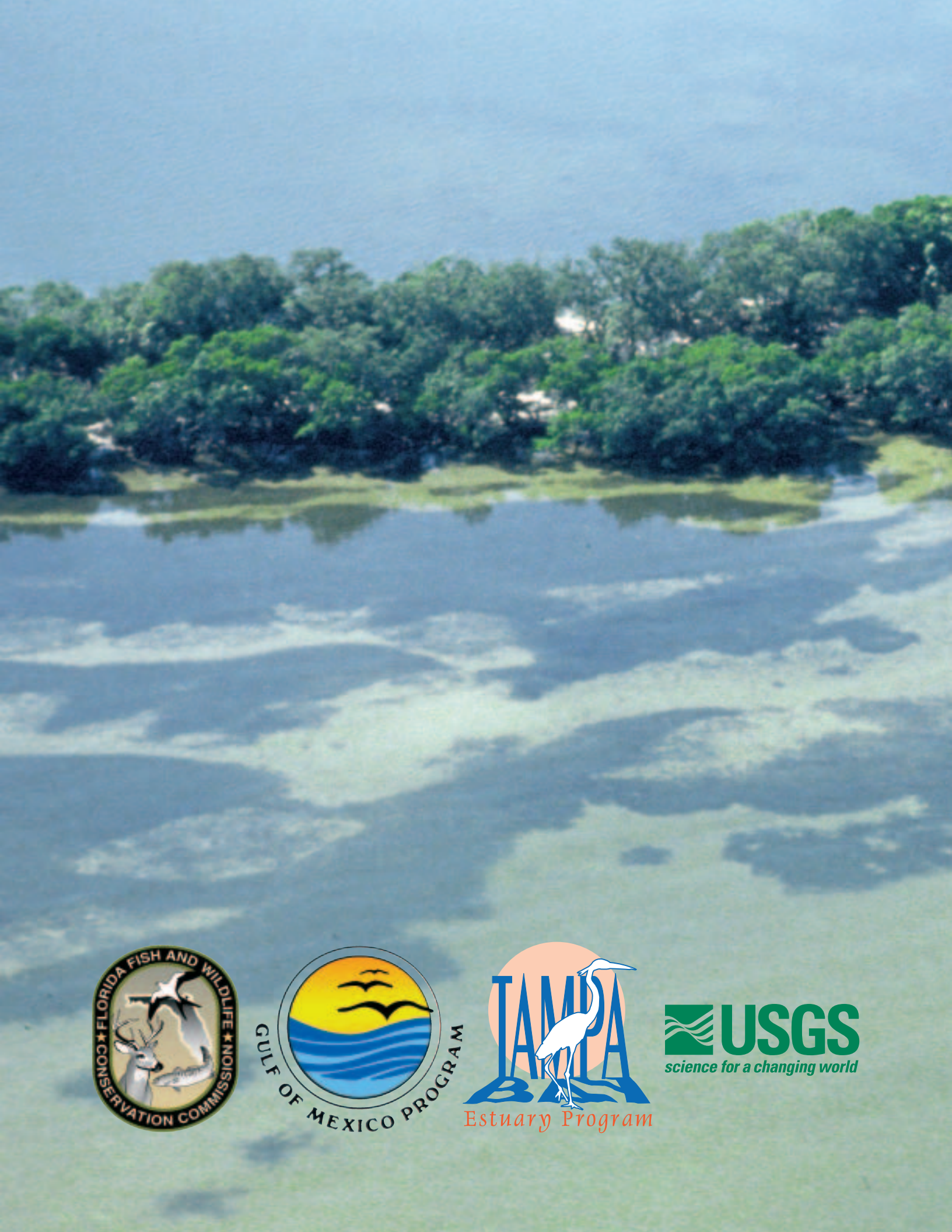# SEAGRASS COMMUNITIES
of the **GULF COAST**
of **FLORIDA:**
STATUS
and *ECOLOGY*

August 2004

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GEROLD MORRISON

SEAGRASS COMMUNITIES of the GULF COAST of FLORIDA: *STATUS* and *ECOLOGY*

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FOREWORD

The waters along Florida's Gulf of Mexico coastline, which stretches from the tropical Florida Keys in the south to the temperate Panhandle in the north, contain the most extensive and diverse seagrass meadows in the United States. Seagrass meadows rival or exceed most kinds of agriculture in their productivity and also provide unique aesthetic and recreational opportunities. The importance of seagrasses as food, shelter, and essential nursery habitats for commercial- and recreational-fishery species and for the many other organisms that live and feed in seagrass beds is well known. A single acre of seagrass can produce over 10 tons of leaves per year and can support as many as 40 thousand fish and 50 million invertebrates. This high level of production and biodiversity has led to the view that seagrass communities are the marine equivalent of tropical rainforests.

The importance of seagrasses to society has become fully recognized by government agencies. Seagrasses are now receiving focused attention from environmental managers, who require integrated science to aid in developing seagrass-protection programs. Studies concerning the ecology, biology, and management of Gulf-coast seagrasses are increasingly diverse and complex; yet a synthesis of this research has not been prepared since the late 1980s. The need for an up-to-date synthesis has resulted in the production of this document, which compiles and organizes the many diverse research efforts that have been accomplished for this region since that time.

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ACKNOWLEDGEMENTS

*I*NTRODUCTION

The goals of this review are to update what has become known about seagrasses since the publication of Zieman and Zieman's review in 1989 and to assess the current status of seagrass habitats on the Gulf coast of Florida.

⤷ Published studies about seagrasses have increased substantially since the 1960s.

⤷ Seagrass losses on Florida's Gulf coast, documented in the 1970s and 1980s, became the basis for state and local government involvement in developing management approaches.

⤷ Whether continuous or patchy in plant coverage, all seagrass communities should be viewed as having the same valued functions, such as serving as nurseries.

⤷ At least thirteen ecological roles have been assigned to seagrass communities, including roles as primary producers, as habitat for animals and plants, and as support for food webs.

⤷ Florida Gulf-coast seagrass communities support multimillion-dollar commercial and recreational industries, especially with regard to fishing.

Turtlegrass, *Thalassia testudinum*
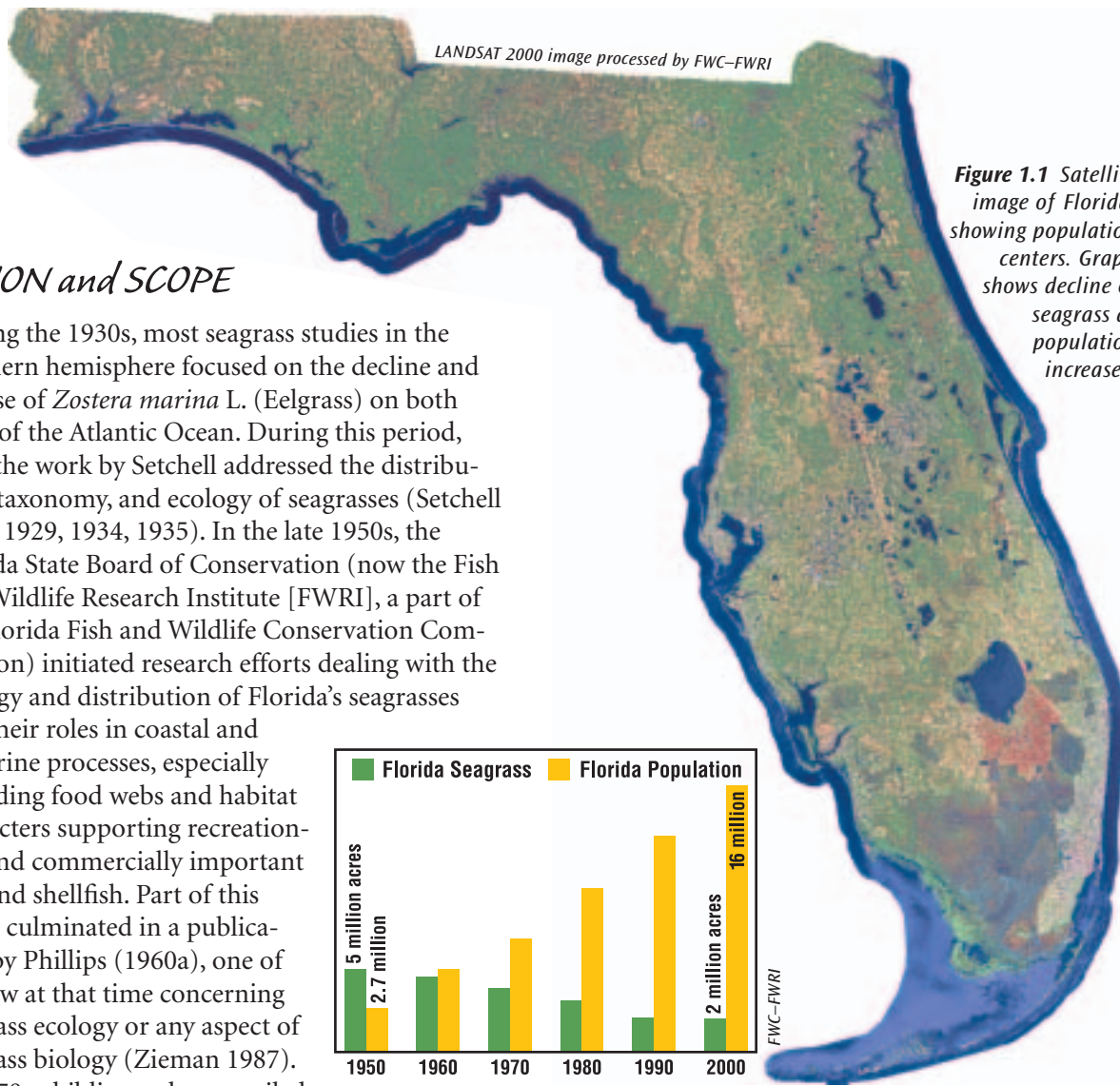*Ron Phillips photo*

Figure 1.1 Satellite image of Florida, showing population centers. Graph shows decline of seagrass as population increases.

VISION and SCOPE

During the 1930s, most seagrass studies in the northern hemisphere focused on the decline and demise of *Zostera marina* L. (Eelgrass) on both sides of the Atlantic Ocean. During this period, only the work by Setchell addressed the distribution, taxonomy, and ecology of seagrasses (Setchell 1920, 1929, 1934, 1935). In the late 1950s, the Florida State Board of Conservation (now the Fish and Wildlife Research Institute [FWRI], a part of the Florida Fish and Wildlife Conservation Commission) initiated research efforts dealing with the ecology and distribution of Florida's seagrasses and their roles in coastal and estuarine processes, especially regarding food webs and habitat characters supporting recreationally and commercially important fish and shellfish. Part of this effort culminated in a publication by Phillips (1960a), one of the few at that time concerning seagrass ecology or any aspect of seagrass biology (Zieman 1987). In 1978, a bibliography compiled by the Seagrass Ecosystem Study listed over 1,400 titles worldwide (Bridges *et al.* 1978), and by 1982, a community profile of south Florida seagrasses contained over 550 references (Zieman 1982).

In a summary of seagrass studies published over a period of 25 years, Zieman (1987) found that initially nearly all seagrass literature was descriptive and qualitative. By 1970, most published works were quantitative, and development of conceptual models had begun. By 1980, increasingly robust models of the mechanisms by which seagrass systems develop and maintain their productivity were being proposed and used as guides for developing proposed research (*e.g.,* McMillan 1978, 1980).

By 1982, scientists, resource managers, and agency personnel monitoring and managing bays and estuaries on the Atlantic and Gulf of Mexico coastlines of Florida, such as for the Indian River Lagoon, Charlotte Harbor, Sarasota Bay, Tampa Bay, and Pensacola Bay, noted dramatic seagrass losses. Starting around 1950, those areas experi-

encing large population increases also experienced seagrass losses, probably as a result of increasing development pressure (Figure 1.1). To address seagrass losses in the State of Florida, management programs were initiated between 1985 and 1995 to conserve and restore seagrass communities. The State's Surface Water Improvement and Management (SWIM) programs, within the Water Management Districts, address seagrass conservation issues statewide. Federally sponsored National Estuary Programs (NEPs) were designated for four specific estuaries: Tampa Bay National Estuary Program (TBNEP, now TBEP), Sarasota Bay National Estuary Program (SBNEP), Charlotte Harbor National Estuary Program (CHNEP), and Indian River Lagoon Program (IRLP). Since that time, considerable research, particularly regarding the light requirements of different seagrass species, has been conducted. This work was stimulated by the development of goals and targets established by the SWIM Districts and NEPs with respect to reducing eutrophication and nutrient loadings in

Figure 1.2 *Demarcated watersheds of Florida's Gulf coast.*

the major bays and estuaries. In several of these estuaries, the large seagrass losses observed in the early 1980s have halted, and moderate gains in seagrass extents have been occurring since about 1988 in some areas.

Although many recent studies concerning seagrass ecology and biology along Florida's Gulf coast have been and are being conducted, a synthesis of this information has not been compiled since the 1989 publication of "Ecology of the Seagrass Meadows of the West Coast of Florida: A Community Profile" by Zieman and Zieman. Several resource-management and science programs have identified the need for an updated synthesis of seagrass information:

↪ The FWC Fish and Wildlife Research Institute has developed a framework for a statewide Seagrass Conservation Plan (Morrison *et al.* 2003a).

↪ In August 2000, over 70 seagrass scientists and managers attended a Seagrass Management Symposium convened by the Tampa Bay Estuary Program (Greening 2002a). Workshop participants identified, as a first and critical step in seagrass management, the need for a compilation of scientific information on Florida's seagrasses published since the review by Zieman and Zieman (1989).

↪ The US Geological Survey's (USGS) Coastal and Marine Geology Program initiated a "Gulf of Mexico Estuaries Assessment" in 2001, using Tampa Bay as the subject of a pilot study. An initial element of the study is to develop a "synthesis report" and web-based information bank that would link directly to the USGS National Estuaries Assessment.

↪ The Gulf of Mexico Program (GMP) made a commitment that "By 2004, the GMP will com-

plete development of an updated gulf-wide characterization of the status and trends of seagrasses and coastal wetlands" (Gulf of Mexico Program 2003).

Knowledge of seagrass ecology and distribution within Florida has progressed substantially in the last 20 years. The objective of this publication is to summarize available data and information about seagrass research performed along the Gulf coast of Florida since 1985. Literature and studies published prior to 1985 are summarized in Zieman and Zieman (1989), which is available from the FWC Fish and Wildlife Research Institute Web site (www.floridamarine.org). The geographical scope of this document extends from Florida Bay and the Florida Keys at the southern extreme northward and westward through the Florida Panhandle to the Alabama border (Figure 1.2). Although the distance is only about 700 km (435 miles) from Florida Bay to Apalachicola Bay (extending over 6.5° of latitude), the aquatic climate changes dramatically. In Florida Bay, conditions are tropical, whereas in the Panhandle region, conditions are temperate and delimit the northern distribution in the Gulf for several Florida seagrass species, including *Thalassia testudinum* (Turtlegrass; Figure 1.3) and *Syringodium filiforme* (Manateegrass; Figure 1.4).

Figure 1.3 Thalassia testudinum *(Turtlegrass)*

Figure 1.4 Syringodium filiforme *(Manateegrass)*

Figure 1.5 A mixture of patchy and continuous seagrasses along a mangrove shoreline in Tampa Bay, Florida.

DEFINITION of SEAGRASS HABITAT

Simply put, habitat is where an organism resides. Nevertheless, habitat is not only where organisms live but also includes how they live there. Seagrass habitat is an ecological function provided by seagrasses. It is the location where certain organisms can thrive (survive, grow, and reproduce).

Seagrass habitat is defined in this document as a physical space containing seagrasses in sufficient quantity and pattern to produce the appropriate structural and physiological characteristics to support organisms typical of seagrass communities. These characteristics include food webs based on organic-matter production, nutrient cycling, detritus production, shelter, and sediment formation.

Continuous-coverage beds as well as patchy beds of seagrasses provide critical and valued habitat functions. Fonseca *et al.* (1998) found that scattered or patchy *Z. marina* beds covered many thousands of acres of estuarine seafloor in North Carolina, had shoot densities and primary production equivalent to those of continuous-coverage beds, had significantly greater below-ground biomass than did continuous-coverage beds, and often supported densities of economically valuable animal species, *e.g.,* pink shrimp, similar to those of continuous-coverage seagrass beds. They concluded that seagrass habitat must be recognized as indicating not only continuous-coverage seagrass beds, but also chronically patchy areas, therein considering the unvegetated spaces between vegetation as seagrass habitat as well (Figure 1.5).

Thus, the value of seagrass habitat should not be judged on the basis of seagrass densities or patterns, but upon the provided functions. In this document, any reference to areas covered by seagrass means seagrass habitat, as long as valued functions are present and measurable. One should consider that patchy seagrass beds perhaps represent areas in the process of recovering from past disturbances, or they may be areas held in a patchy pattern because of the characteristics of the present physical environment. In any event, patchy seagrasses support valued animals and plants and display typical seagrass functions.

ECOLOGICAL and ECONOMIC IMPORTANCE of SEAGRASS COMMUNITIES

Seagrasses are a vital component of Florida's coastal ecology and economy. They provide nutrition and shelter to animals that are important to marine fisheries, provide critical habitat for many other animals (*e.g.,* wading birds, manatees, and sea turtles), and improve water quality (Thayer *et al.* 1997,1999; Livingston 1990; Kenworthy *et al.* 1988b; McMichael and Peters 1989; Stedman and Hanson 1997; Valentine *et al.* 1997). For example, Heck *et al.* (2003) found a strong link between seagrass abundance and those of juvenile finfish and shellfish that was related to habitat structure.

In systems where seagrasses occur, nearly all of the commercially and recreationally valuable estuarine and marine animals depend on seagrass beds as refuge or habitat for parts or all of their life cycles (Kikuchi and Peres 1977; Thayer *et al.* 1978, 1984; Kikuchi 1980; Ogden 1980; Thayer and

Ustach 1981; Phillips 1984). As reported by Wingrove (1999) in the Florida Keys, hundreds of fish species, including many of commercial value, rely on seagrass habitats during some parts of their life cycles. Seagrasses help support a thriving, multimillion-dollar recreational fishery including, as an example, the shallow-water seagrass flats fishery seeking bonefish and tarpon. In addition, over 30 species of tropical invertebrates that depend on seagrasses are collected in the Florida Keys annually for the marine aquarium industry.

