 km from the southwest coast of India. It is oriented along a north–south axis, with an island on the east and a shallow lagoon enclosed by a coral reef on the west (Fig. 1). The lagoon is about 4,500 m long, 1,200 m wide, and has an average depth of 2 m. The enclosing reef (about 300 m wide) has a 60-m gap at its northwest point, forming the main entrance to the lagoon. At Kavaratti the maximum tidal range is about 1.7 m. In the lagoon there is a continuous unidirectional flow towards the entrance, created by the heavy surf breaking across the reef (1 wave/8–10 sec) and pouring into the lagoon. In November the average current velocity in the lagoon was 10 cm/sec (5 cm/sec at the southwest corner, accelerating to 20.4 cm/sec near the entrance). At low water the reef is exposed; at high water it is submerged. The lagoon has a luxuriant growth of benthic algae and macrophytes. All along the reef, corals are the dominant animals, although their growth is patchy except at the southwest point.

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METHODS

Water samples were collected from the surface and 4–5 liters were filtered through Whatman GF/C pads coated with 2 ml of a 1% suspension of $MgCO_3$. The particulate matter deposited on filter pads was analyzed for organic carbon by wet oxidation with a mixture of chromic acid and sulfuric acid followed by titration with 0.1 N ferrous ammonium sulfate (1 ml of ferrous ammonium sulfate = 300 μg C, Steele and Baird 1965). Another subsample of 5 liters or more was filtered for the estimation of chlorophyll *a* (Steele and Baird 1965); at some stations (Fig. 1) ^{14}C assimilation was also measured.

RESULTS

The concentration of particulate organic carbon in the ocean water, 12 km northwest of the atoll, was relatively low and

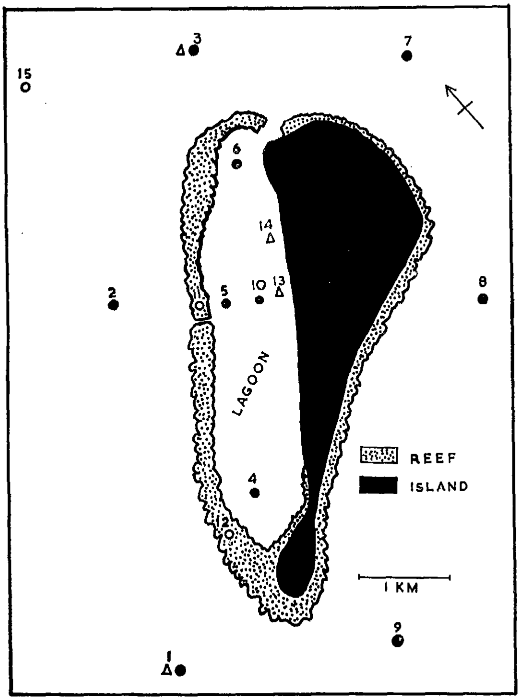

FIG. 1. Kavaratti Atoll showing the relative position of reef, lagoon, and island and the positions of sampling stations. Stations 1–10 (solid circles)—particulate organic carbon and chlorophyll *a* were measured; stations 11 and 12 over the reef and station 15 about 2 km away (open circles)—only particulate organic carbon was measured. Stations 1, 3, 13, and 14 (open triangles)—chlorophyll *a* and ^{14}C uptake were measured. Runs were made from stations 1–3 and 4–6 to measure fractions of particulate organic carbon added to the water as it flows over the reef.

showed no significant change along a transect to the atoll until within 6 km of the area. From about 2 km off the atoll, the values increased progressively and the highest concentrations were recorded over the reef and in the lagoon (Fig. 2). This clearly suggests that the increase in the particulate carbon was due to the influence of the reef community, as a consequence of the transport of water over the reef and its reentry into the surrounding sea.

The chlorophyll *a* values in the area (Fig. 3) were extremely low and agreed with those previously recorded from coral reef waters (Jeffrey 1968). The assimilation of ^{14}C at different stations in the lagoon and open sea (*see* Fig. 1) was directly related to chlorophyll *a* (Fig. 3B). Thus it appears that the chlorophyll represents a live phytoplankton community, but at levels so low, and so unrelated to the particulate carbon (Fig. 3A), as to add further support to the view that material from the reef, not phytoplankton, accounts for the particulate levels.

To assess quantitatively the fraction of particulate matter added to the water as it traverses the reef, two runs were made from stations 1 to 3 outside the reef and from opposite stations 4 to 6 inside the lagoon (Fig. 1). The total time taken for working 6 stations in each run was about 2.25 hr. The first run was made at night on 3–4 December 1968, the second the following morning (Table 1). The results show that, both during day and night, there was appreciably more particulate carbon at the stations inside the lagoon.

