Browsing patterns of herbivorous fishes in a

*Halodule uninervis* seagrass bed of a

Pacific island coral reef (Guam, Micronesia)

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ABSTRACT: Browsing patterns of herbivorous fishes were investigated in a seagrass bed (*Halodule uninervis*) near Guam (Micronesia). Artificial reefs of three sizes were set out to determine 1) if browsing is greater around reefs than in the open seagrass, and 2) if browsing pressure is related to reef size. Browsing levels around the two smaller reefs were similar to that recorded in the open seagrass. Fish browsing activity was greater around the largest reef, and a nearly barren sand halo was created within 80 days. Changes in hydrography due to the presence of the largest reef was not a factor in halo formation. Fishes were also demonstrated to concentrate browsing in sheared areas which were similar to developing sand halos. Seagrass preference experiments tested whether fishes preferred epiphytized or nonepiphytized blades of *Halodule uninervis*. The results indicated that fishes overwhelmingly preferred nonepiphytized blades. When sheared-area and preference results are considered collectively, it is apparent that browsers preferred younger *Halodule* blades. Halo formation is greatly influenced by reef-size threshold and browser preferences for nonepiphytized seagrass.

Title: Browsing Patterns of Herbivorous Fishes in a *Halodule uninervis* Seagrass Bed of a Pacific Island Coral Reef (Guam, Micronesia).

Approved: [Signature]

Charles E. Birkeland, Chairman, Thesis Committee

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apparent that browsers preferred younger *Halodule* blades. These results are supported by foraging theory. Halo formation is discussed in terms of reef-size threshold and browser preferences for nonepiphytized seagrass.
BROWSING PATTERNS OF HERBIVOROUS FISHES IN A
HALODULE UNINERVIS SEAGRASS BED OF
A PACIFIC ISLAND CORAL REEF (GUAM, MICRONESIA)

By

PAUL D. GATES

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University of Hawaii Sea Grant College Program

Project: Are Population Densities of Herbivorous Reef Fishes Determined by the Productivity of the Habitat?

Project no.: UG/R-7
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INTRODUCTION

The role of herbivory in seagrass beds near Caribbean coral reefs has been studied intensively (Randall 1965, Ogden et al. 1973, Ogden and Zieman 1977, Ogden and Lobel 1978, Lobel and Ogden 1981, Tribble 1981, Hay 1984). Particular interest has focused on the conspicuous bare strips of sand or sand halos which separate reefs from seagrass beds. The origin of these seagrass-free zones has been a point of contention. Initial observations implied that these seagrass-free strips resulted from daytime browsing of reef-based herbivorous fishes, particularly scarids and acanthurids (Randall 1965, Earle 1972). However, later work concluded that sea urchins were the primary agents of halo formation (Ogden et al. 1973). Although this evidence linked herbivory by fish and urchins to halo formation, Ogden and Zieman (1977) cautioned researchers not to overlook the role of physical factors. They demonstrated that seagrass-free zones surrounding reefs could arise entirely by the action of physical forces.

It was pointed out by Hay (1984) that many of these early studies on herbivory were conducted in heavily overfished areas where urchins were extremely abundant. These two features might limit the general applicability of any conclusions concerning seagrass herbivory derived from work at these locales. Furthermore, most early investigations assessed the impact of herbivory by either urchins or fishes, but not both. In light of this, recent
research has addressed the relative impact of seagrass browsing by both urchins and fishes (Tribble 1981, Hay 1984).

Also, recent information has been collected over a much greater area, although still limited primarily to the Caribbean. Tribble (1981) focused on three locations along a single reef in the San Blas islands, while Hay (1984) examined herbivory on numerous reefs over a variety of reef zones. Both investigators reported that browsing by herbivorous fishes was significantly more important than herbivory by urchins in creating and maintaining seagrass-free zones around undisturbed reefs. These results contrasted sharply with those from reefs in overfished waters where much of the earlier work took place.

