

## Mucus Production by Corals Exposed during an Extreme Low Tide<sup>1</sup>

DAVID A. KRUPP<sup>2</sup>

**ABSTRACT:** An extreme low tide resulted in the severe exposure of corals on the reef flat surrounding Coconut Island in Kaneohe Bay, Oahu, Hawaii. The exposed corals produced vast quantities of mucus that aggregated as mucous ropes near the shoreline. These mucous ropes were heavily laden with carbonate sediments, amorphous materials, microflora, and microfauna. Compared to the purified liquid mucus of the coral *Fungia scutaria*, the consolidated mucous ropes were rich in organic material and phosphorus. Pure mucus was relatively low in trophic quality. While the pure mucus may provide corals with some protection against desiccation, it is not a particularly rich food source for reef heterotrophs. Perhaps the most important role of coral mucus is the consolidation of microscopic organic particulates into macroscopic aggregates of considerably higher trophic quality than the pure mucus itself.

THE CONTINUOUS PRODUCTION AND SLOUGHING away of mucus from reef corals may be an important component of reef trophic dynamics (Johannes 1967, Coles and Strathmann 1973, Benson and Muscatine 1974). This hypothesis is supported by observations of animals feeding on coral mucus (Gerlach 1961, Johannes 1967, Knudsen 1967, Preston 1971, Benson and Muscatine 1974, Hobson 1974, Richman, Loya, and Slobodkin 1975, Patton 1976, Reese 1977, Gottfried and Roman 1983) and by evidence for bacterial utilization of mucous components (Coles and Strathmann 1973, Ducklow and Mitchell 1979b, Rublee et al. 1980, Pascal and Vacelet 1982). Consequently, considerable research has been undertaken to evaluate and quantify the trophic quality of coral mucus (Johannes 1967, Coles and Strathmann 1973, Benson and Muscatine 1974, Richman, Loya, and Slobodkin 1975, Daumas and Thomassin 1977, Ducklow and Mitchell 1979a,b, Pascal 1981, Pascal and Vacelet 1982, Daumas, Galois, and Thomassin

1982, Krupp 1982, 1984, Gottfried and Roman 1983).

The consensus has been that coral mucus represents a high energy, nutrient-rich food source for reef organisms (e.g., Benson and Muscatine 1974, Daumas and Thomassin 1977, Ducklow and Mitchell 1979a). Unfortunately, past analyses may have been confounded by contamination in the samples of mucus studied (Krupp 1982). Thus, coral mucus may actually be relatively poor in trophic quality. An hypothesis is currently being developed suggesting that nonmucous materials suspended in or adsorbed to the mucus, rather than the polysaccharide-protein complex comprising pure mucus, give mucous flocs or aggregates stripped from corals their suggested high trophic quality.

An extreme low tide resulting in excessive production of mucus by exposed reef corals provided an opportunity to examine the composition of naturally produced mucous aggregates. In addition, analyses were performed on purified mucus from the solitary coral, *Fungia scutaria*, for comparison.

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<sup>2</sup>Hawaii Institute of Marine Biology, P. O. Box 1346, Kaneohe, Hawaii 96744.

### MATERIALS AND METHODS

The extreme low tides occurred in Kaneohe Bay, Oahu, Hawaii, from 30 May to 5 June

1981. Visual and photographic observations were made while walking along the eastern and southeastern coasts of Coconut Island where the Hawaii Institute of Marine Biology is located in Kaneohe Bay.

Mucous strands, sloughed from corals in situ, were collected with a glass syringe for microscopic examination. Aggregated mucous ropes gathering at the shoreline were stable enough in structure for collection by hand. These materials were either examined immediately or fixed in 10% formalin seawater.

Dry weight yields of the mucous rope material were determined on samples that were blotted dry to remove excess water. Each wet sample was then dried to constant weight at 60°C. Samples of the mucous ropes were also analyzed for inorganic ash and organic C, N, and P content after centrifuging ( $5520 \times G$  at 5°C for 15 minutes) from seawater. The ash content of this material was determined as the weight left after combustion in a muffle furnace at 500°C for 3 hours (Coles and Strathmann 1973). Carbon and nitrogen determinations were performed using a Hewlett Packard 185B CHN Analyzer according to the methodology of Hirota and Szyper (1976). Organically bound phosphorus was liberated from samples using a two-step sulfuric-persulfate digestive procedure (U.S. Environmental Protection Agency 1974, American Public Health Assoc. 1976) requiring an initial hydrolysis in boiling concentrated sulfuric acid, followed by oxidation in potassium persulfate. The final hydrolysate was neutralized, and the orthophosphate produced was assayed on a Technicon Autoanalyzer II System (procedure modified slightly from Strickland and Parsons 1972).