The production of particulate carbon by the reef was calculated as:

Mean difference of particulate carbon (mg/cm^3) between sea and lagoon × mean depth over the reef (cm) × average current velocity (cm/sec) = production of particulate carbon (mg cm^{-1} sec^{-1}). This was 0.089 g C m^{-2} hr^{-1} for the night run and 0.101 g C m^{-2} hr^{-1} for the day (avg = 0.095 g C m^{-2} hr^{-1}).

Gross primary production of the reef community was determined in November along the same track by measuring changes in the oxygen concentration of water flowing over the reef during the day and at night (for method *see* Sargent and Austin 1949, 1954). This gave a value of 0.513 g C m^{-2} hr^{-1}. The factor for converting the oxygen values to carbon was 0.375/PQ where the value of PQ was taken as 1.2.

From these data it would appear that the production of particulate carbon by the reef community is about 20% of its gross production, which is equivalent to about 95% of coral respiration as determined from the flow studies at night (respiration = 0.100 g C m^{-2} hr^{-1}). Johannes (1967) estimated that the export of particulate

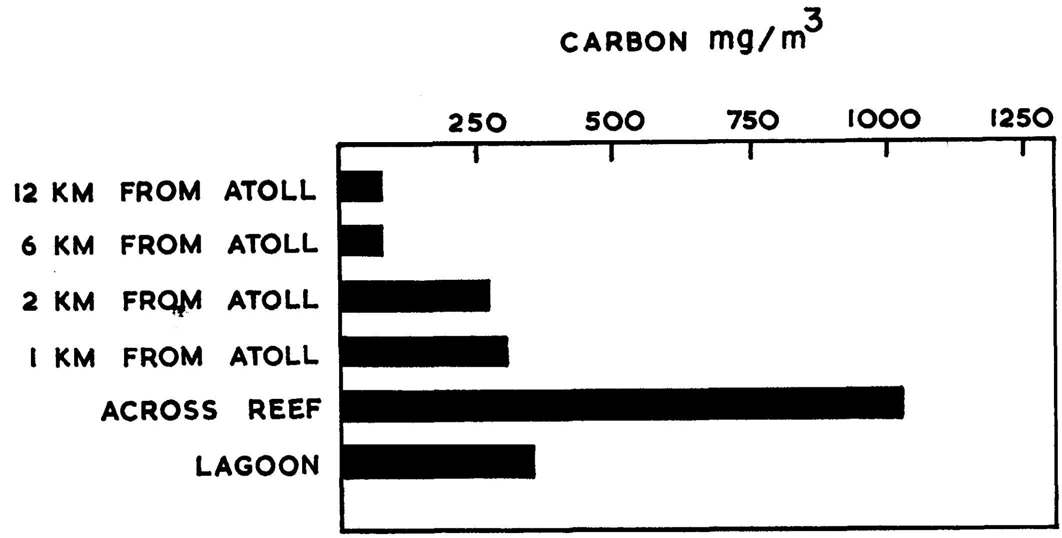

FIG. 2. Relative concentrations of particulate organic carbon in the surrounding sea and at different sites. Each value is a mean of 4–5 measurements.

matter (which he indicates is predominantly mucus) is about 2% of the reef production on Eniwetok Atoll (Marshall Islands) which amounts to 40% of coral respiration. This may be an underestimate, for Johannes correlated his values of mucus transport with estimates of reef production made many years ago (Odum and Odum 1955). Nevertheless, both our observations and those of Johannes clearly indicate that an appreciable proportion of the reef productivity is released in the form of particulate matter.

DISCUSSION

The results indicate a high rate of production of particulate matter by the reef on Kavaratti. In certain areas of the lagoon we have confirmed the occurrence of large quantities of mucus and aggregates by underwater observations where particles were "often sufficiently abundant to limit visibility, creating the visual impression of an underwater snowstorm" (Johannes 1967, p. 190). The shallowness of the lagoon and intense clarity of the water make it easy to see patches of particulate matter, especially at the southwest point of the lagoon. We filtered a small quantity of water (5–10 ml) from the reef flat through a membrane filter and cleared it with Tween 20; we could then see the particles with a microscope. The size and form of these aggregates were similar to those described by Riley (1963).

