Changes in the Distribution of Seagrass Species along Florida's Central Gulf Coast: Iverson and Bittaker Revisited

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ABSTRACT: A broad-scale survey of seagrass species composition and distribution along Florida's central Gulf Coast (known as the Big Bend region) was conducted in the summer of 2000 to address growing concerns over the potential effects of increased nutrient loading from adjacent coastal rivers. Iverson and Bittaker (1986) originally surveyed seagrass distribution in this region between 1974–1980. We revisited 188 stations from the original survey, recording the presence or absence of all seagrass species. Although factors such as accuracy of station relocation, differences in sampling effort among studies, and length of time between surveys preclude statistical comparisons, several interesting patterns emerged. While the total number of stations occupied by the three most common seagrass species, *Thalassia testudinum, Syringodium filiforme*, and *Halodule wrightii*, was similar between the two time periods, we observed a change in the number of records of each species as well as changes in distribution with depth. *T. testudinum* and *Halophila engelmanni* occurrence declined in the deepest areas of the region, while the number of stations occupied by *S. filiforme* and *H. wrightii* increased in nearby areas. We observed several localized areas of seagrass loss, frequently associated with the mouths of coastal rivers. These results suggest that increased nutrient loading to coastal rivers that discharge into the Big Bend area may be affecting seagrasses by increasing phytoplankton abundance in the water column, thus changing water clarity characteristics of the region.

Introduction

Florida's north central Gulf coastline, commonly referred to as the Big Bend (Anclote Key north to Apalachee Bay), includes the second largest expanse of seagrass habitat in the eastern Gulf of Mexico. Iverson and Bittaker (1986) conducted a broad-scale survey of seagrass distribution of this region in the late 1970s. In that report, the authors recorded the distribution of six of seven Florida species of seagrass within this area, and estimated total seagrass coverage at about 3,000 km².

Seagrass beds are essential to the ecological integrity and health of Florida's estuarine and nearshore coastal ecosystems. Along Florida's Gulf Coast, seagrasses provide refuge and forage habitat for many ecologically and economically important fauna, such as scallops, shrimps, blue crabs, manatees, and turtles (Killam et al. 1992). A number of researchers have documented degradation or destruction of many of Florida's seagrass ecosystems, including areas in Apalachee Bay (Zimmerman and Livingston 1976), Tampa Bay (Lewis and Estevez 1988), and Florida Bay (e.g., Robblee et al. 1991). In many of these cases, increased nutrient loading or other anthropogenic insult is blamed for the loss.

Seagrass survival, growth, and production are influenced by irradiance levels (reviewed by Duarte 1991), sediment nutrient availability (Short 1987; Williams 1990), water flow (Fonseca et al. 1983; Fonseca and Bell 1998), temperature (Masini et al. 1995), and salinity (Walker and McComb 1990). Among these, light is most often recognized as the major determinant of seagrass distribution (Duarte 1991). The amount of light available for photosynthesis is influenced by water clarity, which is largely a function of turbidity. Reduced water clarity caused by increased phytoplankton abundance or suspended sediment, often associated with anthropogenic disturbance of nearshore ecosystems, appears to be the most widespread mechanism threatening seagrass health (Short and Wyllie-Echeverria 1996). Epiphytic algae growth may affect seagrass photosynthetic potential by intercepting incident light (Den Hartog 1979; Tomasko and Lapointe 1991).

Though the addition of nutrients alone does not always lead to a decline in seagrass health (e.g., Erftemeijer et al. 1994), increases in phytoplank-

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ton production and epiphytic abundance on seagrass leaves generally result from increased nutrient delivery to a system. Numerous researchers have documented changes in seagrass ecosystems across large geographic extents due to various causes. Den Hartog and Polderman (1975) postulated that anthropogenic pollution, expressed as a change in water quality, was behind the widespread effects of the seagrass wasting disease and regional declines in seagrass coverage observed in the 1930s and later. Livingston (1984) described numerous long-term detrimental effects of pollution (as a change in water quality) on seagrass ecosystems along the northern Gulf Coast of Florida. Dennison et al. (1993) linked physical habitat requirements of submersed aquatic vegetation to a variety of water quality standards, including nutrient content, and argued that the connection between seagrass condition and water quality parameters was so consistent that changes in seagrass cover, particularly along their depth limit, may be an early sign of degenerating water quality. Fourqurean et al. (1995) reported a change in seagrass species composition of a seagrass bed in Florida Bay due to increased nutrient input. Short and Burdick (1996) provided evidence relating loss of seagrass cover and increased fragmentation of seagrass beds to urban development and increased nutrient input into receiving waters, while Tomasko et al. (1996) reported a negative correlation between seagrass biomass and productivity and watershed nutrient loading.

