Sparisoma viride (Bonnaterre), the Stoplight Parrotfish[1]), a major Sediment Producer on Coral Reefs of Bermuda ?[2])

By Reinhart A. Gygi[3])

ABSTRACT

A constantly regrowing dentition enables *S. viride* to erode and triturate reef rock or calcarenite of any hardness. Smooth-scoured surfaces of subtidal calcarenite and algal–vermetid rock off Bermuda's wave-swept south shore appear to be largely the result of abrasion by grazing herbivorous or omnivorous fish. The erosion rate was estimated in Gravelly Bay on the south shore where *S. viride* feed almost exclusively on algae. There most of the algae are filamentous and form a short-cut overgrowth on hard calcareous substrates of calcarenite or biolithite. The fish scrape away algae and some of the rock below with strong, beak-like jaws, and crush the mouthful in the pharyngeal mill. Swallowed rock bits are used as a milling agent to rip up algal cells. They outweigh nutrients in the digestive system about 3 to 1 (dry weight), and make up 4% of the fishes' wet body weight. Grain sizes range from less than a micron to 5 mm.

If the excreted sediment were deposited on an area equal to the area of erosion, then 2.1 metric tons or 0.12 mm of sediment with a porosity of 40% were laid down per hectar per year, which is equivalent to 1.2 m of uncompacted sediment per 10,000 years or about 100 m of limestone per one million years. This rate of a single scarid species indicates that parrotfish are a geologically significant agent in the transformation of reefs into sediment.

S. viride prefer agitated water near exposed reefs and shorelines. There the proportion of reworked sediment to detritus from erosion is lowest in the excrements. The erosion rate calculated for Gravelly Bay therefore appears to be above average to high. Boring by the sponge *Cliona lampa* under optimal conditions may proceed at a hundred times the maximum abrasion rate of *S. viride*. Fish erosion and sedimentation are conspicuous, but in Bermuda possibly of less quantitative importance than erosion and sedimentation by subtidal borers and etching by algal rhizoids.

The Rauracian Reef complex (Upper Jurassic) of northwestern Switzerland is in many respects similar to Bermuda. It is conceivable that fish of the genera *Mesodon* and *Microdon* (family Pycnodontidae) on these reefs had an ecologic position comparable to recent Scaridae. However, their capacity in the production of reef-derived sediment must have been inferior to that of modern scarids.

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[1]) The species name is used according to Winn & Bardach (1957).

[2]) Contribution No. 606, Bermuda Biological Station, St. George's West, Bermuda.

[3]) Naturhistorisches Museum, Department of Geology, Basel (Switzerland).

Introduction

At the present time there is no agreement about the relative importance of physical or chemical versus biogenic processes in marine erosion of reefs or subtidal carbonate rock. LADD, TRACEY, WELLS & EMERY (1950) made no reference to organisms when describing reef erosion and sedimentation on a Pacific atoll. FAIRBRIDGE (1952) as well as REVELLE & EMERY (1958) point out the chemical component of marine erosion. HODGKIN (1964, p. 390) thinks that "corrosion" is responsible for erosion of coastal limestone in Western Australia. STANLEY & SWIFT (1967, p. 679) write about the "smooth-scoured surfaces at the top and the base of the reef" off the south coast of Bermuda as being "morphological forms produced or strongly modified by mechanical erosion...". A second group of authors gave examples of the joint action of organisms and waves causing erosion of marine calcareous coasts or reefs. BERTRAM (1934) reviewed boring algae and animals of the Red Sea and noticed that coral colonies, broken off from the Ghardaqa reefs by waves, had their holdfast weakened by boring sponges and molluscs. The undercutting of coastal cliffs is due to boring algae soften-ing the rock to a depth of 5 mm and grazing chitons (*Acanthochiton spinigera*) rasping the surface. The powerful radula of *Acanthochiton* carves shallow, parallel grooves into the rock, and its faeces are entirely made up of calcareous matter (p. 1022 f.). GINSBURG (1953, p. 63) confirms that mechanical erosion by waves or rasping organisms is accelerated by boring plants or animals weakening their rock substrate. In the same article (p. 68) the author assumes that microorganisms are the dominant eroding agent in the intertidal zone (cf. NADSON 1927, p. 1016, and PURDY & KORNICKER 1958, p. 98), and macroorganisms in the subtidal zone. STEPHENSON & STEPHENSON (1954, p. 80) interpreted the smooth intertidal and subtidal surface of the algal–vermetid crusts and reefs off the south shore of Bermuda to be partly an effect of wave action, but also of erosion by chitons, snails, crabs, and fish. The authors observed these animals feeding on the algal growth covering the rock surface where they leave con-spicuous scars. ODUM & ODUM (1955, p. 317) thought that the windward reef of Eniwetok Atoll is eroded by "current abrasion and the complex of bacteria and boring algae". Some types of algal skeleton may be transformed into sediment when after death of the plant the organic integumenta decay and the skeletal elements disinte-grate (CHAVE 1960, p. 18). By this process coarse bioclastic sediment is formed by

Halimeda and lime mud by *Penicillus*. Emery (1962, p. 28) observed in Cocos Lagoon of Guam that only organisms or hurricane waves are able to degrade coral or coralline algae to bioclastic sediment. Grazing fish leave parallel scratches on coral and encrusting algae (see also Bakus 1966, Fig. 1 and 2). Grabau assumed early in this century that "perhaps by far the largest contribution of coral sand and mud is made by the activities of organisms" (republication of 1960, p. 415).

Evidence for direct biogenic erosion without other intervening factors has accumulated since April 1836 when Darwin, during the circumnavigation of the globe aboard H.M.S. Beagle, recognized the production of fine-grained sediment by two species of *Scarus* (coral-grazing parrotfish) on Keeling Atoll alias Cocos Island, Indian Ocean (Darwin 1842, p. 14). Darwin also emphasized the role of rock-boring worms and molluscs in the mechanical breakdown of reefs (cf. Wood-Jones 1910, p. 264 f.). Brunelli (1928) credited the supratidal snail *Littorina* with production of depressions in sandstone of the Mediterranean coast of Italy. Otter (1937) described a variety of rock-boring organisms of the Great Barrier Reef, Australia. Hartman (1958) demonstrated that the boring sponge *Cliona celata* produces particles from 30 to 70 microns in size (for photographs see Cobb 1969). An investigation by Warburton (1958) indicates that at least 90% of the material removed by *Cliona* is particulate. Hunt (1969) observed *Echinometra lucunter*, a rock-boring sea urchin of Bermuda, producing sand grains from 0.5 to 2 mm in size. Gygi (1969c, p. 33) found that boring organisms produce sand and rubble as a by-product when causing heavily bored shells of the snail *Strombus gigas* eventually to crumble. James (1970, p. 25) reported that the boring worm *Eunice schemacephala* produces pellets as large as 500 microns in size.

Biogenic erosion (cf. Neumann 1966, p. 92) as such is now a well-documented process. Part of the sediment on and around living coral reefs appears to be produced by the almost spontaneous post-mortem disintegration of fragile algal skeletons and by the activity of boring organisms as well as rock-grazing and sediment-ingesting animals. But few attempts have been made to estimate the rate of erosion. Probably the first research of this kind was undertaken by C. Reid. Jehu (1918), quoting Reid, wrote that the seabed of cherty chalk off the coast of Norfolk, England, appears to be eroding at a rate of 1 to 2 cm per year by the action of rock-boring molluscs. Emery (1946) studied depressions with an elevated rim in Cretaceous and Eocene sandstone with about 8% $CaCO_3$ in the intertidal zone at La Jolla and Point Loma, California. In nearly all of the depressions were *Littorina planaxis*, a grazing gastropod. The intestines of the animals contained a mixture of sand grains and sessile blue-green algae. The animals had an individual average of 0.00012 g of sand in their intestines (p. 216). They are capable of eroding about 500 kg of sandstone per year in an area of 30 by 100 meters, equivalent to 1.66 metric tons per hectar per year (p. 217). Emery assumed that CO_2 produced overnight by the organisms in the basins caused solution of $CaCO_3$ in the rock substrate, thus weakening the rock surface and making abrasion by gastropod radulae possible. North (1954) studied *Littorina planaxis* in the same area as Emery, but found an individual mean sediment content of 1.6 mg in the intestines and an erosion rate of 1 cm every 40 years, or 6.25 metric tons per hectar per year. North's result is based on a calculation of the standing crop of *L. planaxis* and measurements of the time required for overturning the gut contents by

staining the substrate. HODGKIN (1964) measured the erosion rate in the intertidal zone of an eolianite cliff with about 80% carbonate content at Point Peron, Western Australia. The rock surface there is covered by "the usual dense growth of filamentous blue-green algae", and thin, patchy *Lithothamnion* encrusts the lower part of the intertidal zone (p. 388). The mainly hard eolianite is eroded slightly above mean sea level at a mean rate of 1 mm per year by "corrosion" (p. 390). Since boring algae appear to be ubiquitous in the intertidal zone of tropical limestone coasts, the erosion rate measured by HODGKIN is likely to be the effect of boring and rasping organisms. NEUMANN (1966), working in Harrington Sound, Bermuda, found that the calcarenite cliffs in the subtidal zone are receding at a rate of more than 1 cm per year. The erosion is demonstrated to be caused by the boring sponge *Cliona lampa*, which from 1 m² of substrate may produce nearly 6 kg of fine sediment in 100 days (p. 106 f.), equalling about 210 metric tons per hectar per year. *Bioerosion* is suggested (p. 92) as a term for the removal of consolidated mineral or lithic substrate by the direct action of organisms. HUNT (1969, p. 39) estimated that it takes the urchin *Echinometra lucunter* about ten years to excavate a boring of roughly 100 cubic inches out of clacarenite at Bermuda's south shore (for a photograph of boring echinoids see FAIRBRIDGE 1952). Evidence of recent research indicates that organisms are dominant in shallow-water carbonate degradation. Essential mechanical abrasion of carbonates occurs only in shallow water, especially on beaches. Prominent chemical dissolution is restricted to the deep sea (MILLIMAN 1974, p. 268).

Fish were chosen for the present bioerosion estimate because their eroding activity, unlike boring organisms, can be observed directly. Scaridae appear to be most important in respect to erosion capacity. There are still taxonomical problems with this family (WINN & BARDACH 1957, SCHULTZ 1958), but both sexes of adult *S. viride* can be identified at first glance underwater, and the fish mainly graze on hard substrates in water usually less than 10 meters deep.

