

A Global Crisis for Seagrass Ecosystems

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Seagrasses, marine flowering plants, have a long evolutionary history but are now challenged with rapid environmental changes as a result of coastal human population pressures. Seagrasses provide key ecological services, including organic carbon production and export, nutrient cycling, sediment stabilization, enhanced biodiversity, and trophic transfers to adjacent habitats in tropical and temperate regions. They also serve as “coastal canaries,” global biological sentinels of increasing anthropogenic influences in coastal ecosystems, with large-scale losses reported worldwide. Multiple stressors, including sediment and nutrient runoff, physical disturbance, invasive species, disease, commercial fishing practices, aquaculture, overgrazing, algal blooms, and global warming, cause seagrass declines at scales of square meters to hundreds of square kilometers. Reported seagrass losses have led to increased awareness of the need for seagrass protection, monitoring, management, and restoration. However, seagrass science, which has rapidly grown, is disconnected from public awareness of seagrasses, which has lagged behind awareness of other coastal ecosystems. There is a critical need for a targeted global conservation effort that includes a reduction of watershed nutrient and sediment inputs to seagrass habitats and a targeted educational program informing regulators and the public of the value of seagrass meadows.

Keywords: seagrass, decline, sentinels, ecological services, monitoring

Seagrasses—a unique group of flowering plants that have adapted to exist fully submersed in the sea—profoundly influence the physical, chemical, and biological environments in coastal waters, acting as ecological engineers (*sensu* Wright and Jones 2006) and providing numerous important ecological services to the marine environment (Costanza et al. 1997). Seagrasses alter water flow, nutrient cycling, and food web structure (Hemminga and Duarte 2000). They are an important food source for megaherbivores such as green sea turtles, dugongs, and manatees, and provide critical habitat for many animals, including commercially and recreationally important fishery species (figure 1; Beck et al. 2001). They also stabilize sediments and produce large

quantities of organic carbon. However, seagrasses and these associated ecosystem services are under direct threat from a host of anthropogenic influences.

Seagrasses are distributed across the globe (figure 2), but unlike other taxonomic groups with worldwide distribution, they exhibit low taxonomic diversity (approximately 60 species worldwide, compared with approximately 250,000 terrestrial angiosperms). The three independent lineages of seagrass (Hydrocharitaceae, Cymodoceaceae complex, and Zosteraceae) evolved from a single lineage of monocotyledonous flowering plants between 70 million and 100 million years ago (figure 3a; Les et al. 1997). This is in stark contrast to other plant groups that have colonized the marine envi-

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Figure 1. Examples of seagrass meadows and associated animals. (a) Seahorse (*Hippocampus* sp.) in temperate *Cymodocea nodosa* meadow, Mediterranean Sea. Photograph: Gérard Pergent. (b) School of zebrafish (*Girella zebra*) over a temperate *Posidonia australis* meadow, Western Australia. Photograph: Gary A. Kendrick. (c) Manatee (*Trichechus manatus*) feeding in a tropical *Thalassia testudinum* meadow, Puerto Rico. Photograph: James Reid. (d) Green sea turtle (*Chelonia mydas*) feeding in a tropical *T. testudinum* meadow, Yucatán. Photograph: Robert P. van Dam.

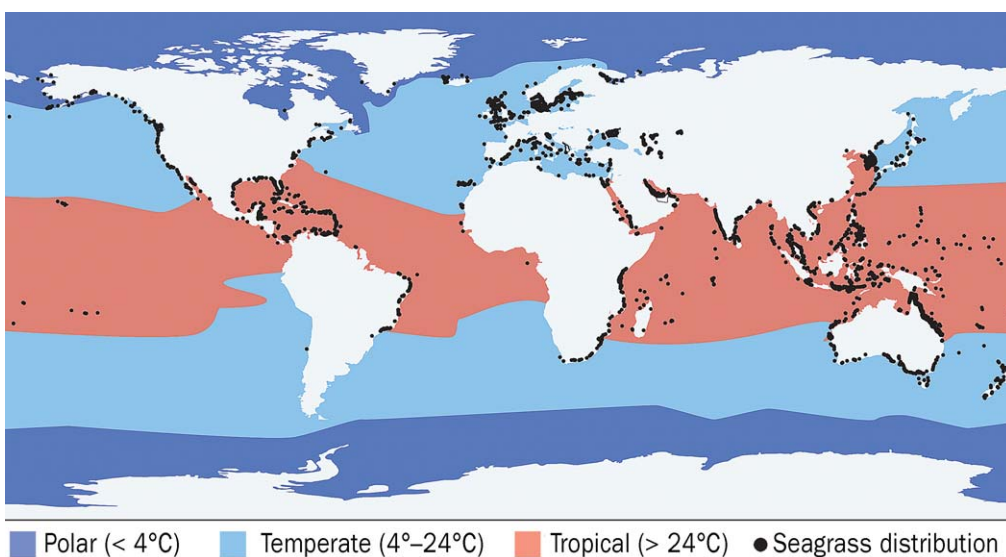


Figure 2. Current global distribution of seagrass in relation to mean ocean temperature. Regional divisions are based on polar (< 4 degrees Celsius [°C]), temperate (4°C–24°C), and tropical (> 24°C) climate (Green and Short 2003).

ronment, such as salt marsh plants, mangroves, and marine algae, which are descended from multiple and diverse evolutionary lineages. In spite of their low species diversity and unique physiological characteristics, seagrasses have successfully colonized all but the most polar seas (figure 2). Compared with seagrass meadows, the other major coastal marine habitats are geographically restricted to much smaller latitudinal ranges (mangroves and coral reefs in tropical regions, kelp beds and salt marshes in temperate regions).

Seagrasses have developed unique ecological, physiological, and morphological adaptations to a completely submerged existence, including internal gas transport, epidermal chloroplasts, submarine pollination, and marine dispersal (den Hartog 1970, Les et al. 1997). To provide oxygen to their roots and rhizomes, often growing in highly reducing sediments with toxic sulfide levels, and to support large amounts of nonphotosynthetic tissue (Terrados et al. 1999), seagrasses require some of the highest light levels of any plant group worldwide (approaching 25% of incident radiation in some seagrass species, compared with 1% or less for other angiosperm species; Dennison et al. 1993). These extremely high light requirements mean that seagrasses are acutely responsive to environmental changes, especially those that alter water clarity. Although it is true that the global distribution and abundance of seagrasses have changed over evolutionary time in response to sea-level change, physical modification of coastlines (figure 3a, 3b), and global changes in atmospheric carbon dioxide (CO₂) concentration and water temperature (figure 3c; Crowley 1990, Berner and Kothavala 2001), the very gradual changes in environmental conditions over the history of seagrass evolution are overshadowed by current changes to the coastal zone resulting from increased human pressures. These pressures result in the degradation of estuaries and coastal seas, producing changes to species and habitats

(Lotze et al. 2006). These rapid contemporary changes have been caused by a multitude of mechanisms, including increased nutrient and sediment runoff, invasive species, hydrological alterations, and commercial fishing practices. As a result, reported seagrass losses worldwide have been accumulating.

