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PN-AAM-540
ISN=2785

Handbook of Seagrass Biology: An Ecosystem Perspective

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1960

Garland STPM Press • New York & London

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Faunal Relationships in Caribbean Seagrass Beds

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Introduction

Seagrass beds are common coastal zone features in the oceans of the world. They form highly productive systems, in protected shallow waters, with diverse assemblages of organisms. Seagrasses are the one major community type held in common by both temperate and tropical seas. Such identity provides the possibility that the organisms inhabiting temperate and tropical seagrass beds have been subjected to similar selective pressures and that our knowledge of one may be relatively easily extended in fact or by analogy to the other.

In nearshore environments, seagrass blades act as baffles slowing water movement and increasing sedimentation of organic and inorganic material in the beds (Wood *et al.*, 1969; Zieman, 1972). A tangled network of roots and rhizomes holds this sediment and creates an organic and nutrient-rich environment within the fine sediments of the beds. This resource is exploited by a complex fauna of detritivores. The high productivity of seagrass beds is channeled in two major directions, i.e., to the detritus food chain and to direct consumers. In addition there is a considerable export of organic material to other systems. The quantitative details of these pathways are just beginning to be known, but the seagrass beds are largely detrital systems. The environment created by the high standing stock of leaves in most grass beds provides a large surface area for the attachment of a diverse sessile flora and fauna while the shelter and food provided by the leaves and their epiphytes are exploited

by many large motile organisms, most notably echinoderms, gastropods, and fishes.

In the tropics, seagrass beds are prominent features in the Indo-Pacific and the Caribbean. With the possible exception of the Indo-Pacific seagrass beds of Madagascar and the Seychelles (Kikuchi and Pérès, 1973; Taylor and Lewis, 1970), tropical seagrass communities have been most thoroughly studied in the Caribbean and adjacent waters, especially Florida. While the studies of the two major regions are not equally advanced, a major difference between them is beginning to emerge. Caribbean seagrass beds are apparently unique for the number and variety of organisms feeding exclusively or nearly exclusively on the grasses and their epiphytes (Kikuchi and Pérès, 1973; Ogden, 1976). For this reason a major portion of this chapter will be devoted to the role of macroconsumers in Caribbean seagrass beds.

Caribbean Seagrass Beds

Caribbean seagrass beds are generally mixed associations of three seagrass species. The dominant species is turtle grass, *Thalassia testudinum* König (Phillips, 1960; den Hartog, 1970). Manatee grass *Syringodium filiforme* Kutzing and shoal grass *Halodule wrightii* Ascherson are commonly found in lower abundance in beds of *Thalassia*. A fourth genus, *Halophila*, including the species *decipiens* and *baillonis*, is generally not present in mixed beds of the above species, but is found in turbid shallow waters, or as deep as 50 m or more in dense beds in clear water. A successional sequence is recognized, involving these three major species of seagrasses, which runs from *Halodule* to *Syringodium* to *Thalassia* (den Hartog, 1970). This sequence can often be seen from the edge to the center of established seagrass beds or during the recovery phase of damaged seagrass beds. It must also be noted that in the American tropics there is a pronounced latitudinal gradient in the development of seagrass beds. This gradient is not completely understood, but involves seagrass community structure, extent and importance of ties to surrounding communities, and number of direct consumers of seagrasses. Generally, the complexity of the seagrass community increases from the subtropics to the tropics.

Community Structure and Species Composition

The high productivity of the seagrasses sustains a complex association of organisms, including a rich resident epifauna and infauna as well as more mobile forms, both pelagic (e.g. fishes, turtles, and some shrimps) and benthic (e.g. crabs, some shrimps, large gastropods), whose abundance and activity may vary conspicuously on a daily or seasonal basis. Many of the smaller resident benthic forms are microphagous feeders, taking particulate organic material, living and dead, either suspended in the

water or present as surface deposits (e.g. bivalve molluscs, gastropods, ascidians, and such polychaetes as serpulids, sabellids, terebellids, and pectinariids).

Species lists accompany most works dealing with seagrasses and their associated animal populations. In Florida, invertebrate species lists have been provided by several authors (Voss and Voss, 1955; Bloom *et al.*, 1972; Dragovitch and Kelly, 1964). Hooks *et al.* (1976) provide a list of epibenthic macroinvertebrates from both a polluted estuary and an unpolluted estuary in northwestern Florida, while Santos and Simon (1974) provide a systematic and trophic-type species list of the polychaetes of Tampa Bay. Other lists include those of Rodriguez (1959) in Venezuela, Orth (1971) in Bermuda, Heck (1977) in Panama, and Jackson (1973) in Jamaica. The latter suggests that the species listed comprise the great majority of infaunal and semi-infaunal bivalve species to be found in the shallow water *Thalassia* communities of the Caribbean. Studies concerned primarily with fishes have also yielded lists (Reid 1954; Sykes and Finucane, 1966; Carr and Adams, 1973). Randall (1967) provided a large species list of coral reef fishes some of which are closely associated with nearby grass beds. Tabb and Manning (1961) and Tabb *et al.* (1962) provide an extensive list of species (both fishes and invertebrates) present in northern Florida Bay, while Brook (1975) accumulated a large species list of invertebrates and fishes present in the *Thalassia* beds of Card Sound, Florida.

