Benthic Habitat: Seagrasses

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In a nutshell

- Seagrasses provide habitat for fish and invertebrates and play a major role in maintaining water quality by taking up and transforming nutrients.
- People value seagrasses as a place to find large numbers and a variety of fish, for stabilizing sediments, as critical habitat for protected species, and as a natural filter for wastewater and stormwater.
- The damage to the bottom from recreational and commercial activities in seagrass beds can lead to complete loss of seagrass beds from heavily affected areas.
- Eutrophication of coastal waters, often related to increasing human development, has been implicated in the loss of seagrasses in many areas of the world, including South Florida.

There are few places on earth where seagrass beds are as expansive as the nearshore marine ecosystem of South Florida. With 14,622 km^2 of seagrasses in South Florida, this area ranks among the most expansive documented seagrass beds on Earth, comparable to the back-reef environment of the Great Barrier Reef in Australia (Lee Long et al., 1996) and the Miskito Bank of Nicaragua (Phillips *et al.,* 1982). Accordingly, the economic impact and ecological importance of the South Florida seagrass beds are significant (Zieman, 1982). Over half of all employment in the Florida Keys is dependent on outdoor recreation (NOAA, 1996). For the larger part, these outdoor activities rely on the clear waters and healthy marine habitats in the nearshore marine environment. Fisheries landings in the Florida Keys total over 12×10^6 kg annually of mostly seagrass-associated organisms (Bohnsack *et al.,* 1994).

Five species of rooted aquatic vascular plants, or seagrasses, are commonly found in South Florida: *Thalassia testudinum, Syringodium filiforme, Halodule wrightii, Halophila decipiens,* and *Ruppia maritima*. One additional species, *Halophila johnsonii,* occurs in the extreme northern Biscayne Bay and India River Lagoon. Seagrass communities are found from the mangrove-lined estuaries of Florida Bay, the Shark River drainage, and the Ten Thousand Islands out to back-reef environments and open continental shelf waters (Figure 1). T. testudinum is often dominant in areas of stable salinity and stable sediments. *H. wrightii* and *S. filiforme* are often found in deeper water and areas that are more frequently disturbed, and the *Halophila* species are generally restricted to low-light environments (<15 percent of surface irradiance) and turbid shallow waters. In general, *R. maritima* is restricted to areas near freshwater sources. The total seagrass habitat in the South Florida region covers least 17,620 km^2 of semicontinuous beds.

Seagrasses Support Fisheries and Maintain Water Quality

Most of the value of commercial fisheries landings in the Florida Keys comes from either seagrass resident species (e.g., pink shrimp) or from species that rely on seagrasses

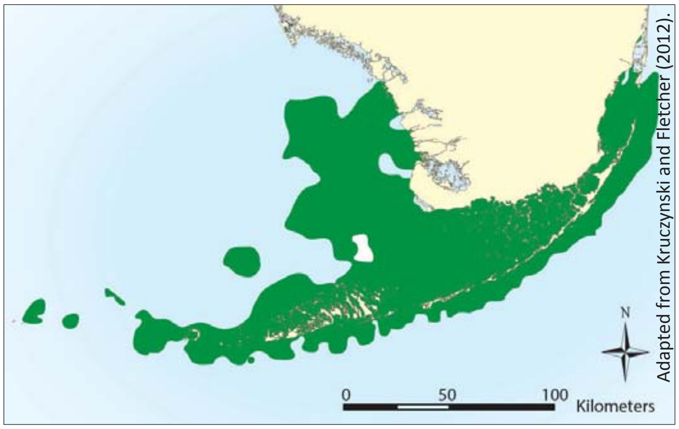

Figure 1. Distribution of seagrass beds in the Florida Keys marine ecosystem.

for nurseries for their early life stages (e.g., Caribbean spiny lobster, grouper). We know of no assessments of the commercial value of commercial landings of seagrass-dependent species in South Florida, but one study from subtropical Australia concluded that the fisheries value of seagrass beds was $3,500 per hectare per year (Watson *et al.,* 1993). Extrapolating this areal value to the extent of seagrasses in South Florida results in a potential fisheries value of $6.3 billion per year. Seagrass beds are recognized as among the most productive (Zieman and Wetzel, 1980) and economically valuable (Costanza *et al.,* 1997) of ecosystems, and the economy of the Florida Keys is inextricably tied to seagrass beds and other nearshore benthic marine habitats. The proximity of seagrass meadows to coral reef and mangrove ecosystems provides critical feeding grounds and nursery areas for species who rest on coral reefs or in mangroves as adults (Beck *et al.,* 2001). These associations are essential in maintaining the abundance of some coral reef and mangrove species (Valentine and Heck, 2005).

