

12.3 APPLICATION OF A SEAGRASS MANAGEMENT MODEL

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MANY LARGE SEAGRASS systems, such as Florida Bay in south Florida, are undergoing severe degradation, with controversy raging as to the possible causes (e.g., water-quality issues of hypersalinity versus eutrophication). To date, no one has considered the possible implication of destructive fishing (e.g., overharvesting of large herbivorous conch [*Strombus* spp.]) as well as the trapping of herbivorous pinfish (Atlantic, Sparidae) and the netting of rabbitfish (Pacific, Siganidae) and mullet (pantropical, Mugilidae) for seagrass fitness. The protection of beneficial herbivores could present a serious conservation and management issue that is presently receiving little attention.

Aside from catastrophic events such as hurricanes, the major direct source of seagrass mortality and degradation is excessive overgrowth by filamentous and frondose (fleshy) forms of epiphytic algae. Epiphyte loading has been documented to decrease the productivity of seagrasses (e.g., Gacia et al. 1999), as well as to inhibit both subterranean (e.g., Tomasko and Lapointe 1991) and emergent (e.g., Howard and Short 1986) growth. Since epiphytes diminish the light energy and nutrients reaching the host plant, they may indirectly influence seagrass abundance, distribution, and productivity, as well as both sexual and vegetative reproduction (Orth and Montfrans 1984). This phenomenon is especially pronounced in south Florida and the Florida Keys on grass flats impacted by humans where filamentous and frondose algae overgrow and smother the rooted seagrasses (Tomasko and Lapointe 1991). The result is reduced seagrass cover, biomass, habitat diversity, and biological diversity. Although the problem is controversial, most scientists agree that it is largely related to anthropogenic effects on an interactive complex of factors that threatens the pristine conditions under which seagrass systems flourish.

A corollary of the relative dominance model (RDM) for biotic reefs (see section 12.2; Littler and Littler 1984a) is proposed here as a testable paradigm for the major structuring components of tropical seagrass ecosystems (fig. 12.2). These vast grass beds represent the shallow, sedimentary-bottom biological equivalent of coral reefs. Healthy seagrass ecosystems, where marine vascular plants provide more than 50% of the cover, occur where nutrient pollution and destructive fishing (by hand-collecting conch and poisoning, netting, trapping, or dynamiting fish) are either low or absent.

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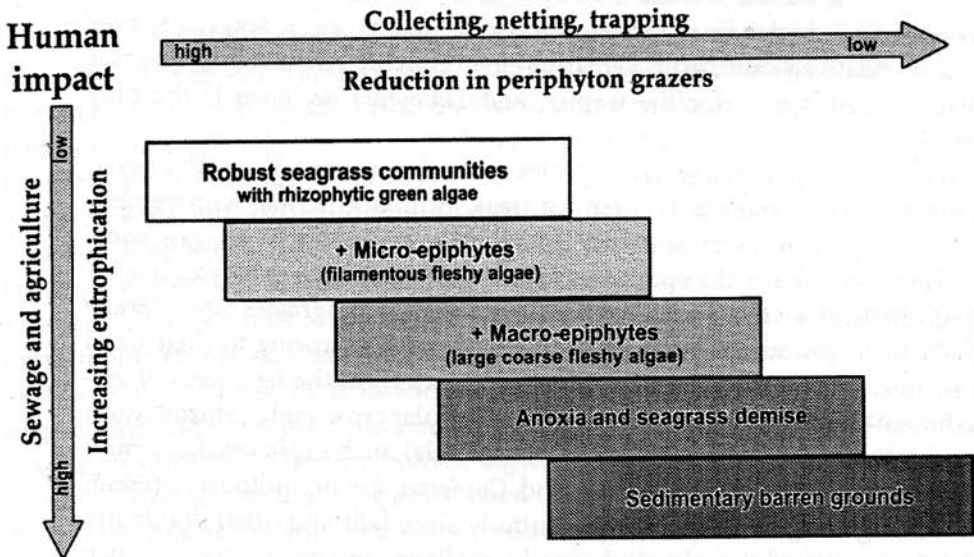


