TROPHIC STRUCTURE AND PRODUCTIVITY OF A WINDWARD CORAL REEF COMMUNITY ON ENIWETOK ATOLL[1]

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INTRODUCTION

The coral reef communities of the world are tremendously varied associations of plants and animals growing luxuriantly in tropical waters of impoverished plankton content. Under intense equatorial insolation the plants apparently grow rapidly and are eaten rapidly. Save for fluctuations the reef seems unchanged year after year, and reefs apparently persist, at least intermittently, for millions of years. With such long periods of time, adjustments in organismal components have produced a biota with a successful competitive adjustment in a relatively constant environment. The reef community is famous for its immense concentrations of life and its complexity.

Perhaps in the structure of organization of this relatively isolated system man can learn about optima for utilizing sunlight and raw materials, for mankind's great civilization is not in steady state and its relation with nature seems to fluctuate erratically and dangerously. What, then, is the relationship between organic productivity, energetic efficiency, and the standing crop structure of a coral reef community? How are steady state equilibria such as the reef ecosystem self adjusted?

Since nuclear explosion tests are being conducted in the vicinity of these inherently stable reef communities, a unique opportunity is provided for critical assays of the effects of radiations due to fission products *on whole populations and entire ecological systems in the field.* In the present paper some results are presented of a variety of measurements made on an Eniwetok Atoll reef which as yet has been little affected by nuclear explosions. These measurements represent both a multiple approach to the problem of obtaining practical assays of total function which will aid future comparisons between the normal and the irradiated reef ecosystems, and also a continuing effort by many to answer the questions posed in the preceding paragraph.

THE PROBLEM OF RELATING STANDING CROP AND PRODUCTION

In recent years rapid advances in technique and approach have permitted the measurement of the metabolism and productivity (rate of production) of aquatic communities and their components. Ingenious methods such as used by Sargent & Austin (1949, 1954) building on the work of Mayor (1924), Yonge (1940), and others, have permitted estimates of the productivity of coral reefs. Intense postwar interest in the tropical Pacific by geologist and biologist alike has led to new and detailed popu-

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lation and zonational study of reef fauna and flora such as by Ladd, *et al.* (1950), Tracey, *et al.* (1948), Emery, *et al.* (1954), Wells (1951), Doty & Morrison (1954), and Cloud (1952, 1954). It seems now time to determine the relationship between the standing crop, defined as the dry biomass of existing organisms per area, and productivity, defined as the rate of manufacture of dry biomass per area.

It has long been felt that the productivity of the various trophic levels of a community is very roughly proportional to the standing crop being maintained although the reason has not been entirely clear. Many have confused these entirely different properties of ecosystems. The distributions of standing crop may be represented graphically by trophic level so as to form block diagrams in the shape of pyramids. For a discussion of pyramids and production see Odum, E. P. (1953). In another communication by Odum & Pinkerton (1955) theoretical reasoning based on the second law of thermodynamics is presented to show that systems of many types when in open steady state tend to adjust to maximum output of energy consistent with available input energy and a corresponding low but optimum efficiency. If steady state systems tend to be similarly self adjusted regarding efficiency of energy utilization between trophic levels, then there is theoretical reason for expecting pyramids of biomass to be similar for components with similar metabolic rates. It is pertinent that somewhat similar pyramids have been found in Silver Springs, Florida, a rich constant-temperature aquatic community in slightly pulsing steady state (Odum, H. T. 1953), and in successional terrestrial communities in the Savannah River Atomic Energy Commission area of South Carolina (Odum, E. P. 1954).

ACKNOWLEDGMENTS

This study was supported by the U. S. Atomic Energy Commission through a contract (No. AT(07-2)-10) between the AEC and the University of Georgia. We are grateful for the courtesies and aids provided by AEC personnel at Eniwetok, especially, T. Hardison, E. Wynkoop, J. C. Kyriacopulos, R. Taft, and D. Ellif. It is a pleasure to acknowledge the many stimulating discussions, help, and encouragement provided us during the course of this study by experienced reef scientists: R. W. Hiatt, M. S. Doty, and T. S. Austin in Hawaii; L. Donaldson, K. Lohman, A. Weylander of the Univ. of Washington; D. W. Strasburg, Duke Univ.; L. R. Blinks, Stanford Univ.; and H. Ladd, U. S. G. S. in Washington, D. C.

We are also indebted to L. D. Tuthill, Department of Zoology and R. W. Hiatt, Director of the Marine Laboratory of the University of Hawaii for providing facilities for the work done in Hawaii.

Identifications of organisms were provided by F. M. Bayer (corals), M. Doty (algae), C. E. Cuttress (anemones), R. Hiatt (invertebrates), and A. Weylander (fish). Code numbers have been assigned to unidentified corals along with tentative names to specimens deposited with the U. S. National Museum.

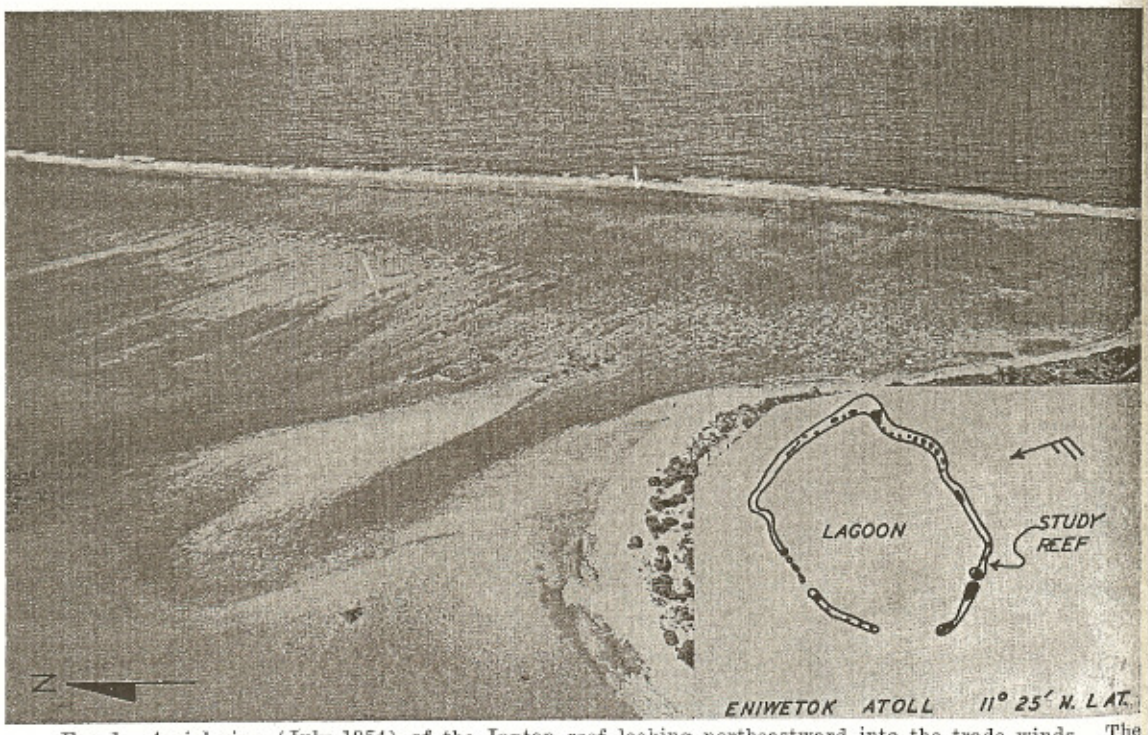

FIG. 1. Aerial view (July 1954) of the Japtan reef looking northeastward into the trade winds. The study transect is delimited by the two arrows. The insert shows the position of the Japtan reef in Eniwetok Atoll with wind direction indicated.

GENERAL PROCEDURES

During a six weeks' period at the Atomic Energy Commission Eniwetok Marine station a transect of quadrats marked by iron stakes was established on a relatively undisturbed and fairly typical inter-island reef shown in Figure 1. Many varied sampling procedures were combined to estimate the standing crop of the major component groups of the reef biota. Then chemical methods were used upstream and downstream to estimate the primary production and total respiratory metabolism of the reef. From these standing crop and productivity estimates, the turnover was obtained. Productivity data were combined with calculated light intensities to obtain an estimate of energetic efficiency.

In this approach it was imperative that a wide variety of methods be used all at the same time on the same area. Thus, fewer replications were made than would be required to obtain maximum accuracy from each method. Therefore it is the orders of magnitude which mainly emerge, but care is taken to base conclusions only on large, probably significant differences. Details of methods used are outlined in appropriate sections which follow.

The taxonomic composition of the reef community is tremendously varied from spot to spot whereas we believe the biomass per area is more constant. Weight estimates by trophic level based on our few quadrats are thus probably representative, but the quadrats should not be considered as population estimates by species. Many more quadrats would be required to estimate the densities of individual populations.

The 20 ft by 20 ft quadrat maps in Figure 5 were made in the field with pencil on acetate boards so that drawings could be made underwater using face masks.

Drs. R. W. Hiatt and M. S. Doty, who visited the reef, agreed with the authors that the quadrats mapped were fair samples regarding percentage of coral and general physiography.

THE WINDWARD REEF COMMUNITY, ZONATION

The study reef (Fig. 1) is a part of the ring of submerged reefs which connects the small islands that make up Eniwetok Atoll. The transect is located ¼ mile north of Japtan Island (Lady Slipper or Muti Island on some maps), on the eastern and windward edge of the atoll where the reef is 1500 ft wide (455 m). Most previous study transects of atoll reef communities have been made on island reefs where the water must break onto the reef and then return in the same path as an undertow. In contrast, this transect, like that of Sargent & Austin (1949), is across an inter-island reef where the water moves in only one direction from east to west with the wind; that is, from the open sea into the lagoon. On Eniwetok Atoll, the inter-island reef is actually the important predominant type.

As pointed out by Cloud (1954), many island reefs actually represent eroding reefs which were elevated above the water surface by a six-foot fall in ocean level which began at the end of the postglacial thermal maximum about 3000 years ago. These reefs are now in the process of being worn down. Only the front edge of present-day island reefs of Eniwetok support actively growing reef-building corals and algae, whereas many of the inter-island reefs support a vigorous community throughout. Consequently, the inter-island reef more nearly represents the "climax" or "steady state" community under present water level conditions. From the standpoint of productivity and metabolism it is quite clear that the inter-island reef is much more typical of an active coral community than is the half-dead, decadent island reef. These latter reefs, of course, may again become active when sufficiently worn down or if there is a future rise in sea level.

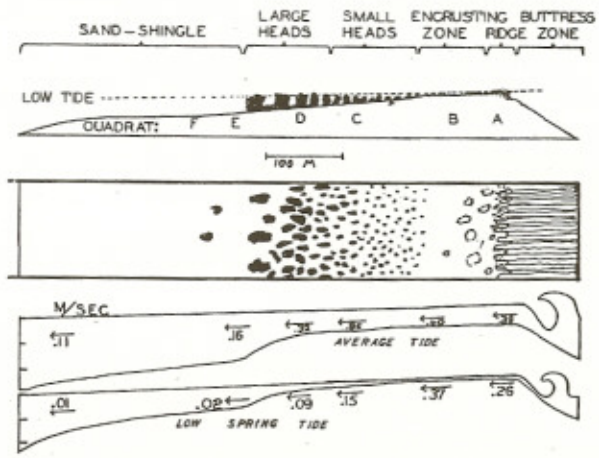

FIG. 2. Diagram showing the physiographic zones of the reef in surface and cross section view, and the average current velocities in m/sec. The approximate location of the 6 quadrats is indicated in the upper diagram.

The transect of stakes was erected in a line parallel to the steady current traversing the reef. At no time during our observation were there tide pools with entirely stationary water. The zonation is very distinctive and apparently regulated by current velocities that decrease downstream as the depth increases. The descriptions of island reef zonation by Cloud (1952), Banner & Randall (1952), and Wells (1951) show very few similarities with the inter-island zonation on this reef, which is not surprising in view of points raised in the preceding paragraph. Tracey, Ladd & Hoffmeister (1948) class this type of inter-island reef as type IA.

As diagramed in Figure 2 and shown in aerial photographs and horizontal views in Figures 3-5, there are six physiographic zones as described briefly below.

WINDWARD BUTTRESS ZONE

The only information on the leading front of the reef comes from the aerial photograph in Figure 4 which shows the surge channels and buttresses running at least 200 ft (66 m) to seaward. It was not possible to sample this area because the algal ridge breakers could not be crossed.

Brief glimpses from a helicopter suggest that there is about a half coverage of coral in this zone.

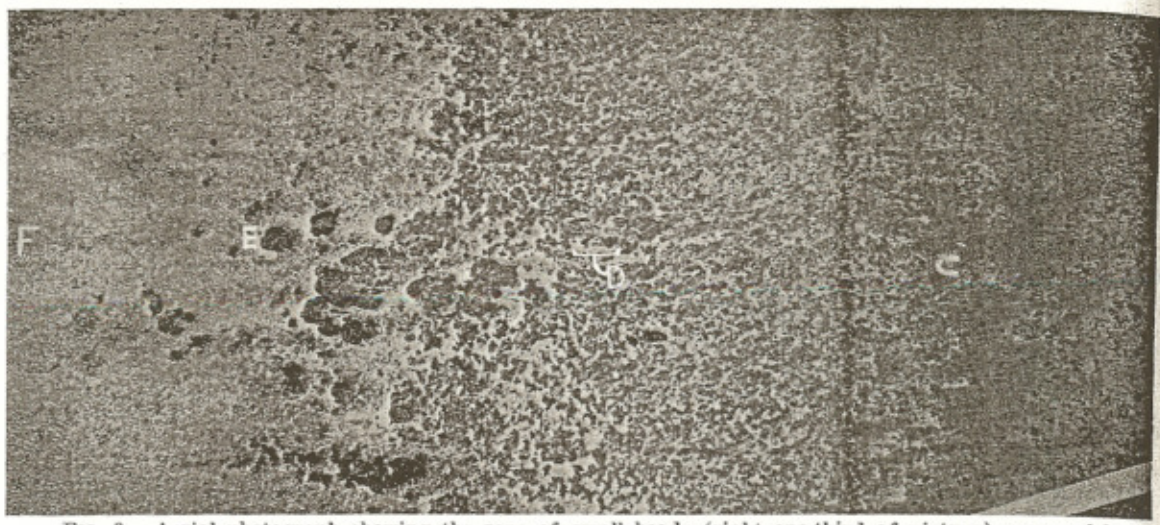

FIG. 3. Aerial photograph showing the zone of small heads (right one-third of picture), zone of large heads (center), and zone of sand-shingle of the down stream reef (left). Water flows from right to left. Zones of Quadrat C-F are marked.

Mayor (1925) found primarily species of *Acropora* in such an area.

CORAL-ALGAL RIDGE

In contrast to the massive algal ridges which have been described for windward reefs of Bikini and other atolls (Taylor 1950), the front ridge on the inter-island reef is a low, narrow ill-defined strip of limestone about 50 ft wide. The irregular surface is covered largely with corals and soft algae. The calcareous red algae (chiefly Porolithon), which are so prominent on Bikini reefs, are found mainly in small patches below the other algae or down in crevices. Our reef is an example of the principle (Tracey, *et al.* 1948; Ladd, *et al.* 1950; Cloud 1954) that inter-island reefs do not have so extensive an algal ridge or so elaborate a tunnel structure as do the island reefs. This is reasonable because the undertow on the inter-island reef is less on the front since much of the water goes over rather than back through. However, even the island reefs on Eniwetok have less calcareous superstructure than Bikini although much more than on our inter-island transect area. The lack of extensive superstructure may make the crossing of the algal ridge by a swimmer more difficult. The foam and combers on algal-coral ridges diminish the light penetration significantly and possibly cause the red algae to dominate.

The yellow encrusting *Acropora palmerae* (B-1),* small clumps of Pocillopora (A-1), and an encrusting form of *Millepora platyphylla* (B-2) are the chief corals which may cover up to half of the area of the ridge zone. Otherwise the ridge is covered with a thick mat of fleshy algae such as *Dictyosphaeria intermedia, Zonaria variegata,* Ceramium, Dictyota, and *Caulerpa elongata.* A characteristic feature is large purple sea urchins (*Heterocentrotus trigonarius*) which wedge themselves into holes under the pounding surf. Rotenone sampling revealed a prevalence of small blennies and groupers. Sampling work on the ridge was possible only for a half hour during each low spring tide. The ridge is marked by white surf in Figures 1 and 4. Some idea of the distribution of coral and the much folded algal surfaces can be obtained in the diagram of Quadrat A in Figure 5.

ENCRUSTING ZONE

The first 200 ft (66 m) downstream from the ridge is a high, gently sloping plateau that at low spring tide is covered with only 6 in. of water. It is relatively the smoothest area with corals being either of a flat encrusting growth form or restricted to low rounded "heads" but little raised above the general reef surface. The range between tops of heads and ridges and the bottoms of depressions is only about one foot. As on the coral-algal ridge zone sheets of yellow Acropora and Millepora are conspicuous. In addition, there are scattered low, rounded heads of *Porites lobata* (B-6) and several species of favids (B-3, B-4, B-5). As shown in Figure 5, quadrat B, living coral colonies on these low heads are often crescent or doughnut shaped probably because the higher center portions are killed periodically by exposure during exceptionally low spring tides.

