Marine Community Ecology

Edited by

Mark D. Bertness
Brown University

Steven D. Gaines
University of California at Santa Barbara

Mark E. Hay
Georgia Institute of Technology

ABOUT THE COVER

A diverse coral reef community at Manado, Indonesia.
Photograph by Mike Severns/Tom Stack & Associates.

MARINE COMMUNITY ECOLOGY

Seagrass Community Ecology

Susan L. Williams and Kenneth L. Heck, Jr.

*F*or a long time, seagrass communities remained largely unstudied by ecologists, probably because seagrasses usually exist at depths requiring the use of SCUBA. Uniformly green and almost impenetrably dense, seagrass beds hide the life teeming within them very well. The 1970s brought an explosion of research, and the abundance of organisms within seagrass communities became widely acknowledged among marine scientists. Why seagrass beds should support such abundant life became a major research question concerning habitat utilization and function, including trophic support, refuge from predation, recruitment, and provision of nursery areas. This question has dominated seagrass community ecology and is the framework for this chapter.

Within the general question of habitat utilization and function, we chose to focus on several specific topics in marine community ecology to highlight significant contributions from seagrass studies. First, some of the most comprehensive analyses of detrital food webs originated from seagrass beds, along with salt marshes. At least half of the prodigious primary production of seagrasses enters the food chain as detritus. Seagrass studies helped to establish stable isotopes as food web tracers in ecology. Second, seagrass studies demonstrated that inconspicuous but highly productive and palatable microalgae provide an important source of food for consumers. Third, seagrass beds provide some examples of apparently rare marine trophic cascades, where the primary control of the community clearly resides in the effects of higher-order trophic levels. Fourth, seagrass studies have contributed greatly to understanding how structural complexity in the habitat influences the distribution and abundance of organisms. Fifth, recent experimental manipulations in seagrass beds have provided examples of the complex nature of ecological interactions between native and non-native species.

Until recently, knowledge about marine non-native species has been limited primarily to their distribution, abundance, and perhaps origin, and ecological interactions have only been hypothesized (Steneck and Carlton, this volume).

Finally, seagrass communities provide some of the most comprehensive examples of the acid test of ecological understanding—marine habitat restoration. Seagrass community research is driven increasingly by the accelerating loss of seagrass habitat and associated species of economic value and, in the United States, the legislative mandate to mitigate intentional loss of seagrass ecosystems (Orth and Moore 1983; Robblee et al. 1991; Walker and McComb 1992; Short and Wyllie-Echeverria 1996). Ecologists need to understand the community consequences of seagrass decline. Mechanistic understanding of the community is required for effective mitigation and restoration and to achieve ecological functions (e.g., primary production, trophic support) that are equivalent to those in the seagrass beds replaced, that is, functional equivalency. What kinds of functions lead to the biological wealth of relatively undisturbed seagrass beds?

INTRODUCTION TO SEAGRASS COMMUNITIES

Our description of seagrass communities will be brief because excellent references exist (McRoy and Helferrich 1977; Phillips and McRoy 1980; Phillips 1984; Thayer et al. 1984; Larkum et al. 1989; Zieman and Zieman 1989). Seagrasses are clonal marine flowering plants and occur in shallow soft-sediment habitats along the shores of bays and estuaries throughout most of the world. The notable exceptions are the surfgrasses (*Phyllospadix* spp.) and *Amphibolis* spp., which grow on hard substrata. There are between 50–60 seagrass species in the families Hydrocharitaceae and Pota-

mogetonaceae. Seagrasses are primarily subtidal, but they can extend also into the intertidal zone. In subtropical and tropical meadows, several seagrass species typically coexist. Although temperate meadows in the northern hemisphere tend to be dominated by a single genus, either *Zostera* (eelgrass) in sediments or *Phyllospadix* (surfgrass) on rocks in the north Pacific, a careful observer will find that even these beds are not monospecific (Figure 12.1). *Ruppia maritima* (widgeongrass or ditch grass) frequently coexists with eelgrass on a seasonal or perennial basis, depending on the locale. Up to three species of surfgrass intergrade across the depth distribution of surfgrass beds in North America and, depending on the substratum, can be mixed with eelgrass at

some sites. On the northeast coast of Japan, five species of eelgrass occur, each with a distinct growth form, and up to three species (e.g., *Zostera marina*, *Z. caulescens*, and *Z. caespitosa*) can be found in a bed (Aioi and Komatsu 1996; Iizumi 1996; S. Williams pers. obs.).

All seagrass beds also include many kinds of algae. Algal epiphytes use seagrass leaves and rhizomes as substrata and include microscopic and small filamentous forms as well as larger blades and corticated thalli. For example, Humm (1964) reported 113 species of algal epiphytes on turtlegrass (*Thalassia*) in Biscayne Bay, Florida, and Ballantine and Humm recorded 66 epiphytic algal species in a seagrass bed on the west coast of Florida (1975). The epiphytes composed from...
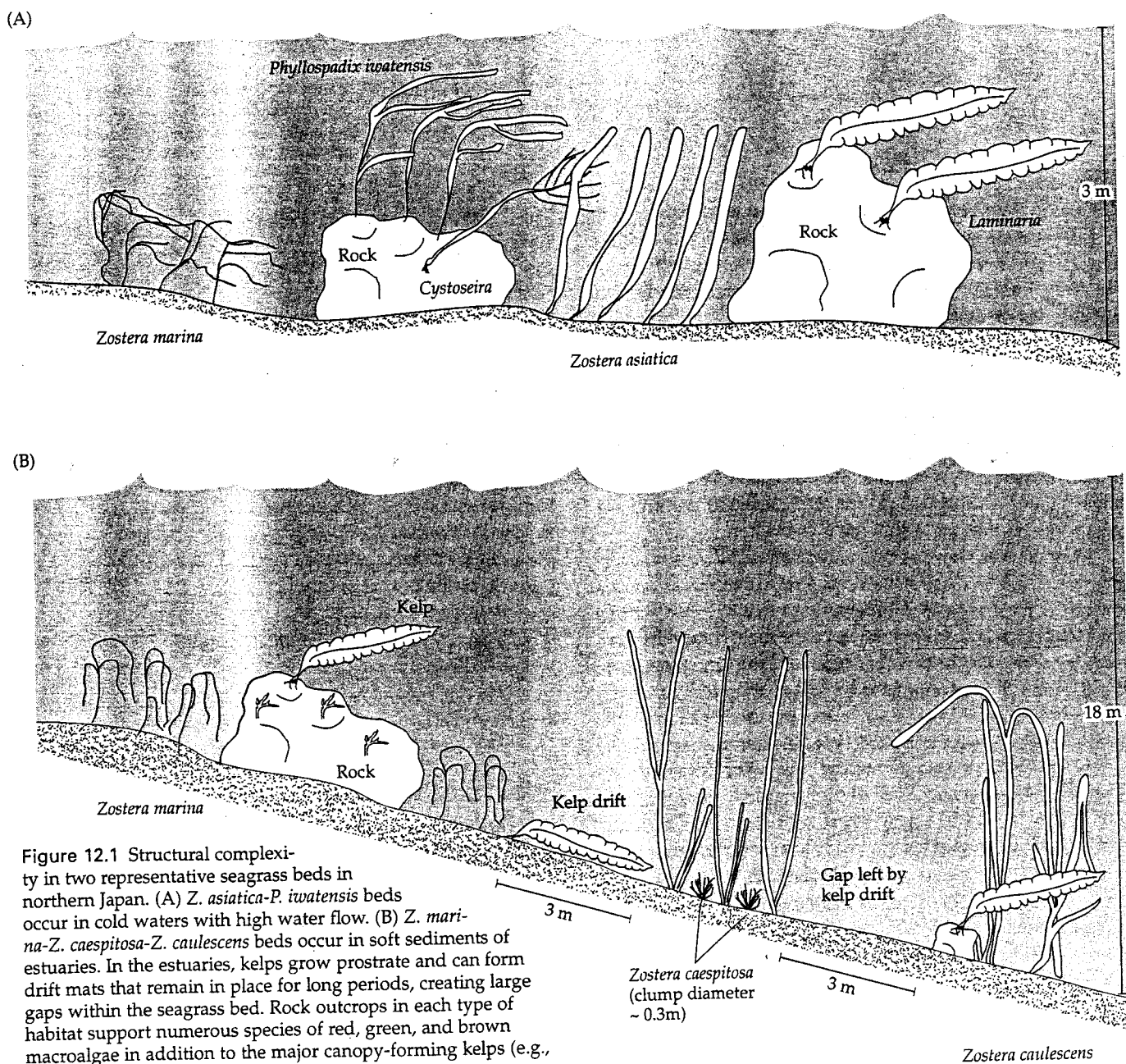
Figure 12.1 Structural complexity in two representative seagrass beds in northern Japan. (A) *Z. asiatica-P. iwatensis* beds occur in cold waters with high water flow. (B) *Z. marina-Z. caespitosa-Z. caulescens* beds occur in soft sediments of estuaries. In the estuaries, kelps grow prostrate and can form drift mats that remain in place for long periods, creating large gaps within the seagrass bed. Rock outcrops in each type of habitat support numerous species of red, green, and brown macroalgae in addition to the major canopy-forming kelps (e.g., *Laminaria* spp.) and rockweeds (*Cystoseira* spp.).

