

REEF CORALS: AUTOTROPHS OR HETEROTROPHS?

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Some recent studies² seem to indicate that the nutritional economy of reef corals is for all practical purposes to be considered autotrophic due to their zooxanthellae (Fig. 1). For example, Franzisket (1969a, 1970) claims to have demonstrated that some Hawaiian reef corals can achieve net growth in the total absence of particulate food, while Johannes and Coles (1969) state that the energy requirements of Bermudian reef corals are in some cases more than an order of magnitude greater than could be provided by the zooplankton which the investigators were able to catch with a fine net.

In spite of their supposedly autotrophic economy, the reef corals have not developed any of the behavioral and structural specializations for such a way of life. In this respect they differ fundamentally from *Xenia hicksoni* and *Clavularia hamra* (Octocorallia, Alcyonacea) (Gohar, 1940, 1948) and *Zoanthus sociatus* (Hexacorallia, Zoanthidea) (Von Holt and Von Holt, 1968a, b), unrelated anthozoans which have independently evolved a more or less complete nutritional dependence upon their contained zooxanthellae. Available data is summarized in Table I. These species have never been observed to feed, and there is a more or less marked reduction of structures and functions associated with the usual predatory feeding habits in Cnidaria; for example, they do not respond to any of the known tactile and chemical stimuli that trigger feeding behavior in related carnivorous species; they do not ingest particulate matter, and are unable to either digest or assimilate food artificially placed into their coelenteron by means of a canula (Goreau and Goreau, unpublished).

The reef corals are, by contrast, superbly efficient and voracious carnivores that will accept practically any kind of particulate animal food (Yonge, 1930a, 1930b; Yonge and Nicholls 1930, 1931). Feeding occurs in several different ways, depending on the species: in the majority, the food is swept into the coelenteron by means of ciliary currents, (sometimes involving reversal as in *Fungia*), while in some corals the tentacles convey the food directly to the mouth (Yonge, 1930a). Most species are also capable of extracoelenteric digestion of food matter outside the body by means of mesenterial filaments extruded through temporary openings (Fig. 2) at any place on the colony surface (Duerden, 1902; Matthai, 1918; Goreau, 1956). Reef corals obtain food via this ancillary route and also use the extruded filaments as weapons, primarily against other corals the tissues of which they may digest (Lang, 1969, 1970).

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² See also the paper by V. B. Pearse and L. Muscatine (dedicated to the late T. F. Goreau) on pages 350-363, and that by P. V. Fankboner on pages 222-234 of this issue—*Editor*.

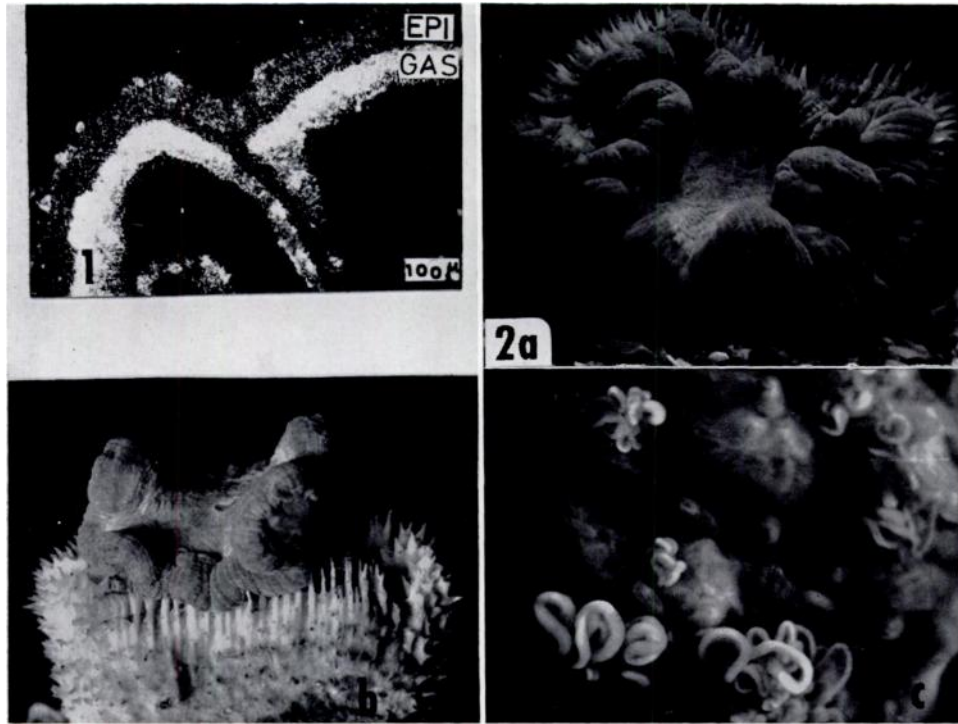


FIGURE 1. Autoradiogram of carbon¹⁴ labelled *Fungia scutaria*. The coral was exposed to ¹⁴CO₂ in sunlight for ten minutes and washed in running sea water for thirty minutes before fixation. The area seen under dark field illumination and focused on the plane of emulsion shows the concentration of silver grains over the carbon¹⁴ labelled zooxanthellae of the gastrodermis. The scale represents 100 μ. Specimens exposed in the dark showed no fixation of the isotope.

FIGURE 2. *Mussa angulosa* under severe starvation gradually loses contact with the skeleton (a) (b), eventually sinking to the bottom of the aquarium, still alive. When offered crab juice this free specimen extruded its mesenterial filaments (c) through the epithelium of the calicoblast. Some colonies lose their zooxanthellae, some keep them, but in the most severe cases of starvation only the stomodeum and a few filaments remain. Later only bits of mesenterial filaments curl about. However they all showed feeding responses when crab meat or amino acids were added. These filaments persist for a few days.