Filamentous red, brown, green, and blue-green algae form heavy encrusting mats over all of the zone which is not covered by coral, there being no areas of white sand as in the back reef zones. Small sea anemones are abundant, occurring in clusters throughout the algal mat. These belong to the genus *Actiniogeton* (Carlgren 1938), and apparently represent an undescribed species according to Charles E. Cutress who is currently working on this material. These anemones are remarkable in that they coat themselves with calcareous sand grains which are permeated with

* Code numbers refer to specimens deposited in the U. S. National Museum where final or more complete identification will be made when taxonomy of Marshall Island corals becomes better known.

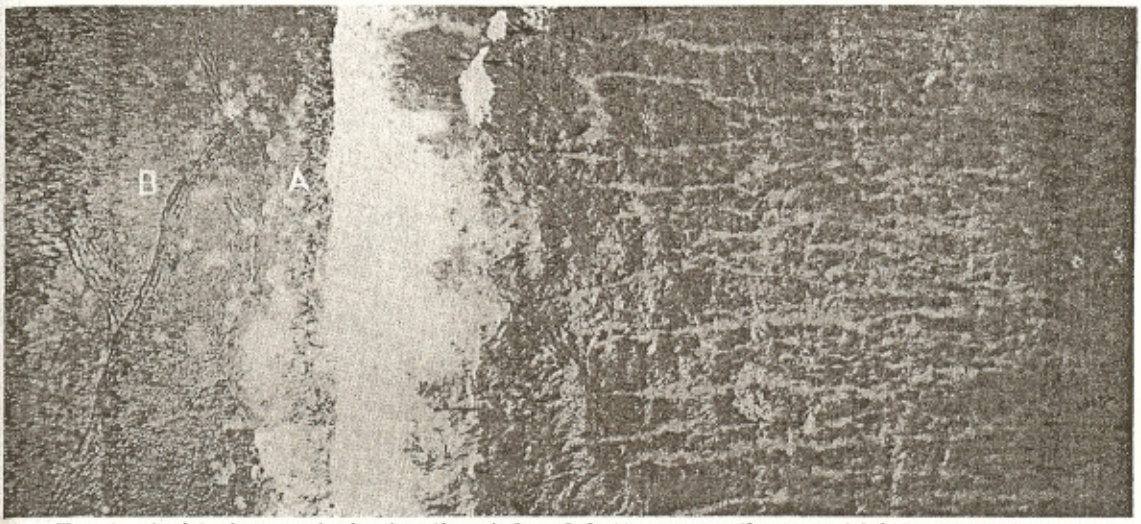

FIG. 4. Aerial photograph showing the windward buttresses on the east (right), the surf zone, the algal ridge (just to left of white line of surf), and the encrusting zone (left of ridge and covered with light-colored splotches of encrusting coral). Water leaving the zones pictured here flows downstream across zones pictured in Figure 3. Quadrats A and B are marked.

filamentous algae of the same type as found in the skeletons of corals.

Corals cover much less than half of the surface area (Fig. 5, quadrat B). From the air the zone has a wine-red color (algae) splotched with yellow (corals). The zone receives pulses of foam-water as the breakers throw rolls of water up on the plateau. Since there is a distinct slope the current is always strong even at low spring tide when the water pours steadily across like a broad mountain stream rippling over a rocky bed. Visual observation indicates that fish are not numerous in this shallow, rough-water zone, although schools of parrot fish were observed to cross the area and small fish were found in the few crevices which are available. The encrusting zone is visible just back of the line of breakers in Figure 4.

ZONE OF SMALLER HEADS

Fairly abruptly beyond the sloping plateau (encrusting zone) the water begins to deepen and the current diminishes accordingly. Coral heads become taller and more numerous but are still only a foot or so in diameter and height. The non-coral surfaces become lighter in color with less algal matting and more sand and more fragments of calcareous skeletons (rubble and shingle). As one moves downstream, the heads become larger and are coalesced into compound heads, often composed of several species. Quadrat C, Figure 5, is located near the lagoonward part of this zone. The numerous small heads and the formation of larger heads are well shown in this figure. Encrusting forms of Acropora, so prominent in the previous two zones, are absent. Massive, rounded heads of large calyx favids (C-2, C-3 *Favia pallida*, C-4, C-5 *Cyphastrea serailia*, C-7) reach maximum abundance in this zone. *Porites lobata* continues to be an important species, while colonies of the short, branching forms of Acropora first make their appearance in numbers (Figure 5). Large branched Acroporas (*A. gemmifera*, C-10), which become more important in the next zone, are present in small numbers.

Small fishes are numerous in this zone and large fish come into the area when the current is not too strong. Two individuals of the poisonous stone fish, *Scorpaena gibbosa*, were found resting on the top of dead portions of heads when quadrat C was being mapped. So well did these fish blend with the background that one was at first sketched in as part of the reef structure before disturbance caused it to change its position!

The zone of small heads is well shown in the aerial photograph in Figure 3.

ZONE OF LARGER HEADS

As the water depth increases and the current becomes much less, the heads become massive compound structures, 2 to 4 ft or more in height and 2 to 20 ft in diameter, with channels of white sand and cobble floor in between the heads (quadrat D, Figure 5). Branching corals predominate, such as *Acropora gemmifera* (D-7), *A. cymbicyathus* (D-9), Pocillopora, Stylophora, and others, but massive types such as Porites and Montipora are present. There is a distinct Millepora zone composed of *M. platyphylla* (E-1) and the "stinging coral" *M. murrayi* (E-2) at the back edge of the zone of larger heads. The blue coral, *Heliopora caerulea* (E-3), is fairly common, while large heads of *Turbinaria mesenterina* (E-4) represent the last important coral formations as one passes into the next zone in the lagoon. Quadrat D lies in the front part of the zone of large heads where Milleporas are less prominent.

Mounds of coral shingle (dead coral fragments, usually permeated with living filamentous algae) form the central mass upon which smaller live heads form wreaths. At low spring tide the branching type corals

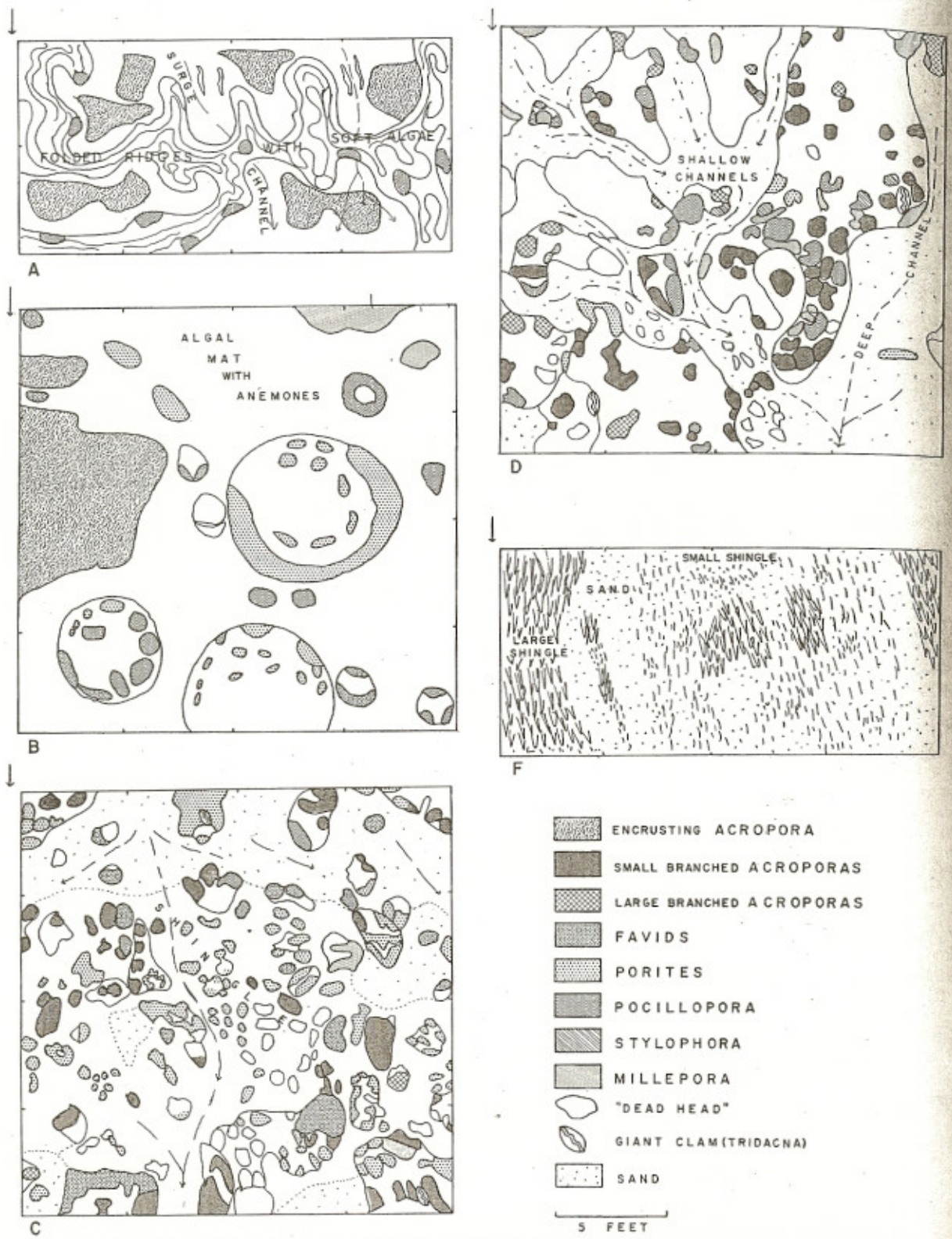

FIGURE 5. Quadrat maps showing distribution of corals and other major habitat features from front to back of the reef (see Fig. 2, upper diagram, for the approximate location of quadrats on the reef). Quadrat A, coral-algal ridge; quadrat B, encrusting zone; quadrat C, zone of small heads, quadrat D, zone of large heads; quadrat F, zone of sand and shingle.

on the tops of these compound heads break the surface, whereas the reef floor is 3 ft submerged. Swimming becomes easy in this zone. The majority of parrot fishes and surgeon fishes browse and school here. In superficial visual appearance, this zone is a beautiful jungle of live coral and fishes although as shown later, in terms of live protoplasm the plant world nevertheless dominates as usual. This zone as seen in Figure 3 is about 400 ft wide.

Zone of Sand and Shingle

With gradually increasing depth and diminishing current, both the small and the larger coral heads, live and dead complexes, come to an abrupt end. A long flat shelf slopes lagoonward for 500 ft or more, covered with coarse and fine sand made up of fragments carried downstream from the front reef. Foraminifera of large types are abundant (Table 7). The fishes decrease except for the schools of sardine-like fishes that feed on the downstream drifting fragments of pseudoplankton and a few larger carnivorous fishes, including sharks, which cruise here. The area is predominantly white except for filamentous algae in the larger coral shingle fragments. Beyond the 500 ft of this long bare shelf there is a sharp steepening of slope for over 100 ft (33 m) down to the irregular lagoon floor. As seen from a helicopter the steepening of the slope is sharply marked by a border of the green turbidity of the lagoon water as the floor drops out of visible range.

The over-all change from the dark color of encrusting filamentous algae of the front reef to the white color of the back reef, where the filamentous algae are mainly within the dead and porous calcareous fragments, suggests a transition from a water-filtering source of nutrients up front to a sub-surface decomposition source of plant requirements on the back zone. It will be shown that the quantitative totals of over-all plant protoplasm per area are similar in order of magnitude.

Current Velocities

In the course of the study, 26 dye current measurements were made in different zones and time. Fluorescein dye (from air-sea rescue kits) was released into the water by one observer and the time required to travel a measured distance to a second observer was determined. The maximum current measured was 1.44 m/sec across the reef during a high water neap tide. Currents probably twice this velocity were encountered in incoming spring tides when the observers were too busy hastening to shore to get a measurement. The lowest velocity measured on the front reef encrusting zone was 0.18 m/sec; the lowest in the back reef lagoon shelf zone was 0.009 m/sec. The mean of eleven measurements on the encrusting zone was 0.49 m/sec. The 5 ft-deep water of high spring tides probably permits strong flow over the reef although no measurements were made at this time. The larger fish which are unable to hide behind small bumps and coral heads apparently could not browse on the middle reef when the current was running over 0.3 m/sec, for no larger fishes were observed in these zones at this time.

As a rough estimate of comparative and average currents, measurements made of water transport at a neap tide at one station are converted by calculation of depth effect into velocities for the different zones and reported in Figure 2. Currents change so rapidly with time in the tidal cycle that this is the only way to make a synoptic comparison. As indicated above it was difficult to obtain measurements during high water spring tide without being washed off the reef.

TROPHIC STRUCTURE

Plant and Animal Components in Live Coral; The Predominance of Plant Protoplasm

Early taxonomists classified corals as plants, as in John Ray's system (Nordenskiold 1932), because of their vegetative appearance. Later, corals were found to be coelenterates and thus classified as animals. Yet their ecological roles that resemble plants remained a point of interest such as their predominance in the community and their practice of laying down carbonaceous substance in quantity sufficient to maintain the community substrate. Then, when the symbiotic zooxanthellae were found in the tissues of the animal polyp, it became evident that, metabolically, corals might be part-plant and contribute to the primary production of the community. Yonge, Yonge & Nicholls (1932); Kawaguti (1937); and others have shown that corals do indeed produce an excess of oxygen over carbon-dioxide during the daytime, although most measurements show that production does not quite equal respiration over a 24-hr period.

On ecological grounds, zooxanthellae, to match coral respiration, must either carry out photosynthesis many times faster than corals respire or exceed the coral animal protoplasm several times if a pyramid of mass should exist as required by the second law of thermodynamics for most systems. Yet corals have been shown to come close to achieving a balance between photosynthesis and respiration while possessing seemingly only a small amount of plant tissue in the form of scattered single algal cells restricted to the endoderm of the polyp.

However, there is yet a second plant component characteristic of corals, the significance of which seems to have been overlooked. When one breaks open a fresh, live coral head, conspicuous green bands are seen in the skeleton of the living polyp zone and also in the concentric layers in the older skeleton well below the zone of animal tissue as shown in Figures 6 and 7. These bands are not due to the yellow-brown, rounded zooxanthellae cells, but to a network of bright green filamentous algae growing in the pores of the inert skeleton (Fig. 7E). Although sometimes located as much as 2 or 3 cm below the surface, these algae growing within the translucent aragonite skeleton are, nevertheless, within light range of the intense penetrating tropical sun. All of the species of hard aragonite corals, examined at Eniwetok including hydrozoan, octocoral, and hexacoral groups contained

these filamentous green algae in abundance. Only Dendrophyllia, growing in the shade in Hawaii, was different in not possessing either the zooxanthellae or the filamentous greens of the skeleton.

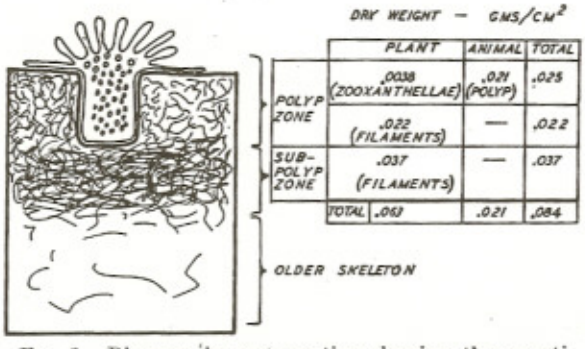

FIG. 6. Diagram in cross section showing the quantitative distribution of plant (algal) and animal (coral polyp) tissue in a generalized live coral head. Data on plant and animal biomass are from Table 4.

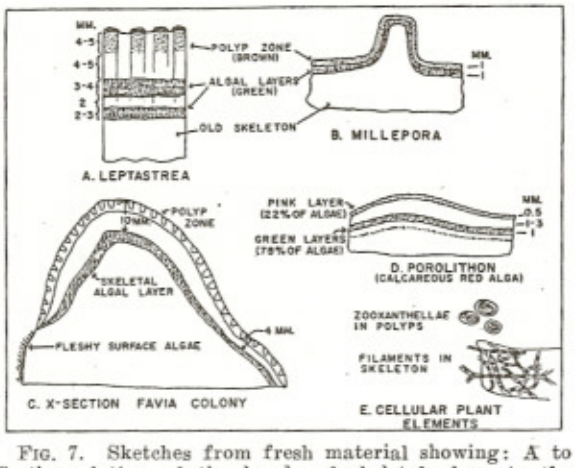

FIG. 7. Sketches from fresh material showing: A to C, the relation of the bands of skeletal algae to the polyp zone in three genera of corals. D, sub-surface green bands in the skeleton of calcareous red algae. E, the two major types of symbiotic plant material in coral colonies.

