

QUANTIFYING HERBIVORY ON CORAL REEFS:
JUST SCRATCHING THE SURFACE AND STILL BITING OFF
MORE THAN WE CAN CHEW

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ABSTRACT

Herbivory was quantified using six different techniques simultaneously at nine discrete sites along a coral reef system on the Caribbean island of St. Croix. In order to study diverse assemblages of herbivores and algae, functional groups were used for both. The groups are based on shapes and structural properties of the algae and feeding capabilities of the herbivores.

Herbivory was most frequent and intense in the shallow forereef sites where an average of over 5,000 herbivorous fish bites per meter square per hour was recorded. Although most of these were from herbivorous fishes that do not denude primary substratum (i.e., small damselfishes), this site also had the highest frequency of grazing from herbivores capable of denuding (i.e., yellowtail damselfish and tangs) and excavating the calcareous substratum (parrotfishes, urchins and limpets). Herbivory from all sources decreased in backreef, shallow algal ridge, and deep wall-reef habitats. The latter sites had the lowest levels of grazing.

Herbivory on macrophytes was assessed using a Thalassia bioassay technique but the results at the forereef sites contradicted those of all other techniques. Caution is suggested in applying this technique as a single measure of herbivory.

INTRODUCTION

The process of herbivory is generally thought to be of primary importance to the distribution and abundance of benthic algae on coral reefs (reviewed by Lubchenco and Gaines 1981). While the units of measure and methods for determining the abundance of algal prey are well established, no such convention exists for determining the impact of their herbivorous predators. Measurements of percent cover, biomass, or number of individuals when applied to assemblages of reef dwelling herbivores are of dubious meaning for quantifying herbivory. For instance, how many foraging urchins equal the impact of a 20 kg parrotfish? The "apples and oranges" involved here result from trying to force units and techniques which are designed to determine patterns in herbivore abundance on the process of herbivory.

Ecological processes are factors that result in observed patterns. It is generally assumed that the abundance of herbivores corresponds with their impact on algae. This assumption has never been tested. In this paper, I will report on several techniques used simultaneously on a single reef system in order to measure the impact of a diverse assemblage of herbivores on an assemblage of reef-dwelling algae. I will also provide an argument for considering this topic at a "functional group" level so that herbivores with similar effects and algae with similar ecological properties are treated together.

ORGANISMS, STUDY SITES, AND METHODS

Functional Groups

Since herbivory involves the interaction of two diverse groups of organisms, "functional group" subdivisions will be used. Algae have been subdivided into such groups based on shared anatomical and morphological characteristics (see Littler and Littler 1980, Steneck and Watling 1982). For the purposes of this paper, I will simplify these subdivisions to three groups: 1) ALGAL TURFS (diverse, microscopic

filaments; e.g., Polysiphonia, Spacelaria, and Taenioma), 2) MACROPHYTES (larger, more ridged forms; e.g., Laurencia, Dictyota, Jania, and Asperogopsis), and 3) ENCRUSTING CORALLINES (calcareous algal crusts; Porolithon, Neogoniolithon and Paragoniolithon). Note that the "turfs" referred to here follow Neushul 1967, Randall 1967, Dahl 1972, John and Pople 1973, Van den Hoek *et al.* 1975, Adey *et al.* 1977, Benayahu and Loya 1977, Pichon and Morrisey 1981, but not Hay 1981a). Among the ecological properties correlated with algal functional groups (and this simplified scheme) is toughness of the thallus. From an herbivore's perspective turfs are easiest to consume, macrophytes intermediate and coralline crusts most difficult (Littler and Littler 1980, Steneck and Watling 1982, Littler *et al.* 1983).

Herbivores fall into three categories with respect to grazing (Steneck 1983, see Table 1 for species): 1) NON-DENUDING (those incapable of, or unlikely to, denude the substratum of algae; e.g., some damselfishes [Eupomacentrus], amphipods and polychaetes; Brawley and Adey 1977, Kaufman 1977), 2) DENUDING (those that denude the substratum of turfs and smaller macroalgae but are incapable of excavating corallines and large leathery macrophytes; e.g., yellowtail damselfish [Microspathodon], tangs [Acanthurus] several non-limpet archaeogastropods and mesogastropods; Randall 1967, Jones 1968), and 3) EXCAVATING (those capable of consuming even the toughest forms of algae, such as encrusting corallines e.g., limpets [Acmaea], chitons, some regular echinoids [Diadema] and parrotfishes [Scarus and Sparisoma]; Randall 1967). For a more complete discussion of these categories see Steneck 1983.