These diverse feeding mechanisms are supplemented by an exquisitely perceptive chemotactic sense. In several species of Jamaican reef corals (*Manicina areolata*, *Cladocora arbuscula*, *Eusmilia fastigiata*, *Isophyllia sinuosa*, *Mussa angulosa* and *Scolymia lacera*) we found some years ago that very low concentrations of amino acids such as glycine, alanine, phenylalanine and lucine could trigger off typical feeding responses; *i.e.*, opening and eversion of the stomodeum, swelling of the coenosarc, extension of tentacles and sometimes extrusion of mesenterial filaments. *M. areolata* responded in this manner to alanine and glycine at concentrations as low as 10⁻⁹ M, whereas glucose, sucrose, glycerol and mannitol did not have any effect at high concentrations. Mariscal and Lenhoff (1968) ob-

TABLE I
*Available data on nutritional adaptation and absorption in
 Scleractinia, Alcyonacea and Zoanthidea*

Taxonomy	Zooxanthellae	Absorption of crab juice and india ink into filaments	Uptake of ^3H leucine into the epidermis	Uptake of ^{14}C by zooxanthellae	Feeding response to crab meat or amino acids	Nematocysts
Scleractinia:						
Hermatypes:						
<i>Fungia</i>	+	+++	+++	++	+++	+++
<i>Stylophora</i>	+	+++	+++	++	+++	+++
Ahermatype:						
<i>Tubastrea</i>	0	+++	+++	0	+++	+++
Alcyonacea:						
<i>Xenia</i>	+	0	?	+++	0	0
Zoanthidea:						
<i>Z. sociatus</i>	+	?	?	+++	?	disordered
<i>P. caribbae</i>	+	+++	?	+	+++	++
<i>P. grandis</i>	+	+++	?	+	+++	++

Other morphological correlates with xanthellar symbiosis are:

- (1) *Xenia*: no nematocysts, reduced filaments, no septal lobes,
- (2) *Zoanthus*: nematocysts, but these are in a disordered position and in places where they do no good; filaments reduced but lobes are very large. All stages of pycnosis, degeneration, fragmentation and extrusion of zooxanthellae were observed in the mesenterial lobes.

Feeding reaction:

- (1) *Corals*: Dilatation and extension of stomodeum, imbibition of water, sometimes erection of tentacles or shooting of the mesenteries through mouth or body wall;
- (2) *Xeniids*: Rhythmic movement of tentacles of anthocodia;
- (3) *Zoanthids*: *Zoanthus sociatus*: none,
Palythoa caribbae: Dilatation of mouth, strongly inward movement of water at ciliate groove, curling over of the tentacular rim,
Palythoa grandis: same as *P. caribbae*.

served that concentrations as low as 10^{-7} M proline resulted in feeding responses in *Cyphastrea ocellina*, *Pocillopora damicornis* and *Fungia scutaria*.

Responses similar to those caused by amino acids are produced in corals by seawater in which there had previously been zooplankton. We have often observed that corals will expand under natural conditions in apparent anticipation of plankton; evidently this is due to their ability to sense the diffuse cloud of metabolites, including amino acids, that usually surrounds plankton swarms (Hellebust, 1965). It would indeed be surprising if, as Johannes and Coles (1969) have speculated, the corals have retained these capabilities merely to obtain trace nutrients such as phosphorus from their prey while the bulk of their nutrition comes from the zooxanthellae! Yet, there is no need for such a roundabout way to obtain phosphorus since reef corals, but *not* ahermatypes, in the light are known to take up inorganic phosphate from the medium, this being a function of the zooxanthellae, not the coral host (Yonge and Nicholls, 1931). The fully autotrophic xeniid alcyonaceans and *Zoanthus* are evidently able to obtain all their trace nutrients directly from the seawater. As regards the possible need for organic phosphorus, Von Holt (1968) has shown that in *Zoanthus* there is a transfer of nucleoside polyphosphate from algal symbiont to animal host. If the reef corals were truly

as autotrophic as Franzisket and Johannes believe, the question arises why have they not evolved similar more direct mechanisms for obtaining critical nutrients directly from their symbionts?

OBSERVATIONS

The boundary layer water and its relation to the trophic structure of the reef

The evidence so far cited has not resolved the conflict between the apparent low productivity of tropical ocean surface waters (Fleming, 1954; Sargent and Austin, 1949, 1954) and the need for organic nutrients by the benthonic fauna in the reef ecosystem. This consists of the corals and a diverse assemblage of filter, detritus, suspension and deposit feeders as well as predacious carnivores, the majority without zooxanthellae which might serve as ancillary food source. Recent reviews by Bakus (1969) and Stoddart (1969) have demonstrated how little quantitative information is available on the trophic cycles within the reef biotope, largely because the pathways themselves are still largely unknown. Oceanic reef ecosystems appear on the whole to be autotrophic units operating at very high levels of productivity, turnover rate and efficiency (Odum and Odum, 1955; Kohn and Helfrich, 1957) whereas at least some smaller reefs off high islands may be non-autotrophic (Goreau, Torres, Mas and Ramos, 1960; Gordon and Kelley, 1962). In view of the low trophic potential of the tropical oceanic waters, high localized productivity of reefs can only be achieved through coupled internal recycling systems that reduce external losses of free energy to a minimum and thus maintain the local nutrient levels at high steady state values.

The existence of such internal cycles is reflected in the marked differences that may be observed between the outside ocean water and the water circulating within the reef which will be referred to here as the boundary layer water. Whereas the former is clear and deficient in plankton and other suspended matter, the latter is relatively turbid due to the much higher concentrations of suspended particulates, consisting of both inorganic and organic detritus stirred up by the turbulence, or added to the water by benthonic biota. Near high islands, both particulate and dissolved nutrients in the sea are increased by run-off from the land. The boundary layer water also contains a relatively high concentration of zooplankters, swarms of which shelter and feed within the multitude of crevices and other microhabitats of the reef frame. This environment is extremely difficult to sample quantitatively, but can be readily observed by anyone diving on the reef.