While zooxanthellae have long been considered symbiotic or mutualistic with coelenterate polyps, the possibility that the filamentous skeletal algae might also be symbiotic or at least important to the nutrition of the coral colony has been little considered. Indeed, most writers refer to these conspicuous algae as "boring algae" and consider them as parasitic agents which weaken the skeleton and hinder the growth of the coral colony. Duerden (1905) found two kinds of filaments, one with cross walls, one without. As one of the first to describe the filamentous skeletal algae, he stated that they "invade the coral-lum, weakening it if having no other effect." This view seems but little challenged although Edmondson (1929) stated that his evidence was not conclusive that these algae check the metabolism since he found that some "heavily infested" colonies showed good coral growth in the laboratory. It may well be, that the boring filamentous algae of live corals are beneficial, and at least under conditions existing on this study reef, contribute to the survival and rapid growth of major reef builders. Thus, there is a sharp contrast between the boring algae in live corals and the different species boring in dead coral. The species of algae which have been described as boring in calcareous substrates are listed by Utseumy (1942).

The evidence that there is a predominance of producing plant protoplasm rather than coelenterate polyp protoplasm in a live coral head is based on high chlorophyll content found in the non-polyp parts of live coral heads relative to dry weight estimates of animal polyps. The dry weight of producing plant tissue was determined from the chlorophyll values with the graph in Figure 8 on the assumption that algae in the coral skeleton and polyps have a chlorophyll-dry weight ratio similar to free-living algae. Details of the method used are given below in the section on primary producers. Rough quantitative estimates of the dry weight of the animal-polyp component of a coral head were obtained by estimating the volume of the coral head occupied by polyps and assuming that the dry weight to volume ratio of anemones represents that of coral polyps. The polyp volume was estimated by a vaseline method. Further details on estimation of polyp volumes and dry weights are given in the section on coral polyps. Rough estimates of zooxanthellae dry weights were obtained from chlorophyll extraction of isolated polyps of a large polyp species (Lobophyllia) and from histological sections pictured by Yonge, Yonge & Nicholls (1931) and further described in the following section on producers. The data on plant and animal components are given in Tables 1, 2 and 4.

The estimate of .075 gm/cm² residue after treatment with 20% nitric acid (Mayor 1924) compares well with the finding of .062 gm/cm² mean loss on ignition (Table 2) as an estimate of total biomass.

The diagram in Figure 6 and the mean estimates of protoplasmic components in Table 4 summarize the data and present a general picture of the coral head, which is almost a whole ecological community in itself with producer, herbivore, and carnivore roles all in one. The essential components thus appear to be: (a) animal (non-photosynthetic) tissue, (b) zooxanthellae, (c) filamentous green algae in the sub-surface skeleton and between polyps, (d) bacterial components which are not estimated in this study but which may be of importance.

The important quantitative conclusion from Table 4 is that the total plant protoplasm exceeds the animal biomass (about 3 to 1) and the filamentous green algae have a greater biomass than the zooxanthellae (about 16 to 1). If the filamentous skeletal algae are considered an integral part of the coral colony along with the zooxanthellae, a reasonable biomass pyramid is obtained which is in line with the high photosynthetic activity shown by most coral colonies.

Comparison of live and dead corals provides indirect evidence of symbiotic relationship between

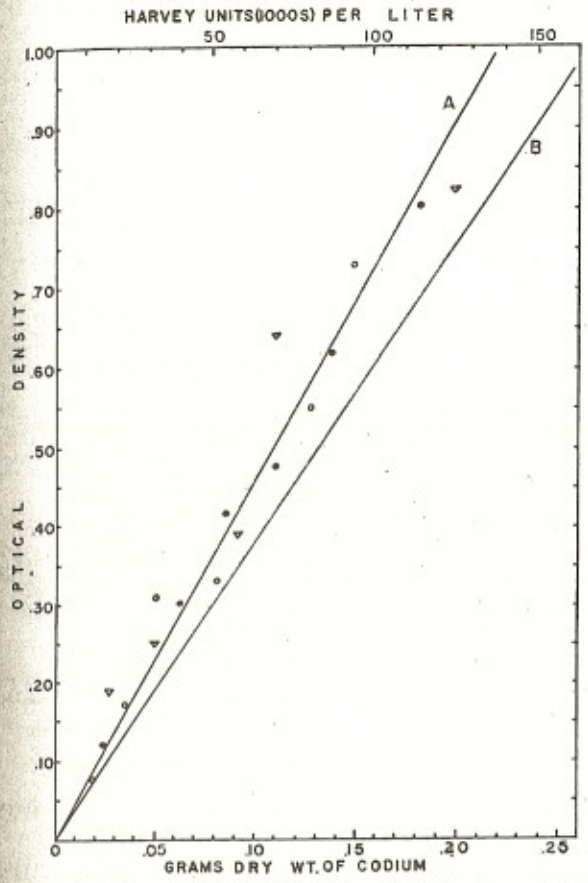

FIG. 8. Curve (A) relating chlorophyll to dry weight of *Codium edule*. This graph was used as a means of obtaining rough estimates of the dry plant protoplasm in coral heads and other calcareous substrates. The curve is based on three replications as indicated by the three types of symbols. B is correction for average loss of color on drying. See text for further explanation.

coral animals and filamentous algae in the skeleton. Algae occur in characteristic bands under living polyps (Figs. 6 & 7) and the bands show patterns which are characteristic for a given species. These sub-surface bands disappear if the coral animals above them died to be replaced by other algae which grow on and near the surface of the dead skeleton. Thus, the bands are not present on the sides of the head where there are no live polyps (Fig. 7C). Although no attempt was made to classify the filaments, the microscopic appearance of algae in bands under live polyps is clearly different from that of algae growing on and in dead coral material. Dead corals included boring greens, reds, and blue-greens, whereas the live corals observed contained only greens.

These observations suggest the hypothesis that skeletal algae, as well as zooxanthellae, have a symbiotic relationship with coral animals. Nutrients of coral metabolism may readily diffuse through the porous skeleton to the algae. The coral skeleton provides matrix and some enclosed nutrient, and the polyp-protoplasmic sheet on the outside protects the delicate filaments from competition, browsing, and

Table 1. Quantitative distribution of algae in corals.

	Percent of Total Algae	
	Polyp Layer	Sub-polyp Layer
A. Vertical Distribution of Algae in Massive Corals		
Leptastrea sp. (B-3)	40	60
Faria sp. (C-3)	34	66
Porites sp. (B-6)	40	60
Porites sp. (B-6)	46	54
Turbinaria mesenterina (E-4)	43	57
Mean	41	59

	Percent of Total Algae	
	In Branches	In Basal Zones
B. Distribution of Algae in Branching Corals		
Acropora sp. (D-9)	59	41
Acropora sp. (D-9)	57	43
Pocillopora sp. (C-8)	68	32
Lobophyllia sp.	66	34
Mean	62	38

C. Zooxanthellae in Coral Animal Tissue

Percent zooxanthellae in a coral planula*	27%
Percent zooxanthellae in a coral polyp (estimated from histological cross section)*	14%
Mean of extraction of two *Lobophyllia* polyps	16%

	Individual No. 1		Individual No. 2		Mean	
D. Biomass Distribution in *Lobophyllia*, Gms/cm²						
Biomass in Polyps:						
Zooxanthellae in polyps	.013	13%	.018	19%	.016	21%
Animal tissue in polyps	.041	97%	.077	81%	.059	79%
Total biomass of polyp	.054	100%	.095	100%	.075	100%
Comparison of Zooxanthellae and Algal filaments outside Polyps:						
Zooxanthellae in polyps	.013	31%	.018	18%	.016	19%
Algal filaments	.029	69%	.084	82%	.067	81%
Total plant biomass	.042	100%	.102	100%	.083	100%

Distribution of Plant Biomass:		
Zooxanthellae in polyps	.013	31%
Filaments around polyps	.015	36%
Filaments below polyps	.014	33%
Total plant biomass	.042	100%
Comparison of Animal and Plant Biomass:		
Animal biomass (from Table 4)	.042	46%
Total plant biomass	.083	54%
Total plant and animal biomass	.155	100%

*Calculated from data of Yonge et al. (1931).

intense sunlight (note from figure 7C that algal bands are deeper in the skeleton at the apex where light intensity is greatest).

From the quantities of algae present relative to coral protoplasm, it would be supposed that coral animals benefit from diffusion of organic substances from the algae but direct evidence of this was not obtained. Coral animals would still need to obtain some food and critical nutrients such as nitrogen by ingesting plankton, since there is not enough plant material to completely support the coral and since the coral requires a higher nitrogen content. Also, it is possible that the sub-surface algae raise the pH

TABLE 2. Quantitative estimates of animal tissue in coral polyp zones gm/cm².

Species	Depth of Polyp Zone cm	Total Biomass (Loss on Ignition*)	Plant Biomass (Extract Methods; Tables 1 & 5)	Animal Biomass in Gm/cm²			
				By subtraction (Total Minus Plants)	By Estimate of Polyp Volumes† (See Table 3)	By Direct weighing of isolated polyps‡	Mean Animal Biomass
Pocillopora (C-8)	.1	.035	.036	−.001	.0015	....	.007
Millepora (B-2)	.15	.044	....	....	.007	....	.007
Porites (D-2)	.2	.043	.016	.027	.009	....	.018
Heliopora (E-3)	.3	.043	....	....	.0144	....	.014
Leptastrea (B-5)	.4	.062	.019	.043	....	....	.043
Astreopora (M-30)	.5	.045	....	....	.015	....	.015
Turbinaria (E-4)	.8	.062	.026	.036	.019	....	.027
Favia (C-3)	1.0	.050	.019	.031	.029	.015	.025
Lobophyllia	2.2	.173	.081	.092	.064	.059	.072
Mean of corals	.64	.062	....	....	....	....	.025
Anemone-sand grain—algae complex	.5	.086	....	....	....	.034	....

*Loss on ignition in furnance at 600°C.
†Volume of polyp zone assumed to be filled with protoplasm like that of sea anemones growing on the reef with a density of about 1 and a 15.1% dry weight of wet weight. (Similar dry weights of wet weights are summarized for other Coelenterates by Vinogradov, 1953.) Estimates with 15% error of underestimation due to dry tissue in pores possibly cancelled by pore space occupied by plant filaments and zooxanthellae.
‡It is not possible to separate all of the polyp out, even in large polyp species. Possible compensation comes from using weights rather than loss on ignition of separated polyps.

TABLE 3. Density, porosity, loss on ignition of skeletons.

Species and Zone		Skeletal Density gm/cc	Gross Dry Density gm/cc	Porosity in % (vaseline method)			Loss on Ignition % (of dry)
				A	B	Mean	
FRESH DRIED LIVING CORALS							
Pocillopora	branch	2.09	1.86	10.0	12.4	11.2	4.9
Millepora	polyp zone	....	1.51	....	....	33.3	8.9
	whole	2.27	1.42	....	....	37.6	....
Porites	polyp zone	2.38	1.66	30.4	30.4	30.4	12.7
	Algal zone	1.98	1.50	17.4	26.5	22.0	4.7
	layer 3	2.08	1.70	15.4	21.0	18.2	4.5
	layer 4	2.33	1.72	24.4	26.0	25.2	4.4
	layer 5 (eroded)	2.24	1.68	20.1	32.2 (hole)	26.1	3.9
Leptastrea (B-3)	polyp zone	2.38	1.82	....	....	23.3	4.1
	algal zone	2.28	2.12	....	....	7.0	2.6
	sub-algal	2.47	2.18	....	....	11.6	1.7
Heliopora	polyp zone	2.89	1.63	....	....	31.9	8.9
	whole	2.42	2.24	....	....	7.1	....
Astreopora	polyp zone	2.51	1.99	22.6	18.1	20.3	4.8
Turbinaria	polyp zone	2.44	1.90	....	....	22.0	4.5
	whole	....	1.50	....	....	38.7	....
Favia (C-3)	polyp and algal zone	2.33	1.83	22.2	20.2	21.4	5.4
Lobophyllia	polyp zone	2.18	1.64	25.1	24.7	24.9	4.8
FRESHLY DRIED ALGAL SKELETON							
Porolithon		2.38	2.20	....	....	7.8	4.5
SKELETONS FROM REEF MASS, 20 FT DEEP IN DYNAMITE HOLE							
Porolithon		2.64	2.53	....	....	3.2	3.9
Favia?		2.38	2.22	....	....	6.7	2.9
MEAN OF POLYP ZONES (7)		2.44	1.73	....	....	26.6	7.0
MEAN OF SUB-POLYP ALGAL ZONES (2)		2.13	1.81	....	....	14.5	7.3
MEAN OF SUB-ALGAL LAYER ZONES (3)		2.29	1.87	....	....	18.3	3.5

TABLE 4. Summary of components of biomass in corals, mean data. Figures given: in gm/cm² dry weight and in percent of total biomass.

		Plants Tissue	Animals Tissue	Total Biomass
Polyp Zone	In Polyps	.0038* (zooxanthellae) 4.5%	.021† 25%	.025 30%
	Between Polyps	.022‡ (filaments) 26%	....	.022 26%
	Total in Polyp Zone	.026‡ 31%	.021 25%	.047‡ (.062§) 56%
Sub-polyp Zone		.037** (filaments) 44%	....	.037 44%
Total Biomass Outside Polyps		.059 70%	....	.059 70%
Total of all Layers		.063†† 75%	.021 25%	.084 100%

*Mean of zooxanthellae extracted from Lobophyllia (13% and 19% of polyps in Table 1) and calculated from Yonge (14% of polyps in Table 1). 15.3% of .025 gms/cm² polyps (from Table 2).
†.025 gms/cm² polyps (from Table 2) minus zooxanthellae estimate .0038 gms/cm².
‡Total plant estimate for the polyp zone minus zooxanthellae estimate.
‡41% (from Table 1) of Plants are in Polyp zone; mean plant estimate per area of coral .063 gms/cm² from Table 5.
‡Sum of plants and animal estimates.
§Total organic matter estimate based on loss on ignition at 600°C for comparison. (from table 2)
**59% of plants in sub-polyp algal zone (from Table 1); mean plant estimate per area of coral, .063 gms/cm² from Table 5.
††From Table 5.

(and thus slow skeletal decomposition) or actually contribute directly to the skeleton formation of the coral complex. Certainly evidence is lacking that the presence of algae in any way weakens the live skeleton so long as the coral-algal complex is intact. The high strontium content of aragonite coral skeletons being in the same or higher ratio to calcium as the sea water (9.23 atoms per 1000 atoms) is unusual for calcareous animals. The similar high ratio in the green calcareous alga Halimeda suggest some similarity in the deposition process of corals and Halimeda that might be explained by a role of the green filamentous algae in deposition in the coral. Since the green filaments are tightly enclosed within the coral colony, any organic matter produced by them as growth or surplus diffusable products cannot escape without going through the enclosing polyp zone. There is no room for such growth except as the whole colony grows and there is no visible accumulation of organic products. The situation leads to the supposition that either the plants are growing close to the compensation point or are supplying coral animal polyps with organic materials. Since there are often several bands of healthy green filaments, it is possible that, if the deepest band were at the compensation point, the top bands would be making an excess which was being used by the corals and deeper algae.

From the standpoint of the entire reef ecosystem it does not matter how much food made by algae within the live coral head is used by coral animals directly. Only by considering the large amount of producer tissue in a coral head is it possible to explain the great preponderance of organisms classed as animals. Thus the coral reef is like most known self-sufficient ecosystems in having a much greater weight of plant biomass than animal biomass.

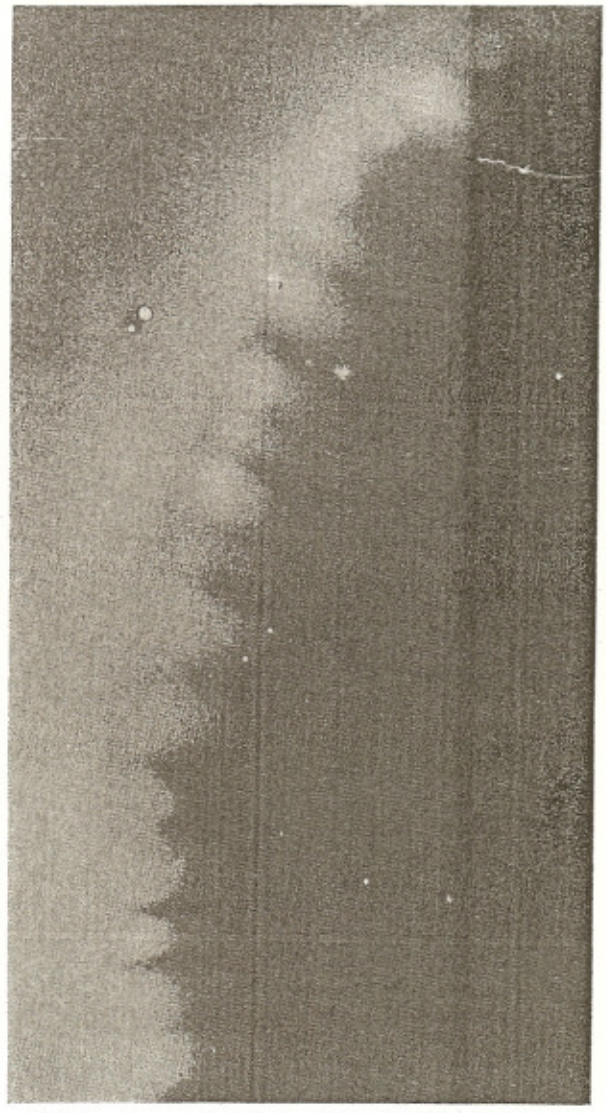

FIG. 9. A positive print of an autoradiogram of a section of a coral head (Goniastrea) after two days' exposure; light areas indicate exposed and dark areas unexposed film. Note that the surface polyp zone, but not the subsurface algal bands (see Fig. 7), exhibited considerable radioactivity.

