

The Feeding Habits of Fishes and Primary Production at Eniwetok, Marshall Islands¹

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Introduction

Results of experiments on rasping and grazing fishes at Fanning Island, central Pacific, during mid-1963 led to the conclusion that certain families of coral reef fishes are a powerful influence in controlling, directly or indirectly, the survival and distribution of many shallow-water reef sponges (Bakus, 1964). Moreover, additional observations and a survey of the literature suggested that rasping, grazing, and predaceous reef fishes probably have played an important role by acting as agents of natural selection, leading to the evolution of protective mechanisms and habits among certain tropical shallow-water invertebrates. A more recent publication (Bakus, 1966) presented quantitative information and evidence from literature for further support of this hypothesis. The object of the present work is to compare the rasping behavior of fishes at Eniwetok Atoll with that of Fanning Island (both atolls).

During July 1965 I had the opportunity to make numerous observations on grazing fishes at several of the approximately 38 islands of Eniwetok Atoll (Woodbury, 1964). Underwater photographs and movies were taken of grazing fishes and of the effects of grazing on benthic algae. The terms "rasping" and "grazing" are used as synonyms and applied to those fishes that actually scrape the substratum while feeding. Other observed feeding types not included in this category are: "browsers" which consume benthic algae but do not scour the substratum and "predators" which usually consume mobile invertebrates and vertebrates although they may also bite and consume sessile organisms.

Investigations on Grazing and Predaceous Fishes and Descriptions of Study Areas

1. Lagoon in the region of the Eniwetok Marine Biological Laboratory, Eniwetok Island.

The area adjacent to the laboratory was surveyed from the uppermost littoral to about 36 m offshore where the depth ranges from 0 to approximately 4.5 m. The bottom consists of a dead coral shelf uncovered at low tide, and as one proceeds into the lagoon, this is followed by zones of dead corals, sand, and more dead corals. The dead coral substratum has a dense but thin mat of algae growing on it. The calcareous green alga *Halimeda* is common in small patches.

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There are a few scattered live but small table *Acropora* and a few exposed invertebrates, chiefly gastropods. The variety of fishes is striking in this region of few living corals but the numbers of each species of fish are relatively small. Common representatives in the deeper areas (3 to 4.5 m) include surgeonfishes (Acanthuridae), damselfishes (Pomacentridae), squirrelfishes (Holocentridae), parrotfishes (Scaridae), triggerfishes (Balistidae) and wrasses (Labridae). Many fishes were grazing and browsing on the algal mat living on dead corals. Manini or Convict Fish (*Acanthurus triostegus*) often foraged in schools comprised of 5-20 individuals in water less than 2 m deep. When water covered the coral shelf at the laboratory Manini were often seen browsing there. Parrotfishes (*Scarus* spp.) and surgeonfishes (*Naso lituratus*) grazed and browsed at intermittent times.

Approximately 200 m northwest of the laboratory is a short concrete fishing pier. The concrete shelf there as well as adjacent dead coral heads were covered with an algal mat. Numerous fishes frequented this point. Small schools of Manini often browsed on the algae growing on the concrete shelf. Parrotfishes were commonly observed in the area.

2. Reef flat of Eniwetok Island.

The outer reef is characterized by an upper zone of coral cobble about 6 m wide below which is often a 3-5 m wide zone of sand. This is followed by a reef flat (old limestone pavement) that consists of a gently sloping micro-undulated substratum of dead coral upon which grows a veneer of algae, largely blue-green, especially in the upper reaches. The reef flat extends seaward a distance of about 40 m (in the more undisturbed southeastern half of the island) before merging with the abrupt uplift of old algal ridge. There is about 31-46 m of irregular and cavernous algal ridge, with open surge channels and other partially enclosed byways beneath the porous ridge. The scarcity of living corals on the reef flat and the algal ridge perhaps is due in part to the toxic effects of oil from a tanker wrecked prior to 1954 (see Emery, Tracy and Ladd, 1954: 182). Even *Porolithon*-type algae are poorly represented along the algal ridge. An account of the geology of Eniwetok Atoll and descriptions of traverses across reefs and along shores are given by Emery, Tracy and Ladd (1954: 91-100, 182-190).

The most striking phenomenon about the reef flat is the innumerable toothmarks that range from the uppermost reaches of the dead coral substratum (*Nerita plicata* zone) to the outer edge of the algal ridge, and beyond. On the incoming tide Manini in large schools gradually browse their way to the uppermost reaches of the reef flat. Behind the Manini are large schools (perhaps 300-400 fishes) of *Acanthurus guttatus* that are also actively browsing and grazing on benthic algae. Here and there the two species overlap and are observed browsing and grazing together but the smaller Manini is most often the first browser to advance in with the tide when both species are present. Depending on the specific locality, *A. guttatus* are usually first to advance inshore when Manini are absent. Behind *A. guttatus* are numerous schools of parrotfishes (*Scarus* spp.). They tend to remain in slightly deeper water until the water is from mid-high to high tidal level at which time they tend to venture in towards shore, although preferring to remain offshore a short distance. On one occasion they were observed to be about 3 m from the water's edge during the highest tide. Examination of stomach contents from fishes of the reef flat indicated that juvenile *Acanthurus triostegus*