Short *et al.* (2000) list ecological services provided by seagrasses (modified here):

- Primary production (food for animals and support for fisheries and wildlife)
- Canopy structure (habitat, refuge, nursery, settlement and support of fisheries)
- Epibenthic and benthic production (support of food webs and fishery support)
- Nutrient and contaminant filtration (improved water quality, support of adjacent habitats, support of fisheries)
- Sediment filtration and trapping (improved water quality, countered sea-level rise, support of adjacent habitats)
- Epiphytic substratum (support of secondary production, production of carbonate sediment, support of fisheries)
- Oxygen production (improved water quality, support of adjacent habitats, support of fisheries)
- Organic-matter production and export (support of estuarine and offshore food webs, support of adjacent habitats, support of fisheries)
- Nutrient regeneration and recycling (support of primary production, support of adjacent habitats, support of fisheries)
- Organic-matter accumulation (support of food webs, countered sea-level rise, support of fisheries)
- Dampening of waves and currents (prevention of erosion/resuspension, support of adjacent habitats, increased sedimentation)
- Seed production/vegetative expansion (self-maintenance of habitat, support of wildlife)
- Self-sustaining ecosystem (recreation, education, landscape-level biodiversity)

Costanza *et al.* (1997) and Costanza (1999) stated that, for the entire biosphere, the economic value of all ecosystem services for 16 biomes is in the range of 16 to 54 trillion US $ y^{-1}, with an average of 33 trillion US $ y^{-1}. They considered this to be a minimum estimate. The value of coastal environments, including estuaries, coastal wetlands (mangroves and salt marshes), seagrass beds and algae, coral reefs, and continental shelves, is of a disproportionately high value. These communities cover only 6.4% of the world's surface, but they are responsible for 43% of the estimated value of the world's ecological services.

In Florida, seagrass beds are directly responsible for bringing in millions of dollars annually from out-of-state and resident recreational boaters and fishermen and commercial fishermen (Bell 1993; Milon and Thunberg 1993; Virnstein and Morris 1996; Virnstein 1999; Wingrove 1999; Thomas and Stratis 2001). Seagrass beds on the Gulf coast of Florida are important not only for the ecological services they provide, but for the economic health of the state and region.

DOCUMENT CONTENT

The focus of this review is the biology and ecology of seagrasses and of seagrass communities on Florida's Gulf coast.

Chapter 2 considers distribution of the Florida Gulf coast seagrasses and reports the trends in areal extents of seagrass beds, as recorded by monitoring efforts of various local and regional programs. Chapter 3 synthesizes new information regarding autecology and presents what is known regarding genetic analyses of Florida seagrasses. These genetic techniques were not applied to seagrasses prior to the 1990s. Chapter 4 addresses the ecological roles of seagrass communities, of their macroalgal components (epiphytic and drift), and of adjacent coastal communities (mangroves and salt marshes). Chapter 5 focuses on the natural and anthropogenic effects on Florida seagrasses. The Appendix presents keys to the Florida seagrass species and presents brief taxonomic descriptions for the families, genera, and species (includes figures).

A companion document entitled "The Florida Seagrass Manager's Toolkit" (Morrison *et al.* 2003b) addresses seagrass management in Florida and is available at www.floridamarine.org.

DISTRIBUTION, STATUS, and TRENDS

⤳ Florida's Gulf coast can be divided into four regions—South Florida, Gulf Peninsula, Big Bend, and Panhandle—for the purpose of assessing near-shore seagrass community status and trends.

⤳ Aerial photography taken during the 1990s revealed that the South Florida region contained the majority (65%) of the Gulf coast's seagrass coverage, followed by the Big Bend (28%), Gulf Peninsula (5%), and Panhandle (2%) regions.

⤳ The most abundant seagrass species on the Florida Gulf coast are *Thalassia testudinum, Syringodium filiforme,* and *Halodule wrightii,* each of which principally has a tropical to subtropical distribution. Two other species (*Halophila engelmannii* and *H. decipiens*) also occur in the area, in near-shore meadows dominated by *T. testudinum* and *S. filiforme* and in deeper waters where the latter two species are absent.

⤳ A substantial decline in seagrass coverage has occurred in the South Florida region over the past 15 years, following a dramatic "die-off" that began in Florida Bay during 1987.

⤳ In the Gulf Peninsula region between *ca*. 1959 and 1982, mapping efforts in Tampa Bay, Sarasota Bay and Greater Charlotte Harbor revealed reductions in seagrass coverage. However, difficulty in obtaining accurate coverage estimates from the 1950s-era maps has complicated attempts to quantify these declines, particularly in the Greater Charlotte Harbor area.

⤳ Increasing coverage trends have occurred in Tampa Bay and Sarasota Bay since 1982 in response to improved management of nitrogen loadings and increasing water clarity. Increased rainfall, stormwater runoff, and nutrient loadings associated with the 1997–1998 *El Niño* event interrupted the trends in seagrass coverage gains, but they appear to have resumed in recent years.

⤳ Several other areas within the Gulf Peninsula region—including Charlotte Harbor Proper and Lemon Bay—have been mapped approximately biennially since 1988. No significant seagrass coverage trends have been reported from these recent mapping efforts.

⤳ The Big Bend region is a unique "zero-energy" coastline and contains Florida's second-largest near-shore seagrass bed. The region has received relatively little research and management attention. The only long-term seagrass coverage changes reported have been localized losses attributed to the effects of an industrial facility that discharges to the Fenholloway River and Apalachee Bay.

⤳ In portions of the Panhandle region, which is also poorly studied, seagrass coverage may be increasing in some low-salinity areas and declining in some areas of higher salinity.

⤳ In addition to these near-shore seagrass resources, recent work on the West Florida Shelf indicates the presence of extensive, seasonal, deep-water *Halophila* beds, which may exceed four hundred thousand hectares (one million acres).

Shoalgrass, *Halodule wrightii*
Ron Phillips photo

DISTRIBUTION

Seagrasses are a relatively small group of flowering plants that have adapted to survive and reproduce in the marine environment. They are present in all coastal states of the U.S., with the exception of Georgia and South Carolina, where a combination of freshwater inflows, high turbidity, and large tidal amplitude restricts their occurrence (Thayer *et al.* 1997).

The most abundant taxa in Florida's near-shore waters are *T. testudinum, S. filiforme,* and *H. wrightii,* each of which principally has a tropical to subtropical distribution (Zieman and Zieman 1989). *Thalassia testudinum* (Turtlegrass) is the largest of these species, with long strap-shaped leaves and robust rhizomes (see Appendix for taxonomic keys, descriptions, and illustrations). Extensive seagrass beds are usually dominated by this species, either alone or in combination with other species, such as *Syringodium filiforme. Syringodium filiforme* (Manateegrass) can be distinguished by its cylindrical (terete) leaves that, because they are brittle and buoyant, are frequently broken off from the parent plant and dispersed widely by winds and currents. *Halodule wrightii* (Shoalgrass) has flat, narrow leaves and a shallow root system. It is thought to be an early successional species in the development of seagrass beds in the Gulf of Mexico and Caribbean Sea.

Three other species, *Halophila engelmannii* (Stargrass), *H. decipiens* (Paddlegrass), and *H. johnsonii* (Johnson's Seagrass), are also found in Florida's coastal waters. In the Big Bend region, *H. engelmannii* and *H. decipiens* are scattered throughout beds dominated by *T. testudinum* and *S. filiforme* but also occur in deeper water where these latter two species are absent (Iverson and Bittaker 1986). *Halophila decipiens* has been found in the Big Bend and Tampa Bay regions and at depths to 90 m near the Dry Tortugas (Zieman 1982), and it forms single-species stands in depths of 20 m or more, beyond the deep edge of the extensive *T. testudinum/S. filiforme* beds (Zieman and Zieman 1989, Dawes and Lawrence 1990). *Halophila johnsonii* is a relatively newly described species and is morphologically similar to *H. decipiens* (Eiseman and McMillan 1980). *Halophila johnsonii* is now listed as a threatened species by the National Marine Fisheries Service (NMFS; 2002) and is

apparently an endemic whose range is restricted to the lagoon systems of Florida's southeastern (Atlantic) coast. It has not been documented to occur on the Gulf coast (NMFS 2002), and recent evidence suggests it is genetically indistinguishable from *H. ovalis,* a species of the Indo-Pacific region (Waycott *et al.* 2002).

A seventh species, *Ruppia maritima* (Widgeongrass), is a euryhaline plant that is often encountered in the waters of Florida's Gulf coast, particularly in estuaries such as Homosassa Bay (Koch and Dawes 1991a, b) and Tampa Bay (Lazar and Dawes 1991). This species can form dense beds, as found in upper Tampa Bay (Lazar and Dawes 1991). In recognition of its broad salinity tolerance, some authors have suggested that *R. maritima* may be thought of as a freshwater species that is also capable of living in saline environments, rather than a seagrass in the strictest sense (*e.g.,* Zieman 1982, Kuo and den Hartog 2001).

In addition to seagrasses, drift and attached seaweeds also make up an important component of the total submerged aquatic vegetation (SAV) in many areas of Florida (Dawes *et al.* 1987, Dawes 1986). In the Big Bend region, for example, benthic green algae in the order Caulerpales— including *Halimeda incrassata,* seven species of *Caulerpa,* and two species each of *Udotea, Penicillus,* and *Codium*—are important associates in the region's seagrass beds, with standing crops exceeding those of seagrasses in some areas (Mattson 2000).

Depth-related zonation patterns of Gulf-coast seagrass beds (Figure 2.1) have been described by Lewis *et al.* (1985a), Iverson and Bittaker (1986), Zieman and Zieman (1989), and Mattson (2000). As a general rule, *H. wrightii* and *R. maritima* tend to be more abundant in shallow inshore areas because they tolerate frequent tidal exposure and low salinities. *Thalassia testudinum* and *S. filiforme*
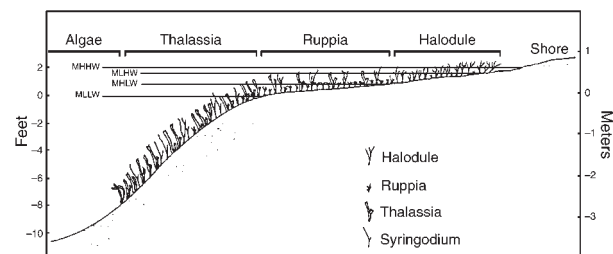

Fig 2.1 *An example of an inshore-offshore seagrass zonation profile on Florida's Gulf coast (from McNulty* et al. *1972).*
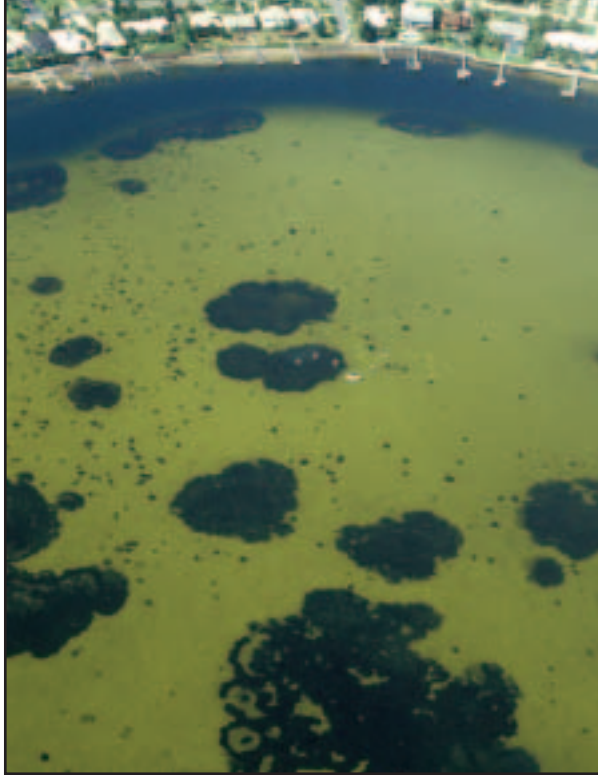
Fig 2.2 *Dense seagrass beds begin as patches that coalesce into a larger, more genetically diverse meadow.*

reach their highest abundance and biomass in slightly deeper areas, often forming dense single- or mixed-species stands (Figure 2.2). In some areas, *H. wrightii* exhibits a second abundance peak along the deep-water edge of *T. testudinum/S. filiforme* meadows (Iverson and Bittaker 1986, Zieman and Zieman 1989). *Halophila* spp. form sparse beds in deeper waters outside these meadows (Zieman and Zieman 1989, Fonseca *et al.* 2001). In the Big Bend region and Tampa Bay, *H. engelmannii* also occurs in low-salinity areas (<5 ppt) within 1–2 km of river mouths, where an ability to tolerate low light levels in waters of relatively high color may be an important factor explaining its persistence (Dawes 1967, Zimmerman and Livingston 1976, Mattson 2000).

When considering the distribution of seagrasses on Florida's Gulf coast, dividing the area into four regions is helpful. Regions defined by Sargent *et al.* (1995) are summarized in Table 2.1 and Figure 2.3:

↘ South Florida (Florida Keys and Florida Bay to Estero Bay)
↘ Gulf Peninsula (Estero Bay to Anclote Key)
↘ Big Bend (Anclote Key to Ochlockonee Point)
↘ Panhandle (Ochlockonee Point to the Florida-Alabama border)

The spatial distribution and areal extent of seagrasses vary substantially between these regions (Zieman 1982, Iverson and Bittaker 1986, Sargent

et al. 1995). Recent status and trends in seagrass coverage at this geographic scale are summarized in the following section.

REGIONAL STATUS and TRENDS

Sargent *et al.* (1995) estimated that, on a statewide basis, Florida's near-shore coastal waters support approximately 1.1 million ha (2.7 million acres) of seagrass. This statewide estimate includes 0.8 million ha (1.9 million acres) of dense and relatively easily mapped seagrasses in state waters where visibility allowed interpretation of bottom communities (within 14.4 km [9 miles] of shore along the Gulf coast). It also includes, in portions of the South Florida region, an estimated 0.3 million ha (0.8 million acres) of sparse and incompletely mapped seagrass beds that are interspersed with hard-bottom communities and are thus difficult to map accurately. This estimate does not include the sparse beds that occur in deeper waters on portions of the West Florida Shelf (Sargent *et al.* 1995).

Along the state's Gulf coast, the coverage of the sparse deep-water beds of the West Florida Shelf and the small, patchy mixed-species beds that occur intermixed with hard bottom outside the main seagrass beds in Florida Bay remain the largest question marks in the effort to develop accurate estimates of overall seagrass coverage. For example, recent assessments indicate that the total area of deep-water beds in the Gulf-coast region may be on the order of 0.4 million ha (1 million acres), which would place them, on a worldwide basis, among the most extensive seagrass habitats currently known (Fonseca *et al.* 2001).

During the 1990s, aerial photographs were used to produce digitized maps of seagrass coverage for

Table 2.1 Extent of seagrass coverage and aerial photography dates in four regions of Florida's Gulf coast (Madley *et al.* 2003).

Region	Seagrass (hectares)	Seagrass (acres)
Panhandle (1992)	17,474	43,178
Big Bend (1992)	247,598	611,815
Gulf Peninsula (1999)	43,323	107,051
South Florida (1992, 1995)	574,875	1,420,517
Gulf coast total	883,270	2,182,561
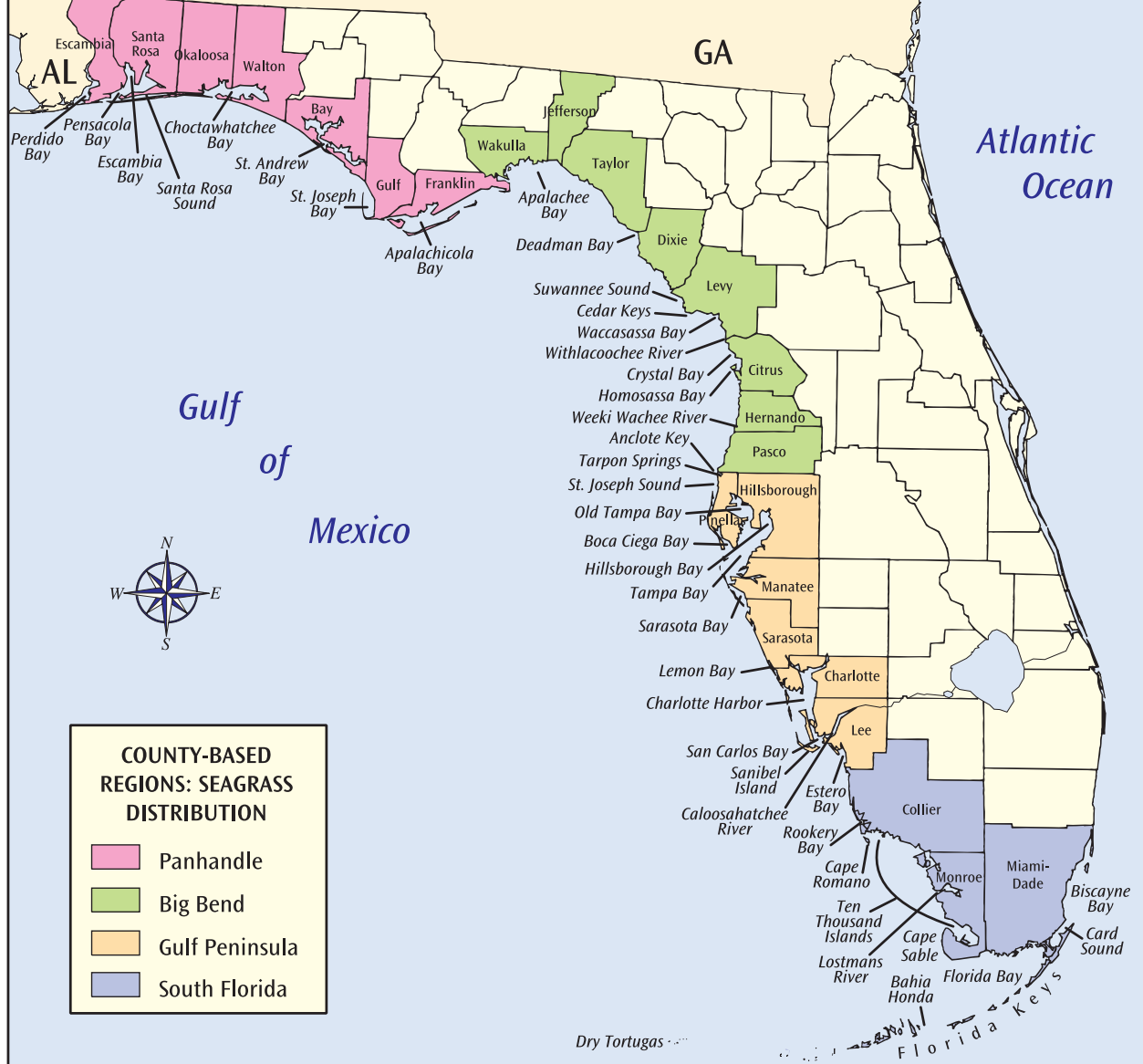
Fig 2.3 *County-based regions used to describe seagrass distributions along the Gulf coast of Florida (after Sargent* et al. *1995) and containing locations referred to in the text.*

each of the regions shown in Figure 2.3. The dates of these mapping efforts and their results are summarized in Table 2.1. The South Florida region contained the majority (65%) of the Gulf coast's seagrass coverage, followed by the Big Bend (28%), Gulf Peninsula (5%), and Panhandle (2%) regions.