Seagrasses maintain water quality. They trap sediments produced in other parts of the ecosystem (Kennedy *et al.,* 2010) and decrease sediment resuspension (Green *et al.,* 1997), thereby contributing to clearer water. They are also sites of active nutrient uptake to fuel their high primary productivity; nutrients taken up by seagrasses cannot be used by phytoplankton and macroalgae. The importance of seagrasses to water quality in South Florida was made clear following the seagrass dieoff that occurred in Florida Bay in the late 1980s (Robblee *et al.,* 1991). The loss of the nutrient retention and sediment stabilization provided by the dense seagrass meadows of western Florida Bay resulted in orders-of-magnitude increases in turbidity and phytoplankton concentrations in the water column that persisted for a decade following the dieoff (Boyer *et al.,* 1999). This decrease in water clarity led to a further decline and change in community composition of the seagrasses that survived the dieoff (Hall *et al.,* 1999). Such a change in state is reminiscent of the multiple stable states experienced by some lakes that alternate between multi-year periods of clear water and high benthic vegetation abundances and multi-year periods of very turbid water and no benthic vegetation (Scheffer *et al.,* 2001). If such large-scale losses of seagrasses occurred throughout the Florida Keys, the degradation in water quality would undoubtedly have severe impacts on the coral reefs of the region, which surely would not survive a multi-year stable state of the coastal waters of the Florida Keys dominated by high turbidity and abundant phytoplankton.

Attributes People Care About

Seagrasses in the Florida Keys support attributes of the marine environment that people care about. These attributes are directly related to ecosystem services provided by the Florida Keys marine ecosystem:

- Abundance and large variety of fish
- Intact habitat for quick species recovery
- Coastal erosion and storm protection
- Critical habitat for protected species
- Natural filter for wastewater and stormwater runoff
- Carbon sequestration

Abundance and Large Variety of Fish

Seagrass beds are important locations for recreational fisherman in the Florida Keys. Biodiversity is much higher and animal densities are orders of magnitude higher in seagrass beds than in surrounding unvegetated sediment (see Hemminga and Duarte, 2000, for a review). The money spent on owning and operating private vessels in the region is at least partly motivated by those targeting seagrass ecosystems for their recreational opportunities. Further, the guided fishing charter industry in the Florida Keys is largely dedicated to taking customers to seagrass ecosystems to catch game fish including tarpon, permit, bonefish and snook, all seagrass-resident species.

Intact Habitat for Quick Species Recovery

As a vital component of the mangrove-seagrass-coral reef habitat mosaic that makes up the South Florida nearshore marine ecosystem, seagrass meadows are vital to the resilience of the ecosystem to disturbance. Given their ability to stabilize sediments and trap suspended particles, they prevent storm resuspension of sediments, erosion, and the consequent decreases in water clarity that would accompany them; hence, the presence of seagrass meadows protect the coral reefs from disturbance-generated water quality degradation and they protect the shoreline from storm-driven erosion. An example of the importance of seagrasses for protecting against sediment resuspension and erosion was provided when a large area of seagrass meadows north of Marathon were overgrazed by sea urchins in the late 1990s. Following the overgrazing, 5-10 cm of sediment was lost and algae in the water column tripled (Peterson *et al.,* 2002).

Since many of the fish that live on Florida's coral reefs leave the reefs and feed in seagrass beds (Robblee and Zieman, 1984), seagrasses promote healthy reef ecosystems; without the seagrasses, fish stocks on coral reefs may not be able to rebound following disturbances. Many of the commercially important species also depend on seagrasses at some stage in their like cycle, including Caribbean spiny lobsters, mangrove snappers, and queen conch. Without seagrasses, such species could not recover from disturbance.

Coastal Erosion and Storm Protection

By reducing wave height, current velocities, and sediment resuspension, seagrass meadows protect shorelines from erosion, saving coastal communities the tremendous capital they would need to repair erosion of the coastline. In fact, seagrasses are a much more economical means of protecting coastal properties than building seawalls and armoring coastlines with riprap, since seagrass beds require no expenditure of capital for maintenance and can self-adjust to rising sea levels by the accretion of sediments in the seagrass beds. The human-built erosion-control structures require resources to be spent to maintain them and, as the sea level rises, they will need to be redesigned and rebuilt.

Critical Habitat for Protected Species

The world's only threatened marine plant species, Johnson's seagrass (*Halophila johnsonii*), is one of the seagrasses of South Florida that occurs in protected marine waters and estuaries from Key Biscayne northward to the Indian River Lagoon. Seagrass beds of South Florida are essential habitat for the endangered green sea turtle and the West Indian manatee. They also support many threatened species including Nassau grouper and queen conch. Bottlenose dolphins feed extensively in seagrass meadows. Wading birds such as great white herons, great blue herons, little blue herons, great egrets, snowy egrets, reddish egrets, and American flamingos all feed in seagrass-covered shallows.

Natural Filter

Seagrass meadows are among the most active sites of bacterial nutrient cycling in the coastal ocean. Rapid growth rates of seagrasses and associated micro- and macroalgae take up readily available plant nutrients, like dissolved inorganic phosphorus, nitrate, and ammonium, out of the water. The efficient trapping of particles by the seagrasses provides another flux of particulate forms of plant nutrients and organic matter by the seagrass ecosystem.