Nutrient concentrations are increasing in many of the rivers that feed the coastal waters along Florida's central Gulf Coast (Ham and Hatzell 1996; Jones et al. 1997), and increases in nutrient loads to coastal waters in the region potentially threaten the seagrass beds along this portion of Florida's Gulf Coast (Frazer et al. 2001). Because seagrasses are often used to ascertain impacts resulting from increased anthropogenic nutrient inputs, we repeated, in large part, the broad-scale survey completed over 25 yr ago by Iverson and Bittaker to determine if a change in seagrass distribution and species had occurred. Approximately two hundred stations along the Big Bend coast of Florida, from Piney Point (north of the Steinhatchee River) to Anclote Key (just north of Tampa Bay) were revisited, and the presence or absence of seagrasses was recorded. Returning to these stations enabled us to update information regarding the distribution and species composition of seagrass communities along Florida's central Gulf coast, and provided the opportunity to assess changes that may have occurred as a result of increased nutrient inputs.

Materials and Methods

Iverson and Bittaker (1986) conducted surveys of seagrass distribution along the northwest Gulf coast of Florida from Apalachee Bay south to Anclote Key in October of each year between 1974-1980. Between July and September 2000, we revisited 188 of these sampling stations, recording the presence or absence of all seagrass species along 250 km of coastline within an area of approximately 6,000 km². The exact coordinates of the Iverson and Bittaker sampling stations were not available (Bittaker personal communication), but were estimated by two methods: digitization of the original map from Figure 1 of their text, and then assigning map coordinates to the image using the available latitude-longitude graticules, or estimation via triangulation from well-defined land forms. One short SCUBA dive or up to 3 snorkel dives were made at each sampling station, and the presence or absence of any submersed aquatic vegetation was noted. If any vegetation was present, additional search time was devoted to detect as many species of seagrass as possible. Surveyors were not told where to expect to find seagrass from the original survey to standardize the survey effort at each station.

Water depth was recorded to the nearest 0.5 m at each station. To compare depth distributions of species between the historical and current surveys, we assumed the depth at each station to be the same between time periods. No mention of standardizing depth to any elevation datum was made in the original report. Mean tidal range for the Big Bend coastline is 0.85 m (National Ocean Service unpublished material).

Results

The presence or absence of four species of seagrasses, Thalassia testudinum, Syringodium filiforme, Halodule wrightii, and Halophila engelmanni, was recorded at 188 sampling stations. We cataloged a cumulative total of 158 records of presence at 85 stations of the three most common seagrass species, T. testudinum, S. filiforme, and H. wrightii, a slight increase from 149 records at 79 stations made by Iverson and Bittaker (1986) (Table 1). We made fewer observations of the three less common species, including no records of Halophila decipiens or Ruppia maritima in 2000.

We recorded *T. testudinum* at 54 of 188 stations (29% occurrence; Fig. 1) between depths of 0.5 m (station 161) and 7.3 m (station 45), compared with 63 total observations (34% occurrence) made in the previous study. Fewer observations of *T. testudinum* at depths greater than 3 m were recorded in 2000 than 25 yr ago. In addition, our deepest

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TABLE 1. Summary of observations of seagrass species at 188 sampling locations. The depths represent the maximum depth each species was observed. The depths listed in the 1974–1980 column were determined from the depths we measured at the same stations in 2000.

| | Number of Records | | | Maximum Depth (m) | |
|-----------------------|-------------------|------|----------|-------------------|------|
| | 1974-1980 | 2000 | % Change | 1974-1980 | 2000 |
| Thalassia testudinum | 63 | 54 | -16% | 8.5 | 7.3 |
| Syringodium filiforme | 43 | 51 | +19% | 7.3 | 6.7 |
| Halodule wrightii | 43 | 53 | +23% | 10.6 | 8.3 |
| Halophila engelmanni | 23 | 16 | -30% | 10.6 | 7.0 |
| Halophila decipiens | 1 | 0 | -100% | 9.0 | _ |
| Ruppia maritima | 4 | 0 | -100% | 2.0 | _ |