The depauperate and heavily cropped condition of the shallow reef zones described by Bakus (1967, 1969) for some Pacific reefs, and by Johannes and Coles (1969) for Bermuda have been corroborated by the first author's own observations on parts of the Great Barrier Reef, Eniwetok, Saipan and the Red Sea, and is also observed in the shallow reefs of Jamaica and other Caribbean islands. However, conditions in the deeper parts of the outer reef slope vary considerably from extreme impoverishment as for example in Saipan or Eniwetok to a marked increase in species diversity, size and biomass of the macrobenthos, such as is observed in Jamaica (Goreau and Hartman, 1963; Goreau and Wells, 1967). Here the fore reef slope habitat is characterized by very large and diverse standing crops of corals, sponges, Gorgonacea, anemones, Antipatharia, and various algae such

as *Halimeda* (Goreau and Graham, 1967); the interstices of the reef frame contain an abundant fauna of Foraminifera, sponges (Hartman and Goreau, 1970), hydrozoans, ahermatypic corals, worms, bivalves, brachiopods (Jackson, Goreau and Hartman, 1970), bryozoans, echinoderms, tunicates and arthropods. Only the hermatypic corals, with the great majority of other coelenterates, contain zooxanthellae, the remainder do not. Above sixty meters the corals predominate, below this the sponges prevail although reef corals occur in diminishing amounts to at least one hundred meters.

The boundary layer water is in continuous and dynamic exchange with the reef biota. We established this by releasing small clouds of India ink from syringes in various microhabitats of the Jamaican fore reef slope at depths of 50 to 60 meters where wave turbulence is low. We found that the India ink was cleared from the water within a few minutes, mostly by the sponges. It appears that a continuous downward flow of particulate matter moves from the boundary layer through the reef, recycling nutrients within the benthos. Quantitative measurements of this exchange have now been carried out *in situ* by H. M. Reiswig (Biology Department, Yale University) in Discovery Bay, Jamaica.

Suspended particulate matter in the reef as a possible food source for corals

The particulate suspended organic matter, organic aggregates and dissolved organic substances circulating in the boundary water of the reef may be of crucial importance to the nutrition of the benthonic fauna, corals included. Marshall (1965) showed that the amount of fine suspended organic detrital matter in the waters of Eniwetok Atoll was between one and two orders of magnitude greater than could be collected with the finest plankton nets. In Jamaica, the macroscopic organic particulates consist chiefly of comminuted vegetable matter, fragmented animal remains of diverse origin, faecal pellets, *etc.*, but we have not yet investigated the much larger microscopic and submicroscopic fractions. Coral-browsing acanthurid and scarid fish contribute large volumes of ground-up carbonates to the suspended matter (Bardach, 1961). During periods of rough weather wave turbulence stirs up fine organic detritus, the leptopel, from the bottom sediment, and clouds of this material roll down over the reef communities of the seaward slope into deep water. At the same time, colloidal and dissolved organic matter are aggregated into larger particles at the surface of bubbles stirred up by the surf (Baylor and Sutcliffe, 1963; Riley, 1963). Mucus is secreted into the water in large amounts by benthonic animals in the reef, chiefly sponges, gorgonians, corals and molluscs (Marshall, 1965). Corals and alcyonarians continuously void large numbers of excess zooxanthellae in strings of mucus (Yonge and Nicholls, 1931). The gonadal products of sponges and echinoids periodically reach such high concentrations as seriously to reduce underwater visibility in the vicinity of the reef.

The question of whether any of these diverse organic particulates are available as food to the corals is still undecided. Part of the difficulty in relating reef corals to their potential food supply is a conceptual one. As the result of Yonge's studies (1940), the corals have been thought of principally as specialized planktivorous carnivores. However, we have numerous observations which seem to indicate that many of the reef corals are not restricted in their feeding to zooplankton since they also seem to feed on any organic particulates that happen to be carried into the

coelenteron and from which nutriment may be extracted. In our experience, many reef corals are relatively unspecialized detritus feeders (Fig. 3), capable of utilizing a wide range of organic matter and bacteria (R. A. Kinzie III, Department of Zoology, University of Georgia, personal communication). An example of this is the common Indo-Pacific reef coral *Fungia scutaria* (Goreau, Goreau, Yonge and Neumann, 1970) although it is not yet known what part of its total energy requirements are met from exogenous particulates other than zooplankton.

The uptake of dissolved organic matter by corals

We have not so far considered the possibility of direct utilization of dissolved or colloidal organic matter by scleractinian corals. No attempt will be made here to answer the question of whether there is enough dissolved organic matter of the right kind circulating within the reef to be a significant source of energy for corals; rather we wish to point out that the corals have highly developed structural and functional adaptations for the absorption of dissolved organic matter directly from the sea, and that they can take up compounds such as amino acids



FIGURE 3. *Mcandrina meandrites* f. *danae* behaving as a detritus feeder is seen here sweeping the mud bottom with huge loops of mesenterial filaments extruded through the column wall after crab extract has been added to the media. These corals also showed feeding reactions when offered alanine and glycine.