25–45% of the local algal flora. Free-living macroalgae (as well as periphytic forms) grow from rocks and shells. In temperate beds, large canopy-forming rockweeds (*Cystoseira*, Fucales) and kelps (*Egregia*, *Laminaria*), as well as surfgrass, grow on numerous small (few m²) rock outcrops. In tropical seagrass beds, over a dozen species of siphonous green algae (Caulerpales), which grow from rhizoids anchored in the sediments, form a major component of the community. Attached macroalgae often break off and form large, drifting clumps and mats that are important components in the community. The common macroalgae in drift mats alone represented 13 species of green, brown, and red seaweeds in one study (Williams Cowper 1978). Although the seagrass canopies strongly attenuate light, benthic microalgae also occur commonly in seagrass communities.

Animals in every major Phylum occur within seagrass beds. Animals pack the complex belowground mat of seagrass roots and rhizomes and live attached to or closely associated with the leaves or drift macroalgae (Figure 12.2). More mobile snails, crabs, and fishes cruise through or above the leaf canopy. Seagrass beds also support large populations of migrating waterfowl such as herbivorous swans, ducks, and geese, and predatory wading birds and diving ducks. Raptors such as bald eagles and ospreys feed over the beds. Large vertebrate grazers such as green turtles, dugongs, and manatees rely on seagrass beds for food and habitat; some of these species are threatened or endangered. The majority of the commercially valuable marine species in the United States are found in seagrass communities at some stage in their life histories.

SEAGRASSES AND THE DISTRIBUTION AND ABUNDANCE OF ASSOCIATED ORGANISMS

Seagrass beds harbor higher numbers of animal species and individuals than other marine soft-bottom communities (McRoy and Helferrich 1977) and also support exceptionally high rates of secondary productivity (Pihl-Baden and Pihl 1984; Fredette et al. 1990; Valentine and Heck 1993; Heck et al. 1995). The question of why this should be so fostered research on major aspects of seagrass habitat function, including trophic support, refuge from predation, recruitment, and

Figure 12.2 Pathways of energy flux among major consumer groups in Caribbean seagrass meadows. (Redrawn after Ogden 1980.)
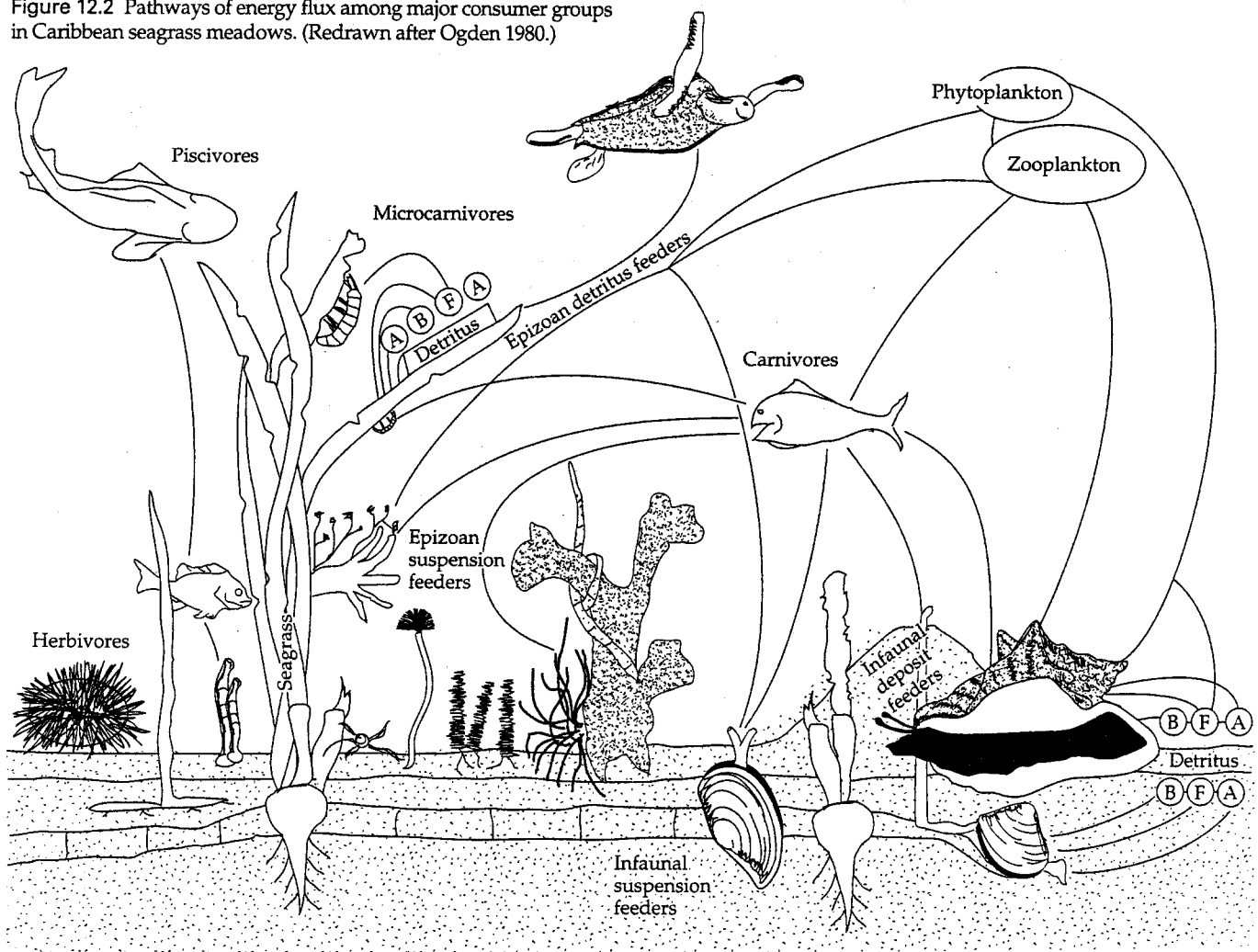
provision of nursery areas. This research has broadened the understanding of how marine plants and animals interact. Herbivory has dominated the study of marine plant-animal interactions, and seagrass studies certainly have contributed to this topic. Extending beyond herbivory, seagrass studies have provided some of the best examples of nontrophic interactions, both positive and negative (e.g., fertilization, bioturbation), that also control the distribution and abundance of associated organisms.

Trophic Support

The prodigious primary production of seagrass ecosystems, reaching up to 8 g C/m^2/d for seagrasses alone (Zieman and Wetzel 1980), is a major aspect of their ecological and economic importance (McRoy and Helferrich 1977; Phillips and McRoy 1980; Larkum et al. 1989). Leaves can grow over 1 cm/d in many cases (Ogden and Ogden 1982; Erftemeijer et al. 1993) and are continuously shed and replaced. Studies of the fate of this primary production have contributed to marine ecology in several major ways. First, the importance of macrophyte detritus as trophic support was quantified. The early debate over whether the detritus itself, or the associated bacteria, was the main source of trophic support for detritivores was resolved in the favor of both in part by studies on the assimilation of eelgrass detritus (Adams and Angelovic 1970; Tenore 1975). Seagrasses have high C:N ratios (Atkinson and Smith 1983), large amounts of structural carbohydrates, and phenolic compounds that reduce their nutritional value relative to many algae (Nicotri 1980), but not salt marsh plants (Buchsbaum et al. 1984). Although many animals directly consume seagrass leaves (McRoy and Helferrich 1977; Ogden 1980; Thayer et al. 1984; Williams 1988; Valentine and Heck 1991), the proportion of leaf biomass production of seagrasses that enters the food web via grazing is typically less than 50% (Cebrián and Duarte 1998).

Belowground seagrass production has not been considered in seagrass trophic support. Although rhizomes grow slowly relative to leaves, the belowground biomass can be an order of magnitude greater than the leaf biomass, thus representing a significant sink for photosynthate (Pangallo and Bell 1988; Powell et al. 1989; Williams 1990; Kenworthy and Schwarzschild 1998). Although rhizomes have high caloric values (Birch 1975), we know of no reports of infauna grazing the living roots and rhizomes. Instead, belowground seagrass production might represent a major source of detritus for infaunal consumers. Belowground biomass forms detritus as the older distal end dies and is replaced by the terminal rhizome meristem (Tomlinson 1974).