Seagrasses as ecological service providers and biological sentinels

Seagrass meadows have important ecological roles in coastal ecosystems and provide high-value ecosystem services compared with other marine and terrestrial habi-

tats (figure 4; Costanza et al. 1997). For example, primary production from seagrasses and their associated macro- and microepiphytes rivals or exceeds that of many cultivated terrestrial ecosystems (Duarte and Chiscano 1999). Seagrasses also provide an enormous source of carbon to the detrital pool, some of which is exported to the deep sea, where it provides a critical supply of organic matter in an extremely food-limited environment (Suchanek et al. 1985). Much of the excess organic carbon produced is buried within seagrass sediments, which are hotspots for carbon sequestration in the biosphere (Duarte et al. 2005). The structural components of seagrass leaves, rhizomes, and roots modify currents and waves, trapping and storing both sediments and nutrients, and effectively filter nutrient inputs to the coastal ocean (Hemminga and Duarte 2000). Biodiversity in seagrass meadows is greater than in adjacent unvegetated areas, and faunal densities are orders of magnitude higher inside the meadows (Hemminga and Duarte 2000). They also serve as a nursery ground, often to juvenile stages of economically important species of finfish and shellfish, although the species vary by region and climate (figure 4; Beck et al. 2001, Heck et al. 2003). The large-scale loss of seagrass that occurred on both sides of the North Atlantic Ocean in the early 1930s, a result of “eelgrass wasting disease” (Rasmussen 1977), had many effects on the ecosystem. Associated with this loss were a collapse of scallop fisheries and dramatic reductions in waterfowl populations. In addition, it resulted in the only known case of an extinction of a marine gastropod (Carlton et al. 1991). Finally, the proximity of seagrass beds to other critical habitats, such as salt marshes (in temperate regions) or mangroves and coral reefs (in tropical regions), facilitates trophic transfers and cross-habitat utilization by fishes and invertebrates (Beck et al. 2001). This provides an energy subsidy that may be essential in maintaining the abundance of some coral reef fish species (Valentine and Heck 2005).

Moreover, seagrasses can be considered as biological sentinels, or “coastal canaries.” Changes in seagrass distribution, such as a reduction in the maximum depth limit (Abal and Dennison 1996) or widespread seagrass loss (Cambridge and McComb 1984), signal important losses of ecosystem services that seagrasses provide. Seagrasses are sessile, essentially integrating the relevant water quality attributes, such as chlorophyll and turbidity, that affect the light reaching their leaves. Several features of seagrasses and seagrass meadows result in their particular importance in this regard. The widespread distribution of seagrasses throughout tropical and temperate regions (figure 2) allows better assessment of larger-scale trends than do other comparable coastal habitats, such as mangrove, corals, or salt marsh plants, which are limited to only one of these broad geographic regions. Seagrasses also live in

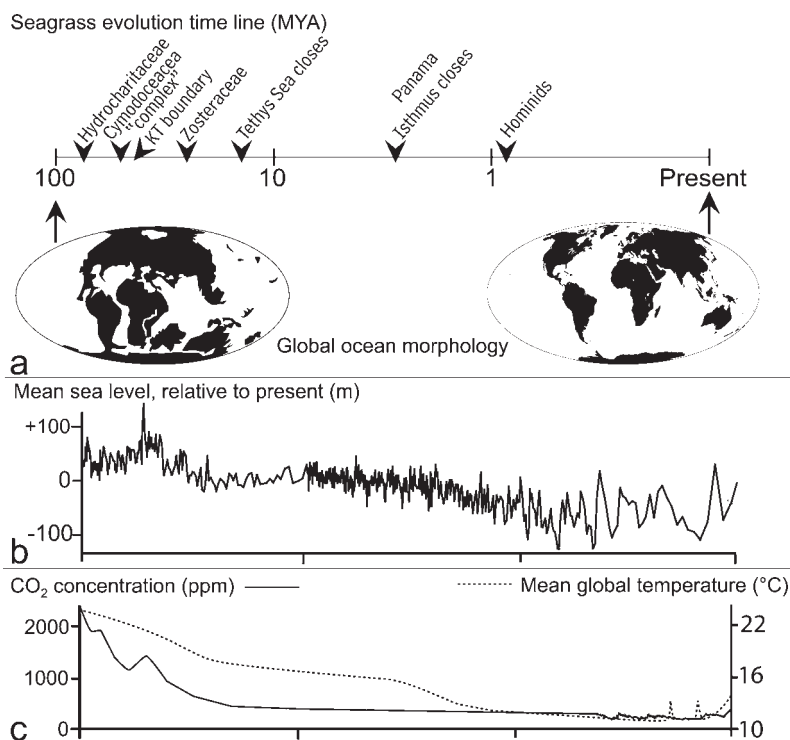


Figure 3. Seagrass evolution time line for the past 100 million years during periods of changing (a) global ocean structure (Dietz and Holden 1970), (b) mean sea level (Miller et al. 2005), and (c) atmospheric carbon dioxide (CO₂) concentration (Berner and Kothavala 2001) and mean global temperature (Crowley 1990). Abbreviations: °C, degrees Celsius; KT, Cretaceous–Tertiary (approximately 65 million years ago [MYA]); m, meters; ppm, parts per million.

shallow, protected coastal waters, directly in the path of watershed nutrient and sediment inputs, and are therefore highly susceptible to these inputs (figure 4), unlike mangrove forests (which are largely unaffected by water quality) or coral reefs (which occur farther away from the inputs).