Study Sites

This study was conducted at nine sites in three locations along the north shore of St. Croix (Fig. 1). The locations were selected as representative of three common reef types in the Caribbean 1) Algal Ridge (Boiler Bay), 2) Bank barrier-reef (Tague Bay), and 3) Deep wall-reef (Salt River Canyon). All three are geographically close to one another, thus giving them about the same exposure to light, destructive storms and recruitment events.

The predominant algal growth form at the bank-barrier and deep wall-reef sites are turfs with an average canopy height of 2mm. Turfs are highly diverse with about 30 to 50 species found in an average four square centimeter area (Adey and Steneck in ms.). Species composition is temporally variable with up to an 80% change in community dominance every 3-4 months (Steneck in prep.). Patches of encrusting coralline algae are also scattered throughout. Macroalgae are only abundant in places at the algal ridge site (see Connor and Adey 1977).

At each site, circular slabs of coral (1 cm thick, and 10 cm diameter) were placed on racks and affixed to the reef (locations and depths in Fig. 1). The plates were placed in December of 1979, and most of the experiments were conducted more than three years later from March to May 1982. At the time of the experiments, the coral plates had the same algal community structure, canopy height, and biomass as the surrounding substrata. All the plates at the nine stations were covered with the same (algal turf) functional group. Details of specific experiments are described below where appropriate.

RESULTS AND DISCUSSION

To reduce some of the variables related to herbivory, the study was conducted at one spot and at one time at each of the nine sites. Several of the experiments ran simultaneously, focusing on the same six (100 to 200 cm sq.) planar coral plate surfaces or their surrounding areas.

TABLE 1
HERBIVORES OBSERVED IN THIS STUDY

NON-DENUDING HERBIVORES

FISHES:	REFERENCES
<u>Eupomacentrus dorsopunicans</u> (dusky damselfish)	Randall 1967, Pers. Obs.
<u>Eupomacentrus planifrons</u> (threespot damselfish)	Brawley and Adey 1977, Kaufman 1977
<u>Eupomacentrus variabilis</u> (cocoa damselfish)	Randall 1967, Pers. Obs.
<u>Eupomacentrus leucostictus</u> (beaugregory)	Randall 1967, Pers. Obs.
GASTROPODS:	
<u>Fissurella angusta</u> (keyhole limpet)	Steneck and Adey 1982