The importance of detritus in seagrass beds was inferred for a long time because of the sheer amount of detritus formed and the biomass and dominance of detritivores in seagrass beds (Petersen and Boyson Jensen 1911; Howard 1982). Seagrass ecosystems thus provided a model to analyze detrital food webs using stable isotopic ratios. Confirmation of the source of plant detritus is difficult because it is basically unidentifiable once in a consumer's gut. However, detritus

retains the unique stable isotope signature laid down by the plant's physiology, and thus stable isotopes can be used to differentiate the source of the primary production at successively higher levels in the food web. Stable isotope analysis of seagrass food webs confirmed that seagrasses provided a major source of organic matter for detritivores, but mixed diets were also common (Thayer et al. 1978; Fry and Parker 1979; McConnaughey and McRoy 1979; Fry et al. 1983; Nichols et al. 1985). Stable isotopes also helped in determining situations where other primary producers become more important (Stephenson et al. 1986). Stable isotope ratios provided a valuable tracer for shrimp migrations and feeding areas and helped identify the functional importance of seagrass beds as feeding grounds for commercial species (Fry 1981; Zieman et al. 1984b; Loneragan et al. 1997). Utilization of seagrass detritus by large invertebrates in the deep sea was elucidated through stable isotopic analyses (Suchanek et al. 1985). Ruckelshaus et al. (1993) combined isotopic analyses with measures of food quality and quantity to challenge the paradigm that the suspended pool of organic particles in estuaries is a well-mixed "soup" for filter feeders. Instead, habitat patches (e.g., mudflats, channels in salt marshes, eelgrass beds, or neritic zones) locally differed in the quality and quantity of suspended food particles. These differences were realized in the growth of filter-feeders, including the mussel *Mytilus galloprovencialis*, which grew best in eelgrass habitat (Ruckelshaus et al. 1993).

Studies of the fate of primary production in seagrass beds also contributed to a growing understanding that inconspicuous microalgae are very productive and important sources of high-quality food for benthic marine consumers (Fry 1984; Kitting et al. 1984; Moncreiff et al. 1992). In comparison to seagrass beds, the trophic importance of algal epiphytes in kelp beds and other macroalgal systems is poorly understood (Brawley and Fei 1987). In these systems, stable isotope analyses cannot be used as successfully to identify the relative trophic importance of small algae because their isotopic signatures overlap with those of the macroalgae.

The primary production of algal epiphytes can represent a substantial component of the total primary production of a seagrass bed, sometimes matching or exceeding that of the seagrasses (Morgan and Kitting 1984; Mazella and Alberte 1986; Thom 1990a). Epiphytic algae are an important determinant of epifauna abundance (Hall and Bell 1988; Edgar 1990). Typically comprising diatoms and other unicellular species as well as small filaments (Coleman and Burkholder 1995), algal epiphytes can have low biomass that belies their trophic significance (Jernakoff et al. 1996). Algal epiphytes have very high biomass-specific rates of primary production and can replace their standing stock within a few days (Borum 1987; Sand-Jensen and Borum 1991). In addition, the biomass represents higher nutritional quality for consumers (Zimmerman et al. 1979), being relatively rich in nitrogen and low in structural carbohydrates compared to seagrasses and macroalgae and the detritus they form (Nicotri 1980; Klumpp et al. 1989; Duarte 1992; Enríquez et al. 1993).

Epiphytes also apparently lack the phenolic compounds found in seagrasses that can inhibit grazing on living and recently dead leaves (Harrison 1982). Although very few studies have directly assessed the nutritional content of epiphytes (Nichols et al. 1985, 1986), data for diatoms and other microalgae or small filamentous species should be representative of similar epiphyte species. Most of the mesoconsumers such as caprellids and gammarids are small enough to select algae from the epiphyte matrix, which also includes sediment particles and detritus (Harrison 1977; Zimmerman et al. 1979; Caine 1980; Howard 1982; Kitting et al. 1984). Because consumers select algae from the matrix, values for organic content, proteins, and carbohydrates derived from the intact matrix probably underestimate its nutritional quality for the meso- and micrograzers.

Trophic Interactions

Although the focus on detrital food webs might predominate in seagrass ecology, it was always apparent that seagrass vegetation and the associated community could be controlled by herbivores because of dramatic examples of overgrazing by large invertebrates such as sea urchins (Camp et al. 1973; Valentine and Heck 1991) and vertebrates such as birds, sea turtles, and marine mammals (Thayer et al. 1982a,b). Despite these dramatic examples, there has been a tendency to treat herbivore control of seagrasses as an anomaly. It has been argued that a historically important top predator was missing (in the case of sea urchins) or that the environment represented some otherwise "special case." In fact, these "special cases" might better represent seagrass communities of the past when large herbivorous vertebrates (waterfowl, manatees, sea turtles) were numerous (Jackson 1997).

In addition to controlling the distribution and abundance of seagrasses, animals also influence the population biology of clonal seagrasses. The influence of herbivores on the population biology of seagrasses represents a relatively unexplored research area, but one with some interesting parallels to terrestrial ecosystems such as grasslands with intense grazing. Physiological integration within a seagrass clone (Harrison 1978; Iizumi and Hattori 1982; Tomasko and Dawes 1989a; Pedersen and Borum 1993) helps it withstand grazing. When photosynthetic tissues are removed, physiological readjustments occur among leaves, leaf shoots, and rhizomes (Dawes and Lawrence 1979; Dawes et al. 1979; Tomasko and Dawes 1989b). After adjustment, the remaining ungrazed shoots can exhibit increased rates of photosynthesis and production of nitrogen-rich young leaves. The new growth is higher-quality forage for sea turtles, which repeatedly return to feed on it (Bjorndal 1980; Thayer et al. 1982b, 1984; Zieman et al. 1984a). Because internal adjustments to grazing cannot be sustained indefinitely, there is a broad range of plant responses to grazing intensity. For example, heavy grazing by sea turtles (Williams 1988), sea urchins (Heck and Valentine 1995), and dugongs (Preen 1995) can lead to reduced seagrass standing crop, and intense grazing during fall and winter can lead to local disap-

pearance of seagrasses (Greenway 1974; Heck and Valentine 1995). However, intermediate levels of grazing can stimulate the production of new shoots and areal productivity, especially during periods of high growth (Valentine et al. 1997). Similarly, seven seagrass species in a variety of locations, subjected to a one-time experimental cropping of up to 100% of the aboveground shoot biomass, showed little evidence of negative effects on regrowth rates. Instead, regrowth rates at the highest levels of cropping were often greater than those with lower rates of biomass removal (Cebrián et al. 1998). Just as noted in terrestrial systems (McNaughton 1983; Belsky 1986; Huntley 1991; Herms and Mattson 1992), there is a continuum of seagrass responses to grazing pressure, ranging from negligible effects on shoot production at low intensity, to stimulatory effects at intermediate intensity and negative effects at high intensity. Although the ability of seagrasses to withstand grazing pressure appears to be related to the amount of belowground rhizome storage capacity (Dawes and Lawrence 1979; Dawes et al. 1979; Heck and Valentine 1995; Cebrián et al. 1998), this needs to be substantiated by experiments.

Animals also can influence the sexual reproduction of seagrasses. Polychaetes inhabiting eelgrass inflorescences (Hellwig-Armonies 1988) prey upon flowers and seeds (M. Herndon, pers. com.). Although there are few published studies on seagrass seedling recruitment in the field, seed predators can limit seedling recruitment (Fishman and Orth 1996). Although herbivores defoliate seagrasses, they also can exert a positive effect on seagrass population growth rates, persistence, and, conceivably, genetic diversity. Animals, by creating gaps in the canopy, can enhance the recruitment of seagrass; seed germination and seedling survival for *Zostera* spp. are significantly higher in gaps (Ewanchuk 1995, Peterken and Conacher 1997, Williams, unpubl. data).

The view that seagrass communities are not controlled by consumers recently achieved the status of a paradigm, with the advent of declines in seagrass vegetation (Orth and Moore 1983; Short et al. 1986; Robblee et al. 1991; Cambridge and McComb 1992; Short and Wyllie-Echeverria 1996) and the search for causes. Seagrasses require large quantities of light to support their rapid growth rates (McRoy and McMillan 1977; Kenworthy and Haunert 1991). When the attenuation of light increases as phytoplankton and epiphytes bloom under eutrophication or as sedimentation increases, seagrass distribution and abundance is clearly reduced (Dennison et al. 1993; Short et al. 1995; Moore et al. 1996; Olesen 1996). Hence, emphasis has been placed on physicochemical control of seagrass communities. However, the issue is more complex and interesting when subtle biological interactions between seagrasses, shading epiphytes, herbivores, and perhaps top predators are considered. Mesoherbivores clearly can control the growth of seagrass leaves by removing epiphytes (Neckles et al.1993; Williams and Ruckelshaus 1993; reviewed by Jernakoff et al. 1996), and thus can mitigate the negative effects of increasing eutrophication. Grazers similarly can control macroalgae that bloom in re-

sponse to eutrophication (Hauxwell et al. 1998). Epiphyte-grazer interactions need to be incorporated in models devised as management tools to predict seagrass distribution (Wetzel and Neckles 1986; Williams and Ruckelshaus 1993). Models promised for management are often based primarily on water column attenuation of light or water column nutrient concentrations. These models will be less useful where mesograzers control epiphytes.