Previous work on fish erosion

The pioneer observations of fish erosion by DARWIN (1842) have since been questioned by many authors and were almost forgotten, when COUSTEAU, a pioneer in diving with SCUBA equipment, again drew attention to parrotfish grazing on living corals of the Red Sea. COUSTEAU (1952, p. 454) saw the animals biting into coral colonies where they left white scars, and observed individuals excreting clouds of lime (see also CLOUD 1952). NESTEROFF (1955, p. 29), a scientist member of COUSTEAU's expedition to the Red Sea, described these observations in detail. NEWELL (1956, p. 360) established that parrotfish carve grooves as much as 0.5 mm deep into reef rock and illustrated the scars (Pl. 43). CLOUD (1959, p. 399) estimated that at Saipan, Mariana Islands, fish grazing on coral–algal rock or living coral might excrete an individual average of about 30 grams per day of new sediment (dry weight), contributing annually 1100 to 1600 metric tons of sand and fine gravel per square mile to the shoal bottom sediments. This would be equivalent to 5200 kg per hectare per year, or an annual mean sediment accretion rate of 0.2 to 0.3 mm. HIATT & STRASBURG stated in their ecological monograph on reef fish of the Marshall Islands (1960, p. 103), that "All parrot fish examined had scraped coral polyps, mostly from the

massive, glomerate corals, particularly members of the coral genera *Porites, Astraea-pora*, and *Montipora*. The beak marks on these heads, and on the rather smooth, algal covered reef rock, are very striking, ...". The authors observed the fish underwater and saw them voiding great masses of calcareous powder at rather frequent intervals. They have little doubt that parrotfish contribute substantially to the formation of fine sand. BARDACH (1961, p. 98) measured the rate at which calcareous material passes through the intestines of grazing omnivorous reef fish from a patch reef in the North Lagoon of Bermuda. He calculated 2300 kg of calcareous matter to be excreted per hectar per year, part of which is redeposited sediment. STEPHENSON (1961) inferred that at Heron Island, Australia, grazing fish were the main eroding agent on a beach rock surface at low water level of nip tide, and reported a rate of about 0.5 mm per year. EMERY (1962, p. 28) remarked that coral-grazing fish are obvious sediment producers. He confirmed that the numerous parallel scratches on corals and encrusting red algae were made by these fish. NEUMANN (1966, p. 101), referring to EMERY, mentioned similar closely-spaced and random scrape markings he found to be a common feature of subtidal surfaces off Bermuda's south shore.

Data on the diet of parrotfish are scarce. BOULENGER (1922, p. 674) writes: "Parrot-wrasses feed mostly on vegetable matter, corals, and hard-shelled Mollusca, for crushing which their dentition is well adapted." SUYEHIRO (1942) listed the parrotfish *Leptoscarus japonicus* on page 281, Table 48, in a column of fish who "bite off animals on rock", but had only found "sea weeds" in the stomach of six individuals of the species he had bought at the fish market and opened (p. 181). The fish were caught north of the northern limit of coral reef growth. Off the Marshall Islands HIATT & STRASBURG (1960) recognized predominantly herbivorous parrotfish as for instance *Cryptotomus spinidens*, as well as mostly coral-eaters like the very common *Scarus sordidus*. All species observed eat coral and algae in various proportions and had a large or even "a great amount of calcareous powder" in the intestines, particularly the individuals containing algal filaments. TALBOT (1965, p. 456) included all *Scarus* species of Tutia Reef at 8° S, Tansania (East Africa) in the group of "coral feeders". BOULENGER's assertion that parrotfish eat hard-shelled molluscs to our knowledge has not been confirmed by underwater observation or inspection of intestine contents.

Methods

Observations on the erosion rate of *S. viride* were made at Bermuda's south shore in the area between Gravelly Bay and the cup reefs of the outer reef tract, where the fish predominantly feed on hard substrates. Here the subtidal surfaces of calcarenite and the dead parts of reefs are detritus-free except for sand and fine gravel bound in a growth of soft algae (cf. OERTEL 1970, p. 100) which is ubiquitous on subtidal calcarenite or dead reef rock. The area was mapped based on a vertical aerial photograph kindly lent by the Public Works Department, and detailed inclined photographs taken from different angles at 590 m altitude. On the aerial photographs of this area, underwater features show up clearly to a depth of about 10 m (Fig. 3). The distortion of the photographs was rectified with a grid constructed by means of a reconnaissance survey on land. The outlines of underwater features were then traced on an acryl board with sand-blasted faces. This was taken underwater for detailed mapping.

Soundings were made with a hand-held line marked at one-meter intervals. SCUBA[4]) equipment was indispensable when using heavy tools to take rock samples from the sea floor and reefs. SCUBA gear was also used for a part of the underwater photography and some observations of feeding habits in deeper water.

The erosion rate was estimated by establishing the standing crop of *S. viride* in different habitats, by recording the food materials ingested by 38 fish, and by calculating the average carbonate content of the fishes' intestines. The time required for turning over the intestinal contents was not measured, because this difficult procedure had recently been done by BARDACH with parrotfish of Bermuda. For the calculations of sediment excretion it is assumed that *S. viride* turn their intestinal contents over once a day, according to BARDACH (1961, p. 98). The estimate of the erosion rate is based only on male (green) *S. viride* in order to avoid possible uncertainty which might be caused by dissent about the question whether *S. viride* and *S. abildgaardi* are conspecific or not (see WINN & BARDACH 1957, SCHULTZ 1958, and BÖHLKE & CHAPLIN 1970).

The standing crop in Gravelly Bay was recorded at two stations: No. 1 on a smooth strip of algal–vermetid rock, where the corners of a 8 by 8 m area (64 m²) were marked by three conspicuous rock protuberances (scarred with a chisel) and a large sea rod (see map, Fig. 4). This area was completely visible at one glance. Station No. 2 is a small, elongate patch reef with a surface area of about 100 m², which could be completely surveyed within ten seconds by swimming around the reef. The fish were counted alternating between the stations at different times of the day between 10 a.m. and 3 p.m. during September 1972. The standing crop was also established on Grid Reef in the North Lagoon in August 1968. The unofficial name refers to a cable network marking five parallel lanes 3 m wide and 50 m long on the reef top. Here, the standing crop of *S. viride* was determined by swimming along the lanes and counting fish present. The method was introduced by BROCK (1954) and used by BARDACH (1959).

The feeding habits were recorded on all of the studied sites by following an individual fish as long as possible, by snorkeling in shallow water on the reef tops, or with SCUBA equipment along the faces of reefs in the North Lagoon. It is practical to define the feeding time as the number of bites a fish applies to food, the time spent for a bite being about one second. Each bite observed when following a fish was recorded with a pencil on a plastic note board by a dash into prepared columns for five different kinds of food (see Table 1, p. 348), together with the times indicating the beginning and end of the observation of the fish. Samples of coral–algal reef rock covered by algal growth were pryed off at Gravelly Bay from a patch reef with a steel bar. The samples were taken ashore in a plastic bag, and the sediment was washed out in the laboratory. This and measuring the area of the sample's algal growth gave the amount of mud, sand and fine gravel held by the algae per square meter on the otherwise detritus-free rock surfaces of the south shore. The mean area scraped bare per bite by *S. viride* had to be established in order to calculate the quantity of calcareous detritus ingested daily from the algal growth on dead reef rock or calcarenite. For investigation of the carbonate particles in the intestines, the fish were

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[4]) An underwater breathing apparatus with a tank filled with compressed air.

caught with a spear. Care had to be taken to hit the fish in the backbone directly behind the head in order to kill them instantly and also to prevent excretion of faeces or loss of intestinal contents through injuries to the gut. The number of fish which could be taken in this manner without having excreted before capture was limited, because many fish already excreted when being followed with the spear or when they were hit. An inadequate number of fish was taken from Gravelly Bay because spear-fishing at that location was possible only with special permission. The digestive tract of the fish was taken out and straightened, then divided into three segments of equivalent length. To check for carbonate solution in the gut, the grain size distribution of the carbonates was determined separately in each segment by wet sieving after treatment with sodium hypochlorite and alcohol to remove organic matter. Plant fibers not destroyed by sodium hypochlorite aggregated into small puffs when the dried sieves were shaken and could then be hand-picked. Rock samples were pryed or chiseled off where fish were seen to leave particularly large scars after biting into algal-covered rock or living coral. After removing organic matter with sodium hypochlorite and drying the samples, equivalent scars were carved out and the released calcium carbonate was weighed. This gave the approximate maximum of solid carbonate *in situ* a fish can remove by a single bite.

Habitats of *S. viride* in Bermuda

General setting of Bermuda

The Bermuda reefs and islands rest on the more or less flat top of a truncated volcanic seamount. The activity of the volcano has ceased in the Tertiary; GEES (1970, p. 93) has measured a basalt from a borehole near Gibb's Hill lighthouse (Fig. 1) at a depth of 715 feet (a marginal part of the cone) to be $34.4 \pm 3 \times 10^6$ years old. Another basalt sample from a hole at the causeway across Ferry Reach (depth 140–145 feet) yielded an age of $52.4 \pm 2.5 \times 10^6$ years. The Bermuda platform is elliptical with the long axis of roughly 40 km running from the southwest to northeast, and a maximum width of about 20 km. The irregular basalt surface is covered by a 20 to more than 100 m thick layer of partly marine and partly terrestrial calcarenite or Pleistocene age. The islands on the southeastern edge of the platform are indurated, coastal eolian sand dunes formed during interglacial high stands of the sea (MAC-KENZIE 1964; LAND, MACKENZIE & GOULD 1967). North Rock (see Fig. 1) is a small relic of eolian limestone within the northern fringing reef (VERRIL 1907). The Bermuda platform appears to be tectonically stable (VACHER 1971) and has been dry during the Wisconsin glaciation (cf. MILLIMAN & EMERY 1968). Today it is submerged to a depth of generally 18 m, forming the bottom of the North Lagoon and a terrace 850 m to 5.6 km wide seaward from the outermost reefs (STANLEY & SWIFT 1968, p. 493). These reefs (locally referred to as "ledge flats") girdle the North Lagoon and the islands forming an almost continuous band, the only major gaps being at the east (leeward, see Fig. 2) end of the platform. This reef tract may follow the course of preexisting submerged eolianite dunes (see STANLEY & SWIFT 1967, p. 679), as well as some of the lagoon reefs arranged in an arch, like for instance Three Hills Shoals (Fig. 1). But at least the upper part of Bermuda reefs are Holocene growth forms with a
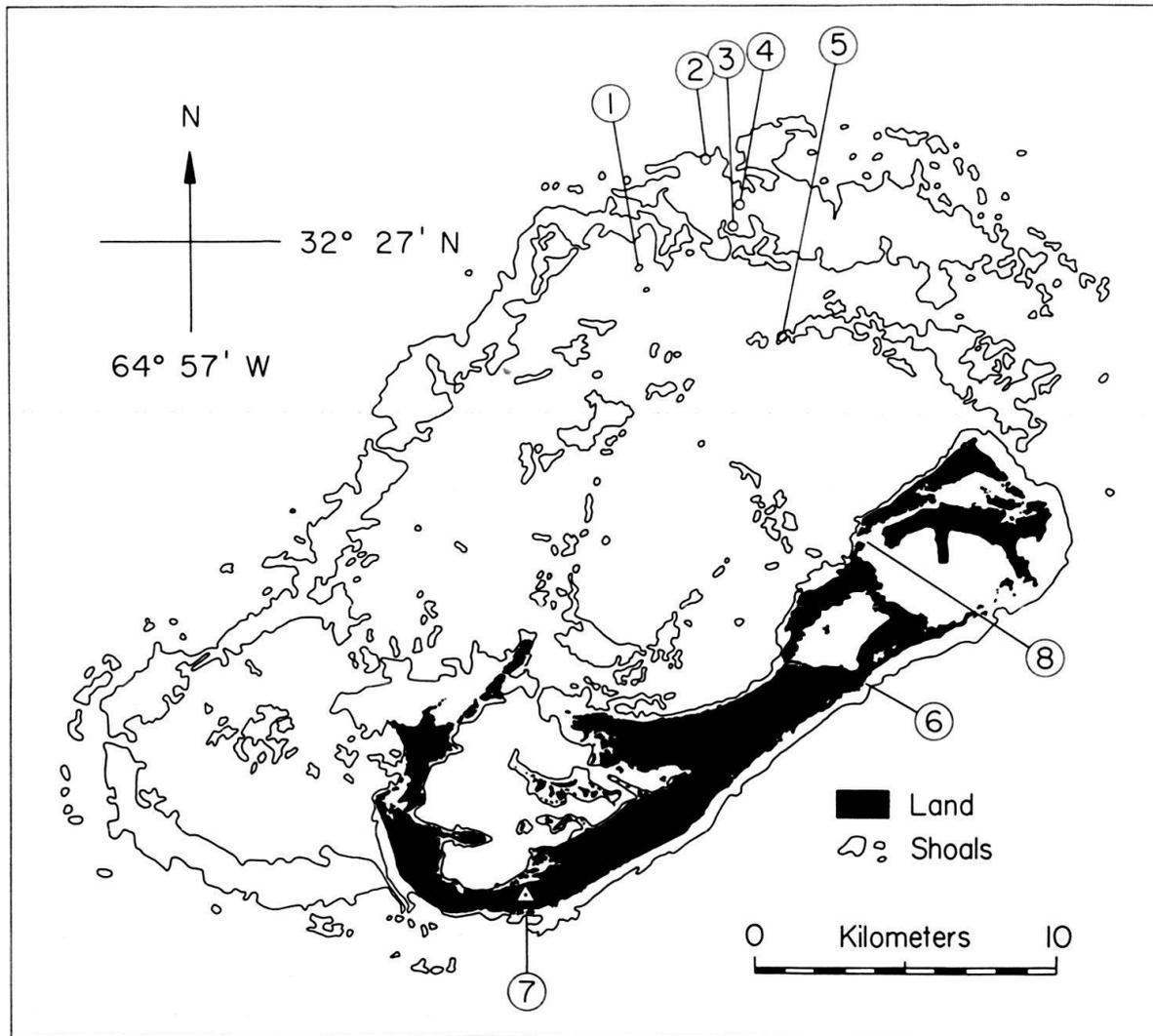
Fig. 1. Map of Bermuda.