are strictly browsers; adults have algae and a few small coral fragments in their digestive tracts. Medium to large-sized *Acanthurus guttatus* graze significant quantities of coral fragments along with benthic algae. Small toothmarks predominate from the upper limit of the reef flat seaward approximately 18 m. These are believed to be caused by the grazing activities of *Acanthurus guttatus* and probably juvenile scarids. Below this zone are intermixed tooth scars of acanthurids and scarids. The algal ridge, surge channels and associated pools show an abundance of the rather deeply grooved parrotfish toothmarks. It is of interest to note that a large gastropod, *Thais armigera*, collected on the outer reef flat, had several tooth scrapings on the shell; the shell supported a growth of algae.

Because parrotfishes comprise one of the dominant families of grazers and represent the largest of the grazing fishes, a survey was conducted in order to determine the density of Scaridae on the reef flat adjacent to a road running from the southeast end of the island airstrip to about 400 m from the northeast end of the airfield, a total distance of one statute mile (1609 m). A binocular and hand counter were used to record the number of fishes observed. It was soon determined that observations could not be conducted properly during periods of relatively high wind velocity, high or low tide (accompanied by either considerable surf or lack of water), and cloudy overhead sky or rain. As time progressed the number of color phases of scarids detected increased from 2 to 3 (bright green, pale green, purple brown) and the overall efficiency in detecting scarids improved considerably. It was discovered that observations with a binocular, made from a jeep, were only effective from the uppermost water line to the beginning of the algal ridge, a 40 m wide strip of reef flat. Moreover, the best time for surveying in regard to tide, surf, and the grazing habits of the fishes was the 45-minute observation period from 3-1/2 to 2-3/4 hours before high tide.

Table 1. Population Density of Scaridae on the Reef Flat of Eniwetok Island*.

Date	Time Surveyed	Color Forms Observed and Counted	No. of Parrotfishes Counted
7 July 1965	11 A. M. to 12 Noon. 3 $\frac{1}{2}$ to 2 $\frac{1}{4}$ hrs. before high tide	2 (bright green and purple brown)	93
11 July 1965	2:30 P. M. to 3 P. M. 1 to $\frac{1}{2}$ hr. before high tide	2 "	58
14 July 1965	2:20 P. M. to 3 P. M. 3 to 2 $\frac{1}{4}$ hrs. before high tide	2 "	138
18 July 1965	4 P. M. to 4:45 P. M. 3 $\frac{1}{2}$ to 2-3/4 hrs. before high tide	2 "	343
19 July 1965	4:15 P. M. to 5 P. M. 3 $\frac{1}{2}$ to 2-3/4 hrs. before high tide	3 (bright green, pale green, and purple brown)	523
27 July 1965	1:15 P. M. to 2 P. M. 3 hrs. to 2 $\frac{1}{4}$ hrs. before high tide	3 "	242

* Population densities are given for a portion of the reef flat measuring 40 m. wide and 1609 m. (1 statute mile) long, located adjacent to the airstrip.

Table 1 presents the data. From underwater observations on scarids in many areas I am fairly certain that the highest density observed on the reef flat through a binocular is substantially less than the mean numbers of parrotfishes actually occurring in this region at these times. If the assumption is made that 523 scarids graze on this area of reef flat, a rough estimate of the population density of large grazing parrotfishes is 1 fish per 123 m² during a tidal cycle.

3. Quarry and adjacent reef flat of northeast Eniwetok Island.

The quarry represents an excavation carried out in the 1950's by the Holmes and Narver Engineering Corporation. It occupies an area of once normal reef flat and now measures roughly 45 m wide by 90 m long and ranges to a greatest depth of about 5 m at high tide. During July water temperatures ranged from 28–31°C. and salinities from 33.6–35.4‰ with mean values of 29°C. and 34.4‰ respectively. The substratum consists of innumerable dead coral fragments and fossil rubble interdigitated with deeper channels of sand. Live corals such as *Acropora*, *Pocillopora* and *Montipora* are sparsely distributed except in a few restricted regions where they are moderately numerous. The part of the quarry nearest shore is bordered by a few narrow tongues of reef flat where many Manini browse at high tide. Manini were also observed browsing in the quarry in large numbers at depths of from 1–2 m. Numerous families of fishes are represented in the quarry. The area is exceptionally rich at high tide when everything from blennies (*Istiblennius* spp.), small grazing surgeonfishes (*Acanthurus* spp.) and top herring (*Sprattelloides delicatulus*) to nearly 2 m-long black-tip sharks (*Carcharinus melanopterus*) may be observed. A representative collection of over 100 species of fishes was made in mid-July by the use of rotenone (Chemfish) and by spearing; many of the animals were taken from the quarry. These specimens are identified and now reside in the ichthyological preserves of the Los Angeles County Museum. Among the characteristic bottom feeders in the quarry are Scaridae (*Scarus* spp.), Balistidae (*Rhinecanthus aculeatus*, *R. rectangulus*), Acanthuridae (several species including *Acanthurus guttatus*, *A. triostegus* and *Ctenochaetus aliala*), Labridae (numerous species), Siganidae (*Siganus rostratus*) and Mullidae (*Parupeneus cyclostomus*). The greatest concentration of grazers, especially scarids, on an incoming tide was located at the outer edge of the quarry where the water was most turbulent.