Fig. 1. Differences in distribution between surveys of four species of seagrass, *Thalassia testudinum, Syringodium filiforme, Halodule wrightii*, and *Halophila engelmanni*. Solid circles indicate presence in both surveys, open circles indicate absence from both surveys, solid up-pointing arrows indicate new record, and open down-pointing arrows indicate loss or failure to observe. Dotted lines delineate the 6- and 9-m isobaths.



Fig. 2. Comparison of the frequency of distribution of four species of seagrass by depth: *Thalassia testudinum, Syringodium filiforme, Halodule wrightii,* and *Halophila engelmanni.*

observation of this species was approximately 1 m shallower than in the previous study (Fig. 2).

S. filiforme occurred at 51 of our stations (27% occurrence; Fig. 1), an increase from 43 records as reported in the previous study (23% occurrence). In 2000, S. filiforme was distributed in water of depths that ranged from 2 m to 7 m. In the earlier study S. filiforme was recorded at depths between 2 m and 8 m (Fig. 2).

We recorded *H. wrightii* at 53 stations (28% occurrence; Fig. 1), while it was recorded at 43 stations (23% occurrence) 25 yr ago. *H. wrightii* occurred at depths between 2 m and 11 m in the previous study, at least 2 m deeper than our deepest record of approximately 8.5 m (Fig. 2).

H. engelmanni was recorded at 16 of 188 stations (8% occurrence), only two-thirds of the 23 stations in the previous study (12% occurrence). In general, the loss of records occurred either along the coastline of the northern half of our study area, or from the deepest, offshore regions of the southern half (Fig. 1). The latter observation accounts for a loss of at least 3 m from the maximum depth of distribution of this species (Fig. 2).

The occurrence of T testudinum along the 6-m isobath from 20 to 30 km offshore in the southern third of our study area decreased considerably. These contiguous records of absence occur in some of the deepest areas where this species was recorded between 1974 and 1980. In addition to the absence of T testudinum, we recorded an increase in H urightii occurrence at 8 of our stations and an increase in S. filiforme at 5 stations (Fig. 3). These changes resulted in 5 stations where T testudinum was not recorded, but either S filiforme or H urightii or both was observed.

Discussion

Because Big Bend bathymetry is characterized by a very gentle slope, increasing about 1 m in depth per 5 km distance from shore, relatively large distances from shore result in only subtle changes in depth. Though they observed seagrasses in deeper waters, Iverson and Bittaker (1986) described an "outer limit" of seagrass bed development, where seagrass occupied at least 80% of the bottom. For much of the southern portion of our study area, this outer limit corresponded with the 6-m isobath. It follows that even a small decrease in water clarity could decrease the potential habitat of dense seagrass coverage by several hundred square km off the coasts of counties south of Crystal River. Our data suggest the extent of abundant seagrass distribution may have retreated some distance shallower than the 6-m isobath.

Our observations indicate that the four most common seagrasses within our sampling area along Florida's central Gulf Coast have experienced a reduction in their maximum depth of occurrence over the last 25 yr. Light is generally recognized as the factor most often controlling seagrass depth distributions (e.g., Duarte 1991), and reduced water clarity due to increased phytoplankton abundance and suspended solids seems to be the most widespread mechanism threatening seagrass health (Short and Wyllie-Echeverria 1996). We hypothesize that increased nutrient loading to the region may have resulted in an increase in phytoplankton abundance and possibly periphyton abundance on seagrass blades (Den Hartog 1979;



Fig. 3. Locations where *Thalassia testudinum* was present in the historical study, but replaced by *Syringodium filiforme* (S) or *Halodule wrightii* (H), or both species in the current survey. Dotted lines delineate the 6- and 9-m isobaths.