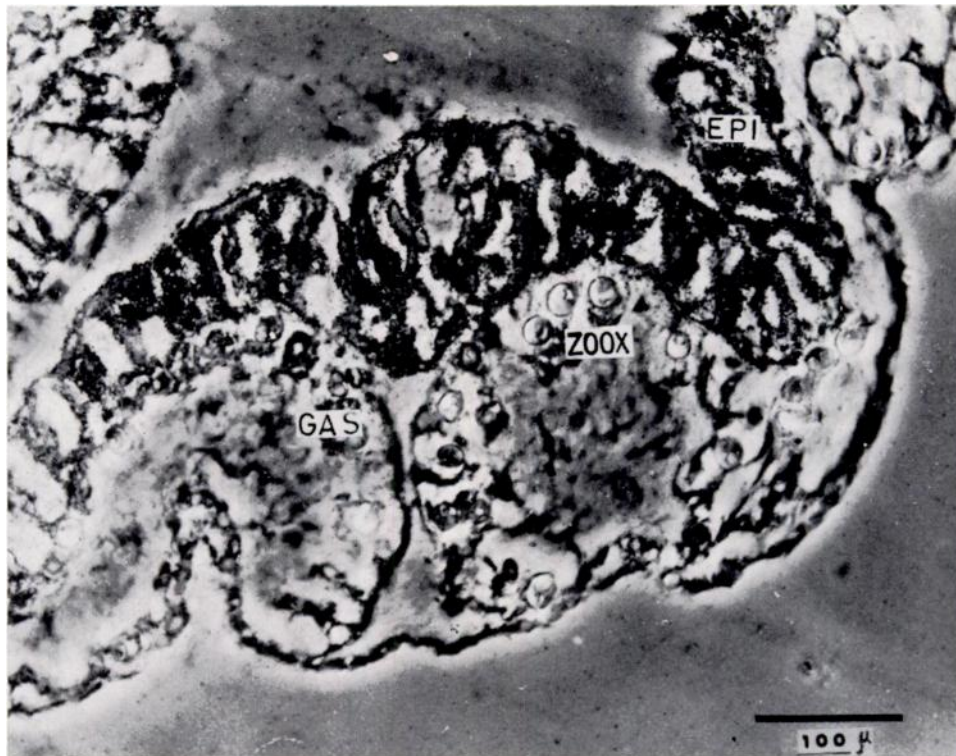


FIGURE 4. Autoradiogram of *Fungia scutaria* exposed to ^3H leucine in sunlight for 1 hour, then washed in running sea water. The radioactivity is restricted to the epidermal cells as shown by the distribution of the dark silver grains in the overlying emulsion. Activity first appeared in the tall epidermal cells, then spread over the cellular tissue except for the zooxanthellae, mesoglea and mucus glands. Compare this with figures 6 and 7 for alkaline phosphatase and P.A.S. The dark control shows the same pattern of activity; phase contrast.

from extremely dilute solution. There is also some preliminary evidence that certain Gorgonacea and Zoanthidea have similar abilities.

In the stony corals, the absorption of dissolved organic matter takes place mainly in the epidermis of the column wall, tentacles, oral disc and stomodaeum, *i.e.*, the entire surface in direct contact with the external medium. Autoradiography of the reef corals exposed to very low concentrations of tritiated DL leucine in sea water for one hour and fixed at varying times after labelling show that the activity is initially fixed in the tall columnar cells of the epidermis, whereas much less is present in the gastrodermis, very little in the mesogloea and none in the zooxanthellae (Fig. 4). Twenty-four hours after labelling the activity is more uniformly spread throughout the cellular tissues, except for the zooxanthellae. Epidermal uptake of amino acids by corals is independent of light intensity and absorption occurs even when the leucine concentration is below the threshold of chemotactic response of the test species, *Fungia scutaria*, about $3:10^{-9}$ M. Absorption of glucose has since been observed by Stephens (1962).

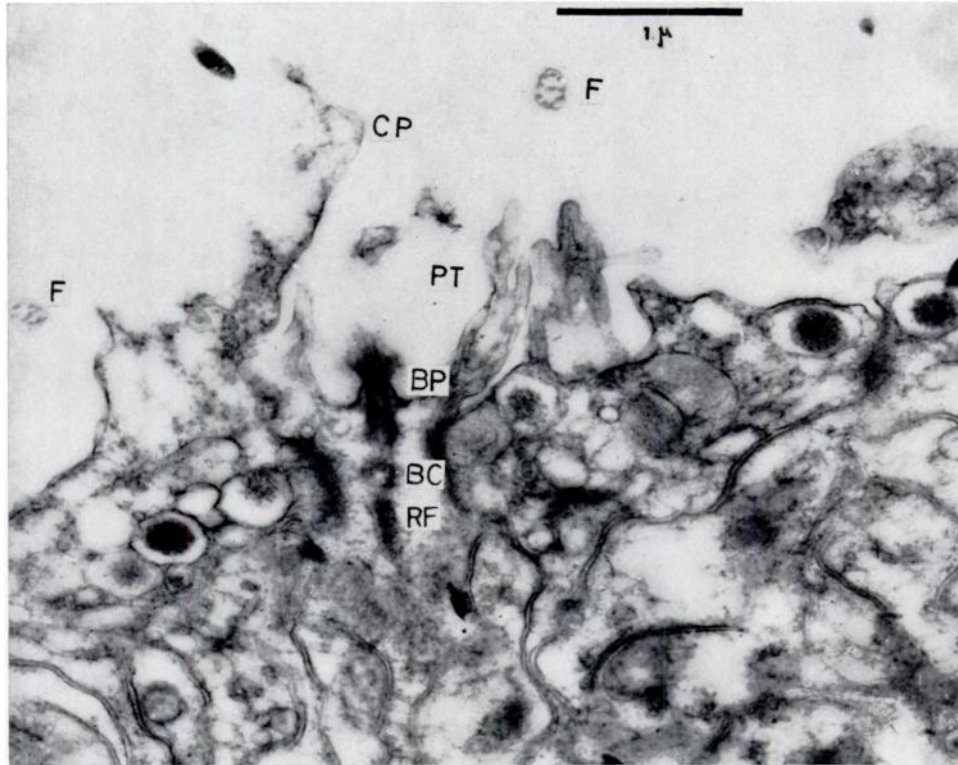


FIGURE 5. Electronmicrograph of the epidermal border of *Astrangia danae* tangentially cut. The epidermis consists of tall columnar cells with a finely granular cytoplasm the free surface of which bears a single flagellum (f) set into a shallow pit (pt) bordered by a circllet of nine to twelve microvilli. The microvilli are especially conspicuous on the collar processes (cp). At the base of the flagellum are shown the basal plate (b.p), basal corpuscle (b.c.) and rootlet fibre (r.f.). The latter has a periodicity of about 670 Å. The arrangement of the microvilli suggests they are modified collars reminiscent of those of choanocytes. The surface membrane shows numerous and very variable cytoplasmic extensions and invaginations suggestive of micropinacytosis. The cell membranes are continuous and show no protoplasmic bridging or syncytial structures.

