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ECOLOGICAL ASPECTS OF CORAL REEF - SEAGRASS BED CONTACTS IN THE CARIBBEAN

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Introduction

The coral reef community with its diversity of forms has provided a focus for many community ecology studies. The reef community can have close contacts with surrounding communities such as seagrass beds or mangroves but the extent or importance of such contacts is rarely easily evaluated. Recent studies showing the effects of the close physical proximity of coral reefs and seagrass beds in the Caribbean provide ample evidence of biological contact between the communities. It remains to evaluate the ecological importance of the contact.

Seagrass beds in the Caribbean are composed of mixed associations of marine spermatophytes of three major species, turtle grass, Thalassia testudinum König, manatee grass, Syringodium filiforme Kützting and shoal grass, Halodule wrightii Ascherson (1, 2). They are most conspicuously linked with coral reefs in waters less than 10 m deep. The seagrasses in shallow water occasionally grow up to the bases of nearby reefs, but are usually separated by a narrow (<10 m) band, or halo, of open sand or heavily grazed seagrass. Below approximately 10 m, Thalassia declines in density and Syringodium is the dominant species to about 20 m. Deeper sandy slopes may be covered with an additional species Halophila, which grows in monospecific beds to 35 m and may also be found in shallow water in highly disturbed or turbid conditions (1, 2).

Seagrasses are rooted plants and depend on nutrients from the sediments (3, 4). Where sediments are thin (< 3 cm) or disturbed by current flow or extensive bioturbation, seagrass beds cannot establish themselves (4, 5). When seagrass beds are damaged by natural or man-induced disturbances, they do not quickly recover. Pusey (pers. comm.) comments that oil exploration shot holes in seagrass beds in British Honduras could still be seen in aerial photographs after 10 to 15 years. The shot holes (about 10 m² in area) are colonized by calcareous green algae with a sharp edge at the healthy seagrass bed. The high biomass, productivity and turnover rate of plant material within seagrass beds creates a storehouse of organic material that nourishes a detritus-based food chain of great complexity (6, 7, 8, 9). The blades also provide shelter and surface area for attachment of numerous sessile and motile epibionts (1, 10).

Caribbean seagrass beds are apparently unique for the number of consumers which feed directly on seagrasses, their epiphytes, and associated macroalgae (11, 12, 13). Earlier work done mainly in Florida minimized the importance of this aspect of seagrass ecology (4) but closer

examination indicates an increased role of direct consumers with decreasing latitude (Ogden, unpub.). It is interesting to note the release in relatively recent history of seagrass beds in certain areas of the Caribbean from intensive grazing by the green turtle (Chelonia mydas) and by large herbivorous fishes, the stocks of which are severely reduced throughout their ranges (13, 14). Many of these direct consumers are coral reef dwellers, but the beds shelter a variety of resident and juvenile fishes and invertebrates of small size.

In this paper a brief review of some recent published and unpublished work will be given in an attempt to provide a basis for evaluation of the ecological significance of the seagrass bed - coral reef association in the Caribbean.

Halos

Halos consisting of bands of bare sand or heavily grazed grass have long been noted as conspicuous features of coral reefs where they contact seagrass beds. The biological origin of halos (14, 15) has been studied but clearly physical factors of wave action and current are also involved.

The bases of bank barrier reefs or extended fringing reefs on St. Croix, U.S.V.I. often have a wide band of rippled, coarse, and poorly sorted sand in backreef and forereef areas which contact seagrass beds. There is no grazed stubble of seagrass present within this zone and the edge of the grassbed has a sharp relief of 10-30 cm. Close examination of the halo areas by day and night indicates that while larger herbivorous fishes will venture across the zone to feed in the distant seagrass beds by day, there are no nocturnal forays of sea urchins across the sand zone.

Inferential evidence for the importance of waves and currents in the formation of halos was obtained following the construction of a series of small (40-160 block) concrete block artificial reefs placed within a Thalassia and Syringodium bed at depths of 12 to 15 m on the north coast of St. Croix, U.S.V.I. (Ogden and Gladfelter, unpub.). During the first 6 months (July to December 1976) following construction, the reefs placed at a depth of approximately 12 m rapidly developed a halo about 1 m wide in which ripples formed and the rhizomes of the grasses (usually 10-30 cm deep) were exposed. Water movement around the reefs excavated sand from under these reefs causing collapse of the block structure. Deeper reefs at approximately 15 m were not

undermined by sand movement and had macroalgae and grazed grasses growing to the reef base. For the particular wind and wave regime during the observation period it appears that current and wave action were effective in moving sand near the shallower reefs but not near the deeper reefs.