Several observations gave some indication of the voracity of certain fishes in the quarry. Few soft-bodied invertebrates were exposed to the numerous grazers and predators living there during the day. When rocks were overturned several species of wrasses and certain trigger-fishes would often consume some of the organisms that were exposed (e.g., ophiuroids) but the abundant 5 cm-long brown sea cucumber, *Holothuria difficilis*, appeared to be avoided by fishes. William Bussing (personal communication) overturned coral slabs and observed that 2 cm-wide crabs were readily consumed by several species of wrasses and sand perches (*Parapercis montillae*). On 11 July 1965 William Bussing called my attention to numerous *Abudefduf septemfasciatus* that were guarding ova attached to the wall at the inner end of the quarry. The thin egg masses were purple and each consisted of several thousand ova. When the guarding fishes were closely approached they retreated from their egg mass and immediately several species of wrasses, numerous small blue pomacentrids (*Abudefduf glaucus*) and even other individuals of *A. septemfasciatus* ate the eggs voraciously. On other occasions

slabs were overturned and wrasses were usually the first fishes to consume organisms adhering to the exposed undersurface. The larger acanthurids and scarids were rather reluctant to move into the area to graze, perhaps because of the proximity of the observer. Mature or larger parrotfishes were often difficult to approach closely for observations or photography. In contrast, the medium-sized species of parrotfishes at Fanning Island could be approached readily (Bakus, 1964).

4. Parry Island.

Evidence of grazing activities was widespread on the seaward reef flat where innumerable fish toothmarks were observed up to the highest water line. *Acanthurus triostegus* and *A. guttatus* were observed browsing and grazing in large numbers. Scarids were observed grazing in considerable numbers at the northeast end of the island.

A shallow pool located adjacent to the Parry Island quarry contained numerous sponges, ophiuroids, and moderate numbers of crabs, polychaetes and flatworms but practically all representatives of these groups were well hidden under coral rocks. On 13 July William Bussing called my attention to a pomacentrid (*Abudefduf septemfasciatus*) that was guarding a mass of thousands of eggs under a coral rock. Several *Abudefduf glaucous* were attempting to swim in and consume the eggs. As we approached closer the guarding fish saw us, swam away, and *A. glaucous* immediately began feeding on the eggs.

5. Japtan Island.

This island was visited on two occasions. The northeast end consists of an extensive reef flat of coral rubble and boulders. Fish toothmarks were extremely numerous from the highest level of coral boulders to a distance of at least 50 m offshore (See fig. 1). Parrotfishes were abundant in the area on the incoming tide and grazing actively. Although invertebrates were moderately numerous to abundant on the undersides of boulders very few were observed on the surface where they would be exposed to potential grazers and predators.

6. Japtan Reef.

This region was visited on one occasion, approximately where Odum and Odum (1955) conducted their investigations on reef productivity. The specific area observed was comparable to their "zone of larger coral heads." Numerous schools of scarids and smaller aggregates of acanthurids grazed on the substratum or rubble bottom between large patches of coral. The algae *Caulerpa*, *Halimeda* and *Turbinaria* were growing in moderate numbers especially in depressions within the extensive, generally level-topped coral patches. The area contained far more exposed algae than any other region visited at Eniwetok Atoll but the standing crop did not appear to be comparable to that of shallow sublittoral algae on rocky substrata along temperate coasts I have visited. Fishes apparently do not often consume these genera of algae, in part because of their location in coral pockets and the prevailing strong current velocity. Moreover, *Turbinaria* and *Halimeda* may not be desirable as a food source because of their deposits of calcium carbonate. A large *Tridacna maxima* collected from the reef had moderate numbers of fish toothmarks on both valves.

7. Chinimi Island.

Chinimi is characterized by having a magnificent development and diversity



Fig. 1. A coral slab (60 by 36 cm) in situ in the littoral zone at the northeast end of Japtan Island. Note the numerous white streaks that represent the toothmarks of parrotfishes which have been grazing on algae.

of corals off the northwest end (lagoon) to a depth of about 6 m and this supports a large variety of fishes. Parrotfishes (*Scarus* spp.) were common and actively grazing, primarily on the substrata of dead corals and on the bases of living corals. Acanthurids (*Ctenochaetus aliala* and others) browsed in a similar manner. Fishes of the species *Monotaxis grandoculis* (Family Sparidae) were common here but not observed grazing. The only live coral fishes were observed biting was *Porites*. *Porites* displayed moderate numbers of toothmarks, although a few toothmarks were observed on many of the other genera of corals. As is other areas, few readily edible invertebrates were exposed.