Samples of mucus from the solitary coral *Fungia scutaria* were purified of particulate contamination by centrifugation and of salts by dialysis (Krupp 1982). Slow speed centrifugation removes the particulate contamination without sedimenting the mucus (Lewis 1973, 1976) because freshly collected mucus forms a viscous solution rather than a particulate suspension. On the other hand, old mucus or highly contaminated mucus seems to undergo a polymerization process (Ducklow and

Mitchell 1979a) that causes it to sediment at low centrifugation speeds.

The dry weight yield of the "pure" lyophilized mucus was determined as a percentage of the weight of the corresponding volume of the mucus before centrifugation. Inorganic ash and the relative organic C, N, and P were determined on lyophilized mucus as described above for the mucous ropes.

Callianassid shrimps, *Callianassa placida*, observed pulling the mucous ropes into their burrows were collected by enticing them from their burrows with pieces of mucous ropes or algal fragments. These shrimps were fixed in 10% formalin seawater for 24 hours before dissecting their guts and squeezing out the contents for examination.

## RESULTS

### *Reef Descriptions*

The mucous aggregates formed on the reef and were blown inshore, where they were rolled into mucous ropes. These ropes accumulated in a coastal pocket on the southeastern side of the island and along the eastern (seaward) coast of a thin peninsula that encloses the eastern side of a long narrow lagoon at Coconut Island (Figure 1). Flotsam normally accumulates at these sites because of the configuration of the coastlines, the prevailing wind direction, and the current patterns over the adjacent fringing reefs.

The eastern reef is narrow with a central dredged trench (approximately 1–2 m below reef surface) along its length. The reef substrate seaward of this trench forms a compact calcareous bench composed predominantly of incrusting calcareous red algae and the corals *Porites compressa* and *Pocillopora damicornis*. The shoreward margin of the trench is formed by extensive *Porites compressa* colonies which give way to a bottom of gravel and sand with isolated heads of *Porites compressa*, *Pocillopora damicornis*, and *Montipora verrucosa*. Patches of zoanthids are also scattered sparsely across the reef. *Porites compressa* is the dominant coral.