An internal use and reuse of nutrients in a living coral is suggested by the autoradiogram (positive) in Figure 9 which is typical of ten made from corals from the generally (low level) radioactive Japtan reef. The radioactivity is entirely restricted to the animal polyp zone. Whereas algae on dead reef surfaces were intensely radioactive, these forms beneath the corals are apparently not in nutrient contact with the outside water except through the coelenterate tissues. This may be interpreted as an evidence that

the coral algal filaments receive nutrients from the corals. By this view the radioactive elements in the polyps are not of the type which are released by the corals during their daily metabolic cycles. Cerium and praesodymium have been strongly implicated as main components to previous reef radioactivity (Blinks 1952; Donaldson *et al.* 1950). Apparently the calcophile elements like calcium and strontium are not retained but rapidly exchanged away by the high non-radioactive concentrations in the flux of sea water over the reef.

Although the filaments and zooxanthellae are small in size, their photosynthetic rates on a dry plant weight basis (Mayor 1924) are not nearly as high as free algae growing in nature as quoted by Verduin (1952); thus, for the same production per area, more biomass is required than in a plankton population, for example.

If the filamentous algae are truly mutualistic with corals then there may be no need to create separate taxonomic names for them. The coral-algal complex could be considered as a single species entity as is the fungal-algal complex of lichens, and the established names for the corals used to cover both elements.

PRIMARY PRODUCERS

In the previous section the complex association of plants and animals in a live coral head was discussed with a new viewpoint. In this section all of the main groups of primary producers (plants) are described and quantitative estimates are presented in Table 5.

The main primary producers grouped ecologically are as follows:

(1) filamentous algae in live corals.

(2) zooxanthellae in coral polyps.

(3) algae matted as an encrustation on and in the dead rigid porous reef substrate surface in the swift current zone.

(4) Encrusting fleshy green types such as Dictyosphaeria, Zonaria, and Caulerpa attached to the irregular surface, with encrusting calcareous reds such as Porolithon and Lithophyllum mostly beneath.

(5) Small algae in and on loose coral shingle (broken coral pieces) lying in channels and in areas between coral heads.

(6) Small filamentous algae in and on "dead heads." (A dead head is defined as a coral formation no longer containing living coral polyps but still standing erect on the surface of the reef.)

(7) Large conspicuous bunches of branching algae attached around dead heads including genera such as Codium, Asparagopsis, and Halimeda.

(8) Algae in the coarse, white, calcareous sand which covers inter-coral areas of the back reef.

(9) Zooxanthellae and filamentous algae in animals other than coral polyps such as sea anemones and giant clams (Tridacna, etc.).

(10) Planktonic algae derived from the open sea and the much larger quantity of pseudoplankton breaking off the other sessile masses. Sargent & Austin (1949) showed the relative insignificance of the plankton production in the reef's metabolism. The relative sparsity of true plankton is suggested by the absence of attached plankton feeding molluscs, hydroids, tunicates, and ectoprocts on the glass slides as reported in Table 6. The attachment aufwuchs was entirely autotrophic.

A reef community resembles a complex, tropical, terrestrial community in that it is not dominated by one or two producer species, but there is considerable diversity and variation from place to place. On the reef, for example, the myriads of tiny blue green,

TABLE 5. Primary producers of the reef.

1. ALGAE IN LIVING CORALS (filaments in skeleton and zooxanthellae in polyps)	Quadrat	Gms. Dry Wt. per cm²
(a) Massive Scleractinia		
Leptastrea (B-3)	B-C	0.049
	B-C	0.038
	B-C	0.049
	B-C	0.037
	B-C	0.033
	B	0.076
Favia (C-3)	B-C	0.054
	B-C	0.060
	B-C	0.058
Favia (B-4, green species)	B-C	0.116
	C	0.135
Porites lobata (C-1)	C-D	0.044
	C-D	0.040
	B	0.043
Porites lobata (in deep water)	E	0.016
Turbinaria mesenterina (E-4)	E	0.060
Acropora palmerae (B-1, encrusting form)	B	0.036
Mean of Massive Scleractinia	..	0.056
(b) Branching Scleractinia		
Acropora cymbicyathus (D-9)	D	0.038
	D	0.048
Pocillopora (C-8)	C	0.077
	C	0.038
	A	0.043
Lobophyllia	*	0.124
	*	0.053
Mean of Branching Scleractinia	..	0.060
(c) Octocorallia and Milleporina		
Heliopora caerulea (E-3)	D	0.056
Millepora platyphylla (B-2),		
encrusting section	D	0.029
vertical branch	E	0.094
Millepora murrayi (E-2),		
encrusting section	E	0.078
encrusting section	E	0.080
encrusting section	E	0.065
encrusting section	E	0.041
vertical branch	E	0.117
vertical branch	E	0.074
Mean of Octocorallia and Milleporina	..	0.070
Mean of all corals (33 specimens, 12 species)	..	0.063

TABLE 5. Primary Producers of the Reef (Continued).

2. ALGAE IN REEF SUBSTRATES	Quadrat	Gms. Dry Wt. per cm²
Reef floor—with fleshy algal mat	A	0.062
Reef floor—with fleshy algal mat	A	0.041
Reef floor—*Porolithon* encrusted	A	0.042
Reef projection, upper plus under surface	A	0.092
Reef projection, upper plus under surface	A	0.080
Reef floor—with fleshy algal mat	B	0.072
Reef floor—with anemones on surface	B	0.070
Reef floor—very porous	C	0.122
Algal mat separated from reef surface	B	0.008
Algal mat separated from reef surface	B	0.007
Algal mat separated from reef surface	C	0.004
Algal mat separated from reef surface	C	0.003
Porolithon separated from reef surface	A	0.030
Rubble (Shingle), new, non-porous	C	0.029
Rubble (Shingle), old, porous	C	0.047
Rubble (Shingle), old, porous	D	0.066
Rubble (Shingle), old, porous	D	0.060
Rubble (Shingle), old, porous and eroded	D	0.141
Rubble—buried 25 cm deep in dead head	D	0.028
Rubble (Shingle), old, porous	F	0.110
Deadhead—surface and internal algae	D	0.049
Deadhead—internal algae only, surface "grazed" by fish	D	0.042
Deadhead—	D	0.061
Deadhead projection, upper plus under surface	D	0.160
Sand—deep channel	D	0.0019
Sand—shallow channel	D	0.017
Sand—deep channel	F	0.009
Mean—reef floor	A-C	0.073
Mean—old shingle	C-F	0.085
Mean—deadheads	D	0.078
Mean—sand	D-F	0.009

3. ALGAE IN AMINALS OTHER THAN CORALS	Quadrat	Gms. Dry Wt. per cm²
Anemones—sand complex; zooxanthellae in polyps and filamentous algae in attached sand grains.		
Sample 1—zooxanthellae in polyps plus filamentous in attached sand	B	0.037
Sample 2—zooxanthellae in polyps plus filamentous in attached sand	B	0.025
Sample 3—zooxanthellae in polyps only	B	0.030
filamentous in attached sand	B	0.017
Total	B	0.047
Sample 4—zooxanthellae in polyps only	B	0.045
filamentous in attached sand	B	0.019
Total	B	0.064
Giant clam (Tridacna)		
Algae in mantle exposed to sun when shell fully open	D	0.052
Algae in calareous shell of same specimen	D	0.031

*From lee reef at Rigili Island

TABLE 6. Reef fouling on glass slides submerged 21 days. (Each figure unless otherwise indicated is the mean of 5 counts; slides submerged July 3 to July 24, 1954; counts in numbers of individuals per cm².)

	Front Reef Encrusting Zone	Back Reef Zone of Large Heads	Slides imbedded in coarse bottom sand
Station designation (quadrat)	B-1	D	C
Depth of water over slides at low-water spring tide in cm	10	30	20
Larger algae (greater than 5 microns) individuals/cm²:			
Greens (*Enteromorpha*, siphonaceous)	97	33	0
Browns (*Ectocarpus* and others)	290	53	133
Reds (filaments and calcareous pieces)	2	26	0
Blue-Greens	47	39	3
Diatoms	0	693	20
Smaller algae (less than 5 microns)			
Greens	1.2×10^5	9.0×10^5	15.4×10^5
Blue-Greens	2.4×10^5	$.2 \times 10^5$	6.6×10^5
Encrusting diatoms	52.8×10^5	5.4×10^5	$.4 \times 10^5$
Bacteria	4.4×10^8	2.4×10^8	1.2×10^8
Ciliates, nematodes, other similar sized soft bodied animals	600	132	15
Foraminifera (small sized types)	.6	.4	0
Dry weight of algal protoplasmic biomass by chlorophyll method in mg/cm²	2.5	1.6	..
Plankton feeders such as barnacles, molluscs, ectoprocts, hydroids, tunicates	0	0	0

brown, red, and green algal filaments embedded in live and dead calcareous materials have been little studied, yet they make up a large part of the food making biomass of the reef community. Some idea of this component can be gained from counts of attached algae on glass slides (Table 6). In spite of the great diversity in species there seems to be a fairly uniform distribution of producer biomass as estimated with the chlorophyll method. Particularly since the living primary producers are so completely interwoven with animal material and in dead skeletal material, the chlorophyll extracting method seemed to be the most practical way of obtaining quantitative estimations readily comparable with other communities. To permit comparison with other areas the chlorophyll methods are outlined in some detail. It is recognized that chlorophyll is not a perfect measure of the active plant protoplasm and that it varies considerably with species, physiologic age, and growth conditions.

All values for irregular shapes are reported in gms dry weight per area of the horizontal plane covered. (This surface is much less than the surface area of the irregular object.) For corals a small block was cut out with a hacksaw and the area of the block's projection on the horizontal surface was measured.. The block was cut deep enough to include all visible green material (25 mm usually sufficed for massive corals, deeper sectioning was required for branching forms). It was later found that some algae occur even below the visible green zones but the amount is so small as to be scarcely measurable with the methods used. The block was pulverized with a

hammer, ground up in a mortar and extracted with successive washings of acetone until all the chlorophyll had been removed. The extract was filtered into a test tube, adjusted to 20 ml and read photometrically. Reef substrates, rubble and dead heads were also cut into blocks with a measured surface area and treated in the same way, care being taken not to lose the algae growing on the surface. Sand from a measured area was removed into a bottle and then ground and extracted in the same manner. It was found that materials must be extracted fresh, preferably not more than 12 hours after collection. Oven-dried materials invariably gave lower values than comparable fresh materials. For corals and most reef materials a piece with a surface area between 1 and 4 sq cm was required for extraction with 20 ml of acetone.

In the massive corals, algae are concentrated in layers just beneath the surface (Fig. 7) while in branched corals it is distributed along the branches with less concentration at the base and with relatively little at the exposed tips of branches. In fact in some branched forms the algae are so diffuse that the intensely green solutions derived from pale pieces of coral are surprising. A "block" of a branching coral type such as Acropora or Pocillopora, as used for extraction, consisted of a vertical branch together with the basal section from which the branch arose. The cross sectional surface area of such a block (including all branches in the imaginary prism directly above the measured area on the horizontal) was considered comparable with the surface area of flat encrusting corals, since the amount of light per square centimeter of horizontal surface should be similar.

To convert photometric readings into biomass of producing tissue, a calibration curve was determined from acetone extracts of known dry weights of an arbitrarily chosen alga abundantly available in the field. *Codium edule* was selected as a standard and a relatively constant relation was found between chlorophyll content and dry weight (Fig. 8). A small portable colorimeter was used at first until a Coleman Spectrophotometer Model 6 became available. Codium used for calibration was freshly collected and paired, duplicate pieces were respectively dried and extracted for chlorophyll. Since a 20% loss of chlorophyll was found in pieces oven dried at 100° C for 6 hr, all extractions based on oven dried materials must be corrected for loss on drying. Figure 8 shows the calibration curve for optical density at 670 millimicrons as a function of Codium dry weight based on 3 replications on 3 different batches of material. A straight line results with monochromatic light. With the colorimeter first used, a reproducible curved line was obtained for absorption as a function of dry weight of Codium. The line allowing 20% correction for loss of chlorophyll on drying is also drawn in Figure 8. A series of nickel-chromium solutions was made as reference standards and readings equivalent to dry weights of Codium were included in Figure 8 (upper scale). 10,000 Harvey units/1 were made up with 4.3 gm/1 nickel sulfate and .25 gm/1 potassium dichromate. Since the readings reported in Figure 8 were made with a spectrophotometer as 670 millimicrons instead of visually as originally defined (Harvey 1934), these are not Harvey units as usually used as a measure of chlorophyll but considerably different. Measurements made later on the nickel-chromium solution with a Beckman model DU spectrophotometer indicate that the optical densities in Figure 8 were made with an optical path of about 2 cm. From Richards (1952) these densities indicate an order of magnitude of .7 mg chlorophyll/gm dry Codium.

The values for algal dry weights obtained with the above methods are given in Tables 1 and 5 arranged according to the general producing types previously listed. These dry weights may be overestimates since the small filamentous strands, so important in many reef materials, are smaller and thus likely to have a lower dry protoplasmic weight-chlorophyll ratio than that characteristic of the standard used, Codium. No correction was made for ash in Codium.

The following tentative conclusions are indicated from these data about primary producers:

1. There is a striking similarity between values obtained with different species of corals. When expressed in terms of cross-sectional area projected on the horizontal, the branching types as compared with flat or rounder massive types were little if any higher in algal content even though much more calcareous matter was extracted and even though the actual surface area of branching forms exposed to the water was much greater. The branching life-form may be an advantage to the animal part of the coral in catching plankton from deep water and possibly useful to plant components in obtaining nutrients. The functional plant producers, however, seem to be regulated by the available light and are more widely dispersed in the branching forms. Thus, in general, the chlorophyll, per area perpendicular to the sun, is suprisingly uniform. The chlorophyll per area of a steady-state community may be expected to have a uniformity and greater significance than in transient bloom populations and laboratory cultures. It may be a better measure of producers and productivity under these more constant conditions.

2. While the algal content of different species of corals was of the same general order of magnitude, distinct species differences are indicated. Thus among the massive corals an unidentified species of Favid (code #B—4) had about twice the algal content of other species of favids (Table 5). This coral is very green in appearance with abundant green algae and zooxanthellae in the surface in the polyp zone as well as in the subsurface zone. Among the branching types, Millepora appears to be high and in both species (*M. platyphylla, M. murrayi*) the tall vertical branches were found to contain more algae per cm^2 cross section than flat portions of the same colony. A wide 100 fold range of production and respiration values had been established for corals by Kawaguti (1937).

3. In so far as our small number of samples shows.

there was little evident difference in producer content of live corals in different zones of the reef which range from ½ to 4 ft deep at low spring tide. Similarly, the corals collected in Kaneohe bay in Oahu, Hawaii although from more turbid water gave similar orders of magnitude of chlorophyll content for comparable species.

4. The white sand area of the back reef was the only major area of the reef which had a definitely lower biomass of producer protoplasm.

5. From the data on glass slide attachment in Table 6, about twice the growth of encrusting algae was obtained in the front reef as on the back reef correlating with the predominance of encrusting forms up front with boring forms in back.

CORALS AS CONSUMERS

Estimates based on mapped quadrats (Figure 5) indicate, along with cursory survey, that most of the reef surface is between 16% and 50% covered with live coral. Although the living part of a coral is more plant than animal there is, nevertheless, an important total weight of animal coral. It has been repeatedly shown (Mayor 1924, Edmondson 1929, Yonge 1930) that coral polyps are in part carnivores in trophic classification, since they catch zooplankton, especially at night. And if the inferences of the previous sections and of previous authors (reviewed in Yonge 1930, Kawaguti 1937) are correct, a coral animal polyp is very much an herbivore because of nutrition received from symbiotic algae. Thus, the animal part of a coral is partly divided in trophic classification between two trophic levels, herbivores and carnivores. Three procedures were used to obtain an estimate of the dry weight of the consumer fraction in live coral.

