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The role of herbivorous fishes and urchins in coral reef communities*

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Synopsis

Herbivorous fishes and invertebrates are conspicuous elements of coral reef communities where they predominate both in numbers and biomass. Herbivores and the coral reef algae on which they feed represent a co-evolved system of defense and counter-defense. Algal species have developed toxic, structural, spatial and temporal defense or escape mechanisms, while the herbivores employ strategies that involve anatomical, physiological and behavioral adaptations. Current research demonstrates that many reef fishes are highly selective in the algae they consume. Food selection in these fishes may be correlated with their morphological and digestive capabilities to rupture algal cell walls. Sea urchins select more in accordance with relative abundance, although certain algal species are clearly avoided.

The determinants of community structure on coral reefs have yet to be established but evidence indicates a strong influence by herbivores. Reef herbivores may reduce the abundance of certain competitively superior algae, thus allowing corals and cementing coralline algae to survive. We discuss how the foraging activities of tropical marine herbivores affect the distribution and abundance of algae and how these activities contribute to the development of coral reef structure and the fish assemblages which are intimately associated with reef structure.

Introduction

Coral reefs contain the most diverse assemblages of organisms in the marine world. About 15–25% of the

fish species diversity and biomass on these reefs consists of herbivorous fishes in the families Scaridae, Acanthuridae, and Pomacentridae, in addition to other families which derive at least part of their energy from benthic plants (Bakus 1964). Adjoining seagrass beds, particularly conspicuous in the Caribbean, have small resident species of herbivorous fishes and are heavily exploited by larger fishes from nearby reefs (Ogden & Zieman 1977). The tropical situation contrasts dramatically with temperate waters where herbivorous fishes are either absent or where plants are taken incidental to invertebrate feeding (Bakus 1964). Thus herbivorous fishes are largely confined to tropical regions where they play a major role in the transformation of energy fixed by benthic plants.

Also conspicuous in the tropical system are the herbivorous invertebrates, particularly the regular sea urchins. An extensive literature has developed around the relationships of algae and sea urchins (see Lawrence 1975). There is often difficulty in separating the effects of sea urchins from those of fishes; as the urchins are more easily manipulated, they have been much more intensively studied (e.g. Ogden 1976, Vadas, in press).

Within the coral reefs and seagrass beds of the tropics, the activities of herbivores tend to be concentrated in the top 20 m of water. This is the region of greatest development and highest productivity of benthic plants. Below these depths herbivorous fishes and invertebrates do occur, but are much less prominent.

The following is a brief review of the functional morphology, feeding behavior and ecology, and the influence of herbivores on plant distribution and community structure. Our purpose is to present what

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evidence is known, while recognizing that these data do not yet explain the whole story. As much as this is a review, we are also describing the direction of our own research.

General characteristics of herbivorous fishes

Much of the diversity among modern acanthopterygian fishes involves adaptations associated with feeding and with living on coral reefs. The teleost radiation began during the Jurassic period but these fishes did not become successful on reefs until acquiring the morphological advances which distinguished the acanthopterygians during the Cretaceous (Romer 1966). These were carnivorous fishes. Hobson (1974) has discussed the evolution of predaceous reef fishes. Herbivorous fishes appear to be one of the most recent trophic innovations attained during the second coral reef epoch beginning in the Eocene. **Few taxa are herbivorous, but they often predominate on coral reefs (Randall 1963, Hobson 1974).**

Superficially, herbivorous fishes differ from ancestral predaceous forms in the structure of the mouth. Predators generally possess gaping jaws with teeth suited for grasping prey (e.g. barracudas, eels, etc.). More specialized predators are adept at 'inhaling' prey by rapid expansion of the buccal cavity (e.g. anglerfish, groupers, trumpetfish, etc.). They do not necessarily have grasping teeth but may have reduced rasping teeth instead. In contrast, fishes which eat plants have short, blunt snouts with teeth side by side to form a cropping edge. In its most extreme form, represented by the scarids, the teeth have totally fused to form a beak with which these fishes bite into the inorganic substratum and obtain algal mat and endolithic algae.

Four morphological trends characterize the alimentary tract of herbivorous fishes (Lobel in prep.):

- 1) An elastic stomach and long intestine (e.g. damselfishes, some surgeonfishes).
- 2) A thick-walled stomach and long intestine (e.g. some surgeonfishes, some angelfishes).
- 3) A pharyngeal mill and long intestine but no stomach (e.g. scarids).
- 4) A pharyngeal mill and an elastic stomach with a long intestine (e.g. some cichlids).

The first three types are found among reef fishes. The fourth type, characteristic of cichlids, is restricted to freshwaters and will not be considered here.

Cellulase or comparable enzymes are lacking and microflora are not present in sufficient quantity to

break down algal cell walls during the time food is in the gut of a fish (Phillips 1969). Stickney & Shumway (1974) found traces of microfloral cellulase in the guts of some estuarine fishes, but found no correlation between cellulase activity and the food habits of the fish. *Mugil cephalus* was the only herbivore of 17 fishes with cellulase activity. Odum (1970) has shown that flagellates occur in the intestine of *M. cephalus*, but the possible role of microorganisms in digestion has not been evaluated.

Studies conducted thus far are too limited to make generalizations concerning how fish herbivores utilize plant material. The possibility that bacteria and protozoans that can break down cellulose and other polysaccharides are present in the guts of herbivorous fishes has not been adequately explored and should not be dismissed yet.

Fishes may utilize a chemical mechanism to rupture cell walls. Moriarty (1973) and Bowen (1976) have demonstrated that extreme acidity in the stomach of freshwater cichlids (*Tilapia nilotica* and *T. mossambica*)* functions to lyse the cell walls of blue-green algae, detrital bacteria and some green algae. The possible functions of pH and alimentary morphology in herbivorous reef fishes in relationship to the foods they eat is currently under investigation (Lobel in prep.).

Herbivorous fishes are classed as 'browsers' or 'grazers' according to their ingestion of inorganic substratum (Hiatt & Strasburg 1960, Jones 1968). Grazers pick up large quantities of the inorganic substratum while feeding either by rasping or sucking. Browsers bite or tear benthic macro-algae while rarely ingesting any inorganic material. The thick-walled, gizzard-like stomach which *may* be capable of trituration (its function has not yet been demonstrated) and the grinding pharyngeal mill are common to most grazers. Fishes with thin-walled stomachs are generally browsers. Fishes with gizzard-like stomachs have shorter intestinal lengths than species with thin-walled stomachs, suggesting that food is better prepared for digestion in fishes possibly capable of trituration (Jones 1968). The abilities of different fishes to break down plants differ significantly but may be partially compensated for by the length of time the food remains in the gut. Where a fish lacks the necessary mechanics or pH for quick breakdown of plants, it may lengthen the time in which food is in the intestine. Such seems to be the strategy of fishes on a high fat or waxy diet (Patton & Benson 1975).