Diversity and abundance are basic parameters of community structure, and have been measured in a number of seagrass habitats. Brook (1975) noted a seasonal trend in diversity of invertebrates in a subtropical *Thalassia* bed. Diversity was highest in November followed by a low in June while abundance demonstrated almost the reverse pattern. Heck (1977) also noted seasonality of invertebrate abundance in Panama. Orth (1971) found diversity of infauna higher in *Thalassia* beds than in adjacent bare sand areas. Jackson (1972) found diversity of a shallow water *Thalassia* mollusc community to increase on an offshore transect and assumed that this trend was due to increasing stability. Greater abundance was reported inshore than offshore. Roessler and Zieman (1969) and Thorhaug *et al.* (1973) report diversity and abundance of algae, seagrass and animals reduced in the region of heated effluent entering Biscayne Bay. Hooks *et al.* (1976) noted that diversity of a *Thalassia* community did not significantly vary with pulp mill pollution but that abundance was greatly reduced.

Food Chains and Energy Flow

It is estimated that a large percentage of the *Thalassia* blade production enters the detrital food chain (Wood *et al.*, 1969). There are essentially two pathways leading to detritus. First, the leaf may remain on the plant

until it falls off and is broken down over a period of months by bacteria and fungi which have the capability of digesting the cellulose structure of the leaf. Second, the leaf may be consumed by a large herbivore which digests its epiphytes and cell contents, but is unable, through a lack of cellulose-digesting enzymes, to break down the leaf structure. The fragmentation of the leaf in feeding and subsequent defecation, however, undoubtedly speeds the breakdown process by bacteria in the sediments. Our knowledge of both of these pathways is minimal.

Dense populations of bacteria are associated with *Thalassia* (Burkholder *et al.*, 1959). These bacteria form a major source of food for detritus feeders living within the sediments (Fenchel, 1970). These include a great variety of polychaetes, crustaceans, bivalves, and gastropods (O'Gower and Wacasey, 1967; Orth, 1971; Brook, 1975). These consumers strip the bacteria from leaf detritus and the fecal pellets are subsequently reingested following recolonization by bacteria (Fenchel, 1970). Some fishes, notably the mullet *Mugil cephalus*, are detritus feeders (Odum, 1970) and several large invertebrates such as the gastropod *Strombus gigas*, and the asteroid *Oreaster reticulatus* take detritus as part of their food from the surface of seagrasses and sediments.

The seagrass leaf provides a large surface area for the attachment of a variety of plants and animals. Chief among the plants are crustose coralline algae such as *Leptoporolithon* and *Tenaria*, and various filamentous algae (chiefly reds—Rhodophyta) (Humm, 1964; Adey, personal communication). The seagrass plant may provide something more than just living space to these epiphytes as there is some evidence that seagrasses transport nutrients from the sediments through the plant and release them into the surrounding water (McRoy and Barsdate, 1970). These nutrients may enhance the growth of epiphytes. The animal epibionts are sessile, particulate feeders such as forams, sponges, hydroids, and anemones, or motile crustacea which are carnivores or herbivores feeding on the leaf or on epiphytic plants.

The invertebrate epifauna of tropical seagrass beds may be divided into those which use the beds as shelter and those which feed directly upon seagrasses or their epiphytes. Sessile epifauna living within *Thalassia* beds in the Caribbean includes the stony corals *Manicina*, *Porites*, *Siderastrea*, and *Cladocora*, sponges, tunicates, and anemones. These are largely particulate feeders. Motile invertebrate epifauna feeding upon grasses and epiphytes consists of the echinoids, notably *Tripneustes ventricosus* (Fig. 1) and *Lytechinus variegatus*, the large gastropod *Strombus gigas* (Fig. 2) and the asteroid *Oreaster reticulatus* (Fig. 3). Nocturnal migrations and foraging of the echinoid *Diadema antillarum* from reefs to seagrass beds were found to be responsible for the formation of halos around some Caribbean reefs (Ogden *et al.*, 1973) (Figs. 4 and 5). The large irregular echinoid *Meoma ventricosa* feeds on sediment and can be

Fig. 3. The large asteroid *Oreaster reticulatus* (approx. 25 cm) in a *Thalassia* bed. *Oreaster* feeds by everting its stomach on seagrass associated algae and epiphytes. It also feeds on detritus on sandy surfaces.

Fig. 4. The echinoid *Diadema antillarum* (test diameter approx. 6 cm) in a *Thalassia* bed at the edge of a patch reef at night. Hundreds of these sea urchins move from reefs into surrounding seagrass beds to feed at night. A characteristic "halo" or grazed zone results from this feeding.

abundant in thin seagrass beds. Other invertebrates such as a variety of crabs, shrimps and gastropods are carnivores feeding on small members of the *Thalassia* community. The large gastropod *Cassis tuberosa* (Fig. 6) feeds on the echinoids of seagrass beds (Hughes and Hughes, 1971), particularly *Tripneustes* and *Lytechinus*. The bored and cleaned tests of these echinoids are a common feature of seagrass beds.

The fishes and other vertebrates associated with *Thalassia* beds in the Caribbean form a conspicuous and highly mobile group. They move between reef or mangrove habitats and grass beds often in a diel cycle. Chief among the herbivores feeding directly on grasses and epiphytes are the parrotfishes (Scaridae) (Fig. 7) and the surgeonfishes (Acanthuridae) (Fig. 8). Many fishes, such as surgeonfishes, puffers, and snappers, are present in grass beds as juveniles taking both food and shelter from the dense leaf canopy. Seagrass beds also support a relatively rich fauna of permanent residents including parrotfishes, razorfishes, pipefishes, porgies, eels, and wrasses.