The high primary productivity of seagrasses supplies abundant organic carbon for bacteria to use as an energy source. Rapid oxidation of this organic matter leads to very low oxygen concentrations and hypoxic/anoxic conditions in the sediments of seagrasses. Hence, bacteria that are able to use other chemical species to oxidize the organic matter are particularly important. Nitrate and sulfate are rapidly consumed in seagrass sediments, producing N_2, which returns to the atmosphere, and a sulfide ion that either diffuses out of the sediment or combines with metal cations to form minerals in the sediment.

These processes (the immobilization of dissolved inorganic nutrients, the transformation of dissolved nitrogen to atmospheric gas, etc.) are the processes that humans design waste treatment plants to accomplish. It has been estimated that it would cost $19,002 per year (1994 U.S. dollars) to build and maintain a sewage treatment plant to perform the same nutrient regulation functions as are performed by each hectare of seagrass (Costanza *et al.,* 1997). Extrapolating this areal value of the nutrient regulation processes of seagrasses to the extent of seagrasses in South Florida, the value of the nutrient regulation services provided by the seagrasses of the region is $34 billion per year (in 1994 U.S. dollars). This nutrient regulation protects coastal water quality from degradation.

Carbon Sequestration

Seagrass beds are very productive ecosystems, and they are an important net sink of CO_2 for the global carbon budget (Duarte *et al.,* 2010). The carbon sequestered in seagrass beds is stored mostly in the form of particulate organic matter in the sediments; seagrass meadows of South Florida contain, on average, about as much stored carbon per hectare as temperate forests. Their status as a net sink means that seagrasses act to buffer the global ecosystem against anthropogenic climate change. Globally, seagrass meadows tend to be autotrophic ecosystems with a mean, net community production (NCP) of 27.2 ± 5.8 mmol O_2 m^{-2} day^{-1}. The global NCP of seagrass meadows ranges (95 percent c.l. of mean values) from 20.73-101.39 Tg C yr^{-1}. Extrapolating from the mean areal rates of NCP and estimates of the area of seagrass meadows in South Florida results in an estimate of 1.2-3.0 Tg C yr^{-1} removed from the atmosphere by the seagrass ecosystems of South Florida. The global historic loss of 29 percent of the seagrass area (Waycott *et al.,* 2009) represents, therefore, a major loss of intense natural carbon sinks in the biosphere.

Attributes We Can Measure

The U.S. EPA established a monitoring program in 1995 designed to define the status and trends of seagrass communities in the Florida Keys National Marine Sanctuary (FKNMS) as part of the agency's comprehensive Water Quality Protection Plan for the sanctuary (Fourqurean and Rutten, 2003). The monitoring program addresses concerns over eutrophication and its impact on the status of seagrass communities in the FKNMS. The monitoring program was designed to determine regional-scale gradients in the status of seagrass by compiling data on these attributes of the seagrass beds:

- Spatial extent
- Depth distribution
- Biomass
- Species composition
- Elemental and isotopic composition
- Genetic diversity

Each of these parameters can be explicitly linked to environmental factors of known management concern and are explicitly linked to the structure and function of seagrass meadows.

Spatial Extent

In many coastal ecosystems, the interaction of the high light requirement of seagrasses, water clarity, and water depth control the spatial extent of seagrass ecosystems. For example, in Tampa Bay, the areal extent of seagrasses shrank by 70 percent in the 1960s and 1970s in response to decreases in water clarity. Subsequent improvements to wastewater treatment led to a partial recovery of the lost seagrasses as water quality improved (Greening and Janicki, 2006). Seagrass beds can also shrink from the deliberate or accidental destruction of the habitat. Dredging and filling of seagrasses for coastal construction and navigation were commonplace prior to the 1960s (Short and Wyllie-Echeverria, 1996), and repeated erosion caused by acute vessel groundings and chronic "prop scarring" by boats operating in shallow water continues to result in large decreases in the areal extent of seagrasses (Sargent *et al.,* 1995).

Depth Distributions

As a group, seagrasses have a very high requirement for light compared to other plants growing in low-light environments. This is likely because of the large proportion of seagrass biomass that is buried in the sediment as root and rhizome tissues, the general scarcity of oxygen in marine sediments in which those below-ground tissues are buried, and the absorption of light by sediments and organisms that foul the seagrass leaves. Where both phytoplankton, macroalgae, and typical terrestrial shade-adapted plants require less than 1 percent of incident sunlight to thrive, seagrasses require 10 percent or more (Duarte, 1991). Note, however, that there are important species-specific differences in light requirements among the seagrasses common in South Florida. *T. testudinum* requires more light and, therefore, is restricted to shallower locations than either *H. wrightii* or *S. filiforme* (Wiginton and McMillan, 1979), and the species of *Halophila* that occur in South Florida require even less light (about 5-8 percent of surface irradiance in South Florida, J.W. Fourqurean, unpublished data).