* = *Sarotherodon*.

In general, herbivorous fishes have a low assimilation efficiency and high ingestion rate with a retention time of a few hours. Maximum nutrient absorption apparently results from a large and continuous ingestion rate and short retention time. Assimilation efficiency is probably high for a few components of the diet but rather low when the entire bulk of ingested material is examined (Odum 1970).

Differences in morphology of the alimentary tract and a diversity of feeding mechanisms may reflect an ability by reef fishes to consume and utilize certain types of algae. These differences may serve as a basis from which to evaluate competitive interactions and the effect of fishes on the distribution and abundance of particular algae.

Feeding behavior and feeding ecology of herbivorous fishes

Herbivorous fishes are conspicuous and active during the day. As twilight progresses, they seek hiding places within the reef, often moving over relatively long distances. At night they are generally inactive.

Table 1. Habitat and foraging strategy of herbivorous fishes (see text for references and details).

Habitat	Foraging strategy	Fishes
Shallow reef	Single and mixed species aggregations	surgeonfishes, parrotfishes, angelfishes
	Territorial	damselfishes, small parrotfishes
	Home range	angelfishes, surgeonfishes
Deep reef	Home range	angelfishes, surgeonfishes
	Single and mixed species aggregations	parrotfishes
Sand	Wide roaming schools and aggregations	mullet, milkfish, surgeonfish
Intertidal at high tide	Single and mixed species aggregations	sea chubs, parrotfishes, surgeonfishes
	Territorial	surgeonfishes, damselfishes
Seagrass	Home range	parrotfishes, surgeonfishes

During the day, herbivorous fishes have essentially three foraging strategies: territorial defense, group foraging and individual home ranges. The strategy adopted appears to relate to habitat type as much as to taxonomic status (Table 1).

Territorial behavior

The most conspicuous holders of feeding territories on a reef are the damselfishes (Pomacentridae). These fishes have been the object of intensive behavioral study, but their ecology and relationships with algae are only just coming to be known.

The territories of pomacentrids are easily defined by a patch of algae often of characteristic color and consistency. The algae in pomacentrid territories are known for only a few cases (Foster 1972, Belk 1974, Brawley & Adey 1977, Ogden, unpubl.); no published studies have as yet confirmed that the algae present in territories are actually consumed by the resident, although we have observed such feeding. Stomach contents of territorial pomacentrids contain some invertebrates, but their presence in the territories and importance of these to the nutrition of the fish has not yet been shown.

Several studies (Vine 1974, Moran & Sale 1977, Ebersole, in press) have shown conclusively that the pomacentrid territory is primarily a feeding territory and secondarily a nest site. The activities of *Eupomacentrus planifrons* in the Caribbean can lead to the destruction of corals and to the subsequent formation of new territory space (Kaufman 1977). Settling plates placed within territories rapidly develop algal growths more characteristic of territories than outlying areas (Vine 1974) and there is some suggestion that the fish may take an active role in 'weeding' its territory (Foster 1972, Ogden, unpubl.). Removal of a damselfish will lead to territory expansion by contiguous territory holders, or to rapid reduction of the algal biomass within the territory by scarid and acanthurid foraging groups. The presence of high densities of territorial pomacentrids in certain reef areas may consequently affect reef productivity, coral growth, nitrogen fixation, and reef cementation (Vine 1974, Kaufman 1977, Brawley & Adey 1977).

Territoriality will be advantageous if the actions of a fish increase the yield of the guarded resource. We therefore do not expect nor do we find territorial herbivores in deep water (> 30m) where such defense would not significantly increase the standing crop of algae in the territory (Vine 1974). Standing crop and

territory size are inversely correlated (Syrop 1974). Since the rate of growth of algae decreases with depth, we would expect larger territories in deeper water. Vine (1974) found a sharp decline in algal growth on protected plates at depths greater than 12 m. At 20 m there was no significant difference between standing crops of algae on protected vs. exposed plates. This matches the lower distributional limit of territorial, herbivorous pomacentrids, but not of other herbivores such as pomacanthids in Hawaii (Gosline 1965). Standing crop on exposed vs. protected plates may give a measure of algal replacement rates and implies that territory size is not only dependent on the standing crop but also on the replacement or growth rate of the algae.

The minimum size of an herbivore's territory should approximate the bioenergetic requirements of the resident divided by the maximum sustainable yield of the territory minus that which is predictably lost to intruders. Fluctuations in territory size may reflect changes in benthic productivity, degree of intrusion, and metabolic requirements of the resident at various reproductive and growth stages. The maximum size of a territory approaches the limit of area that a resident can economically defend.

While pomacentrids are the most conspicuous reef-associated territory holders, scarids are also known to hold feeding territories. Ogden & Buckman (1973) and Buckman & Ogden (1973) showed that *Scarus croicensis* will hold territories that appear to serve dual functions of feeding and reproduction. These territories are defended against conspecifics and other benthic feeding fishes (Robertson et al. 1976). The food supply in this species consisted of filamentous algae, diatoms and flocculent material that covered the reef surface. The sites in Panama were close to large rivers which periodically brought in abundant sediments. Interestingly, in St. Croix, U.S. Virgin Islands, *S. croicensis* is less common and does not hold territories. This may be due to the more dispersed nature of the available food (Ogden, unpubl.).

Foraging groups

Foraging groups of variable size are characteristic of the families Scardiae and Acanthuridae in tropical waters. These groups may be homotypic or heterotypic. Where heterotypic the groups often consist of several herbivorous species as well as a few carnivores which presumably feed upon invertebrates and small fishes disturbed by the foraging group (Eibl-Eibesfeldt 1965, Hobson 1974, Ogden & Buckman 1973,

Robertson et al. 1976, Alevizon 1976). The groups probably serve a dual function. Aggregations provide some protection from predators while they also serve to increase individual feeding efficiency, especially in areas where territorial fishes control much of the surface available for feeding (Barlow 1974, Robertson et al. 1976, Morse 1977).

In the Pacific, aggregating *Acanthurus* spp. are the most devastating invaders of algal territories. In particular, *Acanthurus triostegus* forms the nucleus of many mixed species aggregations. Other herbivorous species join the aggregation and feed along with *A. triostegus*. Benthic foraging predators, such as labrids and aulostomids, also accompany the aggregation (Hobson 1974). The feeding aggregation swarms over the reef and descends onto lush algal patches, which are usually defended by pomacentrids. At first the territorial pomacentrid will vigorously attack the marauders, but after a few moments the resident waits listlessly until they are gone. The number of attacks by the resident fish per fish in an aggregation are not enough to drive the aggregation away (Barlow 1974). Other acanthurids are more solitary and graze over the reef in general.

