

Appendix G. Sources of Energy and Predators and Associations of Corals (Source: GMFMC and SAFMC 1982).

SOURCES OF ENERGY IN CORALS

1.0 Scleractinia

1.1 Light

Fundamental to the flow of energy through the reef ecosystem is the symbiotic relationship with zooxanthellae characteristic of all shallow-water hermatypic corals. These algae are capable of producing more oxygen that is consumed by the algae and coral host combined (Yonge, et al., 1932; Odum and Odum, 1955; Kanwisher and Wainwright, 1967). But more important to corals, and the communities which they form, is the carbon fixed during the process of photosynthesis. Evidence that zooxanthellae can release photosynthetically fixed organic compounds to their hosts is well documented, as is the effect of zooxanthellae on nutrient recycling and enhancement of calcification (reviewed by Muscatine, 1973). The indispensability of the symbiosis, however, is one of the sources of controversy noted above.

While it appears that supplemental sources of nutrition are taken in addition to the amount supplied by zooxanthellae, the overall question of indispensability of such exogenous food to the existence of scleractinians is still debated. Yonge and Nicholls (1931) concluded that scleractinians can live for several months in complete darkness as long as food is provided. Conversely, Kawaguti (1964) observed that four genera of Pacific corals kept for more than 15 months in the light but without food appeared healthy and increased their numbers of polyps (note: although zooplankton were withheld as a food source, bacteria may have been present and consumed in Kawaguti's work]. Franzisket (1969; 1970) showed that Hawaiian corals performed in the same fashion and noted that corals kept in the dark for two months exhibited symptoms of atrophy. Connell (in Muscatine, 1973) excluded light from a section of the Great Barrier Reef using an opaque dome without affecting ambient currents and food supply. During three and one-half months in the shade, corals expelled their zooxanthellae and all colonies died. Control colonies under transparent domes survived. Lewis (1974) found that planulae of *Favia fragum* could not survive more than three months if not provided with both food (*Artemia*) and light (12h:12h, light:dark photoperiod).

1.2 Zooplankton

Opinions differ on the adequacy of zooplankton in satisfying the food requirements of coral and other benthic invertebrates on reefs (Lewis, 1977). Johannes (1974) has argued that the biomass of zooplankton over coral reefs is insufficient to supply energy needs although it may be important as a source of essential nutrients. In this view reef corals are "autotrophic" and depend extensively upon energy supplied by their zooxanthellae.

The early papers of Sargent and Austin (1949, 1954) indicated that the zooplankton biomass of surrounding waters at Rongelap in the Pacific were too small to support all the benthic invertebrates on the reef. Johannes, et al. (1970) calculated that zooplankton on a Bermuda reef were not sufficiently abundant to support the energy needs of the corals present as indicated by their rates of respiration. Johannes and Tepley (1974) found that the zooplankton biomass present could supply only 20 percent of the daily requirements for respiration in the Pacific coral, *Porites lobata*, and Porter (1974) estimated that during a two-hour feeding period at sunset, the small star coral (*Montastraea annularis*) could capture only between 0.2 percent and 11 percent of the total daily food required for energy used in respiration.

Although the supply of oceanic zooplankton appears to be inadequate to support reef secondary production, reefs undoubtedly produce their own zooplankton (Porter, et al., 1977;

Porter and Porter, 1977). Sale, McWilliam and Anderson (1976) found that there was a resident plankton community at Heron Island, Australia, which was more abundant and richer in species than the offshore community.

They suggested that this plankton community was retained on the reef by local circulation or by behavioral responses and was a potential source of food for the sessile reef organisms. This aspect of reef zooplankton ecology may be of quantitative significance when its impact is more fully evaluated.

The view that reef corals are not wholly "autotrophic" in their nutrition has been summarized by Goreau, et al. (1971). They regard corals as specialized carnivores without structural modifications for an autotrophic existence depending primarily upon zooplankton for their food. The work of Coles (1969) supports this view. He found that reef corals were able to ingest more than sufficient numbers of brine shrimp to cover their energy expenditure in respiration with energy left for storage and growth. Furthermore, Goreau, et al. (1971) considered that reef corals may act as unspecialized detritus feeders upon a wide range of organic matter or may even utilize dissolved or colloidal organic matter. Lewis and Price (1975) discussed suspension feeding strategies in Atlantic reef corals.