Biomass

The biomass of seagrasses is a function of the supply of the necessary resources for seagrass growth (most importantly, light and nutrients), as well as the loss rate of seagrass leaves (both due to physical processes and herbivory) and environmental conditions like temperature and salinity. In the very nutrient-poor areas of South Florida, an increase in nutrient availability leads to an increase in biomass of the seagrass beds (Fourqurean *et al.,* 1992b; Ferdie and Fourqurean, 2004; Armitage *et al.,* 2005). As the habitat value of the seagrass bed is partially a function of the biomass of the seagrasses, changes in biomass will affect the animals resident in the seagrass beds and the structure of the food webs they support (Hemminga and Duarte, 2000; Gil *et al.,* 2006).

Species Composition

Knowledge of the species composition and their relative abundance, and how these factors change in time, provides an insight into the ecological health of seagrass meadows. The pattern of the anthropogenically-driven loss of seagrass beds across the globe leads to a generalized model of the effects of nutrient loading on seagrass beds (Duarte, 1995). In general, eutrophication in aquatic environments shifts the competitive balance to faster-growing primary producers. The consequence of this generality in seagrass-dominated environments is that seagrasses are the dominant primary producers in low-nutrient conditions. As nutrient availability increases, there is an increase in the importance of macroalgae, both free-living and epiphytic, with a concomitant decrease in seagrasses because of competition for light. Macroalgae lose out to even faster-growing microalgae as nutrient availability continues to increase: first, epiphytic microalgae replace epiphytic macroalgae on seagrasses; then planktonic microalgae bloom and deprive all benthic plants of light under the most eutrophic conditions.

Using knowledge of the life history characteristics of local species and experimental and distributional evidence, this general model can be adapted to seagrass beds of South Florida. The South Florida case is more complicated than the general case described above because there are six common seagrass species in South Florida, and these species have different nutrient and light requirements; hence, they have differing responses to eutrophication. Large expanses of the shallow marine environments in South Florida are so oligotrophic that biomass and growth of even the slowest-growing local seagrass species, *T. testudinum*, are nutrient-limited (Fourqurean *et al.,* 1992a; Fourqurean *et al.,* 1992b). At this very oligotrophic end of the spectrum, increases in nutrient availability actually cause increases in seagrass biomass and growth rate (Powell *et al.,* 1989). As nutrient availability increases beyond what is required by a dense stand of *T. testudinum*, there are other seagrass species that will out-compete it. At locations with more constant marine conditions, there is evidence that *S. filiforme* may be a superior competitor to *T. testudinum* in areas of enhanced nutrient availability (Williams, 1987).

In estuarine areas of South Florida, nutrient addition experiments show that *H. wrightii* will prevail over *T. testudinum* under fertilized conditions (Fourqurean *et al.,* 1995). Evidence from the distribution of primary producers around point-sources of nutrient input show that in estuarine areas there are zones of dominance of different species with respect to nutrient availability, from *T. testudinum* at lowest nutrient availability, to *H. wrightii* at higher availability, to *Ruppia maritima* at higher availability, followed by a microalgae-dominated zone at highest nutrient availabilities (Powell *et al.,* 1991). The abundance of macroalgal epiphytes also increases along the same gradient, up until the point that microalgae become dominant (Frankovich and Fourqurean, 1997). Consequently, the relative importance of the various primary producers can be used to assess the trophic state of the community (Fourqurean and Rutten, 2003). Trends towards dominance by faster-growing species and a decrease in the dominance of slow-growing turtlegrass indicate increases in nutrients, driving a change in seagrass meadows.

Elemental and Isotopic Composition

Tissue nutrient concentrations can be monitored to assess the relative availability of nutrients to the plants. For phytoplankton communities, this idea is captured in the interpretation of elemental ratios compared to the familiar "Redfield ratio" of 106C:16N:P (Redfield, 1958). Similar analyses can be made with data from seagrasses and macroalgae with the recognition that the taxon-specific "Redfield ratio" may be different from the phytoplankton ratio (Atkinson and Smith, 1983; Duarte, 1992; Gerloff and Krombholtz, 1966). For the seagrass *T. testudinum*, the critical ratio of nitrogen:phosphorus (N:P) in green leaves that indicates a balance in the availability of N and P is ca. 30:1, and monitoring deviations from this ratio can be used to infer whether N or P availabilities are limiting this species' growth (Fourqurean *et al.,* 2005). Hence, *T. testudinum* is likely to be replaced by faster-growing competitors if nutrient availability is such that the N:P ratio of its leaves is ca. 30:1. A change in the N:P ratio in time to a value closer to 30:1 is indicative of increased nutrient availability or decreased light availability. The spatial pattern in the N:P ratio can be used to infer sources of nutrients for supporting primary production in the ecosystem (Fourqurean *et al.,* 1997; Fourqurean and Zieman, 2002; Fourqurean *et al.* 1992a).