There is a striking size distribution of fishes inhabiting seagrass beds. Large predators such as barracudas, jacks, and mackerels may restrict the size classes of fishes in seagrass beds to those small enough to hide in grass blades and those too large to serve as prey. Fishes approximately 15–30 cm long are apparently restricted to areas of shelter by day and may move into the beds at night when predation is less intense (Ogden and Zieman, 1977). Some large fishes hunting in seagrass beds have unusual feeding habits. Large rays, such as the southern stingray *(Dasyatis americana)* (Fig. 9) and the spotted eagle ray *(Aetobatis narinari)* are predators of the infauna of *Thalassia* beds, particularly molluscs. In the course of feeding they often excavate large holes up to 1 m deep in sparsely grass-covered sediment with a combined flapping and shoveling action of the pectoral fins.

Other more spectacular vertebrates associated with *Thalassia* in the Caribbean are the turtles, particularly the green turtle *Chelonia mydas*, and the manatee *Trichechus* spp. While populations of the green turtle are presently low in many areas of the Caribbean, green turtles are still regularly observed. The impact of turtle feeding on seagrasses has never been fully evaluated, but the existence of well-documented and protected colonies such as at Tortugero in Costa Rica and large captive mariculture populations in the Cayman Islands and the Bahamas may provide areas for observation and experimentation. Manatees were once common in the mainland areas bordering the Caribbean and are now confined to a few locations, notably Florida and Venezuela (Bertram and Bertram, 1968). They were probably never important seagrass consumers in the smaller islands of the West Indies.

There have been few studies which have attempted to document quantitatively the fate of the blade production in *Thalassia*. Greenway (1976)

Fig. 9. The southern stingray *Dasyatis americana* (approx. 50 cm across) feeds on molluscan infauna of *Thalassia* beds and sandy bottoms by excavating with its nose and large pectoral fins. Large holes can result from such excavations.

working with *Thalassia* in Kingston Harbor, Jamaica, found a blade production of 53.8 g/m²/wk, of which 24.0 g/m²/wk was eaten by the sea urchin *Lytechinus variegatus*, 0.06 g/m²/wk was eaten by the parrotfish *Sparisoma radians*, and 29.7 g/m²/wk went to detritus. This preliminary work undoubtedly overemphasizes the quantity of material entering the grazing food chain for seagrass beds in general in the Caribbean. Urchin densities in Greenway's study area averaged 24/m². Normally, urchins are much less abundant in seagrass beds.

Links with Surrounding Communities

The seagrass community can have close ties with surrounding communities such as coral reefs and mangroves. The importance of these ties is particularly evident in the nutrient-poor waters of the tropics. Shallow tropical waters are characterized by an abundance of herbivores, many of which dwell on 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.

The importance of export of leaf material from *Thalassia* beds probably varies widely depending upon season, wave action, and storm activity. *Thalassia* leaves have been found floating far at sea and at abyssal

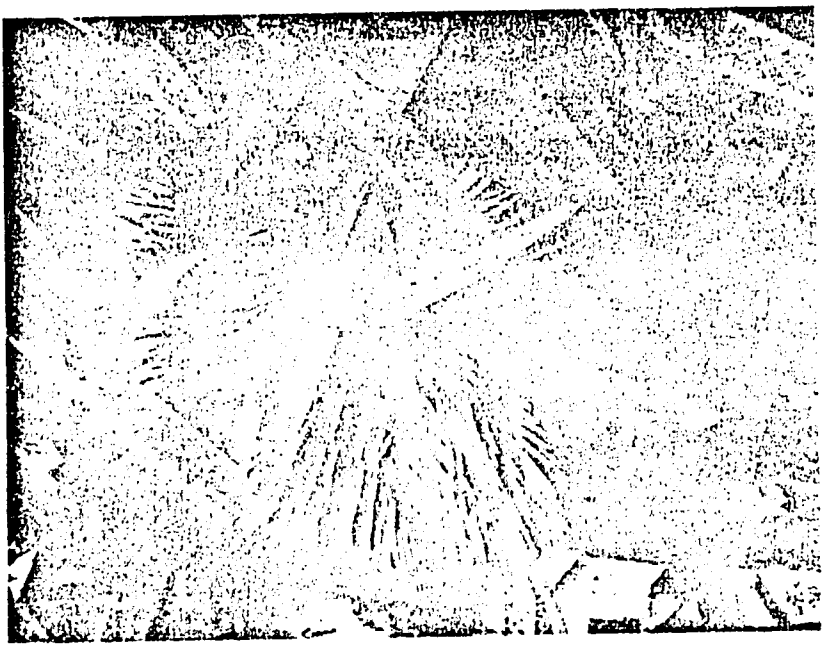

Fig. 1. The echinoid *Tripneustes ventricosus* (test diameter approx. 10 cm) in typical inactive daytime position in a *Thalassia* bed. The grass blades are held over the test by the tube feet, forming a cover. The animals uncover and move about at night feeding on *Thalassia* and epiphytes.

Fig. 2. A juvenile *Strombus gigas* (15 cm) in partially buried daytime position in a seagrass bed. This large, conspicuous and commercially important gastropod feeds upon the epiphytes of *Thalassia* and upon detritus in sand.

depth (Menzies *et al.*, 1967; see also Chapter 11). They certainly provide some level of energy input to distant communities. *Thalassia* leaves are also cast ashore in windrows and form along with other species of seagrasses and algae an organically rich substrate that can be exploited by organisms inhabiting the beach strand, particularly amphipods, isopods, and insects. Abbott *et al.* (1974) found that the urchin *Echinometra lucunter* captured seagrasses from the drift in significant amounts, particularly during winter periods of high wind and heavy wave action.