1	"One-Hectar Reef" of BARDACH (1959)	*5*	Three Hills Shoals reefs
2	North Rock	*6*	Gravelly Bay
3	"Grid Reef"	*7*	Gibb's Hill lighthouse
4	"Make-Do Reef"	*8*	The Causeway

wave-resistant organic framework (WILSON 1969, p. 62, Fig. 5; SCOFFIN 1972; cup reefs of GINSBURG & SCHROEDER 1973). The string of cup reefs, especially along the south shore, may be interpreted as an ill-developed analogon to the *Lithothamnion* ridge of Pacific atolls. Cup reefs are only known from Bermuda.

Parrotfish were studied on three reefs in the North Lagoon (see Fig. 1) and at North Rock. The domain best suited for detailed fish-observation is between Gravelly Bay and the outer reef tract off Bermuda's south shore, where all types of parrotfish substrates occur within a small area (Fig. 4) and are easily accessible by swimming from John Smith's Beach.

Physiography of Gravelly Bay

Pleistocene calcarenite makes up the rocky shore of Gravelly Bay and the cliffs of Canton Point. The inner part of the bay is but 1.2 m deep and has a calcarenite
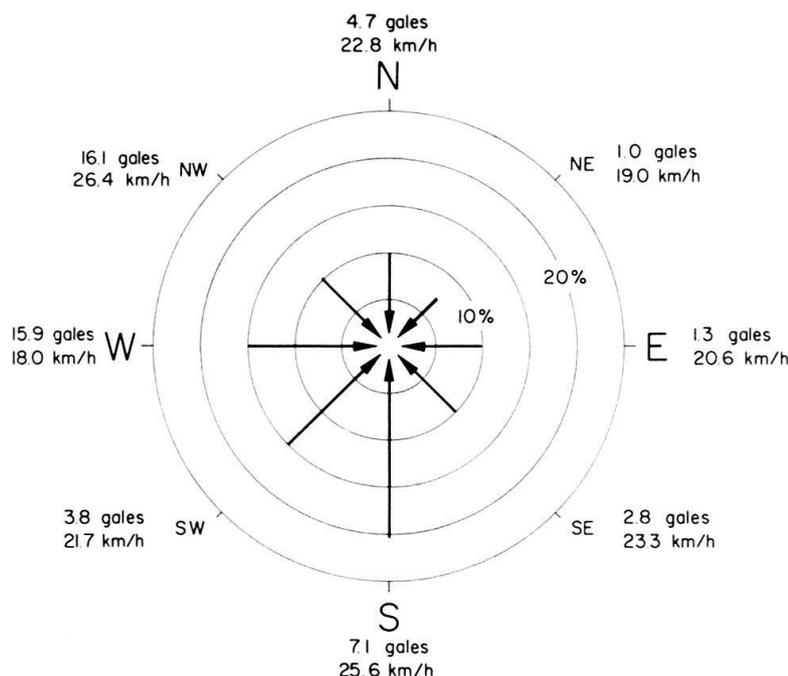
Fig. 2. Frequency distribution in percent of hourly wind direction and average speed of wind for the eight prime points of the compass recorded at St. George's, Bermuda, from August, 1932 to April, 1954; km/h = kilometers per hour. Average numbers of gales are given for the period 1932–1947. After MACKENZIE 1964.

floor locally encrusted by coralline algae. There are a few patches of sand and some gravel. Downward from the lower half of the intertidal zone, the cliffs at Canton Point and at the south side of the bay are covered by an intergrowth of encrusting organisms, principally crustose coralline algae and the attached vermetid gastropod *Dendropoma irregulare* (some data about zonation of the intertidal and supratidal of Canton Point are given by CHARLTON 1969, p. 30). The organisms build up projecting lips or benches first described and figured by PRAT (1935, p. 269 f.), and again by OERTEL (1970, p. 102). Comparable structures of the Mediterranean have been published by SAFRIEL (1966) and others. These bio-constructional lips are best developed around Canton Point, and cross Gravelly Bay in a line just above the 2 meters depth contour (see map, Fig. 4), marking the edge of a subrecent terrace of submarine planation. A ridge of this algal–vermetid rock extends from Canton Point about 40 m out to the southeast and ends on a smooth surface of the same material at 2.2–2.5 m depth with elevated marginal lips. This rock type is almost identical with the cup-reef rock published in detail by GINSBURG & SCHROEDER (1973). The smooth calcarenite floor of outer Gravelly Bay, largely 3 m deep, supports a scarce growth of mostly single colonies of the massive corals *Diploria strigosa*, *D. labyrinthiformis*, and *Porites asteroides*. The rock between the corals is covered by a short-cut growth of mostly blue-green algae. The first small coral–algal patch reefs appear at the outer edge of the 3 m erosion terrace. Data by REDFIELD (1967, Fig. 1) and NEUMANN (1971, p. 42) indicate that the terrace is less than 4000 years old. Below an escarpment is a third calcarenite terrace with its surface at a depth of 6 to 6.5 m. Sand-filled channels dissect this terrace. The small patch reefs of its inner part merge towards the edge of

Fig. 3. Inclined aerial view of Gravelly Bay from an altitude of 590 m. Emerging cup reefs ("boilers"), sand holes, and patch reefs in the lagoon channel (center right) are clearly visible (see Fig. 4). – Photograph by the author.

the sand-filled lagoon channel into a continuous coral–algal reef. The coral–algal reefs of Bermuda never grow into the intertidal zone as do coral reefs in equatorial seas. PRAT (1935, p. 280) relates this fact to the low air temperatures during the winter months. Minimum air temperatures in Bermuda are normally not below 8 °C, but an extreme of 0 °C has been recorded. Water temperature, according to PRAT, does not drop below 16 °C. Bermuda's latitude is more than 32 °N (cf. Fig. 1).

Opposite the lagoon channel, a continuous coral–algal growth extends to the "breakers" or cup reefs of the outer reef tract. The surface is very irregular and rugged, from 1.5 to 5 m deep, and interrupted by few, 8 to 9 m deep sand holes. STANLEY & SWIFT (1968, p. 486) reported "patches of exposed stratified sandstone" in narrow passages between cup reefs of this area at depths exceeding 50 ft, but did not give the exact location of the outcrops. The cup reefs in front of Gravelly Bay are not arranged in a single row as further to the southwest. The outer wall of an individual cup reef rises vertically or more often overhangingly and ends in a bulging lip which encloses a semicircular or lobate depression. Of the reefs in the front line, the seaward lips emerge at low tide and cause the waves to break (thus the local name "breakers"). The landward lips are usually lower. The cup reefs behind the front line are less developed with lips lower than low tide level. Further back towards the lagoon channel there are even lower, presumably dead cup reefs encroached by coral. On the terrace seaward of the outer reef tract, there is an expanse of hummocky coral–algal growth which comes to within 9 m of the surface. It is interrupted by few sand-floored holes with the sediment surface at 14 m depth (cf. STANLEY & SWIFT 1967, p. 678). The sediment there and within the lagoon channel is coarse and mostly rippled at intervals of 20–40 cm. Towards John Smith's Beach it becomes gradually finer and better sorted. Part of the flat sand surfaces and also some of the rippled sand is covered by algal mats. The green filaments of *Cladophoropsis membranacea* make the sand coherent to a depth of 1–2 cm; they grow to about the same length above the sediment surface (see GEBELEIN 1969, p. 55).

The standing crop of *S. viride* was established on the two most important types of substrate. The first station is on a strip of smooth, algal–vermetid rock southeast of Canton Point which is separated from deeper water to the northeast by a steeply rising wall about one meter in height made up of the same material (No. 1 on map, Fig. 4). Towards Gravelly Bay is a cavernous, elongate mound of algal–vermetid rock and an elevation equal to the wall. The cavities are inhabited by many *Diadema antillarum*, an urchin with brittle spines up to 30 cm long. A single individual of the boring urchin *Echinometra lucunter* was found in a small, isolated mound. *Homotrema rubrum*, an attached foraminifer, occurs on the protected underside of rock protrusions. Living coralline algae cover only about 1–2% of the intensely scratched rock surface. Orifices of vermetids project slightly, but are masked by a thick algal growth thriving on dead biolithite rock, mainly of filamentous green and blue-green algae, *Eucheme isiforme*, and by isolated small tufts of green, red-tipped *Cladophora catenifera*. Other erect algae are *Dictyota* sp. and *Padina* sp. These are always small and do not cover more than a few percent of the rock. Scleractinian corals occupy about 5% of the surface: *Diploria strigosa*, *D. labyrinthiformis*, *Porites asteroides*, *Favia fragum*, *Siderastrea siderea*, and *Isophyllia* sp., *Plexaurella* sp., a purple sea rod (alcyonarian coral), is not abundant.