Tomasko and Lapointe 1991) which has changed the light regime available to seagrasses at depth. There have been several regional reports indicating that nutrient concentrations (nitrate, in particular) in rivers that discharge directly into the Gulf of Mexico along Florida's Big Bend coast have increased over the last several decades (Ham and Hatzell 1996; Jones et al. 1997), and our hypothesis is consistent with the findings in these reports. There is no comparable water quality data available for the coastal region of interest to corroborate the hypothesis that increased nutrient loading has resulted in increased phytoplankton biomass and reduced light availability at depth. This information should be a priority for subsequent investigators whose aim is to more fully understand these changes in depth distribution of seagrasses.

In several locations, the distribution of *H. wrightii* and *S. filiforme* increased where *T. testudinum* experienced marked losses. *H. wrightii* has higher nutrient requirements than *T. testudinum* (Fourqurean et al. 1995), and the loss of the latter species (perhaps due to decreased available light) may have allowed for the successful re-colonization by *H. wrightii* given adequate nutrient conditions. Gallegos et al. (1994) described how pioneer seagrass species—i.e., S. filiforme and H. wrightii—exhibit higher growth and turnover rates than T. testudinum, supporting the concept that both the former species are colonizers of habitats with higher nutrient availability or lower light. In an example where light was not likely a factor, Fourqurean et al. (1995) reported how H. wrightii out-competed T. testudinum in the presence of increased or excess nutrients. Under those conditions, H. wrightii remained the dominant (biomass) seagrass up to 8 yr after the removal of the nutrient source. These observations support our idea of a regional shift from a high-light, nutrient-poor system characterized by T. testudinum to a lower light, higher nutrient system favoring S. filiforme and H. wrightii.

Our proposition of the effects of decreased light are further supported by a review of the life histories of these seagrasses. *T. testudinum*, though capable of rapid blade growth, also has long-lived short shoots, up to 7 yr in the northern Gulf of Mexico (Eleuterius 1987), while *S. filiforme* and *H.* wrightii have comparatively shorter-lived shoots, i.e., about 1-3 yr (Eleuterius 1987; Gallegos et al. 1994). This suggests that *T. testudinum* may exhibit less rapid appearance or disappearance than *S. filiforme* or *H. wrightii*. Our observed decrease in the offshore extent of *T. testudinum* suggests longerterm and more chronic stress, perhaps as a consequence of decreased light availability.

It is important to note that we recorded more locations with S. filiforme and H. wrightii than did Iverson and Bittaker (1986). This suggests light is not limiting the distribution of all seagrasses in some parts of our study area. Williams (1987) demonstrated that T. testudinum may outcompete S. filiforme given plentiful nutrients and light. Buesa (1975) reported that S. filiforme grows well in lowerlit areas where T. testudinum may be light-limited, an observation supported by the mean maximum depth limits of colonization summarized by Duarte (1991). There is considerable overlap in the recorded depth ranges of these species, and Williams (1987) observed how seagrasses partition sediments (and thus nutrient availability) given adequate light for photosynthesis. T. testudinum occurred with other seagrass species in almost 90% of our observations, while Iverson and Bittaker recorded only 75% co-occurrence in their study. Around Florida, Phillips (1960) noted small amounts of S. filiforme and H. wrightii in seagrass areas dominated by T. testudinum, north of the Anclote Keys, and Zieman et al. (1989) recorded species co-occurrence at only 45 of 108 stations (42%stations) in Florida Bay. In light of Williams' experimental results and the differences between our observations and those of the original Iverson and Bittaker surveys, we conclude that mixed assemblages of seagrass species are not uncommon in our area, rather the presence of 2 or 3 species of seagrass in the same location is the rule instead of the exception.

Our results also indicate that seagrasses were not necessarily present at the same locations between the historic and current surveys. We recorded Ttestudinum at 54 stations, but only 39 stations were common to both surveys; and we recorded H. wrightii at a total of 53 stations, but only 16 stations were common to both surveys. While the net records of seagrass presence were similar between surveys, the actual locations of seagrass presence were variable. This suggests a dynamic that warrants further investigation. It is possible that sediment characteristics are more highly variable, both in space and time, than previously recognized or appreciated. It is also possible that sexual reproduction among the seagrasses observed in this region is a common occurrence and may be an under-appreciated aspect of their life history. Quantitative data concerning the frequency and intensity of sexual reproduction, seed dispersal and subsequent germination of new plants are sparse in this region (Moffler and Durako 1987; Mattson 2000).