Another feature that makes seagrasses a valuable biological indicator is that they integrate environmental impacts over measurable and definable timescales (Longstaff and Dennison 1999, Carruthers et al. 2002), and a number of key examples support this concept. Increased coastal development leading to nutrient inputs in Cockburn Sound, Australia, led to large-scale losses of seagrass into the 1990s, and seagrasses remain at low levels in the area today (Walker et al. 2006). The loss of seagrass led to sediment resuspension, hampering restoration efforts and negatively affecting fish populations. In this region of Australia, if seagrass density drops below the 25th percentile of the long-term average for two consecutive years, remedial action is now mandated by law in confronting diffuse sources of pollution. Because of the susceptibility of seagrasses to such stresses and the high level of ecosystem services they provide, seagrasses are also used as one of the five sensitive indicators of pollution in the US National Estuarine Eutrophication Assessment (Bricker et al. 2003). And in the Chesapeake Bay, historical levels of

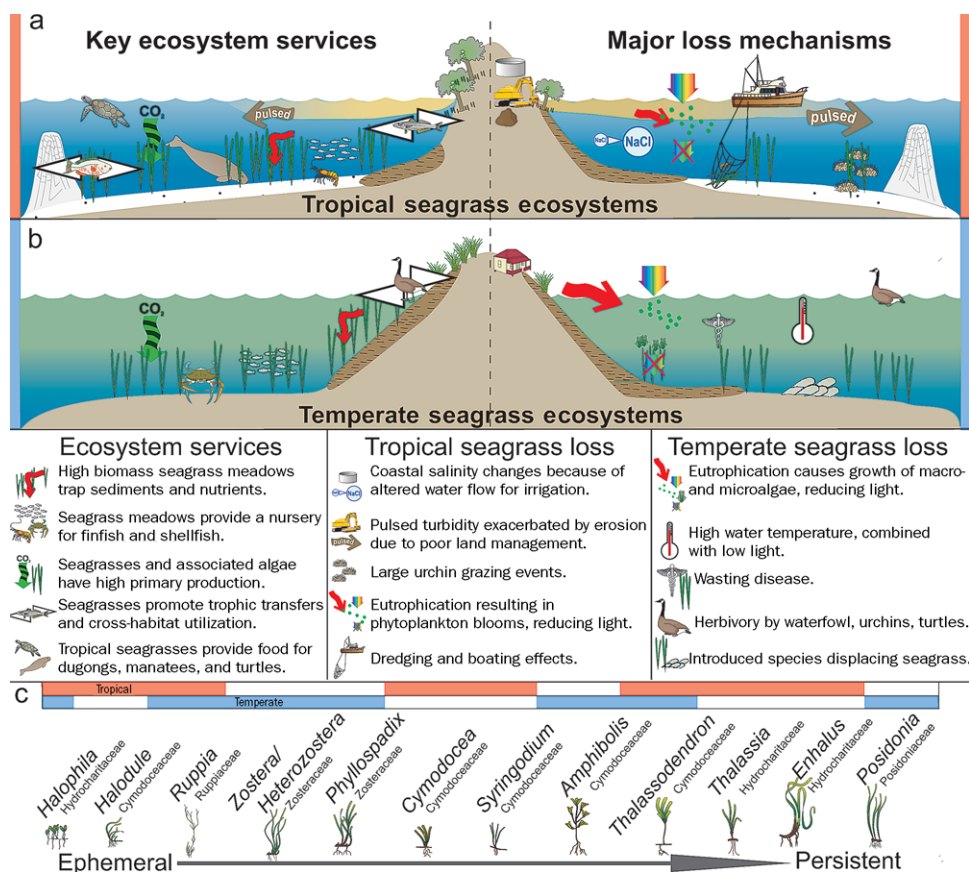


Figure 4. Conceptual diagrams for (a) tropical and (b) temperate seagrass ecosystems, detailing key ecosystem services and major mechanisms of seagrass loss. (c) Temperate and tropical seagrass genera (and family names), from ephemeral to persistent.

seagrass abundance (based on an assessment of historical photography) are being used as a target for the attainment of improved water quality from comprehensive nutrient and sediment management strategies (Orth et al. 2002).

The challenge of rapid environmental changes

Seagrasses now live in a marine environment with a lower mean temperature and lower availability of CO_2 than were experienced by their ancestors (Beer and Koch 1996). The recent trends of increasing global temperature, sea-level rise, and CO_2 concentrations (figure 3c, 5a, 5b) could result in environments that are potentially more conducive for many seagrass species. However, as a result of increased human population (figure 5c) and concomitant increased anthropogenic pressure to the coastal zone, the rates of change in coastal waters today are much faster than those experienced in the previous 100 million years of evolutionary history, and may well be too fast to allow these species to adapt. Where human activities have led to a reduction in the genetic diversity of seagrasses, these species' adaptation could be compromised (Williams 2001). In many areas, human alterations to the coastal zone (coastal hardening through breakwaters, harbors, and groins) have led to a situation that

prevents the shoreward migration of the seagrasses necessitated by sea-level rise. In addition, significant seagrass habitat continues to be lost to coastal development (marinas, canal estates, and industry), leading to meadow fragmentation, with unknown consequences for long-term survival (Fonseca et al. 2000).

Seagrass meadows are increasingly being recognized for their dynamic nature, in many cases on an interannual basis, with a dynamic equilibrium at broad spatial scales (square kilometers) even in areas where water quality remains high (Fonseca et al. 2000, Kendrick et al. 2000). But this awareness is being overshadowed by rapid, large-scale seagrass losses over relatively short temporal scales throughout the world, in places such as the European Mediterranean (Marbà et al. 2005), Japan (Environment Agency of Japan 2000), the Chesapeake Bay (Orth and Moore 1983) and Florida Bay (Fourqurean and Robblee 1999) in North America, and Cockburn Sound (Walker et al. 2006) and Western Port (Bulthuis 1983) in Australia. Although there are places where seagrass loss has been reversed following improvements in water quality, such as Tampa Bay, North America (Tomasko et al. 2005), and Hervey Bay, Australia (Preen and Marsh 1995), the number of declines far exceeds the reported increases, leading to

the concern that seagrasses are experiencing a global crisis (table 1; Short and Wyllie-Echeverria 1996, Duarte 1999, 2002, Green and Short 2003).

Multiple stressors behind seagrass declines

Environmental, biological, and extreme climatological events have been identified as causes of seagrass losses in temperate and tropical regions (table 1). Threats from global climate change (e.g., increases in sea surface temperature, sea level, and frequency and intensity of storms and associated surge and swells), from regional shifts in water quality (e.g., in the Chesapeake Bay; Kemp et al. 2005), and from more localized impacts due to increased loading of sediment, contaminants, and nutrients (figure 6a) reaching coastal environments (e.g., Cockburn Sound; Walker et al. 2006) have had demonstrable impacts on the health of seagrass-dominated coastal ecosystems worldwide (table 1). These global, regional, and local stressors can all independently result in large-scale seagrass loss; however, seagrasses are often simultaneously influenced by multiple stressors at different temporal and spatial scales, and studies that examine the interacting impacts of multiple stressors are lacking. In all regions, the environmental effects of excess nutrients or sediments are the most common and significant causes of seagrass decline, and result in small to very large areas of seagrass being lost. The direct influence of other organisms (e.g., brown tides, urchin overgrazing, and disease) has also led to large-scale losses and, when acting in concert with suspended sediments and nutrients, can accelerate the trajectory of seagrass loss for the area in question. The greater diversity of causes attributed to seagrass declines in temperate regions most likely reflects the much greater research and monitoring effort in Europe, North America, and southern Australia (Duarte 1999), rather than greater susceptibility in these regions (table 1).