The southeastern reef, which is the same

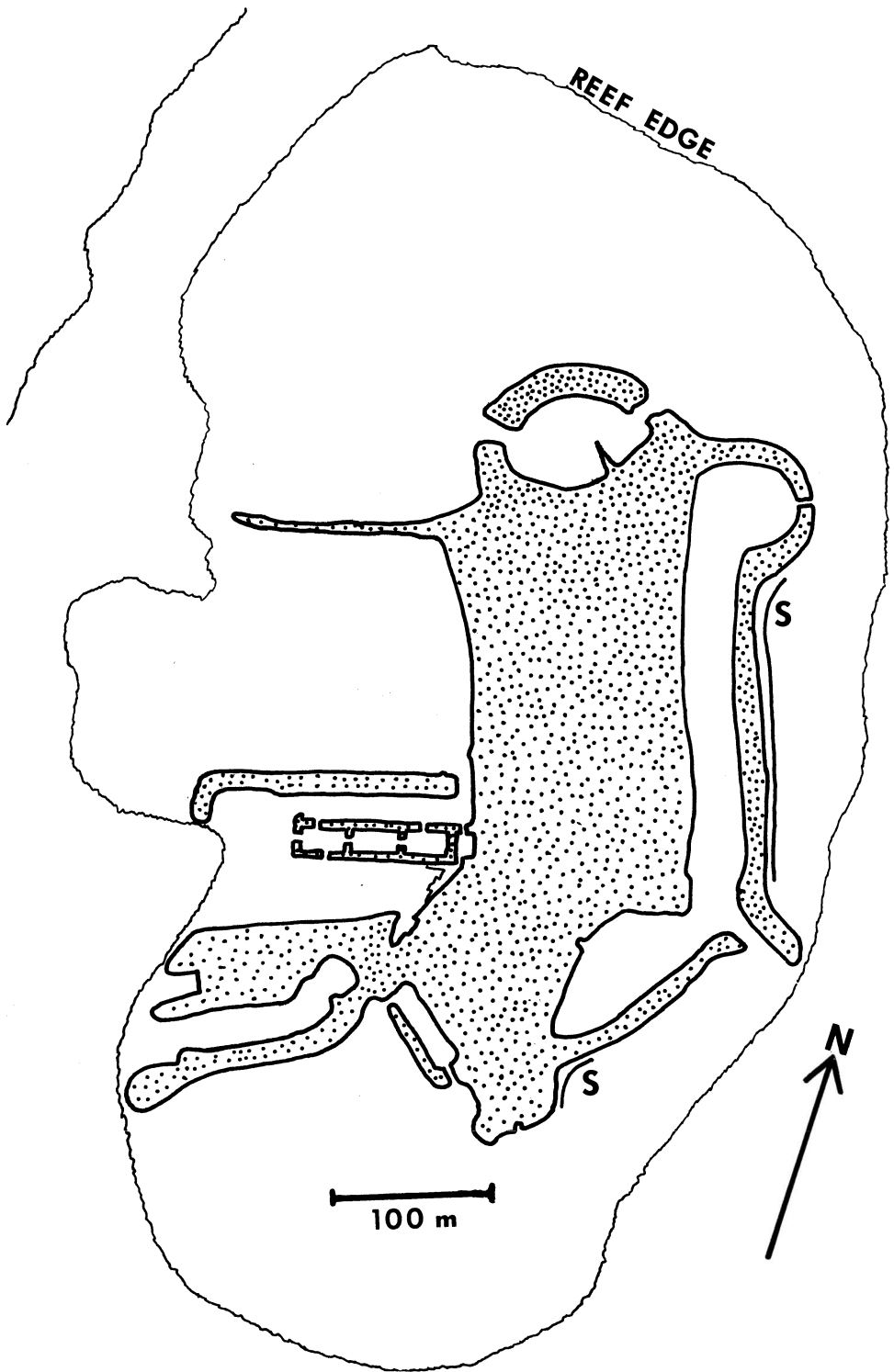


FIGURE 1. Locations of mucous rope accumulation on the reefs at Coconut Island, Kaneohe Bay, Oahu (S, mucous ropes).