Electronmicroscopy provides some of the most persuasive evidence that reef corals possess the necessary structural organization for transport of dissolved organic matter across the epidermal barrier. In all species so far examined the epidermis is shown to consist of tall columnar cells the free surface of which bears a single flagellum set into a shallow pit bordered by a circllet of nine to twelve microvilli about 2μ long and 100μ in diameter (Goreau and Philpot, 1956). The arrangement of the microvilli (Fig. 5) suggests they are a modified collar reminiscent of that of choanocytes. The surface membrane shows numerous and very variable cytoplasmic extensions and invaginations suggestive of micropinacytosis. Just beneath the surface are mitochondria and endoplasmic reticulum. Thus, not only are the epidermal cells shown to have a surface area many times greater than purely geometric estimates based on light microscopy would indicate, but their ultrastructure is suggestive of a very dynamic cell boundary across

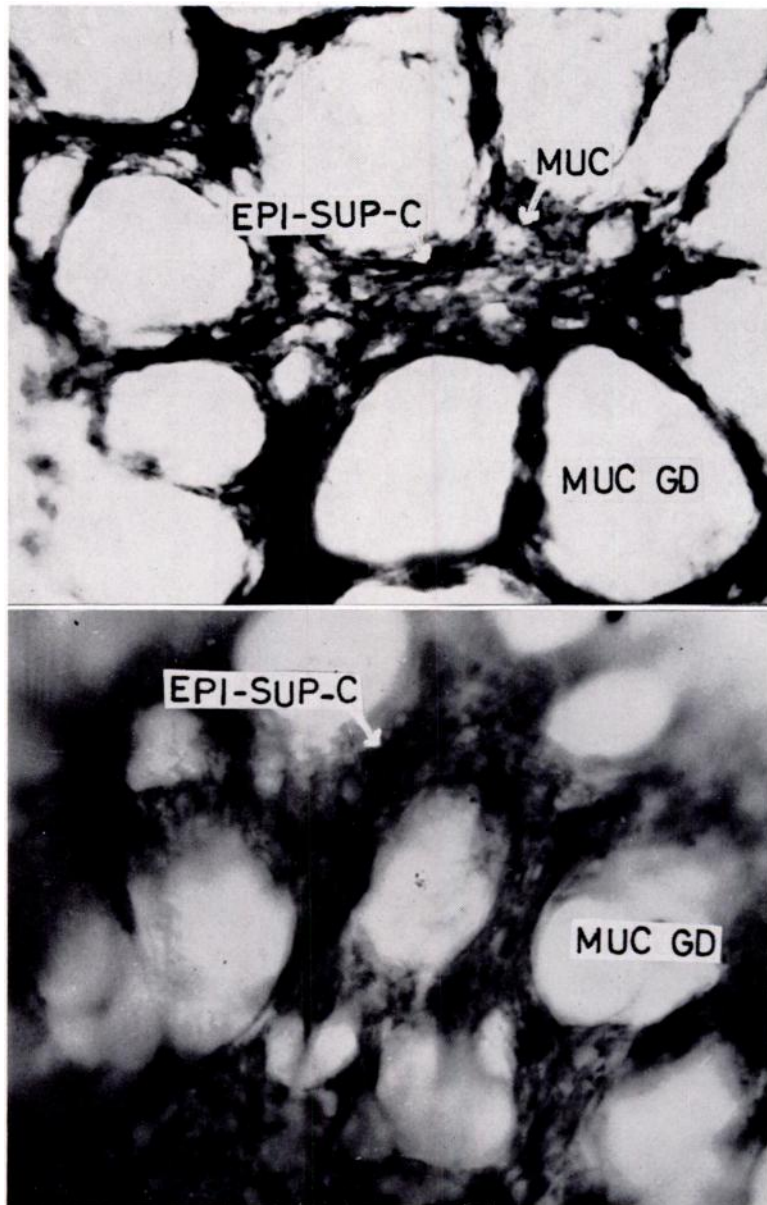


FIGURE 6. Tangential section through the epidermis of *Colpophyllia natans*, stained for alkaline phosphatase and counterstained with eosin Y. The large lacunae represent mature mucus glands (muc gd). The phosphatase activity is confined to the supporting cells (epi sup c) here seen in cross section. Note that the enzyme has a reticular localization in what appear to be cell membranes. The small phosphatase negative vacuoles (muc) may be due to an early stage in the formation of mucus; magnification is $\times 5000$.

FIGURE 7. Tangential section through the epidermis of *Colpophyllia natans* stained with P. A. S. Compare with figure 6 which shows a serial section stained for phosphatases, and note that both this enzyme and the P. A. S. reactive substance have a similar localization confined to the supporting cells (epi sup c). The mucus glands (muc gd) are negative; magnification is $\times 3600$.

which active transport takes place: the data from the amino acid uptake experiments suggest that the net flux is from outside to inside.