The second station is a small patch reef, 6.5 by 6 m and 4 m high (No. 2 on map, Fig. 4). The shape of the structure appears to be strongly influenced by the prevailing subnormal-to-coast direction of the surge (see cross-sections and plan view, Fig. 5). Living scleractinian corals and hydrozoans make up about 8% of the surface: *Diploria strigosa*, *D. labyrinthiformis*, *Favia fragum*, *Porites asteroides*, *Siderastrea siderea*, *Isophyllia* sp., *Montastrea cavernosa*, and *Millepora* sp. Alcyonarian corals like *Plexaurella* sp. (sea rod) and small specimens of *Rhipidogorgia flabellum* (sea fan) are not abundant. Living coralline algae have a light violet tinge and occupy about 5% of the surface. Small tufts of *Dictyota dentata* are not more than 10 cm tall and cover another 5% of the reef. A growth of filamentous blue-green algae up to 2 cm thick, intermingled with a few *Cladophora catenifera*, grows on more than 80% of the reef's surface. *Diadema antillarum* inhabits some of the larger cavities.

Reefs north of Bermuda

The reef studied on Three Hills Shoals (Fig. 1) has a diameter at the base of 60 m and rises to within 3 m from low tide level. The reef top has an irregular relief of 1–2 meters with a few small depressions containing sand littered with coarse coral debris. Living scleractinian coral, alcyonarians and intricately branching *Millepora* occupy about 15% of the surface. Dead reef rock is covered by erect uncalcified algae growing as much as 20 cm tall, mainly *Dictyota* sp., *Caulerpa* sp., and some attached *Sargassum*

Key to fig. 4

Supratidal zone
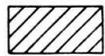
Calcarenite

Beach sand

Intertidal and subtidal zones

Calcarenite

Calcarenite with conspicuous bedding

Calcarenite covered by thin veneer of sand

Calcarenite with scarce growth of scleractinian coral
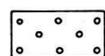
Coral-algal rock: Knobs, patch reefs, or hummocky expanse
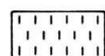
Algal-vermetid rock: Crusts, lips, or cup reefs
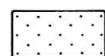
Sand and fine-grained rubble

——— Clear boundary

- - - - - Gradational boundary

Lip of algal-vermetid buildup

Lip of presumed cup reef

~ Ripple of sand or fine-grained rubble

Algal mat on rippled sand or rubble

Algal mat on flat sand or rubble

· · · Algal nodules
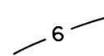
6 Depth contour plotted at one meter intervals below MHWS

× 4 m Sounding in meters

① Fish counting station
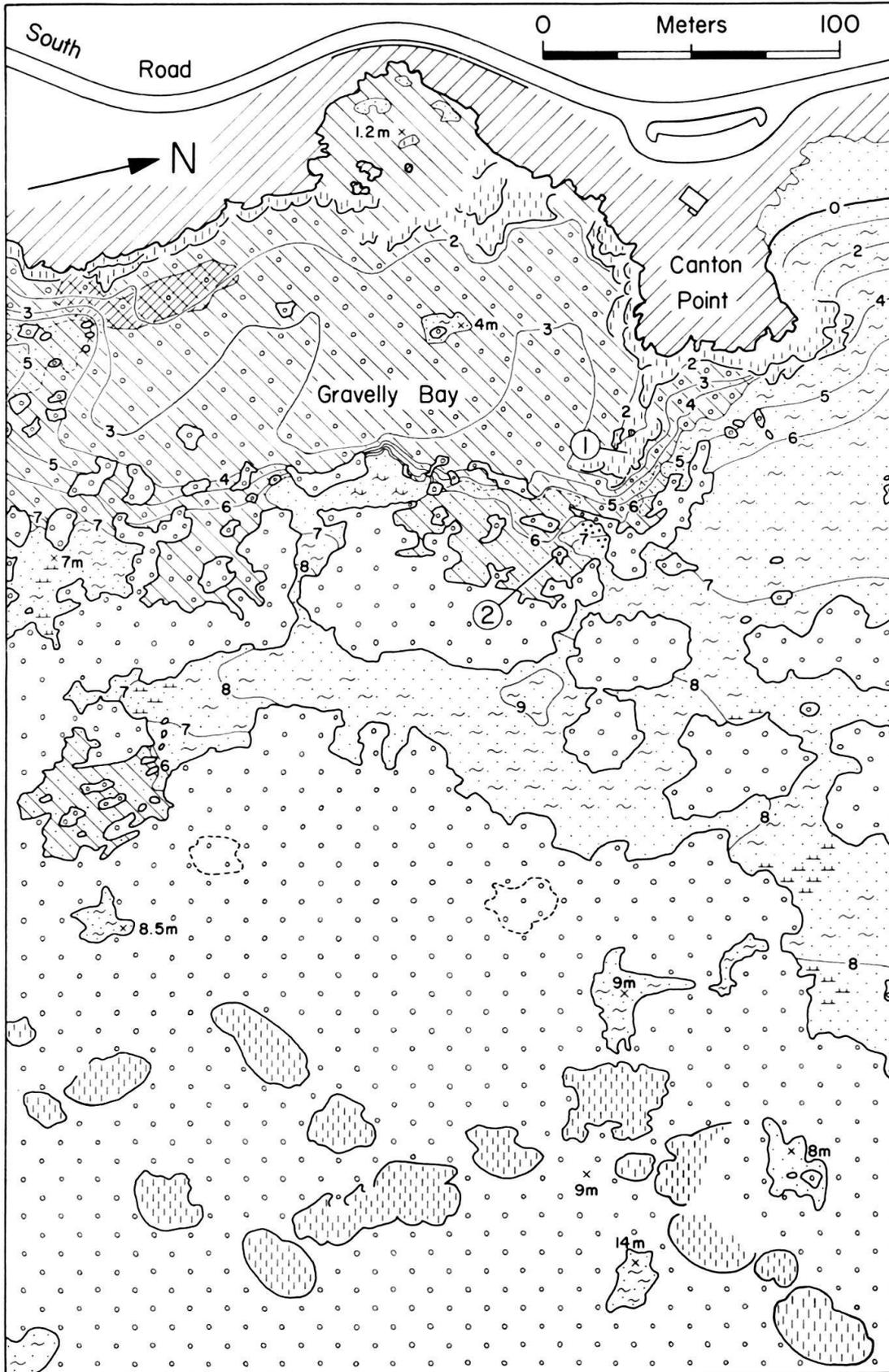
Fig. 4. Map of Gravelly Bay (south shore, see Fig. 1).

sp. A variety of sponges lives within the lush algal meadow. Sediment fans slope down from the reef faces to the 15 m deep lagoon floor. The sediment talus supports a dense growth of *Halimeda* ssp., *Penicillus* sp., sponges and some *Oculina* sp., a branching coral (cf. WILSON 1969, p. 60).

Grid Reef (see GARRETT et al. 1971, Fig. 4) rises from the bottom of the lagoon, which is 18 meters deep at that location, to within less than one meter from low tide level. From a depth of about 10 m downward the base of the reef is masked by an initially steeply inclined apron of gravel- to mud-size reef detritus which grades into the level lagoon floor. The sediment slope is littered by a few blocks of reef rock up to two meters in diameter. The reef faces rise 6 m more or less vertically to a depth of about 4 m, then level off to the rugged reef top. The top of the reef is almost circular with a diameter of about 120 m. It consists of coral–algal knobs, concentrated near the margin to form a nearly continuous fringing ridge. In the interior an irregular pattern of winding and branching channels extends between the less densely spaced knobs, the shallow channels being rock-floored, and those deeper than 3 meters having a level sand bottom.

Make-Do Reef (GARRETT et al. 1971, Fig. 17) is about 700 m long and more than 150 m wide in its southern part. The fringing ridge is similar to that on Grid Reef, but from the ridge inward the knobs are spaced at rapidly increasing intervals, giving room to a vast central sand plain at a depth of 4 to 4.5 m, with only a few turret-shaped knobs. On this plain the uppermost 5 mm of the sand are slightly coherent and have a pale greenish tinge. BATHURST (1967, p. 737) emphasized that this type of mat "is presumably the main source of food" for sand-grazing animals including fish. LAFON (1969, p. 23) observed that flagellates might be important producers of sediment-binding slime on the bottom of two bays on Bermuda's north shore, and reported "small fish that constantly nibble at the bottom" (p. 24). PATRIQUIN (1969, p. 95) found a colonial, unicellular blue-green alga embedded in a matrix of gelatinous material to form patchy mats on Grid Reef.

On Grid and Make-Do reefs living coral and *Millepora* cover as much as 45% of the hard substrate on the deep water side of the fringing ridge (GARRETT et al. 1971, p. 651). As much as 50% of the surface of some of the isolated knobs on the central sand plain of Make-Do Reef is occupied by scleractinian and alcyonarian coral, and *Millepora*. The dead reef rock on the top of Grid and Make-Do reefs is predominantly overgrown by filamentous algae or juvenile specimens of erect algae like *Dictyota*. Tall growths of *Dictyota* are to be found on the deeper part of the reef faces below about 5 meters depth.

Habits and abundance of *S. viride*

Parrotfish spend the night sleeping in reef cavities (see photograph by SCHROEDER & STARCK 1964, p. 136, and STARCK & DAVIS 1966). Species of *Sparisoma* apparently do not produce a mucuous cocoon for sleeping (WINN & BARDACH 1960, p. 31, see also WINN 1955). In the morning *S. viride* probably become active about sunrise and leave their cavern to graze. In Gravelly Bay the fish were seen feeding 20 minutes after sunrise. Shortly before sunset they return to their sleeping places. Reefs larger than one hectar like Grid or Make-Do Reef possibly support their own population of *S. viride*, because none of the species were seen in deeper water around these reefs.

W E

Plan view

Principal direction of surge

W E N S
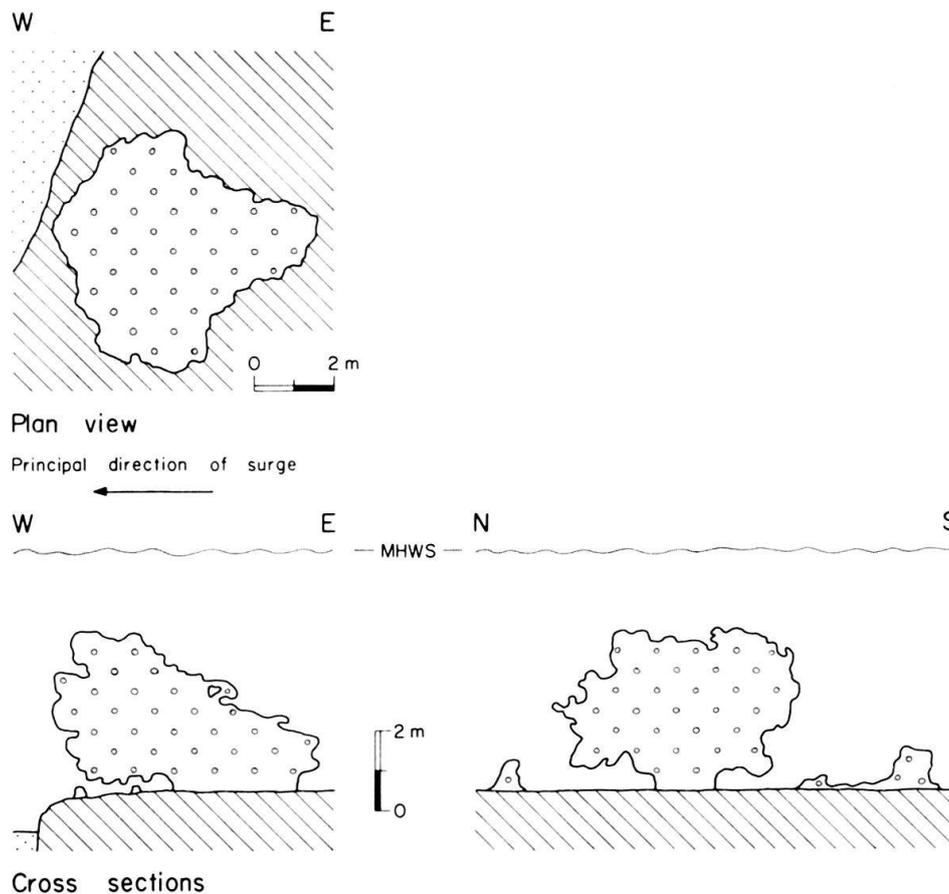
— MHWS —

Cross sections

Fig. 5. Plan view and cross sections of a small patch reef in Gravelly Bay (= station No. 2 in Fig. 4). For key see Figure 4.