Carnivores exploiting seagrass beds long distances from reefs at night include the grunts (Pomadasyidae), the snappers (Lutjanidae), and the squirrelfishes (Holocentridae) (Starck and Davis, 1966; Starck, 1969). Ogden and Ehrlich (1977) describe the nocturnal migrations of resting schools of juvenile (< 15 cm) grunts consisting primarily of french grunts *Haemulon flavolineatum* and white 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 (Fig. 10). The distances traveled may be 1 km or farther. The migrating grunt schools break up and the fishes feed individually on seagrass-associated invertebrates through the night, gathering and returning to the reef on the same pathways at dawn. Grunt schools from a number of reefs may partition the available seagrass feeding areas by the use of ritualized migrations along specific pathways (Ogden and Zieman, 1977).

Randall (1963) 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 (Randall, 1963; Ogden and Zieman, 1977) indicate that reef fish biomass is clearly enhanced by seagrass beds. Some investigators 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 (Ogden and Zieman, 1977).

Seagrasses have been noted to serve as nursery grounds (Kikuchi, 1974; Phillips, 1960). The seasonal fluxes in fishes and macroinvertebrates have already been mentioned. Carr and Adams (1972, 1973) have studied the feeding juvenile fishes present in a grass bed in Florida while Sykes and Finucane (1966) list fishes important in Gulf of Mexico fisheries present as juveniles in seagrass beds. Kikuchi (1974) notes the

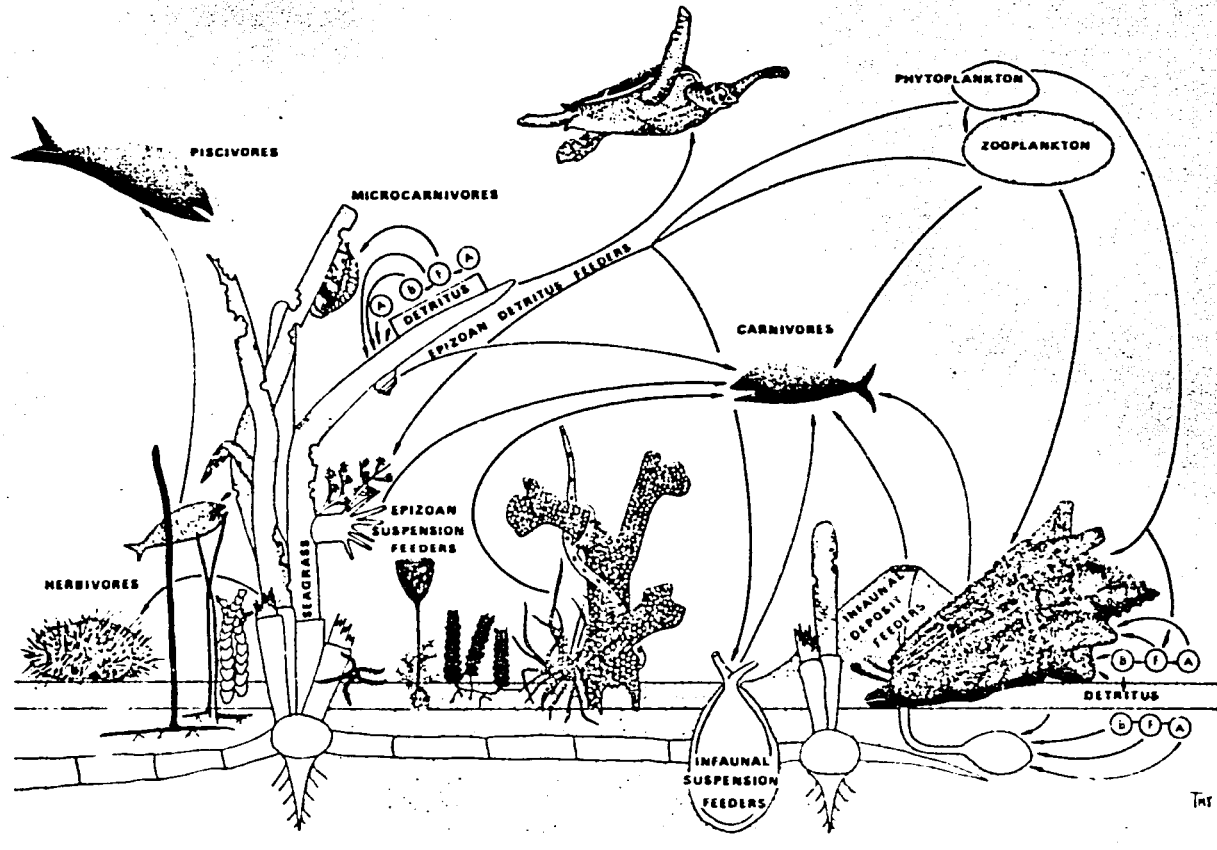

Fig. 11. Energy flow in a Caribbean seagrass bed (after Brasier, 1975). A = algae; B = bacteria; F = fungi. This scheme would differ in a subtropical seagrass bed by the elimination of fishes and turtles and by considerably less diversity in associated plants and animals.