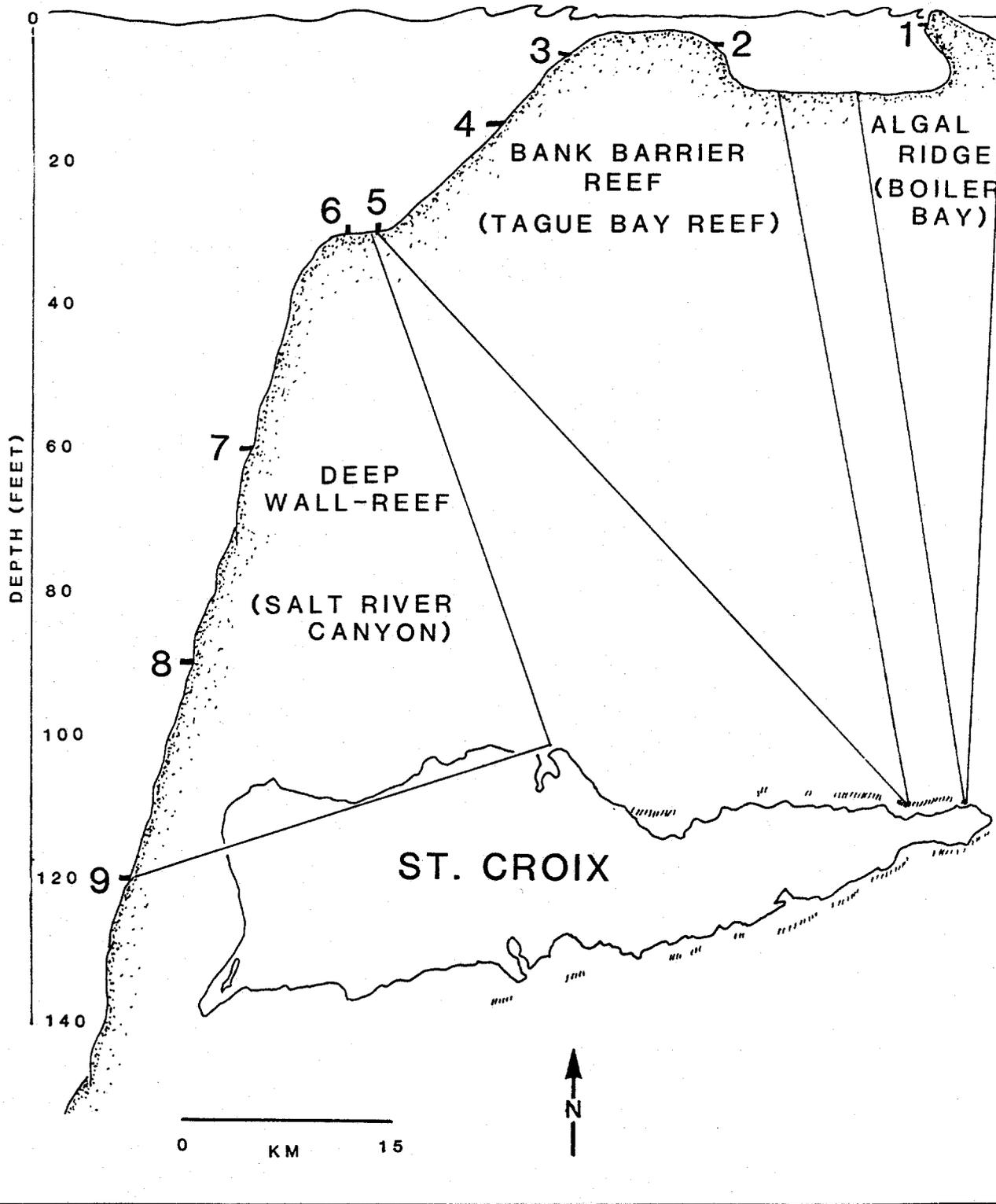
DENUDING HERBIVORES

FISHES:	REFERENCES
<u>Microspathodon chrysurus</u> (yellowtail damselfish)	Randall 1967, Steneck 1983
<u>Ophioblennius atlanticus</u> (redlip blenny)	Randall 1967, Steneck 1983
<u>Acanthurus bahianus</u> (ocean surgeon)	Randall 1967, Steneck 1983
<u>Acanthurus coeruleus</u> (blue tang)	Randall 1967, Steneck 1983

EXCAVATING HERBIVORES

FISHES:	REFERENCES
<u>Scarus croicensis</u> (striped parrotfish)	Randall 1967, Steneck 1983
<u>Sparisoma chrysopterum</u> (redtail parrotfish)	Randall 1967, Steneck 1983
<u>Sparisoma viride</u> (stoplight parrotfish)	Randall 1967, Steneck 1983
ECHINOIDS:	
<u>Diadema antillarum</u> (long-spined sea urchin)	Steneck 1983
GASTROPODS:	
<u>Acmaea pustulata</u> (limpet)	Steneck and Watling 1982, Steneck 1983

FIGURE 1. Diagrammatic composite representation of reef transects along the north of St. Croix. Numbers correspond to study sites in Table 2.



Observing Herbivory

Quantifying fish grazing employed two methods. The first involved watching each rack of six coral plates at each station for five-minute intervals several times a day and recording which species fed on them. The second method is identical to the first except that an underwater time-lapse movie camera takes the place of a diver. Each movie lapses between 10 and 12 hours and generates 3600 observations (frames). During the movies, divers avoided the area except to simultaneously count fish bites over a few five minute intervals. Since the plate areas are known, the number of bites per square meter per hour can be determined for both techniques.

Fish grazing was greatest in shallow forereef habitats and least at depth (Table 2). Mean grazing frequencies of over 5,000 bites per meter square per hour were recorded using visual and time-lapse techniques in 1982 and visually in 1981. At the algal ridge and bank barrier-reef sites grazing was predominantly from non-denuding herbivores (i.e., Eupomacentrus). This group of damselfishes (four species) accounted for 72% (± 30) and 50% (± 22) of the bites observed at this site visually and on film, respectively. Pomacentrid grazing on the deep wall-reef was relatively low (6% ± 12). Denuding herbivores (particularly Microspathodon) were most abundant at the mid-depth forereef site. Excavating herbivores (Scarus and Sparisoma) were most abundant at the shallow forereef site. Juveniles of this group were the primary herbivores at the deep wall-reef sites.