The general conclusions regarding the importance of zooplankton to support reef production indicate that while there is a substantial removal of plankton by benthic organisms, zooplankton biomass from oceanic water flowing over reefs is too low even to supply the daily energy requirements of the corals present. Additional food must be supplied by resident plankton and other external sources.

1.3 Bacteria

It has been pointed out by DiSalvo (1973) and Sorokin (1973c) that there are very few quantitative data on the role of microbial populations in the productivity of coral reefs. One cannot conceive of such complex systems without micro-organisms functioning as organic decomposers, nitrogen fixers and in biogeochemical processes. Large numbers of bacteria on reef surfaces were reported by Odum and Odum (1955) and bacteria have been implicated in the high respiration rates of coral communities noted by Sargent and Austin (1949). The work of DiSalvo (1973, 1974) has been concerned with the diversity and abundance of bacteria on coral reefs while Sorokin (1973a, b; 1974) has emphasized the role of bacteria in secondary production in reef organisms, i.e., in transforming detritus to microbial biomass.

DiSalvo (1973, 1974) suggested that the finely divided sediments in reef spaces and cavities functioned as "regenerative surfaces" and that the rapid rates of oxygen consumption occurring in these cavities indicated rapid organic decomposition. Plate count of sediments at the bases of coral heads showed densities of 10^7 to 10^8 bacteria/g dry matter and among them were forms capable of digesting chitin and other organic compounds, reducing nitrates and digesting gelatin and agar.

The bacteria in reef sediments and in internal cavities are considered to have a role in nutrient regeneration (DiSalvo, 1974). Pools of dissolved nitrogen and amino nitrogen were found in sediments and in dead coral heads. Quantitative estimates gave value of 33 g-atoms of phosphorus and 30 moles of amino nitrogen/m² dead coral surfaces. His results show that bacteria may thus be important in cycling of nutrients in the reef system.

Sorokin (1973a, b, c; 1974) has stressed that the biomass of bacteria in reef sediments and in shallow coastal water corresponds with their importance in processes of mineralization and nutrient cycling on reefs. They are also considered important as food for secondary consumers. Results of feeding experiments (Sorokin, 1973a) showed that six species of reef

corals could consume bacterioplankton. Other forms which were able to filter bacterioplankton from water were the tunicate *Ascidia nigra*, the sponge *Toxadocea violacea*, and the oyster *Crassostrea gigas*. Sorokin (1973a) regarded the bacterioplankton as being a high-quality food adequate in amount to supply a large percentage of the total energy needs of suspension feeders on the reef. A general scheme illustrating trophic relationships has been attempted by Sorokin (1973c). This study emphasized the importance of micro-organisms and the process of decomposition. It also suggested a shortage of phytoplankton as primary producers in the reef ecosystem and hence the minor importance of the phytoplankton/zooplankton trophic relationship.

1.4 Detritus

The quantitative significance of detritus as food for coral and other benthic organisms on the reef has not been evaluated. However, there is a good deal of evidence to indicate that suspended detritus is abundant in the water flowing over reefs.

Glynn (1973) found that dry biomass of suspended matter passing over a reef in Puerto Rico exceeded the dry biomass of net plankton by an order of magnitude or more. Evidence from examination of Millipore filters, plankton-pigment concentrations and productivity measurements indicated that the suspended matter was primarily detritus. The flux of suspended matter amounted to between 20 to 40g dry wt/m²/day and there was no evidence of depletion of detrital material within the water mass flowing over the reef. In fact, there are a number of studies which show an increase in detritus available to suspension feeders after water has crossed a reef (Lewis, 1977).