Furthermore, the assumption that epiphyte-associated declines in seagrasses are due to bottom-up control by eutrophication needs to be evaluated against alternative hypotheses. For example, the papers cited in the preceding paragraph indicate that mesograzers can and do control epiphyte biomass. Mesograzers can exhibit nonlinear functional responses to increased resource availability (Nelson 1997), although the numerical responses are poorly known. In addition, Edgar (1993), after estimating food consumption by amphipods and gastropods, concluded that mesograzers are probably food-limited in Australian seagrass meadows. This raises the question of why mesograzers do not respond sufficiently to the eutrophication-induced algal proliferation to ultimately reestablish grazer control. An alternative to the conventional wisdom of bottom-up control of seagrasses in eutrophic environments may provide the explanation that overfishing of top predators might lead to a cascading effect in which epiphytes are released from grazing when small fishes increase and in turn control the abundance of meso- and microherbivores, such as isopods, caprellids, and amphipods (Figure 12.3). Data in partial support of this alternative hypothesis have recently been published (Heck et al. 2000), and confirmatory evidence for trophic cascades from freshwater macrophyte beds (Bronmark et al. 1992; Martin et al. 1992; McCollum et al. 1998) suggests that it deserves serious consideration.

In developing a general understanding of trophic interactions and community structure (e.g., Paine 1980; Polis 1994; Polis and Strong 1996), seagrass communities with their great diversity and abundance of organisms offer promising but unexplored model systems. On a gradient of primary production (Oksanen et al. 1981), they represent high end-point members. As discussed above, the wide variation between the relative importance of detritus versus living plants in supporting food webs should be useful in evaluating the effects of detritus and omnivory on trophic structure. There is exceptional functional diversity at the primary producer level because seagrasses themselves vary in nutritional value (Birch 1975; Irving et al. 1988), and they are associated with many different forms of algae, as we discussed previously. Epiphytes take on greater significance in seagrass beds than in other marine communities. This plant diversity can facilitate coexistence among very similar species of sea urchin consumers (Keller 1983). The combination of vascular plants and diverse forms of algae might also explain why seagrass beds not only support most of the kinds of animals found in the rocky, intertidal seaweed beds and unvegetated soft sediments, but also sea turtles, sirenians, and waterfowl not typically found in these other communities.
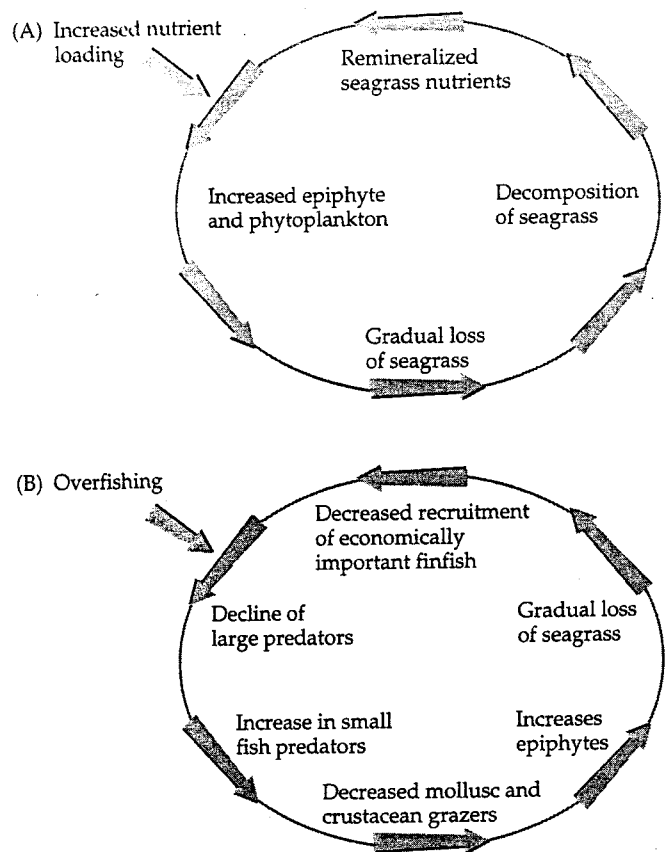

Figure 12.3 Models for the separate effects of increased nutrient loading (A) and overfishing (B) on seagrass ecosystems. Overfishing is hypothesized to initiate cascading trophic effects that lead to algal overgrowth and seagrass loss. The combined effects are expected to lead to accelerated seagrass loss.

Nursery and Refuge Function

Seagrass meadows support populations of invertebrates and small fishes that are substantially more abundant (often by an order of magnitude or more) than on nearby unvegetated substrata (Orth 1977; Virnstein et al. 1983; Orth et al. 1984; Heck et al. 1997). This is especially true of epifauna, but characteristic of infauna as well. In addition, because many of these animals are present as juveniles, seagrass beds often are described as "nursery grounds," (or said to play a "nursery role" in coastal waters), where nursery grounds are understood to be places where young animals survive and grow at exceptionally high rates (see Kikuchi 1980; Thayer et al. 1984; Zieman and Zieman 1989). The "nursery grounds" concept forms the primary basis for the protection and conservation of seagrass habitats, which are declining worldwide (Hinrichsen 1998). As such, it is being subjected to increasing scrutiny and, as noted following, there are inconsistencies in the existing data.

However, there is strong and consistent experimental evidence that seagrasses provide protection for a variety of small invertebrates from actively foraging fish predators (see reviews by Orth et al. 1984; Heck and Crowder 1991) and that

increasing amounts of vegetation provide increasing refuge from predators. Nevertheless, there is considerable variation in the protective function of vegetation among seasons and years (Heck and Wilson 1987), among seagrass species, and among individual suites of predators and prey in precisely how vegetation affects the outcome of predator-prey interactions (Heck and Crowder 1991). Most often there is threshold density of vegetation that is necessary before a significant reduction in predation effectiveness is noted, and different seagrass species provide varying amounts of protection, depending on the species-specific visual acuities, sizes, and behavior of predator and prey taxa (Heck and Crowder 1991; Orth 1992). The only published exception to this relationship showed that increasing vegetation density did not hinder the effectiveness of an ambush predator, the seahorse *Hippocampus erectus*, foraging on small caridean shrimp (James and Heck 1994). This result verified an earlier hypothesis that the success of ambush predators, in contrast to what was known about active foragers, might not be negatively affected by increasing seagrass biomass (Heck and Orth 1980). The rationale for the hypothesized difference between ambushers and active foragers was that prey would have increasing difficult times detecting the presence of ambushers as seagrass biomass increased, and at some point the advantage of inhabiting seagrass would switch from prey to predator.

Although fewer studies have investigated the form of the relationship between belowground biomass and the protection received by infaunal seagrass associates, the existing evidence, although published some time ago, suggests that the root-rhizome complex does reduce predator success (reviewed by Orth et al. 1984).

Given the nearly universal acceptance of the "nursery grounds" concept, it is somewhat surprising that there is only equivocal evidence that organisms grow at accelerated rates in seagrass habitats than elsewhere. In fact, nearly half the comparisons of invertebrate and fish growth rates in seagrass and on unvegetated substrate have found either no significant difference among substrata or significantly greater growth on unvegetated substrata (Heck et al. 1997). Included in the taxa studied are organisms as diverse as suspension-feeding bivalves, predatory penaeid shrimp and portunid crabs, and several species of small predatory fishes, indicating that these results are not taxon-specific. Therefore, the evidence for the role of food in the nursery grounds concept is far less compelling than the role of seagrass as shelter from predation.

In addition, there is a growing recognition that commercially important species in some areas do not appear to rely on seagrass meadows as important nursery grounds. For example, there are few commercially important species in Cape Cod waters that appear to rely heavily on seagrass nursery habitats (Heck et al. 1989; Heck et al. 1995). Similarly, there is little evidence for a significant seagrass nursery function in temperate Australia (Edgar and Shaw 1995; Gillanders and Kingsford 1996). At present the evidence for the seagrass "nursery grounds" concept seems to come consistently from warm subtropical and tropical latitudes and to be much less obvious in temperate and boreal latitudes. This may be explained by the existence of latitudinal gradients in predation pressure, with higher rates characteristic of tropical regions (cf. Bertness et al. 1981; Menge and Lubchenco 1981; Heck and Wilson 1987). Such higher predation rates may strongly select for shelter occupation in tropical taxa and may also lead to competition for hiding places among taxa at great risk to predation. Although competition for access to seagrass habitat and escape from predation has been demonstrated among seagrass-associated caridean shrimps (Coen et al. 1981; Tayasu et al. 1996), competition has been investigated very infrequently among seagrass animal associates and remains a fertile area for study.

Nontrophic Interactions between Plants and Animals

Seagrass communities provide ecologists with numerous opportunities in which to study nontrophic interactions between plants and animals and also the indirect effects, sensu Wooten (1994) and Menge (1995), of ecological interactions. Nontrophic interactions between seagrasses and animals also can exert major control over the distribution and growth of seagrasses. Well before recent emphasis on ecosystem engineers (Jones et al. 1994), it was known from seagrass studies that faunal feeding and burrowing could limit the distribution and growth of seagrasses and associated macroalgae (Ogden et al. 1973; Orth 1975; Suchanek 1983; Williams et al. 1985; Valentine et al. 1994). Mussels growing within seagrass beds can alleviate nutrient limitation of seagrass growth (Reusch et al. 1994; Reusch and Williams 1998; Peterson and Heck 1999). Mussels filter organic matter in the water column and transfer it to the sediments as feces and pseudofeces, which after remineralization increase porewater nutrients for seagrasses. Mussel-seagrass interactions are complex, because the same mussels can affect seagrasses in negative ways, depending on the densities of both interactors, the habitat structure, and the season. Eventually, mussels can replace seagrass beds, particularly in the face of frequent disturbances of seagrasses, because mussels can recruit and grow much more rapidly than seagrasses. Even without disturbance, mussel recruitment into seagrass beds can be so strong at times that the seagrass canopy collapses and eventually degrades (Sewell 1996, Williams, pers. obs.). Another indirect but potentially major influence of suspension feeders in seagrass beds is their potential to mediate deleterious phytoplankton-seagrass interactions in eutrophic estuaries (Lemmens et al. 1996).