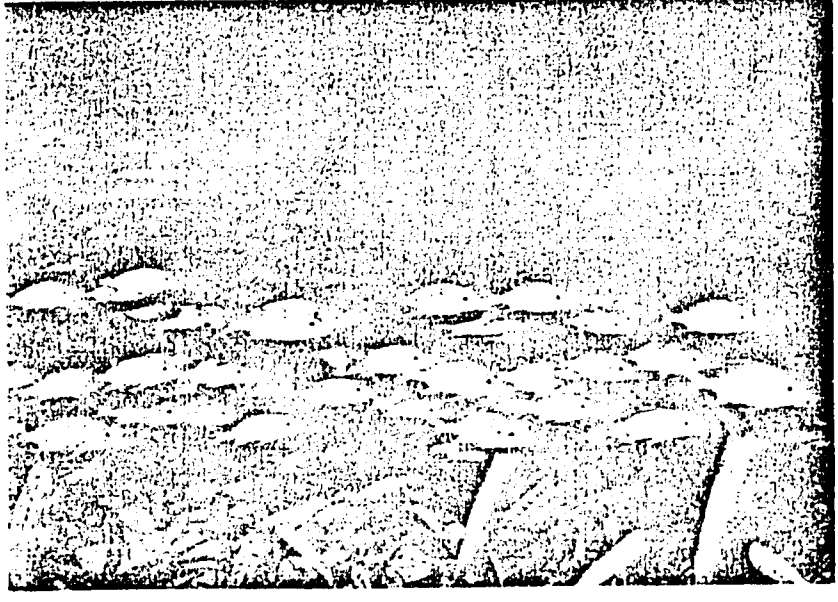

Fig. 10. A mixed migrating group of juvenile french grunts *(Haemulon flavolineatum)* and white grunts *(H. plumieri)* (approx. 10 cm) in column formation at dusk heading from a reef daytime resting area into a *Thalassia* bed. These nocturnal migrations extend for at least several hundred meters from the reef and follow definite pathways. Grunts feed on nocturnally active epifauna and infauna in seagrass beds.

seasonal presence of fishes of commercial value in *Zostera* beds of Japan.

Figure 11 presents a graphic summary of trophic relations and energy flow within a Caribbean seagrass bed. Within the subtropics this scheme would be modified chiefly by the elimination of direct consumers of seagrasses (see Brasier, 1975).

Macroconsumers of Seagrass in the Caribbean

Caribbean seagrass beds are apparently unique for the numbers and variety of direct consumers of blade tissue. These large consumers including sea urchins, conchs, fishes, and turtles are among the most conspicuous representatives of the local fauna and also include many commercially important species. Their relationships with seagrass beds are worthy of close attention.

The Green Turtle

The green turtle *(Chelonia mydas)* is the most abundant large vertebrate consumer of seagrasses in the world. Populations of the green turtle have been greatly reduced throughout its range, but there are a few areas such

as Tortuguero on the Caribbean coast of Costa Rica where fairly large populations can still be found. Green turtles apparently have habitual feeding areas. They have been known to return to particular grass flats after capture and displacement over several miles (Carr and Caldwell, 1956). Impounded turtles show favored feeding areas resulting in patches of heavily grazed grass while other areas are untouched (Bjorndal, personal communication). The principal feeding ground for a large colony of green turtles nesting at Tortuguero is located in luxuriant *Thalassia* beds in the Miskito and Sandy Bay Cays some miles off the coast of Nicaragua. Green turtles feed mainly by day, although some feeding is done at night (Carr, 1952; Bjorndal, personal communication).

Turtle grazing creates very conspicuous scars in grass beds. In the Port Moresby region of New Guinea, turtles, and perhaps dugongs, leave the only really visible signs of grazing in beds of *Thalassia* and *Enhalus* (Johnstone, personal communication). Turtle grazing in the Caribbean is evidenced by cutoff *Thalassia* stubble 2–4 cm long, some uprooted plants and some floating leaf debris created when sections are bitten out of the leaves (Carr, personal communication). This debris which rises to the surface and floats away may be a significant percentage of the amount grazed (Bjorndal, personal communication). Ogden and Robblee (unpublished) have observed circular areas about 2 m in diameter in dense *Thalassia* with a stubble of square cut blades 2–4 cm long that are probably caused by turtle grazing. Apparently no one has attempted to estimate the feeding intensity and impact of green turtles on seagrasses in the Caribbean, although several such studies are in progress or in the planning stage (Bjorndal, personal communication; Hirth, personal communication).

The most extensive information on the stomach contents of the green turtle in the Caribbean has been collected by Mortimer (personal communication) as part of her master's thesis at the University of Florida. At turtle slaughterhouses in Nicaragua, Mortimer collected 202 stomachs of green turtles captured at Miskito and Sandy Bay Cays. The components of each stomach were sorted into species categories, dried to a constant weight, and the percentage contribution of each species to the total gut contents was recorded. *Thalassia* contributed an average percentage of 87.3% (range 0%–99.9%) to the diets of the turtles examined. Only *Thalassia* blades were consumed, rhizomes were not found. *Thalassia* occurred in 99% of the stomachs. *Syringodium* occurred in 51% of the stomachs and constituted an average of 2.6% (range 0%–99%) of the diet. Both blades and rhizomes of *Syringodium* were consumed, the rhizome material accounting for 8.6% of the total material present. *Halodule* occurred in 26.7% of the stomachs and contributed an average of less than 1% (range 0%–25%) to the diet. As with *Syringodium*, both blades and rhizomes were consumed, with rhizomes accounting for less

than 1% of the material. The remainder of the diet (9.4%) consisted of over 30 species of benthic algae (mainly Chlorophyta), and invertebrates, mainly sponges. Thus, the diet of the green turtle in the western Caribbean consists almost entirely of *Thalassia* blades. Surprisingly, Mortimer found that epiphytes contributed almost nothing to the total biomass as the blades were nearly free of epiphytic growth. In another study, Ferreira (1968) examined the stomach contents of 94 specimens from Brazil and found a predominance of benthic algae with some *Halodule wrightii* as a secondary food source.