SOUTH FLORIDA

The South Florida region (Figure 2.3) includes the coastal waters of Collier, Monroe, and Miami-Dade counties (Table 2.1). The portion that lies immediately south of Cape Romano includes the Ten Thousand Islands, an area that is dominated by mangrove islands and tidal channels but that also contains patches of seagrasses and some large seagrass beds (*e.g.,* as reported from the Lostmans River area by Dawes *et al.* 1995). The Florida Bay

portion, which lies south of Cape Sable and west of the Florida Keys, is a carbonate-sediment-based system that supports extensive seagrass beds.

Based on monitoring data collected annually from 1974 through 1980, Iverson and Bittaker (1986) noted that, in addition to their greater extent, the 0.5 million-ha (1.4 million-acre) Florida Bay seagrass meadows also had about two to four times the short-shoot densities of *T. testudinum* and *S. filiforme* as occurred in the 0.3 million ha (741,000 acre) Big Bend meadows. They hypothesized that the density differences observed in the two areas may be a consequence of greater seasonal variations in solar radiation and water temperature in the Big Bend, which is at the northern limits of tropical American seagrasses (Iverson and Bittaker 1986).

Seagrass coverage and condition in the South
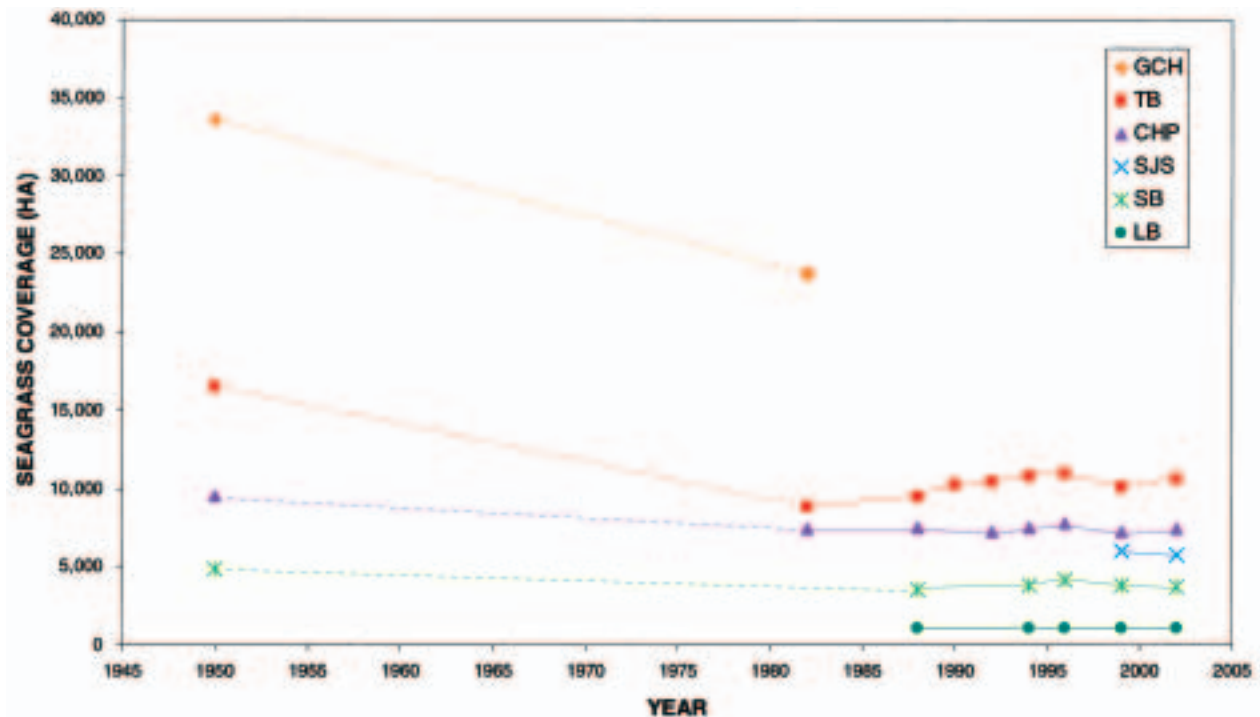
Figure 2.4 *Time series of mapped seagrass coverage within major coastal water bodies of the Gulf Peninsula region (GCH = Greater Charlotte Harbor; TB = Tampa Bay; CHP = Charlotte Harbor Proper; SJS = St. Joseph Sound; SB = Sarasota Bay; LB = Lemon Bay) from* ca. *1950 through 2002. The 1950 values were developed using mapping methods that differ from those currently in use and should be viewed as approximations. (Data sources: FWRI, SWFWMD)*

Florida region have changed since the 1974–1980 period documented by Iverson and Bittaker (1986). A dramatic decline in coverage began in western Florida Bay during the summer of 1987 (Hall *et al.* 1999). Seagrasses in the bay were apparently subjected to decreased light availability resulting from resuspended sediments and widespread, persistent microalgal and cyanobacterial blooms. Bay-wide surveys in 1984 and 1994 indicated that the biomass of *T. testudinum, S. filiforme,* and *H. wrightii* declined by 28%, 88%, and 92%, respectively, during that 10-year period. The spatial patterns of seagrass losses suggested that chronic light reductions, which affected all species, and "die-off" (rapid, unexplained plant mortality), which also affected *T. testudinum,* most likely caused the overall decline. Although the loss rate has slowed considerably in recent years, die-off and regression of seagrasses are still occurring in parts of the bay (see also Chapter 5).

GULF PENINSULA

The Gulf Peninsula region lies between Estero Bay

and Anclote Key (Figure 2.3) and includes the coastal waters of Lee, Charlotte, Sarasota, Manatee, Hillsborough and Pinellas counties. This region is a moderate-energy coastline, with extensive sand beaches and barrier islands that enclose two large estuarine embayments (Tampa Bay and Charlotte Harbor) and many smaller lagoons (*e.g.,* Estero Bay, San Carlos Bay, Matlacha Pass, Pine Island Sound, Lemon Bay, Sarasota Bay, and St. Joseph Sound) containing the majority of the region's seagrass beds. Recent seagrass-coverage trends in this region appear somewhat irregular, apparently responding to site-specific situations within the different estuary and lagoon systems.

For Tampa Bay, Sarasota Bay, and the Greater Charlotte Harbor system, the earliest photography-based seagrass coverage maps for the region were developed by the FWRI, using aerial photographs taken in the late 1940s and early 1950s and again in 1982 (Harris *et al.* 1983, Tampa Bay Regional Planning Council [TBRPC] 1984, Janicki *et al.* 1994). Maps were subsequently prepared by the Southwest Florida Water Management District (SWFWMD) for Tampa Bay (for the years 1988,

1990, 1992, 1994, 1996, 1999, and 2002), Charlotte Harbor (1988, 1992, 1994, 1996, 1999, and 2002), Sarasota Bay (1988, 1994, 1996, 1999, and 2002), Lemon Bay (1988, 1994, 1996, 1999, and 2002), and St. Joseph Sound (1999 and 2002) (TBNEP 1996, Kurz *et al.* 2000, D. Tomasko *pers. comm.*). Time series of seagrass coverages based on these maps are shown in Figure 2.4.

In Tampa Bay, approximately 46% (7,452 ha or 18,400 acres) of the existing seagrass coverage was lost between *ca.* 1950 and 1982 (Figure 2.4) from the combined effects of dredging and reductions in water clarity (Haddad 1989). Coverage losses in Tampa Bay over longer time periods are difficult to estimate with any accuracy, because of the sparseness of data and absence of aerial photography prior to *ca.* 1950. Indirect methods suggest, however, that as much as 81% of predevelopment coverage may have been lost during the years 1879 through 1982 (Lewis *et al.* 1991).

Between 1982 and 1996 Tampa Bay regained approximately 2,090 ha (5,160 acres) of seagrass, apparently in response to management efforts that led to reduced nutrient loadings and increased water clarity. Reduced nutrient loadings and increased seagrass coverage were also observed in Sarasota Bay during the same period (Tomasko *et al.* 1996). Seagrass coverage then declined in both estuaries, apparently in response to the heavy rainfall and increased stormwater runoff that occurred during the 1997–1998 *El Niño* event (Johansson 2002a).

Seagrass coverage increased once again in Tampa Bay during the 1999–2002 mapping period, as water clarity improved during the relatively dry years that occurred following the cessation of the 1997–1998 *El Niño* event. During this period the total mapped coverage in the bay increased by 501 ha (1,237 acres), to 10,561 ha (26,078 acres). In Sarasota Bay, on the other hand, the total mapped coverage declined slightly between 1999 and 2002, from 4,799 ha (11,850 acres) to 4,740 ha (11,703 acres). Seagrass coalescence occurred in both estuaries during the 1999–2002 mapping period, through a net increase in the coverage of continuous (as opposed to patchy) seagrass beds (D. Tomasko *pers. comm.*).

The documented increases in seagrass coverage in Tampa Bay and the slight increase in Sarasota Bay between 1982 and 2002 apparently occurred in response to improved management of anthropogenic nitrogen loads to both estuaries (Tomasko *et al.* 1996). Through the Grizzle-Figg Act (403.086 Florida Statutes), the Florida Legislature required that all sewage treatment plants discharging to the two estuaries and their tributaries must provide advanced wastewater treatment (AWT) prior to discharge. The City of Tampa upgraded its sewage treatment plant to AWT in 1979, greatly reducing the amount of nitrogen entering Tampa Bay from that source. The City of St. Petersburg implemented a wastewater reuse program which almost eliminated its direct wastewater discharges to Tampa Bay. Similar improvements to sewage treatment plants in Pinellas, Hillsborough, Manatee, and Sarasota counties also helped improve water quality in the receiving estuaries. By the early 1990s, water clarity in some of the most degraded portions of Tampa Bay had already begun to improve (Johansson 1991, TBNEP 1996).

Improved management of seagrass communities has been identified as a priority issue in Tampa Bay and Sarasota Bay and is being addressed through broad-based stakeholder groups. Both systems are part of the U.S. EPA's National Estuary Program, which helps to coordinate the management activities of local, state, and federal agencies and the private sector. The Tampa Bay Estuary Program is pursuing a resource-based management strategy that seeks to limit anthropogenic nitrogen loadings at levels needed to achieve its seagrass-coverage goal of 15,400 ha (38,000 acre), representing 95% of the seagrass coverage that was mapped in the Bay in 1950 (TBNEP 1996, Johansson and Greening 2000). The Sarasota Bay National Estuary Program has adopted a technology-based strategy that seeks to control nitrogen loadings through the adoption of "best available technology" for anthropogenic nitrogen sources in the contributing watershed (SBNEP 1995).

Nitrogen-management strategies are effective seagrass restoration tools in Tampa Bay and Sarasota Bay. Because phytoplankton are important sources of light attenuation in both estuaries, by controlling nitrogen inputs, managers can reduce phytoplankton biomass, increase water clarity, and increase the bay-bottom area that receives sufficient sunlight to support seagrasses (*e.g.,* Johansson and Greening 2000). A similar situation appears to exist in Lemon Bay, where phytoplank-

ton are also a major source of light attenuation (Tomasko *et al.* 2001). In Charlotte Harbor, however, light attenuation is affected more by water "color"—naturally elevated levels of dissolved organic matter discharged from extensive wetlands in the Peace and Myakka river systems—than by phytoplankton abundance (McPherson and Miller 1994). Because of its large watershed, Charlotte Harbor also experiences large seasonal and annual variations in fresh-water inflow, producing large fluctuations in salinity that can be stressful to seagrasses (Tomasko and Hall 1999). The nitrogen-based management strategies developed for Tampa Bay and Sarasota Bay may thus have limited applicability for Charlotte Harbor (D. Tomasko *pers. comm.*).

The time series of mapped seagrass coverage in portions of the Charlotte Harbor system is shown in Figure 2.4. Much of the reduction in coverage in Greater Charlotte Harbor (which includes San Carlos Bay, Matlacha Pass, and Pine Island Sound, in addition to Charlotte Harbor Proper) between *ca.* 1950 and 1982 occurred in the southern portion of the system, particularly in Pine Island Sound and San Carlos Bay. This reduction has been linked, circumstantially, to a series of large-scale anthropogenic activities that occurred in the area during the 1960s, including dredging of the Intracoastal Waterway, construction of the Sanibel causeway, and installation of dam and lock structures in the lower Caloosahatchee River (Harris *et al.* 1983). In addition to direct destruction of seagrass habitats, these projects have been postulated to have indirectly altered the water clarity, salinity, hydrodynamics and flushing characteristics of the area in ways that made it less conducive to seagrass growth and survival (Harris *et al.* 1983). Due to difficulties encountered in interpreting and digitizing the aerial photographs that were taken in the area during the *ca.* 1950 period, however, the coverage values shown for the Greater Charlotte Harbor system in that period in Figure 2.4 should be viewed as rough approximations (Harris *et al.* 1983).

No geographically and technically consistent mapping of seagrass coverage throughout the Greater Charlotte Harbor system has been conducted since 1982. The northern portion of the system—which falls largely within the SWFWMD and is referred to locally as Charlotte Harbor Proper—has been mapped approximately biennially since 1988 by the SWFWMD (Kurz *et al.* 2000). From 1988 through 2002, seagrass coverage in this area fluctuated between 7,200 ha (17,800 acres) and 7,800 ha (19,300 acres), with no apparent upward or downward trends (Figure 2.4). Lemon Bay has been mapped over the same time period and has shown relatively small fluctuations around an average value of 1,058 ha (2,600 acres), with no apparent trends (Figure 2.4).

Mapping data from St. Joseph Sound near Clearwater are available only for the years 1999 and 2002, when an average of 5,840 ha (14,400 acres) were recorded (Figure 2.4).

BIG BEND

The Big Bend region extends from Anclote Key northwestward to Ochlockonee Point in the Panhandle region (Figure 2.3) and includes the coastal waters of Pasco, Hernando, Citrus, Levy, Dixie, Taylor, Jefferson, and Wakulla counties. Zieman and Zieman (1989) note that this portion of the coast is unique in that it is an extensive area, with no offshore barrier islands, where a number of rivers, creeks, and marshes discharge directly into the Gulf of Mexico. It is also one of the few examples of a "zero-energy" coastline, with average breaker heights of 3–4 cm or less and little littoral transport of sand (Murali 1982). Factors contributing to the low-energy characteristics of the area include a wide and gently sloping shelf, divergence of approaching wave trains into a large coastal concavity, the location of the coast in a generally upwind direction, and the wave dampening effects of old submerged beaches and seagrass meadows (Murali 1982).

The region is an environmentally diverse area that can be divided into five subregions (Mattson 2000). The Springs Coast subregion, which extends from Anclote Key northward to the mouth of the Withlacoochee River, is dominated by flows from a series of short, spring-fed river systems: the Weeki Wachee, Chassahowitzka, Homosassa, and Crystal rivers. Concentrations of nitrate nitrogen have been increasing steadily in these rivers in recent decades, due to increasing anthropogenic nitrogen discharges in their highly karstic watersheds and spring recharge areas (Katz e*t al.* 1997). The limestone bedrock and sediments of this portion of the coast are rich in carbonates, however, and tend to

bind inorganic phosphorus from the water column. Because inorganic phosphorus is less available in the water column, primary production of near-shore aquatic ecosystems are tilted from N-limitation toward P-limitation (Hauxwell *et al.* 2001).

The four subregions north of the Springs Coast subregion are Waccasassa Bay, Suwannee Sound and adjacent coastal waters, Deadman Bay, and Apalachee Bay (Mattson 2000). Discharges from river systems in these subregions tend to be high in color during periods of high flow, a factor that apparently contributes to relatively low seagrass coverage in the vicinity of the river mouths (Mattson 2000).

Although the inshore and offshore seagrass beds of the Big Bend are among the largest in the eastern Gulf of Mexico (Iverson and Bittaker 1986), the region has received relatively little management attention (Mattson 2000). Several mapping surveys have been conducted, but most have covered only a limited portion of the region and have produced highly variable coverage estimates (Mattson 2000). The most extensive, region-wide mapping efforts have been carried out by Iverson and Bittaker (1986) and Sargent *et al.* (1995), producing coverage estimates of 300,000 ha (741,000 acres) and 334,842 ha (827,000 acres), respectively. Neither of these estimates includes the sparse, deep-water seagrass beds that are located offshore. For the entire West Florida Shelf, Fonseca *et al.* (2001) estimated the areal coverage of deep-water *H. decipiens* beds at 0.4 million ha (1 million acres), which would place them among the largest seagrass communities in the world.

In a general sense, the Big Bend area has been described as one of the least polluted coastal regions of the continental United States (Livingston 1990). However, the Fenholloway River—a tributary to Apalachee Bay—is an exception to this generalization, receiving discharges from an industrial facility that are high in color and contain elevated levels of sulfate, BOD, suspended solids and nutrients (Mattson 2000). These discharges have apparently caused localized reductions in water clarity and seagrass coverage in portions of Apalachee Bay (Livingston 1993, Livingston *et al.* 1998).

PANHANDLE

The Panhandle region extends from Ochlockonee Point westward to the Florida-Alabama border (Figure 2.3) and includes the coastal waters of Franklin, Gulf, Bay, Walton, Okaloosa, Santa Rosa, and Escambia counties. It resembles the Gulf Peninsula region in being a moderate-energy coastline with extensive sand beaches and barrier islands enclosing protected estuaries and lagoons (*e.g.,* Apalachicola Bay, St. Joseph Bay, St. Andrew Bay, Choctawhatchee Bay, Santa Rosa Sound, Escambia Bay, and Pensacola Bay) that contain the region's seagrass beds. Like the Big Bend region, it is the subject of limited recent research and management activity.