We recorded more stations with seagrasses in the southern half of our study area than in the north half. Examples of the community shift from T testudinum to H. wrightii or S. filiforme were more numerous in the south than in the north. Iverson and Bittaker (1986) measured a higher light extinction coefficient at northern stations (north of Crystal River, approximately 29°N) than southern stations. While they did not report which component of light was most responsible for this difference in attenuation (e.g., scattering, color; see Kirk 1994), there are differences in characteristic land cover and watersheds which may partially explain this difference. Rivers draining into the northern half of our study area are higher in color (Frazer et al. 1998), a reflection of differences in watershed size and dominant vegetation. As a result of tropical storm events, the plume from the Suwannee River (approximately 29°20'N) may extend 20 km or more from the coast, exporting colored dissolved organic material and light-scattering particles into the offshore environment (Bledsoe and Phlips 2000), and further increasing light attenuation. Most of the rivers in the southern half of the region are short and fed by artesian springs, contributing little colored dissolved organic material or suspended particles to nearshore areas. This natural difference within the study area is important to consider when designing future research plans aimed at describing seagrass ecology in the region. Changes in the land cover and land use surrounding these coastal rivers should be monitored and managed with care.

Two characteristics of the data sets precluded a rigorous statistical comparison: precise station locations were not available to us, and the original authors pooled their data across 6 yr (to minimize interannual variability), while we had only a single observation during a single year at each station. By pooling data, Iverson and Bittaker (1986) biased their reports to records of presence. In other words, a single observation of presence of a seagrass species during any one of 6 yr yielded a present value, even if the species was not recorded at any other time during the surveys. That we recorded more stations having seagrass present in a single survey suggests that there may be more seagrassincreased distribution across the region-than when the original surveys were conducted. Most of the stations where we did not record formerly present seagrass species were contiguous; i.e., immediately adjacent to river mouths and along the deep edge of T. testudinum distribution. This lends credence to the assertion that seagrasses have disappeared from these areas over the time interval between the present and historical surveys, and that our observations do not represent sporadic or short-term changes in distribution.

While a number of studies conducted during the last three decades have estimated seagrass abundance along the Big Bend coast of Florida, research into other aspects of seagrass ecology-e.g., seagrass productivity, reproduction, and speciesspecific light requirements—have been conducted only sporadically, and never along the entire coastline. This study establishes a new baseline against which future changes in the regional seagrass ecosystem might be gauged. More inclusive investigations involving the simultaneous measurement of nutrients, phytoplankton abundance, epiphyte growth on seagrass blades, and light levels carried out on a spatial scale similar to this and the historical survey by Iverson and Bittaker (1986) will be necessary to monitor the effects of management actions and development in a region where the watershed includes many thousands of square km of south Georgia and central and north Florida.

LITERATURE CITED

- BLEDSOE, E. L. AND E. J. PHLIPS. 2000. Relationships between phytoplankton standing crop and physical, chemical, and biological gradients in the Suwannee River and plume region, U.S.A. *Estuaries* 23:458–473.
- BUESA, R. J. 1975. Population and biological data on turtle grass (*Thalassia testudinum* Koenig, 1805) on the Northwestern Cuban shelf. Aquaculture 4:207–226.
- DEN HARTOG, C. 1979. Seagrasses and seagrass ecosystems, an appraisal of the research approach. Aquatic Botany 6:105-117.
- DEN HARTOG, C. AND P. J. G. POLDERMAN. 1975. Changes in the

seagrass populations of the Dutch Waddenzee. Aquatic Botany 1:141-147.