First, the volume of the polyps was estimated by filling the pores of a slice of coral from the polyp zone with melted vaseline. From the amount of vaseline filling the pores, the polyp zone porosity is determined as an upper limit to the polyp volume. One source of error, the inclusion of pores not occupied by polyps, may be cancelled by the error of not including pores partly blocked by animal and plant dry-residues. In drying, shrinkage of polyps may be expected to be greater than shrinkage of algal filaments within the skeleton. Thus, a rough upper limit figure for primarily animal volume (with enclosed zooxanthellae) may be obtained. The steps in this procedure are as follows: (1) cut a slice of polyp zone with hacksaw, measure surface area, dry, and weigh; (2) place in melted vaseline in oven 6 hours until permeated, remove, cool, wipe all excess vaseline off the outside, weigh; (3) the figure for vaseline in pores obtained by subtraction of weights, should be divided by the density of the vaseline to obtain the volume occupied; (4) multiply the volume by the dry weight equivalent for anemones and divide by the area to obtain final figure for dry weight polyp per square centimeter.

For two species with large polyps, it was possible to tease out the protoplasm and obtain a dry weight directly.

In the procedure for the third method of estimating polyp biomass, the chlorophyll-based estimate of the plant part of the polyp zone is subtracted from the total loss on ignition (600°C). This method assumes that most of the loss on ignition of the polyp zone is due to ashing of live plant and animal tissues.

Some estimates for polyp weights from the three methods outlined above are given in Table 2, where they are in sufficient agreement to permit some confidence in the order of magnitude at least. The predominance of plants over the animal component seems clear.

The role of current in limiting coral distribution is supported by their distribution relative to currents at low tide (Fig. 2). Values for the quadrats show a decrease in coral coverage as the current decreases. Since ample light for photosynthesis penetrates the clear waters of the back reef it would seem likely that current is a major factor in the decrease of coral coverage.

CONSUMERS OTHER THAN CORALS

Although the trophic relationships of most of the higher organisms on the reef are very imperfectly known, an attempt has nevertheless been made to make rough groupings by trophic level as to herbivores, carnivores, and decomposers. Drs. Hiatt and Weylander generously gave their help on this, drawing on studies of food relationships in preparation.

Each of the groups required a suitable means of obtaining a weight estimate per area. It must be realized that the great clarity of water permits face mask work with as great visual intimacy as on a terrestrial quadrat. In Tables 7-12 are presented the results of the various estimates by methods briefly listed with trophic levels below. Where an organism eats the matting of algae with included small invertebrates, an omnivore classification might be correct except that by weight most of this material is plant. So, such consumers are classed as herbivores. For example, a negligible biomass estimate was obtained for microcrustacea in algal mats.

The following are the groupings and methods used for estimating trophic components. Since considerable doubt exists as to the trophic relationships, the groupings are kept separate in the presentation to

TABLE 7. Benthic Foraminifera; counts of individuals /cm². (Counts of representative algal mats and sand patches have been multiplied by the coverage of these areas in the quadrats.)

Quadrat	Coverage of sands or mats containing Foraminifera	Small Forams .01 cm size	Large Forams .1 cm size
B (Front, encrusting)	70%	25	0
C (Small Heads)	34%	2	5
D (Large Heads)	34%	2	32
E (Sand-Shingle)	67%	3	54

TABLE 8. Dry biomass estimates on quadrat A on the algal-coral ridge.

Biomass Component	Quantity measured, calculation	Mean Biomass averaged over the Quadrat gms/m²
PRODUCERS		
Algae in corals	Coral coverage estimated 50% (Fig.5) Algae in non branching coral .063 gms/cm² (Table 5)	315.
Fleshy and calcareous Algae in crust and subcrust	Algae coverage estimated 50% (Fig. 5) .064 gms/cm² (Table 5 average Quad. A reef floor)	320.
Total Estimate of Producers		635.
HERBIVORES PREDOMINATELY		
Slate pencil urchins (*Heterocentrotus trigonarius*)	Quadrat count: 6(5, 5, 8) individuals/9 m² 59.3 gms loss on ignition/individual	39.4
Gammarids and other small crustacea	Mean of 2 methods A. 16 individuals/9 cm²; .0004 gms loss on ignitson/individual	
	B. .086 gms/.04 m² collected sample	4.7
Animal tissue in corals (partly carnivore but classed as predominately herbivore because of symbiotic algae)	50% coverage (Fig. 5); .021 gms/cm² (Table 4)	105.
Parrot fish	Visual counts: .4 individual/28 m²; 9.3 gms loss on ignition/individual	0.1
Total Estimate of Herbivores		149.
CARNIVORES PREDOMINATELY		
Annelids, mostly of Nereid type	.65 gms/.04 m² sample	16.1
Small crabs and other similar sized crustacea	.28 gms loss on ignition/.04 m²	7.
Total Estimate of Carnivores		13.1
Total Biomass H/P .24; C/H .09.		807.

Table 9. Dry biomass on quadrat B on the encrusting zone.

Biomass Component	Quantity Measured, basis for calculation	Mean Biomass averaged over the Quadrat gm/m²
PRIMARY PRODUCERS		
Slab of reef rock surface containing substrate boring algae and mats of encrusting algae	70% coverage; (Fig. 5) Chlorophyll extract estimate: .072 gm/cm²	804.
Slab of reef floor covered with anemone—algal permeated grain complex	Coverage 7.0%; chlorophyll extract estimate .070 gm/cm²	49.
Halimeda clumps	Coverage 1%; .036 gm/cm² loss on ignition of clump	4.
Algae in corals	Coverage of corals 22% Mean biomass of algae in non-branching corals. .063 gm/cm² (Table 5)	139.
Total Estimate of Primary Producers		696.
HERBIVORES PREDOMINATELY		
Animal tissue in corals (partly carnivores; classed as herbivore due to symbiosis with algae)	Coverage of corals 22% (Fig. 5) .021 gm/cm² animal tissue in coral (Table 4)	46.
Snails (*Thais*)	Counts: 16.5 (16, 17) individuals/1.44 m²; .094 gm dry tissue/individual	1.
Sedentery annelids in reef floor	Visual count: 65/1.44 m² of non coral area; 70% coverage; .12 gm dry/individual	4.
Cucumbers	Count: 3/36 m²; 2.4 gm/indiv. loss on ignition	.2
Parrot fishes	.4 individuals/28 m²; 9.3 gm loss on ignition/individual	.1
Ophiuroids in coral heads	Coverage of suitable heads 8.6%; 1.59 gm loss on ignition in sample head .04 m²	3.4
Anemones (also carnivores; partly herbivores because of symbiotic algae)	.043 gm loss on ignition/individual 7.0% coverage of anemone complex; 17 individuals/120 cm² of anemone area	4.3
Total Estimate of Herbivores		59.0
CARNIVORES PREDOMINATELY		
Nereid type annelids in coral heads	Coverage of heads 8.6%; 1.86 gm loss on ignition/.04 m² head	4.
Small crustacea, crabs in coral heads	.22 gm loss on ignition/.04 m²; coverage of heads 8.6%	.5
Total estimates of carnivores other than corals and anemones		4.5

permit rearrangements as further knowledge becomes available.

HERBIVORES

Small herbivorous fishes, including primarily surgeons and damsels, were counted on the 20 ft quadrats visually and converted to dry weight using the mean dry weight per fish found in a rotenoned sample. A similar method of visual census of coral reef fish has been recently described by Brock (1954). Three species, namely, *Acanthurus elongatus, Pomocentrus jenkensi,* and *P. vauili,* made up a large percentage by weight of small herbivorous fishes at quadrat C and D as shown by rotenone samples.

Large herbivorous fishes, including especially surgeons, damsels, parrot fish, and butterfly fishes were rapidly counted with 360° underwater vision. The area of this sample was estimated from horizontal visibility measurement, and the dry weight per fish was determined from a sample of 12 speared fish of the same general size. *Scarus sordidus, S. erithrodon, Chaetodon auriga, C. ephippium, C. trifasciatus, Centropyge flavissimus, Naso lituratus, Acanthurus olivaceusm,* and *Ctenochaetus striatus* were important species in this group.

TABLE 10. Dry biomass estimates on quadrat C on the zone of smaller heads.

Biomass Component	Quantity Measured, basis for calculation	Mean Biomass averaged over the Quadrat gm/m²
PRIMARY PRODUCERS		
Algae in live coral	Coverage of coral 19% (Fig. 5) .062 gm/cm² dry algae in coral (Table 5)...	118.
Coral shingle permeated and encrusted with algae	Coverage of shingle 47%; .038 gm/cm² dry algae in shingle.....	178.
Algae in and on hard reef floor	Coverage of algal encrusted floor-rock 23%; .122 gm/cm² dry algae.....	286.
Algae in and on small dead-heads (Quadrat C dead-heads like reef floor in respect to algae)	Coverage of dead-heads 11%; .122 gm/cm² dry algae.....	134.
Giant clam algae	.2% coverage; .052 gm/cm² of exposed mantle photosynthetic surface...	1.
Total Estimate of Producers..	.....	717.
HERBIVORES PREDOMINATELY		
Small cucumbers in dead-heads	3 individuals/0.26 m² of head; 2.4 gm loss on ignition/individual; 11% coverage of dead and live coral heads..	31.
Small cucumbers around corals and in shingle	20 individuals/18 m²; 4.8 gm loss on ignition/individual.....	5.3
Large cucumbers	14 individuals/18 m²; 17.7 gm loss on ignition/individual.....	14.
Small urchins in dead heads (*Echinothrix*)	1.01 gm (4 individuals) loss on ignition in 260 cm²; 11% coverage of dead heads	4.2
Large urchins (*Echinothrix*)	56 individuals/18 m²; .61 gms loss on ignition per individual.....	1.9
Tridacna (small) (herbivorous because of symbiotic algae)	3 individuals/36 m²; 12.7 gm dry/individual minus 1 gm /m²plant in clam (see above).....	.1
Annelids in dead heads	20 gm dry (19, 21)/100 cm² dead head; 11% coverage of dead heads; loss on ignition 57%; 70% herbivores..	9.0
Sedentary annelids on hard reef floor	.126 gm loss on ignition/30 cm² of reef flat; coverage 23%.....	10.4
Sponges	10 cc volume/36 m²; 7.9% of wet is loss on ignition.....	.02
Small gastropods (*Thais* and *Conry*)	6 individuals/18 m²; .089 gm loss on ignition/individual.....	.03
Animal tissue in corals	19% coverage of coral; .021 gm/cm² animal tissue in coral.....	40.
Smaller fishes	Visual counts: 25 (21, 23, 24, 25, 34, 34, 17, 33) fish/36 m²; 2.42 gms dry/individual and 61% herbivores based on poisoned sample.....	1.0
Larger fishes	Visual counts: 52 (35, 40, 65, 75, 43)/692 m² area of horizontal visibility in all directions. 120 gm dry weight/individual; 90% herbivorous; large fishes absent from area 1/3 of time during maximum currents.....	5.0
Total Estimate of Herbivores.	.....	122.
CARNIVORES PREDOMINATELY		
Molluscs	6 individuals/18 m²; .09 gm loss on ignition/individual.....	.03
Small starfish	11 individuals/18 m²; 1.0 gm loss on ignition/individual.....	.6
Large starfish	1 individual/36 m²; 106 gm loss on ignition/individual.....	3.0
Smaller fishes	39% of fish counted (see herbivorous fishes above).....	.65
Larger fishes	10% of fish counted (see herbivorous fishes above).....	.7
	1 stone fish/36 m² (100 gm dry) (A stone fish was twice taken from the quadrat area during two days' work)	2.8
Annelids	Estimated 30% of annelids in dead heads (see herbivorous annelids above).	4.0
Total Estimate of Carnivores.	.....	11.2

It can be noted that attempting to poison out quadrats or other measured areas with rotenone proved to be a poor census method in itself, but was a valuable adjunct to visual counts. Many of the larger herbivorous fishes, which abound in coral reefs, travel in active schools and quickly move out of a limited poisoned area. But after the active fishes were censused by repeated counts rotenoning the quadrats revealed the hidden element of small fishes which could then be added to the population estimate.

Herbivorous molluscs, sea urchins, sea cucumbers, brittle stars, and other large invertebrates were counted by hand in subquadrats as the observer carefully took the superstructure of the reef apart, lifting dead material, and breaking open heads with a hammer. The loss on ignition value (600°C) for an average sized organism was used as a rough estimate of live protoplasm to convert numbers of each phyletic type into biomass. Herbivorous molluscs were primarily Thais, Cypraea, and Tridacna.

In the *Herbivorous annelids* were somewhat arbitrarily included all those annelids in sedentary tubes and all those without pharyngeal jaws. These were estimated from sample heads of measured horizontal area coverage carried back to the laboratory and broken open. Allowing the head to stand in stagnant water was found effective in inducing the annelid component to crawl out into the surrounding water prior to death. With estimates of the coverage of

TABLE 11. Dry biomass estimates for quadrat D on the zone of complex larger heads.

Biomass Component	Measurement; Basis for Calculation	Mean Biomass averaged over the Quadrat gms/m²
PRIMARY PRODUCERS		
Algae in live coral	Coverage of live Coral 16% (Fig. 5) .062 gm dry algae/cm² coral (Table 4)	100.
Algae in shingle (dead coral fragments)	Coverage 10%; .089 gm/cm² algae in shingle (Table 5)	89.
Algae in tall complex dead heads, encrusting and permeating	Coverage of dead heads; 40%; .049 gm/cm² algae in and on dead heads	197.
Halimeda clumps in dead heads	Coverage of dead heads 40%; .013 gms loss on ignition *Halimeda*/cm² head	52.
Fleshy algae on lower dead parts of tall live heads	Coverage of live heads 16%; 7.5 gms loss on ignition/400 cm² live head	30.
Algae permeating and encrusting dead cobble under live heads	Coverage of live heads 16%; .028 gm/cm² algae in sample 25 cm deep in head	45.
Algae in white sand in channels	Coverage of sand 34%; .009 gm/cm² Algae in sand (Table 5)	31.
Fleshy algae (Codium) on dead-heads along their lateral slopes	Coverage of dead-heads 40%; Estimated fraction of dead-heads with fleshy algae 30%; 36.5 gm dry algae/400 cm² sample	107.
Algae in *Tridacna*	Coverage of *Tridacna* .3%; .040 gm/cm² dry algae in *Tridacna*	1.2
Total estimate of primary producers		652.
HERBIVORES PREDOMINATELY		
Sponges in dead-heads	Coverage of dead-heads 40%; 4.0 gm (4, 9, 3, 2) loss on ignition/.04 m²	40.
Sponges in live heads	Coverage of tall live heads 16%; 7.0 gm loss on ignition/.04 m²	28.
Midget cucumbers in dead-heads	.27 gm loss on ignition/.04 m²; coverage of dead heads 40%	2.7
Small cucumbers in and around heads	2.4 gm loss on ignition/individual; 4 individuals/2.25 m²	4.3
Small urchins in dead-heads	.13 gm (.19, .06) loss on ignition/.04 m²; dead-head coverage 40%	1.3
Ophiuroids and urchins in live heads	.53 gm loss on ignition/.04 m²; live-head coverage 16%	2.1
Urchins around heads	27 individuals/2.25 m² subquadrat; .61 gm loss on ignition/individual	7.3
Ophiuroids around heads	36 individuals/2.25 m² subquadrat; .40 gm loss on ignition/individual	6.4
Herbivorous annelids in dead-heads	.10 (.09, .11) gm loss on ignition/.04 m²; coverage of dead heads 40%	1.0
Herbivorous annelids in live heads	Coverage of live heads 16%; .14 gm loss on ignition/.04 m²	.6
Small herbivorous crustacea in dead-heads	Coverage of dead heads 40%; .17 gm/.04 m² loss on ignition	1.7
Small mollusks in dead heads (herbivores)	Coverage of dead heads 40%; .55 gm loss on ignition/.04 m²	5.5
Small mollusks in live heads	.09 gm loss on ignition/.04 m²; Coverage of live heads 16%	.4
Animal part of corals	Coverage of live coral 16%; .021 gm/cm² animal tissue in live coral (Table 4) Surface of branching corals about 3 times area covered horizontally	99.
Small herbivorous fishes	Counts on quadrats: 71 individuals/36 m²; 2.42 gm dry/individual	4.8
Large herbivorous fishes	Counts per 600 m² horizontally visible area; 30 (24, 25, 33, 27, 42) fishes; estimated 3/4 herbivorous; 120 gm dry/fish	4.5
Tridacna	.163 gm/cm² dry	4.9
Total Estimate of Herbivores		126.
CARNIVORES PREDOMINATELY		
Annelids and nemerteans in dead-heads.	.07 (.05, .08) gm loss on ignition/.04 m²; coverage of dead-heads 40%	.7
Annelids and nemerteans in live heads	.07 gm loss on ignition/.04 m²; coverage of live heads 16%	.3
Small crabs and shrimp in live heads	Coverage of live heads 16% 1.05 gm loss on ignition/400 cm²	4.2
Small crabs around heads	4 individuals/2.25 m²; .15 gm loss on ignition/individual	.3
Small crabs in dead-heads	.07 gm loss on ignition/.04 m²; coverage of dead-heads 40%	.7
Carnivorous mollusks around heads	5 individuals/2.25 m²; .06 gm loss on ignition tissue/individual	.13
Carnivorous mollusks in dead-heads	.5 gm loss on ignition/.04 m²; coverage of dead heads 40%	5.0
Small carnivorous fishes	5.3 individuals/36 m²;2.42 gm dry/individual	.34
Larger carnivorous fishes	1/4 of fishes counted in visible horizontal area (See herbivorous fishes above)	1.5
Total estimate of carnivores		13.1

the type of head counted from quadrat maps, these head counts for live and dead head-types were converted into over-all weights per area using loss on ignition values. A correction by counting was made

TABLE 12. Dry biomass estimates on quadrat E—F on the sand-shingle zones of the back reef. (Data combined from open areas of Stations E and F.)