The diurnal and nocturnal feeding forays of fishes and sea urchins from reefs to grassbeds are clearly involved in halo formation particularly in shallow water (< 10 m). Randall (16) lists over 30 species of fishes which had seagrasses as part of their gut contents. Most of these graze the grasses in situ but some of them feed on floating or broken off leaves. Organisms appear to be chiefly involved in halo formation about patch reefs. Randall (14) concluded that the diurnal feeding activities of reef fishes, particularly parrotfishes and surgeonfishes, which venture only 10 m or so from the protection of the reef are responsible for halo formation about patch reefs. Ogden *et al.* (15) showed that in some areas nocturnal forays of the sea urchin *Diadema antillarum* from the reef to the seagrass bed at dusk and back at dawn were involved in halo formation. Elimination of all of the sea urchins from an experimental reef led to the elimination of the halo within 6 months.

Halos of biological origin are often irregular in outline, the irregularities coinciding with the ease with which sea urchins can migrate to the seagrass beds. For example, where dense stands of *Acropora palmata* occur at the edge of patch reefs the halo can be very narrow and few urchins are observed in this area at night. Conversely, where the reef is a gentle slope and movement is unobstructed the halo can be as much as 10 m wide (15; Ogden, unpubl.). Such halos are rarely denuded of seagrasses. Although blade density is 1/2 to 1/3 of the surrounding bed, there is no relief at the edge of the thicker grassbed. Blade morphology within the halo is usually quite different from blades in open grassbeds. The blades form a flat curl and tend to lie flat on the bottom. This blade form may be attributed to grazing and to higher reflected light intensities within the cleared halo areas (Zieman, in prep.).

Exploitation of Seagrass Beds by Reef Fishes

With the exception of exploitation of seagrass beds within the halo region, utilization of seagrass beds at longer distances from reefs is primarily by larger herbivorous fishes which are day-active and by the nocturnal migrations from reefs of carnivorous fishes feeding on the invertebrate fauna of the beds.

The seagrass bed is a two-dimensional environment for a fish too large (> 20 cm) to hide among the blades. The importance of shelter is seen by the tight clustering of fishes about coral fragments, depressions, or other objects where they occur or are placed within seagrass

beds. Exploitation of seagrass beds by day-active herbivorous fishes is limited to small (< 15 cm) resident species (eg. bucktooth parrotfish, *Sparisoma radians*) and to very large (> 40 cm) reef species (eg. rainbow parrotfish, *Scarus guacamaia*). Mid-range size fishes (20 - 40 cm) are virtually excluded from open seagrass beds and are limited to feeding within halos. Large predaceous fishes such as the great barracuda (*Sphyraena barracuda*), large jacks (*Caranx* spp.) and mackerel (*Scomberomorus* spp.) roam from reefs long distances into seagrass beds and are most surely involved in this exclusion.

Figure 1 shows the effects of exploitation of different areas within the grass beds by different populations or size classes of parrotfish. More than 400 *Thalassia* blades were collected at four stations along a transect from the reef edge (PR-3, see Fig. 2) towards the center of the bed and the number and width of bite marks was recorded. The station 0.5 m from the reef shows the wide bite widths resulting from the populations of larger parrotfish from the reef habitat, whereas the 20 and 60 m stations show the narrow bites from the resident *Sparisoma radians* populations in the grass beds. The 4 m station clearly shows the mixing of the two groups, not only by the intermediate average width, but by the greater variation in bite width indicating the overlap of two separate size groups of herbivores. Grazing intensity, both number of bites per leaf and percentage of leaves with bites, reaches a maximum deeper into the grass bed. The 4 m station where the size group overlap shows the minimum exploitation by herbivorous fishes.

Carnivores exploiting seagrass beds long distances from reefs at night include the grunts (Pomadasyidae), the snappers (Lutjanidae) and the squirrelfishes (Holocentridae), usually of juvenile size. Ogden and Ehrlich (17) describe the nocturnal migrations of resting schools of juvenile (< 15 cm) grunts consisting primarily of french grunts (*Haemulon flavolineatum*) and whit grunts (*H. plumieri*). These species form large heterotypic resting schools associated with particular coral formations on a series of patch reefs within Tague Bay, St. Croix, U.S.V.I. As dusk approaches, the grunt schools stream over the reef to specific assembly points on the reef edge and then migrate into the surrounding seagrass beds on pathways that remain constant for years. The distances traveled may be 1 km or farther. The migrating grunt schools break up and the fishes feed individually through the night, gathering and returning to the reef on same pathways at dawn.