A. triostegus is also unique in that it does not possess a muscular stomach as do many other acanthurids (Randall 1961, Jones 1968). Its alimentary morphology appears functionally similar to that of the herbivorous pomacentrids. Unlike the highly aggressive pomacentrids, *A. triostegus* is passive, a necessary prerequisite for group cohesion.

There is a possible correlation between the occurrence of aggregations and the density of territorial herbivores (Barlow 1974). The herbivorous *Acanthurus nigrofuscus* defends territories much like a pomacentrid. *A. triostegus* will form aggregations where *A. nigrofuscus* is abundant but is solitary where *A. nigrofuscus* is rare. Too much crucial evidence is missing, however, to identify the relationship as causal or merely incidental to some other factor such as food availability, threat from predation, or time of day of observation. Another territorial herbivore is *Acanthurus lineatus* (Nursall 1974). These fish are found just below the intertidal zone. They are most territorial during high tide and become less defensive with a change in habitat due to low tide. During high tide, *A. lineatus* are especially aggressive toward transient scarids which enter the reef flat in aggregations to graze at that time (Nursall 1974). Other tidal zone fishes display similar behavioral responses to changing water levels (Gibson 1969, Nursall 1974).

Heterotypic schools have been described as traveling together but separating into smaller single species groups while actually feeding. The smaller groups reunite when moving to a new location. A further breakdown by size was apparent with small *Scarus croicensis* separating from larger individuals of the same species while feeding, but joining together with larger *S. croicensis* for 'travel' (Earle 1972 and pers. comm.).

Depletion of food in one particular locality is probably not the reason for movement by an herbivore aggregation. The first few fishes may leave a location for a variety of reasons and other fish may respond to these departing movements and follow. Thus a mechanism involved in group cohesion may prevent an algal patch from being overgrazed past its regenerative potential. At least enough resource is expected to remain to provide the essential nutrition for the territory resident while the territory recovers. A similar phenomenon has been noted for bird flocks (Moynihan 1962, Morse 1970, 1977).

Home range

Many reef fishes are known to limit their movements to a specific reef area in which their feeding is concentrated (Reese 1973, 1977, Sale 1977). Although these fishes may defend their 'home' against potential food competitors, as is the case for some chaetodontids (Reese 1975), others do not, such as the pomacanthid *Centropyge* (Lobel ms.). An animal with a feeding home range may be territorial over some other limited resource such as a shelter or nesting site. Concerning food, a home range seems to differ from a feeding territory in at least three ways. The home range does not increase the productivity of the food

resource and stronger defense would not likely do so either. Home ranges are not defended against all potential food competitors; the species attacked are usually of close taxonomic relationship and possibly competitors for shelter or spawning sites. Finally, home range behavior develops where food is not the limiting factor for the species population or where food resources are not widely utilized by other species.

Selectivity in feeding by herbivorous fishes

Major studies have been conducted on the trophic habits of tropical fish communities in the Pacific (Hiatt & Strasburg 1960, Hobson 1974) and the Caribbean (Randall 1967, Carr & Adams 1973). These have included examination of herbivorous fishes. Stomach-content data alone provide only limited information and have led to the notion that most herbivorous fishes are generalist feeders. Detailed field studies involving both stomach contents and availability are lacking; there have been few complete studies of feeding preferences in herbivorous fishes (Table 2).

The common Pacific surgeonfish, *Acanthurus triostegus*, appears to prefer the algae which it can most readily utilize. *A. triostegus* is able to digest the proteins of *Enteromorpha* and *Polysiphonia* and some carbohydrates of *Enteromorpha*, but is unable to utilize *Sargassum* (Pfeffer 1963). It is possible that the restricted release of reducing groups by *Sargassum* is due to its storage of polysaccharides as polymers of mannuronic acid rather than as glucose (Blinks 1951, Pfeffer 1963). Bile from the gall bladder is able to kill *Enteromorpha*, *Polysiphonia*, and *Sargassum*, but not the blue-green alga *Phormidium*. There was no evidence that the cell walls were digested, although the

Table 2. Plants preferred by fishes during choice experiments.

Family	Species	Habitat	Preferred plant (genus)	Total No. plants Tested	Authority
Acanthuridae	<i>Acanthurus triostegus</i>	Pacific reefs	<i>Polysiphonia</i> & <i>Enteromorpha</i>	29	Randall 1961
Scaridae	<i>Sparisoma radians</i>	Caribbean seagrass beds	<i>Thalassia</i>	9	Lobel & Ogden (in prep.)
Siganidae	<i>Siganus spinus</i>	Pacific reefs	<i>Enteromorpha</i>	62	Bryan 1975
	<i>Siganus rostratus</i>	Pacific reefs	<i>Enteromorpha</i>	56	Tsuda & Bryan 1973
Pomacanthidae	<i>Pomacanthus arcuatus</i>	Caribbean reefs	<i>Codium</i>	11	Earle 1972

cytoplasmic structure was disrupted and the cell contents clumped into a central mass (Pfeffer 1963). Randall (1961) demonstrated that blue-greens and a red alga, *Asparagopsis* (known for its ketone content) were not eaten by *A. triostegus*. The brown algae were only sparingly consumed. The preference for algal species seems to correlate with the ability of a fish to kill and digest the algae.

Although the evidence is weak, it appears that not all preferred algae are of equal value and if given an opportunity, a fish will feed on an alga in proportion to its food value. *A. triostegus* died after two months when fed only *Enteromorpha* sp., while fish fed only *Polysiphonia* sp. lived four months until sacrificed (Pfeffer 1963). Pfeffer determined that *Polysiphonia* contained more protein than *Enteromorpha*. Unfortunately, it is not known whether three times the quantity of *Enteromorpha* will maintain fish as well as one unit of *Polysiphonia*. *Polysiphonia* appears to be a more important energy source and is eaten in greater amounts than *Enteromorpha* when both are offered in copious amounts (Tandall 1961). It may be significant that *Polysiphonia* is usually encrusted with epiphytes which may add nutrition while *Enteromorpha* is not (Pfeffer 1963). Both *Polysiphonia* and *Enteromorpha* are preferred food by *A. triostegus* over other algae when presented a choice in an aquarium (Randall 1961).