Biomass Component	Measurement; Basis for Calculation	Mean Biomass averaged over the whole Quadrat gm/m²
PRIMARY PRODUCERS		
Algae in sand	Coverage of Sand 67%; .009 gm/cm²; dry algae in sand (Table 5)	60.
Algae in shingle	Coverage of shingle 33%; .110 gm/cm²; dry algae in shingle (Table 5)	331.
Total estimate of producer biomass		391.
HERBIVORES PREDOMINATELY		
Small herbivore fishes	Count 23 (31, 15) individuals/36 m² quadrat; 2.42 gm dry/average sized fish	1.5
Schools of sardine-herring fishes	Count of schools 1.2 (1, 1, 2, 1, 1) per 600 m² horizontal visible area; About 100 fish/school; 1 gm/fish	.2
Large herbivore fishes	Count 16 (16, 14, 17, 15) individuals per 600 m² horizontal visible area; 240 gm dry weight per fish	6.4
Total estimate of herbivores		8.1
CARNIVORES PREDOMINATELY		
Larger fishes other than sharks	3.2 (4, 0, 6, 3) individuals counted per 600 m² horizontal visible area; 240 gm dry weight/fish	1.3
Sharks observed while walking across back reef zones	Counts per 20 minutes observation: 1.6 (1, 1, 0, 5, 1) individuals per 600 m² visible area; 90 degrees visibility at one time; each individual in sight about 30 seconds; Weight per shark about 50 lbs wet or 4540 gm dry (20% of wet) (Vinogradov 1953)	prorated on time and area basis 1.2
Total estimate of Carnivores		2.5
DECOMPOSERS		
Foraminifera	Counts: 54/cm² area 1.33×10^4 gm loss on ignition/individual (13.5%) 67% coverage	48.

for tube worms imbedded in the hard base reef of the front quadrats.

Small *Herbivorous crustacea,* including mainly shrimps and gammarids, were estimated in the same manner as herbivorous annelids.

Micro-crustacea in the algal encrusting mats were estimated from some counts in samples scraped from measured areas. Only 237 (361, 120, 180, 288) were found per 28 cm². Estimating .02 cm x .01 cm x .01 cm as the size of these small species and allowing 14% dry tissue in wet volume (Vinogradov 1953), a negligible biomass of .022 gms/m² is found.

CARNIVORES (OTHER THAN CORALS)

Small carnivorous fishes, including mainly wrasses, groupers, and small moray eels, were estimated by means of counts and rotenone as described for herbivorous fishes. *Gymnothorax buroensis, Thalassoma quinquevittata, Epinephalus hexagonatus, E. spilotoceps, E. merra, Amblycirrhites arcatus, Scorpaena parvipinnis,* and *S. gibbosa* were examples of fishes in this ecological group.

Large carnivorous fishes, including a variety of species with no one type predominating, were very roughly estimated by counts as with the herbivorous fishes. A rough estimate of shark biomass was obtained as follows: The time sharks were in view during the 15 minute underwater walk to and from the area across the back reef zone was recorded. The fraction of the time when a shark was observed was assumed to be the fraction of one shark's range in view. The area of visibility of an observer looking from side to side through a face mask was assumed as ¼ of 360 deg. The average shark had an estimated weight of about 50 lbs. wet. Moray eels were estimated from the rotenone samples on the surely underestimating assumption that all the morays had climbed out into the channels to die. A rough estimate of area effectively rotenoned was used.

Carnivorous annelids including mainly the nereids were estimated as described for herbivorous annelids.

Carnivorous crustacea including mainly small crabs were estimated as described for herbivorous crustacea.

Carnivorous molluscs primarily Conus were estimated as described for herbivorous molluscs.

One series of night counts was made to estimate the larger night invertebrates. The basis for estimation was the number seen in walking a known distance where estimated visibility for bright eye reflections with an underwater flashlight is about 2 ft as a band along the path. A count of 6 individuals (4 spiny lobsters, 2 large crabs)/720m² was obtained. One individual weighed 150 gm wet with about 35 gms organic matter as estimated by loss on ignition. Thus about .3 gms/m² was observed.

DECOMPOSERS

Decomposers are here identified as that trophic group that subsists on the leakage from other food chains of dead organic matter no longer clearly assignable to a living group of producers, herbivores or carnivores. Included in this group are the bacteria, blennies, and foraminifera. Many others act as decomposers in part of their diet in nature, as when sea cucumbers eat sand, but in most of these cases a majority of the nutrition is from living algae. All algae are considered producers even though some may erode calcareous skeletons. The following were the only efforts made to assess the decomposer part of the community.

Bacteria. Counts of bacteria on glass slides suspended three weeks indicated an 80% coverage. What proportion of these were autotrophs of photosynthetic or chemosynthetic type is not known. As a possible upper limit, the surfaces of all reef objects (about 3 times horizontal area in complex zones) may be assumed to be bacterial covered to the same extent.

Allowing .05 gm/cm³ dry weight and a one micron thickness of bacteria an estimate of their possible biomass of .1 gm/m² results. We have no idea of the bacterial populations within skeletons.

Foraminifera. The foraminifera of the front reef algal mats are very small forms (.1 mm) characteristic of plankton and probably maintained by influx of oceanic water in the strong flow in this area. The forams of the sandy back reef are large benthic types like Calcarina (1. mm). Rough counts (Table 7) and loss on ignition values for these components permit rough estimate of their contribution to the biomass. The nutritive source for the large foram biomass (Table 12) on the back reef is not known.

Blennies. Following food studies by Strasburg (1953), the blennies which are numerous in rotenone samples from the algal ridge zone can be grouped as partly decomposers because of their eating of precipitated detritus (leptopel).

These exploratory estimates were mainly incidental to our study. An understanding of the trophic relationships of the bacteria and foraminifera on reefs is urgently needed. From estimates available, these components do not represent a large biomass in comparison to the other trophic levels. However the high metabolic rates of the small decomposers life system greatly magnifies the effect of a small biomass.

Biomass Pyramids

Finally, the quantitative trophic structure of the reef community can be set out as a pyramid of mass. The estimates of biomass by trophic level as estimated in the previous sections are combined in the graphs of Figure 10. In spite of the various errors in the necessarily crude estimates, a general pyramid structure clearly results in all cases as predicted by ecological theory. Furthermore, these pyramids are not quantitatively too different on a weight basis from quadrat to quadrat even though entirely different types of reef community components are represented. Thus the combined mean estimates in the composite pyramid (Fig. 10) gives a reasonable picture of relationships of standing crops. Even if any one of the minor estimates were as much as two fold in error, the general shape of the pyramids would be unchanged. If the chlorophyll to organic matter ratio (Fig. 8) has been underestimated by using Codium, the correct pyramids may be steeper than shown in Figure 10. The ratios of standing crop between trophic levels is H/P 18.9%; C/H 8.3%. Decomposer estimates do not include all components and are left out of the pyramids. Although the reef in gross appearance is what is usually described as a coral reef (rather than an algal reef), and although even the front breaker ridge is in gross appearance half coral, the pyramids show that on a live protoplasmic basis the usual predominance of producer algae exists. This is partly due to the prevalence of plant protoplasm in coral and partly due to large concentrations of matted algae in and on all the reef surfaces.

The pyramids of biomass structures show up even within some taxonomic groups. In the fishes, for example, there is a striking predominance on a weight basis of herbivorous parrot fishes, surgeons, damsels and butterfly fishes in comparison to wrasses, groupers and other carnivores. The numerous, beautiful schools of brilliant herbivorous fishes are indeed the "cows" of the reef.

The single coral is first a producer, to a lesser extent (in many cases) an herbivore, and somewhat a carnivore, thus giving something of a pyramid within one coral head. Indeed the isolated coral heads growing in Eniwetok atoll lagoon practically constitute a whole community since the plankton is scarce and so much of the metabolism is internally complete, thus fitting community definition. This need not be true of all coral heads everywhere and is most certainly not the case for clusters of non-photosynthetic Dendrophyllia growing in deeper waters at Bikini or in shadows of ledges in Hawaii.

COMMUNITY METABOLISM

Having demonstrated roughly the trophic structure of the coral reef, consideration may be given the rates at which the community is operating, its productivity, its metabolism, its turnover, and the efficiency of its primary production. Although there is consensus that individual corals are not quite inherently self sufficient in production, the work of Sargent & Austin (1949, 1954) suggests that the whole reef does subsist on its own primary production. They showed, using black bottles, that the production values of water in both the open sea and lagoon side of the reef were far too small to be of significance in comparison to the production of the whole reef, although this did not prove that plankton passing over the reef was not quantitatively an important source of nutrition. Their production measurements only meant that production by the plankton while passing over the reef was small relative to the attached community below. Whether the large volume of water filtered by the reef was contributing appreciable energy sources from organic matter previously accumulated in the water was not settled. Whether the reef lives entirely on its own production or not, it is likely that it derives critical nutrients from the strong flow over the community.

In this study, to assess the contribution of the inflowing water to the reef metabolism, measurements of several variables were made in incoming sea water (represented by water in the windward channel south of Japtan island), in water crossing the front reef after passing through the breaker zone, and in water leaving the reef over the back reef zone (Table 13). The general water characteristics are summarized in Table 14. Discussion follows on the significance of the changes observed as indicated in Figure 11

Sargent & Austin (1949) interpreted their high values of organic matter on the front reef as due to the trajectory of the water in passing through several turbulent eddys in the breaker zone at which time some of the production of the buttress zone was con-

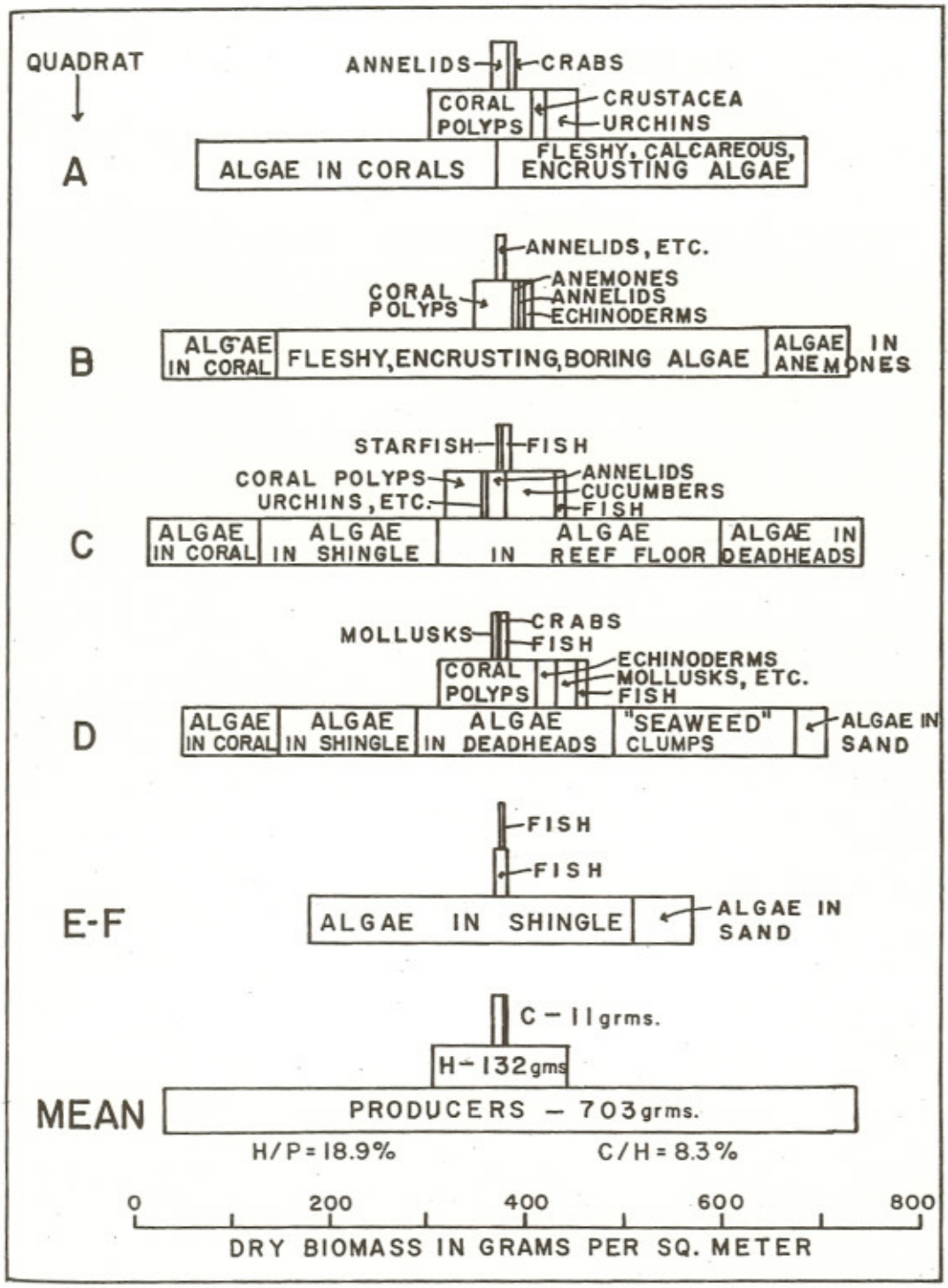

FIGURE 10. Pyramids of biomass resulting from estimates of the dry weight of living materials (excluding, of course, dead skeletal materials associated with protoplasm). For each quadrat, A-F, the weight of "producers" (bottom layer of pyramid), the "herbivores" (H) (middle layer), and the "carnivores" (C) (top layer) is shown, and also the average dry biomass for the reef.

TABLE 13. Plankton characteristics across the reef, July 1954.

Station, circumstance	Volume Filtered m^3	Dry Weight gm/m^3	Loss on ignition gm/m^3	Washed ash (dry) gm/m^3	Plant Fraction (Extract method) %	Radio-activity Thsds. counts min/m^3
OCEANIC WATER (taken from M boat in Japtan—Parry channel)						
10:30 p.m. (night), July 19, falling spring tide:						
Sample 1	6.1	.0120	.0041	....	5.5%	....
Sample 2	6.1	.0121	.0042	.0059	....	13.5
2:00 p.m. July 17, rising spring tide:						
Sample 1	6.1	.0177	.0064	....	6.5%	....
Sample 2	6.1	.0099	.0036	.0054	....	24.1
Mean Oceanic Water	....	.0129	.00457	.0057	6.0%	18.8
WATER CROSSING ALGAL-CORAL RIDGE						
Midnight, July 19, turning low spring tide	3.6	.057	.030	.023	41.2%	188.
2:10 a.m. (night), July 19, rising spring tide	5.0	.063	.033	....	29.7%	....
Noon, July 17, turning low spring tide	4.4	.358	.175	.181	28.7%	1081.
10:45 a.m. July 27, falling spring tide	9.0	.039	.021	.0168	57.2%	73.
Mean of water crossing algal ridge	....	.129	.064	.074	39.2%	447.
WATER CROSSING END OF ENCRUSTING ZONE (Station B-2)						
4:00 p.m., July 13, falling neap tide	21.8	.079	.022	.0236	8.1%	....
WATER CROSSING ZONE OF LARGE HEADS (Station D)						
July 13, turning high neap tide:						
Sample 1, 3:00 p.m.	30.0	.024	.0079	.0034	32.3%	....
Sample 2, 3:20 p. m.	30.0	.027	.0099	.0054	30.6%	....
July 19, rising spring tide, Night:						
Sample 1, 1:00 a.m.	1.68	.054	.0327	....	3.3%	....
Sample 2, 1:37 a.m.	2.65	.034	.0199	.0081	....	52.
July 17, turning low spring tide:						
Sample 1, 10:53 a.m.	11.9	.0129	.0052	....	20.7%	....
Sample 2, 12:40 a.m.	5.9	.035	.0139	.0171	....	77.
July 27, falling spring tide:						
9:45 a.m.	3.0	.037	.0184	.0125	....	34.
Mean of water crossing large head zone	....	.032	.0154	.0093	22.0%	54.
WATER CROSSING ZONE OF SAND AND SHINGLE OF THE BACK REEF SHELF (Station E)						
July 27, falling spring tide, 8:50 a.m.	4.0	.022	.0119	.0042	....	35.

tinually being added. The plankton data suggests this picture to be correct for coarse plankton. Organic matter data are inconclusive as to whether the far larger dissolved organic-matter fraction changes in crossing the reef.

As the water passes the shallow portions of the reef, much plankton is removed. That which remains is exposed to settling in the quieter back waters and to the schools of small anchovy type fish of the back reef zone. The presence of some open-sea plankters in the samples of the back reef indicate that a few individuals do cross the reef without being removed. In general the reef is a highly efficient filter even though the water crosses the reef in 15 to 20 minutes.