Atlantic reef corals have been shown by Lewis and Price (1975, 1976) to behave as suspension feeders. By means of nets and strands of mucus they are able to capture a wide range of particulate material and larger plankton with their tentacles. Thus, when the biomass of zooplankton is too low to support the nutritional needs of corals (Johannes, 1974; Porter, 1974), other sources of food may be available to them. While those species with long active tentacles obtain food by means of tentacle capture and by mucus filaments, species with short tentacles such as the *Agariciidae* appear to feed entirely by suspension feeding. Lewis (1976, 1977) has shown experimentally that some Atlantic reef corals are able to clear the surrounding water of particulate material in amounts just enough to supply their daily maintenance requirements.

Some interest has been shown in the potential nutrient significance of the mucus that is produced in copious amounts by most reef corals. Johannes (1967) observed mucus released by corals and the subsequent formation of aggregates of mucus and entrapped particles. Marshall (1972) found considerable quantities of zooxanthellae in mucus discharged from coral heads. Suspended mucus strings were examined by Coles and Strathmann (1973) and found to have significantly higher organic carbon and nitrogen contents than suspended particles in the surrounding water. Benson and Muscatine (1974) found that the mucus from a variety of corals contained wax esters and they also observed that reef fish fed on the coral mucus. This is apparently one route by which energy-rich products of coral metabolism are transferred to higher trophic levels.

This raises the possibility of a detritus-based food chain such as exists in mangrove swamps (Odum and Heald, 1975). Feeding strategies for particulate food sources other than zooplankton are different from strategies in which zooplankton is the main food source (Jorgensen, 1966). Filter feeding, a type of suspension feeding, is one way of capturing particulate matter and Crisp (1975) has commented on the fact that suspension feeders require less energy for feeding than do zooplankton feeders. The proportion of ciliary-mucoid

suspension feeders (including corals) and filter feeders on reefs has been estimated by Glynn (in Lewis, 1977). Glynn also found that the total biomass of the macrobiota at Panama was 441 g protein/m². Of this, 285.5 g consisted of corals and 14.6 g of other suspension feeders. If, as Crisp (1975) suggests, suspension feeders are intrinsically efficient converters of energy, then such a feeding strategy based on suspended detritus is particularly suitable for zooplankton-poor tropical waters. With this view in mind Lewis (1977) outlined trophic relationships within a coral reef community, incorporating detritus as a food source.

1.5 Dissolved Organics

As yet there is no conclusive proof that corals use dissolved organic matter as food. Stephens and Schinske (1961) and Stephen (1962, 1968) discussed the problems that must be overcome in determining the extent of net utilization of a particular dissolved organic substance. As stated by Muscatine (1973), experiments have yet to be conducted with appropriate concentrations. Release as well as uptake of the material has not been determined, so that net gain, if any, is unknown. Finally, there is no documentation that absorbed organic material participates in the metabolism of the host.

2.0 Alcyonaria

Alcyonarian corals have been considered carnivorous along with the rest of the coelenterates (Hyman, 1940). There is evidence that at least in some species, this statement is valid. Both Bayer (1956) and Grigg (1970) reported that *Leptogorgia virgulata* and *Muricea* spp., respectively, prey extensively on shelled bivalve larvae. Grigg found through hypochlorite digests of polyps that this item constituted 90 percent of the diet of both *M. californica* and *M. fruticosa* but concluded that only one percent of metabolic needs were met in this fashion. Experimental work showed that microzooplankton and particulate organic matter were also consumed and probably represented the bulk of the diet of these species.