Based on aerial photography taken in 1992–1993, Sargent *et al.* (1995) estimated that 19,509 ha (48,170 acres) of seagrasses were present in the coastal waters of the Panhandle region. No region-wide coverage estimates have apparently been produced since that time. Lores *et al.* (2000) assessed recent coverage trends in seagrasses and other SAV in the Escambia-Pensacola Bay portion of the region, and provided the following summary:

⤵ SAV in the Escambia-Pensacola Bay System underwent a substantial decline in the late 1940s through the early 1970s;

⤵ Although scientific documentation of SAV distribution since that time is lacking, some observations suggest SAV growth in the oligohaline regions of estuaries in northwestern Florida has shown recent improvements (*e.g.,* in Mobile Bay [Alabama], Escambia Bay, and Perdido Bay);

⤵ Evidence suggests these same areas are also losing SAV in the euryhaline regions;

⤵ Improvements in water quality of the upper bay regions is thought to be leading to recovery of low-salinity seagrasses; and

⤵ Continuing increases in coastal development in the lower bay region, with resulting increased nutrient input and sediment loading/resuspension, may be having an adverse impact on the health and productivity of high-salinity seagrasses such as *T. testudinum.*

AUTECOLOGY and POPULATION GENETICS

- Flowering is known in all six species of seagrasses on the Gulf coast of Florida, but *Thalassia testudinum* produces fewer fruits at higher latitudes (north of Tampa Bay).

- Genetic information for Florida seagrasses exists only for *T. testudinum*, with lower genetic diversity observed in its northern populations. This may be a result of the lower level of seed production and, therefore, more dependence on vegetative expansion for reproduction.

- Genetic data are needed for more populations and for other seagrass species.

- The clonal nature of seagrasses allows transport of soluble carbohydrates, proteins, and nitrogen (as glutamine) to stressed short-shoot and long-shoot rhizome meristems.

- Depth distribution of *T. testudinum* is influenced by a variety of factors, including water transparency, epiphyte load of the leaf blades, and water movement.

- Salinity variations affect the local distributions of seagrasses. *T. testudinum* does not survive if held in culture for over 6 weeks in 6 ppt seawater. In the field, other factors will raise that threshold. More data are needed regarding osmoregulation in euryhaline species such as *Halodule wrightii*.

- Higher sulfide levels in the sediment are toxic to *T. testudinum*, occur in areas of eutrophication in a number of Gulf-coast estuaries, and may play a role in the patchy nature of seagrass communities.

- Moderate grazing by invertebrates (especially sea urchins), fish, sea turtles, and manatees may enhance seagrass-bed development and species diversity.

- Stable isotope ratios can be used to trace the flow of organic components in seagrass beds, although macroalgae may have similar isotopic signatures.

- Carbon fixation by most seagrasses occurs via the C_3 pathway. However, it is debatable whether a modified form of the C_4 pathway exists in some species.

- Entire-plant carbon budgets of *T. testudinum* and *H. wrightii* show that below-ground components account for over 50% of a plant's respiration.

Widgeongrass, *Ruppia maritima*
Ron Phillips photo

SEAGRASS MORPHOLOGY and ANATOMY

Detailed descriptions of seagrass morphology and anatomy can be found in den Hartog (1970), Ancibar (1979), Tomlinson (1980, 1982), and Kuo and McComb (1989). Also see the Appendix, Taxonomy of Florida Seagrasses, in this document. The basic construction of *most* seagrasses (Arber 1920) is an indeterminate horizontal stem (plagiotropic rhizome or long shoot) that periodically produces determinate erect stems (orthotropic rhizomes or short shoots) having leaves and flowers. Adventitious roots develop from both types of rhizome. Rhizomes are usually cylindrical and below the sediment surface in species with robust morphologies. In contrast, rhizomes of species with more delicate morphologies (*e.g., H. decipiens* and *H. johnsonii*) often occur above the sediment surface. Rhizome growth is either sympodial (*e.g., H. wrightii* and *R. maritima*) or monopodial (*e.g., T. testudinum* and *S. filiforme*). Leaves of the Gulf-coast Florida species differ greatly in morphology, being long, wide and thick in *T. testudinum;* long, narrow, and thin in *H. wrightii* and *R. maritima;* long, rigid, and cylindrical in *S. filiforme;* and short, thin, and membranaceous in species of *Halophila.*

The rhizomes of Florida seagrasses are herbaceous, with little fiber tissue. In seagrasses similar to *T. testudinum,* the vascular stele and fiber bundles in the cortexes of the blades, short shoots, and rhizomes are poorly lignified (Dawes 1986). Epidermal cells of seagrass blades lack stomata and associated guard cells, contain most of the blades' chloroplasts, and have a thick outer cell wall covered by a thin, porous cuticle. As determined by uptake studies (Larkum *et al.* 1989), the cuticle apparently does not prevent absorption (*e.g.,* of CO_2, cadmium, or manganese) by the blade. As with those of *T. testudinum,* the epidermal cells of *R. maritima* may be involved in osmoregulation. Epidermal cells of *R. maritima* blades that are grown in higher salinities (*e.g.,* 32 ppt) develop masses of gelatinous polysaccharides and form cell-wall ingrowths that may be involved in ion binding and exchange between the seawater and cytoplasm (Kruzcynski 1994).

SEXUAL REPRODUCTION

Although sexual reproduction is known in all the
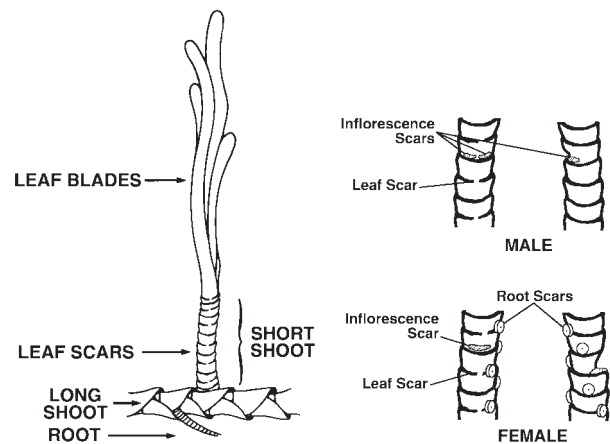
Figure 3.1 *Inflorescence, leaf, and root scars on short shoots of* Thalassia testudinum *(modified from Witz 1994).*

seagrass species of Florida, with the possible exception of *H. johnsonii* (see Appendix), data on flowering and seed production and survival are limited (Ferguson *et al.* 1993). Leaf and inflorescence scars (Figure 3.1) have been used to determine short-shoot age, sex, and frequency of flowering in *T. testudinum* (Cox and Tomlinson 1988; van Tussenbroek 1994; Witz and Dawes 1995), with short shoots that produce female flowers often having narrower leaves than short shoots that produce male flowers (Durako and Moffler 1985). Inflorescence scars on short shoots of *T. testudinum* (Fig 3.1) suggest that abundant flowering occurs in northern areas along Florida's Gulf coast (*e.g.,* St. Joseph Bay and Apalachee Bay) and throughout the Florida Keys (C. Dawes *pers. obs.*), yet flowering and seed production have not been documented for most *T. testudinum* beds along the northern Gulf coast. In contrast, in May or June of each year, thousands of *T. testudinum* seeds may occur in the beach wrack at Mathieson Hammock near Miami and in the wrack lines in the Florida Keys (C. Dawes *pers. obs.;* Lewis and Phillips 1980), and countless more are eaten by birds (Fishman and Orth 1996).

Seagrass flowering and fruiting occur annually between February and August along the Gulf coast of Florida (Phillips 1960c; Durako and Moffler 1987; Witz and Dawes 1995) and on the Caribbean coast of Mexico (van Tussenbroek 1994). Photoperiod does not appear to influence the onset of flowering in *T. testudinum* (Moffler and Durako 1987), *S. filiforme,* or *H. wrightii* (McMillan 1982), as these three species flowered under continuous light. Instead, water temperature influences flower development (Moffler and Durako 1987), and all species in Florida flower within a temperature range of 20°–26°C (McMillan 1982). Lower water temperatures (10° to 18°C) in the winter in the

Tampa Bay area may cause *T. testudinum* to flower later in the spring than it does in the Florida Keys, causing immature fruits to dehisce early in response to rapidly rising water temperatures in May and June (Witz and Dawes 1995).

Seed germination has not been studied in most Florida Gulf-coast seagrass species. *Ruppia maritima* seed germination is influenced by salinity and temperature but not by photoperiod. Seeds collected from the sediment at the mouth of the Weeki Wachee River germinated at all temperatures (17°, 23°, and 39°C) and in 0 and 15 ppt but not 30 ppt salinities. In contrast, seeds from North Carolina germinated in all temperature and salinity combinations (Koch and Dawes 1991a). Studies on fish predation of *R. maritima* seeds demonstrated that they can pass through the gut and thus be dispersed (Agami and Waisel 1988). The importance of seed reserves as an early source of carbohydrate energy for seedlings of *T. testudinum* was proposed by Durako and Sackett (1993). Seedlings had a lower carbon isotopic fractionation ($\delta^{13}C_{plant} - \delta^{13}C_{source} = 15.4$ ppt) than did one-year-old plants (21.0 ppt), possibly indicating a shift from using carbon reserves in the seed to taking up CO_2 from the water column. However, the one-year-old plants were cultured under artificial conditions and were preconditioned, which may have altered their fractionation level.

ASEXUAL REPRODUCTION and CLONAL BIOLOGY

Vegetative growth by the long-shoot rhizome is thought to be the principal means of expansion for Gulf-coast seagrasses, in light of the curtailment of sexual reproduction explained above. Seagrass short shoots can be regarded as ramets, and the clonal group of ramets connected by long-shoot rhizomes derived from a single propagule is considered to be the genet (see Harper 1990). Rhizome extension is the basis for vegetative expansion in all seagrasses (Tomlinson 1974; Dawes 1998a; Andorfer and Dawes 2002; Dawes and Andorfer 2002).

Two possible advantages in being clonal are the ability to carry out vegetative expansion or foraging (Cain 1994) and the ability to share resources between ramets of the same genet growing in areas of stress or low nutrients (Tomasko and Dawes 1989; Wijesinghe and Handel 1994; Andorfer

2000). Short shoots of *T. testudinum* near Mullet Key in Tampa Bay were isolated from others by severing the long-shoot rhizome on each side of the short-shoots that were then shaded. These short shoots had significantly lower blade growth than did shaded short shoots that were connected to other short shoots (Tomasko and Dawes 1989). Rhizomes adjacent to shaded short shoots were depleted of soluble carbohydrates and proteins, while the rhizome portion beyond the severed short shoots was not, suggesting that sugars and amino acids stored in the adjacent rhizomes could be mobilized.

Laboratory culture studies using the stable nitrogen isotope $^{15}NO_3$ demonstrated that nitrogen in the form of glutamine was translocated from the fourth-oldest ramet of *T. testudinum* to the growing long-shoot rhizome meristem (Andorfer 2000). Further, leaf regrowth, after the four youngest short shoots were clipped, was supported by carbon fixed in the fifth short shoot and transported to it via the rhizome. This high degree of short-shoot integration, over a distance of five ramets, demonstrates the importance of the physiological integration that allows *T. testudinum* to expand through regions of low light or nutrients and to tolerate periods of intense grazing (Andorfer 2000). These studies support earlier findings for *T. testudinum* subjected to weekly clipping of blades (Dawes and Lawrence 1979) and for *S. filiforme* in the Indian River Lagoon subjected to shading of connected and severed short shoots (Rey and Stephens 1996). In the latter study, soluble-carbohydrate levels declined from 26.5% to 18.4% and then stabilized in rhizomes connected to shaded short shoots; this suggests movement of soluble carbohydrate from adjacent non-shaded short shoots, thus showing physiological integration of the genet.

Production of new long-shoot rhizome branches by *T. testudinum* occurs principally at the long-shoot meristem and rarely occurs through branching of the older long-shoot rhizome. Dawes and Andorfer (2002) found that older short shoots were more likely to produce a new long-shoot rhizome than were younger ones and that initiation of rhizomes was suppressed unless the existing long-shoot meristem was removed. The presence of "inactive" or dormant short shoots and rhizomes on *T. testudinum* suggests that a meristem bank may exist in *T. testudinum* beds, as was found

on the Caribbean coast of Mexico (van Tussenbroek 1996a). Just what role these inactive short shoots play in vegetative expansion in a seagrass bed is yet unknown. Perhaps, under certain conditions, the dormant short shoots will again resume growth and produce new blades or rhizome meristems. Further, seagrasses differ in rhizome-branch frequency. For example, *H. wrightii* rhizomes branch frequently and grow rapidly, whereas those of *T. testudinum* do not. Species that exhibit more aggressive growth are often chosen for restoration in Florida. Thus *H. wrightii* is more often selected for restoration projects than *T. testudinum,* although the latter species forms the dominant beds in Florida and contains the greatest diversity of species (Zieman and Zieman 1989). The types of growth (foraging) strategies of seagrasses are the same as those of terrestrial clonal plants. Rhizomes of *H. wrightii* show a "guerrilla"-type growth by branching frequently and spreading rapidly. In contrast, *T. testudinum* rhizomes show a "phalanx"-type growth, growing linearly and with few lateral axes (Dawes 1998a).

EVOLUTION and GENETICS

The discovery of fossil seagrasses in the Avon Park formation in Florida (Lumbert *et al.* 1984) indicates that species of *Thalassodendron* and *Cymodocea* occurred with *T. testudinum* in the late Middle Eocene (*ca.* 40 million ybp). These fossils were preserved as carbonized imprints within the bedding planes of a micritic dolomitic limestone in a rock outcrop of the Ocala Arch in central Florida, which contains the oldest exposed rocks in the state. Generic determinations were certain, except for one of the fossils, and species identifications were questionable for two of the fossils. The fossils were identified as *Thalassodendron auriculaleporis* den Hartog, *Cymodocea floridana* den Hartog, *T. testudinum*, *Cymodocea* sp., *Halodule* sp., and an unknown Zosteroid.

Species of *Thalassodendron* and *Cymodocea* presently occur only in the Old World tropics (Indo-Pacific region), indicating that a more diverse seagrass flora existed in the Caribbean Sea in the past. One hypothesis suggests that they disappeared from the Caribbean region when the Central American isthmus elevated and separated the Atlantic and Pacific oceans, changing dominant circulation patterns, which caused Caribbean

water temperatures to fall. Evidentially, an extensive and diverse seagrass flora existed in central Florida in the past, judging by the abundance and extent of the fossilized seagrasses and by the diversity of less well-preserved animals from seagrass beds (two families of foraminifera, some bivalves, a bryozoan, a crab carapace, and possibly an ostracod). The fossil findings support the vicariance model of Heck and McCoy (1979), who proposed that the present-day distribution of seagrass species is a product of continental drift, speciation, and extinction. Hypotheses regarding the origin of seagrasses include evolution from salt-tolerant terrestrial shrubs (den Hartog 1970) or from freshwater hydrophilous ancestors (Cox and Humphries 1993).

Comparison of isozymes of various enzymes and molecular-DNA techniques have been used to examine genetic diversity within and between present-day seagrass populations and species in Florida and the Caribbean region. Early isozyme studies examined genetic differences between Caribbean Sea and Gulf of Mexico populations of *T. testudinum, S. filiforme,* and *H. wrightii* but found little intraspecific variation (McMillan 1980). The studies supported McMillan's (1978) earlier culture experiments, which revealed that leaf width was influenced by the immediate environment and not by genetic differences between plants.

Being the dominant seagrass in Florida and the Caribbean (Zieman and Zieman 1989), *T. testudinum* has been the principal species to have its genetic diversity measured using isozymes (Schlueter and Guttman 1998) and molecular-DNA approaches (Kirsten *et al.* 1998; Davis *et al.* 1999; Waycott and Barnes 2001). Allozyme loci of 14 enzymes in 18 populations in the lower Florida Keys indicated that asexual reproduction is probably the basis for the low genetic diversity there and for a trend towards genetic uniformity (Schlueter and Guttman 1998). Allozyme and Amplified Fragment-Length Polymorphism (AFLP) analyses were used to compare genetic diversities of *T. testudinum* from two sites in Panama and from another in Bermuda (Waycott and Barnes 2001). The authors found high levels of genetic uniformity, and they suggested that it is due to vegetative-fragment dispersal, even over a distance of 2,700 km.

In contrast to isozyme and allozyme studies, two other molecular DNA studies found a higher
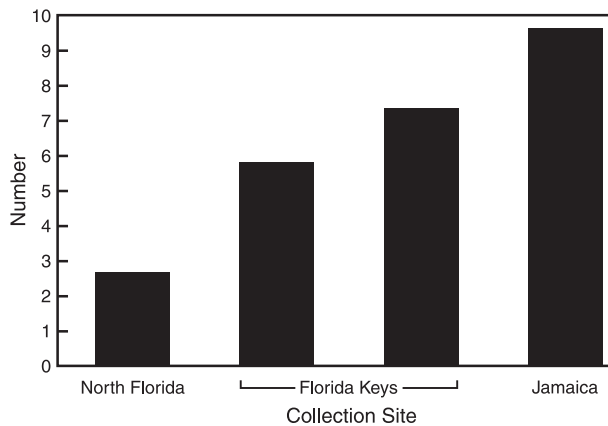
Figure 3.2 *Randomly amplified polymorphic DNA (RAPD) phenotypes within four populations of* Thalassia testudinum. *(Modified from Kirsten* et al. *1998)*

level of genetic diversity within populations of *T. testudinum,* rather than between geographically distinct ones. Randomly Amplified Polymorphic DNA (RAPD) analysis showed high genetic diversity within two proximal Florida Keys populations (*e.g.,* Fiesta Key and Craig Key) and within another northern population off the Steinhatchee River (as Apalachicola Bay in Kirsten *et al.* 1998). Further, almost all samples from an outlier Jamaican population and the two Florida Keys sites were distinct genetic individuals within and between the three populations. This is in contrast to the northern population that had the fewest RAPD phenotypes (Figure 3.2). The lower within-community genetic diversity of northern populations of *T. testudinum* may reflect the limited introduction of new genets (*e.g.,* drift plants) or a low level of flowering and seed production, perhaps because of less-than-optimum water temperatures or water transparencies. A second study on *T. testudinum,* using DNA-fingerprinting techniques, concentrated on clonal variation in populations in Florida Bay and found discrete beds that were not genetically uniform (Davis *et al.* 1999), again emphasizing the role of sexual reproduction in maintaining population genetic variation. Thus, beds of *T. testudinum* in more tropical regions contain a greater number of distinct genets than do beds at higher latitudes. The difference in genetic diversity between tropical and subtropical beds may reflect a lower rate of seed production in more northern sites, as shown for seagrasses in Tampa Bay (Witz 1994; Witz and Dawes 1995). This may explain the lower genetic diversity for the northern population of *T. testudinum* found off the Steinhatchee River

(Kirsten *et al.* 1998). The concept that sexual reproduction is less likely to be successful when an organism encounters less-than-optimal temperatures was described by Gessner (1970). However, little is known about flowering and the production of viable seeds on most of the Gulf coast of Florida, with the exception of some data for Tampa Bay and the Florida Keys.