Because the tidal cycle creates a variation in the current the reef plankton is highly variable. At very low tides the breakers up front pull off usual quantities of algae but since little water is being thrown up and over the reef, they accumulate in the breaker eddies until the incoming tide at which time the plankton is unusually heavy in the water first coming over the reef. Some such variation may account for the organic values of Sargent & Austin (1949) which were too high on the front reef relative to the back reef to match the known respiration of the reef. The high plankton values in Sample 1, 2:00 p.m. July 17 (Table 13) are due to the effect described above. The data in Figure 11 show similar patterns across the reef for loss on ignition, chlorophyll extracts of the plankton, and plankton radioactivity.

FLUX OF LARGER PLANKTON

Plankton samples were made with a #10 net. On the reef the net could be set on a stake to permit the

TABLE 14. Chemical levels in Eniwetok waters.

Component	Analyses	Mean	Range
Organic Matter, alkaline permanganate method, in mg/l	13	.96	.74—1.41
Nitrate nitrogen, strychnidine method, in mg atoms/m^3	24	.44	.06—1.0
Inorganic phosphorus, ammonium molybdate method in mg atoms/m^3	29	.32	.26—.64
Total phosphorus, acid digested, in mg atoms/m^3	6	1.7	0—3.4
Dissolved oxygen, Winkler method, in mg/l.			
(1) Incoming Ocean Water (from channel)	8	6.54	6.38—6.68
(2) Algal-coral Ridge	12	6.50	6.09—6.97
(3) Back Reef zone of Large Heads			
Daytime	19	7.31	6.22—8.59
Night	6	5.37	4.89—6.26
pH (Beckman Model G)			
Daytime			
Incoming Ocean Water (from channel)	5	8.21	8.19—8.22
Algal-coral ridge	5	8.21	8.18—8.24
Back Reef zone of large heads	5	8.32	8.30—8.33
Night			
Incoming Ocean Water (from channel)	2	8.19	8.18—8.19
Algal-coral ridge	2	8.16	8.14—8.17
Back Reef Zone of large heads	2	8.10	8.10—8.10
Temperature in degrees Fahrenheit			
Incoming ocean water (from channel)	2	82.6	82.6—82.7
Algal-coral ridge	2	82.9	82.7—83.0
Back reef zone of large heads			
Daytime	3	84.1	83.5—84.6
Nighttime	1	82.2	.....

strong current to flow through. The channel samples were taken from a boat. The volume of water passing through the net was determined by placing a drop of dye (air-sea-rescue dye marker, fluorescein) in the mouth of the net and counting the seconds required for the dye to wash through the net. The current on the reef was always sufficient to give a satisfactory sample of plankton after 10 to 40 minutes. The current outside the net was simultaneously determined with the dye method in order that computations of total plankton flux could be made. The average time for five dye spots to cross a distance of 20 ft was used to determine water velocity.

Qualitatively, net plankton of the incoming water was characterized by pteropods, calanoid copepods, radiolaria, and tiny filamentous algae. The reef plankton after passing the surf zone was conspicuously different being made up of large fragments of filamentous algae derived from the buttress-breaker zone of the reef. The data (Table 13, Fig. 11) clearly indicate a very large increase of large-sized plankton as the water crosses the breaker zone and a rapid loss of most of this plankton in crossing the rest of the reef. Thus the reef consumes its own pseudoplankton. Since the amount of plankton leaving the reef at the back is about the same or slightly greater than that in the incoming water, it seems that the reef is indeed energetically self-sustaining and deriving no net gain of larger planktonic material from the inflowing water. The data, however, do not entirely eliminate the possibility of a gain from nannoplankton and dissolved organic matter.

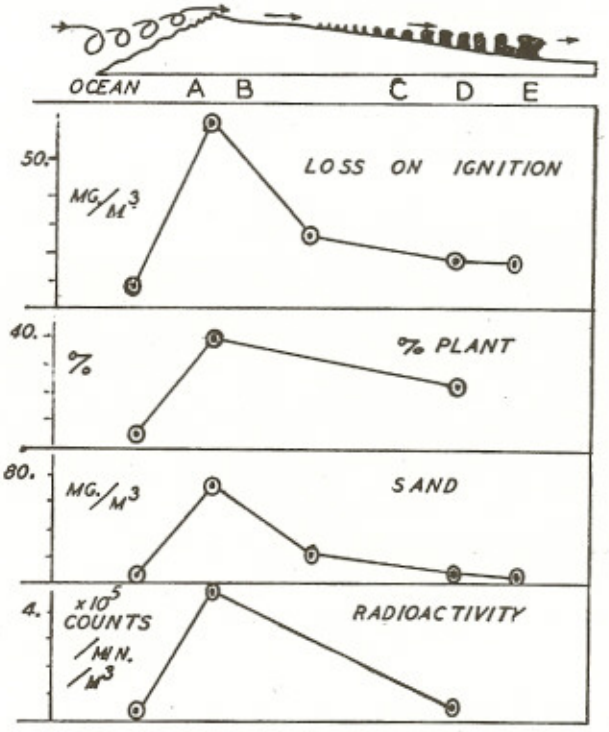

Fig. 11. Changes in water content as it crosses the reef in regard to: loss on ignition of net plankton and seston; green plant content (estimated by chlorophyll content) of net plankton; suspended sand; radioactivity.

TOTAL ORGANIC MATTER

A few measurements to determine the order of magnitude of the total organic matter were made with the alkaline permanganate method of Benson & Hicks (1931). Samples (100 cc) were digested 30 minutes at 95°C with standardized permanganate and sodium hydroxide. The ferrous sulfate was added in an amount equivalent to the permanganate. Oxidation-reduction conditions were adjusted with manganous salts and phosphoric acid to prevent oxidation of the chloride. The excess ferrous sulfate was titrated with more permanganate to determine the permanganate lost during digestion. A mean value of about 1 mg/l of oxygen consumed was found (Table 14). The values obtained with this very rough procedure were fairly consistent and probably give the general order of magnitude of dissolved organic matter. Significantly, the values were similar to those obtained by Johnstone with BOD determinations (Sargent & Austin 1949). We did not find the great difference between front and back reef found by Sargent & Austin although our permanganate method should probably not be relied upon as accurate enough to delimit a difference of less than 1 ppm. As in other kinds of water, the dissolved organic matter is much greater, though less conspicuous, than the particulate matter. Motoda (1938) found 2.0-3.1 mg/l, 35 day BOD, in open sea water at Palao and 5.5 mg/l in the bay.

PRODUCTION AND RESPIRATION BY THE FLOW METHOD

Sargent & Austin (1949) used an ingenious flow-rate method to measure the over-all production and respiration of the coral reef at Rongelap Atoll, Marshall islands. A similar method has been used by H. T. Odum in Silver Springs, Florida (1953, 1954). The oxygen content of the water upstream and downstream is measured simultaneously. The oxygen increase between stations during the day is the net photosynthetic production of the community. The oxygen decrease between stations during the night is the total respiration of the community. By taking a series of measurements over the daily cycle, one obtains the course of production during the day. Measurement of the current transport permits calculation of total reef metabolism. The respiration at night plus the net production during the day gives the total production. By comparing the area of the graph between the day curve and the zero line with areas of the graph under the zero line at night one can obtain an indication of what part of the excess production during the day is used up by respiration during the night.

A series of such measurements was made on several different days of typical cloud cover of from 1/10 to 3/10 small cumulus and 1/10 to 4/10 high and middle cloudiness, and also at night. These values are expressed on an area basis in Figure 12 following their conversion from depth and current measurements. The curve obtained by Sargent and Austin for their reef is also plotted in Figure 12.

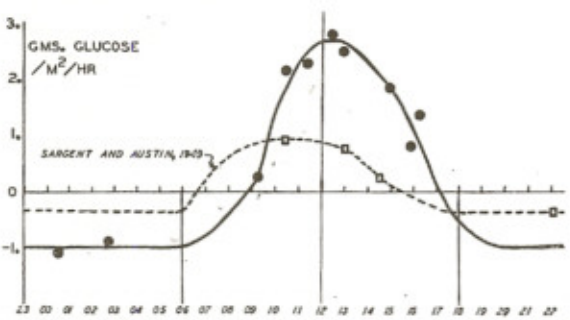

FIG. 12. Graph of primary production and respiration on the middle reef between the coral-algal ridge and quadrat D. A similar curve from Rongelap Atoll is recalculated from Sargent & Austin (1949).

Besides small errors due to inherent fluctuations and variability of oxygen samples and methods, current and depth measurements, and cloud cover changes, there is a major source of error that tends to cause values of production and respiration to be too small. This is the diffusion of oxygen from and to the atmosphere. This error is greatest when the displacement of the gaseous content of the water from equilibrium with the atmosphere is greatest. Thus the error in decreasing the production estimate is greater than that in the respiration since greater displacement from equilibrium occurs. Furthermore, during the day's production a carpet of bubbles of oxygen is observed to form over the algal-mat surfaces particularly on the front reef. These bubbles are continually breaking off and reach the surface without dissolving so that some of the oxygen is lost, further lowering the estimate of production below the correct figure. The diffusion error is further discussed in the section on over-all balance sheet for the reef.

Our curve of reef production for the middle reef (Fig. 12) permits the following interpretations: (1) The productivity of the reef is very high, greater than 24 gms/m²/day or 74,300 lbs/Acre/yr. (2) The productivity is greater than that of Silver Springs, Florida, which is very nutrient-rich with a relatively constant temperature, and supports a similarly autotrophic community with a production of 50,000 lbs/Acre/yr (Odum, H. T. 1953-54). Silver Springs has a higher summer production rate but a smaller annual total due to the small insolation of the winter. The reef production is greater than other marine localities reported. In comparison to the open tropical waters such as that flowing onto the reef (.2 gms/m²/day; Sargent & Austin 1949), this reef is 120 times more productive. (3) The Japtan reef has twice the production value per area by the flow method as the Rongelap reef studied by Sargent & Austin. The larger production of the reef per area is matched by a larger respiration per area in comparison to the reef studied by Sargent & Austin and therefore suggests a greater biomass per area. Sargent & Austin (1954) describe their reef as relatively barren. (4) There is a lag between the sun's light intensity and the oxygen production as measured in the water above the reef each day. It is likely that part of this lag is due to the location of many of the primary producers down in the calcareous reef surface, sands, and below the coral polyps.

In view of the evidence for a lag in gaseous exchange, a symmetrical morning and afternoon production curve seems incorrect even though Yonge & Nicholls (1931) showed that isolated single corals in the sun may reach maximum photosynthesis in the morning. Thus Sargent & Austin's production curve, drawn through three afternoon points, probably shows too much productive area. It seems likely that their reef possessed little or no excess of production over respiration and may not have been depositing stored organic biomass.

PRODUCTION EXPERIMENTS IN SUBMERGED BELL JARS AND PLASTIC BAGS

Following experience in Silver Springs, efforts were made to enclose reef components with glass jars, and to sample the water before and after periods of production and respiration. After many difficulties a diaphragm of inner-tube rubber placed outside of the glass jar was found to make a seal between the jar and the hard irregular reef floor. Sand and boulders heaped over the ring-shaped rubber border prevented active circulation of the water outside the jar with the interior water. A rubber tube with an

opening inside the jar and one outside the jar permitted sampling. Water samples were drawn out with a type of sampler developed at Silver Springs by which the observer draws water through two bottles on a stick by sucking on a tube. The bottle nearest the bell jar source is used for Winkler oxygen determinations after the second bottle has filled.

The unexpected results given in Table 15 for experiments on the reef seem to demonstrate a lag effect as also evidenced in the flow measurements discussed in the previous section. When black covers were put over corals or reef surfaces during the day, oxygen, presumably from sub-surface bubbles, continued to be evolved for over an hour. Supporting this interpretation is the observation that myriads of little bubbles rise from the interior of Millepora or Acropora fingers when they are broken during the day. The hard bumps of the reef surface that do not even look green externally, as well as the algal mats of the front reef, are coated with bubbles during the middle of the day. These bubbles on bare looking places are probably coming from the subcrustal green algal layers previously described in the primary producer discussion.

To determine whether reef components had an over-all net production or respiration, plastic bag experiments were conducted in the field. Following the suggestion of Dr. Max Doty, 6 x 6 in. plastic bags were tied around small coral and algal heads with rubber bands and observed a day later. The bubbles which accumulated in the bags are assumed to have been initially formed of oxygen because release of other gases seems unlikely. Carbon-dioxide would not be released in a gaseous form through basic sea water. Since no temperature changes could occur in this field arrangement, air components would not be released from solution. Once a gaseous phase was formed other dissolved gases might enter. No extensive decay is suspected that might produce large quantities of hydrogen, methane or other gas. As positive evidence that these bubbles contain considerable oxygen, water drawn from bags with bubbles was super-saturated whereas water drawn from bags without bubbles was undersaturated. However, after a gaseous phase had been formed, other dissolved gases would diffuse in. Visual estimates were made of the volume of bubbles in the bags after one day. Note (Table 16), that the dead heads with encrusting algae have a large net bubble-production whereas the corals had slight or no production even though 2 hrs

TABLE 15. Lag in gas exchange between reef and water. (Oxygen changes in dark and light bell jars on reef substrates.)

Surface	Preceding Light Regime	During Measurements	Time Lapse Minutes	Oxygen Change gms/m²/hr
Sand-shingle	7 hr light	dark	31	+.73
Sand-shingle	31 min dark	light	30	−.24
Dead-heads	7 hr light	dark	31	+.085
Dead-heads	3 hr light	dark	73	+.125

TABLE 16. Volume of bubbles accumulating in plastic bags over reef heads. Bubbles estimated at noon.

	Time exposed hrs	Volume of bubbles cc
Dead heads permeated and encrusted with algae	26	15
	74	12
	26	25
Halimeda bunch	26	2
Bag of foraminiferal sand	26	.1
Live corals		
Millepora	26	.5
Porites	26	1.0
Heliopora	26	1.0
Acropora (read at 9:00 a.m.)	70	0
Acropora	50	.1
soft coral (*Lobophytum*)	26	.1
Control bag	26	.1

of sunlight of a second day were included in more than one day's measurement. This seems to indicate that photosynthesis in situ does not exceed respiration in many corals although it does match a large fraction of the respiration. It is possible that the role of photosynthesis is greater in the clear waters of the Marshalls than in more turbid waters in some other areas. Perhaps fortunately for corals, decreasing light, due to greater turbidity is often accompanied by increasing plankton content.

PHOSPHORUS AND NITROGEN

To establish the general nutrient level on the reef, a few analyses were made of inorganic phosphorus, organic phosphorus, and nitrate nitrogen. Methods used were rough adaptations of the ammonium molybdate-stannous chloride method for phosphorus (Robinson & Kemmerer 1930) and the strychnidine method for nitrate (Zwicker & Robinson 1944). Samples were necessarily determined 1 to 6 hrs after collection. Some loss due to uptake by bottle walls may have occurred. As expected for a central tropical ocean the incoming waters had extremely low values of both nutrient elements. Although the concentrations were in the lower limits of sensitivity of the methods, the values reported in Table 14 possibly are of valid order of magnitude.

Considering the productivity, as established, the required nutrients can be accounted for as follows. If the mean nitrogen content of the producing algae is 3.0% (½ protein), then .72 gms/m²/day nitrogen is required. Considering the width (Table 17) and volume transport of water (3. x 10^4 m³/day), only .6 gms/m²/day nitrogen could be supplied from inorganic nitrate even if it were all captured and used. It is not all used since it was detected in a concentration of the same order of magnitude in back-reef water. Using open-ocean values (Sverdrup, *et al.* 1946) .1 gm/m³ total organic nitrogen is found in water with about 2.0 gms/m³ total organic matter. Using this nitrogen/organic matter ratio of 5% and a total organic matter content of 1 gm/m³ (as determined, Table 14), about 4.7 gms/m²/day could be

TABLE 17. Balance sheet for the Japtan inter-island reef in July. From algal-coral ridge to the end of the zone of large heads, this zone is 322 m² long.

	gm/m²/day
INCOME*	
Planktonic organic matter (Table 13) from breaker zone	2.0‡
Primary production (measured as oxygen, calculated as glucose:	
Net (uncorrected) daytime production	14.0
Respiration during daytime	10.0
Total income	26.0
LOSSES*	
Planktonic organic matter lost to lagoon (Table 13)	0.4‡
Total respiration in 24 hr	24.0
Total outgo	24.4

*Dissolved Organic Matter; 0.96 gm/m³ (Table 14) (no significant difference between influx and outflux; analytical method not precise enough, however, to delimit.)

‡The mean water flux during plankton sampling was 425m³/hr across a band of reef 1 m wide.

acquired by the reef if all the nitrogenous organic matter were taken up. To meet the need of .72 gms/m²/day, therefore, much of the incoming organic matter would have to be taken out. Our few analyses showed no evidence of this magnitude of organic-matter uptake although Sargent & Austin had some evidence of large uptake. It seems equally likely that there is cyclic re-use of nitrogen along with some nitrogen fixation by the abundant blue greens of the front reef. That the surface encrusting algae are so definitely correlated with high current velocity, however, suggests the need for taking out some nutrients of organic or inorganic nature from the low nutrient water. As indicated in Table 5, however, the surface encrusting algae, although conspicuous, are relatively unimportant on a biomass basis in comparison to the algae permeating the calcareous substrates, living and dead. They may, however, have higher metabolic rates than the imbedded algae.