These observations raise questions as to the mechanism involved in the formation of particulate organic matter and its importance in the ecology of the reef community. Sheldon, Evelyn, and Parsons (1967) have demonstrated in the laboratory that particle formation in seawater can occur in the absence of any external agency excepting bacteria and that the mechanism is greatly enhanced by an addition of soluble carbon, such as glycine. It has recently been reported that symbiotic zooxanthellae imprisoned in corals excrete soluble substances (mainly glycerol) in appreciable quantities (Muscatine 1967). Thus the presence of large quantities of dissolved organic matter may accelerate the formation of particulate matter near the reef. An abundance of calcium carbonate particles in coral reef waters, forming nuclei around which dissolved matter may be adsorbed, is another likely factor (Marshall 1968). Continuous bubbles produced by the surf and their role in the formation of organic aggregates (Baylor and Sutcliffe

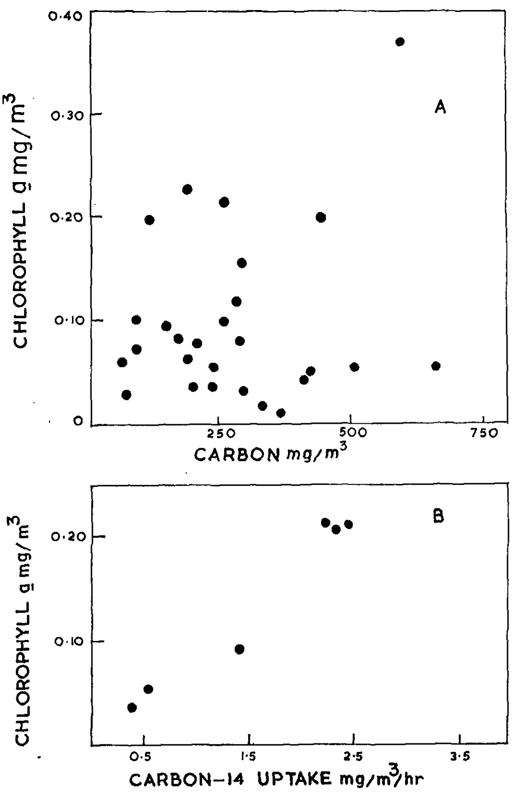

FIG. 3. A. Relation between particulate organic carbon and chlorophyll *a* in water samples taken from stations 1–10. B. Relation between ^{14}C assimilation and chlorophyll *a* at stations 1, 3, 13, and 14.

TABLE 1. *Concentrations of particulate organic carbon obtained at different stations (in parentheses) in the sea and in the lagoon during two runs*

Date (1968) and time (hours)	Carbon (mg/m³)	
	Sea	Lagoon
	Night	
3–4 Dec		
2245–0050	(1) 203	(4) 300
	(2) 188	(5) 507
	(3) 370	(6) 260
Avg	254	356
	Day	
4 Dec		
1117–1345	(1) 240	(4) 450
	(2) 173	(5) 282
	(3) 263	(6) 294
Avg	225	342

1963) is yet another possibility. The abundance of mucus secreted by the corals may be another factor responsible for increasing the load of particulate matter. Mucus entraps detrital particles and bacteria and the entire mass may be broken down into smaller and smaller particles by the surf action across the reef. Marshall (1969) observed that in several species of corals kept in captivity, mucus production is greatly increased when the corals are exposed to jets of water simulating wave action. Under such treatment both the dissolved and particulate organic content of the water in which the corals were kept increased substantially. Whatever the mechanism involved in the formation of particles in seawater may be, and it may include one or a combination of several possibilities, the processes may well occur more readily in the vicinity of coral reefs.

The availability of particulate material may be important to the widely debated problem of coral nutrition. Corals possess an elaborate system of catching their prey and are well known to be zooplankton feeders (Yonge 1930, 1963), but the evidence as to the abundance of zooplankton near the coral reefs has been conflicting. Some authors have found large quantities of zooplankton (Russell 1934; Emery 1968), while others have reported extremely low concentrations (Sargent and Austin 1954; Odum and Odum 1955). If large concentrations of zooplankton do exist, what would be the source of their energy in such coral reef waters of impoverished phytoplankton content? One answer seems to lie in the possibility that the reef may play a recycling role, in which the particulate matter that the reef produces serves as a source of food for the zooplankton and other filter feeders of the reef community. Johannes (1967) found that *Artemia* nauplii kept in tanks containing coral mucus grew faster and lived longer than those in control tanks. Perhaps the occurrence of dense concentrations of zooplankton near the coral reef, noticed by Emery (1968) and more recently by Tranter and

George (1969) at Kavaratti during October 1968, may be due to the presence of large quantities of particulate matter as a readily available food. The particulate production in corals thus becomes an interesting adaptation, providing a potential source of energy to the zooplankton and thus providing a partial energy return to the corals as they feed on the plankton.

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