In addition to elemental stoichiometry, ratios of the stable isotopes of carbon and nitrogen have proven useful indicators of the supply and processing of nutrients. Stable isotope ratios in macrophytes and consumers have proven valuable in tracing the flow of energy in marine food webs (Peterson *et al.,* 1985; Peterson, 1999). Stable isotope ratios can also be used to identify nutrient sources and processing in ecosystems. For example, 13C/12C ratios in macrophytes have been used to identify the importance of allochthonous carbon to marine ecosystems (Zieman *et al.,* 1984; Lin *et al.,* 1991; Hemminga *et al.,* 1994). Since discrimination against uptake of 13C is partly a function on the demand for CO_2 used in photosynthesis, there is a relationship between the stable C isotope content of seagrasses and the amount of light that reaches the plants, with isotopically lighter tissues resulting from low light (Grice *et al.,* 1996).

Bacterially-mediated processing of N can strongly influence stable N isotope ratios and, as a consequence, the spatial pattern in 15N/14N ratios in macrophytes can be used to infer ecosystem-scale processing of organic matter (Fourqurean *et al.,* 1997). Carbon and nitrogen isotopes have been used in both paleoceanography and paleolimnology to infer changes in water column nutrient cycles (e.g., Schelske and Hodell, 1991). Owing to the isotopically heavy N associated with many anthropogenic nutrient sources, stable isotopes of N in macrophytes are potentially invaluable tools for gauging the impact of man on coastal water bodies (McClelland and Valiela, 1998a, 1998b). This tool is potentially of primary importance because of the magnitude of the impact man is having on coastal water bodies through anthropogenically-increased N loading (Paerl, 1997; Vitousek *et al.,* 1997; Tilman *et al.,* 2001).

Genetic Diversity

The genetic diversity of seagrasses can have important ecological consequences for seagrass ecosystems (see Hughes *et al.,* 2008 for a review). For instance, genetically-diverse plant populations can be more successful at reproducing (Ellstrand and Antonovics, 1985; Johnson *et al.,* 2006). In addition, genetic diversity can increase the habitat value of seagrass meadows by increasing the diversity and abundance of associated invertebrates (Hughes and Stachowicz, 2004; Reusch *et al.,* 2005). Furthermore, genetic diversity can increase the stability of systems and enhance resistance to or recovery from disturbance (Hughes and Stachowicz, 2004). In this way, genetic diversity is an important determinant of the way seagrass ecosystems can respond to anthropogenic and natural pressures on the ecosystem.

Light penetration through the water column is a function of the amount of particulate and dissolved substances in the water, two important aspects of water quality that affect seagrass resources. As water clarity decreases, seagrass depth distributions will also decrease. Additionally, nutrient availability has a direct impact on seagrass light requirements and, therefore, depth distribution that is independent of its influence on water clarity. High nutrient availability leads to epiphyte overgrowth of seagrass leaves (Tomasko and Lapointe, 1991). These epiphytes directly block light from seagrass leaves (Frankovich and Zieman, 2005).

Drivers of Change in Seagrass Beds

Pressures affecting seagrass beds in the Florida Keys marine ecosystem can be traced to two sets of drivers: near-field drivers that act within the region of the Florida Keys and Dry Tortugas and far-field drivers that operate at regional and global scales Near-field drivers include fishing and other, more general effects of development of the Keys on the surrounding waters. Far-field drivers include regional inputs of nutrients, which contribute to a general increase in nutrient concentrations in the coastal ocean, climate change, and the effects of rising carbon dioxide concentrations on ocean water chemistry. While climate change and changes to ocean water chemistry are of concern, their current impact on seagrasses in the Florida Keys is probably not as large as the other drivers of change, like water quality degradation and direct removal of seagrasses due to boat groundings and propeller scarring.

Fisheries, Species Extinction, and Changes in the Food Web

While the net effect of humans altering food webs is not certain, in all likelihood our current seagrass ecosystems are different now than they were before human alteration of coastal food webs through selective harvesting of the large predators and herbivores from the ecosystem. Humans have been harvesting food from the ocean for millennia. Besides the impacts on populations of currently targeted species detailed in the Fish and Shellfish ICEM submodel, the systematic depletion of larger-bodied organisms by humans has drastically altered food webs in the world's oceans (Jackson, 2001; Jackson *et al.,* 2001; Baum *et al.,* 2003; Myers and Worm, 2003). These altered food webs can change the functioning of coastal ecosystems (Worm *et al.,* 2000) and can even have effects that cascade downward to the structure of the seagrass beds (Jackson, 2001). The loss of top predators, like sharks and large groupers, may increase the population of smaller herbivores, resulting in more grazing of seagrass beds. Given that these smaller herbivores exhibit a preference for fast-growing, high nutrient-content seagrasses, changes in predators could result in a change in species composition of the seagrass beds (Armitage and Fourqurean, 2006). In contrast, the marked population reductions of large herbivores, like green sea turtles and manatees from pre-Columbian times, may have resulted in a decrease in grazing and an overgrowth of seagrasses beyond their historic extent (Jackson, 2001).