- DENNISON, W. C., R. J. ORTH, K. A. MOORE, J. C. STEVENSON, V. COARTER, S. KOLLAR, P. W. BERGSTROM, AND R. A. BATTUK. 1993. Assessing water quality with submersed aquatic vegetation. *Bioscience* 43:86–91.
- DUARTE, C. M. 1991. Seagrass depth limits. Aquatic Botany 40: 363-377.
- ELEUTERIUS, L. N. 1987. Seagrass ecology along the coasts of Alabama, Louisiana, and Mississippi, p. 11–20. *In* M. J. Durako, R. C. Phillips, and R. R. Lewis, III (eds.), Proceedings of the Symposium on Subtropical-Tropical Seagrasses of the Southeastern United States. Florida Marine Research Publication No. 42. Florida Department of Natural Resources, St. Petersburg, Florida.
- ERFTEMEIJER, P. L. A., J. STAPEL, M. J. E. SMEKENS, AND W. M. E. DROSSAERT. 1994. The limited effect of in situ phosphorus and nitrogen additions to seagrass beds on carbonate and terrigenous sediments in South Sulawesi, Indonesia. *Journal* of *Experimental Marine Biology and Ecology* 182:123–140.
- FONSECA, M. S. AND S. S. BELL. 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. Marine Ecology Progress Series 171:109–121.
- FONSECA, M. S., J. C. ZIEMAN, G. W. THAYER, AND J. S. FISHER. 1983. The role of current velocity in structuring eelgrass (Zostera marina L.) meadows. Estuarine, Coastal and Shelf Science 17: 367–380.
- FOURQUREAN, J. W., G. V. N. POWELL, W. J. KENWORTHY, AND J. C. ZIEMAN. 1995. The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thal*assia testudinum and *Halodule wrightii* in Florida Bay. Oikos 72: 349-358.
- FRAZER, T. K., M. V. HOYER, S. K. NOTESTEIN, D. E. CANFIELD, JR., F. E. VOSE, W. R. LEAVENS, S. B. BLITCH, AND J. CONTI. 1998. Nitrogen, phosphorus, and chlorophyll relations in selected rivers and nearshore coastal waters along the Big Bend Region of Florida. Final report. Suwannee River Water Management District, Live Oak, Florida and Southwest Florida Water Management District, Brooksville, Florida.
- FRAZER, T. K., M. V. HOYER, S. K. NOTESTEIN, J. A. HALE, AND D. E. CANFIELD, JR. 2001. Physical, chemical and vegetative characteristics of five Gulf coast rivers. Final Report. Southwest Florida Water Management District, Brooksville, Florida.
- GALLECOS, M. E., M. MERINO, A. RODRIGUEZ, N. MARBA, AND C. M. DUARTE. 1994. Growth patterns and demography of pioneer Caribbean seagrasses Halodule wrightii and Syringodium filiforme. Marine Ecological Progress Series 109:99–104.
- HAM, L. K. AND H. H. HATZELL. 1996. Analysis of nutrients in the surface waters of the Georgia-Florida Coastal Plain study unit, 1970–91. Water-Resources Investigations Report 96-4037. U.S. Geological Survey, Tallahassee, Florida.
- IVERSON, R. L. AND H. F. BITTAKER. 1986. Seagrass distribution and abundance in eastern Gulf of Mexico waters. *Estuarine*, *Coastal and Shelf Science* 22:577–602.
- JONES, G. W., S. B. UPCHURCH, K. M. CHAMPION, AND D. J. DE-WITT. 1997. Water-quality and hydrology of the Homosassa, Chassahowitzka, Weeki Wachee, and Aripeka Spring complexes, Citrus and Hernando Counties, Florida (origin of increasing nitrate concentrations). Ambient Ground-Water Quality Monitoring Program. Southwest Florida Water Management District, Brooksville, Florida.
- KILLAM, K. A., R. J. HOCHBERG, AND E. C. RZEMIEN. 1992. Synthesis of basic life histories of Tampa Bay species. Technical publication #10-92. Tampa Bay National Estuary Program, St. Petersburg, Florida.
- KIRK, J. T. O. 1994. Light and Photosynthesis in Aquatic Ecosystems, 2nd edition. Cambridge University Press, New York.
- LEWIS, III, R. R. AND E. D. ESTEVEZ. 1988. The ecology of Tampa Bay, Florida: An estuarine profile. Biological Report No. 85

(7.18). U.S. Fish and Wildlife Service. National Wetlands Research Center, Slidell, Louisiana.