Extreme climatic events (e.g., hurricanes, tsunamis) also can have large-scale impacts on seagrass communities and subsequent effects on the ecosystem services provided by seagrass meadows (table 1, figure 4). In the case of the pulsed turbidity events following the passage of tropical storms in Hervey

Seagrass–human interaction time line (YBP)

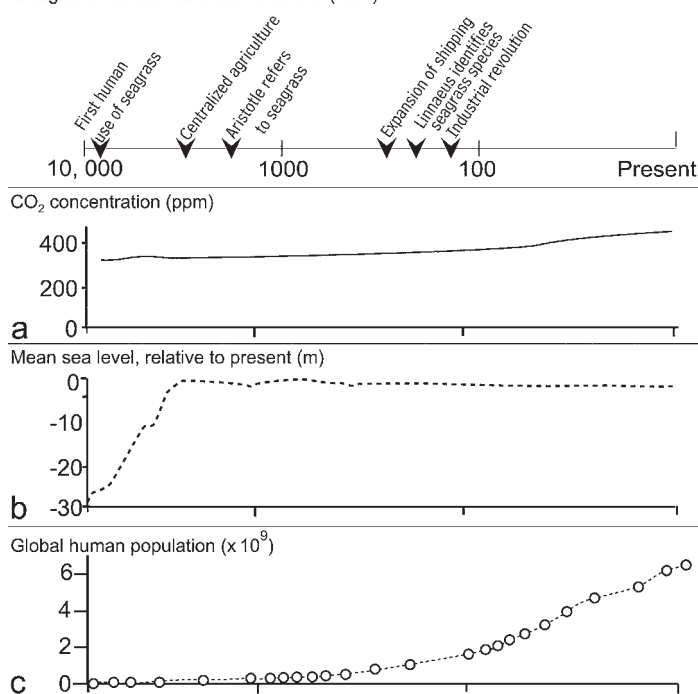


Figure 5. Seagrass–human interaction time line for the past 10,000 years, showing (a) carbon dioxide (CO_2) concentrations (Thoning et al. 1989, Petit et al. 1999), (b) mean sea level (Fleming et al. 1998), and (c) global human population (Cohen et al. 1995). Abbreviations: m, meters; ppm, parts per million; YBP, years before the present.

Bay, Australia, which resulted in 1000 km² of seagrass loss, high mortality and emigration of dugong eventually occurred (Preen and Marsh 1995). Recently, greater attention has focused on the role of top-down control in seagrass declines, as cascading effects on trophic dynamics follow the loss of higher-level consumers in seagrasses and other ecosystems (Heck et al. 2000, Jackson et al. 2001). Thus, seagrasses are being influenced by both bottom-up and top-down processes (Heck and Orth 2006). Although our primary focus here is on the seagrasses themselves, seagrass-associated species are also threatened or vulnerable to extinction. Eleven of 28 fish

Table 1. A synthesis of 47 representative case studies of seagrass loss.

| Area lost (km ²) | Major mechanisms of loss (number of reports) | | |
|------------------------------|--|---|---------------------------|
| | Environmental | Biological | Extreme events |
| <i>Temperate region</i> | | | |
| < 1.0 | Dredging, hydrological, dune migration (7) | Herbivory, introduced species, bioturbation (7) | Ice scour, heat waves (2) |
| 1.0–100 | Eutrophication, sediment deposition (4) | Brown tide (1) | No data |
| > 100 | Eutrophication, sea-level rise, high temperature (5) | Wasting disease (1) | No data |
| <i>Tropical region</i> | | | |
| < 1.0 | Vessel grounding, thermal pollution (5) | Herbivory (3) | No data |
| 1.0–100 | Eutrophication, boating, sedimentation (6) | Brown tide, urchin herbivory (2) | No data |
| > 100 | Hydrological, sediment resuspension (3) | No data | Pulsed turbidity (1) |

Note: The seagrass genera studied in temperate regions include *Cymodocea*, *Halodule*, *Heterozostera/Zostera*, *Posidonia*, *Syringodium*, and *Thalassia*; genera studied in tropical regions include *Halodule*, *Halophila*, *Syringodium*, *Thalassia*, and *Zostera*. An expanded table detailing the results of each study can be found at www.vims.edu/bio/sav/bioscience_global_crisis_table_1.pdf.

species vulnerable to extinction in the United States use seagrass habitat during at least part of their life cycle (Musick et al. 2000).

In addition to the well-documented causes of seagrass declines, other threats to these species are emerging. Over the last 20 years, introductions of nonnative marine species have arisen as a major environmental challenge for the world's oceans (Carlton 1989). Such introductions are accelerating worldwide (Ruiz et al. 2000), a trend that will continue as the pathways for introductions widen and proliferate and as intervention lags (figure 6b; Naylor et al. 2001, Levine and D'Antonio 2003, Padilla and Williams 2004). At least 28 non-native species have become established in seagrass beds worldwide, of which 64% have documented or inferred negative effects (figure 6b). The concern about this emerging threat to seagrass beds is that, whereas it is possible to reverse eutro-

phication or cease dredge-and-fill activities, it is virtually impossible to remove a nonnative species after establishment and spread (Lodge et al. 2006). Lastly, the rapid expansion of fish farming and other aquaculture practices (e.g., shellfish culture) can have serious consequences on local populations of seagrasses through physical disturbance or increased deposition of organic matter and nutrients (Marbà et al. 2006).

Seagrass monitoring, management, protection, and restoration

Reported cases of seagrass loss have increased almost tenfold over the last 40 years in both tropical and temperate regions (figure 6c), suggesting increased rates of seagrass decline worldwide. In response to seagrass loss caused by increasing anthropogenic stresses on coastal seagrass meadows, during

the last decade there has been a major increase in the number of marine protected areas that include seagrass (figure 6d) and in seagrass monitoring (figure 6e) and restoration projects throughout the world. The current challenges are to synthesize this information to enhance our understanding of global seagrass processes, threats, and change, and to apply this knowledge to develop effective resource management programs. Efforts to protect seagrasses now include 19 monitoring programs that encompass 30 seagrass species in 44 countries (approximately 2000 sites).

Perhaps the most difficult issue facing resource managers as they try to protect seagrasses is in implementing management plans to reduce nutrients and sediments from both diffuse and point sources in surrounding watersheds, especially where watersheds cross jurisdictional boundaries. Seagrass distribution and abundance are being successfully incorporated into water quality management programs and environmental impact studies in several areas, notably the Chesapeake Bay and Florida in North America, and Moreton Bay and the Great Barrier Reef Marine Park in Australia (Kenworthy et al. 2006). Management applications are based on the foundation of seagrass knowledge developed in each of those areas and are aimed at establishing water quality standards to conserve and restore seagrasses (Dennison et al. 1993, Coles and Fortes 2001, Kenworthy et al. 2006).