There is also the possibility that fisheries activities that lead to the loss of filter feeding organisms, like sponges and mussels, could negatively affect seagrasses. The loss of the filtering activity of these organisms can lead to decreases in water clarity. Such a cascade of effects has been hypothesized as an important driver behind seagrass losses in Florida Bay in the late 1980s and early 1990s where blooms of noxious blue-green algae caused the death of most of the sponge community in western Florida Bay (Butler *et al.,* 1995). The subsequent loss of sponge filtration decreased the effective time required for sponges to filter the water column of Florida Bay (Peterson *et al.,* 2006).

Coastal Development

Urban/suburban development of the Florida Keys poses threats to seagrass beds. It is obvious that dredging of seagrass beds to aid in access by boats and filling seagrass beds for construction lead directly to seagrass losses, but there are other effects of increasing coastal development. Armoring of the shoreline with seawalls and docks increases the reflection of wave energy and increases erosion rates in nearshore seagrass beds. As human populations increase, nutrient loading will increase. Additional cover of impervious surfaces can increase the amount of stormwater runoff, and increased use of those surfaces by the growing population can lead to an increase in sediment and toxic chemicals in the runoff. A growing fleet of recreational vessels increases the chances of both intentional and accidental impacts of those boats on the seagrass beds.

The near-field effects of human activity in the Florida Keys and surrounding waters has the potential to deleteriously affect seagrasses. Increasing human population density in coastal regions has often led to eutrophication, which can reduce the light available for seagrasses; eutrophication has been implicated in the loss of seagrasses from many areas of the world. Dredging and filling of coastal areas for navigation and development can directly remove potential seagrass habitat, alter hydrological conditions that lead to erosion, and cause a reduction in light available to seagrasses by increasing turbidity. Recreational and commercial use of seagrass beds can also damage them. For example, contact of the bottom by outboard motors can cause scars that can take years to recover; the cumulative impacts of such frequent events can lead to a complete loss of seagrass beds from heavily-trafficked areas.

Climate Change

Since the Industrial Revolution of the early 1800s, widespread fossil fuel combustion has contributed large quantities of carbon dioxide to both atmospheric and oceanic reservoirs around the globe. Present day atmospheric CO_2 concentrations of 385 ppm represent a near 30 percent increase over pre-industrial values, with concentrations forecast to surpass 700 ppm by the end of the century (IPCC, 2007). Global sea surface temperatures are responding to these increases in CO_2 concentrations, with projected increases in sea surface temperatures of a few degrees Celsius by the end of the century (IPCC, 2007).

Changes in Ocean Water Chemistry

Roughly 30 percent of the anthropogenically-released CO_2 has been absorbed by the global oceans (Feely *et al.,* 2004), with severe consequences for the carbonate chemistry of the surface waters (Sabine *et al.,* 2004). Furthermore, CO_2-mediated increases in the abundance of H+ ions are expected to dramatically reduce oceanic pH, with forecasts of a 0.5 unit reduction by the year 2100 (Sabine *et al.,* 2004).

Several studies have suggested that altered pCO_2 values within coastal environments may impact the functioning of both aquatic and marine plant communities (e.g., Kleypas and Yates, 2009; Martin *et al.,* 2008; Palacios and Zimmerman, 2007; Short and Neckles, 1999; Zimmerman *et al.,* 1997). External increases in CO_2 and HCO_3^- concentrations have the ability to increase seagrass production (Hall-Spencer *et al.,* 2008), leaf photosynthetic rates (Beer and Koch, 1996; Durako, 1993; Invers *et al.,* 1997; Zimmerman *et al.,* 1997), and plant reproductive output (Palacios and Zimmerman, 2007). Submerged macrophytes comprise much of the coastal benthic community around the globe and are important contributors to the carbon sink capacity of the world's oceans (Duarte *et al.,* 2010); thus, similar to declines in reef calcification, changes in oceanic pCO_2 may additionally have widespread implications for these productive and economically-important ecosystems. CO_2-mediated growth responses can be rapidly constrained by the availability of other essential resources, such as water and/or nutrients (Diaz *et al.,* 1993).

Changes in Salinity and Temperature

Increasing sea surface temperatures may negatively impact seagrasses in the region. This point was illustrated by the loss of the largest stands of seagrasses due to the discharge of heated water from the Turkey Point Nuclear Power Plant on the shores of Biscayne Bay in the 1960s (see review by Zieman and Wood, 1975). A rise of only 3°C caused mortality of macroalgae, and a modest 4°C rise in temperatures killed nearly all plants and animals in the seagrass bed.

In addition to the relatively direct changes in pCO_2 and temperature associated with climate change, it is anticipated that the timing and amount of rainfall and evaporation will change as well (IPCC, 2007). These changes in the freshwater budget of coastal Florida have the potential to change the salinity climate and nutrient supply in coastal seagrass beds. Species composition of seagrass beds is influenced by the salinity climate, with increases in the amount and variability in runoff leading to a change from *T. testudinum*-dominated seagrass beds to ones dominated by *H. wrightii* (Fourqurean *et al.,* 2003). Anthropogenic decreases in freshwater flow into Florida Bay played a major role in the shift of the seagrass communities of eastern Florida Bay from a *H. wrightii*-dominated state in the 1970s to a *T. testudinum*-dominated state in the 1980s (Schmidt, 1979; Zieman, 1982).