- LIVINGSTON, R. J. 1984. The relationship of physical factors and biological response in coastal seagrass meadows. *Estuaries* 7: 377–390.
- MASINI, R. J., J. L. CARY, C. J. SIMPSON, AND A. J. MCCOMB. 1995. Effects of light and temperature on the photosynthesis of temperate meadow-forming seagrasses in Western Australia. *Aquatic Botany* 49:239–254.
- MATTSON, R. A. 2000. Seagrass ecosystem characteristics and research and management needs in the Florida Big Bend, p. 259–277. In S. A. Bortone (ed.), Seagrasses: Monitoring, Ecology, Physiology, and Management. CRC Press, Boca Raton, Florida.
- MOFFLER, M. D. AND M. J. DURAKO. 1987. Reproductive biology of the tropical-subtropical seagrasses of the Southeastern United States, p. 77–88. In M. J. Durako, R. C. Phillips, and R. R. Lewis, III (eds.), Proceedings of the Symposium on Tropical-Subtropical Seagrasses of the Southeastern United States. Seagrasses of the Southeastern United States. Florida Marine Research Publication No. 42. Florida Marine Research, St. Petersburg, Florida.
- PHILLIPS, R. C. 1960. Observations on the ecology and distribution of the Florida seagrasses. Professional Paper Series 2. Florida Board of Conservation, Marine Laboratory, St. Petersburg, Florida.
- ROBBLEE, M. B., T. R. BARBER, P. R. CARLSON, JR., M. J. DURAKO, J. W. FOURQUREAN, L. K. MUEHLSTEIN, D. PORTER, L. A. YAR-BRO, R. T. ZIEMAN, AND J. C. ZIEMAN. 1991. Mass mortality of the tropical seagrass *Thalassia testudinum* in Florida Bay (USA). *Marine Ecology Progress Series* 71:297–299.
- SHORT, F. T. 1987. Effects of sediment nutrients on seagrasses: Literature review and mesocosm experiment. Aquatic Botany 27:41–57.
- SHORT, F. T. AND D. M. BURDICK. 1996. Quantifying eelgrass habitat loss in relation to housing development and nitrogen loading in Waquoti Bay, Massachusetts. *Estuaries* 19:730–739.
- SHORT, F. T. AND S. WYLLIE-ECHEVERRIA. 1996. Natural and hu-

man-induced disturbance of seagrasses. Environmental Conservation 23:17-27.

- TOMASKO, D. A., C. J. DAWES, AND M. O. HALL. 1996. The effects of anthropogenic nutrient enrichment on turtle grass (*Thal-assia testudinum*) in Sarasota Bay, Florida. *Estuaries* 19:448–456.
- TOMASKO, D. A. AND B. E. LAPOINTE. 1991. Productivity and biomass of *Thalassia testudinum* as related to water column nutrient availability and epiphyte levels: Field observations and experimental studies. *Marine Ecology Progress Series* 75:9–17.
- WALKER, D. I. AND A. J. MCCOMB. 1990. Salinity response of the seagrass Amphibolis antarctica (Labill) Sonder and Aschers— An experimental validation of field results. Aquatic Botany 23: 13–26.
- WILLIAMS, S. L. 1987. Competition between the seagrasses Thalassia testudinum and Syringodium filiforme in a Caribbean lagoon. Marine Ecology Progress Series 35:91–98.
- WILLIAMS, S. L. 1990. Experimental studies of Caribbean seagrass bed development. *Ecological Monographs* 60:449–469.
- ZIEMAN, J. C., J. W. FOURQUREAN, AND R. L. IVERSON. 1989. Distribution, abundance, and productivity of seagrasses and macroalgae in Florida Bay. *Bulletin of Marine Science* 44:292–311.
- ZIMMERMAN, M. S. AND R. J. LIVINGSTON. 1976. The effects of kraft mill effluents on benthic macrophyte assemblages in a shallow bay system (Apalachee Bay, North Florida, U.S.A.). *Marine Biology* 34:297–312.

Sources of Unpublished Materials

- BITTAKER, H. F. Personal Communication. South Florida Water Management District, 3301 Gun Club Road, West Palm Beach, Florida 33406.
- NATIONAL OCEAN SERVICE. Unpublished Material. 2003 Station information for the Cedar Key, Florida, tidal station benchmark. U.S. Department of Commerce. Available: http://www.co-ops. nos.noaa.gov/data_options.shtml? stn = 8727520+Cedar+ Key,+FL.

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