Figure 12.2 Predicted changes in the relative dominance of seagrasses, rhizophytic algae, and epiphytes as a result of the predominant forcing functions of declining water-column quality (eutrophication) and herbivory. All four functional indicator groups of primary producers are present all the time in seagrass beds, but dominate most often under the interacting conditions indicated. The complex interacting vectors of long-term water-column eutrophication and declining herbivory (either naturally or anthropogenically derived) are postulated to produce competitive shifts away from seagrass/rhizophytic algae domination on healthy grass beds toward various phases of epiphytic algal dominance. Hypothetically, one vector can partially offset the other (e.g., high herbivory may delay the impact of elevated water-column nutrients, or low water-column nutrients may offset the impact of reduced herbivory). Latent trajectories are most often catalyzed or accelerated by large-scale stochastic disturbances such as tropical storms, salinity fluctuations, diseases, and global-warming phenomena. Degree of desirability, from a management perspective, is shown by light to dark shading.

NATURAL HISTORY OF THE SEAGRASS ECOSYSTEM

Seagrasses (Magnoliophyta) are the only submerged marine plants having true roots, stems, and leaves, and contain an abundance of vascular tissues as well as inconspicuous flowers. Seagrasses are derived from two monocot plant families, the Hydrocharitaceae and the Potamogetonaceae, and are the only flowering plants to have colonized (presumably from terrestrial estuaries) the depths of the oceans, occurring down to 40 m deep. Seagrasses have a coarse, fibrous, grasslike texture and are apple green or grass green. Like all higher-plant groups, they contain many of the same pigments as their relatives, the Chlorophyta (green algae). Species of the strap-shaped forms are often distinguished by the number of veins running lengthwise in the blades. In oval-bladed species, the numbers and angles of lateral veinlets branching from the main vein or midrib are diagnostic. Most species have a well-developed runner (rhizome) system that binds and consolidates sedimentary bottoms, thereby adding protection and a sheltered environment for the many organ-

isms that live in the stabilized sand, thick foliage, or extensive root systems. There are only about 48 species in 12 genera worldwide; nevertheless, seagrasses play major roles in relatively calm, tropical marine environments. Areas of high seagrass endemism are not known for the tropics, and *Halophila decipiens* is the only pantropical seagrass.

Like mangrove forest trees, seagrass species themselves are not diverse; however, these relatively large marine plants cover vast areas, forming grass flats with tremendous biomass and primary productivity. Most of the considerable seagrass community diversity resides in the epiphytic biota, particularly algal epiphytes but including invertebrates. The blades of the strap-shaped seagrasses are literally conveyor belts of various stages in early to late succession, owing to their basal growth by intercalary meristems (like terrestrial grasses). In the healthiest of systems, sediment-dwelling, siphonaceous (lacking cellular cross walls), rhizomatous forms (= rhizophytes) of Bryopsidales (green seaweeds), such as *Halimeda*, *Avrainvillea*, *Udotea*, *Penicillus*, *Rhipocephalus*, and *Caulerpa*, are ubiquitously present, scattered among the grass blades. Conspicuously abundant and often dominant, seagrasses form vast meadows in sandy or silty shallows, and certain species, such as *Thalassodendron ciliatum*, can even overgrow hard carbonate substrates. The most luxurious and spatially complex seagrass beds occur in clear shallow waters and serve as habitats and nursery grounds for juvenile and adult stages of a myriad of epiphytes, fishes, and invertebrates. They are the feeding grounds of some of the most sought-after sport fishes (e.g., tarpon, bonefish, and permit), and this high-dollar catch-and-release fishery provides an attractive tourism incentive to managers of tropical marine resources worldwide. Tropical seagrasses also serve as important food sources for "charismatic" large animals, such as sea turtles, parrot fish, manatees, and dugongs (sea cows). The seeds of *Enhalus* species are gathered and eaten by South Pacific islanders.