Another study (Angel 2002) using RAPD analysis compared three populations of *H. wrightii* from Texas (Christmas Bay, Corpus Christi) and from Florida (Florida Bay). All individuals appeared to have unique genotypes, with plants from Corpus Cristi more closely clustered to those of Florida Bay, which Angel suggested was due to similar habitats that acted as a selective force. The molecular phylogeny of 11 species of *Halophila* found that *H. decipiens* and *H. engelmannii* were distinct species and that there was a 100% overlap between populations of the former species between populations from Australia, the Caribbean, and Florida (Waycott *et al.* 2002). Further, the internal transcribed spacer (ITS) region of the ribosomal DNA indicated that *H. johnsonii* from the Indian River in Florida could not be distinguished from *H. ovalis* and needs further study.

PHYSIOLOGICAL ECOLOGY

At least five abiotic properties influence the morphological and anatomical adaptations of seagrasses (Dawes 1998a), including the (1) osmotic effects of salt water; (2) availability of dissolved CO_2 and nutrients; (3) intensity and quality of illumination; (4) density (greater than air) and mechanical drag of an aqueous medium; and (5) effects of an aquatic medium on the dispersal of pollen and seeds.

The general physical requirements of five Florida seagrass species were discussed in Phillips (1960a). Seagrasses show physiological adaptations to a variety of abiotic and biotic conditions, including salinity, temperature, water motion, anoxia, nutrient limitation, epiphytes, irradiance, infection, and herbivory (Kuo and den Hartog 1989). The most-studied factor has been the relationship between light and the depth distribution of seagrasses. Nevertheless, other physical, geological, and chemical characters must be examined to explain the patchy distribution of seagrasses on the Gulf coast of Florida (Koch 2001). Koch identified
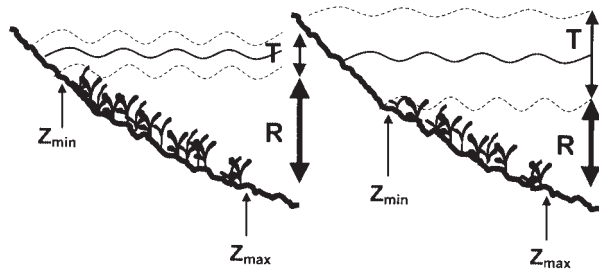
Figure 3.3 *Influence of tidal range on seagrass depth distribution. Minimum depth is deeper with greater tidal range (Koch 2001). Reprinted with permission from Estuarine Research Federation.*

Figure 3.4 *Influence of wave energy on seagrass depth distribution. Greater wave energy and deeper wave-mixing depths result in deeper minimum depths (Koch 2001). Reprinted with permission from Estuarine Research Federation.*

tidal amplitude (Figure 3.3) and wave energy (Figure 3.4) as two factors that influence seagrass depth distribution. Tolerances to common abiotic factors may differ between populations of a species from different environments, as shown for *R. maritima* grown from seed (Koch and Dawes 1991b). Different strains grown from seeds collected in the Weeki Wachee River estuary and from North Carolina had growth rates that were similar under different combinations of temperature and photoperiod but differed with regard to salinity. This was also reported in earlier studies for other species (McMillan 1979, 1984). In those studies, different strains of *T. testudinum, S. filiforme,* and *H. wrightii* showed different tolerances to temperature, and these tolerances were often related to distinct environmental origins. These findings suggest that transplanting from one area to a different site at greater distances (*e.g.,* seeds from Biscayne Bay to Tampa Bay) may not be as successful as when using local plants.

A large global-level literature base shows the critical effects of water quality on the presence, growth, and vitality of seagrasses. Adequate light transmission is vital to the presence of seagrasses and affects the density and biomass of seagrasses at all depths (Dixon and Leverone 1991; Duarte 1991; Johansson 1991; Kenworthy and Haunert 1991; Lapointe and Clark 1992; Tomasko 1992, 2002; Lapointe *et al.* 1994; Fletcher and Fletcher 1995; Kenworthy and Fonseca 1996; Kurz *et al.* 1999, 2000; Dixon 2000; Neely 2000). Depth determinations (±10 cm) can be obtained with a mapping-grade differential Global Positioning System, carrier-phase equipment and surveyed benchmarks (Johansson 2002b). In Tampa Bay, the deep edges for *H. wrightii* ranged from –0.30 to –0.76 m below mean low water (MLW), from –1.19 to
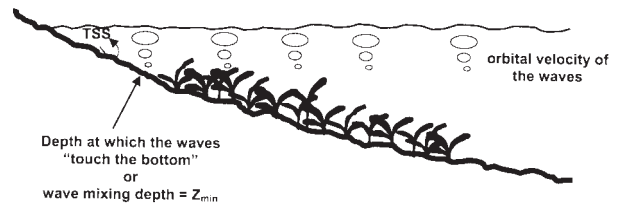
–1.96 m for *S. filiforme,* and from –0.57 to –1.73 m for *T. testudinum.* The maximum depth of *T. testudinum* at Port Manatee in Tampa Bay was –1.6 m, in agreement with the above determinations carried out before the 1997–1998 *El Niño* event (Dixon and Leverone 1995). The shallowest deep edges for all three species occurred at the northernmost sites, and the deepest deep edges were near the mouth of Tampa Bay, where more oceanic (clear water) conditions exist.

Neely (2000) demonstrated an inverse relationship between light reduction and short-shoot numbers for *H. wrightii* in Tampa Bay. Leaves on plants exposed to a 43% light reduction were longer than those on shoots in control plots or in other light-reduction treatments. Her experiments showed that loss of biomass was a result of winter die-back and also occurred with a >60% reduction in light. The data showed that epiphytes and surface scattering of light must be accounted for when calculating carbon budgets. Durako and Hall (1992) found that for *T. testudinum* the carbon supply became nonlimiting when light was reduced to levels that limited photosynthetic rates. Tomasko (1992) demonstrated that *H. wrightii,* when growing under a canopy of *T. testudinum* leaves, had longer rhizome internodes, less frequent branching, and lower above-ground to below-ground biomass ratios than when growing alone. Studies by Sand-Jensen (1977, 1990), Cambridge *et al.* (1986), and Tomasko and Lapointe (1991) showed that heavy epiphyte loads on seagrass leaves are indicative of nutrient over-loading in the water column and, therefore, eutrophication, *i.e.,* poor water quality (see Chapter 5). In addition to the adverse effects of nutrient-enriched water on photosynthetic functioning of seagrass leaves, increased levels of nutrients can result in high epiphyte loads that shade and weigh down the leaves, further lowering them in the water column.

Table 3.1 Light requirements of Florida seagrasses.

Species and Sites	Minimum Light Requirement (percentage of total surface irradiance)	Reference
Thalassia testudinum		
Big Bend area, FL	15.3%	Iverson and Bittaker (1986), as reported by Duarte (1991) and by Dennison *et al.* (1993)
Northwest Cuba	23.5%	Duarte (1991)
Puerto Rico	24.4%	Duarte (1991)
Charlotte Harbor, FL	20%	Tomasko and Hall (1999)
Tampa Bay, FL	22.5%	Dixon and Leverone (1995)
Tampa Bay, FL	20.1% (annual mean)	Dixon (2000)
Corpus Christi Bay, TX	14% (4% survival after 12 months)	Czerny and Dunton (1995)
Syringodium filiforme		
Florida Bay, FL	18.3%	Iverson and Bittaker (1986) as reported by Duarte (1991)
Indian River Lagoon, FL	17.2%	Duarte (1991) *pers. comm.* from J. Kenworthy (1990)
Indian River Lagoon, FL (southern region)	24%–37%	Kenworthy and Fonseca (1996)
Halodule wrightii		
Indian River Lagoon, FL	17.2%	Dennison *et al.* (1993) *pers. comm.* from J. Kenworthy (1990)
Florida Bay, FL	10%–20%	Fourqurean and Zieman (1991)
Laguna Madre, TX	7%–23%	Tomasko and Dunton (1991); Dunton (1994); Czerny and Dunton (1995)

The relationship between light, both quantity and quality, and the depth at which seagrasses grow was the subject of two workshops in Florida in the 1990s, one sponsored by NOAA (Kenworthy and Haunert 1991) and the other by the Indian River Lagoon National Estuary Program (Morris and Tomasko 1993). Even though they can grow under high irradiences, seagrasses are regarded as shade plants (Hillman *et al.* 1989), with compensation values (I_c) of 25 to 50 µmole-photons m^{-2} s^{-1} and saturation irradiances (I_k) of <200 µmole-photons m^{-2} s^{-1}. Studies comparing photosynthetic responses of seagrasses to different irradiance levels (*i.e.,* I_c, I_k, and P_{max} levels) often show a relationship to temperature and salinity, as seen for two species of *Halophila* (Dawes *et al.* 1989). For example, the estuarine, intertidal populations of *H. johnsonii* in the Indian River Lagoon tolerate a wide range of temperatures (10°, 20°, and 30°C) and salinities (15, 25, and 35 ppt) and did not become photoinhibited by high photosynthetically active radiation (PAR; *ca.* 500 µmole-photons m^{-2} s^{-1}). In contrast, *H. decipiens* from deeper, nonestu-arine Gulf-coast populations were intolerant of a 10°C temperature, 15 and 25 ppt salinity, and PAR above 300 µmole-photons m^{-2} s^{-1} (Dawes *et al.* 1989).

Depth distributions of Florida's seagrasses are governed by PAR levels in Tampa Bay (Miller and McPherson 1995; Dixon and Leverone 1995, 1997; Dixon 2002) and the Indian River Lagoon (Gallegos and Kenworthy 1996). Recent work has demonstrated more specific light requirements for the dominant seagrass species (Table 3.1). PAR levels measured at the deep edges of *T. testudinum* beds in Tampa Bay were significantly higher than the required average light level of 11% (of surface value) proposed for seagrasses by Duarte (1991). Also, *T. testudinum* in Florida Bay (Fourqurean and Zieman 1991) and Caribbean seagrasses (Onuf 1994) required at least 22% of surface PAR levels, when whole-plant requirements and average daily irradiances were considered. Continuous *in situ* measurements of underwater PAR levels for one year at the shallow and deep edges of four *T. testudinum* beds in Tampa Bay also indicated the
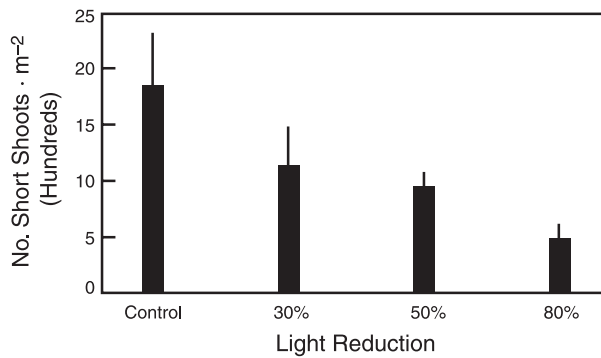
Figure 3.5 *Average density (short shoots m⁻²) of* Halodule wrightii *at control and three increasing levels of shading (30, 50, 80%) in Tampa Bay seagrass beds (± 1 S.D.). (Modified from Neely 2000)*

maximum depth limit in the bay occurred at about 20.5% of subsurface PAR (Dixon and Leverone 1995, 1997). Another study on irradiance in the more oceanic waters at the mouth of Tampa Bay showed that, using 20% light penetration as the threshold, sufficient light was available for *T. testudinum* beds to extend to two meters of depth (Miller and McPherson 1995). That depth is similar to measured seagrass-bed depth limits, which ranged from 1.98 to 2.37 m in estuaries (Dixon and Leverone 1995). Evaluating short-shoot density, Neely (2000) found that shallow, monospecific beds of *H. wrightii* showed a direct relationship between density and irradiance level at Mullet Key in Tampa Bay (Figure 3.5). The same level of density reduction with shading occurred in the cool and warm seasons, although summer short-shoot densities were almost twice those of the winter densities, indicating the critical effect that underwater irradiance has on seagrasses. Similar declines in leaf growth, short-shoot density, biomass and primary production have been caused by shading *T. testudinum* (Lee and Dunton 1997; Kraemer and Hanisak 2000) and *H. wrightii* (Czerny and Dunton 1995).

Light attenuation that limits seagrass depth distribution can result from a variety of sources (Kenworthy and Haunert 1991; Morris and Tomasko 1993). One factor governing light effects on seagrass depth distribution is the level of epiphytic biomass. The average annual attenuation by epiphytes on water-column PAR levels available to *T. testudinum* blades was from 32%–47% in Tampa Bay, 40%–56% in Sarasota Bay, and 21%–44% in Charlotte Harbor (Dixon and Leverone 1997). Variation in epiphyte loads on *T. testudinum*

blades resulted in a 7%–67% seasonal range in PAR attenuation in Tampa Bay, 13%–99% in Sarasota Bay, and 6%-89% in Charlotte Harbor (Dixon and Leverone 1997). Thus, in determining seagrass light requirements, seasonal levels of epiphyte loads should be considered in addition to the actual PAR levels (Dixon 2002).

Other factors shown to have critical effects on light available to seagrass, in a light model developed for the Indian River Lagoon, were total suspended solids (*e.g.,* tripton or non-algal particulate matter) and chlorophyll *a* concentration, which were the dominant causes of light attenuation affecting seagrass depth distribution (Christian and Sheng 2002). Attenuation of light by turbidity is a critical abiotic factor governing availability of light to seagrasses, as shown by the effects of dredging in the Laguna Madre of Texas that resulted in the decline of *H. wrightii* (Onuf 1994). Depth distribution, biomass, and photosynthetic responses were compared for shallow and deep populations of *T. testudinum* on the Gulf coast of Florida (Dawes and Tomasko 1988; Dawes 1998b). In general, biomass decreased while chlorophyll *a* increased with greater depth (Table 3.2), and the ratio of above- to below-ground biomass remained similar.

Also, light quality (*i.e.,* wave-length distribution) and PAR affect seagrass growth. Exposure of *H. wrightii, H. engelmannii,* and *S. filiforme* to UV-A and PAR irradiation resulted in photosynthesis inhibition in the latter species (Trocine *et al.* 1982). A low ratio of red:far-red wave lengths reduced branching and node formation in *R. maritima,* a response that may allow plants shaded by larger plants to escape by emphasizing horizontal rhizome elongation (Rose and Durako 1994). A similar response by *H. wrightii,* when shaded by *T. testudinum,* was noted in the Florida Keys (Tomasko 1992).

Photosynthetic responses have been used to evaluate seagrass tolerances to salinity and temperature variations (Dawes *et al.* 1987, 1989). Estuarine populations of *H. engelmannii* and *H. johnsonii* from the Gulf coast and Indian River Lagoon of Florida, respectively, had broader tolerances to a range of temperatures and salinities when compared to Gulf-coast oceanic populations of *H. engelmannii* and *H. decipiens.* Differences in photosynthetic factors (*e.g.,* P_{max}, α, I_k) were evident with freshly collected plants and after culturing

Table 3.2 Photosynthetic characters (P_{max}, alpha, I_c, total chlorophyll), primary production, and leaf growth (± S.D.) of *Thalassia testudinum* in deep- and shallow-water populations at two Florida Gulf-coast sites.

Site	Leaf Relative Growth Rate (mg dw · g dw^{-1} · d^{-1})	Primary Production (g dw · m^{-2} · d^{-1})	Total Chl (mg · g dw^{-1})
Egmont Key			
Shallow (–0.4 m)	28.7 (5.4)	11.71	4.86 (0.99)
Deep (–2.5 m)	27.4 (6.3)	8.17	3.92 (1.28)
Anclote Key			
Shallow (–1.0 m)	31.1 (9.3)	1.39	3.00 (0.84)
Deep (–2.5 m)	20.5 (0.3)*	1.00	2.39 (0.70)

Site	P_{max} (mg O$_2$ · g dw^{-1} · h^{-1})	I_c (μE · m^{-2} · s^{-1})	Alpha (P_{max}/I_c)
Egmont Key			
Shallow	4.54 (0.70)	39	0.063
Deep	6.31 (1.21)	45	0.069
Anclote Key			
Shallow	6.08 (0.92)	32	0.103
Deep	2.60 (0.33)*	24	0.097

Modified from Dawes and Tomasko (1988). * = probability <0.01

plants under common garden conditions for a number of weeks using various combinations of temperature and salinity. Salinity tolerance of *T. testudinum* from San Carlos Bay in the Caloosahatchee River Estuary in southwest Florida was assessed using long-shoot rhizomes bearing two to four short shoots (Doering and Chamberlain 2000). After a four-week acclimatization period in ambient seawater (35 ppt) in the laboratory, salinity was changed daily in 1.5 ppt increments.
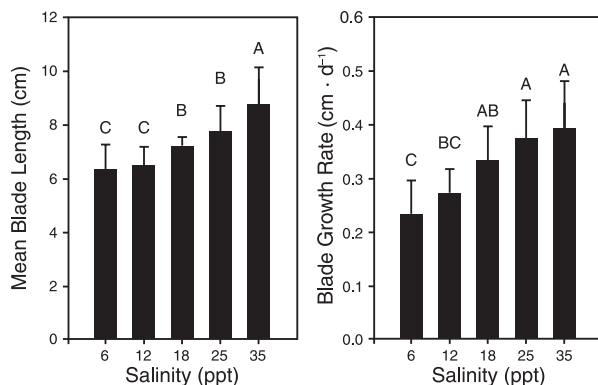
Figure 3.6 *Blade length and mean blade elongation rates for* Thalassia testudinum *cultured for 43 days in salinities ranging from 6 to 35 ppt. Letters indicate statistical differences between treatments and means, different letters are statistically different (*P < 0.05*). (Modified from Doering and Chamberlain 2000)*

Regardless of other variables, blade length decreased (Figure 3.6) and blade production ended after 43 days in the lowest (6 ppt) salinity. Blade length was positively correlated with salinity after 43 days of exposure. Also, the number of blades per short shoot and blade biomass were similar in 12, 18, 25, and 35 ppt salinities after 43 days of exposure (data not shown).