Not all algae consumed by fishes may be intentionally eaten. The presence of some organisms in the guts of fishes may be simply incidental. Study of *A. triostegus* in the Line Islands revealed that 40 species of algae were eaten, exceeding the number previously known from that region (Dawson, Alleem & Halstead 1955). Of all the algae the five most abundant in the stomach contents were *Pterocladia* sp., *Sphacelaria furcigera*, *Lyngbya majuscula* (and/or *L. aestuaria*), *Bryopsis pennata* and *Lophosiphonia* sp.. After reviewing this study and from his own work Randall (1961) suggested that many algae were consumed by the fish incidentally according to their abundance on the reefs. At least *Lyngbya* spp. were avoided by *A. triostegus* in aquaria. *Lyngbya* and *Asparagopsis* (also not eaten; see above) are two out of three algae which commonly reach a height of 5 cm or more in Hawaii (Randall 1961). The third species is a red alga, *Plocamium sandvicense*, which has not been tested for palatability to fish. It appears as if some of the material ingested by fish are types which would be avoided if possible. In Hawaii, Jones (1968) found only 40 out of the 160-odd algal genera available to browsing acanthurids in fish's stomachs. In the individual algal divi-

sions, 6 of 16 available browns, 9 of 27 greens, 15 of 97 reds and 2 of 24 blue-greens were eaten.

Siganids are the only other marine fish herbivores whose food habits, preferences and assimilation efficiencies are known, principally from the studies of Tsuda & Bryan (1973) and Bryan (1975). Their work was prompted by the yearly occurrence of nearly 13 million juvenile siganids appearing on the reef flats of Guam. Soon after the population explosion, the reef flats were defoliated, especially of preferred species of algae. Dead individuals of *Siganus spinus* were collected, 74% of which contained no food in their guts. The rest contained only a small amount of filamentous and non-calcareous fleshy algae. The initial swarm, however, consisted of two siganid species, *Siganus spinus* and *S. rostratus* = (*S. argenteus*). Tsuda & Bryan (1973) speculated that the larger *S. rostratus* was able to outcompete *S. spinus* for food. They qualitatively state that *S. rostratus* is more aggressive; however, no empirical evidence is presented that interference competition is occurring. It may be that *S. rostratus* is actually more efficient at assimilating the same and/or more species of algae and consequently attains larger size.

In preference trials, the siganids chose mostly the same algae. Both fishes chose the algae (1) *Enteromorpha* (2) *Feldmannia* and *Derbesia*, and (3) *Cladophoropsis membranacea* (Tsuda & Bryan 1973). Differences between the fishes appeared in the avoidance of a different alga by each. *Siganus spinus* did not eat *Clorodesmis fastigiata* while *Siganus rostrata* did. *Siganus rostrata* did not eat *Polysiphonia* while *Siganus spinus* did (Tsuda & Bryan 1973, Bryan 1975). Only 12 of 56 algal genera offered were always completely eaten by both siganids.

Tsuda & Bryan (1973) noticed that the algae, *Enteromorpha*, *Caulerpa*, *Boodlea*, and *Cladophoropsis* were the first to vanish from the reef flats with the appearance of the siganid swarms. Thus, it appears that algae which were preferentially chosen by fishes in the laboratory were also heavily grazed upon in the field. Both siganid species fed preferentially on filamentous algae but generally did not eat blue-greens or calcareous algae. This agrees with Randall's (1961) observation that blue-greens are among the most abundant algae on reefs and are generally not eaten by fishes.

The preference for a particular alga is not necessarily expressed in the composition of food items found in the guts (Bryan 1975). However, this may be a reflection of the differential digestibility of the items, resulting in the identifiability of the contents.

7,000 *Diadema* from a small patch reef in the Virgin Islands. Dramatic changes occurred very rapidly. Within six months a dense cover of algae obscured the reef surface and even overgrew and killed some of the smaller coral colonies. The halo zone disappeared after six to eight months. Sammarco et al. (1974) compared the same cleared patch reef with nearby 'control' reefs and found not only increased biomass, but also dramatic shifts in dominance and equitability in the algae on the cleared reef. Ogden (unpubl.) has followed this reef for several years subsequent to clearing. The reef has not been recolonized by *Diadema*. The large seagrass-dwelling *Tripneustes ventricosus* has moved from surrounding seagrass beds and taken up residence within the leafy algae on the reef surface. Analogous to the fleshy algal pavements, the reef has become much like a seagrass bed in terms of the response of organisms to its physical structure. *Diadema* is apparently excluded because of its inability to hold itself in position in surge when the substrate is covered with plants. *Tripneustes*, with shorter spines, can easily hold onto the plants with its tube feet and become firmly anchored to the substrate.

Tsuda & Kami (1973) found that selective browsing by herbivorous fishes favors the dominance of blue-green algae. These algae are the persisting forms which are continuously available as food for animals. Apparently few fishes, however, are known to consume these. Within pomacentrid territories, selected species of algae are maintained which are attractive to the majority of herbivorous fishes. Thus it is advantageous for fishes such as acanthurids, siganids and scarids to develop behavioral strategies such as feeding aggregations aimed at overwhelming aggressive pomacentrids. Where reef surfaces are exposed to grazing, the blue-greens composing the turf (rarely exceeding 2 mm in height) and certain macroalgae as *Jania*, *Halimeda*, *Laurencia* and *Caulerpa* (exceeding 10 mm in height) persist (Earle 1972, Dahl 1973, Tsuda & Kami 1973, Belk 1975, Ogden 1976). These species are the types that should be surveyed for possible defensive strategies.

Herbivores have been shown to enhance the productivity of plants in terrestrial and planktonic systems (Mattson & Adey 1975, Dyer & Bokhan 1976, Porter 1976). This effect, occurring in a variety of ways, is the consequence of a long history of co-evolution of herbivore and plant. Herbivory may also enhance nitrogen cycling in plants and positively affect plant production (Mattson & Adey 1977, Owen & Wiegert 1976). The presence in damselfish territo-

ries of certain highly productive species of algae may have an overall effect on reef productivity (Brawley & Adey 1977). Parrotfishes feeding in seagrasses selectively remove the older, more heavily epiphytized leaves, possibly opening up areas for new growth (Ogden, Lobel & Clavijo, unpubl.). Acanthurids feeding selectively on plant epiphytes may enhance individual plant productivity. The heavy grazing characteristic of open reef surfaces leads to the development of a very productive algal mat and holds the plant community in a high-turnover, early successional state.