Biogenic creation of sand halos is not the only aspect of seagrass herbivory which has attracted comment. Observations made during field studies have frequently indicated that most seagrass browsing appears to be concentrated on the tips of heavily epiphytized blades (Ogden and Lobel 1978, Ogden 1980, Lobel and Ogden 1981, Ogden and Ogden 1982, Zieman 1983, van Montfrans et al. 1984). For the most part, however, herbivore preferences, whether between epiphytized or nonepiphytized blades of the same seagrass species or between blades of different species, have not been rigorously tested. In fact, most studies have used only Thalassia testudinum as an assay material for seagrass herbivory. The two notable exceptions
are the efforts of Lobel and Ogden (1981) and Tribble (1981). Lobel and Ogden (1981) demonstrated through laboratory experiments that the bucktoothed parrotfish *Sparisoma radians* preferred blades of *Thalassia testudinum* with epiphytes over a variety of other seagrass types. Tribble's (1981) field studies in the San Blas islands revealed that reef-based herbivorous fishes preferred manatee grass (*Syringodium filiforme*) over *Thalassia*. The preference by fishes for *Syringodium* was responsible for maintaining near-reef zonation of the two seagrasses.

Present knowledge of herbivory in tropical seagrass beds has originated almost entirely from studies in the Caribbean. Perhaps this fact has led to general acceptance of the idea that seagrass feeding in fishes is confined almost exclusively to that region (Ogden and Zieman 1977, Ogden 1980, Ogden and Ogden 1982, Zeiman 1983). Although often stated, this conclusion seems premature, particularly considering the paucity of seagrass studies in the Pacific (Hoese 1978). Until recently, contributions on seagrass-feeding fishes in the Pacific have originated in the temperate waters of Japan (Kikuchi 1974) and southern Australia (Bell et al. 1978). Ogden and Ogden's (1982) work on seagrasses in Palau represents the first study which, at least in part, targeted seagrass browsing by herbivorous fishes in the tropical Pacific.

The present research investigates seagrass browsing by herbivorous fishes in a *Halodule uninervis* bed in the
tropical Pacific. Few seagrass studies have emanated from this region, and none have detailed herbivory on this seagrass species. Research objectives were to determine 1) whether fishes concentrate browsing around artificial patch reefs, and 2) if patch reef size is a partial determinant of browsing pressure. In addition, preference experiments were designed to test the often-reported impression that most browsing of seagrasses is concentrated on heavily epiphytized blade tips.
MATERIALS AND METHODS

Study Site

Field work was conducted exclusively in the seagrass bed which lies approximately 200 m offshore and roughly parallel to the northern lagoonward coast of Cocos Island. Cocos Island is situated 3.2 km southwest of Guam, Mariana Islands, inside a barrier reef system which is contiguous with the island of Guam (Fig. 1). The seagrass bed consists primarily of a vast monotypic stand of *Halodule uninervis* interspersed with small stands of *Halophila minor*. Water depths throughout the seagrass bed range from 2.0 to 2.5 m.

Perhaps the most important single feature of the study site was that urchins occurred in very low abundance. Therefore, it was not necessary to partition the effects of browsing between urchins and fishes. Fishes were most likely to be responsible for any direct seagrass herbivory.

Browsing-Pressure Experiments

Three artificial reefs were constructed within the seagrass bed to detect whether browsing by herbivorous fishes was greater in areas surrounding patch reefs than in open seagrass areas. In order to study browsing pressure as a function of patch reef size artificial reefs of three sizes were constructed. All reefs were constructed with 20.3 cm x 20.3 cm x 40.6 cm double-hollow concrete blocks. The smallest reef consisted of five blocks in two tiers: three on the bottom and two on the top. The intermediate-
Figure 1. Aerial view of the study site. The photo shows the *Halodule uninervis* seagrass beds just offshore of Cocos Island. *Halos* can be seen.
sized reef was constructed from fifteen blocks arranged in three tiers: seven on the bottom, five in the middle, and three on the top. The largest reef was built with forty-five blocks also in a three-tier configuration: twenty on the bottom, fifteen in the middle, and ten on the top (Table 1).

Permanent 10 x 20-cm quadrats were constructed from plastic rods and equipped with legs. Four quadrats were positioned equidistantly around and 10 cm away from each of the three artificial reefs. Reef quadrats were oriented with one narrow end toward the reef. Four open-seagrass quadrats were placed in the seagrass bed away from any rubble or reeflike structure. All of the quadrats were held stationary just at the substrate surface by embedding the legs within the sand.