On the other hand, Pratt (1906) described the morphological "reduction" of the digestive areas in the alcyonacean octocorals *Lobophytum*, *Sacrophyton*, *Alcyonium* and *Sclerophytum*, correlating this in each species with an increase in numbers of zooxanthellae. Pratt conjectured that the needs of growing colonies of *Sclerophytum* could not be satisfied by the small amount of zooplankton actually captured and that nutrition of these species was supported by zooxanthellae. Gohar (1940, 1948) added members of the family Xenidiidae to the species observed by Pratt as having a rich flora of zooxanthellae and also noted that xeniids lacked digestive zones of the mesenterial filaments. These animals were never observed to feed in the laboratory or in the field or to trap and paralyze zooplankters brought into contact with the surface of the animal. Since pulsating colonies ceased to move when placed in the dark but resumed movement when returned to the light, Gohar conjectured that "combustible energy-giving material" is normally supplied by zooxanthellae, rather than zooplankton. Wainwright (1967) reported the gorgonia expanded during the day when plankton was scarce but remained contracted at night showing little feeding activity when zooplankton was most abundant. This was considered to be an adaptation favoring photosynthesis by zooxanthellae during the day, implying a nutritional role for the algae. Similar to the case with scleractinian corals, Kinzie (1970, 1973) has shown that 73 percent of symbiotic gorgonians died after being placed in a light-tight aquarium with running seawater for 83 days. A non-symbiotic species (*Diodogorgia*) was alive and apparently healthy throughout the experiment. Bayer (1954) found evidence that the gorgonians *Plexaura flexuosa* and *Psammogorgia antipathes*, which have especially

abundant zooxanthellae, have lost most, if not all of their nematocysts. In addition, they seem to show a reduction of gastrodermal gland cells, as in the case of the tropical alcyonaceans.

The data here are no less equivocal than in the stony corals. The arguments concerning the daylight expansion of the polyps in so-called "hermatypic gorgonians" (Wainwright, 1967) is countered by Theodor (1977) who found that members of the genus *Pseudopterogorgia* tend to be expanded at night and contracted during the day. The arguments for lack of feeding are often made with the assumption that only animal food is taken. However, Wilson (1884) and Roushdy and Hansen (1961) have both found evidence that octocorals are capable of feeding on phytoplankton. Diatom or detritus capture does not require nematocysts. This correlates well with electron-microscopic observations by Mariscal and Bigger (1977) who found that even asymbiotic octocorals have few nematocysts and no gastrodermal microvilli. In any case, no direct experimental approach has been employed in attempting to define the nutritional requirements in symbiotic *Octocorallia*.

3.0 Antipatharia

Inspection of the tentacular apparatus of *Cirripathes* or any other antipatharian in the study area will reveal large numbers of nematocyst batteries. Thus it is not surprising that Grigg (1965) was able to experimentally feed polyps of *Antipathes grandis* from Hawaii with various zooplankters.

However, Dantan (1921) reported that polyps of a *Leiopathes* contained large numbers of diatoms, often broken and apparently in a state of digestion, along with algal fragments. Although the data do not warrant antipatharians being considered herbivores, omnivorism cannot be ruled out, particularly in view of the recent studies by Lewis (1978) who notes that antipatharians are capable of feeding on fine suspended particulates by means of mucous strands and nets.

PREDATORS AND ASSOCIATIONS OF CORALS

1.0 Scleractinian Predators and Their Effects

1.1 Fishes

Studies by Robertson (1970), Salvini-Plawen (1972) and Patton (1973), have shown that the number of animals specialized to feed on the Scleractinia has been underestimated (Wells, 1957; Yonge, 1963). Some of the observed effects also go far beyond the negligible damage claimed by Yonge (1968). Since many of the known coral predators have been described only relatively recently, it is likely that continued study will add to our knowledge of this feeding habit. The following review will no doubt soon be supplemented by new discoveries.

In Randall's (1967) survey of the food habits of reef fishes small volumes of coral were found in the alimentary tracts of four species: *Scarus coelestinus* Cuvier and Valenciennes and *Sparisoma aurofrenatum* (Cuvier and Valenciennes) (Scaridae), *Chaetodipterus faber* (Broussonet) (Ephippidae), and *Microspathodon chrysurus* (Cuvier and Valenciennes) (Pomacentridae). The only specific coral identified was that of *Oculina diffusa*, a fragment consumed by *C. faber*. In some localities coral consumption by fishes appears greater than indicated by Randall's (1967) study. For example, in Panama (Bakus, 1969) and Bermuda (Gygi, 1969), the rasping of live corals by scarids is commonplace. *Scarus guacamaia* Cuvier rasps *Siderastrea siderea* with fair regularity along much of the north coast of Panama. The summits of large hemispherical colonies are commonly scraped to depths of 2-3 mm; such feeding is often performed by relatively small schools of *S. guacamaia* (five to 15 individuals) which appear to range over extensive areas. *Microspathodon chrysurus* though predominantly