INFLUENCE OF HABITAT STRUCTURE ON THE DISTRIBUTION AND ABUNDANCE OF ORGANISMS

Seagrass beds are structurally complex habitats (Robbins and Bell 1994), and this complexity exists at various spatial scales. Kelp beds and salt marshes also have complex habitat structure, but we argue that seagrass meadows are exceptional

among vegetation-dominated marine habitats. First, seagrasses add structure to both the above- and belowground habitat. Aboveground, structural complexity is afforded by different leaf morphologies within a bed, for example, straplike (e.g., *Zostera, Thalassia, Posidonia*), cylindrical (*Syringodium*), ovoid (*Halophila decipiens*), or clustered (*Amphibolis*). Leaf lengths can also vary; *Zostera marina* varies from a few cm to over 4 m within and among beds. *Zostera caulescens* achieves lengths of nearly 7 m (Aioi et al. 1998; see Figure 12.1). Reproductive shoots add structure because they branch more highly than the vegetative shoots of many species. Such differences in morphology result in quantitative differences in canopy height, area biomass, shoot density, and surface area:volume or SA/biomass ratios. Belowground, rhizomes and roots enmesh to create a solid mat that can extend meters into the sediments. The belowground habitat is structured vertically because the rhizomes of different species occupy relatively distinct layers in the sediment, with the larger species extending deeper (Williams 1990).

The prolific growth of macroalgae and epiphytes adds another element of structural complexity to seagrass beds. Neither seaweed beds nor salt marshes are noted in the literature for the prolific growth of epiphytic algae. Tidal exposure limits the development of algae in salt marshes. Kelps and rockweeds are relatively free of epiphytes compared to seagrasses. Rockweeds shed their outer cell walls and epiphytes on a regular basis, and algal cell wall characteristics or chemicals also might account for the difference in epiphyte development.

There are numerous reports of how grazers and bioturbators, humans anchoring boats, and drifting mats of macroalgae create gaps in seagrass beds. Similar observations are rarer from seaweed-dominated habitats and salt marshes, with the exceptions of disturbances from logs washing ashore in the intertidal and of decomposing wrack mats in salt marshes. Finally, at the largest spatial scale, currents configure seagrass vegetation and soft sediments to create numerous meadow configurations of different vertical relief and ranging from relatively continuous meadows to "leopard skin" patterns. Following, we describe seagrass habitat complexity in detail.

Animals encounter different habitat structure at many spatial scales within a seagrass bed (Table 12.1). At the scale of individual leaf shoots, animals encounter a gradient of epiphytic algal cover increasing toward the leaf tips (Nagle 1968). In moving only a few mm, an animal can encounter an order of magnitude difference in epiphytic algal biomass (Hall and Bell 1988). Over a few cm, animals can encounter different seagrass species as well as epiphytic, benthic, and drifting macroalgae (Figure 12.4, Figure 12.5). The additional structure of rhizophytic seaweeds (Figure 12.6) in the tropics influences the distribution of crustaceans within the seagrass bed. For example, *Penicillus* harbors an order of magnitude more crustaceans than *Halodule* (Stoner 1985). Larger animals moving over many meters also encounter a very heterogeneous environment because the aboveground seagrass biomass is patchily distributed, with a standard deviation typi-

Figure 12.4 A *Thalassia*-dominated bed in the Caribbean (3–5 m water depth). *Thalassia* leaves range between 30–60 cm in height and are encrusted with calcareous red algal crusts. The bed is mixed with *Syringodium, Halimeda*, and epiphytes over a scale of a few cm. *Halodule* is common, but not shown in this photograph.

cally twice the mean (Phillips and McRoy 1980, Figure 12.7). Small gaps are created by bioturbation (Suchanek 1983; Williams et al. 1985, Matsumasa et al. 1992; Valentine et al. 1994), and the vegetation is interrupted by macroalgal and mussel mats (Valentine and Heck 1993; Bell et al. 1995; Holmquist 1997). Large grazers such as dugongs, sea turtles, and geese create mosaics of large areas of leaf shoots cropped

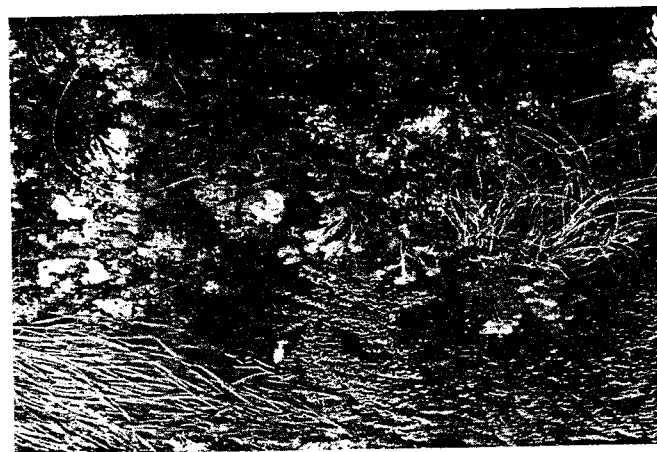
Figure 12.5 A bed of surfgrass (*Phyllospadix torreyi*) in southern California. Long fronds of the rockweed *Cystoseira* (Fucales) are evident at the top left of the photograph. Rocks are also covered with a variety of smaller red and brown seaweeds of different morphologies.

TABLE 12.1 Variation in the structural complexity of seagrass beds is evident at many scales.

Scale	Structures	Characteristics	Variable	Range[a]	Reference
mm^2	Single leaves	Microalgal cover	Biomass	10×	Hall & Bell 1988
cm^2	Leaf shoots	Macroalgal epiphytes			
		Leaf ramet spacing			
		Rhizome packing			
		Shape of leaf, rhizome, thallus			
		No. leaves in shoot			
		Increased epiphytes at tip			
	Algal thalli				
m^2	Aboveground	Leaf canopy	Leaf area	4× within species	McRoy & McMillan 1977
			Leaf biomass	10× within species	McRoy & McMillan 1977
				1000× among spp.	McRoy & McMillan 1977
			Canopy height	10× among spp.	
		Seaweeds			
		Drift algal mats	Biomass	100×	Bell et al. 1995
	Belowground	Vertical rhizome layering			
patch/gap[b]		Grazing scars	Diameter	>10× (turtles)	Ogden et al. 1983
		Bioturbation pits	Diameter	8× (stingray pits)	Valentine et al. 1994
		Callianasid shrimp mounds	No./m^2	16×	Suchanek 1983
		Rocky outcrops with large seaweeds			
		Seagrass patches	Diameter		
km^2	Coastal system	Patch configuration	Bed height/ length	20× (*Zostera*)	Fonseca et al. 1983
			Diameter	500× (*Cymodocea*)	Duarte & Sand-Jensen 1990

[a]*Range* refers to the magnitude of variation in the listed variable that can be encountered at the given scale.
[b]*Patch* refers to a vegetated area; *gap* refers to an unvegetated area.

to, or nearly to, the substratum (Thayer et al. 1984). Physical disturbances such as currents and storms create gaps that cover hundreds of meters (Patriquin 1975; Fonseca et al. 1983; Marbá and Duarte 1995). Humans rival or exceed nature in fragmenting the seagrass landscape by ripping up plants with boat propellers and anchors and by dredging and filling (Thayer et al. 1975; Zieman 1976; Williams 1988).

If the structure of habitat is important to the distribution of organisms at least at some scale, then differences among seagrass species should be reflected in their associated communities (Jernakoff and Nielsen 1998). This prediction assumes that other important parameters, for example, epiphytic food production or predation, are similar. An important research challenge is to test for the effects of parameters that covary with habitat structure. That acknowledged, habitat structure seems to be an important influence on the distribution of organisms within seagrass beds. Evidence for the importance of structure alone comes from studies showing that artificial leaves

support a community of epiphytes and mobile fishes and decapods similar in biomass and species composition to ones associated with natural leaves (Silberstein et al. 1986; Virnstein and Curran 1986; Hall and Bell 1988; Sogard 1989). Seagrass-produced chemicals inhibitory to epiphytes (Harrison 1982; Harrison and Durance 1985) apparently play a minor role in influencing the community.