Salinity affects the local distribution of seagrass species on the Gulf coast of Florida (Phillips 1960b, c), with euryhaline species such as *H. wrightii* able to grow in a broad range of salinities (*e.g.,* 5 to 55 ppt; Dunton 1996). However, the effect on seagrass distribution due to salinity alone is difficult to separate from the effects of other factors, as shown in the general reduction of seagrass beds throughout Tampa Bay after the 1997–1998 *El Niño* event. The 1998 rainfall increase resulted in higher levels of dissolved inorganic nitrogen, chlorophyll *a* (phytoplankton), and color content (tannins) from extensive runoff into the bay (Johansson 2002a), which in turn reduced PAR penetration in the water column. In addition, the increase in rainfall directly lowered salinities, with Middle Tampa Bay salinities declining from a winter high of 30 ppt to 10 ppt by March and then to less than 5 ppt over a two-week period in April, 1998 (Dawes, unpublished data). Therefore, com-

Table 3.3 Structural features of *Ruppia maritima* epidermal cells from a single monoculture grown in 10 ppt and 32 ppt salinity.

Component of Cell Volume	Mean (± SD) at 10 ppt	Mean (± SD) at 32 ppt	Significance Level
Vacuolar volume	28.4% (± 19.8)	9.5% (± 9.3)	$P = 0.03$*
Cell membrane invagination	0.5 μm (± 0.7)	5.0 μm (± 4.2)	$P = 0.001$**
Polysaccharide volume	6.7% (± 3.5)	25.0% (± 13.4)	$P = 0.03$*
Chloroplast volume	8.6% (± 4.8)	13.3% (± 5.1)	$P = 0.02$*
Mitochondria number	12.2 (± 8.9)	17.3 (± 5.5)	$P = 0.03$*

Modified from Kruzcynski (1994). * = significant; ** = highly significant.

bined with higher nutrient loadings and turbidity-caused light attenuation, lower salinities resulted in a die-back of *T. testudinum* in Cockroach Bay by June 1998 and a reduction in seagrass acreage throughout west-central Florida coastal areas (see Chapter 2).

Seagrass osmoregulatory responses to changing salinities involve structural and physiological changes. The epidermal cells of *T. testudinum* and *R. maritima* show cell-wall and organelle modifications when grown or collected in salinities above 30 ppt (Jagels and Barnabas 1989). In *R. maritima,* clones of a single genetic strain cultured in 32 ppt had convoluted cell membranes, smaller vacuoles, and numerous mitochondria associated with the cell membrane (Table 3.3). Also, plasmodesmata were not evident between the epidermal and cortical cells, and a significant increase occurred in acidic mucopolysaccharides associated with the inner cell wall (Kruzcynski 1994). Clones from the same genetic strain of *R. maritima* did not show any of the above features when cultured at a lower salinity (*ca.* 10 ppt). The increase in cell membrane surface area and associated mitochondria are characteristic of cells active in osmoregulation, and acidic carbohydrates may be involved in ion transport and binding (Dawes 1998a). In addition, osmotic roles of the amino acids proline, alanine, and glutamate have been identified in seagrasses (Pulich 1986; Adams and Bate 1994). Pulich (1986) reported that proline functions as an organic osmoticum in *R. maritima, T. testudinum,* and *H. wrightii,* and alanine serves that role in *H. engelmannii.*

Data on temperature effects on seagrasses are limited to studies examining flowering and seed germination (see earlier discussion) and from a study of leaf-blade production near an electricity-generating plant (Barber and Behrens 1985). In the latter study, the productivity of *S. filiforme* increased in cooler months and decreased in warmer months in areas where water temperatures were enhanced by thermal pollution, whereas *T. testudinum* showed little or no response.

Water movement influences the spatial distribution of seagrass beds, in addition to the effects on depth distribution from tidal and wave activity (see also Chapter 5). Water velocities, degree of exposure to waves, and relative water depths strongly affect the distribution of *H. wrightii* and *Z. marina* beds near Beaufort, North Carolina (Fonseca and Bell 1998). Water movement, expressed as blade-friction velocities ($u* = $ cm s^{-1}), reduced boundary-layer effects around the leaf, and photosynthetic rate increased in *T. testudinum,* up to a current velocity of 0.25 cm s^{-1} (Koch 2001). In addition, increased water movement causes a decrease in concentration of sediment sulfide, a phytotoxin. Further, seedlings of *T. testudinum* collected in the Florida Keys showed optimum growth under intermediate flow rates ($u* = 0.3$ cm s^{-1}), whereas stagnant water ($u* = 0.0$) contributed to lower biomass possibly because of increased sulfide levels, and high flow rates ($u* = 1.0$ cm s^{-1}) reduced nutrient availability in the sediment pore water (Koch 1999a). Back-and-forth wave motion increases nutrient exchange between blades and the water column, in contrast to unidirectional movement or currents (skimming) that flow over *T. testudinum* meadows in the Florida Keys (Koch and Gust 1999). When the flow rate ($u*$) equaled 25 cm s^{-1}, the water current began to erode the sand; this caused a 50% reduction in seagrass coverage.

Repeated intertidal exposure, and thus the development of tolerance to desiccation, has been suggested as a causal factor in the ability of

H. wrightii to grow intertidally, where it may form extensive beds, in contrast to the subtidal distribution of *T. testudinum* (Phillips 1960a). However, factors other than desiccation tolerance may play a more critical role in terms of the higher vertical zonation for *H. wrightii,* for example, a greater tolerance to high irradiances and benefits from higher nutrient input from the shore (Björk *et al.* 1999).

Tolerance of exposure to high light levels in shallow or intertidal waters suggests that seagrasses may have evolved photosynthetic mechanisms (*e.g.,* C_4 photosynthesis) that reduce damage by UV radiation or intense PAR. However, photosynthetic mechanisms of all seagrass studied thus far appear to involve carbon-fixation reactions characteristic only of the Calvin cycle (C_3 plants) (Beer *et al.* 1977, 1980; Andrews and Abel 1977; Benedict *et al.* 1980; Durako 1993), with the possible exception of the Mediterranean species, *Cymodocea nodosa* (Beer *et al.* 1980). Carbon fixation in C_3 plants occurs via the Calvin Cycle, in which the enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase (rubisco) initially produces a three-carbon (C_3) compound, phosphoglycerate (Abel and Drew 1989; Beer 1996). However, an earlier study (Benedict and Scott 1976) reported that high levels of labeled carbon (^{14}C-bicarbonate) were incorporated into malate (30%) and aspartate (33%) in *T. testudinum.* These two four-carbon acids are commonly associated with the initial fixation step of the Hatch-Slack pathway of C_4 plants. The process described by Benedict and Scott (1976) for *T. tes-*

Figure 3.7 *Stable-carbon isotope values of seagrasses are influenced by adjacent mangroves.*

tudinum is similar to Crassulacean Acid Metabolism (CAM), which prevents loss of fixed carbon (as CO_2) resulting from photorespiration suffered by plants under high light irradiance. Because seagrass lacunae store respired CO_2, determining the level of photorespiration in seagrass blades is difficult, although it appears to be lower than in susceptible terrestrial plants (Abel and Drew 1989). More studies are needed to determine whether any of the six Gulf-coast species have modified C_4 carbon-fixation pathways. Durako (1993) demonstrated that *T. testudinum* can utilize both bicarbonate (HCO_3^-) and carbon dioxide, with relatively efficient HCO_3^- utilization, despite an apparently low affinity for this form of carbon.

Plants with C_4 photosynthesis have higher (less negative) $\delta^{13}C$ values than those of plants using only the C_3 pathway. It has been shown that seagrasses have $\delta^{13}C$ values similar to those of C_4 plants. The similarity in $\delta^{13}C$ values may be due to diffusional restrictions on carbon movement into the chloroplast in a relatively closed carbon-fixation system rather than reflecting their mode (*e.g.,* C_3 or C_4) of carbon fixation (O'Leary 1988). Overall, average seagrass $\delta^{13}C$ values range between –10 and –11 ppt, showing stable-isotope-ratio signatures that are usually less depleted in ^{13}C than they are in other aquatic primary producers (Hemminga and Mateo 1996). Thus, $\delta^{13}C$ values can be used to trace carbon flow in short-term carbon-allocation and production studies. In contrast to the overall averages for seagrasses given by Hemminga and Mateo, the $\delta^{13}C$ values for *T. testudinum* leaves in south Florida, when growing adjacent to mangroves (Figure 3.7), ranged from –7.3 to –16.3 with stable-isotope ratios of carbon that were similar to those of mangrove detritus (Lin *et al.* 1991). The difference in $\delta^{13}C$ values suggests influence of mangrove detritus on nearby seagrass beds. Macroalgae may have nitrogen stable-isotope ratios similar to those of seagrasses, as shown for $\delta^{15}N$. Using $\delta^{15}N$ values, Dillon *et al.* (2002) determined the sources of nitrogen in Florida. In Sarasota Bay, macroalgae had $\delta^{15}N$ values that averaged +4 per mil greater than those of seagrasses, the higher values being positively correlated with $\delta^{15}N$ values of wastewater discharge and being similar to macroalgae $\delta^{15}N$ values near populated areas in the Florida Keys.

Seagrasses facilitate the transport of inorganic carbon from seawater to the chloroplasts of their

epidermal cells to make up for slow CO_2 diffusion rates and low CO_2 levels in water, as well as for the low affinity of rubisco for CO_2 when the lacunae have high concentrations of O_2 (Beer 1996). More importantly, seagrasses can use HCO_3^- from seawater via carbonic anhydrase-catalyzed extracellular conversions. Unlike seaweeds, which have photosynthetic rates that are saturated by present-day CO_2 levels, seagrasses continue to be CO_2-limited (Beer and Koch 1996). The authors suggest that when seagrasses colonized the sea in the Cretaceous, CO_2 levels were higher. With atmospheric CO_2 levels again increasing, the authors suggest that nearshore beds may expand (but see Beer *et al.* 2003). However, CO_2 concentration in seawater need not be a limiting factor to seagrass growth under low irradiance conditions, as shown by Durako and Hall (1992). Using $\delta^{13}C$ values, they reported that CO_2 concentration in natural seawater was not limiting for *T. testudinum* under low light when photosynthetic rates were low, a relationship that may be relatively common in turbid water.

Entire-plant carbon budgets have been measured for *T. testudinum* in Florida Bay (Fourqurean and Zieman 1991) and for *H. wrightii* in Tampa Bay (Neely 2000). Below-ground biomass (roots, rhizomes, and short shoots) of *T. testudinum* accounted for 85% of the standing stock and 57.5% of total-plant respiration (Fourqurean and Zieman 1991). In contrast, below-ground biomass of *H. wrightii* ranged from 94% (winter) to 69% (summer) in Tampa Bay, with an above-ground productivity of 0.25 g C m^{-2} d^{-1} in September (Neely 2000).

Tomasko and Dunton (1995) compared four methods (blade clip-and-reharvest, above-ground biomass values, leaf-production turnover rates, and below-ground:above-ground-biomass ratios) for estimating diel rates of primary production in *H. wrightii* populations of Texas. The whole-plant biomass and leaf-turnover approaches appeared to be useful tools for estimating productivity in *H. wrightii*. The blade clip-and-reharvest method devised by Virnstein (1982) for determining primary production in narrow-bladed seagrasses such as *H. wrightii,* underestimated primary productivity. Further, they concluded that the H_{sat} model that calculates total PAR for a photoperiod was reliable and accurate in the prediction of daily carbon gain. However, they stated that although the *in*

situ measurement of underwater light levels and P vs. I parameters, as used in Zimmerman *et al.* (1994), is a more rigorous approach for calculating primary production, it requires a large investment of time and resources.

Because of their conspicuous roles in productivity and biomass generation, both the organic composition and the caloric values of seagrasses have been studied (Dawes 1998a). Annual mean caloric values per gram of dry weight (g dry wt) for leaves, short shoots, and rhizomes of *T. testudinum* were 10–13, 8–11, and 12–14 kJ, respectively. Similar values were obtained for *S. filiforme* (10–13, 10–14, and 15–16 kJ, respectively) and *H. wrightii* (13–15, 12–13, and 14–16 kJ, respectively). Another study in seagrass beds between Tarpon Springs and Cedar Key estimated that available kilocalories ranged from a 16-month low of 344 to a high of 1,837 kcal^{-1} m^{-2}, with the highest SAV biomass and caloric values occurring in the late spring and summer (Dawes *et al.* 1987).

Dawes (1998a) found that lipid levels for *T. testudinum, S. filiforme,* and *H. wrightii* were low, ranging from <0.1% to 6.3% of the dry weight for various organs. Soluble protein ranged from 5% to 22% of the dry weight, with leaves having the highest content in all three species. Soluble carbohydrates ranged from 6% to 54% of the dry weight, with rhizomes having the highest levels. Soluble protein and soluble carbohydrate levels show pronounced seasonal and species variations, as summarized by Zieman and Zieman (1989) and Dawes (1998a).

Rhizomes, followed by short shoots, are the principal storage organs for soluble carbohydrates and proteins in *T. testudinum, S. filiforme,* and *H. wrightii* (Dawes and Lawrence 1980) and in *H. engelmannii* (Dawes *et al.* 1987). Further, rhizomes are the source of soluble carbohydrates and proteins for regrowth of cropped blades and for initiation of spring blade growth in *T. testudinum* (Dawes and Lawrence 1979, 1980; Tomasko and Dawes 1989). In a review of carbon, nitrogen, and phosphorus content in the leaves of 27 seagrass species, Duarte (1990) found that they accounted for 34%, 2%, and 0.2% of the dry weight, respectively, with a mean C:N:P ratio of 474:24:1. Although the cell walls of seagrasses contain lignin, celluloses, and hemicelluloses, they are in lower concentrations than in terrestrial monocots (Table 3.4). Soluble, nonstructural carbohydrates (hemi-

Table 3.4 Cell-wall constituents of seagrass leaves, including lignin, cellulose, and soluble carbohydrates.

Species	Site (Ref.)	Lignin	Cellulose	Sol. Carb.
Thalassia testudinum	Florida (1)	0.2–2%	18–32%	1–9%
Syringodium filiforme	Florida (1)	1–3%	19–26%	10–16%
Halodule wrightii	Florida (1)	2–4%	25–33%	4–14%
H. uninervis	Gulf of Acaba (2)	<1%	41%	–
Halophila stipulacea	Gulf of Acaba (2)	2%	36%	–
H. ovalis	Gulf of Acaba (2)	<1%	33%	–
Heterozostera tasmanica	Philip Bay (3)	5%	20%	–

Modified from Dawes (1986). l. Dawes (1986); 2. Baydoun and Brett (1985); 3. Webster and Stone (1994).

celluloses) can account for 1%–16% of cell-wall dry weight in seagrass blades, whereas structural cellulose and lignin account for 18%–40% and 0.2%–5% respectively. By comparison, tropical grasses such as tall fescue (*Festuca arundinacea* Schreb.) and Bermudagrass (*Cynodon dactylon* (L.) Pers.) have 37% and 40% hemicellulose, 32% and 27% cellulose, and 10% and 6% lignin per g dry wt^{-1}, respectively (Dawes 1986). The adaptations of seagrasses to a hydrophytic environment are seen in their flexible blades (*i.e.,* few fiber bundles) and low amounts of lignin. Perhaps the brief life spans of leaves of many seagrass species, *ca.* 15 days in *T. testudinum* (Witz and Dawes 1995; van Tussenbroek 1996b), may not allow time for significant production of lignin to occur, compared to the long leaf life spans (months) of terrestrial plants, thus making seagrass blades more edible to grazers.

RHIZOSPHERE and SEDIMENT DYNAMICS

Seagrasses serve as sediment traps by acting as baffles, causing sediment-laden water to slow and drop its sediment as shown for seagrasses of Florida Bay (Prager and Halley 1999). Even species with diminutive morphologies, such as *H. decipiens,* can reduce sediment movement (Fonseca 1989). However, studies in *T. testudinum* beds in Tampa Bay show that sediment resuspension does occur because of tidal currents, so these communities are both sinks and sources of suspended matter (Koch 1999b).

Seagrasses modify the anaerobic sediment in which they grow. Roots and rhizomes release oxygen translocated from the shoot, cause bioturbation of the soil, and add organic matter via decomposition (Moriarty and Boon 1989). Chem-

ical changes wrought by the below-ground components are critical for plant survival because high levels of sulfides in anoxic reducing sediments are toxic to plants (Erskine and Koch 2000; Koch and Erskine 2001; Carlson *et al.* 2002). The above-cited experiments created sediment sulfide concentrations up to 13.0 mM; natural sulfide levels of healthy seagrass beds in Florida Bay average <2 mM, whereas in areas of seagrass die-off, the phytotoxin averages 4–10 mM (Carlson *et al.* 2002). Some evidence exists that die-off of overdeveloped beds of *T. testudinum* in Florida Bay may be due partly to lowering of plant resistance to the parasite *Labyrinthula* sp. during periods of increased environmental stresses such as high salinity, high or low temperatures, hypoxia, and high sediment sulfides (Durako 1994; Blakesley *et al.* 2002; see Chapter 5). Evidence for sulfide toxicity was found when sulfide addition (6 mM) in tank cultures was combined with high salinity and temperature over a period longer than 28 days (Koch and Erskine 2001), thus mimicking die-off conditions in Florida Bay. Carlson *et al.* 2002 suggested that the higher sensitivity of *T. testudinum* to sulfide levels than that of *H. wrightii* may be due to the former species having a higher below- to above-ground biomass ratio. They also reported high sediment-sulfide levels in other estuaries, including Sarasota Bay, which may help explain the patchy distribution of seagrass beds (Figure 3.8). This suggests that carbonate sediments, as found in Florida Bay, are not the only type of substrate that contain high sulfide concentrations and that seagrass losses (but not die-off) in other areas on Florida's Gulf coast may also reflect sediment conditions. The release of oxygen into its rhizosphere by *T. testudinum* and the resultant decline in sulfides (converted to sulfates) was shown in seagrass beds in Laguna Madre, Texas (Lee and Dunton 2000a).
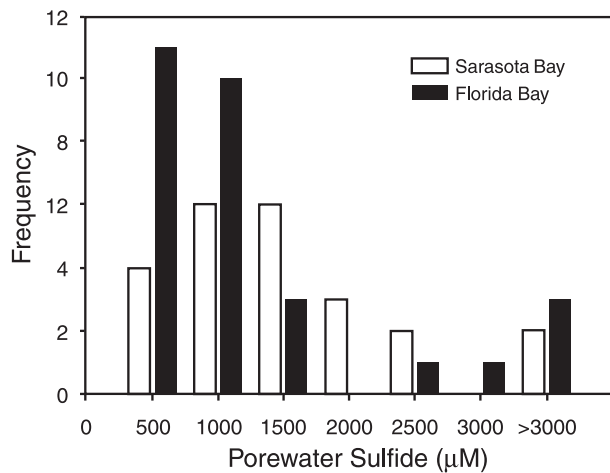
Frequency

12
10
8
12
4
2
0

Sarasota Bay
Florida Bay

0   500   1000 1500 2000 2500 3000 >3000
Porewater Sulfide (µM)

Figure 3.8 *Frequency distribution of pore-water sulfide concentrations in carbonate sediments of Florida Bay (Rabbit Key Basin) and in siliceous, terrigenous sediments of Sarasota Bay (Carlson* et al. *2002).*

Much of the sulfide in anoxic sediments derives from the activities of sulfate-reducing microorganisms. Many microbial associations in the bulk soil and with the plant's roots can provide a means for obtaining scarce nutrients. For example, fungal associations (mycorrhizal) might provide phosphorus or micronutrients. Nielsen *et al.* (1999) hypothesized that the nature of seagrass sediments restricts the development of vesicular-arbuscular mycorrhizae (VAM) because they could not find the association in the rhizosphere of *T. testudinum,* in contrast to their finding that VAM are associated with submergent and emergent freshwater angiosperms. Because they did not find any (VAM) associations with the roots of *T. testudinum,* Nielson *et al.* (1999) suggested that formation of the association was restricted by the combined effects of highly anaerobic nature and high salinity of seagrass sediments.