It is difficult to determine why a better correspondence between visual and time-lapse movie techniques does not exist, since both were conducted at the same time (Table 2). Time-lapse, of course, gives high resolution data over an entire day whereas visual techniques give high resolution over only short intervals spread over several days. The latter technique also requires the presence of a human observer which may suppress normal grazing frequencies during the observation period.

Invertebrate herbivores are easier to count, but more troublesome to actually observe feeding since their mouths are under their bodies. Since they have reduced mobility, their range of grazing influence is relatively restricted. Thus, some indication of their impact can be assessed by determining their population density in a given area.

Excavating invertebrate herbivores (i.e., echinoid Diadema and limpet Acmaea), are most abundant in shallow forereef environments (Table 2). In fact, the two shallowest forereef stations have more echinoids per area than all seven other stations combined. Limpets were only found at the shallowest station.

Impact of Herbivory:

The impact of herbivory requires studying the plants being eaten. Because different functional groups of algae have different structural and morphological properties that contribute to the rate at which they are consumed (discussed above), I will treat three functional groups of algae differently.

In terms of areal coverage, minute turfs are the most abundant algal form on coral reefs. They are impossible to handle without damage so all turf experiments and observations were confined to the coral plates.

To determine herbivore impact on turfs, the rate of biomass loss to herbivores was studied. For this, a set of six plates at each depth (at the deep wall-reef site) was suspended in the water column at the depth they had been growing in for the past three years. An identical set of plates remained on the benthos. No herbivores were observed grazing the suspended plates (nor was there any evidence of grazing using other techniques (i.e., Thalassia bioassay technique, described below). Table 2 shows that there is a steady (nearly linear) decline in the rate of turf algae biomass loss to herbivores with depth. Assuming that the productivity of suspended plates equals that of the benthic plates, the difference in algal biomass after a period of 6 days should indicate the amount of algal biomass that is eaten during that period. Negative numbers indicate that algal growth rate exceeds the

TABLE 2
COMPARISON OF RESULTS IN MEASURING HERBIVORY

STATION NUMBERS	1	2	3	4	5	6	7	8	9
DEPTHS (FEET)	0.5	3.5	5	15	30	30	60	90	120
----- HERBIVORY (BITES/M ² /H) FROM:									
Non-Denuding Fishes									
Visual Obs. 1981	0	0	3,269	170	28				
Visual Obs. 1982	448	273	518	147	230	0	94	0	0
Time-lapse 1982	7,061	1,567	3,325	1,630	1,151				
-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
MEAN	2,503	613	2,371	649	470	0	94	0	0
Denuding Fishes									
Visual Obs. 1981	3	0	2,774	170	28				
Visual Obs. 1982	0	0	532	193	48	39	12	0	0
Time-lapse 1982	936	2,687	0	4,326	1,151				
-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
MEAN	313	896	1,102	1,563	409	39	12	0	0
Excavating Fishes									
Visual Obs. 1981	0	0	2,476	0	0				
Visual Obs. 1982	0	0	27	0	0	79	282	235	0
Time-lapse 1982	0	0	2,660	0	0				
-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
MEAN	0	0	1,721	0	0	70	282	235	0
Total Herbivory From Fishes									
Benthic Plates	2,816	1,509	5,194	2,212	879	118	338	235	0
Suspended Plates						0	0	0	0
Excavating Invertebrates (No/m ²)									
<u>Diadema</u>	0.8	3.8	14.3	17.5	3.9	0.2	0.3	0.5	0
<u>Acmaea</u>	0	0	2	0.3	0	0	0	0	0
----- GRAZING IMPACT ON:									
Algal Turfs (g dry/m ² /day)									
Rate of Turf Biomass Loss						2.8	1.35	0.933	-0.79
Macrophytes (% <u>Thalassia</u> eaten/day)									
On benthos	2.04	14.9	1.45	0.74	49.8	25.2	10.1	3.0	0.69
On Plates	4.8	0.004	1.6	0.79	37.4	16.0	2.2	3.4	1.5
Suspended Plates						0	0	0	0
% Grazed by Fish	100	95	50	50	96	98	100	100	90
Corallines									
% Coralline Grazed	0.6	54.2	82.7	48.0	44.6				
% Grazed by Urchins	0	26.6	57.9	42.0	28.0				

NOTE: Blanks indicate no data

herbivore grazing rate.