ECOLOGY OF THE SEAGRASS ECOSYSTEM

Plant communities are regulated by a combination of top-down controls, involving the activities of predators (herbivores and carnivores), and bottom-up factors, related to resource availability (McQueen et al. 1989). Changes in herbivore populations can cascade through the entire food web (Carpenter et al. 1985), triggering complex interactions depending on the strength (Levitan 1987) and frequency (Threlkeld 1988) of the disturbances (physical removal). In the case of terrestrial plants, Grime (1979) proposed that communities are regulated by the interactions of (1) physical forces that remove biomass and (2) limiting resources that control productivity, in conjunction with (3) competitive interactions. The Grime model was adapted to marine plant communities (Littler and Littler 1984b; Steneck and Dethier 1994) by adding a component for (4) physiological stress. In the management model proposed in figure 12.2, bottom-up nutrient levels enhance plant productivity, whereas the grazing activities of predatory herbivores physically remove plant biomass. These two primary factors hypothetically interact over long time

spans to maintain stable states or to cause phase shifts in tropical seagrass ecosystems. It is postulated that low water-column nutrient levels coupled with high abundances of epiphyte grazers, such as mullet, pinfish, rabbitfish (Pacific only), sea urchins, and gastropods, maintain low standing stocks of competitively superior fleshy epiphytic algae and lead to the relative dominance of seagrasses, such as the turtle grass *Thalassia testudinum*.

Small-scale human perturbations such as anchor and propeller damage or larger-scale activities such as salinity changes and sedimentation also tend to eliminate the slower-growing deeply rooted seagrasses in favor of more ephemeral microscopic or opportunistic macrophytic forms of algae. Aside from uncontrollable catastrophic events such as tropical storms, salinity fluctuations due to drought and flooding, diseases, or global-warming trends, the major reason for seagrass degradation and mortality, from a management perspective, would appear to be excessive overgrowth by fleshy epiphytic algae. Given an overabundance of water-column nutrients (bottom-up), a reduction in grazing (top-down) resulting from destructive fishing or natural causes (e.g., diseases) could potentially shift the relative dominance within seagrass beds to a condition dominated by large masses of microscopic filamentous algae or ultimately to complete inundation by larger frondose macroalgae (fig. 12.2).

MANAGEMENT MODEL

The proposed management model (fig. 12.2) uses the four groups of indicator plants reviewed above to predict the health of a given seagrass ecosystem. The most desirable condition is indicated by clean seagrass stands such as *Thalassia* with diverse green algal rhizophytes (rooted forms) contributing dense cover and biomass in clear waters and anchored in aerobic sediments. Less healthy would be thinner seagrass beds with increased epiphytic loads of small filamentous algal forms. Massive inundation by long filamentous algal forms along with large coarse fleshy epiphytes (or even free-lying unattached fleshy forms) and sparseness of both seagrass and rhizophytic green algal populations would characterize seagrass systems possibly on the verge of collapse, leading ultimately to anoxia and to sedimentary barren grounds.

Large mobile herbivorous fishes such as parrot fish (Scaridae), surgeonfish (Acanthuridae), and rudderfish (Kyphosidae), while beneficial to coral-reef systems, are deadly to palatable seagrasses, as evidenced by ubiquitous "halo effects" (Ogden et al. 1973; see also Littler et al. 1983a for fish-preference ranking). In one study, experimentally elevated nutrient levels increased the palatability and attractiveness of enriched seagrass plots to large herbivorous parrot fish (McGlathery 1995). Fortunately, in healthy systems these fishes are prevented by predatory birds (e.g., osprey, pelicans, herons, cormorants) and carnivorous fish (e.g., barracuda, snapper, grouper, jacks) from straying far from protective reef cover into the relatively open waters over shallow seagrass beds. Thus, seagrass flats with natural carnivore populations are not subject to devastation by powerful grazers. Pristine