The reefs of Gravelly Bay are so small that the fish move from one reef to the other and to calcarenite or algal–vermetid rock surfaces in search of food. *S. viride* (Fig. 6) grazing by themselves may be encountered anywhere during the day, but normally the fish gather in loose aggregations numbering three to more than twenty (Fig. 7a). The number of individuals per aggregation seems to be related to the standing crop of the area: The largest schools were found in the agitated water of Bermuda's southeast coast (in Gavelly Bay as much as 17) and around North Rock (more than 20, cf. NEUMANN 1966, p. 101). There *S. viride* are common, whereas on two reefs of Three Hills Shoals, where the species is not abundant, only a few individuals were seen together. The reefs of Three Hills Shoals are in the more protected southern part of the North Lagoon. *S. viride* appear to stay out of quiet waters between islands like Ferry Reach or the inner part of Castle Harbour. The relative scarcity of *S. viride* on the reefs of Three Hills Shoals cannot be caused by a lack of cavities suitable for sleeping or lack of food. Cavities there are as abundant as on any other reef and algal growth is luxuriant like in inshore waters. In those areas where grazing fish are abundant, the surfaces of calcarenite or dead reef rock have only a short-clipped growth of filamentous algae with occasional tufts of *Dictyota*, *Stypopodium* or small *Cladophora catenifera*, and the rock surface is smooth-scoured, apparently by the dentition of grazing fish (cf. RANDALL 1965, p. 257). On elongate rock projections, large *Scarus* tend to bite always in the same orientation until they

Fig. 6. *Sparisoma viride*, adult, male (length about 35 cm.) – Photograph by Jack McKenny, reprinted
with permission of Skin Diver Magazine.

finally produce blunt edges (Fig. 8). The effect of scratching and scouring by scarid
fish is well demonstrated on algal nodules accumulated in the dead end of a sand
channel in Gravelly Bay (Fig. 9). The upper side of the nodules is smooth-scoured and
scratched with cross-sectioned dead *Homotrema rubrum* on the surface. The unaltered
underside is tuberculate (Fig. 9 b) with *Homotrema* growing in the protected recesses
between tubercles. Other grazing fish such as the surgeonfish *Acanthurus coeruleus*
and *A. chirurgus*, two species seen feeding in mixed aggregations with *S. viride* around
North Rock, certainly contribute to the scouring as well as *Holacanthus bermudensis*,
an angelfish, and others. But their abrasive capacity is probably small when compared
with Scaridae, judging from the size of scars on rock produced by these fish and from
their light body weight.

　　S. viride clip or scrape food and calcareous matter off hard substrates with their
strong jaws equipped with scale-like teeth lined with a form of white dental enamel.
The teeth of each jaw are fused into a cutting plate and give the exposed part of the
dentition the aspect of a beak. The teeth eventually break off and are constantly
replaced, thus keeping the cutting edge sharp and indented (Fig. 10). When the fish
feed on a hard substrate, they open their jaws at a distance of 8–10 cm from the rock
or coral surface and rush forward by a brisk flip of the pectoral fins. At the moment
they hit the rock or coral they close their jaws and by this are bounced back. The
movement is repeated rhythmically (Fig. 7a). The sound of the scratching teeth of a

Fig. 7. Grazing males of *S. viride* on reefs.
a) Northeast Breakers (east of North Rock). – b) Gravelly Bay. Scarred, living colonies of *Porites asteroides* are on the left below the center and at the edge of the picture to the right. – Photographs by the author.
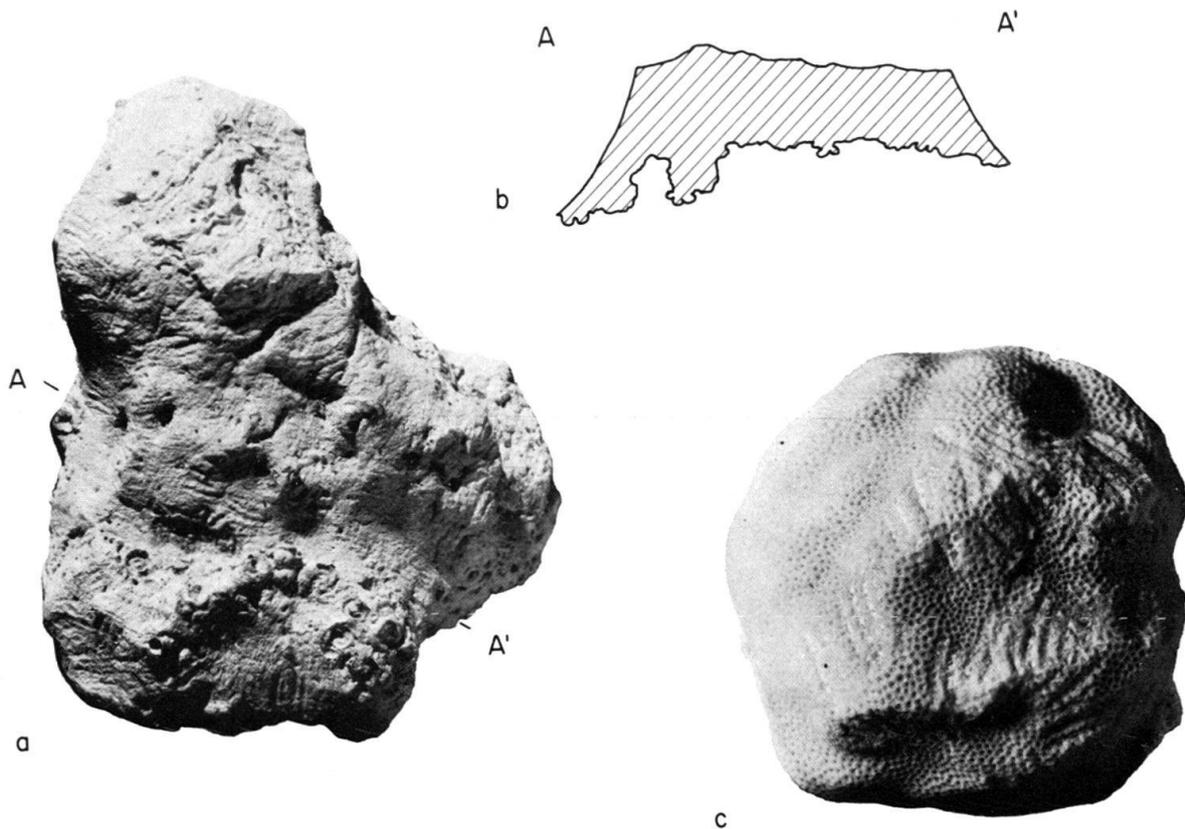
Fig. 8. Bite-scars of scarid fish on hard substrates.

a) Projecting part on lip of a cup reef in front of Gravelly Bay. Blunt, scratched edges are produced by repeated bites in the same orientation by large *Scarus*. Resistant tubes of the vermetid gastropod *Dendropoma irregulare* protrude slightly above the surface. Cross-sectioned *Homotrema rubrum* are mainly near the right edge of the sample. – b) Cross section of sample *a*. – c) Scratched colony of *Porites asteroides*. – About half of natural size. Photographs by W. Suter.

large parrotfish can be heard underwater at a distance of several meters. The dentition of the jaws and the momentum of the body enable the animal to remove as much as 12 milligrams (dry weight) of algal rock per bite, the hardest substrate seen to be attacked, and as much as 28 mg of the more friable aragonite skeleton of living *Porites asteroides*, the only species of scleractinian coral observed to be bitten. The mean erosion per bite is but 5.8 mg (see "Results").

The corresponding figures for large *Scarus* are 82 mg or 213 mg respectively. Friability apparently depends on primary porosity of the different types of skeleton or rock. Abrasion is further facilitated by the secondary porosity caused by boring organisms, mainly clionid sponges and algae. When the fish swallow the mixture of food and carbonate particles, a part of the finest detritus issues through the gills. The faint dust cloud is best visible when the fish feed on short-clipped algal growth holding much sediment as, for instance, in a depression, and it is hardly distinguishable or absent when the fish are grazing on the short algal growth on smooth algal–vermetid rock. After swallowing, the fish crush the mouthful in the pharyngeal mill. Short pauses in feeding, during which the fish stand motionless in the water leisurely opening and closing their jaws are probably used for milling (cf. COUSTEAU 1952, p. 454). The surfaces of the milling organ are covered with tight rows of scale-like pharyngeal

Fig. 9. Algal nodule from sand channel near station No. 2 in Gravelly Bay (see map, Fig. 4). a) Upper side scoured smooth by scarid fish. – b) Tuberculate, unaltered underside. – c) Enlarged detail of *a*. Large voids are primary. A fresh scratch by *Scarus* is visible in the center, by which the otherwise finely pitted surface is ground smooth. Fresh layers of living crustose algae are visible in the lower part of the picture. – d) Cross section of the nodule with a coral fragment as a core. – *a*, *b* and *d* about half of natural size, *c* about natural size. Photographs by W. Suter.

teeth (Fig. 10). At the rear end of the milling surfaces, the teeth are worn and flattened by grinding. From time to time they break away and pass down the intestinal tract. They are constantly replaced in front of the milling surface by fresh teeth with sharp edges. For milling, the lower grinding face is moved back and forth under upward pressure by powerful muscles. The position of the pharyngeal mill within the head of a *Scarus* sp. is shown on an x-ray photograph in MILLIMAN (1974, Pl. 30).