Since the classic studies of Patriquin and Knowles (1972), who used acetylene reduction by the seagrass rhizosphere to infer nitrogen fixation, a number of studies have described nitrogen fixation and nutrient uptake by marine angiosperms in greater detail. Based on acetylene-reduction experiments, Kenworthy *et al.* (1987) determined that bacteria associated with the roots and rhizomes of *T. testudinum* fixed nitrogen. Nitrogen

fixation occurs in *Lyngbya wollei* (Phlips *et al.* 1992), a freshwater cyanobacterium. Perhaps *L. majescula,* a common mat and epiphytic species in seagrass beds of Florida's Gulf coast, has a similar capability.

Seagrasses take up nutrients principally from sediment pore water (*e.g.,* ammonium and phosphorus; Fourqurean *et al.* 1992) but also from the water column (*e.g.,* nitrate and ammonium; Touchette and Burkholder 2000). However, pore-water nutrient concentrations in seagrass beds can vary widely, as shown in Florida Bay, where median values of 0.34 µM for soluble reactive phosphorus and 78.6 µM for ammonium occur (Fourqurean *et al.* 1992). Because of rapid growth rates, seagrasses require large amounts of fixed nitrogen (10 to 450 mg N m^{-2} d^{-1}), with ammonium being the preferred form (Moriarty and Boon 1989). By contrast, nitrate and nitrite concentrations are usually low (<5 µM) in anaerobic sediments, presumably because they are rapidly used by denitrifying and anaerobic bacteria.

Seagrasses show a variety of responses when nutrients become limiting. Phosphorus is usually the most limiting nutrient in seagrass sediments of Florida Bay, where calcium carbonate rapidly binds any free PO$_4^{-3}$ (Powell *et al.* 1989; Short *et al.* 1990; Touchette and Burkholder 2000), and its levels have been correlated with seagrass-bed development (Fourqurean *et al.* 1992). In Florida Bay, phosphorus apparently controls the successional sequence between early-stage *H. wrightii* beds and late-stage *T. testudinum* (Fourqurean *et al.* 1995). The former species tolerates higher nutrients better than *T. testudinum* does and will replace it in areas of natural or anthropogenic eutrophication. Nevertheless, factors other than nutrient levels may contribute to the replacement of *T. testudinum* by *H. wrightii.* Studies in Florida Bay (Carlson *et al.* 2002) reported that higher sulfide levels in the root zone, resulting from enhanced seagrass nutrition, can act as a phytotoxin in sediments and limit *T. testudinum.* By contrast, ammonium deficiency limits growth of *T. testudinum* in Laguna Madre, Texas (Lee and Dunton 2000b) and of *S. filiforme* in the Indian River Lagoon (Short *et al.* 1993).

ECOLOGICAL ROLES

- Biomass production of the three Florida seagrass species with larger statures is highly variable, with highest values reported for each in summer and early fall. Below-ground biomass accounts for 50%–90% of total plant biomass.

- *Thalassia testudinum* produces 10–19 leaf blades per short shoot per year, with lower turnover rates in more northern latitudes. Determinations of leaf production rates for other species are needed.

- Although vegetative growth is the primary method for seagrass expansion, little is known about rhizome extension rates for most species.

- Seagrass communities serve as habitats and nurseries for over 170 species of invertebrates and more than 100 species of fish. About 60 fish species using seagrass beds as habitat have non-commercial values and have poorly known requirements.

- Epiphytic biota are often seasonal, serve as food, and enhance seagrass community structure but may also negatively influence seagrass growth by attenuating light.

- A positive relationship exists between epiphytic load on seagrass blades and nutrient enrichment of their environment, whether the source of the nutrients is natural (*e.g.*, bird rookeries) or human (*e.g.*, septic tanks or stormwater runoff).

- Drift macroalgae deposited on seagrasses can result in seagrass die-back but can also serve as habitat, as nutrient sinks, as food, and as a transport vehicle for invertebrates and fish.

- Unlike overgrazing, which has been documented twice in Florida waters, moderate grazing may enhance the productivity and expansion of *T. testudinum*. The role of secondary metabolites that may reduce grazing in seagrasses is not known.

- Data regarding competition between seagrass species or with their associated macroalgae are limited.

- Animal species using seagrass habitats also often use nearby salt marshes, mangrove forests, and coral reefs.

- The export of inshore seagrass detritus offshore into deep water is poorly documented for Florida waters but may be an important source of organic matter in deep marine systems.

Manateegrass,
Syringodium filiforme,
with drift algae

FWC–FWRI photo

SEAGRASS COMMUNITY ECOLOGY

Like Florida's coastal mangrove and salt-marsh communities, seagrass communities are important primary producers, stabilize mobile sediments, serve as habitats and nurseries, and are direct and indirect food for diverse fauna (Dawes 1998a). Further, the characteristics of seagrasses (*e.g.* short-shoot densities, presence of inflorescence scars, levels of storage products) can aid in determining whether seagrass beds are stressed, thereby contributing to the monitoring of conditions in coastal and estuarine communities (Dennison *et al.* 1993; Dawes 1998a).

In a study of seagrass distributions and conditions on the northeastern Gulf of Mexico, Livingston *et al.* (1998) listed four significant predictors of seagrass community health. These predictors are photic depth, light quality, water quality (color, dissolved organic carbon, and chlorophyll *a*), and sediment characteristics. The principal predictor is light quantity (duration and intensity) in relation to seagrass depth distribution, which is related to water transparency, as shown in the review on seagrass depth limits by Duarte (1991). In this regard, water transparency was found to be the principal factor influencing the depth distributions of *T. testudinum* in Tampa Bay (Dixon and Leverone 1995, 1997) and growth form of *H. wrightii* below a canopy of *T. testudinum* in the Florida Keys (Tomasko 1992). However, light quality influences seagrass morphology as shown by altering the red to far-red ratios in cultures of *Ruppia maritima* (Rose and Durako 1994).

Seagrass communities have been measured for standing stock biomass (g dry wt m^{-2}) and short-shoot densities (numbers m^{-2}). Biomass data are commonly limited to above-ground material, mostly the photosynthetic blade tissue. Such data are available for the larger-stature seagrass species, including *T. testudinum, H. wrightii, R. maritima,* and *S. filiforme* (Table 4.1), but data are usually lacking for the smaller-stature species (*i.e.,* species of *Halophila*). In general, the below-ground biomass (roots and rhizomes) constitutes 50% to 90% of standing stock for the larger-stature species (Zieman and Zieman 1989). For example, total biomass estimates (above and below ground) for *T. testudinum* in Florida Bay ranged from 195 to 2,254 g dry wt m^{-2}, and 85% of this was below ground (Fourqurean and Zieman 1991). Beds of *S. filiforme* in the Indian River Lagoon have an annual mean above-ground leaf biomass of 87 g dry wt m^{-2} (± 151) or 43% of the total, whereas below-ground roots and rhizomes accounted for 117 g dry wt m^{-2} (± 94) or 57% of the total plant biomass (Short *et al.* 1993). Dunton (1990) found that in the Laguna Madre of Texas below-ground biomass for *H. wrightii* was 50% to 85% of the total and for *R. maritima* was 20% to 70% of the total biomass. On Florida's Gulf coast, the greatest leaf biomass for *T. testudinum* occurs in spring and early summer, whereas below-ground biomass (roots and rhizomes) is greatest in the fall (Dawes *et al.* 1985). Unlike below-ground biomass, leaf biomass in *T. testudinum* can show a four-fold seasonal fluctuation, with above- to below-ground ratios of 0.17 to 0.4 in December and 0.4 to 1.0 in April in Tampa Bay (Dixon and Leverone 1995).

Leaf turnover rates were reviewed by Short and Duarte (2001), and techniques to measure leaf growth were compared by Tomasko and Dunton (1995) and van Tussenbroek (1996b). Leaf production (g dry wt shoot^{-1} y^{-1}) in *T. testudinum* was measured by puncturing leaf clusters at their bases and measuring new leaf production after a few days (Tomasko and Dawes 1989). In a review of leaf turnover rates for *T. testudinum,* Marbá *et al.* (1994) reported that 14 to 19 leaves are produced annually by each short shoot. Leaf longevity on short shoots of *T. testudinum* in the Tampa Bay area using leaf-scar chronology was 14.6 days at Sunset Park in Tarpon Springs and 19.2 days in south Tampa Bay (Witz and Dawes 1995) and 24 days in a lagoon in the Yucatán, Mexico (van Tussenbroek 1996b). Leaf production generally ranged between 10 and 19 leaves short shoot^{-1} y^{-1} in Florida Bay (Zieman *et al.* 1989), the Indian River Lagoon (Gacia 1999), Tampa Bay (Witz and Dawes 1995), Charlotte Harbor (Tomasko and Hall 1999), Lower Laguna Madre, Texas (Kaldy *et al.* 1999), and the Caribbean coast of Mexico (Marbá *et al.* 1994; van Tussenbroek 1996b). Populations growing in cooler waters had lower annual rates of leaf production (10–15 leaves shoot^{-1}) for the Indian River Lagoon and the Lower Laguna Madre in Texas compared to those in Tampa Bay. Determination of leaf turnover in narrow-bladed seagrasses, such as *H. wrightii* (Tomasko and Dun-

Table 4.1 Standing stock (biomass) and productivity of southeastern United States seagrasses and closely related species (congeners) from other areas. Procedures differ greatly and influence the ranges in biomass and productivity.

Species	Locality	Biomass (g dry wt · m^{-2})	Productivity (g C · m^{-2} · d^{-1})
Halophila			
H. ovalis	India	48	
	Western Australia	40–60	
H. engelmannii	Texas (Gulf coast)	1.6	
Thalassia			
T. testudinum	Florida (general)	20–8,100	
	Florida (Atlantic coast)	20–1,800	0.9–16.0
	Florida (Gulf coast)	75–8,100	
	SW Florida Bay (Gulf coast)	60–125	
	Indian River, FL (Atlantic coast)	890	
	Corpus Christi, TX (Gulf coast)	454–885	
	Mexico, lagoon (Gulf coast)	420–1,418	
	Mexico, reef (Gulf coast)	573–811	
	Cuba (Caribbean Sea)	20–800	9.3–12.5
T. hemprichii	Queensland, Australia	70	
Syringodium			
S. filiforme	Florida (general)	15–200	
	Indian River, FL (Atlantic coast)	27–81	
S. isoetifolium	New Guinea (East Indies)	327	
Halodule			
H. wrightii	Mullet Key, FL (Gulf coast)	120	0.25
	Florida (general)	0.8	
	North Carolina (Atlantic coast)	105–200	0.5–2.0
	Laguna Madre, TX (Gulf coast)	70–300	
	Mississippi Sound (Gulf coast)	256	
H. uninervis	New Guinea (East Indies)	150	
Ruppia maritima	Texas (Gulf coast)	0–200	

Modified from McRoy and McMillan (1977), Zieman and Wetzel (1980), and Hillman *et al.* (1989).

ton 1995) and *S. filiforme* (Fry and Virnstein 1988), requires using an approach different from the leaf-punch technique. Leaf productivity by *S. filiforme,* determined using leaf clipping and photography, was 1.8 g dry wt m^{-2}d^{-1} (Virnstein 1982; see Short and Duarte 2001 for a detailed review of techniques).

Little is known about rhizome growth rates of Florida's seagrasses, yet this is the sole method for vegetative expansion. Reviews indicate that vegetative growth differs among species, rhizome elongation rates being higher for smaller-stature seagrass species (Marbá and Duarte 1998). In their review, mean rhizome elongation rates were highest for *H. wrightii,* the smallest stature of the larger Caribbean seagrasses (223, range; 81–365 cm yr^{-1}), followed by *S. filiforme* (123, range:

52–182 cm yr^{-1}) and then the largest stature species *T. testudinum* (69, range: 22–152 cm yr^{-1}). Short *et al.* (1993) found that *S. filiforme* rhizome elongation exceeded 100 cm y^{-1} in the Indian River. At Mullet Key in Tampa Bay, rhizome internode length and increase in seagrass patch size for *H. wrightii* were positively correlated; the larger the internodes of *H. wrightii*, the greater the increase in seagrass coverage at the edges of patches (Jensen and Bell 2001). The authors also found that a 100-fold increase in phosphorus, but not nitrogen, resulted in a significant increase in rhizome internode length. Jensen and Bell (2001) suggested that the observed patch-size patterns in seagrass beds (*e.g.* larger landscape features) may be determined by small-scale factors (*e.g.* nutrient availability).

Table 4.2 Densities of macroinvertebrates at various sites in Florida, arranged geographically from the Atlantic coast to the northern Gulf of Mexico. Single-density values are means; ranges generally represent several sampling sites. Several values are derived indirectly.

Study Site	Seagrass Species*	Faunal Group	Mesh Size (mm)	Density (indiv. m^{-2})	Number of Species	Reference
Card Sound	*Tha*	total	0.8	1,085	–	Brook (1977)
Bahia Honda	*Tha*	Amphipoda	1.0	102	5	Nelson (1980)
Florida Bay	*Tha*	total	0.8	2,794	52	Brook (1978)
Rookery Bay	*Hal*	Amphipoda	1.0	910	3	Nelson (1980)
Tampa Bay	*Hal*	Polychaeta	0.62	13,313	44	Santos and Simon (1974)
	Tha	Polychaeta	0.62	33,485		Santos and Simon (1974)
Anclote Anchorage	*Syr*	total	1.0	2,347	68	Mahadevan and Patton (1979)
	Syr	total	0.5	9,538	58	Mahadevan and Patton (1979)
	Tha	total	1.0	3,724	63	Mahadevan and Patton (1979)
	Tha	total	0.5	18,916	50	Mahadevan and Patton (1979)
Apalachee Bay	*Tha/Syr*	total	1.0	1,782 to 2,424	72	Lewis and Stoner (1981)
	Tha/Syr	total	0.5	3,154 to 4,754	86	Lewis and Stoner (1981)
	Tha	total	0.5	16,108	80	Lewis and Stoner (1983)
	Tha/Hal	Crustacea	0.5	6,716	46	Lewis (1984)
	Tha/Syr/Hph	total	0.5	2,827	170	Stoner (1980b)
Apalachicola Bay	*Hal*	total	0.5	38,780	58	Sheridan and Livingston (1983)
St. Andrew Bay	*Tha*	total	0.7	7,567	89	Saloman *et al.* (1982)
	Hal	total	0.7	3,370	67	Saloman *et al.* (1982)
	Tha/Hal	total	0.7	4,192	86	Saloman *et al.* (1982)
Santa Rosa Sound	*Tha*	total	0.5	13,260	144	Morton *et al.* (1986)
	Hal, core	total	0.5	9,020	41	Stoner *et al.* (1983)
	Hal, suction	total	0.5	6,077	37	Stoner *et al.* (1983)

Modified from Virnstein 1987. *Hal = Halodule wrightii, Tha = Thalassia testudinum, Syr = Syringodium filiforme, Hph = Halophila engelmannii.*

STRUCTURE, SHELTER, AND PREDATION

Seagrass beds function both as nurseries (Lewis and Stoner 1981; Lewis 1984; Virnstein 1987; Zieman and Zieman 1989; Fonseca *et al.* 1996b; Bell *et al.* 2001; Heck *et al.* 2003) and as habitats for invertebrates (Greening and Livingston 1982; Virnstein 1987; Valentine and Heck 1993), fish (Stoner 1983; Gilmore 1987), sea turtles (Williams 1988a), and manatees (Lefebvre *et al.* 1989). The role of seagrass meadows as nurseries was reviewed by Heck *et al.* (2003) who reported a strong link between seagrass abundance and abundances of juvenile fin fish and shell fish. The principal factor in this positive correlation was the structure that seagrasses added to the habitat.

Invertebrates add structure and serve as food, thus supporting increased diversity of other forms. For example, high densities of the mussel *Modiolus americanus* in St. Joseph Bay reached 2000 individuals m^{-2}, which enhanced invertebrate diversity and secondary production (Valentine and Heck 1993). The high variation of animal diversities among seagrass sites may be due in part to wave and current activity (Bell *et al.* 1994). The authors found that the mean numbers of fish and copepods and mean numbers of fish species were higher in low-energy seagrass beds (*e.g.,* minimum exposure to wind direction, speed, and effective fetch in Tampa Bay and Onslow Bay, North Carolina). Densities of macroinvertebrates in seagrass beds on Florida's Gulf coast vary widely among sites (Table 4.2), ranging from 910 individuals m^{-2} (Rookery Bay) to 33,485 individuals m^{-2} (Tampa

Bay). Invertebrate communities of seagrass beds in Florida are highly regional, and overlap occurs between subtropical, tropical, and warm-temperate faunas (Virnstein 1987). Holmquist *et al.* (1989) found that seagrass beds in Florida Bay play a secondary role as habitat for decapods and stomatopods compared with their reactions to winter cold fronts as a function of their positions on mud banks. Decapod crustaceans, such as caridean shrimps, usually dominate the larger fauna numerically, similar species of shrimp being widespread in Florida's Gulf-coast seagrass beds (Holmquist *et al.* 1989). The macrofauna varies widely in species composition and animal density over distance and time, including those of amphipods, gastropod molluscs, and polychaete worms (Virnstein 1987).

Because infaunal, epibenthic, and epiphytic animals of seagrass beds are prey for larger animals, fish are abundant there (Gilmore 1987). Principally, the larger-sized fish (*e.g.,* spotted seatrout, *Cynoscion nebulosus*, and pinfish, *Lagodon rhomboides*) have been studied. Smaller nonfishery species (*e.g.,* gobiids, syngnathids), which account for most of the resident species in seagrass beds, are less well known but include over 100 species (Gilmore 1987). As with invertebrates, fish faunas vary with geographic regions on Florida's Gulf coast and include warm-temperate species, eurythermal tropical species, and stenothermal tropical species (Gilmore 1987). Four subenvironments in Florida Bay had an overall average density of 11 fish m^{-2} and a total of 56 species (Sogard *et al.* 1987). The two-year study found seagrass standing crop and litter to be the most important determinates of fish numbers.