A number of seagrass management plans have objectives with quantitative

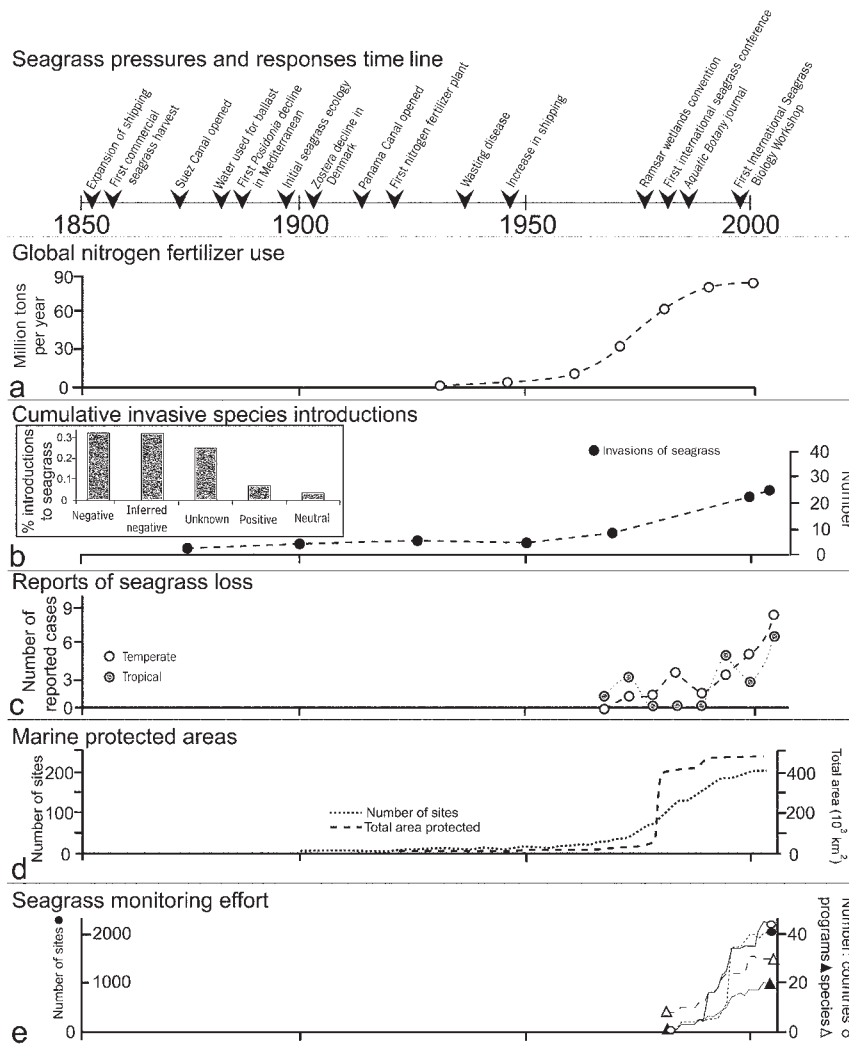


Figure 6. Time line showing pressures on seagrass populations and responses over the last 150 years, including (a) nitrogen fertilizer use (Frink et al. 1999), (b) species introduced to the marine environment (Ruiz et al. 2000), (c) reported cases of seagrass loss in both tropical and temperate regions since 1965, (d) marine protected areas (based on Spalding et al. 2003), and (e) monitoring effort (Duarte et al. 2004).

metrics aimed at restoring seagrass to target levels that allow resource managers, who are making critical decisions, to expend public funds. One key example is the process of seagrass restoration, for which costs are very high (Kenworthy et al. 2006) and success is uncertain. Worldwide, the success of seagrass transplantation and restoration is around 30% (Fonseca et al. 1998), although in some regions higher success rates have been reported (Green and Short 2003). Numerous restoration projects have been attempted or are being planned at mostly small scales (< 1 ha) using a variety of techniques with both adult plants and seeds, although interest in larger-scale transplant programs is growing as resource managers become more aware of the value of seagrass and develop mitigation programs to offset losses from activities such as dredging (Fonseca et al. 1998). However, some species are so difficult to transplant that restoration is not logistically or economically feasible, and longer-term studies that compare the functioning of transplanted areas with that of natural systems are rare (Fonseca et al. 1998).

Seagrass loss is usually the symptom of a larger problem. To effectively reverse the decline of seagrasses, conservation plans must first identify and resolve the problems at a scale that includes the interconnectivity of coastal systems and the mechanisms affecting the declines and gains (e.g., water quality, land use practices). Once this is done, restoration efforts should be balanced against the capacity of seagrasses to recover naturally. Strategic restoration can introduce founder populations that can accelerate the overall recovery of the ecosystem (Orth et al. 2006). At present, our knowledge of the population dynamics of seagrasses remains poor for the majority of species and regions (Kenworthy 2000). As a result, considerable research efforts will be required to guide effective restoration and preserve genetic diversity (Williams 2001). Better ecological information on such approaches is required, and especially the trajectories on how rapidly ecosystem services are restored. Until this is achieved, management

efforts should be aimed at systemwide approaches to protect these ecosystems.

Science and public awareness of seagrasses: A disconnect

Over the last 35 years, scientists have responded to the need for more information on seagrasses and their contribution to the productivity of coastal and estuarine systems with more research and monitoring programs that have resulted in a 100-fold increase in the annual number of papers published during this time period. This increase represents a sustained publication growth rate of 12.8% per year (figure 7a) and includes a seagrass atlas (Green and Short 2003), a methods book (Short and Coles 2001), and two research syntheses (Hemminga and Duarte 2000, Larkum et al. 2006).

Despite the increase in scientific publications on seagrasses, the level of public awareness, as reflected by the number of reports on seagrass ecosystems in the media, is far less than that for other coastal habitats. Salt marshes, mangroves, and coral reefs receive 3-fold to 100-fold more media attention than seagrass ecosystems, although the services provided by seagrasses, together with algal beds, deliver a value at least twice as high as the next most valuable habitat (figure 7b; Costanza et al. 1997). This difference in media attention partly reflects disproportionate research effort, as the number of scientific documents on seagrass is also below those on salt marshes, mangroves, and coral reefs (figure 7b). Reports on seagrasses in the *New York Times* and *National Geographic* are 3 to 50 times lower than those for salt marshes, mangroves, and coral reefs. Nevertheless, these data indicate that translating scientific understanding of seagrass ecosystems into public awareness has not been as effective as for other coastal ecosystems.