The feeding intensity is 7% shortly after sunrise and averages 14% in the morning, goes up to 20% in the afternoon and is about 17% in the average of the whole day. Actually, the fish are almost constantly grazing, because most of the rest of time elapses between bites into food or when the fish move from one feeding spot to another. The feeding period is from about 6.15 a.m. to about 5.45 p.m. or $11^{1}/_{2}$ hours (late August through September). In Bermuda the diet of *S. viride* consists of the following
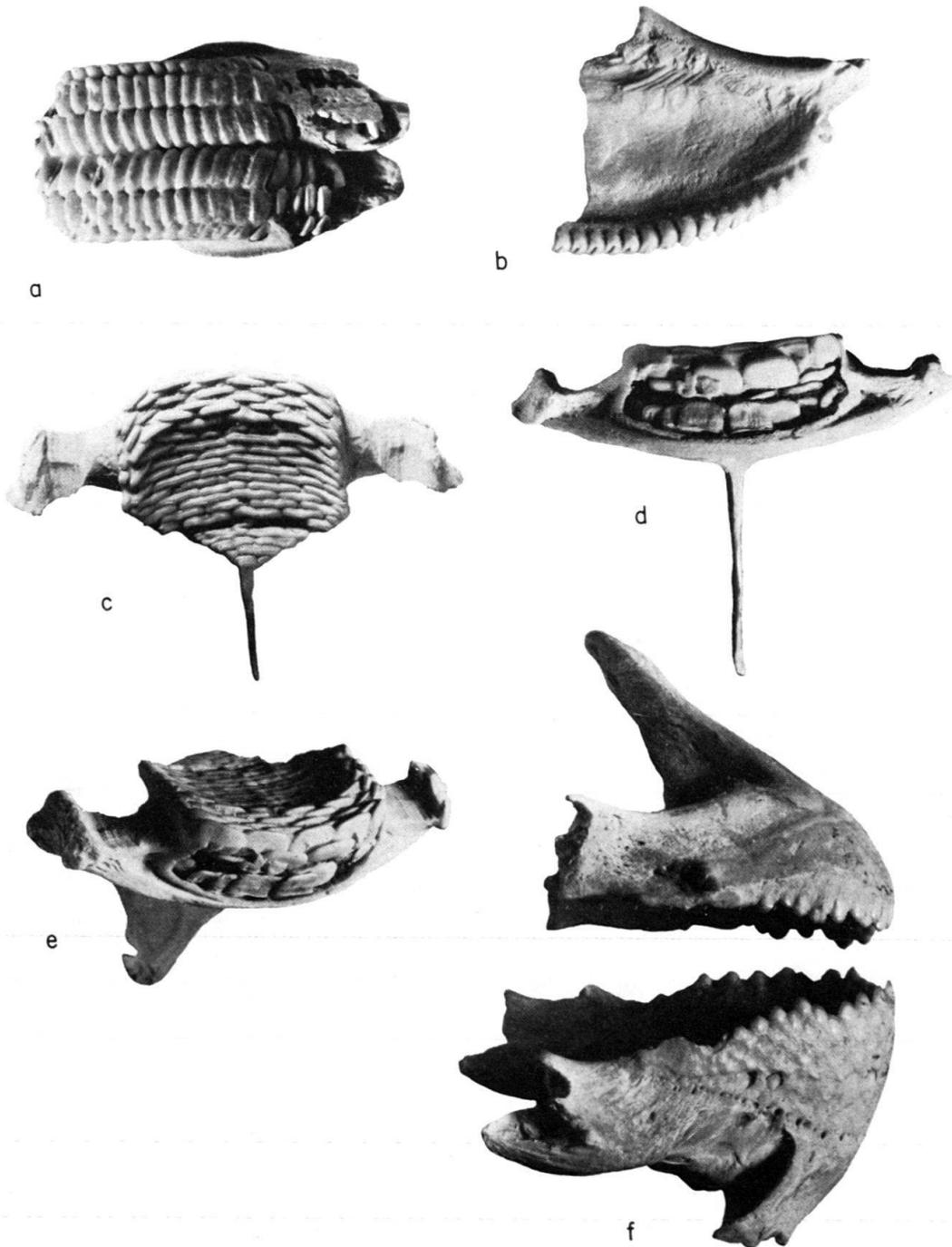
Fig. 10. Jaws and pharyngeal mill of a male *S. viride* (about natural size).

a) Upper grinding surface of the pharyngeal mill. Teeth are regenerated on the right (front) side. The regeneration zone is covered by a thin bony sheet (partly visible) and skin in living fish. – b) Lateral view of the upper grinding surface. – c) Lower grinding surface of the pharyngeal mill. Front side with fresh teeth is up. – d–e) Regeneration zone of the lower grinding surface. New teeth are formed under the front half of the grinding face and from time to time they are pushed up and accreted to the front row of teeth on the face. – f) Upper and lower jaws. The regeneration zone is visible only on the lower jaw. Photographs by W. Suter.

materials: 1. The short-clipped growth of filamentous and juvenile specimens of other algae on calcarenite and biolithite, 2. large erect algae (*Dictyota dentata, Stypopodium zonale*, attached *Sargassum* ssp., *Sargassum natans*), 3. living scleractinian coral (*Porites asteroides*), and living hydrozoans (*Millepora alcicornis*), 4. living alcyonarian coral (*Rhipidogorgia flabellum, Plexaurella* ssp.), and 5. slime- or algal-bound sand (see Table 1). Individual fish were followed during periods from 2 to 15 minutes to record grazing. The food ingested by 22 individuals in Gravelly Bay and 16 on Make-Do Reef is listed in Table 1. The nutrient–calcium carbonate ratio is probably lowest when the fish eat sand. Schools of 10 to 15 individuals on Make-Do Reef were followed for 10 to 15 minutes over the central sand plain. During this time they ate nothing but sand, the uppermost 5 mm of which are slime-bound at this location (see above). In Gravelly Bay the coarse, mostly rippled gravelly sand of the lagoon channel is not eaten by *S. viride*, probably because it contains too little nutrients. Even where the sand is covered by algal mats, it is exceptional to see a fish of this species grazing. Presumably nutrient-rich living coral are only occasionally eaten. Carbonate particles in the intestines of *S. viride* outweigh nutrients about 3 to 1. The gut of one fish from Gravelly Bay contained 24% nutrients and 76% carbonate detritus (dry weight).

The standing crop of *S. viride* in Gravelly Bay was calculated from 130 counts at two stations. 96 fish were counted on the reef (100 m²) and 133 on the patch of algal–vermetid rock (64 m²) corresponding to 207 if calculated to 100 m². The number of fish found on algal–vermetid rock in relation to the patch reef is 2.16 to 1. Around North Rock the species seems to feed mostly on algal–vermetid rock. If the average of the populations on the two types of substrate in Gravelly Bay is regarded as representative, and when the sand-bottom is excluded, the standing crop in this area would be 151 individuals per hectar (see Table 2) or 204 kg (wet weight) per hectar. The average wet weight of 8 male *S. viride* taken from Gravelly Bay was 1.35 kg. The fact that only 12% of the fish counted in the bay were females may mean that the fish commute between different habitats according to the season (cf. BARDACH 1959, p. 82). On Grid Reef ten counts indicated a standing crop of 36 individuals or 50 kg (wet weight) per hectar.

Results

The grain sizes of calcareous matter passing from the pharyngeal mill range from less than one micron to five millimeters. 3 to 5% of all grain sizes found in the intestines of *S. viride* from Gravelly Bay are red fragments of the attached foraminifer *Homotrema rubrum*. The size distribution of the carbonate detritus does not vary systematically from the beginning of the digestive tract to the anus, but there is a relation between the grain size distribution in the gut of the fish and their habitat. The intestines of fish from Gravelly Bay, which feed almost exclusively on hard substrates, usually contain about as many particles smaller than 125 microns as grains of all other sizes. The gut of fish taken on central Make-Do Reef, where 34% of the diet is sand (see Table 1), contained a large amount of sand-size grains from 0.25 to 1 millimeter. Fish from the marginal parts of Make-Do Reef, from Grid Reef and from reefs on Three Hills Shoals had an intermediate grain size distribution of their calcareous material (Fig. 11). Five fish caught in Gravelly Bay between 5 and 5.30

Table 1. *Feeding time proportions of food taken by S. viride in Gravelly Bay and on Make-Do Reef.*

Food materials	Feeding time percentage	
	Gravelly Bay	Make-Do Reef
1. Short-clipped algal growth on calcarenite or biolithite*)	93	44
2. *Stypopodium, Dictyota, Sargassum*	6	21
3. *Porites asteroides* and *Millepora**)	0.9	0.7
4. *Rhipidogorgia flabellum, Plexaurella* ssp.	–	0.3
5. Sand with algal or slime mats	0.1	34
Total observation time	1 h 48 min.	1 h 42 min.

*) Some of the hard calcareous substrate is scraped away by grazing fish and ingested together with this type of food.

p.m. which had not excreted before nor when being speared contained an average of 54.95 g detritus (dry weight) or 4% of their mean wet body weight. The average content of all 23 fish caught in Bermuda at different times of the afternoon from late August through September, including specimens who had excreted when pursued or caught is 42.1 g or 3.1% of their mean wet body weight. This is very close to the 3% given by BARDACH (1961, p. 99).

Table 2. *Standing crop of S. viride in Gravelly Bay and on Grid Reef (explanation in the text).*

	Gravelly Bay South Shore algal–vermetid rock flat	coral–algal patch reef	mean	Grid Reef North Lagoon grid over coral–algal knobs and channels with rock or sand bottom	
mean presence of *S. viride:*					
	64 m²	100 m²	100 m²	750 m²	100 m²
males	1.16	0.86	1.33 ⎫	2.7	0.36
females	0.17	0.10	0.18 ⎭		
calculated number of individuals per hectar:					
males	181	86	133 or 88%		
females	26	10	18 or 12%		
total	207	96	151	36	
standing crop	151 individuals per hectar of 1.35 kg mean wet weight, or 20 g (wet weight) per m²			36 individuals per hectar of 1.40 kg mean wet weight, or 5 g (wet weight) per m²	

Two other points are essential when a calculation of the erosion rate of *S. viride* in Gravelly Bay is attempted: The amount of calcareous detritus held by the short-clipped algal growth on biolithite or calcarenite per square meter, and the quantity of carbonate issuing through the gills when the fish are feeding. Whereas there is no way to assess the carbonate loss through gills in the natural habitat of the fish, the content of detrital carbonate particles held per square meter in the algal growth of otherwise detritus-free reefs or calcarenite of Gravelly Bay can be estimated with
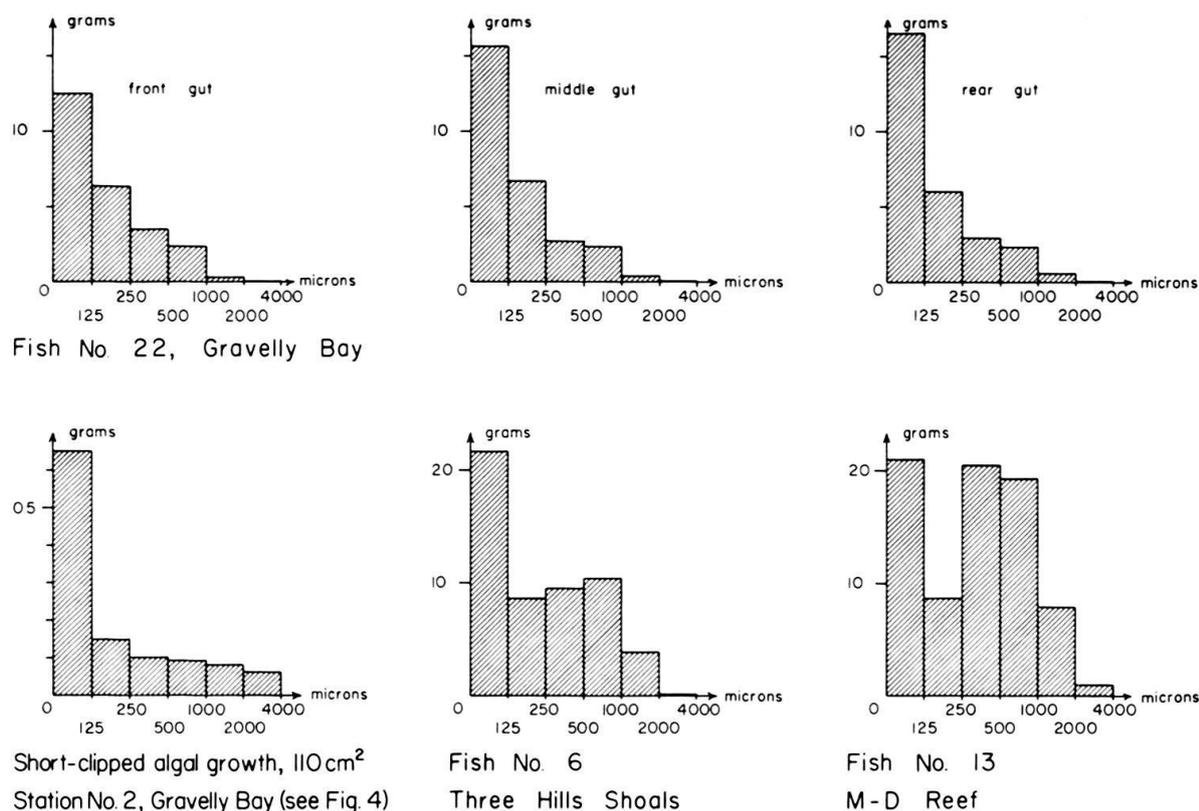
Fig. 11. Histograms of carbonate detritus from the digestive tract of male *S. viride* and from the short-clipped algal growth on a patch reef in Gravelly Bay (station No. 2 on map, Fig. 4).