seagrass beds are, as mentioned earlier, home to large schools of herbivorous rabbitfish, mullet, and pinfish, which feed extensively on epiphytic and filamentous periphyton algae (Odum 1970; Darcy 1985; Gilmore 1988). Numerous gastropods, including the large conchs in the genus *Strombus*, also share this periphyton resource (Stoner and Waite 1991). Herbivorous sea urchins and smaller mesofauna also have the potential to ameliorate the detrimental impact of elevated water-column nutrients associated with epiphyte overgrowth on seagrass communities (Orth and Montfrans 1984; Brawley 1992). The importance of such mesograzers/periphyton interactions seems clear; however, further tests of their impact are needed because of the complexity of food-web interactions in general. Therefore, certain herbivorous fishes and invertebrates lacking powerful biting apparatuses (Orth and Montfrans 1984; Klumpp et al. 1992) have the potential to regulate the more delicate, but harmful, epiphytic algal overgrowth, which should increase seagrass productivity, growth, and reproduction.

The important role of herbivory in eliminating harmful blooms of epiphytes from plant hosts has been demonstrated for frondose algae (e.g., Brawley 1992) and reef-building calcareous algae (Littler et al. 1995), as well as seagrasses (Howard and Short 1986; Sand-Jensen and Borum 1991; Gacia et al. 1999). Under increasing eutrophication (fig. 12.2), a reduction in grazing from overfishing or natural causes (e.g., diseases) could potentially shift the relative dominance within healthy seagrass ecosystems to a condition dominated by microscopic filamentous algae or ultimately to complete inundation by larger frondose macroalgae. Filamentous species are always present naturally but, hypothetically, are cropped to low levels by herbivorous fishes, sea urchins, and gastropods. Severe reductions in grazing could allow the algal biomass to accumulate to an upper limit determined by the second major factor, water-column water quality.

The remarkable feature of seagrasses that allows them to thrive under such nutrient-impoverished water-column conditions is their rooted subterranean system, which gives them access to the relatively nutrient-rich sediment pore waters and which confers a competitive advantage over epiphytic fleshy algae. In seagrass systems, an increase in nutrient supply to the water column leads to increased epiphyte loads on the blades (Sand-Jensen 1977; Cambridge and McComb 1984; Twilley et al. 1985; Silberstein et al. 1986; Tomasko and Lapointe 1991), causing a shift in patterns of primary productivity. Overgrowth by epiphytes reduces light and increases boundary-layer diffusion gradients, inhibiting nutrient and gaseous exchange as well as limiting light energy available for photosynthesis. This effect dramatically reduces both seagrass growth (Kiorboe 1980; Kemp et al. 1983; Short and Short 1984; Gacia et al. 1999) and reproduction (Orth and Montfrans 1984). Thus, low water-column nutrient levels coupled with high levels of periphyton feeders, mostly conch, sea urchins, rabbitfish, mullet, and pinfish, maintain low standing stocks of competitively superior fleshy epiphytic algae and lead to the relative dominance of robust seagrasses such as the turtle grass *Thalassia testudinum*.

Herbivory could also represent an important natural route for the export of nutrients from seagrass beds. Herbivore excretions are exported to surrounding

waters by currents. Because the intrinsic production rate of filamentous and frondose algae is much greater than the lower-producing seagrasses (Littler 1980), the algae can theoretically overgrow and outcompete seagrasses as the dominant space-occupying organisms. Since algae can withstand anoxic conditions that prevail at night during bloom conditions, seagrasses and sessile animals often undergo higher mortality than the algae (Tomascik and Sander 1987; Bell 1991).