herbivorous on epontic diatoms and filamentous algae, frequently feeds on *S. siderea* as well. Juveniles and adults of this fish bite the surface of the corallum vigorously, removing primarily the extended polyps. Corals preyed upon in this manner can be distinguished by the characteristic circular lesions left behind (Glynn, 1973). Juveniles and adults of *Microspathodon* commonly feed on the hydrocoral *Millepora* in Florida (Ciardelli, 1967), adults nest on it, and both juveniles and adults attack *Millepora complanata* in Panama. Other corals observed in Panama with deep rasping marks, similar to those produced by *S. guacamaia*, are *Montastraea annularis*, *Acropora palmata*, *A. cervicornis*, *Agaricia agaricites*, and *Porites furcata*. Mixed schools of *Scarus croicensis*, *Acanthurus chirurgus* (Bloch), *Chaetodon capistratus* Linnaeus, and other species occasionally feed on *A. cervicornis*. Such incidental feeding forays can lead to coral rasping by the scarid and selective removal of polyps by the latter two species (Glynn, 1973). On one occasion a scarid, possibly *Scarus vetula* Bloch and Schneider, was observed to bite off a terminal 2-cm tip of *Porites porites*. On same areas of the reef, *Porites* colonies commonly have many of their terminal branches broken off. This feeding habit was reported long ago in Haiti by Beebe (1928), who observed that scarids (most likely *S. guacamaia*) break off and ingest the terminal branches of corals. The effects of fish predators on *Porites astreoides* have not been reported in the Caribbean, but according to Gygi (1969) *Sparisoma viride* (Bonnaterre) commonly feeds on this coral at Bermuda, removing up to 200 mg with each bite. In addition to direct browsing, Glynn (1974) believes that indirect activity causes detachment of several coral species, notably *Siderastrea radians* and *Favia fragum*. This may be the cause of rounded, mobile coralliths often seen in lagoonal patch reef specimens.

As Yonge (1963) suggested, nematocysts must certainly deter some fishes from feeding on corals. That *Microspathodon* regularly consumes large amounts of the hydrocoral *Millepora*, however, indicates that certain fish species can cope with this potent means of defense. Possibly another effective deterrent that would tend to discourage fish predators is the presence of sharply projecting septa, often with serrated edges, on the corallites of *Mussa*, *Scolymia*, *Isophyllastrea*, *Mycetophyllia* and *Isophyllia*. It may therefore be significant that the coral species most often consumed by large fishes have relatively smooth and unobtrusive surfaces. Reese (1977) has studied the relationship between feeding behavior, substrate type, and coral morphology in the Chaetodontidae fishes of three Pacific areas.

1.2 Invertebrates

Six invertebrate coral predators have been discovered in the Caribbean region since 1962. These include the amphinomid polychaete *Hermodice carunculata* (Pallas), the majid decapod *Mithrax* (*Mithraculus*) *sculptus* (Lamarck), the gastropod mollusks *Coralliophila abbreviata* Lamarck, *C. caribea*

Abbott, and *Calliostoma javanicum* Lamarck, and the echinoid *Diadema antillarum* Philippi. *Hermodice* was first described by Marsden (1962, 1963) to be a habitual predator of *Porites porites* and *P. asteroides*. Subsequent work by Ott and Lewis (1972) and Shinn (1976) showed that several other coral species are preyed upon (although *Hermodice* was found most often on the colonial anemone *Palythoa*). Ebbs (1966) noted that coral browsing may occur in all Atlantic members of the Amphinomidae. Both *P. furcata* and *P. porites* are attacked by *Mithrax*, which severs the polyps with its chelae. This feeding habit, first observed in Puerto Rico (Glynn, 1962), was also seen in Panama, where *Mithrax* commonly preyed upon ramose species of *Porites* (Glynn, 1973). Ward (1965) believed that the mode of feeding of *Coralliophila abbreviata*, involving the dissolution and ingestion of soft tissues, can lead to the death of polyps and eventual destruction of the colony of *Montastraea annularis* (small star