Much of this disconnect between available information and public awareness undoubtedly stems from the invisibility of seagrasses, as they grow underwater, and from the avoidance

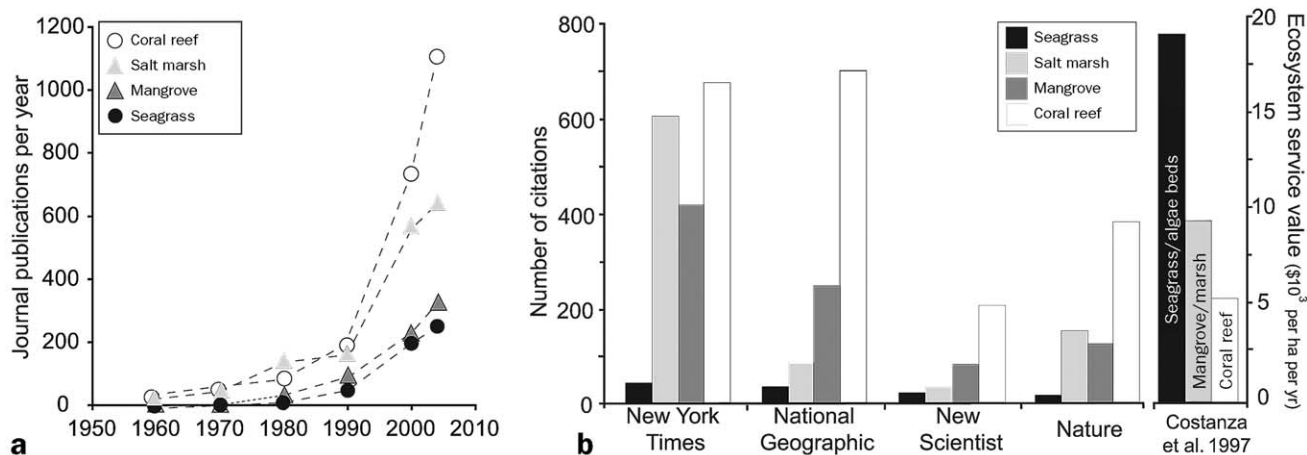


Figure 7. Comparison of seagrass, salt marsh, mangrove, and coral reef habitats in terms of (a) journal publications (Web of Science 1950–2006) and (b) citations in more broadly accessed media (Google and Web of Science), and estimated monetary value of ecosystem services provided by these habitats (Costanza et al. 1997).

of their very shallow habitat by many boaters (unless they run aground, whereupon the boat propellers damage seagrass). In addition, although a high diversity and abundance of organisms live in seagrass beds, the animals are often small and cryptic, in contrast to the large and dazzling organisms that attract the general public to coral reefs. The few charismatic megafauna that do inhabit seagrass meadows (manatees, dugongs, and sea turtles; figure 1) are elusive and not easily viewed in the wild, and because they are endangered by over-harvesting and habitat destruction, they are not nearly as abundant as the fish and invertebrates on coral reefs (Jackson et al. 2001). Without strong public support for seagrasses and the uncharismatic but highly productive animals they shelter, conservation efforts will continue to lag behind those of other key coastal ecosystems.

The need for a global conservation effort for seagrasses

We have presented the case that seagrasses are facing a crisis due to a diverse array of pressures from human activities in the coastal zone, as well as the increased frequency and intensity of natural disasters such as hurricanes, which may also be indirectly associated with human activities (i.e., global warming). Although seagrasses have experienced considerable environmental changes in sea level, CO₂, and temperature over the past 100 million years of their evolutionary history, these historical changes were gradual. How well seagrasses can adapt to the unprecedented rates of change they are currently experiencing is unknown. In view of the many cases of documented seagrass loss, predictions for the future of seagrass-dominated coastal systems cannot be optimistic.

While the global science community has focused on predicting future change to the oceans and to coastal ecosystems for iconic groups like corals, seagrasses have generally been ignored by all but marine scientists, except in the most highly developed countries. Given the importance of seagrasses to humans (Costanza et al. 1997, Larkum et al. 2006), it is imperative to assess the future of seagrasses under the exponentially increasing pressures of human growth and development in the watersheds and coastal zones of the world. A quantitative analysis of seagrass trajectories could form the foundation to incorporate seagrasses into a global science policy for the world's oceans.

Monitoring seagrass meadows is a necessary but insufficient conservation activity, because remedial actions are not fully effective in stopping declines once they are detected (Short and Burdick 1996, Delgado et al. 1999). It will be critically important to forecast the likely cumulative effects of the known and emerging stressors of seagrasses. Present scenarios for future seagrass trends are either of limited geographic extent (Fourqurean et al. 2003) or limited to qualitative statements (Short and Neckles 1999, Duarte 2002, Duarte et al. forthcoming). Quantitative forecasts, together with risk analysis identifying the most vulnerable areas, can inform conservation and management strategies and help determine the most cost-effective allocation of resources to conserve seagrass

ecosystems. Furthermore, developing models that incorporate the landscape scale of seagrass dynamics and can link to watershed runoff models will help inform resource managers about the consequences of various watershed activities on seagrass dynamics.

Our major recommendation is to respond to the global seagrass crisis with extensive conservation efforts involving comprehensive nutrient management schemes, sanctuaries or protected areas, and education for the public and resource managers (Kenworthy et al. 2006). The majority of seagrass losses are a result of human activities in the adjacent watersheds, which lead to increased nutrient and sediment runoff. The isolated case studies of seagrass recoveries when inputs of nutrients (e.g., Tampa Bay, Florida; Tomasko et al. 2005) or sediments (Hervey Bay, Australia; Preen and Marsh 1995) are curtailed demonstrate the potential effectiveness of conservation efforts. The preservation of seagrasses and their associated ecosystem services—in particular, biodiversity, primary and secondary production, nursery habitat, and nutrient and sediment sequestration—should be a global priority. We believe that the crisis facing seagrass ecosystems can be averted with a global conservation effort, and this effort will benefit not just seagrasses and their associated organisms but also the entirety of coastal ecosystems.

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References cited

- Abal EG, Dennison WC. 1996. Seagrass depth range and water quality in Southern Moreton Bay, Queensland, Australia. *Marine and Freshwater Research* 47: 763–771.
- Beck MW, et al. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *BioScience* 51: 633–641.
- Beer S, Koch EW. 1996. Photosynthesis of seagrasses vs. marine macroalgae in globally changing CO₂ environments. *Marine Ecology Progress Series* 141: 199–204.
- Berner RA, Kothavala Z. 2001. GEOCARB III: A revised model of atmospheric CO₂ over Phanerozoic time. *American Journal of Science* 301: 182–204.
- Bricker SB, Ferreira JG, Simas T. 2003. An integrated methodology for assessment of estuarine trophic status. *Ecological Modelling* 169: 39–60.