8. *Rigili Island.*

The upper reef flat around the island was grooved by thousands of toothmarks, up to the highest water line. Manini and scarids were abundant on the incoming tide and the zonation of grazing fishes was similar to that of other islands. The reef flat (seaward), just southwest of an extensive sand spit, at low tide was less than 1 ft. deep over the living *Acropora* beds. Living corals were abundant; several species of *Acropora* were dominants. Numerous scarids (*Scarus* spp.) and acanthurids (*Ctenochaetus aliala* and probably *Acanthurus gahhm*) were observed grazing and browsing, principally on intermittently distributed areas of dead coral pavement and dead branching corals. These genera appeared to represent the most abundant fishes by number and by weight. Scarid toothmarks were observed on live corals but this was limited to round, massive heads of *Porites*.

Sponges were common to abundant under small (<1 m. diameter) dead slabs of table *Acropora* and common under and within live corals. No sponges were

observed to be exposed. Exposed algae contributed relatively little to the overall standing crop. *Halimeda* was moderately common and a filamentous alga that hung between the lower half of the branches of *Acropora* was relatively abundant. On 16 July a 1 m-diameter table *Acropora* was overturned and approximately 6 species of sponges were discovered growing on the underside, in patches measuring up to 13 cm in diameter. Wrasses of several species began feeding on the bottom biota and were soon joined by scarids. The next day the same overturned table *Acropora* was re-examined and it was found that only two small organisms remained, comprising the dull black sponge *Samus anonyma* and the bright yellow sponge *Hippiospongia metachromia*. These apparently were distasteful to the fishes. Toothmarks were evident on the overturned slab. It is of interest to note that practically no sponges were observed exposed in the Eniwetok quarry except for a few specimens of *Hippiospongia metachromia*.

9. Other Regions.

Although I did not visit the far northern islands of Eniwetok Atoll there is little doubt that grazing activity is comparable to that discussed above. This assumption is strengthened by two observations: Dr. Robert Johannes (personal communication) observed that scarids were common on the reef flat of Engebe Island and Darryl Stokes (personal communication) thought that the reef flat of Engebe Island may support a larger population density of scarids than that of Eniwetok Island.

Primary Production in the Benthic Algae on the Reef Flat of Eniwetok Island

On 8 July a triangular exclosure (exclosure No. 1) was arranged on a tongue of reef flat adjacent to the inner end of the Eniwetok quarry. It measured 2 m on a side and consisted of 3 supporting pipes (1 m high) placed into star-drilled holes around which was fastened chicken wire with a greatest mesh size of 36 mm by 26 mm. This is believed to exclude most fishes from algae within the exclosure. Further details on the study area are given in the discussion of the quarry and adjacent reef flat of northeast Eniwetok Island (see above). On 9 July six quadrats, measuring 5 cm on a side (25 cm²) were scraped clean of blue-green algae. The algae were fixed in 7% formalin. The same day exclosure No. 2 was arranged about 30 m southeast of the southern perimeter of the quarry by placing chicken wire around two large separated concrete blocks. The second exclosure was slightly over 1 m high and occupied an area of about 2 m². Algae were removed and preserved in a manner comparable to those of exclosure No. 1. After 17 days the same quadrats in exclosure No. 1 were rescraped clean and 6 additional quadrats were scraped. This procedure was repeated in exclosure No. 2. Photographs were taken at several stages during the experimental work. After returning to the Allan Hancock Foundation the algal samples were dried to constant weights and placed in a muffle furnace (525°C) in order to obtain organic weights. Additional samples were analyzed for carbon content with a Coleman carbon-hydrogen analyzer. Data from the experiments are presented in Table 2.

Exclosure No. 1 was situated high in the intertidal so that the area was often dry during low tide. The algae were exposed to the hot tropical sun as well as

Table 2. Data on the Standing Crop and Primary Production of Blue-green Algae.

Quadrat	Date Scraped	Date Rescraped	Duration of Experiment	Initial Standing Crop g. organic matter per 25 cm ²	Final Standing Crop g. organic matter per 25 cm ²	Primary Production gC/m ² /day
1-A	9 July	26 July	17 days	*0.565	0.054	0.71
1-B	"	"	"	*0.642	0.088	1.16
1-C	"	"	"	*0.534	0.106	1.40
1-D	"	"	"	*1.039	0.133	1.76
1-E	"	"	"	*0.916	0.117	1.55
1-F	"	"	"	*0.581	0.138	1.83
2-A	11 July	27 July	16 days	0.118	0.058	0.77
2-B	11 July	"	16 days	0.120	0.119	1.59
2-C	12 July	"	15 days	0.050	**	
2-D	"	"	"	0.148	0.151	2.15
2-E	"	"	"	0.054	0.046	0.65
2-F	"	"	"	0.279	0.060	0.85
1-A'	26 July			0.188		
1-B'	"			0.157		
1-C'	"			0.235		
1-D'	"			0.192		
1-E'	"			0.198		
1-F'	"			0.226		
2-A'	27 July			0.169		
2-B'	"			0.134		
2-C'	"			0.199		
2-D'	"			0.324		
2-E'	"			0.196		
2-F'	"			0.215		