coral). On the other hand, Robertson (1970) maintains that this species is a well-adapted parasite, causing little damage to polyps. This conclusion is challenged by Ott and Lewis (1972) who documented some damage by *C. abbreviate* to several different corals, especially *M. annularis*. Miller in Glynn (1973) found *Coralliophila abbreviate* and *C. caribea* associated with 14 hermatypes at Discovery Bay, Jamaica, and suggested that the gastropods may feed on plankton ingested by the corals. *Calliostoma javanicum* feeds on *Mussa angulosa* in the laboratory and on *Agaricia spp.* (lettuce coral) in the laboratory and field (Lang, 1970), with a preference for the latter group. Small circular lesions are produced, but it is not yet known which of the soft parts of the coral are ' consumed. *Diadema antillarum* preys on coral at night (Bak and van Eys, 1975) at the same time that it preys on *Thalassia* producing the well known halo effect around patch reefs. Like the scarids (parrot fish), *Diadema* inflict substantial mechanical damage to the corallum, but their impact is greater due to their slow movement and continual feeding pattern.

From the foregoing, it is obvious that several reef animals are adapted to feed on the Scleractinia. Though the actual quantities of coral consumed appear to be slight, there is good evidence that the damaged areas of the corallum that do not undergo regeneration are invaded by other organisms which may overgrow and eventually smother the entire colony. Continuing observations of the rasped surfaces of *Siderastrea siderea* have shown that, while repair normally takes place rapidly (two to three months), some areas suffer irreparable damage. The latter are often invaded initially by a variety of filamentous algae, including members of the Cyanophyceae, Chlorophyceae, Rhodophyceae, and Phaeophyceae, and epontic diatom growths. Large colonies of *Montastraea annularis* with their surfaces in various stages of invasion provide a concrete example of the course of destruction. Scarid nicks often contain mixed growths of filamentous algae and these can be traced through a successional continuum to surfaces highly eroded by boring clionid sponges (Glynn, 1973). Another type of algal invasion is induced by continuous attack on *Acropora cervicornis* (staghorn coral) and *Montastraea annularis* (small star coral) by the threespot damselfish, *Eupomacentrus planifrons*. As described by Kaufman (1977), the fish's continual attack on living and dead corals prevents regeneration of coral tissue and allows "algal lawns" to become established. Feddern (1979, personal communication) claims these "lawns" are cultivated year-round. These "lawns" in turn serve as a food source and egg cultivation space for the fish. Ott and Lewis (1972) find that the blue-green alga *Lyngbia sp.* invades regions of coralla which have been injured due to predation by the polychaete *Hermodice* (see Antonius, 1975). There is no evidence that the algae can expand past the site of injury; however, Antonius (1973, 1976) has described a blue-green alga, *Oscillatoria submembranacea*, which appears to be capable of rapid coenenchymal lysis, and spreading once a foothold on a corallum is gained.

2.0 Other Scleractinian Associations

There is a good deal of evidence from the field indicating that competition for living space is acute among the long-lived benthic populations of coral reefs. It appears that many groups of reef organisms have evolved body morphologies that tend to maximize the area of exposure to light and currents. Certain minimum levels of exposure are necessary for both photosynthetic and suspension feeding forms. Therefore, it is not surprising to find that a variety of strategies are employed to ensure the acquisition of space and access to the surrounding medium, and a subsequent hold on this resource once obtained.

2.1 Competition Among Scleractinian Species

To the rapid and spreading mode of growth employed by many corals as a means of reducing competition for space and light, must now be added the newly discovered adaptation of extra-coelenteric feeding (Lang, 1973). She has found that certain species will extend their mesenterial filaments and digest any living coral tissue from a colony of another species which they can touch, up to about 2 cm away. The species can be arranged in an aggressive hierarchy, each species attacking all others below it in the hierarchy and being attacked by all ranked higher. In general, the massive species of the families Mussidae, Meandrinidae, and Faviidae rank higher than those of other families. This agrees with Connell's (1973) findings that slow-growing massive colonies are not overgrown by the faster growing branching ones, and that in some instances, foliaceous species may inhibit massive ones.