Histochemical studies (Goreau, 1956) have shown that highly active nonspecific alkaline phosphomonoesterases are present in the distal parts of the epidermal cells of corals (Fig. 6). The precise function of these phosphatases is not clear: their extremely sharp and high pH maxima with peaks around pH 11.1 suggest that these enzymes do not act *in vivo* as simple hydrolases, but possibly as phosphotransferases supplying energy for metabolic processes occurring in the outer surface of the epidermis. We have not yet been able to establish on the ultrastructural level whether the alkaline phosphomonoesterase is associated with the microvilli. It is of considerable interest, however, that the localization of the enzyme within the coral epidermis is identical with that of a P. A. S. reactive non-metachromatic neutral mucopolysaccharide (Fig. 7). A similar spatial association of alkaline phosphatase and neutral mucopolysaccharide was found by Moog and Wenger (1952) in absorptive and secretory organs of several vertebrate and invertebrate groups. In spite of their phyletic disparity, the epidermal cells of scleractinian corals and the absorptive epithelia of mammalian kidney and duodenum are remarkably similar in general features of their ultrastructure, histochemistry and functions, having in common a large free surface area due to microvilli, high concentrations of alkaline phosphomonoesterases associated with neutral mucopolysaccharide at the free cell border, and being capable of active transport of dissolved organic substances against a concentration gradient. In view of these considerations, it is not unlikely that these epithelia also perform similar functions.

DISCUSSION

After many years of controversy, much remains to be learnt about the nutrition of hermatypic corals. It is significant that, in distinction to ahermatypes, they exhibit a wide range in size and form of the polyps. This could well indicate a correspondingly wide range of specialization for dealing with food material extending from living animals to detritus and to particulate or dissolved material of animal origin.

Corals such as *Favia*, *Euphyllia* or *Mussa* with large polyps can be observed to feed exclusively on animal prey, *e.g.*, small fish and large zooplanktonic organisms or fragments of flesh (never vegetable matter), in precisely the same manner as do ahermatypic corals such as *Tubastrea* or *Balanophyllia* and all Actiniaria. But, to the extent that these may be available, they may also absorb dissolved or colloidal matter through the epidermis by the mechanisms described above. Where polyps are smaller but still possess adequate tentacles, for instance, *Porites* or *Pocillopora*, and where ciliary currents beat toward instead of away from the mouth (Yonge, 1930a), a primary diet of smaller planktonic animals with particulate and/or dissolved organic matter may reasonably be postulated. In the extreme case of the agaricids (which are very common on reefs) such as *Pavona*, *Psammocora* or *Agaricia* with minute, and in some cases (*e.g.*, *Pachyseris*) non-existent, tentacles around very small mouths, particulate food must consist almost entirely of fine fragments of organic matter from the smallest zooplanktonic organisms downward.

In such corals ciliary currents would appear to assist the boundary layer water

in conveying the finest material across the surface where the stimulus of animal matter in any form (down to amino acids) will cause mouths to open and mesenterial filaments to be extruded through them. These remarkably efficient organs for combined digestion and absorption of animal matter here take over the function of the tentacles. They extend out of the mouth or other openings in the tissue to seize and enwrap food particles which they may digest and absorb outside the coelenteron (Yonge, 1930a; Abe, 1938). In no scleractinian are the filaments reduced as they are in alcyonarians such as *Xenia*.

While it is now abundantly established that material does pass from the zooxanthellae into the tissues of the host coelenterate—actinarian, zoanthid or scleractinian (Goreau and Goreau, 1960; Muscatine, 1967, 1969; Von Holt and Von Holt, 1968; Trench, 1971a, 1971b, 1971c; Lewis and Smith, 1971)—the precise significance of this, in the context of the nutrition of the animal, still remains to be determined. Certainly the few species of temperate water actinians which harbor zooxanthellae appear in no way more efficient than the majority which do not. In the bivalve Tridacnidae there is an equally well established passage of soluble material into the blood stream from zooxanthellae (which are later digested in phagocytic blood cells) (Yonge, 1936; Goreau, Goreau and Yonge, 1966). This material rapidly becomes incorporated into the byssus, crystalline style, periostracum and mucus indicating its possible use in the synthesis of these secretions in a manner similar to that described in the sacoglossan gastropod, *Tridachia* (Trench, 1969; Trench, Greene and Bystrom, 1969).

Maintained in darkness, some scleractinians can survive the eventual loss of the zooxanthellae, others cannot. This may not necessarily imply that the latter are suffering from starvation, it may equally be a consequence of the change in the internal environment. Normally the zooxanthellae automatically remove the waste products of metabolism, notably CO₂ with sources of sulphur, nitrogen and phosphorus needed for protein synthesis. Not all hermatypic scleractinians may have the capacity for the efficient removal of these. Franzisket (1970) describes how, after exposure to darkness and consequent loss of zooxanthellae, the tissues of *Porites* atrophy but when exposed to light and reinfected with algae regeneration rapidly occurred. But it remains to be determined whether atrophy and subsequent recovery were the consequences of removal and then restoration of food supplied by the zooxanthellae or of inadequate metabolism when deprived of the algae which normally remove waste products. The major problems ahead involve adequate evaluation of the precise energy needs of corals and the nature of available supplies—zooplankton and particulate or dissolved organic matter of animal origin—in coral reef seas. The spectacular success as reef builders of the hermatypic Scleractinia has tended to obscure the very small amount of living tissue actually present and so exaggerate the amount of food required.

Apart from the discussion, this paper was in rough draft at the time of Professor Thomas F. Goreau's death. Nora Goreau and Maurice Yonge wish to express their gratitude to Willard Hartman, David Barnes, Judith Lang and Robert Trench for criticism of the manuscript. We acknowledge with thanks the assistance of Peter Hunt who photographed our autoradiogram for Figure 4 and further photographic help from Thomas J. Goreau and E. A. Graham. This

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SUMMARY

The assumption that reef corals are wholly autotrophic due to the presence of zooxanthellae is questioned. Reef corals lack the behavioral and structural specializations for an autotrophic existence comparable to that found in the xeniid octocorals and zoanthideans which appear to depend upon zooxanthellae for their food.