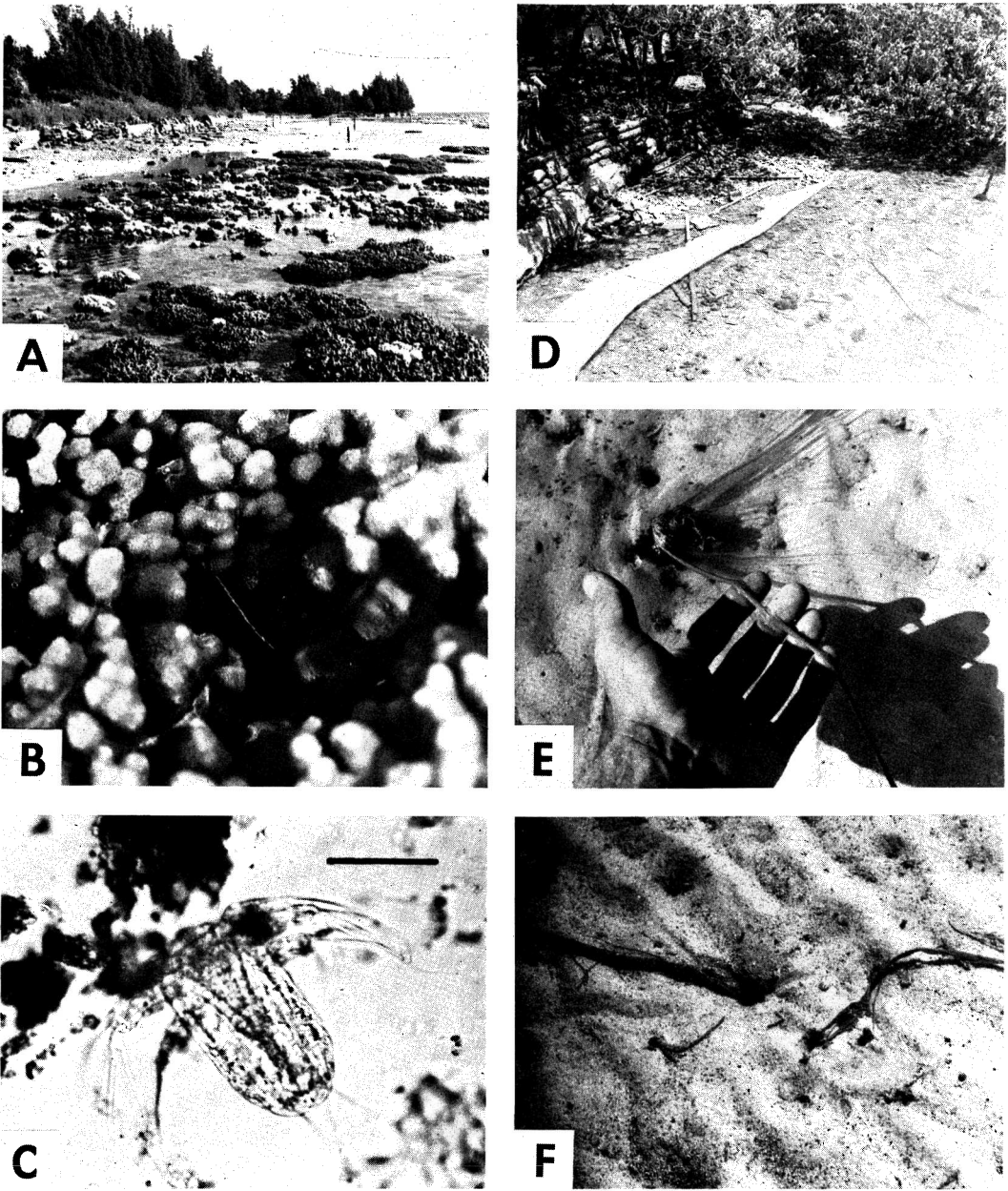


FIGURE 2. Mucus production by corals exposed by an extreme low tide: *A*. typical exposure on the NE reef of Coconut Island; *B*. mucous strand among fingers of *Porites compressa*; *C*. crustacean nauplius associated with a mucous strand (bar represents 50  $\mu\text{m}$ ); *D*. mucous scum accumulation in SE coastal pocket of Coconut Island; *E*. mucous ropes accumulated on exposed sand flats on the NE reef; *F*. Mucous ropes extending into shrimp burrow.

reef studied by Gordon and Kelly (1962), broadens to the south. A deeply dredged trench (approximately 3–4 m below reef) occurs very close to shore in the pocket. The reef edge is composed of cemented calcareous rock with numerous corals. Toward the shoreline the reef is composed mainly of sand with isolated coral heads and patches. *Porites compressa* is the dominant coral on this reef as well.

#### Description of Reef Exposure

All of the extreme low tides (Figure 2A) occurred in the morning during the period from about 30 May to 5 June 1981. Reefs were exposed for a maximum of about 5 hours. During the first several days, the exposure occurred early enough in the day such that the exposed corals were not subjected to severe solar radiation. Many corals were exposed to intense solar radiation on subsequent days because the low tide occurred progressively later. Consequently, the exposed corals exhibited signs of stress and death.

The imperforate coral, *Pocillopora damicornis*, was more susceptible to this exposure than were the perforate corals, *Porites compressa* and *Montipora verrucosa*. Death usually occurred first on the sides facing the morning sun. Many entire heads of *Pocillopora damicornis* were dead by 5 June. Death on colonies of *Porites compressa* and *Montipora verrucosa* was restricted primarily to the tops of these colonies. The dead areas were still noticeable after one year.

#### Process of Mucous Rope Formation

The mucous ropes developed with the rising tide after each low tide. The rising seawater lifted the surface mucus from corals that had been exposed by the low tide. Minute mucous strands were observed among the fingers of these corals (Figure 2B). Microscopic examination of these strands from *Porites compressa* revealed a complex association of fine amorphous threads, sediments, diatoms, zooxanthellae, cnidocysts, filamentous algae, fecal pellets, and small metazoans such as nematodes, polychaete larvae, and crustaceans (Figure 2C).