Figure 2 shows the pattern of exploitation of the seagrass beds of Tague Bay, St. Croix by grunts during November, 1976. The reefs number are the principal reefs which shelter grunts by day. Actual numbers of fishes were not determined, but range from 500 to 1200 for each

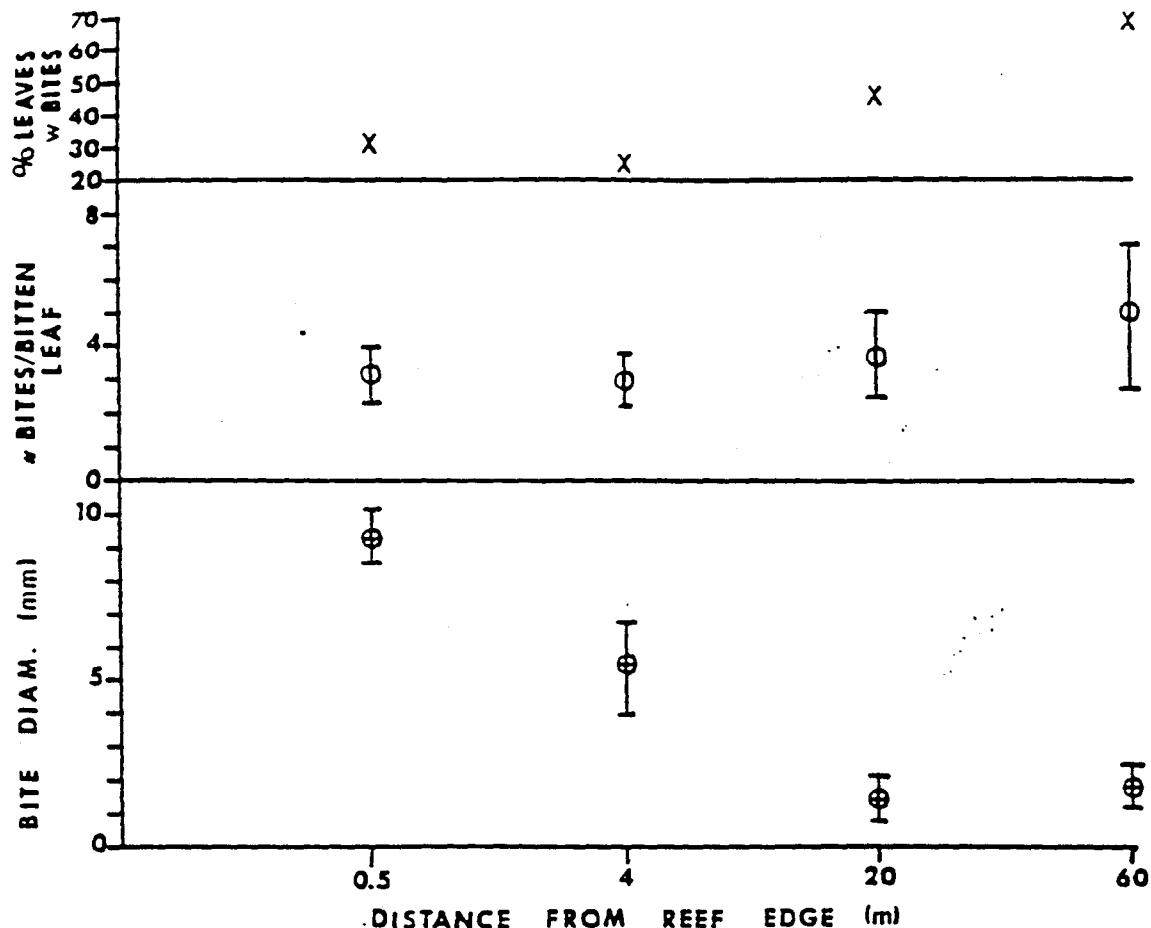


Figure 1. Mean and standard deviation of the parrotfish bite statistics recorded on *Thalassia* blades at four stations along a transect running from Patch Reef 3 into the surrounding seagrass bed. See text for details.

migration path shown. The paths shown were traced by weighted markers dropped by an observer and rechecked by later observation. The migrating schools follow a linear path for 20 to 40 m from the reef and then begin to break up as indicated on the diagram. Within 100 m of the reef the schools originally consisting of hundreds of fish are broken up into groups of less than 20 individuals. The dendritic pattern of the migration was confirmed by placing a net 30 m long at varying distances from patch reef 7 on the path running south towards the shore (see Fig. 2) and perpendicular to the line of travel. The net was deployed before dawn on successive days well before the start of dawn returns to the reef. At 100 m from the reef, about 100 grunts collected on the side of the net away from the reef. At 60 m, 500 grunts were collected, and at 20 m from the reef about 1200 fish representing the entire population of that side of the reef were collected.