Seagrass browsing was evaluated in two ways. The first method provided information on the relative concentration of browsing around each artificial reef and open-seagrass quadrat. The seagrass blades enclosed within each quadrat were counted and then square-cut just below the lowest recognizable bite mark. Blades within each quadrat were reexamined approximately every ten days. On each return visit, the total number of blades within the quadrat and the number of blades containing bite scars were recorded. These data were used to calculate the percentage of blades browsed at each site in order to give an index of browsing pressure. When counts were finished, bite-scarred blades were once
Table 1. Configuration and dimensions of artificial reefs.

<table>
<thead>
<tr>
<th>Site</th>
<th>Total Number of Blocks</th>
<th>Number of Tiers</th>
<th>Number of Blocks per Tier</th>
<th>Circumference (cm)</th>
<th>Reef Height (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef 1</td>
<td>5</td>
<td>2</td>
<td>top 2</td>
<td>171</td>
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<td></td>
<td></td>
<td></td>
<td>bottom 3</td>
<td>220</td>
<td>41</td>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>middle 5</td>
<td>280</td>
<td></td>
</tr>
<tr>
<td>Reef 2</td>
<td>15</td>
<td>3</td>
<td>bottom 7</td>
<td>348</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>top 10</td>
<td>394</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>middle 15</td>
<td>485</td>
<td></td>
</tr>
<tr>
<td>Reef 3</td>
<td>45</td>
<td>3</td>
<td>bottom 20</td>
<td>539</td>
<td>62</td>
</tr>
</tbody>
</table>
again square-cut below the lowest bite mark, and any blades which had sprouted during the preceding ten-day interval were square-cut just below their tips.

Determination of blade-length frequency was the second method used to examine browsing pressure. Seagrass samples were collected at each site on the same days that quadrat data were recorded for that particular site. At each of the artificial reefs, both experimental and control samples were collected. Each of these groups consisted of at least forty stems. The experimental group was haphazardly taken from a band of substrate between 10 and 30 cm surrounding each artificial reef. This interval was identical to that covered by reef quadrats. No stems were collected from inside quadrats. The control stems were gathered haphazardly from an area surrounding the reefs and approximately 3 m distant. Only a single group of forty seagrass stems was collected for the four open-seagrass quadrats, with ten stems taken from the immediate vicinity of each quadrat. Generally two to five, and occasionally six, blades of seagrass are held within a single sheath at the apex of each vertical stem. However, only the length of the longest blade from each stem was used for blade-length frequency analysis. This provided a conservative measure of browsing.

During the later stages of fieldwork it became apparent that the amount of seagrass surrounding Reef 3 was rapidly decreasing, and a sand halo was forming. It seemed
worthwhile to track its rate of progress. Therefore, on the final two collection dates, seagrass blades were sampled at four distances from the reef. The four distances were 10-30 cm, 1, 2, and 3 m. One hundred stems were collected at each distance. Once again, only the length of the longest blade from each stem was recorded. Sampling took place on September 27 and thirteen days later on October 10, 1986.

Sediment Monitoring Procedure

Sediments were monitored at each of the artificial reefs and control quadrats because the presence of artificial reefs might alter regular current patterns which in turn might control local sediment deposition. In some situations novel sediment deposition patterns could produce barren-sand areas around reefs which might be falsely interpreted to be a result of browsing. Sediments were collected at each of the artificial reefs and around the open-seagrass quadrats three times during the course of the study: at the beginning (July 18), at the midway point (August 31), and just prior to termination (October 10). At each reef, four sediment samples were taken on every collection date, and each sample was comprised of four subsamples. Subsamples were taken haphazardly from the 10 to 30 cm band of substrate that surrounded the base of each reef. A single sediment sample, likewise made up of four subsamples, was collected in the immediate vicinity of each of the four open-seagrass quadrats on designated collection
days. All subsamples were taken as cylindrical cores 6.4 cm in diameter and 7.7 cm in depth.