TABLE 1

DRY WEIGHT YIELDS, ASH CONTENTS AND ELEMENTAL COMPOSITIONS FOR AGGREGATED MUCOUS ROPES AND THE PURIFIED MUCUS OF *Fungia scutaria*

	"PURIFIED" <i>Fungia scutaria</i> MUCUS (mean $\pm$ s.d.)	CONSOLIDATED MUCOUS ROPES (mean $\pm$ s.d.)
Dry weight yield (% wet weight) (n = 8)	0.0033 $\pm$ 0.0018	16.6 $\pm$ 4.6 (3)
Ash contents (% dry weight) (14)	17.4 $\pm$ 3.9	81.2 $\pm$ 0.1 (2)
Elemental composition (molar ratios)		
C:N (5)	7.23 $\pm$ 0.98	7.37 (1)*
C:P (5)	286 $\pm$ 30	140 (1)*
N:P (5)	40.9 $\pm$ 9.37	18.9 (1)*

\* Note that there were three replicate determinations for each element (C, N, or P) on a single thoroughly homogenized sample (approximately 200 ml wet volume) of the consolidated mucous ropes. Thus, the molar ratios for this material were calculated from the mean percents that each element contributed to the whole dry weight. The coefficients of variation for these determinations were 0.051, 0.168, and 0.069 for C, N, and P, respectively.

These threads were sloughed away from the corals and combined to form larger aggregates with others. These aggregates floated toward the shoreline where they coalesced into long mucous ropes (Figures 2D,E).

A diverse flora and fauna occurred within these mucous ropes. Numerous ciliates, ostracods, copepods, isopods, decapod larvae and other tiny metazoans were living within the mucous-sediment matrix. None of these organisms appeared to feed directly on this matrix. These ropes were best developed after the reef was entirely covered by the rising tide. The entire process of formation took about 2 hours. The mucous ropes and aggregates were dispersed within 2 hr of maximal development because of increasing surface water agitation accompanying the rising tide and increasing afternoon winds.

#### The Composition of the Mucous Ropes

The dried mucous ropes were composed predominantly of inorganic ash (Table 1) arising from carbonate sediments and sea salts in these samples. By contrast, the desalted,

sediment-purified dry mucus of *Fungia scutaria* contained much less inorganic ash. However, the dry weight yield from a wet sample of the mucous rope (blotted dry) was much greater than the dry weight yield from the purified liquid *Fungia* mucus. Thus, the organic weight yield from a wet sample of the mucous rope greatly exceeded that from the purified *Fungia* mucus, despite the greater ash contents of the mucous ropes.

The relative amounts of organic carbon and nitrogen of both *Fungia scutaria* mucus and the mucous ropes were similar (Table 1), yielding respective molar C:N values of 7.23 and 7.37. However, the phosphorus content of the organic fraction of *Fungia* mucus was half that of the mucous ropes. The molar C:P values were 286 and 140 and the molar N:P values were 40.9 and 18.9, respectively.

#### *Observations on Callianassid Shrimps Gathering Mucous Ropes*

Some of the mucous ropes extended into burrows on the exposed sand flats of the eastern reef (Figure 2F). Continued observations revealed that shrimps, *Callianassa placida*, pulled these ropes into their burrows. It was not certain if these shrimps actually ingested the ropes. Gut contents yielded sediments, amorphous matter, diatom fragments, and macroalgal fragments. A few algal cells resembling zooxanthellae were found in the gut of one animal. While the gut analyses did not absolutely confirm ingestion of the mucous ropes, it was highly probable that the shrimps consumed them.

### DISCUSSION

#### *Mucus Production and Exposure to Air*

The secretion of mucus by corals functions primarily in suspension feeding and sediment clearing (Duerden 1906, Yonge 1930, Marshall and Orr 1931, Abe 1938, Loya 1976, Lewis 1977, Schuhmacher 1977, Fisk 1982). In suspension feeding, small food particles are trapped in a layer of mucus covering the surface epithelium and swept orally by ciliary

activity. Orally directed flow requires an organic stimulus such as prey tissue extract (Duerden 1906, Yonge 1930, Abe 1938).