The action of grazing fishes and invertebrates also enhances the growth and settlement of corals (Stephenson & Searles 1960, Sammarco 1974, Birkeland 1977, Kaufman 1977). Grazing opens up solid substrates upon which corals settle and prevents overgrowth by algae until the colonies escape in size. Birkeland (1977) showed that fishes will graze around newly settled corals without touching or damaging the colony. Grazing may also promote the growth of coralline algae by keeping competitively superior fleshy algae from overgrowing the corallines.

There has been much confusion about whether herbivorous fishes actually eat living corals. Randall (1974) concludes corals are not intentionally consumed by scarids. It is possible that some of the larger scarids are able to bite into living corals because of their stronger jaws, however, corals have not been identified as a main item in the diet (Hiatt & Strasburg 1960, Randall 1967, Hobson 1974). Scarid grazing on carbonate substrates may be a significant factor in their erosion (Bardach 1961, Glynn 1973, Ogden 1977).

Plant-herbivore co-evolution

The diversity of tropical marine plants and the abundance of herbivores has undoubtedly provided a rich background for the evolutionary interplay of plant defenses and herbivore foraging strategies.

According to the scheme we have presented on the morphology of herbivorous fishes, certain algae appear more suitable as food than others. Fishes with only an elastic stomach may be dependent primarily upon their bite as a means of releasing algal cytoplasm. These fishes are expected to select those macroalgae with relatively large cell size. Fishes with a stomach capable of trituration are expected to be able to utilize a different and possibly wider range of algae. This would include smaller cell sizes that could

Table 4. Potential benthic plant defense mechanisms against fishes and urchins (after Vadas, in press).

Defense	Example(s)
Escape in time (highly productive, short-lived)	Small filamentous forms (e.g. <i>Polysiphonia</i> , <i>Herposiphonia</i>)
Escape in space (wave-washed areas, cracks and crevices, from herbivore habitat)	Intertidal algal turfs, cryptic reef species, seagrass beds and associated macroalgae
Structural defense (hard, fleshy or stiff, calcareous, lowered food quality, small cell size)	<i>Turbinaria turbinata</i> , <i>Penicillia</i> , <i>Halimeda</i> , crustose corallines
Chemical defense (unpalatable to toxic)	<i>Sargassum</i> (tannins), <i>Asparagopsis</i> (ketones), <i>Caulerpa</i> (caulerpicin, caulerpin), <i>Laurencia</i> (halogenated compounds), <i>Dictyopteris</i> (dictyopterene), blue-greens (?)

be ground with ingested sand particles in the stomach. Finally, fishes with a pharyngeal mill capable of complete grinding of all foods should have the greatest range of suitable food items. Thus, large-celled macroscopic algae appear most susceptible to all these herbivores, while small-celled algae are possibly least utilized by fishes. Other potential plant defenses (Table 4) include toxicity or chemical defense, cryptic or inaccessible growth, toughness, and lowered caloric value or decreased food quality due to calcification (Paine & Vadas 1969, Ogden 1976, Lobel in prep.).

Caloric value of algal foods has been examined in the temperate zone by Paine & Vadas (1969) and in the Caribbean (Ogden unpubl.). In neither case was the energy content of the food directly correlated with the stomach contents or preferences based on laboratory tests or field availability. Caloric value may not be the most appropriate measure of energy as some of the carbohydrates are bound in structures (e.g. cellulose) which are not equally accessible to all consumers. Some algae may have lowered their food value or desirability by developing a highly silicified or calcified structure, such as *Penicillia* spp. and *Halimeda* spp..

Chemical defenses may exist in benthic marine algae. Many such secondary metabolites found in terrestrial plants are known or presumed to be defensive in nature (Whittaker & Feeny 1971, Freeland & Janzen 1974, Cates & Orians 1975, Levin 1976). Freshwater algae, especially the blue-greens, are also known to be toxic (see Porter 1977). While few marine algae

are known to be toxic or distasteful to herbivorous fishes and invertebrates, many algae produce biologically active compounds which have anti-bacterial or fungicidal properties (Bhakuni & Silva 1974). It seems likely that more intensive study will reveal a rich fabric of chemically-mediated relationships between algae and marine herbivores.

Hashimoto & Fusetani (1972) screened 48 species of algae in the Amami and Tokunoshima Islands and found 38 species that contained toxins lethal to mice or hemolytic to rabbit blood cells. Abbott et al. (1974) and Abbott & Ogden (unpubl.) found that some of the algae avoided by the sea urchin *Echinometra lucunter* contained terpenoids, pungent lipids and other compounds which possibly had a defensive role. Doty & Santos (1970) described the toxic compounds caulerpin and caulerpicin present in the green alga *Caulerpa* and concentrated by an herbivorous saccoglossid gastropod. The compounds may be defensive both in the plant and the invertebrate herbivore. Similarly the toxin known to cause ciguatera in humans who eat certain large predaceous fishes is believed to concentrate biologically in food chains from an origin in blue-green algae or dinoflagellates (Banner 1976).

Ehrlich & Raven (1965) speculated that plant secondary compounds have led to the rich development of insect-plant specializations which are characteristic of the Lepidoptera. The strategies of herbivorous fishes appear to have been very different. In contrast to insects, foraging herbivorous fishes such as the scarids have the ability to move over a wide region while feeding, have an excellent visual sense, and probably have good learning ability. In many ways their strategies may approach those of the mammals discussed by Freeland & Janzen (1974). The guts of herbivorous fishes are long and highly differentiated in some cases. Since they are known to eat some toxic algae they probably can cope with low levels of at least some plant toxins. They have diversified their diets to include a variety of plants and may quickly learn to feed largely on familiar foods. We may expect, however, that temporal differences in plant availability will keep them experimenting with diet and thus remaining flexible. Preferences, where shown by diet/availability studies or direct preference tests, may demonstrate that marine herbivores prefer foods with small amounts of secondary compounds, or select parts of the plants known to be low in such compounds.

On the other hand, the pomacentrids have evolved a strategy of closely tending a patch of bottom and

Thus, what is often identified as a bulk item in the stomach contents may not really indicate what is nutritionally important for growth and reproduction. For example, *Enteromorpha* is the most preferred food of *Siganus spinus* yet it has an intermediate 'importance value' based upon its presence in gut contents (Bryan 1975). Preferred foods are assumed to be so because they are most important to the consumer in bioenergetic terms. The general diet may just reflect what is available in the habitat where the fish is grazing. The test of the assumption that the most preferred food item would also yield the most nutritional value would be to actually maintain consumers on specific diet combinations.