Individual species clearly differentiate seagrass habitat structure based on leaf shoot length, density, or surface area. Stoner (1980) experimentally determined that amphipods differentiate among seagrass structure based on surface area rather than qualitative aspects of leaf shoot morphology. When *Thalassia*, *Halodule*, and *Syringodium* were offered to amphipods in equal biomass, amphipods preferred *Halodule* with its high SA/volume ratio. Amphipods were equally distributed among the three seagrasses when presented in equal surface area. Two species of pipefish select naturally long *Posidonia* or *Zostera* over clipped leaves, and males of one

Figure 12.6 Rhizophytic algae are common in tropical seagrass beds. Two species from the Caribbean: *Halimeda incrassata* (left) and *Penicillus capitatus* (right), both attached to their mass of rhizoids. The maximum aboveground height is around 20 cm.

species and both sexes of the other selected dense seagrass over experimentally thinned plots (Steffe et al. 1989). Pipefish of one species had significantly fuller guts in dense seagrass, suggesting that they captured their principal prey of copepods more efficiently there. This observation is consistent with the work of Thistle et al. (1984) on harpacticoid copepod abundance. Thistle et al. also applied an experimental ap-

Fig. 12.7 Patch and gap structure is demonstrated in a bed of *Halophila decipiens* in the Caribbean (20–30 m water depth). Mounds of callianasid shrimps are visible every few m. The bed contains 7 species of the rhizophytic alga *Caulerpa* and also *Halimeda* and *Penicillus*.

proach to understanding the influence of seagrass structure on harpacticoid copepod abundance. Using live *Syringodium* leaf shoots, mimics, and sediment controls with no structure, they found that copepod abundance and the biomass of bacterial food were higher around leaves and mimics, but there was no difference between them. Thus, the structure of the seagrass, not the release of dissolved organic substrate for bacterial growth, was critical to copepods and their food source. The authors hypothesized that the effect was due to a change in the water flow around the structures. Their hypothesis was supported later by experiments using tube mimics in flumes (Eckman 1985). Around nearby tubular structures such as seagrass leaf shoots, the viscous and diffusional sublayers within the boundary layer are thinner, thereby enhancing the flux of solutes to microbes near the structures. This is just one example of how seagrass structure can change water flow patterns and influence the distribution of animals.

Heterogeneity within seagrass patches can enhance the abundance and secondary production of associated animals. Drift algal mats result in local increases in faunal species and numbers, presumably through provision of additional resources and by increased dispersal of mat-associated animals into the seagrass bed (Virnstein and Howard 1987a, b; Holmquist 1997). However, if mats remain stationary too long and become anoxic, they have the potential to cause the loss of the seagrass (Holmquist 1997). Upright macroalgae (Heck 1979; Stoner and Lewis 1985), sponges and ascidians (Heck and Orth 1980), and mussel patches (Valentine and Heck 1993) within seagrass meadows lead to an enhanced abundance and even secondary production of associated fauna.

Organisms also respond to the larger landscape formed by mosaics of seagrasses patches and gaps. Mobile predators on infauna should be distributed predictably at the edges of a bed where the rhizome mat with associated animals is less dense and thus easier to penetrate. This relationship is upheld for stingrays (Ogden 1980; Valentine et al. 1994) and juveniles of the commercially valuable California halibut (Kramer 1990, pers. com.). The seagrass landscape also affects the growth and survival of bivalve species (Irlandi 1994; Irlandi et al. 1995; Reusch 1998a; Reusch and Williams 1999), copepod recruitment (Bell and Hicks 1991), the recruitment and survival of an epibiotic macroalga (Inglis 1994), and the accumulation of drift algae (Bell et al. 1995). Researchers are just beginning to study the underlying mechanisms for these landscape-scale patterns.

Studies in seagrass beds probably have contributed more to our understanding of the specific ways in which habitat structure influences individual organisms than studies in other benthic habitats. Nonetheless, a major research gap remains: How does habitat structure influence the structure of the associated community? As discussed previously, most of the seagrass studies focus on a single species rather than the community. Is habitat structure a better predictor of seagrass community structure than food availability or predation, which strongly influence community structure in the deep-

sea or rocky intertidal? Habitat structure hypothetically could be the most important determinant of seagrass community structure because it influences both food availability and predation. However, tight correlations between seagrass structural attributes (density, leaf area, canopy height) and community structure and secondary production unfortunately are not very evident (Heck 1979; Virnstein et al. 1984; Bell and Westoby 1986a, b; Virnstein and Howard 1987a, b; Worthington et al. 1992). It would be useful for seagrass management if a few attributes of seagrass vegetation were good predictors of community structure and secondary production. A few such structural predictors could render evaluation of the performance of seagrass mitigations and restorations more cost effective. Recently, Parker et al. (in preparation) determined that the diversity and production of a temperate seagrass epifaunal community depended more on the composition, particularly the morphologies, of the vegetation than on plant diversity per se. Structural complexity both within (density, biomass, leaf area, canopy height) and among (e.g., patch-gap structure) seagrass beds contribute to shaping the community, but the relative contributions of each are incompletely understood. To our knowledge, no appropriate data set exists for a multivariate analysis of the influence of different types and scales of habitat structure on community structure. An experiment that varies structure across the scales is needed but would be very labor intensive.

Community Responses to Seagrass-Induced Alterations in Water Flow Regimes

Along with predation, the dynamic relationship between seagrass beds and the water flow regime is invoked frequently to explain the observed differences both between seagrass and adjacent communities and among different seagrass communities. Seagrass landscapes are molded by water flow; beds become increasingly fragmented as water flows faster, eroding the sediments and belowground biomass (Fonseca et al. 1983). Some mobile organisms such as fishes and pink shrimps are predictably more abundant within low energy, more continuous seagrass beds (Bell et al. 1994; Murphy and Fonseca 1995). Within low-energy beds, these organisms might have reduced costs of mobility and foraging. The sediments have more organic matter that might be important in supporting prey populations.

Within the seagrass canopy, friction with leaf shoots extracts momentum from the flowing water so that the mean water flow speed is slower, mass transport is reduced, and sedimentation of small particles is increased (Burrell and Schubel 1977; Fonseca et al. 1982; Ackerman and Okubo 1993). The exact relationships between seagrass density, canopy height, water depth, seagrass bed dimensions, and various aspects of the water flow regime (mean speeds, variance in speed or turbulence, scales of turbulence, shear stress, mixing, and mass transport) are largely unknown and undoubtedly complex (Fonseca and Fisher 1986; Gambi et al. 1990; Worchester 1995; Koch and Gust 1999). Proper quantification of these relationships is difficult. To date, flumes have

not been scaled appropriately for naturally long seagrass leaves, and leaves interfere with field flow sensors, a problem that needs be resolved. Regardless of a limited quantitative understanding of fluid dynamics in seagrass beds, studies have demonstrated that modification of the flow regime by the seagrass canopy can affect the distribution and abundance of associated organisms, through influences on recruitment or dispersal and/or food supply (Thistle et al. 1984; Eckman 1985; Irlandi and Peterson 1991; Inglis 1994; Bell et al. 1995).

Patterns in the relative abundances of specific animals in seagrass beds with different structure and compared to adjacent unvegetated areas have been explained in light of how seagrass canopies influence recruitment processes through modifying hydrodynamic regimes (Peterson 1986; Eckman 1987; Orth 1992; Grizzle et al. 1996). Recruitment represents the net balance between the flux of larvae into the seagrass bed and the loss of newly settled larvae due to resuspension, assuming competent larvae are passively distributed. The flux increases both with higher larval concentration and higher water flow speeds (lateral advection) into the seagrass beds (Table 12.2). As larvae encounter surfaces on route to their preferred adult habitat (leaves, sediments), shear stress determines whether the larvae will be resuspended from each surface. Both advection and shear stress decrease as water flow slows, as it does as the number of leaf shoots increase in the canopy, but their effects might act in opposition (Table 12.2). Eckman (1987) concluded that advection, thus larval flux, was the dominant influence on bivalves settling on the leaves, because more settled in areas of lower shoot density where flow speeds were higher. In contrast, Peterson (1986) concluded the "baffling" effect of the seagrass shoots resulted in increased adult abundances of *Mercenaria mercenaria* in seagrass sediments, although factors affecting post-settlement survival were equally important in explaining the magnitude of the enhancement. For *Mercenaria*, low shear stress at the bottom of the canopy can be inferred as the overriding hydrodynamic control on recruitment of the clam. For benthic settlers like clams, increased shear stress at the unsuitable leaf surface should facilitate reentry into the water column, but decreased shear stress at the sediments should result in higher settlement due to reduced erosion of settlers. Epiphyte cover complicates the picture by increasing turbulence at the leaf surface (Koch 1994). Finally, geochemical cues for settlement, for example, ammonium concentrations (Woodin et al. 1998), are patchy on very local scales around individual shoots. This is because shoots redirect water flow and create pressure gradients that change the advective flux of dissolved substances from the sediments (Nepf and Koch 1999). Recruitment is a function of the combined hydrodynamic influences at each step on route to the adult habitat of an organism. Determining which step is the most critical one is a major research question. To this end, a sophisticated hydrodynamic settlement-recruitment model, analogous to ones developed for the unvegetated benthos (Denny and Shibata 1989; Gross et al. 1992; Eckman et al. 1994), would help

TABLE 12.2 Influence of hydrodynamics on larval recruitment in seagrass meadows.