While such competitive interactions can be observed among adult corals, they probably also play an important role among young growing forms. An active feeder, for example, would preclude the establishment of subordinate species within its feeding radius. Competitive exclusion by means of predatory interactions occurs most noticeably in the densely populated zones. *Montastraea annularis*, one of the principal reef-building species, is moderately active in extracoelenteric feeding and perhaps owes its presence in the buttress zone and along the seaward slope in part to its ability to compete successfully with more rapidly growing ramose and foliaceous forms (Glynn, 1973).

2.2 Boring Organisms

The importance of boring organisms in corals has been noted in reviews by Otter (1937), Yonge (1963), Goreau and Hartman (1963) and Lewis (1977). A wide variety of organisms including sponges, sipunculid and polychaete worms, molluscs, crustacea and algae are able to bore into corals, by either mechanical or chemical means (or both). Sponges are perhaps the most widespread borers on coral reefs. Rutzler (1971) has found that members of the adociid genus *Siphonodictyon* can excavate both into the living and nonliving portions of colonies of several coral genera. Pre-existing damage to the coral is apparently not a prerequisite for attack. Glynn (1973) noted that when a section of *Cliona sp.* was transplanted from an infected *Siderastrea* to the algal-covered scars of uninfected colonies, the sponge was able to expand over undamaged coral surfaces. The implanted sponge began to grow immediately and expanded 2 cm peripherally in a nine-month period, killing the underlying coral tissue. Neumann (1966) estimated that the sponge *Cliona lampa* can excavate carbonate at the rate of 1 to 1.4 cm yr⁻¹, Hein and Risk (1975) and MacGreachy (1975) estimate that three to 70 percent of the whole corallum may be reworked by clionids, while Hudson (1977) anticipates that a one-meter high coral head could be completely converted to sediment in 150 years or less based on scleroband measurements.

Rates of erosion of reef surfaces are difficult to estimate but Goreau and Hartman (1963) considered the activity of clionid sponges to be a widespread and significant force in the maintenance and formation of Jamaican deep reef communities. In shallow water, weakening of the bases of coral colonies by sponge excavation is perhaps counterbalanced by rapid calcification rates; in deeper water (>30 m or 100 ft), however, calcification is slow, corals become flattened and attached on an edge, the topography is steep, and there is a paucity of frame-cementing biota. All of these factors tend to magnify the effect of boring sponges in this environment.

2.3 Interactions between Corals and Other Sessile Organisms

Careful observation of benthic reef populations reveals frequent instances of unrelated organisms approaching each other in growth and then one overgrowing and excluding its neighbor. While certain corals can coexist for long periods in close contact with alien species, for example, the beneficial association of *Montastraea annularis* with the sponge *Mycale laevis* (Carter) reported by Goreau and Hartman (1966), it appears that there is a tendency for some of the larger algae, sponges, octocorals, and zoanthideans to displace coral growth. This seems to take place in the absence of any detectable pre-existing damage to the coral as noted earlier for destruction initiated through the activities of predators. Some examples follow.

Among algae, *Halimeda opuntia* (Linnaeus) Lamouroux, *Caulerpa racemosa* var. *macrophyssa* (Kützting) Taylor, and *Peyssonnelia rubra* (Irgebille) J. Agardh are commonly found covering large areas of *Porites furcata*. The brown alga *Lobophora variegata* (Lamouroux) Womersley often proliferates over extensive populations. *Chondrilla nucula*, an encrusting sponge and the colonial anemone *Palythoa* sp. can overgrow large tracts of *Porites furcata* and entire colonies of *Siderastrea radians* and *Diploria clivosa*. *Porites* is usually invaded from below, by way of the dead branches; massive corals are invaded from their periphery (Glynn, 1973). The scleraxonians *Briareum asbestinum* (Kinzie, 1970) and *Erythropodium caribaeorum* (Antonius, 1977) may function in the same manner, as may certain didemnid ascidians (Antonius, 1977).