The heterotrophic nutritional activities of reef corals, as observed both in the field and in the laboratory, include the following: (1) specialized carnivorous feeding, primarily on zooplankton, facilitated by ciliated currents and mucus, direct transfer of prey to the mouth by the tentacles, or extracoelenteric feeding by the mesenterial filaments; (2) unspecialized detritus feeding, involving the use of a wide range of organic matter of animal and perhaps of bacterial origin; (3) direct utilization of dissolved or colloidal organic matter as suggested by the uptake of amino acids by the epidermis and by the ultrastructural, histochemical and physiological features of the free cell border.

Water circulating within the reef, the boundary layer water, is in a continuous and dynamic exchange with the trophic structure of the reef, recycling nutrients with the benthos and making the suspended particulate matter a possible food source for corals.

LITERATURE CITED

- ABE, N., 1938. Feeding behaviour and the nematocyst of *Fungia* and 15 other species of corals. *Palao Trop. Biol. Sta. Stud.*, 1: 469-521.
- BAKUS, G. J., 1967. Some relationships of fishes to benthic organisms on coral reefs. *Nature*, 210: 280-284.
- BAKUS, G. J., 1969. Energetics and feeding in shallow marine waters. *Int. Rev. Gen. Exp. Zool.*, 4: 275-369.
- BARDACH, J. E., 1961. Transport of calcareous fragments by reef fishes. *Science*, 133: 98-99.
- BAYLOR, E. R., AND W. H. SUTCLIFFE, 1963. Dissolved organic matter in seawater as a source of particulate food. *Limnol. Oceanogr.*, 8: 369-371.
- DUERDEN, J. E., 1902. West Indian Madreporarian polyps. *Mem. Nat. Acad. Sci.*, 8: 399-597.
- DUERDEN, J. E., 1906. The role of mucus in corals. *Quart. J. Microscop. Sci.*, 49: 591-614.
- FLEMING, M. W., 1954. Plankton of Northern Marshall Islands *U. S. Geol. Surv. Prof. Pap.*, 260(F): 301-314.
- FRANZISKET, L., 1969a. Riff Korallen Können autotroph Leben. *Naturwissenschaften*, 56(3): 144.
- FRANZISKET, L., 1969b. The ratio of photosynthesis to respiration of reef building corals during a 24 hour period. *Forma et Functio*, 1: 153-158.
- FRANZISKET, L., 1970. The atrophy of hermatypic reef corals maintained in darkness and their subsequent regeneration in light. *Int. Rev. Hydrobiol.*, 55: 1-12.
- GOHAR, H. A. F., 1940. Studies on the Xeniidae of the Red Sea. *Publ. Mar. Biol. Sta. Ghardaqa, Red Sea, Egypt*, No. 2: 25-118.
- GOHAR, H. A. F., 1948. A description and some biological studies of a new alcyonarian species *Clavularia hamra* Gohar. *Publ. Mar. Biol. Sta. Ghardaqa, Red Sea, Egypt*, No. 6: 3-33.
- GORDON, M. S., AND H. M. KELLEY, 1962. Primary productivity of an Hawaiian coral reef: a critique of flow respirometry in turbulent waters. *Ecology*, 43: 473-480.

- GOREAU, T. F., 1953. Phosphomonoesterases in reef building corals. *Proc. Nat. Acad. Sci.*, **39**: 1291-1295.
- GOREAU, T. F., 1956. Histochemistry of mucopolysaccharide-like substances and alkaline phosphatase in Madreporaria. *Nature*, **177**: 1029-1030.
- GOREAU, T. F., AND N. I. GOREAU, 1960. Distribution of labelled carbon in reef-building corals with and without zooxanthellae. *Science*, **131**: 668-669.
- GOREAU, T. F., AND E. A. GRAHAM, 1967. A new *Halimeda* from Jamaica. *Bull. Mar. Sci.*, **17**: 432-441.
- GOREAU, T. F., AND W. D. HARTMAN, 1963. Boring sponges as controlling factors in the formation and maintenance of coral reefs. Pages 25-54 in R. F. Sognaes, Ed., *Mechanisms of Hard Tissue Destruction*. Amer. Assoc. Advan. Sci. Publ., No. 75, Washington, D. C.
- GOREAU, T. F., AND D. E. PHILPOT, 1956. Electronmicrographic study of flagellated epithelia in Madreporarian corals. *Exp. Cell Res.*, **10**: 552-555.
- GOREAU, T. F., AND J. W. WELLS, 1967. The shallow water Scleractinia of Jamaica: revised list of species and their vertical distribution ranges. *Bull. Mar. Sci.*, **17**: 442-453.
- GOREAU, T. F., N. I. GOREAU AND C. M. YONGE, 1966. Evidence for a soluble algal factor produced by the zooxanthellae of *Tridacna elongata*. Abstract. *Int. Conf. Trop. Oceanography*, Miami, 1965. [Available from Department of Zoology, University of Edinburgh, Scotland.]
- GOREAU, T. F., N. I. GOREAU, C. M. YONGE AND Y. NEUMANN, 1970. On feeding and nutrition in *Fungiacava cilatensis* Soot-Ryen (Bivalvia, Mytilidae), a commensal living in fungiid corals. *J. Zool. London*, **160**: 159-172.
- GOREAU, T. F., V. TORRES, L. MAS AND E. RAMOS, 1960. On community structure, standing crop and oxygen balance of the Lagoon at Cayo Turrumote, Puerto Rico. (Abstract). *Assoc. Island Mar. Labs. 3rd Meeting*, Jamaica.
- HARTMAN, W. D., AND T. F. GOREAU, 1970. Jamaican coralline sponges: their morphology, ecology and fossil relatives. *Symp. Zool. Soc. London*, **25**: 205-243.
- HELLEBUST, J. A., 1965. Excretion of some organic compounds by marine phytoplankton. *Limnol. Oceanogr.*, **10**: 192-206.
- JACKSON, J. B. C., T. F. GOREAU AND W. D. HARTMAN, 1970. Recent brachiopod sclerospone communities and their palaeoecological implications. (In press)
- JOHANNES, R. E., AND S. L. COLES, 1969. The role of zooplankton in the nutrition of scleractinian corals. [Symp. Corals, Coral Reefs. Jan. 1969]. *Mar. Biol. Assoc. India, Mandapam Camp*, 1969: 8.
- KOHN, A. J., AND P. HELFRICH, 1957. Primary organic productivity of a Hawaiian coral reef. *Limnol. Oceanogr.*, **2**: 241-251.
- LANG, J. C., 1969. New characters for coral taxonomy. (Abstract) *Assoc. Island Mar. Labs. 8th Meeting*, Jamaica.
- LANG, J. C., 1970. Inter-specific aggression within the scleractinian reef corals. *Ph.D. thesis, Yale University*.
- LEWIS, D. H., AND D. C. SMITH, 1971. The autotrophic nutrition of symbiotic marine coelenterates with special reference to hermatypic corals. I. Movement of photosynthetic products between the symbionts. *Proc. Roy Soc. London Series B*, **178**: 111-129.
- MARISCAL, R. N., AND H. M. LENHOFF, 1968. The chemical control of feeding behaviour in *Cyphastrea ocellina* and some other Hawaiian corals. *J. Exp. Biol.*, **49**: 689-699.
- MARSHALL, N., 1965. Detritus over the reef and its potential contribution to adjacent waters of Eniwetok Atoll. *Ecology*, **46**: 343-344.
- MATTHAI, G., 1918. On reactions to stimuli in corals. *Phil. Soc. Proc. Cambridge*, **19**: 164-166.
- MOOG, F., AND E. L. WENGER, 1952. The occurrence of a neutral mucopolysaccharide at sites of high alkaline phosphatase activity. *Amer. J. Anat.*, **90**: 339-378.
- MUSCATINE, L., 1967. Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. *Science*, **156**: 516-519.
- MUSCATINE, L., AND E. CERNICHIARI, 1969. Assimilation of photosynthetic products of zooxanthellae by a reef coral. *Biol. Bull.*, **137**(3): 506-523.