Mechanisms of Change in Seagrass Beds

The principal threats to seagrass beds in Florida Keys marine waters occur through three pathways: eutrophication of the normally oligotrophic Keys marine waters; changes in the food-web; and damage to seagrass beds as the direct result of human activities (Figure 2).

Eutrophication

Three sources of nutrients alter water quality in Florida Keys marine waters and potentially fuel eutrophication. Storm water runoff and domestic and municipal wastewater affect water quality in inshore waters, especially inshore areas like canals, that are poorly flushed by tides. Increased nutrient loads in freshwater inflow from mainland watersheds are another source of increased nutrient concentration in Florida Keys waters. Increased nutrient loads to Florida Shelf waters are the result of changing land use and agricultural practices both in the South Florida region and beyond.

Nutrient loading from both wastewater and stormwater in the Florida Keys has a high potential to negatively affect seagrass beds. The natural state of the nearshore marine waters is one of nutrient limitation of plant (and therefore animal) biomass. The addition of nutrients to the system causes an increase in total plant biomass and a shift in species composition. At the natural low-nutrient state, slow-growing species like *T. testudinum* are the competitively dominant species but, as nutrient availability increases, the competitive dominance shifts to successively faster-growing species. At the highest nutrient loads, phytoplankton, the fastest-growing primary producers, cloud the water and decrease the penetration of light through the water to the bottom, effectively shading out seagrasses and benthic macroalgae.

Changes to the Food Web

While the net effect of humans altering food webs is not certain, in all likelihood our current seagrass ecosystems are different now than they were before human alteration of coastal food webs through selective harvesting of the large predators and herbivores from the ecosystem, as discussed previously.

Damage—Benthic Community

Boating activities, in general, can negatively impact seagrass beds in a number of ways, including: intentional dredging for navigation and harbors; unintentional vessel groundings; increased turbidity from prop wash; nutrient loading from improper disposal of wastes; and unintentional spills of chemicals associated with boats, especially around marinas.

Fishing practices that intentionally disturb the bottom have an impact on seagrass meadows. Cockle and scallop fishing in the North Atlantic have been documented to completely remove the seagrasses that supported these economically important shellfish (Fonseca *et al.,* 1984; De Jonge and De Jonge, 1992). In South Florida, the offshore waters that support the Tortugas shrimp fishery are underlain by extensive meadows of the seagrass *H. decipiens* (Fourqurean *et al.,* 2001). These seagrass resources are undoubtedly repeatedly disturbed by the activities of shrimp trawlers. Similarly, the bait shrimp fishery in Biscayne Bay poses a threat to seagrass meadows. Unintentional consequences of fisheries activities can also impact seagrass beds. Lobster and stone crab traps placed on the bottom can kill the seagrasses beneath them. Storms can drag these traps around the bottom, magnifying their negative effect on the seagrasses.

Seagrass Status and Trends

Concerns for the state of the seagrass beds of South Florida are well-founded. While currently the seagrass beds are nearly continuous and apparently healthy, there is cause for alarm. Despite their recognized importance, worldwide loss of seagrass beds continues at an alarming rate (Short and Wyllie-Echeverria, 1996). This loss has been largely attributed to anthropogenic inputs of sediment and nutrients. The difficulty of monitoring seagrass beds has led to obfuscation of the real extent of seagrass loss, as our best estimates of even the current global extent of this important habitat are within an order of magnitude (Duarte, 2002). In Florida, anthropogenic seagrass losses have been reported in Pensacola Bay, St. Joseph Bay, Tampa Bay, Charlotte Harbor, the Florida Keys, Biscayne Bay, and the Indian River Lagoon (see Sargent *et al.,* 1995; Short and Wyllie-Echeverria, 1996, for reviews), but accurate estimates of the current areal extent of seagrasses even in a populated, first-world location like Florida are only recently available.

While large-scale deterioration of the seagrass beds across the entire South Florida region has yet to occur, localized cases of coastal eutrophication have led to a loss of seagrasses in the study area (Lapointe *et al.,* 1990; Tomasko and Lapointe, 1991; Lapointe and Clark, 1992; Lapointe *et al.,* 1994). The long-lived effects of the dieoff event in Florida Bay underscores the importance of healthy seagrass beds to a sustainable marine ecosystem. A poorly understood dieoff of dense stands of *T. testudinum* in Florida Bay occurred beginning in 1987. The affected area (ca. 4000 ha) was small compared to the total amount of seagrass habitat in South Florida, but the ramifications from this event were great. Turbidity in the water column and algal blooms