CASE STUDY

The interactions between groups of producers (seagrasses and epiphytes) in a nutrient-rich estuarine system were investigated to assess the potential alleviating effects of macroherbivores (this case study is from Gacia et al. 1999). The concept that herbivorous fish can regulate epiphytic algal overgrowth, thereby enhancing primary production and growth of the dominant seagrass (*Thalassia*), was tested. An enclosure experiment was carried out within a monospecific *T. testudinum* meadow in the Indian River Lagoon (IRL), Florida. The Gacia et al. study involved multifaceted approaches including characterization of environmental parameters, particularly those that might be conducive to enhanced epiphytic algal growth; documentation of the abundances of the two predominant herbivorous fish species; assessment of the indirect role of grazers on seagrass primary production and biomass accumulation; and experimental tests of the direct effects of fish grazing on epiphyte biomass, species composition, and relative abundance. The last involved four 2.0-m² exclusion cages (fences) of 2-cm² plastic-coated wire mesh, four open 2.0-m² plots (controls), and four 2.0-m² two-sided cages (cage controls) to control for cage artifacts such as current and light (see fig. 12.3).

It was estimated by Gacia et al. (1999) that within the IRL study area there is an annual load of epiphytic algae of 0.022 g organic dry mass (ODM) per *Thalassia* shoot (blade). Given a mean annual shoot density of 616 shoots per square meter and a shoot turnover rate of 4.1 per year, the minimum annual production of macrophytic epiphytes was estimated at 55 g ODM per square meter per year. These values represent a significant macroepiphyte biomass that falls within the range of total epiphyte production for seagrass beds in Florida Bay (Frankovich and Zieman 1994), while being 40% lower than comparable data provided for *Thalassia hemprichii* beds in Papua New Guinea (Heijs 1987).

The pinfish *Logodon rhomboides* is a ubiquitous omnivorous species in Florida seagrass beds and has a relatively homogeneous distribution in both space and time (Gilmore 1988). Darcy (1985) estimated that *L. rhomboides* has a subsistence feeding rate of 5.75% of body mass per day, and at least 65% of this consumption is algae for the fish sizes excluded from the cages (body mass >90 g per individual). From these data, it was estimated that the potential algal demand needed to sustain the population of pinfish at the IRL study site would be 0.1 g ODM per square meter per day, or about 36 g ODM per square meter per year, which is about 60% of the conservative estimate of epiphyte turnover (55 g ODM per square meter per year). Large schools of herbivorous/detritivorous mullet commonly reside and graze

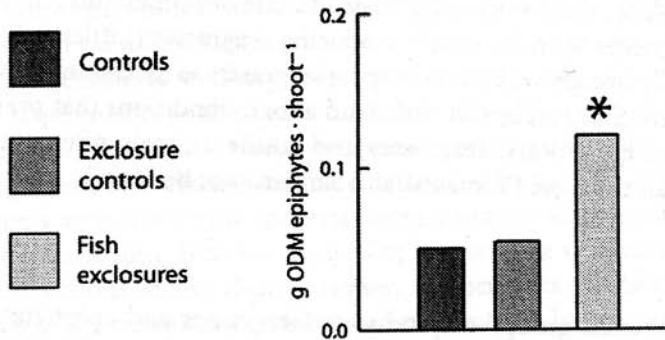


Figure 12.3 Epiphyte growth (mean grams of organic dry mass [weight] per *Thalassia* shoot) from 4 January to 13 March 1995 in the different treatment plots (modified from Gacia et al. 1999). Asterisk indicates significantly higher values for the epiphytic community inside the cage treatments compared to controls (ANOVA, $P < 0.005$).

within seagrass beds throughout the world. The estimated daily algal consumption by striped mullet (*Mugil cephalus*) individuals longer than 20 cm is 9.8% of the body mass (Odum 1970), with a gut-content turnover rate for this size class of five times per day. The estimated algal demand by striped mullet in the immediate IRL study area would be about 6.4 g ODM per square meter per day. Therefore, the total algal biomass required to support the combined demands of the two predominant fish grazers in the seagrass bed studied by Gacia et al. would be about 6.5 g ODM of algal epiphytes per square meter per day.