- ODUM, H. T., AND E. P. ODUM, 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.*, **25**: 291-320.
- RILEY, G. A., 1963. Organic aggregates in seawater and the dynamics of their formation and utilization. *Limnol. Oceanogr.*, **8**: 372-381.
- SARGENT, M. C., AND T. S. AUSTIN, 1949. Organic productivity of an atoll. *Trans. Amer. Geophys. Union*, **30**: 245-249.
- SARGENT, M. C., AND T. S. AUSTIN, 1954. Biologic economy of coral reefs. *U. S. Geol. Surv. Prof. Pap.*, **260**(E): 293-300.
- STEPHENS, G. C., 1962. Uptake of organic matter by aquatic invertebrates. I. Uptake of glucose by the solitary coral *Fungia scutaria*. *Biol. Bull.*, **123**: 648-659.
- STODDART, D. R., 1969. Ecology and morphology of recent coral reefs. *Biol. Rev.*, **44**: 433-498.
- TRENCH, R. K., 1969. Chloroplasts as functional endosymbionts in the mollusc *Tridachia cristata* (Bergh), (Opisthobranchia, Sacoglossa). *Nature*, **222**: 1071-1072.
- TRENCH, R. K., 1971a. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. I. The assimilation of photosynthetic products of zooxanthellae by two marine coelenterates. *Proc. Roy. Soc. London Series B*, **177**: 225-235.
- TRENCH, R. K., 1971b. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. II. Liberation of fixed ^{14}C by zooxanthellae *in vitro*. *Proc. Roy. Soc. London Series B*, **177**: 237-250.
- TRENCH, R. K., 1971c. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. III. The effect of homogenates of host tissues on the excretion of photosynthetic products *in vitro* by zooxanthellae from two marine coelenterates. *Proc. Roy. Soc. London Series B*, **177**: 251-264.
- TRENCH, R. K., R. W. GREENE AND B. G. BYSTROM, 1969. Chloroplasts as functional organelles in animal cells. *J. Cell. Biol.*, **42**: 404-417.
- VON HOLT, C., 1968. Uptake of glycine and release of nucleoside polyphosphates by zooxanthellae. *Comp. Biochem. Physiol.*, **26**: 1071-1079.
- VON HOLT, C., AND M. VON HOLT, 1968a. Transfer of photosynthetic products from zooxanthellae to coelenterate hosts. *Comp. Biochem. Physiol.*, **24**: 73-81.
- VON HOLT, C., AND M. VON HOLT, 1968b. The secretion of organic compounds by zooxanthellae isolated from various types of *Zoanthus*. *Comp. Biochem. Physiol.*, **24**: 83-92.
- YONGE, C. M., 1930a. Studies on the physiology of corals. I. Feeding mechanisms and food. *Sci. Rep. Great Barrier Reef Exped.*, **1**: 13-57.
- YONGE, C. M., 1930b. Studies on the physiology of corals. III. Assimilation and excretion. *Sci. Rep. Great Barrier Reef Exped.*, **1**: 83-91.
- YONGE, C. M., 1936. Mode of life, feeding, digestion and symbiosis with zooxanthellae in the Tridacnidae. *Sci. Rep. Great Barrier Reef Exped (1928-29)*, **1**: 283-321.
- YONGE, C. M., 1940. The biology of reef building corals. *Sci. Rep. Great Barrier Reef Exped.*, **1**: 353-391.
- YONGE, C. M., AND A. G. NICHOLS, 1930. Studies on the physiology of corals. II. Digestive enzymes. *Sci. Rep. Great Barrier Reef Exped.*, **1**: 59-81.
- YONGE, C. M., AND A. G. NICHOLS, 1931. Studies on the physiology of corals. IV. The structure, distribution and physiology of the zooxanthellae. *Sci. Rep. Great Barrier Reef Exped.*, **1**: 135-176.