Sediment samples were returned to the laboratory where they were transferred to large finger bowls and allowed to settle. On the following day, as much of the clear supernatant as possible was siphoned off with small diameter plastic tubing. Samples were air-dried outside for about one week and then placed in an airconditioned office and allowed to dry for several additional days. Finally, to insure thorough disaggregation of sediment particles, samples were placed in a drying oven and left overnight at a constant temperature of 105°C. Next, samples were transferred one at a time directly from the drying oven to a nest of seives and then placed in a Ro-Tap and shaken for 12 minutes. Each sediment size fraction retained by individual seives and the bottom pan was weighed to 0.01 g. These data were used to determine the mean grain size for each sample (Folk and Ward 1957, Royce 1970).

Browsing and Production of Barren Areas

An experiment was designed to determine if fishes concentrate browsing in developing barren-sand areas once formation of these areas has been initiated. If this happens, could this constant browsing of seagrass blades eventually produce a seagrass-free patch? The impact of browsing was determined by comparing seagrass blades growing in protected and open quadrats within developing barren-sand
areas. Four 2-m diameter areas were staked out in the seagrass bed isolated from any patch reef structure. Barren-sand areas were initiated by shearing the seagrass in each area to substrate level. Initial trimmings took place on June 15. These areas remained conspicuous for several months. It took until October before a moderate amount of new seagrass growth was present within the experimental areas. The new growth was primarily blades which protruded directly from the substrate. The final browsing experiment was begun October 1. Blades within each experimental area were sheared to substrate level. Browser-exclusion cages 0.25 m² x 25 cm high, constructed from 1.25-cm mesh hardware cloth were anchored at each site. Likewise, a 0.25 m² open area was staked out adjacent to the cage at each location. On October 12, all four sites were examined. The lengths of the seagrass blades growing within the browser-exclusion cages and open areas were measured. All solitary blades were measured, but only the longest blade was measured when more than one blade originated from the same point. Once the measurements were completed, cages were reanchored in their original locations. Eighteen days later, on November 2, the measurement procedure was repeated.

Seagrass Selectivity Experiments

The seagrass preference experiment offered browsers a choice between heavily epiphytized and clean blades of Halodule uninervis (Fig. 2). Test blades were square cut to
Figure 2. Seagrass-clothespin apparatus used to conduct preference experiments. The nonepiphytized blade sample is on the left.
5-cm lengths with a scalpel blade. One end of each seagrass blade was then placed in a wooden clothespin. Each clothespin was coded with indelible ink to indicate the particular class of seagrass that it held. Seagrass clothespins were set out in pairs within a sand halo that surrounded a small limestone boulder. One clothespin in each pair contained a heavily epiphytized seagrass sample while the other contained an epiphyte-free seagrass blade. The paired blades were placed 2 cm apart in the sand. The clothespins were covered with sand so that only the seagrass blades were visible. A total of fifty pairs of seagrass blades were arranged within the sand halo in a fashion that produced three concentric circles and 17 radiations from the central structure. Thus, but for a single exception, each radiation was comprised of three seagrass clothespin pairs: one located near the central structure, a second positioned between the central structure and the sand halo-seagrass interface, and a third which was placed near the outer edge of the sand halo. The preference experiment began at noon and lasted four hours.

The results of the initial preference experiment indicated that fishes significantly preferred one blade class over the other. Therefore, an additional preference experiment was conducted. This procedure tested whether or not fishes were attracted to cut blades. Cut blades conceivably could exude a chemical that induces fish to prefer them over blades with natural tips. The experimental
design was the same employed in the original experiment with one exception. Test pairs were comprised of only the preferred class of blades. One blade was square-cut as previously, while the other test blade had its natural tip intact.

Herbivorous Fish Observations

Throughout the study interval, observations of fishes were made to determine which species browse seagrass. Individuals from these groups were followed and their browsing behavior was recorded. A small mesh fence net and dip nets were used to collect a representative specimen from species noted to forage on seagrass. These specimens were taken to the University of Guam Marine Laboratory for positive identification.
RESULTS

Browsing Pressure

A G-test (Sokal and Rohlf 1981) performed on the quadrat data from the three reefs and open-seagrass sites revealed a highly significant interaction ($P < 0.001$) among browsing pressure (as measured by bite scars), reef size, and time. Browsing pressure was positively correlated with reef size, but the degree of relation was contingent upon the length of time that the reefs had been in place. When browsing was expressed as a percentage and examined on a date-to-date basis, a fair degree of overlap was recorded among Reef 1, Reef 2, and the open-seagrass quadrats (Figs. 5 - 8). Browsing pressure at Reef 3 was consistently higher than that recorded at any other experimental location.