Hydrodynamic Effects	Hypothetical Influence on Recruitment	Evidence
CANOPY Reduces flow speeds Reduces shear stress	Reduced larval flux Reduced resuspension of settlers on leaf; increased settlement of epiphytic organisms; increased settlement of benthos on unsuitable habitat	Higher settlement in sparse canopies[1]
	Reduced resuspension of settler in sediments; increased settlement of benthos	Higher settlement in seagrass vs. sand[2]
EPIPHYTES Increase leaf shear stress[3]	Increased resuspension of settlers on leaf; reduced settlement of epiphytic organisms; decreased settlement of benthos on unsuitable habitat	
"Monami" (canopy waving)	Increased larval flux[4]	

[1]Eckman 1987
[2]Peterson 1986
[3]Koch 1994
[4]Grizzle et al. 1996
Note: Recruitment is a function of the larval flux and the loss of new settlers due to resuspension. Larval flux is the rate that larvae intercept the substratum, which in turn is a function of larval concentration and mainstream water flow speed.

test the degree to which recruitment reflects the physical environment in a seagrass bed.

If most soft-bottom marine communities are not limited by the supply of propagules or larvae (Olafsson et al. 1994), then the supply of critical resources might be a more important influence on the abundances of organisms in seagrass beds. Nutrients and CO_2 are critical resources for algal epiphytes (Sand-Jensen et al. 1985), just as food is to filter and suspension feeders. Compared to many marine communities, most seagrass communities exist in relatively sheltered environments, with measured freestream flow speeds often less than 0.4 m/s. Sessile organisms within and below the canopy experience even slower flow speeds (references cited previously). Hypothetically, these organisms are subject to physiological limitation by the flux of critical resources. The supply of resources to many organisms within seagrass beds depends on the freestream water flow regime, the hydrodynamics at the water-organism boundary, the ambient resource concentration, and the resource acquisition capacity of the organism. Food flux for suspension feeders increases with water flow speeds, and active suspension feeders are less likely to deplete their food when the boundary layer is thinner under higher flow speeds (Fréchette et al. 1993). Flow speeds in most estuarine seagrass habitats are too slow to reduce particle capture by feeding structures. Beyond these generalizations, it is difficult to predict how the growth of organisms that depend on water flow for food delivery will vary with leaf shoot densities or seagrass patch size. This is illustrated by the wide variation in results from studies of bivalve growth in seagrass beds versus adjacent soft sediments

or among different leaf shoot densities (Kerswill 1949; Peterson et al. 1984; Eckman 1987; Peterson and Beal 1989; Coen and Heck 1991; Irlandi and Peterson 1991; Reusch and Williams 1998). Bivalve growth can increase, decrease, or not change as a function of seagrass cover and flow regimes. Increased growth within slower flow inside the canopy hypothetically reflects the depositional environment that entrains advected food particles (Peterson et al. 1984; Irlandi and Peterson 1991). In addition to food advected into the seagrass bed, these bivalves can utilize suspended benthic microalgae growing within the bed (Judge et al. 1993). What matters to the organism is the food delivered to its feeding ambit. Exactly where the animal resides will be important in determining how water flow affects food delivery. Where food concentrations are very high and densities of filter feeders are relatively low, we would predict that hydrodynamic effects on growth will be minor.

Until both food resources and hydrodynamics are quantified more precisely, the relationships between seagrass cover, water flow modification, and secondary production will not be resolved. To this end, Reusch and Williams (1999) found that the growth of the mussel *Musculista senhousia* in eelgrass beds was proportional to rates of horizontal advection, which decreased as eelgrass patch size increased. The hypothesis that the mussel was limited by a reduced flux of phytoplankton into the eelgrass bed was supported by measurements of reduced chlorophyll concentrations next to and just above the mussels compared to outside the canopy. This hypothesis was verified subsequently when mussels grew faster when experimentally supplemented in situ with phytoplankton (Allen

1999). We believe this is the first *direct* demonstration that the growth and survival of bivalves living in seagrass beds, and indeed in the benthos in general, can be limited by food.

Food availability, whether produced locally or advected in, is apparently important, but is only part of the story. For most of the bivalves studied, predation, which varies with seagrass structure, also had a significant effect on growth due to both direct effects and indirect ones wherein the presence of a predator limited feeding (Coen and Heck 1991; Irlandi and Peterson 1991; Pohl et al. 1991; Reusch 1998b).

LINKAGES AMONG MARINE COMMUNITIES

Seagrass communities can be linked to other marine communities in striking ways through the movement of animals and the export of large quantities of slowly decaying organic matter. Nightly migrations of French and white grunts from their daytime shelter among Caribbean reef corals to adjacent seagrass beds where they feed results in the transfer of nutrients back to the corals, whose growth is thereby increased (Meyer et al. 1983). Fishes living in close association with mangroves or migrating between them and seagrass beds apparently derive most of their trophic support from the seagrass beds (Marguillier et al. 1997). And, we can't resist including this probably unimportant but droll example of trophic transfer from a seagrass community to the squirrels that forage on detached eelgrass leaves in the harbor of Morro Bay, California (Roest 1993).

Seagrass beds export large quantities of leaves that are continuously replaced (Zieman et al. 1979; Josselyn et al. 1983; Bach et al. 1986). Because the leaves are buoyed by internal air channels and are refractory to decomposition, they can be transported far from their origin. A careful look at many deep-sea benthic photographs reveals the presence of seagrass leaves that provide both habitat and trophic support for deep-sea animals (Suchanek et al. 1985). Closer to shore, detrital seagrass mats serve as localized hot spots of secondary production (Vetter 1995). These linkages emphasize that degradation of nearshore seagrass beds can have far-reaching consequences for other marine communities.

ECOLOGICAL INTERACTIONS BETWEEN NATIVE AND NON-NATIVE MARINE SPECIES

Many marine communities have been invaded by non-native species (Steneck and Carlton, this volume), and there is concern that these species might reduce natural levels of biodiversity (Butman and Carlton 1995). In general, manipulative experiments rarely have been used to elucidate the ecological interactions between native and invading species (Kareiva 1996). As an exception to this, seagrass studies have contributed to the understanding that the ecological effects of invading species are complex and not always deleterious (Harrison 1987; Posey 1988; Sewell 1996; Zimmerman et al. 1996; Ceccherelli and Cinelli 1997; Reusch and Williams 1998, 1999). The invasion of *Zostera japonica* in the Pacific Northwest re-

gion of North America in the 1950s afforded the opportunity to study the effects of an invading species on seagrass communities. *Z. japonica* invaded intertidal mudflats located mostly above the upper tidal limit of native *Z. marina*, which was displaced only slightly during the invasion. By modifying the physical structure of the habitat, *Z. japonica* changed the community structure in mostly positive ways, for example, increasing species richness and the abundance of common species, although the abundance of some species declined or did not change (Harrison 1987; Posey 1988). *Z. japonica* also provided waterfowl with increased feeding ground and was easier to access and handle and had higher food quality than *Z. marina* (Baldwin and Lovvorn 1994). The changes were predictable from the ways that seagrasses in general structure the associated community, as discussed above.

Interactions between native *Zostera marina* and the non-native infauna mussel *Musculista senhousia* are more complicated. In the 1920s, *M. senhousia* invaded an astonishing variety of habitats on the west coast of the United States. *M. senhousia* can occur at densities > 15,000 individuals/m^2 in eelgrass beds in southern California, and the abundances of the two species is negatively correlated. The outcome of their interaction is a complicated function of relative plant and animal densities, seasonal shifts in the limiting factor for eelgrass growth, the structure of the eelgrass landscape, food availability for the mussel, and the presence of native gastropod predators (Reusch and Williams 1998, 1999; Reusch 1998b; Allen 1999; Williams and Ebert, unpubl.). The overriding influences are the patch structure of the habitat and food availability. In dense continuous meadows, the mussel starves because of the reduction in water flow, and thus phytoplankton flux into the meadow. Where eelgrass is sparse and patchy, the mussel can achieve densities sufficient to inhibit leaf growth rates. At all densities, the mussel inhibits the growth of eelgrass rhizomes and expansion of the meadow. Over time, the mussel is predicted to win because it recruits extremely well, grows fast and can preempt any habitat where eelgrass, slow to recruit and recover, is disturbed.