some degree of accuracy. It proved to be difficult to dislodge rock samples covered by algae with a hammer and chisel without stirring up sediment out of the growth. No undisturbed samples could be taken from smooth calcarenite or algal–vermetid rock surfaces, because percussions of the sample by the chisel caused sediment to be washed out of the algae by the water current. Two samples with an area of 110 cm² and 1100 cm² respectively of short-cut algal growth, which had been pryed away with a steel bar and little percussion from the upper part of a small patch reef (No. 2 on map, Fig. 4), had a sediment content of 1.24 g and 6.00 g respectively, corresponding to an average of 836 mg per 100 cm². The mean area of short-cut algal growth scraped bare per bite of *S. viride* is 0.3 cm² and holds 2.5 mg of detritus (see below). The quantity of carbonate particles ingested from algal or slime mats in sand channels (0.1%, see Table 1), from alcyonarian coral, or from slightly calcified *Stypopodium* is too insignificant to be included in the following calculation of the erosion rate of *S. viride* in Gravelly Bay:

– Standing crop of *S. viride:* 151 individuals per hectar of hard substrates
– Turnover of intestinal contents: Once a day (see "Discussion")
– Daily feeding period: $11^1/_2$ hours or 41,400 seconds
– Time spent biting into food: 17% of 41,400 sec = 7038 sec when 1 bite is rated at 1 second

- Time spent biting into food[5]) on hard substrates causing erosion: 94% (see Table 1) of 7038 sec = 6616 sec or bites
- Time spent biting into short-clipped algal growth on calcarenite or biolithite[6]): 93% of 7038 sec = 6545 sec or bites
- Mean area of short-clipped algal growth scraped bare per bite: 0.3 cm², or per day per fish: 0.3 cm² × 6545 = 1964 cm² or roughly 0.2 m²
- Mean detritus content of 100 cm² of short-clipped algal growth: 0.836 g
- Detritus ingested per fish per day from short-clipped algal growth: 0.836 g × 19.64 = 16.4 g
- Mean carbonate content of 5 fish caught at the end of the day without having excreted: 54.9 g
- When intake of carbonates from sand, *Stypopodium* or alcyonarian coral is disregarded, then all of the carbonate detritus found in these fish is derived from food materials as listed in footnote No. 5. The mean total amount of

    carbonates ingested per fish per day is: 54.9 g

    Reworked sediment from short-clipped algal growth per fish per day: 16.4 g

    Eroded in situ carbonates per fish per day: 38.5 g
- Mean erosion per bite: 38.5 g : 6616 = 5.8 mg (cf. maximum values given above)
- Erosion per hectar per summer month in Gravelly Bay: 38.5 g × 151 × 30 = 174 kg

Discussion

Variations in the standing crop

The calculated erosion rate is based on observations during only one summer month (September). Very little is known about seasonal variations in the standing crop of *S. viride* in Bermuda. There are two indications that such variations take place: 1. The proportion of males to females is far from being balanced at Bermuda's south shore in September, although it is probably equalized during the mating season (June or July? See WINN & BARDACH 1960, p. 32). 2. BARDACH (1959, p. 82) wrote that most large parrotfish were absent from shallow reefs in the North Lagoon in February 1956. On the other hand, R. Menzies, a professional diver of Hamilton, Bermuda, who assisted the author in September 1972, noticed no difference in the abundance of *S. viride* between summer and winter when diving during the winter of 1972–73 (personal communication). BARDACH's observation in February was made on a shallow reef in the North Lagoon similar to Grid Reef (BARDACH 1958, Fig. 3). At this location low winter air temperatures influence the temperature of relatively quiet surface water more effectively (see BEERS & HERMAN 1969) than at the agitated south shore, where water circulation is always intense. Here seasonal changes in algal growth rates might influence the standing crop of *S. viride* to some degree, because in Gravelly Bay these fishes feed up to 99% on algae (Table 1). The erosion rate probably varies greatly according to the habitat; on Grid Reef the standing crop is

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[5]) Short-clipped algal growth on calcarenite or biolithite, living *Porites asteroides*, and living *Millepora*. With most of the bites into these food materials some of the hard calcareous substrate (calcarenite, biolithite, or skeleton) is scraped away and ingested.

[6]) This type of algal growth holds varying amounts of carbonate detritus.

roughly one fourth that in Gravelly Bay. When the eroded material in relation to sediment reworked by *S. viride* is more than 2:1 (70%) in Gravelly Bay and on Grid Reef is assumed to be 1:3 (25%), then the erosion rate on Grid Reef may be more than ten times smaller than in Gravelly Bay. This difference could be even more pronounced on Make-Do Reef where 34% of the fishes' diet is sand.

Sources of error in the calculation of the erosion rate

A limitation of the above erosion calculation is the insufficient number of fish (5 individuals) on which it is based. The calculation apparently is not biased by solution of carbonate grains within the digestive system (see Fig. 11, fish No. 22). If solution occurred it would reduce the abundance of the finest grains increasingly towards the anus. GOHAR & LATIF (1959), working in the Red Sea, concluded earlier that no carbonate solution takes place in the intestines of parrotfish. When a fish grazing on short-clipped algal growth touches the rock substratum only lightly, leaving a small, hardly perceptible bite-scar, then the proportion of detritus scraped from rock to particles taken from algae will be lower than calculated. When the fish does not reach the rock surface at all, the ratio drops to zero. This probably has only a slight influence on the calculation because it can be heard underwater, especially when diving with SCUBA equipment, that the great majority of bites into short-clipped algal growth hits the rock substrate. Parrotfish jaws bunching together algal filaments with adhering carbonate particles (foraminifers, for instance) may catch more carbonates from algae per bite than are held within the area scraped bare by the closing beak. This potential error is also presumably of minor importance, because detritus in short-clipped algal growth is concentrated near the rock surface. These factors were omitted in the calculation because of the lack of quantitative data. When they are disregarded, the calculated erosion rate tends to increase above the true value.

The following errors have the opposite effect: Small bite-scars on short-clipped algal growth are poorly delimited and likely to be missed. Thus, the average of scar sizes (0.3 cm²) may be overrated, and so would be the proportion of sediment ingested from algal growth to detritus from erosion. Particles smaller than 125 microns make up about half of the sediment held within short-clipped algal growth on patch reefs of Gravelly Bay (Fig. 11). Some of the finest dust probably does not enter the mouth of grazing fish because it swirls up when the jaws hit the rock surface. Although the granulometry of bits scraped from rock surfaces is not known, it is reasonable to assume that a large part of the fine detritus passing through the fishes' gills is derived from short-clipped algal growth. If the dust lost through gills were predominantly detritus from algal growth this could lead to a substantial underestimation of the erosion rate. BARDACH's method of measuring the time for overturning the gut contents by injecting dye into the throat of fish under anesthesia is unsatisfactory because parrotfish are very sensitive to handling. Many of them caught for tagging did not survive the incident (BARDACH 1958, p. 144). The delicate fish, which under natural conditions are almost constantly feeding, probably required a significant amount of time to recover from the anesthesia. The forced feeding interruptions and unwonted food in the laboratory certainly caused an extension of the time required for overturning the intestinal contents. It is very probable that large parrotfish in their

natural habitat turn over their gut contents in less time than measured by BARDACH, this being another factor reducing the calculated erosion rate.

Origin of Homotrema rubrum in sediments of Gravelly Bay

The presence of sand-size, red fragments of *Homotrema rubrum* in the sediments of Gravelly Bay calls for an explanation, because this attached foraminifer under normal conditions (cf. IAMS 1969, p. 72) grows only on the underside of coral colonies, in cavities of reef rock, and on the underside of coralline algal nodules. Calcarenite has a small percentage of *Homotrema* grains, but these are invariably completely bleached out. Red, sand-size grains of *Homotrema* occur in the sediment of the bay bottom, within the algal growth on biolithite and calcarenite, and in sediment-filled voids of reef rock. Since non-biogenic mechanical erosion appears to be of minor importance in Gravelly Bay, except for the intertidal zone and the uppermost part of the subtidal zone of the inner bay, a substantial part of the sand in the bay must be produced by organisms. Clionid sponges may be major subtidal sand producers (see below). They have direct access to surfaces supporting *Homotrema*, but nothing is known about their sand production rate. With the exemption of few algal nodules which occasionally are upturned by storm waves or rays in search of food, living *Homotrema* are out of reach for grazing fish. But samples of bite-scarred, dead bio-lithite with algal growth, or calcarenite encrusted by coralline algae, have several percent of red, cross-cut *Homotrema* grains on the original surface (see Fig. 8a). This apparently means that some parts of the reefs and crusts remain devoid of living coral or encrusting organisms for a time sufficient to allow surface bioerosion to reach the recesses of *Homotrema* (Fig. 8a). More than 90% of the surface of algal–vermetid cup reefs and crusts or lips is dead and covered by a short-clipped algal growth. Large scarid fish are the only sand-producing organisms capable of abrading significant quantities of algal–vermetid rock. The carbonate detritus is probably deposited to a large extent away from where it was eroded (see MACKENZIE et al. 1965, p. 268); part of it is trapped by mostly filamentous algae, and some will seep into voids of reefs and crusts.