3.0 Gorgonian Predators and Associates

The gorgonian octocorals are an important component of the reef and bank community in the study area. Their prominence has enabled them to provide shelter and food for a wide array of casual associates, epizoa and commensals and other symbionts, ranging from other coelenterates to fishes (Bayer, 1961; Salvini-Plawen, 1972). The associates of western Atlantic shallow-water gorgonians, particularly predators and parasites, are described below. The snail *Neosimnia uniplicata* and the shrimp *Neopontonoides beaufortensis* both feed on surface debris and material shed by the gorgonian *Leptogorgia virgulata* off North Carolina. The gastropod appears to incorporate spicular pigments into its own shell, thus acquiring concealing coloration. The nudibranch *Tritonia wellsi* probably feeds directly on *Leptogorgia* tissue (Patton, 1972). Cyclopoid copepods of the family Lamippidae are known to parasitize various octocorals (Zulueta, 1911) and have also been found in the polyps of *Leptogorgia* (Patton, 1972). Several species of *Cyphoma*, an ovulid gastropod, are conspicuous associates of *Pseudopterogorgia*, *Plexaura*, *Plexaurella* and related genera (Bayer, 1961). Kinzie (1970, 1974) has shown that *Cyphoma* is a predator which strips the coenenchyme, laying bare the axial skeleton. He has also described "herding" behavior, whereby *Cyphoma* in groups of up to 24 individuals were capable of completely denuding several gorgonian colonies in a five-week period. Kinzie estimates that damage by *Cyphoma* may be less than the gorgonians' capacity for regeneration. Ott and Lewis (1972) and Birkland (1974) have also noted that the amphinomid worm *Hermodice carunculata* consumes gorgonians in addition to other corals. Morse, et al. (1977) describe algal tumors infesting *Gorgonia ventalina* in the Netherlands Antilles. Bagby (1978) reports considerable numbers of tumors from species of *Pseudoplexaura*, *Pseudopterogorgia*, *Plexaurella*, *Plexaura* and *Muriceopsis* from patch reefs off Key Largo, Florida. Randall (1967) found that the scrawled filefish *Alutera scripta* was the most prominent piscine gorgonian predator among 212 species examined. Ten other fish species had small amounts of gorgonian material in their stomachs but Randall concluded that gorgonians, in spite of their prominence, do not form a significant part of the diets of West Indian reef fishes.

The direct effect of predators and parasites is difficult to assess. However, mechanical damage to the coenenchyme by several sources appears to disrupt the antibiotic properties of the tissue (Burkholder, 1973), allowing the establishment of a variety of invading organisms, particularly *Millepora alcicornis*. Once established, *Millepora* spreads, killing the gorgonia before it. Kinzie (1970) estimated the spreading rate at $244 \text{ cm}^2 \text{ yr}^{-1}$ on a colony of *Gorgonia ventalina* and 1.4 to 0.7 cm yr^{-1} on two tips of a *Plexaurella species*. He also noted that an unidentified keratosid sponge was capable of similar action on deep reef gorgonians in Jamaica. Whether any of these biological interactions is significant compared to periodic storm damage (Cary, 1914) or toppling due to the weakening of the substratum by boring organisms (Kinzie, 1970, 1974), remains to be determined.

4.0 Antipatharian Predators and Associates

Little is known of relationships between black corals and other organisms. Salvini-Plawen (1972) notes a nurse shark, *Nebrius concolor*, feeding on an unnamed antipatharian. Cyclopoid copepods of the family Vahiniidae appear to parasitize the polyps of antipatharians (Humes, 1967). A coralliophilid gastropod, *Rhizochilus antipathicus*, feeds on *Antipathes ericoidea* (Salvini-Plawen, 1972). Other symbionts involving various species and the antipatharian whip *Cirrhopathes* have been described (Davis and Cohen, 1968; Humes, 1973). None of these involve western Atlantic species, although further work on this neglected group will undoubtedly reveal a number of associations in this region. This expectation is heightened by the apparent absence of antibiotic activity in the tissues of a species of *Antipathes sp.* tested by Burkholder (1973).