Range expansions of a limpet (*Tectura depicta*) and an anemone (*Bunodeopsis* sp.) from warmer waters into more northern eelgrass beds in California have contributed to recent and severe declines in eelgrass (Figure 12.8; Sewell 1996; Zimmerman et al. 1996). Both species are cryptogenic, that is, their origin is uncertain. The sudden appearance in Monterrey Bay of the limpet, which is typically found in southern California, is assumed to be in response to ocean warming. The anemone, misidentified for years, is known from tropical locales. Its distribution in San Diego eelgrass beds could represent either a range expansion in response to ocean warming or an introduction. The limpet catastrophically overgrazed its habitat. The anemone blooms in summers to cover virtually all eelgrass leaves, blocking light and causing the canopy to collapse, leading to eelgrass death. Such occurrences of new interactions between eelgrass and animals highlight that, although in general the kinds of interactions between seagrasses and introduced species can be predicted
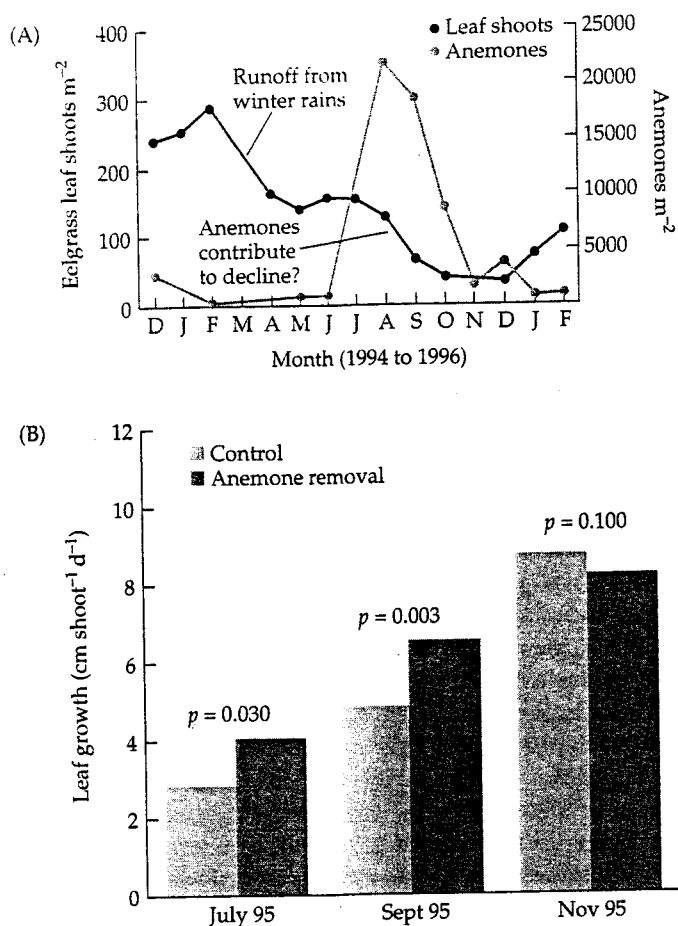
Figure 12.8 Effects of the cryptogenic anemone, *Bunodeopsis* sp., on eelgrass in San Diego, California. (A) Declines in eelgrass leaf shoot density (mean ± se, $n = 40$) coincide with summer increases in anemone density (mean, $n = 20$) in Mission Bay, San Diego. (B) Mean daily eelgrass leaf growth in three experimental removals of the anemones from eelgrass leaves ($n = 4$ treatments in July and September and 6 in November; experiments lasted 8–14 days). Probability levels from an analysis of covariance with leaf width as the covariate. Nonsignificant results of anemone removals in November were attributed to anemone densities that were 75% lower than in earlier experiments. (Data from Sewell 1996.)

from existing knowledge about seagrass communities, there are going to be surprises.

RESTORATION ECOLOGY

Seagrasses, along with mangroves and salt marshes, fall under the legislative mandate of the U.S. Clean Water Act, and thus their deliberate removal must be mitigated. As a result, much research has been devoted to restoration of seagrass ecosystems. Much of this research has been technique-driven and has lead to an understanding of the environmental parameters necessary to support seagrass growth (Fonseca et al. 1988). Here, we will focus on the community-level aspects of seagrass restoration. Establishment of community functions, particularly trophic support, is a primary goal of restoration, but one dif-

ficult to achieve. Designing seagrass beds to maximize functional equivalency requires an exacting knowledge of the mechanisms that result in a particular community and level of secondary production. As described above, ecologists understand the attributes, primarily structural, of the seagrass vegetation that control the distribution and abundance of specific organisms far better than those that influence community structure. Not surprisingly, one species will increase and another decrease as a function of leaf shoot density. This specific knowledge is very useful if mitigation or restoration is directed toward a target species, such as the scallop *Argopecten irradians* (Smith et al. 1989); however, most projects are directed toward community properties such as species diversity and total abundance.

Although there have been numerous seagrass mitigation and restoration projects (Fonseca et al. 1988; Thom 1990b), the results of the required monitoring of community development reside primarily in the gray literature. In the limited published studies, two approaches have been taken to assess the functionality of mitigated or restored beds. First, the community structure (number and density of individuals, number of taxa, species diversity indices) was compared in natural versus planted beds (Homziak et al. 1982; McLaughlin et al. 1983; Fonseca et al. 1990; Fonseca et al. 1996). Trajectories for community development were produced as a function of leaf shoot density (except in McLaughlin et al. 1983). The abundance and diversity of organisms, particularly mobile ones, became similar to natural areas relatively early after planting and, in some cases, before the vegetation had developed fully.

The second approach to evaluating functional equivalency has involved assessing the survival or production of a single species in transplanted versus natural beds (Smith et al. 1989; Bell et al. 1993; Clements et al. 1994). In these studies, the production of animal tissue was used as a measure of equivalency. Both arm regeneration rates for a brittle star and estimated biomass production for a polychaete were greater in transplanted beds of relatively young age (~ 2 years).

The authors just listed pointed out that only young beds were evaluated for functional equivalency. Brown-Peterson et al. (1993) compared 31-year-old seagrass beds that had colonized dredge spoils and suggested that fish community structure differed between these older beds and natural ones. The replicates for one bed type were located at a site physically different from the site for the other bed type, a problem that is common in restoration research. Unless restorations and mitigations are part of an adaptive management program of experimental design and hypothesis testing or are strictly research projects (Bell et al. 1993), they present ecologists with numerous problems of pseudoreplication. The development of restored or mitigated seagrass beds is a successional process (Bell et al. 1993; Montalvo et al. 1997), but unfortunately, seagrass succession has focused primarily on the development of vegetation and nutrient cycling processes (Williams 1990; Pedersen et al. 1997) to the exclusion of the associated animal community.

Studies on the functional equivalency of planted seagrass beds reveal major uncertainties in seagrass community ecology. Although leaf shoot density and perhaps canopy cover can be reasonable predictors of community structure on the scale of a single seagrass bed, the relationship of seagrass vegetation to secondary production is unresolved (Smith et al. 1989; Bell et al. 1993; Clements et al. 1994). Although it is generally assumed that high seagrass primary production supports high secondary production (e.g., Petersen and Boyson Jensen 1911), this relationship needs to be evaluated with more rigor. The study of Lubbers et al. (1990) in natural submersed vascular plant beds in the Chesapeake Bay provides a start. Fish biomass was a positive function of plant biomass. Of greater relevance, overall fish production was higher in vegetated versus nonvegetated sites and tracked seasonal changes in plant biomass changes, and fish guts were fuller. The increased production was largely attributable to higher growth rates, not higher biomass. The diets of several fishes shifted to epifauna in vegetation from infauna in unvegetated areas. Infauna are presumably harder for fishes to find.

Understanding the relationship of secondary to primary production is crucial not only for restoring seagrass beds but also for determining whether declines in fisheries are the result of, or merely correlated with, seagrass declines. This issue is difficult and requires an understanding of population demography and dynamics. Knowing population growth rates would help determine whether changes in numbers of organisms in planted seagrass beds merely reflect a redistribution of biomass from elsewhere. Attainment of functional equivalency will depend to some unknown degree on source populations and their proximity (e.g., Bell and Hicks 1991). A demographic approach to evaluating functional equivalency can help elucidate when immigration is important (Bell et al. 1993). In general, benthic marine ecologists have not linked how demographic changes in the populations that interact in a community ultimately lead to changes in community structure.

and thus radically changing the community. Why epiphytes can escape mesograzer control remains a major research question. Herbivores also influence seagrass physiology and demography, but these aspects deserve more study. Primary production exported from seagrass beds provides important linkages to other nearshore and offshore communities.

Another prevailing influence on seagrass communities is the complex above- and belowground structure of the vegetation. In other marine communities, experiments have verified that competition, predation, recruitment, or food flux control community structure. In seagrass beds, each of these very important processes is strongly modulated by the vegetation structure. The leaf canopy and the associated epiphyte community modify the hydrodynamic regime in very striking, complex ways. Spatial heterogeneity, for example, in the form of macroalgal mats or patches of filter feeders, increases the primary and secondary productivity in seagrass beds. Although ecologists understand the responses of many different species to seagrass habitat structure at a variety of scales, they have not been able to generalize about how habitat complexity influences community structure beyond knowing that with more vegetation, the numbers of individuals and species increase.

Seagrass beds are very susceptible to human influences. Seagrass declines occur when algae overgrow them. Eutrophication has been implicated in algal overgrowth, but this hypothesis needs to be tested against the alternative that the removal of top predators results in algal overgrowth. Introductions of animal species new to a seagrass community have significant, primarily negative effects on seagrasses. In contrast, when non-native seagrass vegetation is introduced to a locale, the overall abundance of other organisms in the community tends to increase. Restoration of seagrass beds offers a unique opportunity to determine how the associated community develops and also to perform controlled manipulations of the structural complexity to test for its influence on community structure.

SUMMARY

The high primary production of seagrass beds and the diversity of primary producers is a major factor of importance for the associated animal communities. Although most of this production enters food webs as detritus, herbivory nonetheless is an important process in seagrass beds. Herbivores can control the distribution and abundance of seagrasses directly as well as indirectly by controlling algal epiphytes. Epiphytic microalgae are more notable than in many other vegetated marine communities because of their role in trophic support and because of their propensity for overgrowing seagrasses

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