It is not known how far grunts travel on their nocturnal migrations, nor exactly where or how they feed. Table 1 shows the results of 3 censuses made on each of two 100 m transects in Tague Bay between 2100 - 2300 hours on 3 separate nights. The area sampled in each transect was approximately 1000 m². There is some indication

Table 1

Night visual censuses (2100-2300 hrs.) of major species of fishes within seagrass beds, Tague Bay, St. Croix, U.S.V.I. Census 5 m on each side of 100 m transect. Mean ± S.D. for 3 censuses (Nov/Dec. 1976).

	T R A N S E C T	
	1	2
<u>Diodon holocanthus</u> ¹		
spiny puffer	26 ± 8	25 ± 2
<u>Holocentrus rufus</u> ¹		
squirrelfish	17 ± 2	13 ± 5
<u>Haemulon plumieri</u> ²		
white grunt	13 ± 8	8 ± 2
<u>Haemulon flavolineatum</u> ²		
french grunt		21 ± 25
<u>Apoogon</u> spp. ³		
cardinalfish	+	++
<u>Fistularia tabacaria</u>		
coronettfish	1 ± 0	0.3 ± 0.6
<u>Pseudupeneus maculatus</u>		
spotted goatfish	1 ± 0.6	0.7 ± 0.6
<u>Ocyurus chrysurus</u> ¹		
yellowtail snapper		2 ± 1

- 1 probably juvenile residents of seagrass beds
 2 observed in seagrass beds only at night
 3 not counted, + indicates relative abundance