Macrophytes are not usually abundant on reefs. In the study areas, macrophytes were most abundant in the intertidal zone of the algal ridges at Boiler Bay (e.g., Gracilaria, Laurencia, Gelidiella, Dictyota and Acanthophora) and to a lesser extent on the Acropora cervicornis in the sand plain in front of the forereef sites (e.g., Asparagopsis, Dictyota and Laurencia). A scattering of macroalgae can also be found at the backreef site (e.g., Acanthophora, Laurencia and Dictyota).

To determine grazing pressure on macrophytes, a Thalassia bioassay technique of Hay (1981b, and Hay et al. 1983) was used. For this, five centimeter long blades of Thalassia were placed in clothes pins. The blades were checked every several hours to determine the amount grazed by herbivores. Bite marks were interpreted as to whether they were from parrotfishes (semicircular bites) or urchins (a shredded appearance) (See Fig. 2 in Hay et al., 1983). At each station, eight blades of Thalassia were affixed to the rack of coral plates and an additional 20 were scattered nearby on the bottom.

The rate of Thalassia loss was greatest at the deepest forereef station (for both those scattered on the bottom and attached to the rack; Table 2). The next highest rate of loss at the Tague Bay stations was in the backreef. In this case however, only those scattered on the bottom were heavily grazed. The deep wall-reef sites showed a consistent decrease in Thalassia grazing with depth. None of the suspended Thalassia blades were grazed.

Nearly all grazing marks were attributable to parrotfishes. No urchin marks were identified on Thalassia blades attached to the racks of coral plates. At benthic stations, however, a few urchin marks were observed. The highest proportion of urchin marks occurred in the shallow forereef stations of the Tague Bay locations (where urchin densities were highest). The 10% urchin bites recorded for the 120' station represents only one urchin-looking bite out of 10 recognizable bites. It is probably an error since no urchins were found below 90'. Other shredding herbivores such as crabs could have been responsible for the marks.

The pattern of Thalassia loss across the Tague Bay reef is opposite that of all other measurements of herbivory. There is no indication from other measures (Table 2) that the deep forereef, and to a lesser extent the backreef, receive as high a rate of predation as the Thalassia bioassay suggests. Conversely, all other techniques indicate that the two shallow forereef stations are most heavily grazed by all herbivore groups rather than minimally grazed as the Thalassia bioassay indicates. There is no question, however, that whatever the Thalassia bioassay measures, it does so consistently and repeatably. It is possible that fishes with a search image for Thalassia, or other conspicuous macrophytes of sand flats or lagoons, are attracted to the Thalassia of this experiment and consume it at a rate unrepresentative of overall grazing rates on the reef.

Relatively few herbivores are capable of excavating crustose coralline crusts (discussed in detail in Steneck 1983). Since crusts can "erase" most graze marks as they grow undisturbed for 10 to 30 days (depending on the depth of the injury and the growth rate of the coralline), marks on corallines are a rough indication of the rate of grazing by excavating herbivores. In addition, the bite marks of the major groups of excavating herbivores (i.e., parrotfishes, urchins, limpets and chitons) are readily identifiable. The pattern of graze marks among excavating herbivores indicates that the greatest grazing pressure occurs in the shallow forereef. Data were not collected for the deep wall-reef site. Overall urchin grazing was most conspicuous on the crusts, with the proportion of graze marks generally corresponding with the abundance of urchins in the area (Table 2).

Patterns of Herbivory on Reefs

Herbivory is greatest in shallow forereef habitats and reduced in shallow algal ridge and backreef habitats. The reduced herbivory around massive algal ridges is likely due to the absence of habitat and refuge space in those environments coupled with the characteristic turbulence (discussed in Steneck and Adey 1976). Backreef habitats are an enigma. They consistently indicate lower levels of grazing (both intensity and frequency) but no simple explanation can be offered. The decrease in herbivory with depth is not surprising since the trophic carrying capacity for herbivores probably diminishes with depth as a function of reduced benthic productivity (Steneck in prep.).

Ecologists are far from agreeing on a method (or methods) for measuring herbivory on reefs. While this does not seem to inhibit publications on the subject, comparisons between reefs are impossible. The simplest and most easily replicated technique, the Thalassia bioassay, is of dubious meaning and must be examined critically in other comparative studies before its general application can be accepted (see Hay 1983 for caveat). The only clear message revealed in this study is that quantifying a process is infinitely more difficult than quantifying patterns in the abundance of herbivores. So far we have only scratched the surface and still we are biting off more than we can chew.

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