* = incomplete combustion

** = excess water prevented scraping

to rainwater from cloudbursts. They comprised two dominant species: *Calothrix crustacea* and *Schizothrix calcicola*. Seawater covered the algae less than 6 hours per day and at high tide the temperatures and salinities in the enclosure were comparable to those of the adjacent quarry (see above). Enclosure No. 2 was located about 40 m from the upper end and 80 m from the lower, end of the reef flat exposed at low tide. Benthic algae (*Calothrix crustacea*, *Schizothrix calcicola*, *Ectocarpus* sp.) were under seawater for longer periods of time but this was not reflected in a greater standing crop or primary production. This was probably due to the presence of small animals (e.g., crabs, blennies) within the enclosure (see below). Blennies, in particular, consume filamentous algae on the reef flat (see Hiatt and Strasburg, 1960: 106-107). The water temperatures and salinities at low tide ranged from 27-34°C. and 33.6-35.4‰, respectively, with mean values of 31°C. and 34.6‰.

After the completion of the experiments it was noted that enclosure No. 1 contained a few 4 mm-long polychaetes and enclosure No. 2 a few small hermit crabs, several sea anemones, one small crab (*Grapsus grapsus*), numerous copepods and several 2 cm-long blennies (*Istiblennius* spp.). Not all the algae on the reef flat were grazed by fishes. One notable exception was a large patch of algae

(*Calothrix crustacea* and *Schizothrix calcicola*) growing under shade near enclosure No. 2.

Discussion

Studies on the feeding habits of fishes by Hiatt and Strasburg (1960) and recent direct observations and experiments on feeding fishes by the present author support the conclusion that marine fishes are influencing profoundly the benthic biota of coral reefs at Eniwetok Atoll. The chief grazers and browsers are parrotfishes and surgeonfishes. This appears to be typical of many tropical coral reefs (Bakus, 1964, 1966), including the Tuamotus (Harry, 1953; 117, 145). Numerous fishes at Eniwetok are predators on invertebrates (see Hiatt and Strasburg, 1960), especially the diurnal wrasses of which there exist a considerable variety. Hobson (1965) found that in tropical fishes off southern Baja California, nocturnal species are predators whereas herbivorous and omnivorous fishes show predominantly diurnal feeding habits. These characteristics would appear to be correlated in part with the fact that certain invertebrates that are members of the cryptofauna (organisms secluded among, under, and within corals) become active and move about at night (see Schroeder, 1965) enabling carnivores, which comprise roughly 65% (Bakus, 1966) of the species of fishes, to acquire an adequate food source. Nevertheless, there probably are numerous invertebrates that live hidden among corals much of the time. Further observations at night are needed to obtain a clearer understanding of interactions between invertebrates and fishes during this time.

One method by which benthic invertebrates may be able to avoid excessive predation is by being poisonous, venomous or distasteful to predators or grazers. This may have been exemplified by a small but abundant sea cucumber, *Holothuria difficilis*, at Eniwetok Atoll. This organism was exposed to many potentially predaceous fishes during both day and night yet was numerous. With a brief gentle handling this holothurian discharged an appreciable quantity of Cuvierian material that was excessively adhesive, apparently a deterrent to many organisms that might attempt to consume them. If the discharge were noxious, something not determined during the present study, it would prove even more effective against predators.

Talbot (1965) reported that about 20% of the fishes by weight are coral feeders at Tutia Reef, Tanganyika, East Africa. When compared to previous reports this appears to be an exceptionally high percentage but Talbot did not indicate the approximate percentage of materials in the digestive tracts that was dead coral. Butterfly fishes (Chaetodontidae) probably consume mostly live coral polyps and perhaps some calcium carbonate fragments whereas parrotfishes, which may comprise the largest family of fishes by weight on coral reefs (Bakus, 1966), appear to consume mostly dead coral in the process of rasping algae and sessile invertebrates from the substratum. At Eniwetok, fish feeding by grazers on living coral was limited largely to *Porites*. At Fanning Island, central Pacific, toothmarks were common on live *Porites* and *Millepora*.

Observations at Eniwetok Atoll and Fanning Island support the hypothesis that the predominant grazing and browsing fishes on the reef flat move into

shallow waters on the incoming tide not to escape predators but to consume the productive primary producers (see below). On many occasions there is either no predation or only an occasional potential predator passing through a particular area. The grazers and browsers at Eniwetok may occur in enormous numbers and may exert considerable effort to arrive at the uppermost reaches of the intertidal zone where they can consume benthic algae. Most of the reef flat on Eniwetok Island and a few other islands (e.g., Parry) is flat and often lacks both living and dead dendritic corals so that little protection is available to these fishes from potential predators.