The blade-length data collected adjacent to artificial reefs and open-seagrass quadrats were compared through analysis of covariance. Highly significant differences were detected among both slopes ($F(3,1430) = 93.536, P < 0.001$) and means ($F(3,1433) = 444.35, P < 0.001$) of lines which regressed blade lengths on time. Initially, this seemed to demonstrate that browsing intensity differed detectably from one experimental location to the next. However, when blade-length data for each artificial reef was compared to blade lengths recorded for their respective controls, a somewhat different picture developed. There were no significant differences between experimental and control
Figure 3. Histograms of data from open-seagrass quadrats. The percentage of blades with bites is listed for each sampling date.
Figure 4. Histograms of data from Reef 1 quadrats. The percentage of blades with bites is listed for each sampling date.
Figure 5. Histograms of data from Reef 2 quadrats. The percentage of blades with bites is listed for each sampling date.
Figure 6. Histograms of data from Reef 3 quadrats. The percentage of blades with bites is listed for each sampling date.
groups at Reef 2 either in mean blade length or regression slopes. At Reef 1 the only difference between experimental and control blade groups was mean blade length, which remained consistent throughout the study. When experimental and control blade-length regressions for Reef 3 were compared, highly significant differences among both means ($F_{1,717}=586.04, P < 0.001$) and slopes ($F_{1,716}=144.12, P < 0.001$) were revealed.

The impact of Reef 3 data on the analysis of covariance results was assessed by running an a posteriori unplanned comparisons test ($T'$-method, Sokol and Rohlf 1981) among the set of regression coefficients. There were no significant differences between Reef 1, Reef 2, and open-seagrass regression slopes. However, pairwise comparisons revealed that the Reef 3 regression slope was significantly different from the regression slopes at all of the other experimental locations ($P < 0.01$ for each site). These results made it clear that Reef 3 data were the primary contributing factors to the significant between-group variance detected by the analysis of covariance (Fig. 9).

Blade-length data collected from the four discrete distances surrounding Reef 3 confirmed that there were significant differences among blade lengths collected at varying distances from the reef ($F_{3,792}=159.97, P < 0.001$, anova). Additionally, blades collected at equal distances from the reef decreased significantly in length over the
Figure 7. Mean blade length of seagrass adjacent to artificial reefs and open-seagrass quadrats through time.
sampling interval ($F(1,792)=42.2$, $P < 0.001$, anova, Fig. 8). Therefore, the halo was progressing outward from the reef.

Artificial reefs were originally set out in the seagrass bed on May 18, 1986, but only quadrat data was collected. The experimental design was modified to incorporate blade-length data, and on July 18, artificial reefs and open-seagrass quadrats were relocated, and the experiment was started over. The patterns that developed during the two months of the original experiment qualitatively resembled those elucidated at the conclusion of the modified experiment. An obvious halo was developing around the largest reef, while there were no noticeable changes in the seagrass surrounding either of the two smaller reefs.

Sediment Monitoring

Grain-size analysis revealed significant differences in the mean particle size among artificial reefs and open-seagrass quadrats ($F(3,11)=13.5$, $P < 0.001$, anova). That relationship was preserved through time. The only significant change in mean grain size during the experimental interval was recorded at Reef 3 ($F(2,9)=4.928$, $P < 0.05$, anova) where grain size increased between both sampling periods (Table 2).

Browsing in Barren Areas

The herbivore-exclusion experiments showed that
Figure 8. Halo formation around Reef 3. Histograms demonstrate the decrease in length of seagrass blades sampled at the same distances from Reef 3 but separated in time. Each histogram is based on 100 blade-lengths.
Table 2. Mean grain size of sediments collected around artificial reefs and open-seagrass quadrats. All grain-size values are mean phi size. There was a significant increase in mean grain size of sediments surrounding Reef 3 ($F_{[2,9]} = 4.927$, $P < .05$ $F_{[2,9]} = 4.26$, anova).