The green turtle is not a true ruminant as it lacks the accessory stomachs characteristic of this digestive system. However, the possibility exists that the green turtle utilizes its caecum for a ruminant-type of digestion (Wood, personal communication). Bjorndal (personal communication) believes that cellulose is digested by turtles, based on the appearance of their feces, and her observations that the cellulose content of the seagrass food was 40% higher than the feces. Perhaps questions concerning the efficiency of utilization of seagrasses by turtles will be answered as the several studies in progress are completed.

It is interesting to speculate on the intensity of pre-Columbian grazing of *Thalassia* by green turtles. Certainly their populations were very high in certain localities (Randall, 1965), but few authors have attempted to discuss carrying capacity. Hirth (FAO, 1968) estimates that in the Gulf of Aden, 1.7 m^2 of dense *Posidonia* leaves yields about 2.3 kg of plant material. This is approximately equivalent to the gut contents of an adult turtle. Adequate data on feeding rate and gut turnover rate are lacking. Frazier (1971) discusses the feeding ecology of *Chelonia* on Aldabra Atoll in the Indian Ocean and gives some very preliminary figures for the carrying capacity of seagrasses for green turtles. Based on about 12 km^2 of dense *(Cymodocea/Thalassia)* seagrass meadows in the lagoon and about 27 km^2 of reef platform and dense algae which are not all prime turtle feeding habitat, Frazier estimates that the plants at Aldabra could support a migrating population of 183,000 turtles or a resident population of 30,000 turtles. It is emphasized that these are estimates based on many assumptions.

Several authors (Wheeler, 1953; Frazier, 1971, for Aldabra; and Carr and Ogren, 1960, for Ascension Island) suggest that the migratory habit of turtles from breeding grounds to feeding grounds evolved because of insufficient food on the breeding grounds to support the huge populations of turtles that occurred there. Clearly in certain areas of the world, the structure of the seagrass ecosystem has undergone great changes with the continuing extirpation of the green turtle. Perhaps marine sanctuaries for the green turtle such as the one recently created at Tortuguero in Costa Rica will allow us to understand fully the dynamics of the turtle-seagrass relationship.

Herbivorous Fishes

Marine plant production in the temperate and subtropical zones is channeled almost exclusively through invertebrates, while tropical areas have a high biomass of herbivorous fishes (Bakus, 1969). As far as is known at the present, seagrass feeding in fishes is confined almost exclusively to the Caribbean (Randall, 1965, 1967; Kikuchi and Pérès, 1973; Ogden, 1976). The major studies that have been done on diets of Caribbean fishes are by Randall (1967) and Carr and Adams (1973). Randall (1967) indicates that over 30 species of Caribbean fishes have seagrasses as part of their gut contents. Of these, parrotfishes (Scaridae) are particularly important consumers, and one species, the bucktooth parrotfish *(Sparisoma radians)* feeds nearly exclusively on seagrasses. Other fishes that are important seagrass consumers are surgeonfishes (Acanthuridae) particularly *Acanthurus bahianus* and *A. chirurgus,* the porgies (Sparidae), especially *Archosargus rhomboidalis,* and the halfbeaks (Hemiramphidae). Almost all of our information on fish-seagrass feeding relationships comes from stomach content analyses. Food choice in relation to available food, or seasonal use of seagrasses by fishes has not yet been studied. Randall (1965) indicated that the movements of fishes, feeding in part on seagrasses, from reefs into seagrass beds are responsible for the formation of "halos" around West Indian patch reefs (Fig. 5). The distribution of sizes of fish bite marks on *Thalassia* blades gets smaller and the overall frequency of bites becomes greater the farther one samples from a reef in a seagrass bed (Ogden and Zieman, 1977).

Fishes in Caribbean seagrass beds tend to be generalist herbivores, selecting plants in approximate relation to their abundance in the field. Their diets often closely reflect the area which they inhabit (Ogden, 1976; Ogden and Lobel, 1978). As a fauna, the fishes are apparently reacting to the structure of the seagrass beds rather than the food sources available. Adey *et al.* (1977) studied the fish fauna of elkhorn coral *(Acropora palmata)* reefs of the Lesser Antilles and contrasted those with "fleshy algal pavement" reefs of the same region which probably were formed after planing off of *Acropora* following storms. The fleshy algal pavements are dominated by dense growths of brown algae, especially *Sargassum.* The fish fauna of the pavements is more typical of that of seagrass beds than coral reefs.

Caribbean herbivorous fishes do display some degree of selectivity in feeding. Ogden (unpublished observation) observed several large rainbow parrotfish swimming over a grass bed area and descending at leisurely intervals to clip off one *Penicillus,* a siphonaceous green alga. Other studies have shown that when offered a choice, *Sparisoma chrysopterum,* the redtail parrotfish, and *S. radians* will select seagrasses with epiphytes (Lobel, Ogden, and Clavijo, unpublished). Studies such as that of Randall (1967) combined with availability data are lacking.