The day following the removal of chickenwire from exclosures Nos. 1 and 2 it was found that fishes had not consumed the comparatively lush algal growth. The algae were thoroughly grazed the second day after removal of the wire. This suggests that behavior patterns may have been selected so that fishes, comprising populations with sizes normal for the region, do not necessarily graze the same areas each day, thus perhaps enabling the available energy sources to have an opportunity to survive and produce. Another aspect of this is that grazers have the potential to strip the reef flat bare but do not, in part because of the energy required to obtain more food after a certain quantity has been removed from an area. Moreover, their feeding periods are restricted by diurnal low tides.

Sponges not consumed by grazing fishes both at Fanning Island and Eniwetok Atoll were yellow or black although different species of Porifera were rejected or ignored in the two regions. I believe that the similarity of colors in the two areas to be a coincidence. This is supported by the observation that there was an abundant black sponge at Fanning Island (*Chondrilla* sp.) that was readily consumed by fishes when made available to them whereas a black dictyoceratid (keratose) sponge was able to grow successfully in the central lagoon under natural conditions in the presence of numerous grazers, indicating that color was not important as a cue. Certain organisms such as sponges are unlikely to have cryptic coloration because many are eaten by indiscriminate consumers. Those organisms not consumed are often rejected by trial and error tasting.

Gilmartin (1960) found that herbivores did not appear to influence the composition of deep water benthic algal communities at Eniwetok Atoll. He concluded that the effects of browsing were probably negligible. His studies were conducted at depths of from 19 to 63 m. This tends to support the idea that most grazers influence the biota principally in relatively shallow waters and particularly in the upper 10 m where their populations are large.

The following sections discuss energetics on the reef flat of Eniwetok Island. Because few data are available it is of interest to speculate about the relationship between production and consumption.

The results of studies on standing crop and primary production in blue-green algae are presented in Table 3. Although blue-green algae are commonly found within live and dead corals, the data on production presented in this paper are considered to be reasonably reliable since algal scrapings removed only small amounts of surface limestone and all quadrats were scraped in the same manner. The mean % of carbon in Cyanophyceae on the middle and upper reef flat is about 55% based on organic weight and about 20% based on dry weight. The

Table 3. Results of Studies on Standing Crop and Primary Production in Blue-green Algae.

Mean % carbon in Exclosure #1 (based on organic wt. of 3 samples)=56.2%

Mean % carbon in Exclosure #2 (based on organic wt. of 3 samples)=53.4%

Mean standing crop (dry wt. of organic matter):

Quadrat Series	Dates	Gms. org. matter per 25 cm ²	Gms. org. matter per m ²
1A to 1F	9 July	*0.713	*285
2A to 2F	11-12 July	0.128	51
1A to 1F	26 July	0.106	42
2A to 2F	27 July	0.087	35
1A' to 1F'	26 July	0.199	80
2A' to 2F'	27 July	0.206	82

Increase in the mean standing crop of organic matter in exclosure #2 during a period of 15 to 16 days=61%

Production for a level substratum:

Exclosure	Method	Net production in gCarbon/m ² /day and (gC/m ² /year)
#1	Settling and growth	1.39 (506)
#2	Settling and growth	1.19 (433)
#2	Difference in mean standing crop	1.06 (386)

*=incomplete combustion

latter figure may appear to be low (see Vinogradov, 1953: 27) but the scraped samples of algae contained calcium carbonate from the surface of the reef pavement. The mean standing crop of organic weight under natural conditions was roughly 50 gms per m². The weight of organic matter reported for quadrat series 1A to 1F was excessively high because of incomplete combustion of algae in the muffle furnace. This was noted as a black precipitate in the crucibles in which the algae had been placed. The occurrence of incomplete combustion was confirmed by examining photographs taken of the exclosures, indicating that the standing crop of algae in the two was comparable under natural conditions. The mean standing crop of organic matter in exclosure No. 2 increased about 61% during a period of 15 to 16 days. This increase of productivity was expressed in grams of carbon (Table 2). The values for percentage carbon content (Table 3) are not entirely correct. The algae scraped from quadrats within the two exclosures was fixed in a seawater-formalin solution. The seawater contained a very low standing crop of phytoplankton which added a minute amount of carbon.