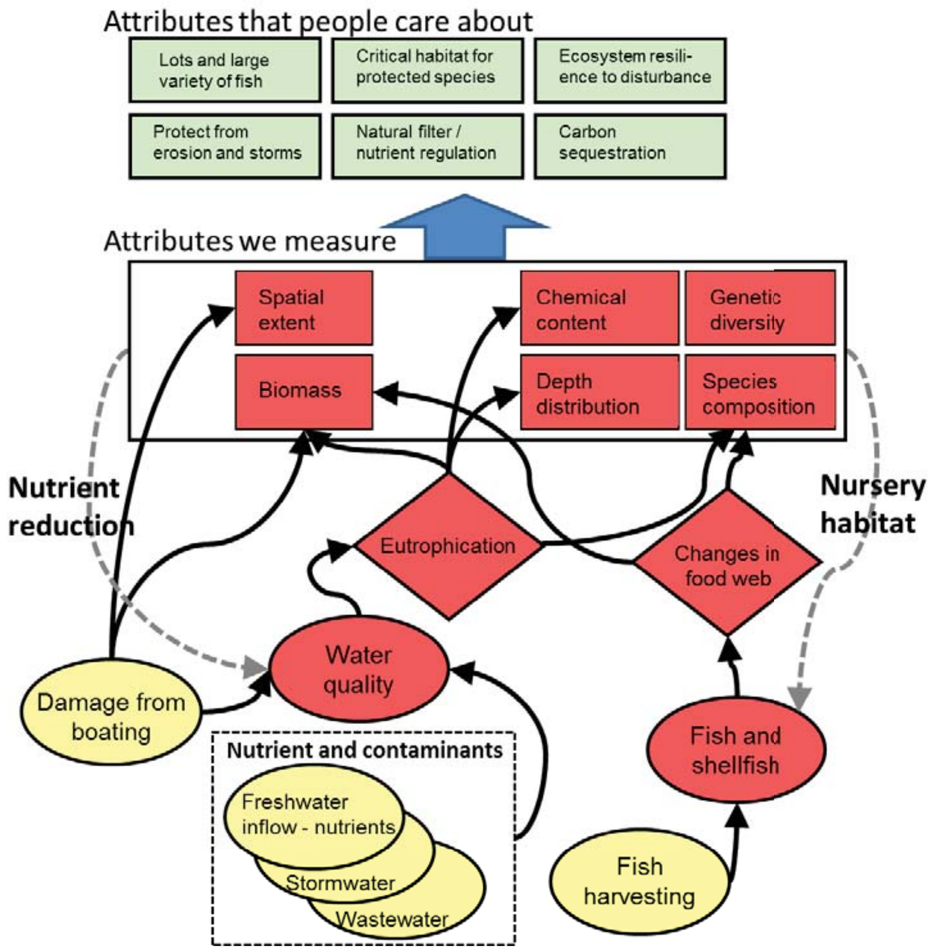

Figure 2. Seagrasses submodel diagram for Florida Keys and Dry Tortugas.

followed the loss of seagrasses (Phlips et al., 1995), leading to a dieoff of sponges (Butler *et al.,* 1995) and a general decline in seagrass beds that survived the initial dieoff in an area of ca. 1000 km^2. Seagrass dieoff in Florida Bay is still poorly understood (Fourqurean and Robblee, 1999), and the increase in turbidity that followed the dieoff continues to effect change in western Florida Bay (Hall *et al.,* 1999; Durako *et al.,* 2002).

While the history of seagrass trajectories in the coastal zone worldwide and in Florida, in particular, is not good, there are some indications that some of these trajectories are reversible. For example, six years after the implementation of sewage collection and treatment and the cessation of the use of septic tanks and cesspits in the Marathon Key area, there are indications that seagrass declines can be reversed (Herbert and Fourqurean, unpublished data). Elemental content and stable carbon isotope ratios indicate a decrease in eutrophication and an increase in light reaching the seagrass meadows nearest the shoreline. Because of the very long residence time of the nutrient phosphorus in seagrass meadows of the Florida Keys (Herbert and Fourqurean, 2008), the species composition of these seagrass beds has yet to revert to the more slow-growing species, but it is expected that this will occur over the next decade.

Topics of Scientific Debate and Uncertainty

While historic changes have elucidated the pathways by which ecosystem structure and function change in response to increased human pressure, we do not have a good idea what pathways these seagrass ecosystems will follow once the human pressures have abated. We know, for instance, that the primary limiting nutrient for most of the region, phosphorus, has a very long residence time in seagrass meadows in South Florida. Understanding the factors controlling the loss of phosphorus from eutrophied systems is critical to projecting pathways of recovery. Further, research is needed on how effective habitat restoration efforts are towards restoring seagrass ecosystem structure and function. We also need a better understanding of how food web alteration has affected the structure and function of seagrass meadows to understand how current fisheries practices and conservation efforts are likely to affect seagrass meadows in the future. For example, it appears that resurgent green sea turtle populations in Bermuda, in the absence of top predators to control their populations, may be contributing to the loss of seagrass beds in that country (Fourqurean *et al.,* 2010). Without a full understanding of food web structure in our coastal systems, there could be unintended consequences in our fisheries and conservation strategies.

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