<table>
<thead>
<tr>
<th>Site</th>
<th>Jul. 18</th>
<th>Aug. 31</th>
<th>Oct. 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open-seagrass</td>
<td>.9158</td>
<td>.9025</td>
<td>.9067</td>
</tr>
<tr>
<td>Reef 1</td>
<td>.7782</td>
<td>.6950</td>
<td>.7083</td>
</tr>
<tr>
<td>Reef 2</td>
<td>.8508</td>
<td>.8650</td>
<td>.7908</td>
</tr>
<tr>
<td>Reef 3</td>
<td>.7250</td>
<td>.8050</td>
<td>.8558</td>
</tr>
</tbody>
</table>
browsing by herbivores can effectively reduce the biomass of seagrass blades in an environment where blades are conspicuous. Seagrass blades protected from herbivory grew significantly longer than blades that were available for browsing ($F_{[1,14]}=98.02, P < 0.0001$, anova) especially by the later sampling date. On October 1, all blades within sheared areas were cut to substrate level. After twelve days the mean length of seagrass blades protected by cages was 47.8 mm, which was 15.9 mm longer than that recorded for unprotected blades (Fig. 9). Eighteen days later, on November 2, the difference between mean lengths of protected and unprotected blades had become three times as great (48.3 mm). The protected blades steadily increased in length, and within a month's time had reached an average length of 73.6 mm. The blades growing in exposed quadrats reached an average length of 31.9 mm after the first twelve days, but in the subsequent eighteen day period they decreased in length by 6.5 mm to an overall average of 25.3 mm (Fig. 9).

There was also a noticeable difference in blade morphology between protected and exposed blades. Protected blades displayed typical blade morphology and were indistinguishable from the majority of blades growing in the open seagrass. Blades which grew in exposed quadrats were much narrower than protected blades (Fig. 10).
Figure 9. The effect of browsing on blade lengths in barren areas. The sample size for each histogram is indicated above it.
Figure 10. Morphological differences between protected and exposed blades in barren areas. Both these blade bundles have been growing for the same period of time. The blade bundle on the right was exposed to browsing. The blade bundle that was protected from browsing (on the left) reflects typical blade morphology.
Seagrass Selectivity

Thirty-five of the 50 samples of *Halodule uninervis* blades without epiphytes had tissue removed. Only 8 of the epiphytized blade samples were missing tissue. Nearly all the blades from which tissue had been removed were characterized by a terminal crescent shaped bite scar. Direct field observations supported the conclusion that scars on sample blades were created through browsing by fishes.

The preference data were analyzed as an either-or situation. Fishes could choose either epiphytized or nonepiphytized seagrass blades. Analysis of the preference data with a goodness of fit test (G-statistic) revealed that herbivorous fishes exhibited a highly significant preference ($P < 0.005$) for nonepiphytized *Halodule uninervis* blades (Table 3).

When cut and natural-tipped blades without epiphytes were compared, fishes did not demonstrate a measurable preference for either (Table 4). Thus, the preference for nonepiphytized blades demonstrated in the first experiment was not simply a preference for recently cut blades.

Observations of Herbivorous Fishes

The most numerous herbivorous fishes noted in the *Halodule uninervis* beds were siganids (rabbitfishes) and scarids (parrotfishes). Two distinct size classes of *Siganus spinus* occurred which were thought to represent two
Table 3. Seagrass selectivity of fishes for either epiphytized or nonepiphytized *Halodule uninervis* blades. A 2 X 2 test of independence using the G-statistic revealed these data significant at the $P < 0.005$ level. (Data $G$-value=29.162, Chi-square with 1 degree of freedom value for significance at $P < 0.005=7.879$).