Sea Urchins

Of the invertebrate consumers of seagrasses, the regular or radial urchins have received the most attention in the Caribbean and elsewhere. Lawrence (1975) has done an exhaustive review of sea urchin-plant feeding relationships of the world. As with the fishes, seagrass feeding among sea urchins appears to be primarily a Caribbean phenomenon. However, sea urchins have been shown to feed on *Zostera* in the North Pacific and upon Indo-Pacific seagrasses. Most studies have been done in the Caribbean where five common species of regular urchins *(Eucidaris tribuloides, Diadema antillarum, Echinometra lucunter, Lytechinus variegatus,* and *Tripneustes ventricosus)* are known to feed on seagrasses (McPherson, 1965, 1968; Randall *et al.*, 1964; Kier and Grant, 1965; Moore and McPherson, 1965; Prim, 1973; Abbott *et al.*, 1974; Ogden *et al.*, 1973; Stevenson and Ufret, 1966; Moore *et al.*, 1963a,b; Greenway, 1976; and many others). Of these, perhaps the most detailed analyses of stomach contents in relation to available food in *D. antillarum, E. lucunter* and *T. ventricosus* have been done at the West Indies Lab on St. Croix (Ogden *et al.*, 1973; Abbott *et al.*, 1974; Odgen and Abbott, unpublished). Each of these three common urchins was found generally to take food in approximate proportion to its abundance in the area where it was found. However, detailed analysis of gut contents and availability of plants in the field indicates some choice on the part of *Diadema* and *Echinometra* (Abbott *et al.*, 1974; Ogden *et al.*, 1973b; Abbott, personal communication). Some plant species are preferred, some are taken at random and others are avoided. Where present in seagrass beds, *T. ventricosus* feeds on seagrasses and epiphytes exclusively, as does *D. antillarum. Echinometra lucunter* is not found in grass beds, but captures over 60% of its food as drift plants, a significant proportion of which are seagrasses. *Diadema antillarum* and *T. ventricosus* are night active animals and move readily between reef and seagrass beds.

Urchin populations have a high reproductive potential, and population explosions of urchins have sometimes been observed. It is tempting to link such explosions with human-induced disturbances such as pollution or elimination of predators, but there are no data to support such speculation. Camp *et al.* (1973) observed population explosions of the urchin *Lytechinus variegatus* along the Gulf Coast of Florida in seagrass beds. Urchin densities between August 1971 and October 1971 averaged a maximum of 636/m^2 and a large area of seagrass bed was damaged. In some cases the basal meristems and short shoots were so damaged that recovery of the bed was doubtful.

Assimilation and Feeding Rate

In spite of the abundance of information that has accumulated in recent

years on seagrass consumers, the question still remains as to the extent to which consumers actually utilize seagrasses. Most recent studies (summarized by Lawrence, 1975) indicate that most seagrass consumers have no enzymes to digest structural carbohydrates and that, with the exception of turtles and possibly manatees, they do not have a gut flora capable of such digestion. Thus, most macroconsumers of seagrasses have two energy sources: cell contents of the seagrasses and of the epiphytes. Seagrasses can support a rich flora of epiphytes (Humm, 1964) and some common animals in seagrass beds such as the queen conch, *Strombus gigas* (Randall, 1965) and juvenile surgeonfishes (Clavijo, 1974) may subsist exclusively upon epiphytes. Most other consumers, however, ingest the whole blade.

One possible means of tracing the energy sources of consumers is to take advantage of the fact that different plants, including the seagrasses, incorporate the stable carbon isotopes C^{13} and C^{12} in different but consistent ratios from the environment. Thus, groups of plants end up with characteristic C^{13}/C^{12} ratios, and their consumers end up with similar ratios (Parker, personal communication). A survey of potential carbon sources for consumers, followed by mass spectrometric analysis of the tissue of the consumers themselves may allow the tracing of food sources between seagrasses vs. epiphytes. McConnaughey (personal communication) reports some success using this method to trace invertebrate consumers of *Zostera* in Alaska.

The feeding rates of macroconsumers of seagrasses are quite high. Moore and McPherson (1965) showed anywhere from 3–6 g wet wt/animal/day was ingested by *Lytechinus variegatus* and *Tripneustes ventricosus*. Parrotfishes feed continually during the day and may void their gut contents many times during a feeding period (Bardach, 1961; Ogden, in press). The quantity of food taken in may allow them to function at a low efficiency. Lawrence (1975) summarized this work for the echinoids. Moore and McPherson (1965) showed absorptive efficiency (a.e. = dry wt food eaten − dry wt feces × 100/dry wt food eaten) to be 50–55% for both *L. variegatus* and *T. ventricosus*. Lowe (1974) indicated an absorptive efficiency (a.e.) of 19 ± 7% for *L. variegatus* feeding on *Thalassia* (a.e. = fraction organic matter in food − fraction organic matter in feces × 100/(1-fraction organic matter in feces) (fraction matter in food)). Gross assimilation efficiencies (g.a.e.) of organic matter for *T. ventricosus* and *L. variegatus* feeding on *Thalassia* were calculated as 3.8% and 3.0%, respectively (g.a.e. = growth as dry org. matter × 100/dry wt ingested food) (Moore *et al.*, 1963a,b). Calculated in another way, gross assimilation efficiency for *L. variegatus* on *Thalassia* was 16% for animals of diameter of 23 mm and 5% for animals with test diameters of 65 mm (g.a.e. = growth in dry wt/m²/30 days × 100 ingested food (dry wt/m²/30 days)) (Moore *et al.*, 1963a).