Ciliary-mucoid removal of sediments is probably more important than the use of mucus in suspension feeding. Corals without this capability might be quickly buried by sediments. In addition, clean tissue surfaces must be maintained for adequate metabolic exchange and to permit light to reach the endosymbiotic zooxanthellae. Thus, rates of reef sedimentation and the abilities of corals to remove sediments are factors important in determining the distributions and abundances of corals across a reef (Darwin 1842, Wood-Jones 1912, Marshall and Orr 1931, Loya and Slobodkin 1971, Loya 1972, 1976, Richman, Loya, and Slobodkin 1975, Schuhmacher 1977, Fisk 1982).

Furthermore, corals increase the production of mucus as a general response to stresses such as high temperatures, altered salinities, and pollution (Marcus and Thornhaug 1982, Mitchell and Chet 1975, Loya and Rinkevich 1980). A blanket of mucus over the surface epithelium may retard many of the detrimental effects of these adverse environmental factors by limiting the diffusion of metabolites in and out of the coral. On the other hand, Segel and Ducklow (1983) have suggested that increased bacterial growth stimulated by the excessive secretion of mucus by corals may be detrimental to the corals.

Because mucus is also extremely hydroscopic, it may serve to maintain moisture in surface tissues of corals during exposure to air. This function is particularly important in certain terrestrial animals such as snails (Machin 1965) and amphibians (Lillywhite 1971) that require moist epithelial tissues for efficient respiration.

Corals with potentials for high rates of mucus production may survive better during periods of exposure. In this respect, mucus may compliment capillarity in perforate corals (Edmondson 1928). *Porites* can form cohesive envelopes of mucus (Lewis 1973) which hypothetically could retard desiccation when exposed to air. *Pocillopora damicornis*, which was more severely stressed by the exposure, does not form similar cohesive en-

velopes nor does it produce copious quantities of mucus. Hodgkin (1959) reported similar destruction of heads of *Pocillopora damicornis* during an extreme low tide near Fremantle, Australia. *Montipora verrucosa* also does not produce discrete envelopes, but appears to produce copious amounts of liquid mucus, which may account for its ability to survive dessication. *Fungia scutaria*, which is the best producer of liquid mucus among Hawaiian corals (Glynn, Hidaka, and Krupp, in preparation), survives experimental dessication better than most other Hawaiian corals (Edmondson 1928).

Specific differences in mucus-producing ability may play a role in determining coral community structure in shallow reef environments. Reef-top environments that are frequently and regularly exposed may be composed of relatively stable populations of corals that produce copious amounts of mucus. Deeper reef-top environments may contain species with poor mucus-producing abilities, but may suffer more severely when exposed during rare and unpredictable extreme low tides.

#### *Composition and Trophic Quality of the Mucous Ropes*

Substantial particulate material adhered to the coral mucus even before the mucus was stripped from the coral surfaces by the rising tide. Some of this material, such as zooxanthellae and cnidocysts, was derived from the corals themselves, while a large fraction appeared to be derived from noncoral sources. Naturally occurring particulate materials of these sorts may be interpreted by the trophic ecologist as augmenting the nutritional quality of the mucus. However, the presence of these particulates, and the difficulty in quantifying their contribution to the total trophic quality, complicates interpretations about the nutritional quality of the coral mucus itself. Thus, previous analyses of coral mucus may have been obscured by the presence of particulate contaminants of both coral and noncoral origin.

The mucus released by stressed corals may be different in composition from mucus se-

creted under natural circumstances (Daumas and Thomassin 1977, Daumas, Galois, and Thomassin 1982, Gottfried and Roman 1983). However, Goreau's (1956) observation of only one type of mucous cell in the external epithelia of 22 species of Atlantic reef corals suggests that there may be only one type of mucus secreted from these epithelia. Verification of this hypothesis remains to be tested using modern histochemical procedures.

Stressing corals yields several results: increased production of mucus, discharge of cnidocysts, and the introduction of damaged tissues into the mucus. The latter two results influence analyses performed upon mucus that has not been purified of these contaminants (Krupp 1982). Compositional differences found between stress-produced mucus and natural mucus are probably more due to stress-induced contaminants and natural contaminants in the mucus than due to intrinsic differences in the two types of mucus.

Furthermore, the low tide conditions which induced the exposed corals to secrete excessive quantities of natural mucus were very stressful. Thus, the comparison being made in the present study is entirely on stress-induced mucus.