- Bulthuis DA. 1983. Effects of *in situ* light reduction on density and growth of the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. *Journal of Experimental Marine Biology and Ecology* 67: 91–103.
- Cambridge ML, McComb AJ. 1984. The loss of seagrasses in Cockburn Sound, Western Australia. 1: The time course and magnitude of seagrass decline in relation to industrial development. *Aquatic Botany* 20: 229–243.
- Carlton JT. 1989. Man's role in changing the face of the ocean: Biological invasions and implications for conservation of near-shore environments. *Conservation Biology* 3: 265–273.
- Carlton JT, Vermeij G, Lindberg DR, Carlton DA, Dudley EC. 1991. The first historical extinction of a marine invertebrate in an ocean basin: The demise of the eelgrass limpet, *Lottia alveus*. *Biological Bulletin* 180: 72–80.
- Carruthers TJB, Dennison WC, Longstaff BJ, Waycott M, Abal EG, McKenzie LJ, Long WJL. 2002. Seagrass habitats of Northeast Australia: Models of key processes and controls. *Bulletin of Marine Science* 71: 1153–1169.
- Cohen JE. 1995. *How Many People Can the Earth Support?* New York: Norton.
- Coles RC, Fortes M. 2001. Protecting seagrass—approaches and methods. Pages 445–463 in Short FT, Coles RG, eds. *Global Seagrass Research Methods*. Amsterdam: Elsevier.
- Costanza R, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253–260.
- Crowley TJ. 1990. Are there any satisfactory geologic analogs for a future greenhouse warming? *Journal of Climate* 3: 1282–1292.
- Delgado O, Ruiz J, Perez M, Romero R, Ballesteros E. 1999. Effects of fish farming on seagrass (*Posidonia oceanica*) in a Mediterranean bay: Seagrass decline after organic loading cessation. *Oceanologica Acta* 22: 109–117.
- den Hartog C. 1970. *The Seagrasses of the World*. Amsterdam: North-Holland.
- Dennison WC, Orth RJ, Moore KA, Stevenson JC, Carter V, Kollar S, Bergstrom PW, Batiuk RA. 1993. Assessing water quality with submersed aquatic vegetation. *BioScience* 43: 86–94.
- Dietz RS, Holdren JC. 1970. Reconstruction of Pangea: Breakup and dispersion of continents, Permian to present. *Journal of Geophysical Research* 75: 4939–4956.
- Duarte CM. 1999. Seagrass ecology at the turn of the millennium: Challenges for the new century. *Aquatic Botany* 65: 7–20.
- . 2002. The future of seagrass meadows. *Environmental Conservation* 29: 192–206.
- Duarte CM, Chiscano CL. 1999. Seagrass biomass and production: A reassessment. *Aquatic Botany* 65: 159–174.
- Duarte CM, Alvarez E, Grau A, Krause-Jensen D. 2004. Which monitoring strategy should be chosen? Pages 41–44 in Borum J, Duarte CM, Krause-Jensen D, Greve TM, eds. *European Seagrasses: An Introduction to Monitoring and Management*. (13 November 2006; www.seagrasses.org/handbook/european_seagrasses_high.pdf)
- Duarte CM, Middelburg J, Caraco N. 2005. Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2: 1–8.
- Duarte CM, Borum J, Short FT, Walker DI. Seagrass ecosystems: Their global status and prospects. In Polunin NVC, ed. *Aquatic Ecosystems: Trends and Global Prospects*. Cambridge (United Kingdom): Cambridge University Press. Forthcoming.
- Environment Agency of Japan. 2000. *Threatened Wildlife of Japan: Red Data Book*. 2nd ed., vol. 8: Vascular Plants. Tokyo: Japan Wildlife Research Center.
- Fleming K, Johnston P, Zwart D, Yokoyama Y, Lambeck K, Chappell J. 1998. Refining the eustatic sea-level curve since the last glacial maximum using far- and intermediate-field sites. *Earth and Planetary Science Letters* 163: 327–342.
- Fonseca MS, Kenworthy WJ, Thayer GW. 1998. *Guidelines for the conservation and restoration of seagrasses in the United States and adjacent waters*. Silver Spring (MD): National Oceanic and Atmospheric Administration (NOAA) Coastal Ocean Office. NOAA Coastal Ocean Program Decision Analysis Series no. 12.
- Fonseca MS, Kenworthy WJ, Whitfield PE. 2000. Temporal dynamics of seagrass landscapes: A preliminary comparison of chronic and extreme disturbance events. *Biologia Marina Mediterranea* 7: 373–376.
- Fourqurean JW, Robblee MB. 1999. Florida Bay: A recent history of ecological changes. *Estuaries* 22: 345–357.
- Fourqurean JW, Boyer JN, Durako MJ, Hefty LN, Peterson BJ. 2003. Forecasting responses of seagrass distributions to changing water quality using monitoring data. *Ecological Applications* 13: 474–489.
- Frink CR, Waggoner PE, Ausubel JH. 1999. Nitrogen fertilizer: Retrospect and prospect. *Proceedings of the National Academy of Sciences* 96: 1175–1180.
- Green EP, Short FT, eds. 2003. *World Atlas of Seagrasses*. Berkeley: University of California Press.
- Heck KL, Orth RJ. 2006. Predation in seagrass beds. Pages 537–550 in Larkum AWD, Orth RJ, Duarte CM, eds. *Seagrasses: Biology, Ecology, and Conservation*. Dordrecht (The Netherlands): Springer.
- Heck KL, Pennock J, Valentine J, Coen L, Sklenar SS. 2000. Effects of nutrient enrichment and large predator removal on seagrass nursery habitats: An experimental assessment. *Limnology and Oceanography* 45: 1041–1057.
- Heck KL, Hays C, Orth RJ. 2003. A critical evaluation of the nursery role hypothesis for seagrass meadows. *Marine Ecology Progress Series* 253: 123–136.
- Hemminga M, Duarte CM. 2000. *Seagrass Ecology*. Cambridge (United Kingdom): Cambridge University Press.
- Jackson JBC, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293: 629–638.
- Kemp WM, et al. 2005. Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. *Marine Ecology Progress Series* 303: 1–19.
- Kendrick GA, Hegge BJ, Wyllie A, Davidson A, Lord DA. 2000. Changes in seagrass cover on Success and Parmelia Banks, Western Australia between 1965 and 1995. *Estuarine, Coastal and Shelf Science* 50: 341–353.
- Kenworthy WJ. 2000. The role of sexual reproduction in maintaining populations of *Halophila decipiens*: Implications for the biodiversity and conservation of tropical seagrass ecosystems. *Pacific Conservation Biology* 5: 260–268.
- Kenworthy WJ, Wyllie-Echeverria S, Coles RG, Pergent G, Pergent-Martini C. 2006. Seagrass conservation biology: An interdisciplinary science for protection of the seagrass biome. Pages 595–623 in Larkum AWD, Orth RJ, Duarte CM, eds. *Seagrasses: Biology, Ecology and Conservation*. Dordrecht (The Netherlands): Springer.
- Larkum WD, Orth RJ, Duarte CM, eds. 2006. *Seagrasses: Biology, Ecology and Conservation*. Dordrecht (The Netherlands): Springer.
- Les DH, Cleland MA, Waycott M. 1997. Phylogenetic studies in the Alismatidae, II: Evolution of the marine angiosperms (seagrasses) and hydrophyly. *Systematic Botany* 22: 443–463.
- Levine JM, D'Antonio CM. 2003. Forecasting biological invasions with increasing international trade. *Conservation Biology* 17: 322–326.
- Lodge DM, et al. 2006. Biological invasions: Recommendations for U.S. policy and management. Position paper, Ecological Society of America. (13 October 2006; http://weblogs.nal.usda.gov/invasivespecies/archives/2006/06/biological_inva.shtml)
- Longstaff BJ, Dennison WC. 1999. Seagrass survival during pulsed turbidity events: The effects of light deprivation on the seagrasses *Halodule pinifolia* and *Halophila ovalis*. *Aquatic Botany* 65: 105–121.
- Lotze HK, et al. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312: 1806–1809.
- Marbà N, Duarte CM, Díaz-Almela E, Terrados J, Álvarez E, Martínez R, Santiago R, Gacia E, Grau AM. 2005. Direct evidence of imbalanced seagrass (*Posidonia oceanica*) shoot population dynamics along the Spanish Mediterranean. *Estuaries* 28: 53–62.
- Marbà N, Santiago R, Díaz-Almela E, Álvarez E, Duarte CM. 2006. Seagrass (*Posidonia oceanica*) vertical growth as an early indicator of fish farm-derived stress. *Estuarine, Coastal and Shelf Science* 67: 475–483.