Selectivity in feeding by sea urchins

The regular sea urchins are the other major group of marine herbivores whose diet and feeding ecology are reasonably well known. In contrast to the herbivorous fishes, the sea urchins are nocturnally active. Their specializations for dealing with plants do not involve the modifications in the morphology of the gut that are present in fishes. The complex jaw apparatus, the Aristotle's lantern, is connected to a short esophagus and then to a thin-walled gut. The jaw scrapes the substrate or bites pieces of plants and a food pellet is formed in the esophagus. Sea urchins are known to have a gut flora which enables the digestion of various sugars, starches, and agar, but they apparently have a very limited ability to digest cellulose (Lawrence 1975, Prim & Lawrence 1975). A cae-

cum which may serve the function of culture of microflora is known in the gut of *Diadema* (Lewis 1964, Lawrence 1975).

The feeding habits and ecology of sea urchins of the Caribbean are summarized in Table 3. Sea urchins appear to be differentiated primarily upon the basis of habitat specialization and much less on the basis of food specialization. *Diadema antillarum* is a reef-dwelling urchin which has the capability to eat whole plants or to subsist upon mat and boring algae in highly overgrazed situations. It is quite mobile and appears in striking numbers in reef areas especially by night (Lewis 1964, Ogden et al. 1973). *Echinometra lucunter* lives in holes or burrows, rarely moving more than a few centimeters at night. A considerable portion of its diet consists of algae captured raptorially from the drift. The spatial separation necessary for this type of feeding is maintained by aggressive behavior (Grünbaum et al. in press). It may overlap in distribution with *Diadema antillarum* in some cases, but is generally confined to wave-washed terraces and reef tops (Abbott et al. 1974). *Tripneustes ventricosus* and *Lytechinus variegatus* are commonly associated with seagrass beds. *Tripneustes* feeds exclusively as a browser on seagrasses and associated macroalgae (Keller 1976, Ogden & Abbott unpubl.). *Lytechinus* is a more generalized feeder and can eat *Thalassia* and macroalgae as well as sand and detritus (Keller 1976).

Feeding preferences have been shown in some of these urchins. *Diadema antillarum* fed upon many algae species in approximate relationship to their abundance on reefs, but some species were avoided, no-

Table 3. Habitat, foraging strategy and preferred food of common Caribbean Sea urchins.

Urchin	Habitat	Foraging strategy	Preferred plants* (genera)	Authority
<i>Diadema antillarum</i>	Reef to 10 m; occasionally found in aggregations in sandy areas	Mobile; generalist; capable of browsing, grazing hard carbonate surfaces, and sand feeding	<i>Herposiphonia</i> , <i>Jania</i> , <i>Thalassia</i>	Ogden, Abbott, & Abbott 1973; Ogden 1976
<i>Echinometra lucunter</i>	Reef to 10 m; most abundant in burrows in wave-washed reef and beachrock	Sedentary; movement restricted to burrow mouth; feeds on drift and attached plants	<i>Dictyota</i> , <i>Jania</i> , <i>Thalassia</i> (drift)	Abbott, Ogden & Abbott 1974
<i>Lytechinus variegatus</i>	Seagrass beds and sandy areas	Mobile; generalist; capable of browsing and sand feeding	---	---
<i>Tripneustes ventricosus</i>	Seagrass beds to 10 m; occasionally on reefs with heavy growth of macroscopic algae	Mobile; diet restricted to seagrasses and macro-algae	<i>Thalassia</i> , <i>Syringodium</i>	Abbott & Ogden (unpubl.)

* Preferences based on percentage of algal species in stomach contents per percentage occurrence of the plant in the habitat.

tably *Penicillis* sp., *Sargassum* spp., *Turbinaria turbinata*, and *Laurencia obtusa* (Ogden et al. 1973, Ogden 1976). When preliminary field preference tests were performed an avoidance of *Laurencia*, *Sargassum* and *Halimeda* was noted (Ogden 1976). The factors involved in this selection are not known, but all of the avoided plants grow abundantly in the presence of urchins. *Penicillis* and *Halimeda* are heavily calcified, *Sargassum* is fleshy and stiff and contains tannins (Ogino 1962), and *Laurencia* is fleshy. Abbott & Ogden (unpubl.) analyzed the diet of *Echinometra lucunter* feeding on attached plants and plants captured from the drift. The urchin showed strong avoidance of *Dictyopteris*, *Sargassum*, and *Chondria*.

Vadas (1968, in press) has shown strong feeding preferences in the temperate sea urchins *Strongylocentrotus drobachiensis* and *S. franciscanus*. Both species prefer the brown alga *Nereocystis luetkeana* and appear to avoid *Agarum fimbriatum*. Feeding preferences did not correlate with caloric content but did correlate strongly with absorption efficiencies, the preferred species being absorbed with greater efficiency by the urchins. Growth and reproduction (gonad index) correlated with the preference rankings. The most preferred species gave the greatest growth rates and gonad indices. Vadas concludes that the urchin preferences lead to an optimization of fitness as measured by growth and reproduction.

Herbivore-plant relationships

Plant distributions

There is abundant evidence that plant distributions in coral reef areas are influenced by grazing and browsing fishes and invertebrates. Reef surfaces usually appear bare and often the tooth marks of fishes and invertebrates can be seen. On closer examination the surface is covered with a thin mat of filamentous algae and the carbonate surface may be extensively pitted with boring forms. A number of studies have used herbivore exclusion cages and in almost every case rapid growth of benthic algae within the cage occurs (Stephenson & Searles 1960, Randall 1961, Earle 1972, Mathiesson et al. 1975). Heavy growths of benthic algae occur where fishes have difficulty feeding, such as the tops of wave washed reefs or intertidal regions or in areas of the reef devoid of shelter. Seagrass beds where they contact reefs in the Caribbean are heavily grazed up to 10 meters from the reef and a characteristic 'halo zone' may develop (Randall

1965, Ogden, Brown & Salesy 1973). Exploitation of beds further from reefs is limited to small resident species capable of hiding in the seagrasses. Large predators such as barracuda and mackerel may be responsible for this pattern by restricting the movements of small fishes (Earle 1972, Ogden & Zieman 1977).

Adey et al. (1976) have described 'fleshy algal pavements' on the Atlantic sides of high islands such as Martinique in the Lesser Antilles in the Caribbean. Dense masses of fleshy algae (up to 4 kg wet wt. m⁻²), including *Sargassum*, *Gracilaria* and many other species, are present from near the surface to 10 to 20 m deep. The algae grow on a pavement of crustose coralline algae covering an *Acropora* framework and may be near a normal live *Acropora palmata* reef with a dense population of grazers. The development of the pavements is open to speculation. A local disturbance such as a storm may have destroyed a section of the original *Acropora* reef. This would destroy habitats utilized by reef grazers, particularly the sea urchin *Diadema* and also herbivorous fishes. The elevated nutrient levels present in the area may have allowed relatively rapid and sustained growth of algae; the grazers could have been prevented from recolonizing by the heavy surge and deep wave base characteristic of the Atlantic coasts of the Antilles. The new equilibrium state attained is quite different from the original reef, and is structurally more similar to a seagrass bed than a coral reef. The fishes occupying the area tend to be those characteristic of seagrass beds (Adey et al. 1976). Fleshy algal pavements are exceptional developments, but they serve as an indication of the balance between herbivory and algal growth characteristic of tropical marine regions.