Sudden blooms in biomass of epiphytic algae correlated (Gacia et al. 1999) with seasonal spikes in dissolved inorganic nitrogen and soluble reactive phosphorus. The nutrient concentrations consistently recorded in the IRL far exceeded the threshold levels conducive to macroalgal proliferation in other tropical seagrass and coral-reef ecosystems (i.e., 0.2 μM soluble reactive phosphorus and 1.0 μM dissolved inorganic nitrogen; Bell 1992; Lapointe et al. 1997). Crossland et al. (1984) also correlated dissolved inorganic nitrogen above the almost undetectable threshold levels of 1.2 μM and soluble reactive phosphorus of 0.22 μM for macroalgal-dominated high-latitude communities of Western Australia. During the early spring, blooms of ephemeral green algal species, mostly of the genera *Cladophora* and *Enteromorpha*, reached peak abundances, with their maximum epiphytic biomass occurring inside the fish-exclusion cages (fig. 12.3). Herbivore pressure on these delicate chlorophytes was critical during the early spring bloom when the epiphyte assemblage was dominated by fleshy forms. These ephemeral forms are delicate, filamentous and thin-tubular species that bloom under eutrophic conditions (Littler and Arnold 1982) and are easily grazed (Littler et al. 1983a). The fish-exclusion experiment (fig. 12.3) strongly supported the hypothesis that epiphytic biomass on seagrass blades would be significantly reduced in the presence of grazers. As predicted, the increased epiphyte loads in the grazer-exclusion cages had an inhibitory effect on leaf growth of *Thalassia* (fig. 12.4A); leaf initiation also was sig-

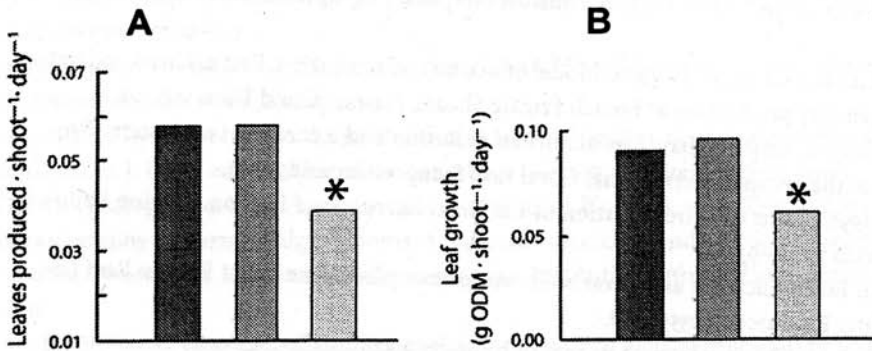


Figure 12.4 Seagrass growth (new *Thalassia* leaves and biomass) from 4 January to 13 March 1995 in the different treatment plots (key same as for fig. 12.3; modified from Gacia et al. 1999). Asterisks indicate significantly lower production of new leaves and new biomass for the plants growing inside the fish enclosure cages (ANOVA, $P < 0.005$) than for accessible plants in the controls.

nificantly reduced (fig. 12.4B) for the nongrazed plants compared to that in the treatments exposed to grazers.

Eutrophication of coastal waters is now seen as one of the most pervasive, worldwide anthropogenic impacts (National Research Council 1994; Vitousek et al. 1997a, 1997b; Jackson et al. 2000; Tilman et al. 2001). Unless major social, economic, and political measures are taken, the escalation of the problem is forecast to worsen in the next decades (Nixon 1995). In light of the growing recognition of the consequences of destructive fishing and increasing pollution on seagrass ecosystems globally (National Research Council 1994), management approaches should include (1) monitoring of herbivore, algal, and seagrass stocks, (2) inventories and assays of the health of herbivore stocks (see section 12.2), (3) characterization of water-column nutrient concentrations and epiphyte tissue analyses for C:N:P ratios, and (4) bioassays using epiphyte physiological responses (i.e., productivity, growth rate, biomass) to experimental nutrient pulses (methods referenced in Lapointe et al. 2004).

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