The productivity of reef flat Cyanophyceae as expressed in Table 3 appears to be low but these figures are misleading since values for net production are listed and the algae grew on a practically level surface. I measured the approximate surface area exposed in a specimen of blue coral (*Heliopora*) taken from Japtan Reef, Eniwetok Atoll, and found that it was about four times that of the bottom surface area covered by the coral (looking down at the coral from above). This is a conservative ratio since *Heliopora* would have less coral surface area per

unit water surface area than that of many species of dendritic *Acropora*. If the assumption is made that net production is about 90% of gross production during exponential growth (see Ryther, 1954) and that the actual surface area occupied by reef flat Cyanophyceae on dead dendritic coral is approximately 3 times (a value chosen in part because the substratum is not entirely dendritic coral) that of what it would be on a flat surface then the gross primary production of these algae, expressed in a manner comparable to that given in much of the literature (i.e., water surface area) would be about 1287 to 1687 grams (conservative estimate) of carbon/m²/year. This compares favorably with the range 1800 to 11,680 grams of carbon/m²/year listed by Gordon and Kelly (1962) for tropical coral reefs; it indicates that the thin veneer of reef flat algae is productive, and suggests that natural selection might have produced certain species of fishes that would swim into very shallow waters to exploit this rich energy source.

The survey conducted on Eniwetok Island to obtain a rough estimate of parrotfishes gave favorable results. If the largest observed fish count is used (see Table 1 and above) the population density of large parrotfishes on the reef flat was about 1 fish per 123 m² Randall (1963), on poisoning reef fishes in the Virgin Islands, obtained a density value of about 1 scarid per 27 to 46 m² based on large fishes having a standard length of about 250 mm. The large parrotfishes (*Scarus brevipilis*) at Eniwetok measured about 330 mm in standard length. Despite the fact that numerous smaller pale scarids were not observed while counting and that the reef flat supported few live corals, the population densities of the two regions are not too dissimilar.

A comparison can be made between primary production and the energy requirements of parrotfishes on the reef flat. Several assumptions must be made because calorimetric values on metabolism in scarids are not available so far as is known. The first problem is to determine how much energy is utilized by parrotfishes. The standard length of larger parrotfishes (based, unfortunately, on only one poisoned specimen collected from a surge channel in the study area) was 330 mm and the wet weight for this length was 1135 gms. The respiratory rates for a puffer at 20°C. and a trout at 15°C., under normal (?) conditions, are 0.06 and 0.349 ml oxygen/g. wet weight/hr. (Prosser and Brown, 1961: 158), respectively. The respiratory rates for a mullet at a temperature of from 24 to 25°C. range from 0.100 to 0.465 ml oxygen/g. wet weight/hr. (Nicol, 1960: 153). Further information on metabolism and bodyweight of fishes is given by Paloheimo and Dickie (1966). Parrotfishes are usually active but perhaps not as active as certain mullets, so I will use a value of 0.25 ml oxygen/g. wet weight/hr. for their diurnal activities since they spend 2/3 to 4/5 of the day grazing (Bardach, 1961). This gives a diurnal oxygen consumption of 0.28 L oxygen/hr/1135 g fish. Herbivores have higher respiratory quotients than carnivores and respiratory quotients in poikilotherms may increase with increasing temperature (Prosser and Brown, 1961: 185). The R. Q. value for fat is 0.71 and for carbohydrates it is 1.0. The R. Q. value for scarids is assumed to approximate 0.9 because their feeding habits are largely herbivorous on the reef flat and because the water temperature there averages about 29°C. At a non-protein R. Q. value of 0.9 the caloric value of 1 L of oxygen used in oxidations of mixtures of carbohydrates and fat is 4.924 kilo-calories (Swift and French, 1954). A 330 mm (1135 g) parrotfish would use

17 k-cal per 12-hour day. If it is assumed that during a 12-hour night the same fish uses 25% of his diurnal energy requirement (Nicol, 1960: 153; Prosser and Brown, 1961: 159) it would require 4 k-cal. This gives a total energy requirement of about 21 k-cal/fish/24 hrs. or about 11,000 k-cal/day for the population of 523 large parrotfishes within the 65,000 m² survey area.

The production of blue-green algae, using the lowest figure available (based on the change in mean standing crop in enclosure No. 2), is about 2 g organic matter/m²/day or 1 gC/m²/day for the survey area. This may be compared with data from Burkholder, Repak, and Sibert (1965) who found that samples of micro-algae from intertidal zones of beaches and mud-flats in Long Island Sound (41°N. latitude) produced an average of about 4.45 mg C/m²/day. These data indicate that littoral blue-green algae on the outer reef at Eniwetok may occasionally be over 200 times more productive than littoral micro-algae from sand and mud flats in Long Island Sound. I was unable to obtain calorimetric values for marine plants but 4 k-cal per gram of ash-free weight probably would be a reasonable estimate (see Golley, 1961: 582). Using this values, the survey area on the reef flat at Eniwetok Island produces roughly 520,000 k-cal per day. Assuming that the larger scarids in the study area represent at least 50% of the biomass of parrotfishes (see Randall, 1963), about 22,000 k-cal/day would be needed to support the standing crop of Scaridae. With the availability of about 520,000 k-cal this leaves a surplus of 498,000 k-cal/day which in part is available to support the very large populations of *Acanthurus triostegus* and *A. guttatus* that frequent the reef flat during the diurnal high tide. From this one can conclude that there is sufficient energy available in the survey area to support the parrotfishes, and apparently enough remaining to support surgeonfishes and other browsers and grazers. It appears likely that these fishes do not have enough time on the reef flat to consume sufficient food for their daily energy requirements; this requires them to continue feeding activities in slightly deeper waters, beyond the algal ridge, during low tide.