Community structure

Beginning with the studies of Paine (1966, 1969) and extended by Vadas (1968, 1977), Dayton (1972) and Menge (in press), consumers have been shown to exert a strong effect upon the structure of marine ecosystems. Invertebrate herbivores present in intermediate densities in intertidal and subtidal areas in the temperate zone consume the fastest growing and most abundant algal species which would otherwise out-compete many slower-growing species. The structure of the system, measured by species diversity, is enhanced by such predation (Paine & Vadas 1969, Menge 1977, Vadas 1977).

Ogden, Brown & Salesky (1973) removed over

encouraging the growth of algal species which are suitable as food. They do not forage for suitable foods and we may expect them to be much more selective and less likely to sample different plant types than such foraging herbivores as the scarids and acanthurids.

Selectivity in the feeding of sea urchins appears to be a compromise between urchin preferences and availability. Sea urchins are mobile, but their movements are much more restricted than fishes. They are non-visual, but appear to be chemosensitive where this sense assists them in locating preferred foods. Vadas (1968, in press) found that *Strongylocentrotus drobachiensis* was strongly attracted to sites where fronds of *Nereocystis* had fallen to the bottom. This preferred food was unpredictably available and the urchins appeared to have a finely developed chemical sense to locate such patches of food. In contrast, *Triplaneustes ventricosus*, which feeds on the superabundant resource of *Thalassia* beds, does not show chemosensitivity to preferred foods in tank or Y-maze tests (Ogden, unpubl.).

The tropical sea urchins are faced with a more diverse food supply than temperate urchins and are relatively incapable of long distance movement and rapid sampling of available foods. These urchins have become generalists in feeding and are capable of getting along on a very wide range of diets. *Diadema*, for example, is capable of feeding on macroscopic plants, algal mats, sand, and will even become carnivorous (Lewis 1964, Ogden et al. 1973). Some preferences are shown, but more dramatic is the tendency to avoid certain genera of algae which then become highly suspect of having strong anti-herbivore defenses.

Conclusions

The preliminary evidence which we have selected and presented here is suggestive of a number of lines of continuing research. Very little is known about the ecology of tropical algal seasonality, reproduction and recruitment, nor especially of the competitive interactions between plant species in reef communities. There appears to be a rich evolutionary interplay between herbivores and algae involving algal structure and chemistry, productivity, and growth habit as well as herbivore feeding strategies and digestive physiology. The herbivores examined in detail so far have shown at least some diet selectivity based on many of these parameters. Detailed studies of herbivore diet, selectivity and sequencing are lacking. Close examina-

tion of the structure, growth, and reproductive strategies of particular algal species in relation to the number of consumers of that species would be very revealing. Herbivores appear to be intimately involved in the community structure of coral reefs; this influence is particularly strong with respect to algal species diversity and the outcome of competitive interactions between algae and stony corals. Manipulations of density of invertebrate herbivores have proven to be very useful in studies of reef community structure. Fishes are less easily manipulated, but the opportunity exists for comparative studies in areas of differing population densities of fish herbivores. Close monitoring of the recruitment of juvenile herbivorous fishes could provide natural experiments in algal-herbivore ecology.

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Questions and answers

Keast: Is the picture of these herbivorous fish much like that in the African ungulate situation, where there is a great amount of actual overlap with certain chosen, favored plants coming through very strongly?

Ogden: There is some beautiful work on the grazing African ungulates and there are some very tempting parallelisms with the Caribbean seagrass system. Caribbean seagrass beds consist of two dominant grasses and a variety of associated algae which are

extensively grazed by a variety of vertebrate and invertebrate herbivores some of which are resident in the beds, some of which venture into the beds short distances from reefs, and others, such as the green turtle, which range very widely. Where we have looked at food preferences, herbivores often show definite preferences for particular components of the vegetation. We are also looking at the influence of herbivores on plant community structure experimentally. Unfortunately we as yet do not know enough to fit our preliminary results into the dynamics of the whole system. One interesting recent observation concerns grazing in seagrass beds by green turtles. Turtles create large patches in the beds by biting off the grasses just above the substrate. The patches persist for several months and appear to be favored areas for fish grazing during recovery.

Brussard: Do any of the algae species that seem to be resistant to generalized herbivore grazing have their own specialist herbivores, analagous to the butterflies in the terrestrial system?

Ogden: Our work has concentrated upon relatively large, mobile herbivores which are clearly generalist feeders. There are some specialist herbivores such as the saccoglossids which eat *Caulerpa* and which are known to concentrate the toxins of the alga, but these specialists are not prominent. Our preliminary data indicate that the generalist herbivores must mix their diets. Where we have conducted feeding experiments with fishes and sea urchins on single plant species, some produce significantly lowered growth rate and others are toxic.

Dale: One slide you had of *Laurencia* with the red tips on its branches made me think that possibly a fish might mistake that for a *Condylactis* anemone, and that might be a mimicry there. Is that conceivable?

Ogden: The picture I showed was quite magnified and the alga is much smaller than the anemone. However, your question brings up an interesting point. Where terrestrial plants are known to be defended by toxic chemicals, we know that these can occur in specific parts of the plant. It is not inconceivable that an alga could advertise its defended parts with striking coloration.

Earle: A special circumstance that may interest the authors exists in the Galapagos Islands and is the subject of research that I have underway at present. Herbivorous fishes, urchins, and in some areas, iguanas,

are conspicuous and abundant in warm surface waters. Volcanic rock substrate is devoid of plants or hosts fast-growing filamentous species or kinds that are not favored as food (including *Sargassum* and certain red algae). A thermocline with a 6° C temperature difference (17° vs 23°) occurs in depths ranging from 20 to 40 m. Below the thermocline, plants are far more abundant and fish herbivores are rare. Algae regarded as 'cold water species' flourish in the colder water, including species of *Desmarestia*, *Laminaria*, *Eisenia*, and numerous large fleshy Rhodophyta.

In the tropics, temperature is rarely as conspicuously influential in shaping plant and herbivore distribution as in this special case, but it is a factor that should be considered in concert with light, substrate, etc.