<table>
<thead>
<tr>
<th>Blade Class</th>
<th>Number of Blades With Tissue Removed</th>
<th>Number of Blades Without Tissue Removed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epiphytized</td>
<td>8</td>
<td>42</td>
</tr>
<tr>
<td>Nonepiphytized</td>
<td>35</td>
<td>15</td>
</tr>
</tbody>
</table>
Table 4. Seagrass selectivity of fishes for either cut or natural-tipped blades of *Halodule uninervis*. A 2 X 2 test of independence on these data using the G-statistic did not indicate that fishes preferred cut over natural-tipped nonepiphytized blades of *Halodule uninervis*. (Data G-value=1.46, Chi-square with 1 degree of freedom value for significance at P < 0.05=3.841)

<table>
<thead>
<tr>
<th>Blade Class</th>
<th>Number of Blades With Tissue Removed</th>
<th>Number of Blades Without Tissue Removed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cut-tipped</td>
<td>26</td>
<td>24</td>
</tr>
<tr>
<td>Natural-tipped</td>
<td>19</td>
<td>31</td>
</tr>
</tbody>
</table>
successive annual recruitments. The most abundant parrotfish species inhabiting the seagrass was *Calotomus spinidens*. Occasionally individual *Leptoscarus vaigiensis* were also observed. Both of these species are members of the subfamily Sparisomatinae, and are related to the buck-toothed parrotfish, *Sparisoma radians*, which is a common dweller of seagrass beds in the Caribbean. *Calotomus spinidens* were observed in schools which roved through the seagrass beds as well as in small groups associated with patch reefs. Roving schools not only foraged in the open seagrass but also around patch reefs. Siganids foraged around patch reefs when they encountered them, although they were not noted to demonstrate any particular affinity for patch reefs.

Numerous individuals of each species were observed browsing on seagrass throughout the course of the study. The smaller rabbitfish nibbled on seagrass blades. It was difficult to determine the exact nature of the bite scars that they created because of their small size and their tendency to browse blades covered with algal epiphytes. The larger siganids took mouth-sized bites from blades which left ragged scalloping along the blade-edges. Rabbitfish were observed foraging on all available portions of *H. uninervis* plants, including stems.

Observations of *C. spinidens* individuals revealed that these fish were capable of removing large amounts of seagrass biomass through the course of daily browsing.
Furthermore, their browsing style did not fit the pattern generally described for fishes which ingest seagrass. C. spinidens did not simply nibble or bite off only the epiphyte-rich distal tips of seagrass blades. Individuals of this species approached the edge of a seagrass blade obliquely from above, as much as 5 cm below the blade tip. Then, with a simultaneous biting and twisting motion, fish would tear the terminal portion away from the rest of the blade. Once this piece was free the fish rotated the blade while retaining the bitten end in its teeth until the blade was directly lined up with its mouth. The fish then consumed the blade by chewing the secured end and working its way to the free end until the entire piece had been ingested. The remaining portion of the seagrass blade was left ornamented with a crescent-shaped bite scar across its freshly created distal tip. These were the types of bite scars observed most often on the seagrass blades used in the preference experiments.
DISCUSSION

A longstanding impression exists that direct herbivory of seagrasses by fishes in tropical waters is confined to the Caribbean (Ogden and Zieman 1977, Ogden 1980, Ogden and Ogden 1982, Zieman 1983). This impression has persisted even though studies regarding seagrass herbivory by fishes in the tropical Pacific are lacking. The evidence presented here suggests that the role of direct herbivory by fishes in seagrass beds near Pacific Ocean coral reefs has been understated. Fishes were found to browse and consume significant amounts of *Halodule uninervis* in the seagrass beds near Cocos island, Guam. The average percentage of blades browsed during this study ranged from nearly 33% in the open seagrass to approximately 70% in the area immediately surrounding the largest artificial reef. Additionally, seagrass consumption by fishes created a conspicuous seagrass-free sand halo around the largest artificial reef. Throughout the Caribbean the presence of sand halos is frequently considered to be an indication of concentrated seagrass herbivory.

Browsing intensity near the artificial reefs was not proportional to reef size below a certain threshold size of reef. The level of browsing pressure around the two smaller reefs was not detectably different from that measured in the open seagrass. In contrast, the largest reef became a focal point for browsing activity which produced a nearly
barren-sand halo around the reef within 80 days. Subsequent observations have confirmed that all the seagrass blades have disappeared, and a sand halo approximately 2.5 meters wide separates the reef from the surrounding seagrass.