Comparison of the erosion rate of S. viride with other eroding organisms

When the erosion rate calculated for *S. viride* in Gravelly Bay is compared with the rate of other eroding organisms, it should be kept in mind that this is the capacity of a single species out of a large group of almost exclusively herbivorous, rock-abrading fish. Most important among these are Scaridae (parrotfish), and to a lesser degree Acanthuridae (surgeonfish). A number of other families are known to carry various amounts of sand (BARDACH 1961, p. 98). In the same paper, BARDACH (p. 99) calculated a redeposition of 600 kg of sediment by all parrotfish species during 8 summer months per hectar or 75 kg per hectar per month. A part of this quantity is derived from erosion. The standing crop of *S. viride* on BARDACH's one-hectar reef is unknown, but the size, physiography, and position of the reef in the lagoon are similar to Grid Reef. If the erosion rate of *S. viride* on BARDACH's reef is assumed to be the same as on Grid Reef or more than ten times smaller than in Gravelly Bay (see above), then

it would be less than 17.4 kg per summer month. NEUMANN (1966, p. 106f.) wrote that the boring[7]) sponge *Cliona lampa* in Bermuda's Harrington Sound is eroding subtidal calcarenite cliffs at a maximum rate of 1.4 cm per year (1 m per 70 years). He calculated a weight loss up to 6.513 kg per m² per 100 days from calcite (Table 2). This corresponds to 19.5 metric tons per hectar per month which would be 112 times the erosion rate of *S. viride* in Gravelly Bay. NEUMANN cautions that the boring rates calculated from his experiments in Harrington Sound may be indicative of initial boring only. The long-term erosion rate within a substrate bored to maximum depth (2 to 3 cm) could be slower. RÜTZLER (1974) found *C. lampa* forma *lampa* only in inshore waters like Harrington Sound, Ferry Reach, Castle Harbour and sheltered bays like Coot Pond at Bermuda's north shore. *Cliona lampa* forma *occulta* appears to occur indiscriminately from Harrington Sound to North Rock as well as at the wave-battered south shore, like most of the other clionids of Bermuda. Only *C. amplicavata* RÜTZLER seems to prefer open to agitated water. But nothing is known about the variation of the biomass of boring sponges per hectar between the different habitats of the Bermuda platform. An observation by TRACEY et al. (1948, p. 876) at Bikini in the Pacific indicates that the bulk of boring organisms prefers protected environments. At Bikini such an area is the sheltered part of the reef with reduced water circulation behind the *Lithothamnion* ridge. Even if NEUMANN's result is valid only for the exceptional habitat of almost completely enclosed Harrington Sound, clionid sponges are possibly more efficient in degrading coral reefs to sediment than fish, at least in Bermuda. Whereas fish only erode directly by gnawing away rock bits and crushing them in the pharyngeal mill, boring sponges release lime mud from their caverns (HARTMAN 1958; GOREAU & HARTMAN 1963, p. 51) as a primary product, and, by causing the heavily perforated substratum eventually to crumble, all grain sizes from sand to rubble and cobbles (cf. BERTRAM 1934, p. 1026) are formed as a secondary sediment which probably makes up a significant portion of the eroded material. This effect is well demonstrated by a number of the queen conch *Strombus gigas* from Ferry Reach and the North Lagoon collected by the author in September 1968. Young specimens with a shell size not exceeding 12 cm had an intact conchiolin periostracum and were not bored. With increasing size of the shell the conchiolin weathers away almost completely, and the calcareous surface is colonized by algae which form a dense growth. The heavy shell of the living snail is bored to within less than one millimeter from the inner surface. After the animal's death clionid sponges perforate the shell to complete disintegration into sand an rubble (GYGI 1969c, p. 33). Another subtidal sand-producing organism is *Echinometra lucunter*, but the sediment production capacity of this sea urchin appears to be of a minor order (HUNT 1969, p. 39). The quantitative importance of another bioerosion process can not even be guessed: In Gravelly Bay the rock surface beneath subtidal growths of filamentous and other algae is pitted by closely-spaced borings with a diameter not greater than 100 microns and a depth of about half a millimeter. Because the rock under fresh, deep fish scratches is not pitted (see Fig. 9c), it is probable that the borings are etched out by the holdfasts of sessile algae. BARNES & TOPINKA (1969, p. 754) described etching of calcareous substrates by

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[7]) The term "boring" is here preferred to "burrowing" (cf. recommendations by CARRIKER & SMITH 1969, p. 1011 f.) in order to make a difference between borings in a hard substrate in contrast to burrows in unconsolidated sediment (see AGER 1963, p. 110, and POHOWSKY 1974, p. 558).

rhizoids of recent *Fucus*, a common littoral alga of the British Isles. GYGI (1969*b*, p. 63) drew attention to similar superficial borings in shallow marine, subtidal rock from the Upper Jurassic of Switzerland. Because in Bermuda extensive parts of the reefs and most of subtidal calcarenite are overgrown by algae, etching by algal rhizoids might be a significant factor in bioerosion and should be taken into account in further work.

Conclusions

Bite-scars by *S. viride* on even the hardest substrates of Gravelly Bay prove that this species is able to erode any calcarenite or biolithite (coral–algal and algal–vermetid). The smooth surfaces of algal–vermetid rock and subtidal calcarenite off the south shore appear to be the result of abrasion by herbivorous fish, not waves as presumed by STANLEY & SWIFT (1967, p. 679; cf. HIATT & STRASBURG 1960, p. 103). The asymmetrical shape of the patch reef figured from Gravelly Bay (Fig. 5) strongly suggests that the structure has been formed by organic accretion rather than erosion as inferred by STANLEY & SWIFT (1967) for "pinnacles", although the reef must have been constantly exposed to surge and bioerosion from the start. Overall asymmetrical growth is probably brought about by preferential breaking away of projecting parts on the wave-exposed side of the reef. It proved to be impossible to calculate the erosion rate of *S. viride* accurately. Because errors in the calculation counteract each other, and because errors reducing the calculated result appear to predominate, the stated figure can be regarded as a minimum and should give at least the order of magnitude of the erosion rate, but this is only valid for Bermuda's south shore. *S. viride* prefer agitated water near exposed reefs and shorelines. These are optimal habitats supporting a maximum standing crop. There the percentage of reworked sediment is lowest in the carbonates excreted by the fish. The erosion rate calculated for Gravelly Bay consequently appears to be above average to high. The rate probably drops rapidly from North Rock towards central North Lagoon. A better estimate of the rate would require more work both in the natural habitat of the fish and in the laboratory with fish kept in aquariums and fed with natural food. However, NEUMANN's experiments demonstrated that measurements in the laboratory may give results which are far from the erosion rate of the organism in its natural environment (NEUMANN 1966, Fig. 10).

It is possible that *S. viride* at the south shore are eroding at an uniform rate the year round. Constant erosion at the rate estimated for September would amount to 12×174 kg = 2088 kg per hectar per year. If the sediment produced were deposited on an area equal in size to the area of erosion, the following rates of deposition would result: when the proportion of excreted aragonite to calcite is assumed to be 1:1, then the mean specific gravity of the calcium carbonate laid down would be at least 2.82. 2088 kg of material of this specific gravity have a volume of 740 liters when porosity is 0. The excreted sediment may have a total porosity (intergranular and within grains) of 40%. The sediment excreted per hectar per year would then have a volume of 1233 liters or roughly 1.2 cubic meters equivalent to 0.12 millimeter of sedimentation per hectar per year or 1.2 meters of uncompacted sediment per 10,000 years. Because no substantial compaction is to be expected during the lithification of this type of sediment, *S. viride* presumably would be able to produce about 100 meters of limestone per one

million years. This rate of a single scarid species indicates that parrotfish are a geologically significant agent in the transformation of reefs into sediment. However, not all scarids appear to be eroding reefs as efficiently as *S. viride*, although two species are much larger. Whereas the wet body weight of adult *S. viride* ranges from 0.60 to 2.18 kg, *Scarus coeruleus* has a maximum wet weight of 10 kg, and *Sc. guacamaia* in Bermuda can grow as heavy as 20 kg (MOWBRAY 1965). While *Sc. guacamaia* appears to feed mostly on reefs and in shallow water where it leaves the biggest bite-scars of all Bermuda scarids, it was frequently seen eating bottom sand with algal mats in Gravelly Bay. *Sc. coeruleus* in this bay was only observed grazing on the bottom, on algal growth either on rock or sand. The body weight of a herbivorous fish and the maximum amount of detritus it can scrape from hard substrate per bite are obviously interrelated (see above).

Because Bermuda is near the northern limit of coral reef growth, coral accretion rates are low as compared with the equatorial parts of the Indo-Pacific Ocean, (see IAMS 1969, Table 1) and fish eat very little coral (Table 1). But on reefs in equatorial seas where predominantly coral-eating parrotfish species occur (HIATT & STRASBURG 1960, p. 103; TALBOT 1965, p. 456), the erosion rate is likely to be considerably higher. Measurement of the rate would be easier on reefs near the equator because of strongly reduced seasonal changes.

Fish erosion and sedimentation are conspicuous, but in Bermuda possibly of less quantitative importance than erosion and sedimentation by subtidal borers and etching by algal rhizoids. Sediments directly produced by subtidal bioerosion are mud, sand and fine gravel from grazing fish and mud from boring sponges. Sand, rubble, and cobbles from clionid sponges and boring algae are sediments indirectly derived from bioerosion (see GYGI 1969c, p. 33, and JAMES 1970, p. 26).

Comparison with a fossil reef (Upper Jurassic) of northern Switzerland

On the Rauracian Reef complex (Oxfordian, Upper Jurassic) of northern Switzerland, an extensive shallow-water platform with small patch reefs (PÜMPIN 1965) was separated from deeper water by a broad belt of coral and hydrozoan growth (ZIEGLER 1962; BOLLIGER & BURRI 1970). Absence of coarse reef detritus on the fore-reef slope indicates that the angle of the talus was gentle. Unlike Pleistocene and Holocene reefs, vertical growth of this Jurassic reef apparently was controlled only by subsidence, and lateral growth by the progress of filling in the fore-reef basin. On the platform sedimentation almost kept up with reef growth and so prevented development of marked differences in elevation between patch reefs and the lagoon floor (PÜMPIN 1965, Fig. 14). It is conceivable that some Jurassic fish were feeding on these reefs in a manner resembling recent Scaridae. *Mesodon* and *Microdon* of the family Pycnodontidae have praemaxillaria equipped with chisel-like teeth (HENNIG 1906) which enabled them, according to a generally accepted opinion, to clip off sessile organisms from their substrate. The massive maxillar dentition was probably used to crush shells of brachiopods, molluscs, and crustaceans. But it cannot be excluded that these fish added coral and algae to their diet, scraping food off the substrate with their praemaxillar teeth including calcium carbonate for milling with the maxillar dentition, thus being sediment producers like recent Scaridae. *Mesodon* sp. has been found by H. Zbinden in a

pisolithic bed in the uppermost St.Ursanne Formation at Ocourt in the back reef realm of the Rauracian Reef complex. Some maxillar teeth of the specimen are ground flat. This is an indication that they have been used not only for crushing shells, but also for milling. However, on several hundred coral colonies from sediment between patch reefs of the middle St.Ursanne Formation, many of them being in a perfect state of preservation, no features could be found which may be interpreted as bite-scars. It is certain that space between glomerate maxillar teeth would have prevented *Mesodon* from triturating carbonate bits as efficiently as modern Scaridae do with their pharyngeal milling surfaces, which are equipped with tight rows of teeth. Pycnodontidae of Central Europe were reef fish (LE DANOIS 1959, p. 1324). They originated late in the Triassic and approached their Upper Jurassic acme in Oxfordian time (op. cit., p. 1322), but their part in the production of reef-derived sediment apparently was not important.

Acknowledgments

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