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Summary

Fish-grazing and rasping behavior at Eniwetok Atoll, Marshall Islands, was comparable to that at Fanning Island, Line Islands. Marine fishes are influencing profoundly the benthic biota of coral reefs at Eniwetok Atoll. The benthic biota is affected principally in relatively shallow waters and particularly in the upper 10 m where their populations are often large. Observations support the hypothesis that the predominant grazing and browsing fishes on the reef flat move into shallow waters on an incoming tide not to escape predators but to consume the productive primary producers.

A visual count of the large parrotfishes on the relatively barren reef flat of Eniwetok Island indicated that their population density was about 1 fish per 123 m². This estimate is not too dissimilar from values given for large scarids on other coral reefs (with a rich development of live corals) where fishes have been poisoned.

The net production of blue-green algae on the reef flat of Eniwetok Island is slightly more than 2 g. organic matter/m²/day or 1 gC/m²/day during July. Speculations made, using the few data available, indicated that the productivity of reef flat Cyanophyceae on Eniwetok Island was roughly 520,000 k-cal/day (conservative estimate) for a study area of about 65,000 m². Energy needed to support parrotfishes within the study area was estimated to be about 22,000 k-cal/day, leaving a surplus of 498,000 k-cal/day, in large part for other grazers and browsers. It is unlikely that parrotfishes have enough time on the reef flat to consume sufficient food for their daily energy requirements; this requires them to continue feeding activities in slightly deeper waters during the diurnal low tide.

Literature Cited

- BAKUS, G. J.** 1964. The effects of fish-grazing on invertebrate evolution in shallow tropical waters. Allan Hancock Foundation Occasional Pap. No. 27: 1-29.
- BAKUS, G. J.** 1966. Some relationships of fishes to benthic organisms on coral reefs. *Nature* 210 (5033): 280-284.
- BARDACH, J. E.** 1961. Transport of calcareous fragments by reef fishes. *Science* 133 (3446): 98-99.
- BURKHOLDER, P. R., A. REPAK and J. SIBERT.** 1965. Studies on some Long Island Sound littoral communities of microorganisms and their primary productivity. *Bull. Torrey Bot. Club* 92 (5): 378-402.
- EMERY, K. O., TRACY, J. I., Jr. and H. S. Ladd.** 1954. Geology of Bikini and nearby atolls. Bikini and nearby atolls: Part I, Geology. *Geol. Surv. Prof. Pap.* 260-A: Wash., D. C.
- GILMARTIN, M.** 1960. The ecological distribution of the deep water algae of Eniwetok atoll. *Ecology* 41 (1): 209-221.
- GOLLEY, F. B.** 1961. Energy values for ecological materials. *Ecology* 42: 581-584.
- GORDON, M. S. and H. M. KELLY.** 1962. Primary productivity of an Hawaiian coral reef: A critique of flow respirometry in turbulent waters. *Ecology* 43 (3): 473-480.
- HARRY, R. R.** 1953. Ichthyological field data of Raroia Atoll, Tuamotu Archipelago. *Atoll Res. Bull.* No. 18: 1-190.

- HIATT, R. W. and D. W. STRASBURG.** 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* **30**: 65-127.
- HOBSON, E. S.** 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia*, 1965 (3): 291-302.
- NICOL, J. A. C.** 1960. The biology of marine animals. Interscience: New York.
- ODUM, H. T. and E. P. ODUM.** 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecol. Monogr.* **25**: 291-320.
- PALOHEIMO, J. E. and L. M. DICKIE.** 1966. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. *J. Fish. Res. Bd. Canada* **23** (6): 869-908.
- PROSSER, C. L. and F. A. BROWN, Jr.** 1962. Comparative animal physiology. Saunders: Philadelphia.
- RANDALL, J.** 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Carib. J. Sci.* **3** (1): 31-48.
- RYTHER, J. H.** 1954. The ratio of photosynthesis to respiration in marine plankton algae and its effect upon the measurement of productivity. *Deep Sea Res.* **2**: 134-139.
- SCHROEDER, R. E.** 1965. Something rich and strange. Harper and Roe: New York.
- SWIFT, R. W. and C. E. FRENCH.** 1954. Energy metabolism and nutrition. Scarecrow: Wash., D. C.
- TALBOT, F. H.** 1965. A description of the coral structure of Tutia Reef (Tanganyika Territory, East Africa), and its fish fauna. *Proc. Zool. Soc. London* **145** (4): 431-470.
- VINOGRADOV, A. P.** 1953. The elementary chemical composition of marine organisms. *Sears Foundation Mem. No.* **2**: 1-647.
- WOODBURY, A. M.** 1964. A review of the ecology of Eniwetok Atoll, Pacific Ocean. *Instit. Environ. Biol. Res. Univ. Utah.* 123 pp.