Coral mucus that has been purified of particulate contamination is actually relatively poor in trophic quality (Krupp 1982). Purified *Fungia* mucus is low in caloric density, energy-rich lipids, and phosphorus. The nitrogen content is lower than typical protein values. Mucus, being a complex association of specific polysaccharides and proteins (Krupp 1982, 1984), is considerably more homogeneous in composition than other potential food sources such as animal and algal tissues. Finally, fresh, unconsolidated mucus is composed of nearly 100% water (Table 1; also Coles and Strathmann 1973). This phenomenon probably results from the extreme hydration of the acidic polysaccharide component (Krupp 1982, 1984) of the mucus.

A low trophic value would appear to be adaptive. Mucus is readily stripped from corals by water motion. Potentially, large quantities are needed to serve several vital functions. Thus, the energetic and nutrient costs due to the production and sloughing-

away of mucus are unavoidable. Corals may minimize these costs by synthesizing a trophically poor mucus. However, there may be biochemical constraints that set the lower limit for these costs.

Perhaps the most important trophic role of coral mucus is serving as an aggregation factor for soluble organics, detritus, microflora, and microfauna. Sorokin (1974) suggested that coral mucus induces bacteria to aggregate. Coral mucus (Ducklow and Mitchell 1979b, Rublee et al. 1980), or small molecular weight substances associated with the mucus (Pascal and Vacelet 1982), do appear to support a substantial bacterial population. Furthermore, Coles and Strathmann (1973) suggested that coral mucous flocs become enriched with nitrogen due to the presence of bacteria. These bacteria and other organisms associated with mucous aggregates may add substantially to the organic content of the mucus.

Coles and Strathmann (1973) actually obtained unusually low C:N values for "aged" mucous flocs suspended in rock pools near Kapoho, Hawaii. Their values ( $4.1 \pm 0.7$ ,  $n = 3$ ) were comparable to values that would be expected for pure protein or protein-rich materials. These mucous flocs were believed to have originated from *Porites lobata* colonies which yielded fresh mucus with a C:N value of 5.9, hence the interpretation of nitrogen enrichment with time. The low C:N value for these mucous flocs is inconsistent with average C:N values of 6.6 to 7.7 obtained for living marine organisms (Redfield 1934, Fleming 1940). As mucous flocs become colonized with microorganisms, their C:N values should approach the average of these microorganisms (e.g., probably between 6.6 and 7.7) rather than approaching typical protein values. *Porites compressa*, which probably contributed the most mucus to the developing mucous ropes examined in the present study, yields mucus with a C:N value of 6.0 (Coles and Strathmann 1973), which is richer in nitrogen than the purified mucus of *Fungia scutaria* (this study; also Coles and Strathmann 1973) and the mucous ropes themselves (this study). Thus, colonization by

microorganisms and adsorption of organic sediments resulted in a C:N value for these mucous ropes that was comparable to living biomass. This interpretation is also supported by a C:P value of 140 for the mucous ropes, since average values for living marine organisms generally range from 106 to 138 (Redfield 1934, Fleming 1940). Furthermore, the higher P content (relative to C) of the mucous ropes over that of the purified mucus of *F. scutaria* suggests that mucous aggregates become enriched with organic phosphorus due to the recruitment of microorganisms. The overall result of colonization with microorganisms and adsorption of organic sediments is to render average values of C:N:P to coral mucous aggregates. Since the C:N:P values of mucophagous organisms is probably near to these averages, the contaminated mucous aggregates may actually be better food sources than the pure mucus.

The particulate material suspended in coral mucus polymerizes liquid mucus into discrete flocs and aggregates by presenting multiple adsorbing sites that cross-link the molecular components of the mucus (Ducklow and Mitchell 1979a). This effect compliments the chemical polymerization that may also occur between these components (Lewis 1976; Allen, Pain, and Robson 1976; Allen 1978; Morris and Rees 1978). Thus, mucous aggregates are really consolidations of liquid mucus and microscopic particulates (including microorganisms) into stable macroscopic structures. These aggregates, representing communities in themselves, may allow exploitations of microscopic food by macrophagous animals such as the shrimp *Callinassa placida* observed collecting mucous ropes in this study.

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