Similar calculations suggest that phosphorus is more abundant relative to needs than nitrogen.

The back reef production is accomplished largely by algae within the calcareous dead parts of corals and other back-reef components. The coverage of coral decreases from nearly 50% of the front reef to 16% of the back reef and finally 0%. Apparently, nutrients caught and stored by the algae and coral of the front reef are passed to the back-reef producers in the form of skeletal fragments. The front reef encrusting-producers, being in shallower water with much swifter currents (Fig. 2), are exposed to greater volume per individual so that the energy of nutrient gathering is partly supplied by the flow system. Thus an adequate nutrient source in water and plankton is available at the front. The nutrient and current regimes are thus entirely different for the front and back-reef producers. The front-reef producers need catch only enough nutrients to balance that leaking off the back reef to maintain the ecosystem. The general habit of the boring producers in all the reef surfaces is most favorable to nutrient conservation. One imagines that at the time of a typhoon or other circumstance bringing richer water to the surface of the ocean, the reef would capture critical nutrients in an efficient manner for future use. Certainly the reef has concentrated radioactivity of multiple types in water that is barely above background as it drifts in 200 mi. from Bikini. Three samples of water, evaporated down without filtering, gave mean radioactivity of 182 counts/min/l (determined by K. Lohman). This was roughly of the same magnitude as the dried-plankton radioactivities per volume (Table 13) estimated with a Beta Gamma survey meter (AEC MOD-SGM-2B). Coral and algal surfaces registered about 300 counts/min/cm² of surface. Thus, plankton radioactivity of a liter of water has an order of magnitude equivalent to that of a cm² of coral surface.

The reef surfaces, living coral, living calcareous algae, and dead skeletons all act as a kind of soil in that they conserve phosphorus nutrients and permit plant biota to burrow in to reach these nutrients. As indicated in Vinogradov (1953), fresh coral skeletons have 1% phosphorus and .01 to .1% aluminum and iron. Calcareous algae contain much less. Green layers of boring algae are found just under the red surfaces of calcareous red algae as well as under the corals (Fig. 7D).

The N/P ratio by atoms is roughly 2.1 (using a nitrogen value inferred from organic matter on the assumption that most is protein), which indicates particularly sparse nitrogen conditions. The large proportion of small blue green algae may suggest a low nitrogen environment.

REEF DEPOSITION, REEF EROSION, pH CHANGES

Although the production and respiration measurements suggest that respiration is not far from a balance with production, there is little clear evidence about the balance between skeletal reef deposition and erosion of any one reef yet studied. Certainly the reef atoll as a whole can maintain its relationship to sea level for long periods of time. As carefully postulated by Mayor (1924), a reef seems to have the mechanism for self regulating its balance of deposition and erosion at about 6 in. below mean low water spring tide. The excess of production or respiration does not in itself indicate whether deposition or erosion is in excess. For example, animals like oysters with entirely respiratory metabolism may nevertheless relegate energy to deposition. Most marine plants with a primarily production-type metabolism do not deposit a skeleton which their metabolism would tend to precipitate in water almost saturated with respect to calcium carbonate, like that at Eniwetok. This might involve an energy expenditure. It is not clear whether reefs, by a succession, destroy themselves by becoming a terrestrial community or whether they form a climax at the 6 in. level below low water spring tide.

Sargent & Austin attempted to estimate reef deposition on the assumption that most of the reef biomass was coral and that their respiration measurements for the whole reef would be extrapolated into a deposition rate, assuming a deposition to respiration ratio typical of corals as measured by previous workers. However, it is clear from the pyramids (Fig. 10) that the majority of the biomass is not coral-animal tissue.

Nor is the metabolism predominately coral. By calculation from Mayor's value for metabolism per living biomass of .43 mg/gm/hr (mean of 4 species) and our figure of .062 gms/cm^2 total biomass in corals, and a coverage of 20% coral, one obtains a respiratory contribution of coral of 53 mg/m^2/hr. This is a relatively small part of the total respiration of the reef determined with the flow method which is about 1.0 gm/m^2/hr.

Sargent & Austin's possible overestimation is partly counteracted by the use of the wrong density. Even so, their over-all estimate of maximum material added (1.4 cm) seems too high, on the basis of their calculations.

As a variation of Mayor's calculation the quadrat estimates of coral coverage were used to estimate rate of coral deposition with a figure for coral growth derived from Mayor (1924). Slightly lower growth rates are found in colder waters (Tamura & Hada 1932, Ying 1934). By recalculating on an area basis and averaging 18 growth values for corals from Mayor, an annual skeletal growth rate of 8.0 cm was obtained. This involved using a dry gross density of coral of 1.9* gm/cc. Most of our reef seems to be built of coral (not calcareous algae) if one can judge by blocks of the reef from the dynamite holes elsewhere on the atoll (Parry island) or from the present composition of most of the reef. Much of the deposition, therefore, comes from the 20% coverage of coral. Therefore, the 8 cm skeletal growth in the areas of coral is spread over the whole area in the form of shingle and dead heads to form a net addition of material of growth of 1.6 cm. Although this rate of increment is almost identical with the one estimated by Sargent & Austin, their apparently less productive reef may actually have a lesser depositional rate.

On the basis of growth rate and coverage estimates, and a density of 1.8, Mayor estimated 0.8 cm annual deposition and simultaneous erosion on his study reef in Samoa.

For the middle reef the estimate of 1.6 cm calcareous deposition amounts to 3.05 gm/cm^2/yr. The over-all income of 26.0 gm/m^2/day (Table 17) is equivalent to .95 gms/cm^2/yr glucose. Thus the biomass initially deposited is only ⅓ of the calcareous deposition. With the water near the inorganic deposition point, little energy is likely to be required for this calcareous deposition. Just how much is not yet known.

This coral increment being added is very likely being eroded just as fast by current abrasion and the complex of bacteria and boring algae that characterize the coral shingle fragments that dominate much of the back reef zones, so neither the above calculation nor Sargent & Austin's evidence is at all indicative of over-all net reef growth or erosion.

Some idea of the magnitude of abrasion taking place on the front buttress zone, which must be balanced by growth to maintain the reef and must be exceeded to produce a reef-growth laterally into the wind, may be obtained from the sand in the reef plankton. The plankton ash in the samples collected at the front and back reef was washed with water leaving a residue consisting mainly of fine calcium carbonate sand that had been suspended in the water passing through the plankton net. The change in this sand fraction in crossing the reef is depicted in Figure 11. Strikingly, the sand content rises in crossing the breaker zone and as the current diminishes on the back reef the sand content falls, thus demonstrating the action of front-reef growth in filling in and cementing the back reef. Since no measurements of sand in plankton were made during the strong currents of high tide, the magnitude of deposition and erosion of reef sand is uncertain.

BALANCE SHEET FOR THE REEF COMMUNITY

Having made various measurements and estimates of photosynthetic rates and metabolic processes, we may now consider the data as a whole to see how nearly balanced are the gains and losses of organic matter on one reef section. In Table 17 the sources of energy storage gain are estimated, including primary photosynthetic production and influx of organic matter in the water. The losses of energy are also listed, including respiration, and outflow of organic matter. The gains and losses are only 4% apart. In view of the rough nature of some of the estimates it is not certain whether this is a significant difference or whether the community is in a perfect steady state with losses matching gains. With the 15-20% lower total insolation in winter (insolation tables, Kennedy 1949) at this latitude than when these measurements were made in July, a lower production but relatively unchanged respiration may be expected to make an annual balance between production and respiration.

This vigorously productive reef is possibly one of those that Cloud (1954) thinks is now in slightly deeper water than the equilibrium depth because of a sea level rise starting about 100 yrs ago. According to this idea the reef may be experiencing a net growth of calcareous matter. However, there is no definite evidence from this study to indicate that the

* In Table 3 are given density measurements of two types. One is the density of the dried skeletal material obtained by weighing wet while suspended in water and by weighing dry. This density which is of interest mineralogically is the weight per volume of the component skeletal septa. The density of a dry gross block including the empty pore spaces is considerably less and is obtained by correcting for pore space. Although the skeletal density (mostly aragonite) is about 2.3 gm/cc (Table 3), with a pore space of 16% the dry blocks of coral have a gross density of only 1.9 gm/cc. This latter density should have been used by Sargent & Austin rather than 2.5 gm/cc in estimating growth increment from weight increases. This error fortunately partly counteracted their error of overestimation of coral populations discussed above. When the pore space is filled with water, the gross wet density is 2.1 gm/cc, a sometimes useful quantity.

reef is not in balance with respect to organic matter. Organic deposition and calcareous deposition are not necessarily in phase.

Similarly, as dicussed in the section on production measurements, a balance between gains and losses may have existed on Sargent & Austin's reef also. The biggest uncertainty in both these studies is still the question of changes in dissolved organic matter in the vast flow of water crossing the reef.

We may tentatively conclude, at least, that the Japtan reef is a true climax community, in the ecological sense, under present ocean level conditions, since there is little if any net increase in living biomass.

EFFICIENCY

From tables of insolation reaching the ground (Kennedy 1949) a figure for insolation reaching the water surface can be obtained, taking into account approximate cloudiness. About ½ of this total insolation is in the visible range (Sverdrup, *et al.* 1946). With a Weston photographic light meter enclosed in a plastic bag a reading above the surface of 1500 fc was obtained compared to 800 fc 50 cm below the surface at quadrat D. Therefore about half of the surface light reaches the average reef depth of 2 ft. From these approximations the energy available to production on the reef can be estimated. For the latitude of Eniwetok in August, these approximations indicate about 1650 KCal/m²/day incoming energy reaching the community. Relative to the 96 KCal/m²/day (24 gm x 4.0 KCal/gm) primary production estimated from oxygen measurements in Table 16 this is about 5.8% efficiency of primary production.

That this efficiency is a low one in comparison to some laboratory experiments (Rabinowitch 1951) and yet higher than average terrestrial agriculture is an important result. Here is an ecosystem which has had millions of years to evolve an effective composition, which is built for a low efficiency. This may be support for the hypothesis (Odum & Pinkerton 1955) that there is an optimum but relatively low efficiency that produces the most effective trophic structure whose survival is based on a high primary productivity.

RELATIONSHIP BETWEEN TROPHIC STRUCTURE AND COMMUNITY METABOLISM

It seems clear that the vast coral reef community is highly productive and not far from a steady state balance of growth and decay. As a community of unquestionable durability and ancient origin, it may be postulated that some kind of optimum adjustment has been evolved. The evolution may be stated in terms of the stability principle (Holmes 1948) as follows: As an open system, the construction of self regulating interactions has led by selective process to the survival of the stable.

In the previous sections a standing crop of living biomass of about 700 gm/m² was found and a total primary productivity (glucose) of 24 gm/m²/day or 8760 gm/m²/yr. The ratio of annual primary production to standing crop is therefore about 12.5 to 1. This ratio can be called the turnover. If there is an underlying relationship of primary production and standing crop under steady-state conditions, an annual turnover value similar to the 12.5 for our reef may be found in other systems where there are similar temperatures, and similar supplementary energies supplied as water currents, and similar sized organisms with similar metabolic rates.

SUMMARY

1. During a mid-summer 6-week period (1954), (1) the standing crop biomass of "producer" and "consumer" organisms of a windward, inter-island coral reef on Eniwetok Atoll was estimated, (2) primary production and total respiration were determined by upstream and downstream chemical measurements, and (3) from these data the turnover and energetic efficiency of the reef ecosystem were calculated.

2. The reef, which has not as yet been directly disturbed by nuclear explosions, exhibited 6 distinct zones as follows: windward buttress zone, coral-algal ridge, encrusting zone, zone of smaller heads, zone of larger heads, zone of sand and shingle (Figs. 2-4). Zonation of this inter-island reef (with its one-direction current system) is very different from zonation on island reefs so abundantly described in the literature. Quadrats were mapped in 5 of the zones (Fig. 5) and standing crop biomass determined for each.

3. Because producers (algae) are so intimately interwoven with animal and dead skeletal material the chlorophyll extraction method appeared to be the most feasible means of estimating producer biomass. Algal dry weight was determined by relating spectrophotometrically, chlorophyll content with known dry weights of a reference species, *Codium edule.*, Various methods were used to estimate major animal components as described in appropriate sections of the paper.

4. On a horizontal surface area basis, the average living coral colony proved to contain three times as much plant as animal tissue, or .063 gm/cm² dry weight of algae as compared with .021 gm of animal polyp (Table 4 & Fig. 6). Zooxanthellae (in the coelenterate polyps) comprised only about 6% of the total plant portion, filamentous green algae embedded in the skeleton making up the bulk of plant material. The evidence indicates that these skeletal algae, often considered "parasitic" or "boring" by previous workers, may be actually mutualistic. The algal-coelenterate complex, therefore, comprises a highly integrated ecological unit (comparable to the algal-fungal complex of a lichen) which permits cyclic use and reuse of food and nutrients necessary for vigorous coral growth in tropical "desert" waters having a very low plankton content. The coral is thus conceived to be almost a whole ecological unit in itself with producer, herbivore (utilizing food from symbiotic algae), and carnivore (plankton feeding at night) aspects.

5. The quantitative coverage of coral (50-16%)

and surface encrusting algae decreased while the amount of subsurface algae increased from front to back across the reef correlated with mean current velocities suggesting a transition from a water filtering source of nutrients up front to a subsurface decomposition source of plant requirements on the back zones.

6. Although species differences were indicated, the algal content of 33 samples of 12 species of corals was rather uniform when calculated as dry biomass on a projected horizontal surface area basis (Table 5). Branching corals contained about the same amount of algae as massive and encrusting corals. Exposed reef surfaces, "deadheads," and shingle contained comparable or somewhat larger amounts of producer tissue; only the calcareous sands of the back reef gave low values.

7. While the kinds of primary producers were quite variable from place to place and zone to zone (10 major types are listed in the ecological classification), the reef, whether covered with coral or not, proved to have a rather uniform content of algae. In other words, the algal standing crop was of a similar order of magnitude (between 0.050 and 0.1 gm/cm^2) throughout, a situation certainly not evident on superficial examination (because a large amount of the green plant material is subsurface).

8. The sessile part of the community is primarily autotrophic with relatively few plankton feeders other than coral polyps; fouling on glass slides was almost entirely algal.

9. In all zones of the reef a trophic structure with a pyramid of biomass was found (Fig. 10). Although entirely different taxonomic components were present in different zones, similar biomass figures were obtained. The mean standing crop for the reef as a whole in gm/m^2 was: producers, 703; herbivores, 132; and carnivores, 11. The ratio between standing-crop trophic levels was H/P, 18.9%, and C/H, 8.3%.

10. A very high total production of about 74,000 lbs/acre/year was obtained with the flow rate method. This represents a turnover (the ratio of annual primary production to average standing crop) of about 12.5 times per year of existing biomass. The figures and the production curve (Fig. 12) provide quantitative criteria for assaying the future effect of nuclear explosions, continued low-level radioactivity, or other factors on the community as a whole.

11. The production on the reef seems to about balance the respiration on the reef (Table 17). The corals do not constitute a dominant part of the whole metabolism. It is concluded that the reef community is, under present ocean levels, a true ecological climax or open steady-state system.

12. The efficiency of primary production computed in terms of the visible light reaching the underwater community is about 6%. This is support for the advocated theory that steady state communities adjust to a moderately low efficiency as a necessary compensation for high total productivity.

13. The reef does not derive a net gain from the larger components of plankton in the water crossing the reef under the stress of the trade winds. Whether a dissolved organic-matter gain is obtained is still uncertain.

14. Individual corals *in situ* in nature, like those in laboratory experiments of other workers, produce an excess of oxygen in the daytime but not over the course of 24 hours (Table 16). The coral with its 3:1 ratio of plants to animals is apparently just about "balanced" in gaseous exchange.

15. The location of the sub-surface boring algae leads to a time lag in gas diffusion with the water crossing the reef and an afternoon community-production maximum (Fig. 12).

16. The nutrient levels of nitrogen and phosphorus are very low (Table 14). Some evidence exists that nitrogen is more scarce relative to plant needs than is phosphorus and must be conserved, fixed, and recirculated.

17. Measurements of low-level radioactivity which was present (Table 13, Fig. 11) provided further evidence of nutrient conservation, and autoradiograms of corals (Fig. 9) provided additional evidence for symbiosis between corals and their skeletal algae.

18. Plankton and eroded sand broken from the front-reef breaker zone is recaptured on the middle-reef zones.

19. Estimates indicate 1.6 cm of calcareous deposition per year but there is no evidence that this is not eroded almost equally rapidly.

20. The Japtan inter-island reef at Eniwetok is primarily a coral reef rather than a calcareous algal reef in the geological reef-forming sense. But like other communities studied (whether aquatic or terrestrial), the Japtan reef has a large predominance of living plant biomass, even though organisms classified as animals are more conspicuous.

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