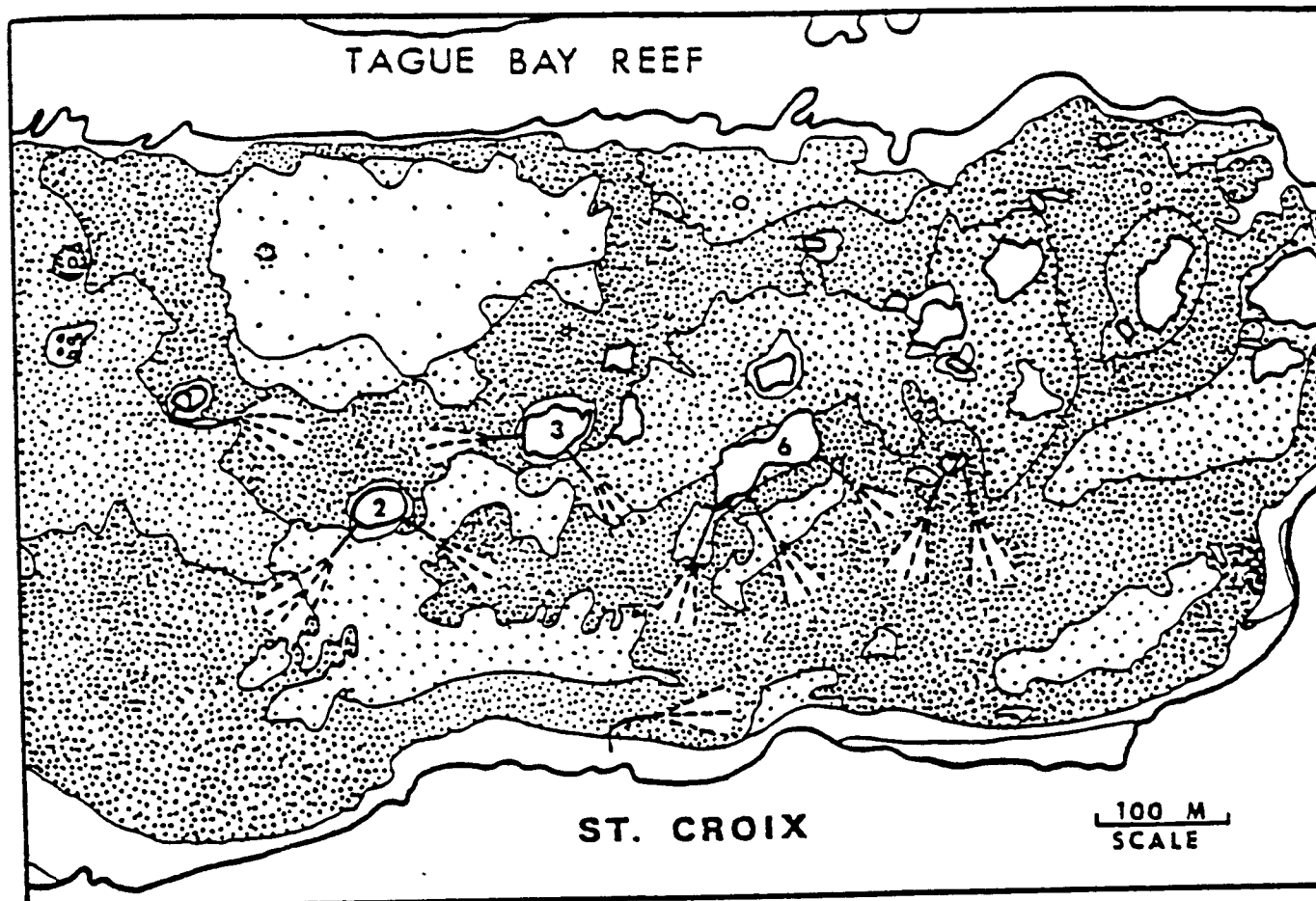


Figure 2. Pattern of diel migration of grunts from a series of reef areas on the northeast coast of St. Croix, U.S.V.I. bounded by seagrass beds. Density of shading is proportional to density of seagrasses.

of a separation in feeding location. No french grunts were observed on transect 1 which is in a thick *Thalassia* bed but many were seen on transect 2 in an area of little *Thalassia*, much open sand and bioturbation from shrimp mounds. This apparent preference of french grunts for more open sandy areas may indicate a partitioning of habitat and diet by the two major species within seagrass beds.

Randall (18) constructed an artificial reef of 800 concrete blocks in a seagrass bed in Lameshur Bay, St. John, U.S.V.I. in 1960. Two years later the fish population of the artificial reef contained 11 times the biomass of the same surface area of natural fringing reef. This difference in biomass was attributed to the proximity of seagrass beds to the artificial reef and the preponderance of night active seagrass bed feeding fishes in its fish populations. Observations in other areas (18, Ogden unpubl.), indicate that reef fish biomass is clearly enhanced by seagrass beds. Some investigators (Johannes, pers. comm.) have speculated that the defecation of these night feeding fishes on reefs by day may be a significant input of organic matter to reefs. This assertion remains open to investigation.

Exploitation of Seagrass Beds by Juvenile and Seasonal Fishes

There is abundant evidence that seagrass beds act as nurseries for certain reef fishes (13). Table 1 shows the spiny puffer (*Diodon*), the squirrelfish and the yellowtail snapper as very prominent members of the night active fish fauna. These are all juveniles in size. Among the day active fishes, all three Atlantic species of *Acanthurus* are present as juveniles in seagrass beds as well as numerous wrasses (*Halichoeres* s). The spiny puffer has arrived in densely packed schools of thousands, presumably newly settled from the plankton, in the area of Tague Bay between June 15 and July 15 each year for the past 3 years. The schools are visible from the air as huge dark spots (Gladfelter, pers. comm.) and gradually disperse over the shallow bay areas floored with seagrasses. Other species, such as the yellow goatfish (*Mulloidichthys martinicus*) may show a similar pattern of settlement from the plankton into seagrass beds.

Conclusions

Seagrass beds are conspicuous features of coastal zones of the world. Their contribution to the enrichment of surrounding waters and

communities is not fully understood, but is particularly evident in the nutrient-poor waters of the Caribbean. Shallow tropical waters are characterized by an abundance of herbivores many of which dwell in reefs but exploit seagrass beds close to the reefs. The resource limitations for organisms on reefs can be severe due to the close couplings of symbiosis in the recycling of energy. The proximity of seagrass beds provides a readily available source of food. In contrast to the closed cycling characteristic of reefs, seagrass beds are more open systems with many organisms from surrounding communities spending their juvenile stages there, feeding, or benefitting from exported organic material. A major factor limiting greater exploitation of seagrass beds appears to be the lack of shelter. Exploitation is limited to small organisms in resident populations, organisms exploiting the periphery of seagrass beds near reefs, and those which venture into the beds only on nighttime feeding forays.

Acknowledgements

We thank Michael Robblee for assistance in all aspects of this study. Numerous undergraduate students at the West Indies Laboratory have assisted in field work as well as friends and colleagues; particularly W. Gladfelter, J. Ebersole, P. Ehrlich, P. Lobel, W. McFarland, J. Lythgoe, N. Ogden, R. Zieman and many others. This work was supported by NSF-IDOE grant #NSF-OCE 76-01304.

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