As reef size increased it also became more likely that the structure affected water movement and sediment deposition. Hydrography may have been the primary factor responsible for the increase in sediment size around the largest reef, but browsing was clearly responsible for halo formation. In fact, browsing may have contributed indirectly to the change in sediment size. The presence of seagrass stabilizes sediments (Ogden 1980, McRoy 1983, Zieman 1983). Rhizomes bind sediment particles, while blades act as baffles which reduce water movement. Browsing activity around Reef 3 continually reduced the amount of seagrass in the immediate area. The blades that did grow near the reef, particularly later on, were not effective in reducing water flow, because they were extremely short and narrow. The sparse, short blades would have permitted local water movement to winnow away the finer sediments from the exposed substrate.

The sand halo that was created through browsing around Reef 3 progressed outwardly from the reef. The halo formed initially because consumption of blade tissue by fishes outpaced blade growth. The experimental shearing of seagrass areas indicated that once a halo develops, it persists, at least over several months, because of the time
required for new blade growth. If seagrass is browsed below the blade-sheath junction, regeneration of blades is a naturally long process (Greenway 1974, this study). Once Halodule uninervis blade bundles were browsed below the blade-sheath junction, the vertical stem which had supported it above the sand withered and broke off at substrate level. New blade growth was initiated below the sand. When blades began to protrude from the substrate, an additional factor figured in halo maintainence. Fishes exhibited a strong inclination to browse seagrass blades growing in conspicuous environments, even though no structure was associated with the area. This behavior appears related to browser preferences. Fishes preferred blades without epiphytes, and young blades are generally epiphyte-free.

The continual browsing of young blades in exposed areas induced morphological changes in subsequent new blade growth. New blades that did grow were narrower than the ones that they replaced. The production of narrower blades most likely resulted from the gradual depletion of stored food reserves in the rhizomes (Greenway 1974, Dawes and Lawrence 1979). Once food reserves had been completely exhausted, the rhizomes probably died back. This would eventually produce an area completely free of seagrass.

Browsing preferences of fishes for nonepiphylitzed seagrass blades figured prominently in the evolution of the halo around Reef 3. The demonstrated preference for nonepiphylitzed blades strictly indicates that fishes are
targeting seagrass and not epiphytes for consumption. The amount of epiphytes growing on a blade offers a rough gauge of blade age. Generally, the older the blade, the more epiphytes growing on it. When the results from the preference experiments and the sheared area experiments are considered collectively, the true preference of fishes appears to be for younger blades. These results are precisely what one would predict on the basis of foraging strategy given the digestive constraints of most fishes (Lobel 1981). Young, regenerated blade tissue has much higher levels of protein and lower levels of ash and structural carbohydrates than older blades (Dawes and Lawrence 1979, Dawes et al. 1979, Björndal 1980). Recropping of Thalassia blades is a foraging strategy of the green turtle, Chelonia mydas. Recropping reduces the fiber content in regenerated blade tissue, which in turn increases blade digestibility (Björndal 1980). Although fishes and turtles digest seagrass in very different manners, fishes that target seagrass for consumption should benefit from changes in nutrient and structural composition of young, regenerated blades.

The field observations of browsing by Calotomus spinidens supports the conclusion that fishes target seagrass for consumption, and that they ingest substantial amounts of normally available, younger blade tissue. It was not possible to tell whether fishes foraging in the open seagrass were selecting younger blades with few epiphytes or
not. However, it was apparent that with each bite these fishes secured large portions of blade tissue. They did not bite off mouth-sized pieces of tissue from heavily epiphytized blade tips. Fishes bit blades well below the tips and secured all of the tissue distal to the bite, thus maximizing the consumption of normally available younger, nonepiphytized blade tissue. Epiphytized, older blade tissue is perhaps ingested as a natural consequence of this foraging manner.

These results indicate that halos produced through browsing by fishes pass through a sequence of intermediate steps. The primary precondition for halo formation is the presence of a sufficiently large reef or structure to concentrate browsing, because halo formation seems to be related to a reef-size threshold. Once that reef-size threshold is surpassed, browsing activity becomes concentrated, and halo formation proceeds to its completion. If the concept of reef-size threshold is valid it has implications for reef management and could potentially prove useful in estimating the abundances of herbivorous fishes in seagrass beds.
REFERENCES CITED