General Aspects of Herbivory in the Caribbean

Herbivores may influence benthic plant communities in subtle ways. Investigations in the temperate zone (Paine and Vadas, 1969; Vadas, 1968) indicated that herbivore grazing of benthic algae may control structure of the algal community in a manner similar to predator control of species diversity among prey populations (this has been called the "keystone species" concept: See Paine, 1966, 1969). Sammarco *et al.* (1974) compared algal community structure on a patch reef (PR-2), cleared of its major plant consumer *Diadema antillarum,* with a series of control reefs heavily grazed by the urchin. Their data show that consumer removal leads to marked shifts in dominance and equitability in the algal community. The ungrazed patch reef (PR-2) became dominated by one species, the phaeophyte *Padina sanctae-crucis.* The authors concluded as have others (Birkeland, personal communication; Sammarco, 1975) that *Diadema* can influence the structure of benthic communities. Studies such as this have not been done in seagrass beds.

Ogden (unpublished) continued study of PR-2 following removal of *Diadema antillarum.* An increase in the population density of fishes was noted on PR-2. These were both plant consumers (especially parrotfishes, Scaridae) and invertebrate feeders (particularly wrasses, Labridae). The former are increasing presumably in response to increased plant food supply while the latter feed on an abundance of invertebrates hiding in the plant cover. Within the past year, 3 years after cleaning, PR-2 has had a great increase in population of *T. ventricosus.* Preliminary studies indicate that its feeding method differs from *D. antillarum* as it scrapes the substrate to a much lesser degree than *Diadema;* an analogy between cows and sheep is tempting. Further studies may illuminate relationships between these important macroconsumers, and their possible competitive interrelationships with grazing fishes (Ogden and Lobel, 1978).

Recent work on interactions between terrestrial herbivores and plants has shown that plants can be defended from herbivore attack by a variety of chemical compounds including alkaloids, terpenes, and phenolic compounds, among others. The herbivores, in turn, can develop mechanisms to detoxify these compounds, rendering plants palatable (Breedlove and Ehrlich, 1968; Feeny, 1975; Frankel, 1959; Freeland and Janzen, 1974; Whittaker and Feeny, 1971). These systems have been said to be "coevolved" and the selective "races" involved have been thought to be a major factor in maintaining organic diversity (Ehrlich and Raven, 1965).

So far, few investigators have applied this view of plant-herbivore interactions to the marine environment. Studies of some invertebrates such as sea cucumbers (Bakus and Green, 1974) have shown a high incidence of toxicity, and this has been related to defense from predation. The

diversity of both plants and herbivores in tropical waters makes this an ideal place to look for such interactions. Preliminary screening has been done with selected species of algae and seagrasses showing that at least some of the plants identified by preference indices or preference testing have toxic or unpalatable compounds present in their tissues (McMillan, unpublished). These plants, at least in some cases, correspond with those avoided in the field or in herbivore preference tests (Ogden, 1976, and unpublished).

Conclusions

The seagrass beds of the Caribbean, dominated by turtle grass *Thalassia testudinum* König, are highly productive, conspicuous features of the coastal zone. This productivity is largely channeled to detritus where a complex fauna in and on the sediments exploits the resource. A relatively small amount of this productivity goes to macroconsumers which include many large, common and commercially important species. Direct consumption of seagrasses is apparently primarily a Caribbean phenomenon. *Thalassia* is exploited by herbivores both for the blade tissue and the epiphyte flora. The relative importance of each in the nutrition of macroconsumers is not known. A third minor pathway for *Thalassia* is export to beach communities and the deep sea.

Of the macroconsumers, fish, echinoids and gastropods are the most important. These herbivores all exploit various portions of the seagrass community, but relatively few are exclusive grass bed dwellers. Their movements, particularly from reef areas to seagrass beds form a conspicuous link between two important communities. Most of the herbivores of grass beds appear to be generalist feeders, but certain species of plants appear to be avoided. These provide some preliminary indications that herbivore-plant relationships in shallow tropical waters may have coevolved in a similar manner to herbivores and plants in the terrestrial environment. As herbivores channel a considerable portion of the energy of the plant world as well as structure the plant community, their activities in turn will affect the organization of higher trophic levels.

Research is needed to understand the quantitative details of the energy pathways in seagrass beds. New techniques involving C^{13}/C^{12} isotope ratios in plants and consumers may help in these efforts. The role of macroconsumers both in structuring the plant community and the higher trophic levels should be worked out. Even in the tropics, seagrasses are seasonal plants and all future studies need to be long term to look at quantitative changes throughout the year. The close association of the three major tropical communities, coral reefs, mangroves and seagrass beds can be seen in a few spectacular examples of animal migrations. The more subtle links will further illuminate the close dependency of these and their central role in the tropical coastal zone.

ACKNOWLEDGMENTS

I thank the Seagrass Ecosystem Study (S.E.S) group, particularly C. Peter McRoy and Ronald Phillips, for including me in their planning sessions and introducing me to the seagrasses. I thank K. Bjorndal and J. Mortimer, both graduate students at the University of Florida, for their excellent assistance with green turtle literature and for use of their unpublished data. A. Carr, H. F. Hirth, I. M. Johnstone, and J. Wood also contributed valuable comments and observations on the green turtle. Numerous students at the West Indies Laboratory have contributed to the development of some of the ideas in this chapter, especially M. Robblee. I have profited greatly from a strong professional and personal association with D. P. Abbott and I. A. Abbott. Many of my ideas were framed through discussions with J. C. Zieman. B. E. Brown provided many constructive comments on the manuscript. This paper is Contribution Number 32 of the West Indies Laboratory, Fairleigh Dickinson University, St. Croix, U.S. Virgin Islands. The review is based, in part, on research supported by the National Science Foundation under Grant No. OCE 76-01304. Any opinions, findings, and conclusions or recommendations expressed in this publication are those of the author and do not necessarily reflect the views of the National Science Foundation or the International Decade of Ocean Exploration.

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