I would like to question the conclusion that 'large-celled macroscopic algae appear most susceptible to all these herbivores, while small-celled algae are possibly least utilized by fishes.' The circumstances are more complex than this generalization implies, so much so, that I think it should be re-evaluated. Species of *Halimeda* have large cells and are calcified except in the youngest stages, and are favored food of parrotfishes. The related genus *Avrainvillea*, not calcified, and species of *Penicillus* (some calcified, some not) curiously are seldom eaten. Filamentous algae — such as species of *Dasya* (red), *Giffordia* (brown), and *Cladophora* (green) tend to have smaller cells, but may also be more 'digestible'. They seem to be readily consumed by various fish herbivores. Some large-celled uncalcified green algae that appear not to be favored as food are species of *Valonia*, *Dictyosphaeria*, and *Microdictyon*. The question is an intriguing one and the point about cells large enough to be macerated and thus more readily digested is a good one. But I feel there are too little data about circumstances too variable to make valid generalizations at this time.

Lobel: My original suggestion [concerning cell size and utilization] was based upon the assumption that fishes are dependent upon the use of dentition, a muscular stomach, or a pharyngeal mill for release of plant cytoplasm from the confines of a cellulose cell wall. A fish should choose a plant based on relative fish-plant morphologies; this is consistent with existing data on the morphology and physiology of herbivorous reef fishes and has been the working hypothesis in my research. Where the observed results differ from the expected based purely on morphological

grounds, we will be led, hopefully, to the discovery of new mechanisms by which fishes cope with plants as food or a reason why fish did not choose a supposedly optimum food (i.e. plant defense mechanisms). We said that cellulases have not yet been found in reef fishes and fish are, therefore, more dependent upon morphological than chemical mechanisms. I will briefly provide one example and one counter-example as points in discussion. These are the results of my current research efforts and will be presented in detail elsewhere (Lobel, in prep.).

First, the counter-example. According to my fish morphology-plant selectivity scheme, herbivorous damselfish (Pomacentridae) should feed preferentially off large celled algae. However, this is clearly *not* the case for the Caribbean *Eupomacentrus planifrons* which feeds principally upon epiphytic blue-green algae growing within its territory (probably *Oscillatoria* sp., mean volume in diet $55 \pm 44\%$, $N = 23$, Lobel, unpubl., and D. R. Robertson, pers. comm.). Utilization of this algae by the damselfish is not explainable using the morphological relationship model. The blue-green algae are of very small relative cell size. This led me to examine other potential digestive strategies, such as the role of pH in the stomach. *E. planifrons* has one of the most acidic stomachs ($\text{pH } 2.38 \pm 0.54$, $N = 12$) I have found among 27 species of Pacific and Caribbean herbivorous fishes. These results strongly suggest a unique alternative digestive mechanism similar to that of the cichlids we mentioned earlier.

Secondly, an example of morphologically based feeding selectivity. We have evaluated the basis for food selection by the Caribbean bucktooth parrotfish, *Sparisoma radians*. Under field conditions, *S. radians* frequently took bites of *Halimeda incrassata*, yet this alga composed only 2 to 3% of a fish's total food intake. In laboratory preference experiments, *H. incrassata* and *Penicillus pyriformis* were the *least* preferred food of nine plants tested. The basis for plant selection in this case was not a function of relative plant cell size (as the model predicted) but was instead correlated with how easily the fish could bite and grind its food. Scarids are unique among herbivorous reef fishes: they can thoroughly macerate food in a pharyngeal mill apparatus. *Halimeda* is heavily calcified and may be 'difficult' and energetically more costly for the fish to handle. This has been demonstrated by calculation of amount of food value per unit effort (incorporating measures of absorption efficiencies, plant toughness, etc.) and by measuring comparative growth of the scarid on single and mixed diets. The results show that while *Halimeda*

was often sampled in the field, it is not a significant nutritional resource for this scarid. However, this does not discount *Halimeda*'s potential value as a supplementary dietary item for essential vitamins and/or minerals.

Another example of algae with very large individual cells are *Caulerpa* spp., which possess a toxin known to affect humans; they are generally avoided by fishes. It appears that both *Halimeda* and *Caulerpa* would be prime food for herbivores were it not for their effective anti-herbivore adaptations. I should mention that neither alga is totally immune to being eaten; Earle is, of course, correct in that *Halimeda* is eaten by some parrotfishes, and *Caulerpa racemosa* is eaten by the Pacific angelfish, *Centropyge flavissimus* (pers. obs.). Thus, these various algal defense mechanisms may function to deter some but not necessarily all herbivores.

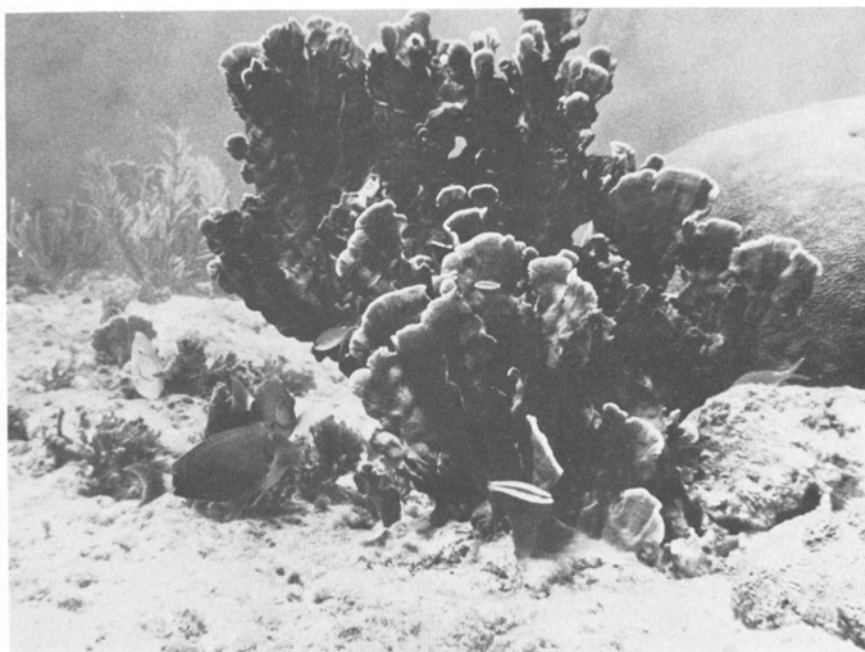
Admittedly, the basic model relating fish and plant morphologies has its limitations. Even so, I have found it to be an effective scheme in which to examine herbivorous fish and plant relationships.

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The photographs were taken in 1965 at Rincon de Guanabo (Cuba) by E.K. Balon.