- Miller KG, Kominz MA, Browning JV, Wright JD, Mountain GS, Katz ME, Sugarman PJ, Cramer BS, Christie-Blick N, Pekar SF. 2005. The Phanerozoic record of global sea-level change. *Science* 310: 1293–1298.
- Musick JA, et al. 2000. Marine, estuarine, and diadromous fish stocks at risk of extinction in North America. *Fisheries* 25: 6–30.
- Naylor R, Williams SL, Strong DR. 2001. Aquaculture—a gateway for exotic species. *Science* 294: 1655–1656.
- Orth RJ, Moore KA. 1983. Chesapeake Bay: An unprecedented decline in submerged aquatic vegetation. *Science* 222: 51–53.
- Orth RJ, Batiuk RA, Bergstrom PW, Moore KA. 2002. A perspective on two decades of policies and regulations influencing the protection and restoration of submerged aquatic vegetation in Chesapeake Bay, USA. *Bulletin of Marine Science* 71: 1391–1403.
- Orth RJ, Luckenbach ML, Marion SR, Moore KA, Wilcox DJ. 2006. Seagrass recovery in the Delmarva coastal bays. *Aquatic Botany* 84: 26–36.
- Padilla DK, Williams SL. 2004. Beyond ballast water: Aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. *Frontiers in Ecology and the Environment* 2: 131–138.
- Petit JR, et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399: 429–436.
- Preen AR, Marsh H. 1995. Responses of dugongs to large-scale loss of seagrass from Hervey Bay, Queensland, Australia. *Wildlife Research* 22: 507–519.
- Rasmussen E. 1977. The wasting disease of eelgrass (*Zostera marina*) and its effects on environmental factors and fauna. Pages 1–51 in McRoy CP, Helfferich C, eds. *Seagrass Ecosystems*. New York: Marcel Dekker.
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH. 2000. Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annual Review of Ecology and Systematics* 31: 481–531.
- Short FT, Burdick DM. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoit Bay, Massachusetts. *Estuaries* 19: 730–739.
- Short FT, Coles RG, eds. 2001. *Global Seagrass Research Methods*. Amsterdam: Elsevier.
- Short FT, Neckles H. 1999. The effects of global climate change on seagrasses. *Aquatic Botany* 63: 169–196.
- Short FT, Wyllie-Echeverria S. 1996. Natural and human-induced disturbance of seagrasses. *Environmental Conservation* 23: 17–27.
- Spalding M, Taylor M, Ravilious C, Short F, Green E. 2003. Global overview: The distribution and status of seagrasses. Pages 5–26 in Green EP, Short FT, eds. *World Atlas of Seagrasses: Present Status and Future Conservation*. Berkeley: University of California Press.
- Suchanek TH, Williams SW, Ogden JC, Hubbard DK, Gill IP. 1985. Utilization of shallow-water seagrass detritus by Caribbean deep-sea macrofauna: $\delta^{13}\text{C}$ evidence. *Deep Sea Research* 32: 2201–2214.
- Terrados J, Duarte CM, Kamp-Nielsen L, Agawin NSR, Gacia E, Lacap D, Fortes MD, Borum J, Lubanski M, Greve T. 1999. Are seagrass growth and survival affected by reducing conditions in the sediment? *Aquatic Botany* 65: 175–197.
- Thoning KW, Tans PP, Komhyr WD. 1989. Atmospheric carbon dioxide at Mauna Loa observatory, 2: Analysis of the NOAA GMCC data, 1974–1985. *Journal of Geophysical Research* 94: 8549–8565.
- Tomasko DA, Corbett CA, Greening HS, Raulerson GE. 2005. Spatial and temporal variation in seagrass coverage in southwest Florida: Assessing the relative effects of anthropogenic nutrient load reductions and rainfall in four contiguous estuaries. *Marine Pollution Bulletin* 50: 797–805.
- Valentine JF, Heck KL. 2005. Perspective review of the impacts of overfishing on coral reef food web linkages. *Coral Reefs* 24: 209–213.
- Walker DI, Kendrick GA, McComb AJ. 2006. Decline and recovery of seagrass ecosystems—the dynamics of change. Pages 551–565 in Larkum AWD, Orth RJ, Duarte CM, eds. *Seagrasses: Biology, Ecology and Conservation*. Dordrecht (The Netherlands): Springer.
- Williams SL. 2001. Reduced genetic diversity in eelgrass transplantations affects both individual and population fitness. *Ecological Applications* 11: 1472–1488.
- Wright JB, Jones CG. 2006. The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *BioScience* 56: 203–209.