Monitoring animal densities and diversity in planted seagrass beds is a useful method for determining habitat restoration success. A study of a three-year-old planted seagrass bed in Tampa Bay (Fonseca *et al.* 1996a, 1996b) found that shrimp, fish, and invertebrate densities were equivalent to those of natural communities, although short-shoot density was only one-third those of natural beds. Another study in Tampa Bay found that higher numbers of polychaetes occurred in two-year-old planted sites than in natural *H. wrightii* beds (Bell *et al.* 1993). The rapid increase of animals in planted beds suggests that the threshold value of habitat structure may be much lower than previously thought and that the lack of correlation between patch size and animal abundance suggests other factors are involved in maintaining animal populations. Clearly, more studies are needed to determine animal population relationships in restored, created, and patchy seagrass beds.

Studies on seasonal animal-population fluctuations and patch formation in seagrass meadows suggest that they are not static, even under "stable" environmental conditions. For example, Tampa Bay seagrass beds experiencing more rapid water movement have a lower number of fish and harpacticoid copepods (Bell *et al.* 2001), which may also be influenced by organic matter content in the sediment. In St. Croix, Virgin Islands, tropical seagrass beds fluctuate in response to seasonal conditions (Williams 1988b). In addition to seasonal changes, severe plant die-off has occurred in Florida Bay, probably hastened by spatial variations in environmental stresses (Durako 1994; Zieman *et al.* 1999; see also Chapter 5). Water-column nutrient increases resulting in eutrophication have been cited as important environmental stressors that can shift species dominance in seagrass beds and influence sulfide production (Carlson *et al.* 2002). Williams (1987) found that *T. testudinum* could shade and replace *S. filiforme* beds in St. Croix. She also reported that the successional sequence from bare sediment began with rhizophytic (psammophytic) algae, then proceeded to *S. filiforme,* and ended with *T. testudinum,* as sediment nutrient concentrations increased over time (Williams 1990). In this regard, considering nutrient increases emanating from bird perches installed in Florida Bay, Fourquean *et al.* (1995) proposed that *H. wrightii* might replace *T. testudinum* in Florida Bay as sediment nutrient levels rise. However, this study did not consider the effect of increased sulfide levels in the sediment (Carlson *et al.* 2002) or the effect of phosphate and nitrate on seagrass growth (Powell *et al.* 1989).

The competition for space or the "space race" is evident by the numbers of macroalgae, cyanobacteria and microalgae (Hall 1988; Harris 1997) that grow on seagrass blades and that show strong seasonal changes. At Egmont Key in Tampa Bay, the five species of cyanobacteria and 20 species of epiphytic macroalgae varied in dominance (by algal division) during a 15-month study of *T. testudinum.* Brown algae dominated during the winter and spring months and cyanobacteria in the
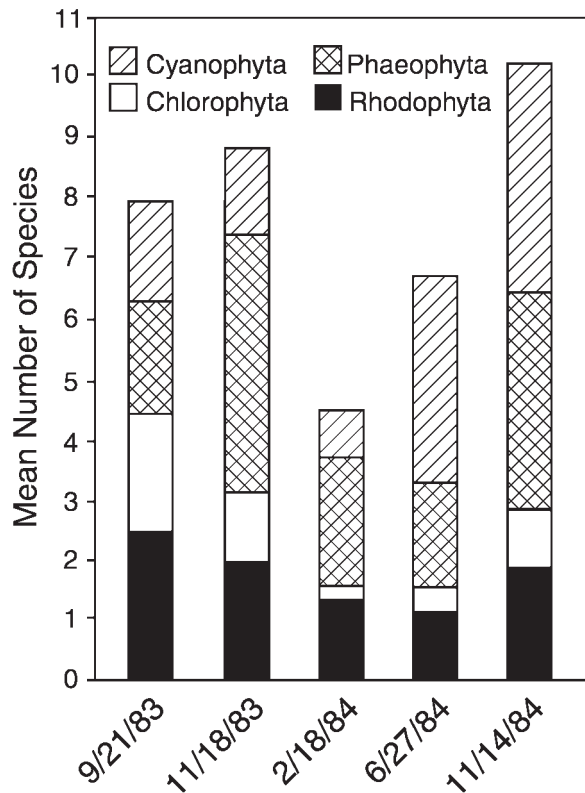
Figure 4.1 *Seasonal variations in the mean numbers of cyanobacteria and macroalgae, grouped by divisions, epiphytic on* Thalassia testudinum *blades at Egmont Key in Tampa Bay over a 15-month period (Hall 1988).*

summer months (Figure 4.1). Hall (1988) divided the algae into those that (1) are characteristically epiphytic on seagrasses; (2) settle and reproduce on seagrass blades, but are commonly epilithic; and (3) germinate on blades and then break free before reproduction. A study of *T. testudinum* beds near Leffis Key and Siesta Key in Sarasota Bay (Table 4.3) found many species of centric and pennate diatoms, six species of cyanobacteria, and 21 species of macroalgae (Harris 1997). Algae epiphytic on *H. wrightii* and *T. testudinum* in Tampa Bay, Sarasota Bay, and Charlotte Harbor (Dixon and Leverone 1995; Dixon and Kirkpatrick 1995, 1999) and Santa Rosa Sound in Pensacola Bay (Macauley *et al.* 1988) change seasonally, species diversity being negatively correlated with water temperature. Gacia *et al.* (1999) found that sheet-like and filamentous species of green-algae genera (*Enteromorpha, Cladophora*) were less resistant to grazing fish than were species of more coarsely branched red-algae genera (*Hypnea, Chondria, Acanthophora*) in the Indian River Lagoon. Algae

epiphytic on seagrass blades can account for 46% of the total biomass and 60% of the benthic primary production, as found using stable-isotope analysis, in *H. wrightii* beds in Mississippi Sound (Moncreiff and Sullivan 2001).

Studies have shown that epiphytes, in combination with PAR attenuation and seasonal low-growth periods, depress blade growth and primary production and reduce the depth of *T. testudinum* in Tampa Bay (Dixon and Leverone 1995, 1997), Florida Bay (Frankovich and Fourqurean 1997), the Florida Keys and Keys in Belize, Central America (Tomasko and Lapointe 1991), and Perdido Key in northwest Florida (Wear *et al.* 1999). Tomasko and Lapointe (1991) found water-column dissolved inorganic nitrogen (DIN) concentration was high near Big Pine Key (3.96 μM), an island in the Florida Keys with over 2,000 septic tanks. This DIN level is similar to that of a mangrove island in Belize (Man-O-War Key) having 75 pairs of nesting frigate birds (3.80 μM). In contrast, DIN levels were low around Cutoe Key (0.50 μM), a remote mangrove island in the Florida Keys. The seagrass beds near Big Pine Key and Man-O-War Key had higher epiphytism, lower short-shoot densities, lower leaf-area indices, and lower biomass in contrast to those near Cutoe Key (Tomasko and Lapointe 1991). Wear *et al.* (1999) reported similar results from an experiment using slow-release fertilizer (Osmocote®) in northwestern Florida at Perdido Key. Nutrification caused significant increases of diatoms, as well as red and brown macroalgae, on blades of *T. testudinum, H. wrightii,* and *S. filiforme* over a 12-month period. Frankovich and Fourqurean (1997) reported that epiphytic loads on *T. testudinum,* along a nutrient-enrichment gradient in Florida Bay, gave similar results to the previous studies, and this study indicated that the effect is localized. The authors concluded that epiphyte levels alone are not as responsive to moderate nutrient enrichment as are other seagrass characters, such as leaf tissue N:C ratios. As noted in Chapter 3, epiphytes of seagrasses reduce water-column PAR by as much as 99% seasonally. The question of whether organic carbon, nitrogen, or phosphorus can be transferred from seagrass blades to the epiphytic community or vice versa is not clear (see Lobban and Harrison 1994).
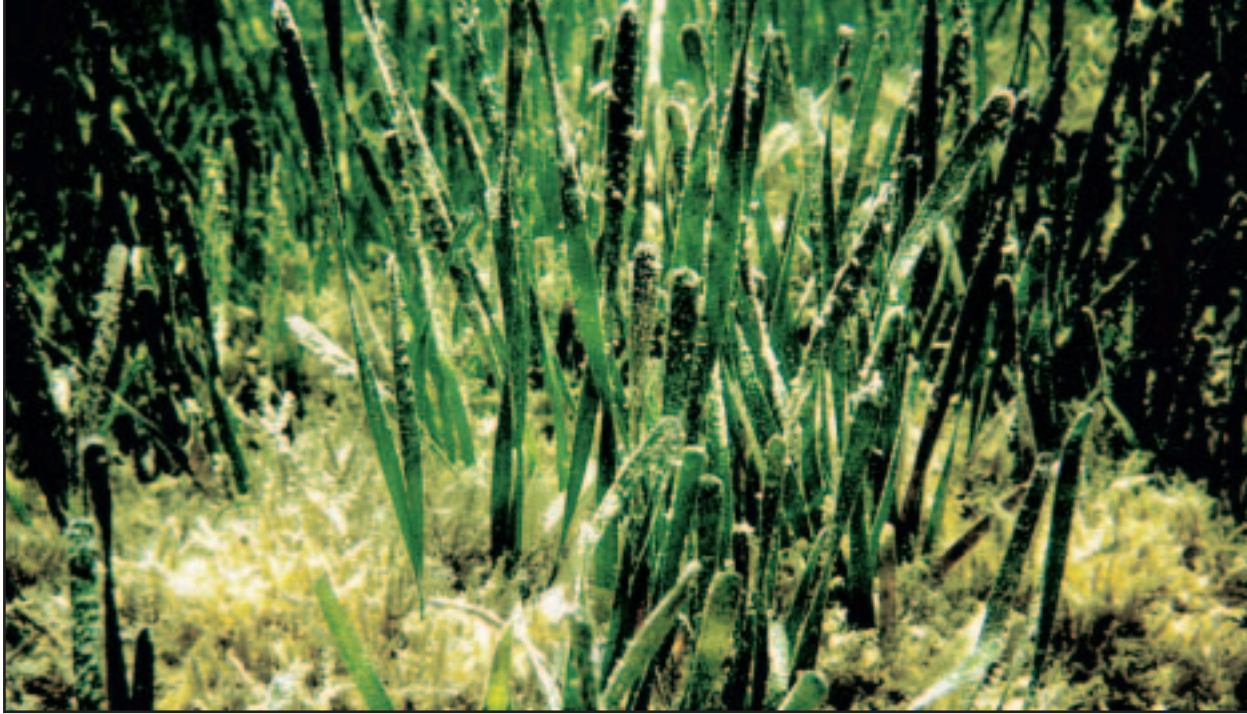
Some of the most abundant invertebrates in

Table 4.3 Epiphytic algae on blades of *Thalassia testudinum* at Leffis Key and Siesta Key in Sarasota Bay (modified from Harris 1997) and at Egmont Key in the mouth of Tampa Bay (modified from Hall 1988).

Species	Leffis Key	Siesta Key	Egmont Key
Cyanobacteria			
Anabaena oscillarioides	x	x	x
Anacystis sp.	x	x	x
Calothrix crustacea	x	x	x
Entophysalis conferta	x		
Microcoleus lyngbyaceus	x	x	x
Porphyrosiphon notarisii	x		
Chlorophyta			
Boodleopsis pusilla	x		
Chaetomorpha minima		x	x
Cladophora spp.	x	x	x
Enteromorpha chaetomorphoides			x
Ulva lactuca	x		
Phaeophyta			
Cladosiphon occidentalis	x		x
Ectocarpus elachistaeformis			x
Ectocarpus rallsiae (as *Giffordia rallsiae*)	x	x	x
Ectocarpus sp. (as *E. rhodochortonoides*)	x	x	x
Hincksia mitchellae (as *Giffordia mitchellae*)	x	x	x
Hummia onusta	x	x	x
Myrionema magnusii (as *M. orbiculare*)	x	x	x
Myriotrichia occidentalis	x	x	x
Rhodophyta			
Acrochaetium spp.	x	x	x
Centroceras clavatum	x	x	x
Ceramium cimbricum (as *C. fastigiatum*)	x	x	x
C. flaccidum (as *C. byssoideum*)	x	x	x
Chondria dasyphylla	x	x	x
Chondrophycus papillosus (as *Laurencia papillosa*)	x		
Erythrotrichia carnea			x
Hydrolithon farinosum (as *Fosliella farinosa*)	x	x	x
Hypnea musciformis	x	x	
Polysiphonia subtilissima	x	x	
Stylonema alsidii (as *Goniotrichum alsidii*)			x

seagrass beds are the meiofauna, including crustaceans (Lewis 1987) and copepods (Hall 1988). Harpacticoid copepods are often the most common animal group associated with seagrasses (Hall and Bell 1988, 1993; Walters and Bell 1986; Walters 1991). One study reported that more than 20,000 harpacticoid copepods migrated h^{-1} m^{-2} from the sediment during the night into the water column, representing over 50% of the total benthic harpacticoid community (Walters and Bell 1986). Further, this postsunset entry into the water column from the sediment involved over 30 species in 15 families (Walters 1991). At Mullet Key in Tampa Bay, artificial blades (green ribbon) with artificial epiphytes (cotton fibers) attached had significantly higher densities, compared to green ribbons alone, of copepods, polychaetes, and nematodes associated with them after three days. This shows that epiphytic biota enhance structural complexity of seagrass blades, thereby increasing habitat values (Hall and Bell 1988). In a similar study, Hall and Bell (1993) showed that the most abundant meiofaunal groups on seagrass blades at Egmont Key were adult harpacticoid copepods, copepod nauplii, and nematodes. They also determined that meiofauna density was most signifi-

Figure 4.2 *Drift algae are entangled by seagrass leaves, as in this* Thalassia testudinum *bed.*

cantly correlated with percentage cover of filamentous algae. A 15-month study of *T. testudinum* blades at Egmont Key at the mouth of Tampa Bay (Hall 1988) showed seasonal shifts in the abundance of nematodes (highest in winter) but not that of harpacticoid copepods and nauplii (abundant throughout the year). Epiphytes trap detritus, which attracts significantly higher numbers of copepods that feed on it (Meyer and Bell 1989). Small grazers (*e.g.,* copepods) can play a role in epiphyte control (Virnstein 1987), as shown for *H. wrightii* plants in the Indian River Lagoon (Howard and Short 1986).

Along with drift macroalgae, rhizophytic (psammophytic) algae may equal or surpass seagrass biomass in Florida Gulf-coast seagrass beds (Dawes *et al.* 1985). With the exception of some tropical coenocytic green algae, macroalgae usually cannot attach to sand or mud. Coenocytic green algae are a diverse group of siphonaceous (lacking internal cell walls) algae placed in the order Caulerpales. They form extensive rhizoid holdfasts and include species of calcified (*Halimeda, Penicillus, Udotea*) and noncalcified (*Caulerpa, Riphilia, Avrainvillea*) genera. Even though rhizophytic coenocytic algae may compete for space and light with seagrasses, they may also serve as pioneer plants, which then may be replaced by seagrasses, as shown in a coral-reef lagoon in St. Croix (Williams 1990).

Over 230 species of unattached macroalgae (drift algae) are known throughout the world (Norton and Mathieson 1983). Drift algae are usually noncalcified, remain infertile, and reproduce vegetatively (Collado-Vides *et al.* 1994). Two studies, one in Tampa Bay, Boca Ciega Bay, and Anclote Anchorage (Phillips 1960b) and the second in Crystal Bay (Phillips 1960c), listed 195 and 46 taxa, respectively, of algae that could not be distinguished as either drift or attached. Drift algae are concentrated in seagrass beds where water-current velocities are reduced and blades will entangle the algae (Figure 4.2). To some extent, seagrass blade size may influence entanglement (Bell *et al.* 1995). Seagrass beds on the Gulf coast of Florida are known to contain from 8 to 65 species of drift algae with the total biomass ranging from 0.002 g to 930 g dry wt m^{-2} (Table 4.4). Brown (2001) found that algal biomass differed for three sites on the Gulf coast of Florida, both by season and by site. Annual means of 6.01, 3.83 g, and 2.25 g dry wt m^{-2} were obtained for Tampa Bay in Cockroach Bay, Tarpon Bay, and Sunset Beach respectively. Although biomass varies with season and site on the Gulf coast, the types and numbers of species are similar (Table 4.4).

Drift algae are an important ecological component of seagrass beds because they serve as habitat, provide transportation, and provide a food source for invertebrates (Ballantine *et al.* 1994; Holmquist 1994; Greenway 1995; Knowles and Bell 1998; Maciá 1999; Brooks and Bell 2001; Rydene and Matheson 2003). In Florida Bay, Holmquist (1994) found 61 invertebrate taxa in drift algae mats in

Table 4.4 Number of drift-algae species and dominant species, biomass, and presence/absence (by division) in seagrass beds on the Gulf coast of Florida. Locations include (1) Anclote Estuary near Tarpon Springs (Hamm and Humm 1976), (2) Hillsborough Bay including studies 2a (Kelly 1995) and 2b (Avery 1997), (3) Sunset Beach at Tarpon Springs (Brown 2001), (4) Cockroach Bay in Tampa Bay (Brown 2001), and (4) Tarpon Bay at Sanibel Island (Brown 2001).

	Locations					
	1	2a	2b	3	4	5
Number of species	65	19	18	9	9	8
Number of dominant species	4	5	9	9	9	8
Mean biomass (g dry wt · m^{-2}) low	–	–	80	0.07	0.0002	0.14
high	–	–	930	6.34	9.45	9.32
Cyanophyta						
Lyngbya majescula					x	x
Chlorophyta						
Caulerpa prolifera			x			
Chaetomorpha crassa			x			
C. gracilis			x			
Chaetomorpha sp.		x				
Enteromorpha spp.						x
Enteromorpha clathrata			x			
Ulva lactuca		x	x		x	
Phaeophyta						
Sargassum pteropleuron				x		
Sargassum spp.	x					
Rhodophyta						
Acanthophora spicifera			x		x	x
Chondrophycus papillosus (as *Laurencia papillosa*)	x					
Digenia simplex	x					
Gracilaria armata					x	x
G. caudata				x	x	x
G. cornea (as *G. debilis*)					x	
Gracilaria spp.		x	x			
Hypnea musciformis				x	x	x
Laurencia intricata (as *Laurencia obtusa*)	x			x		
L. poiteaui				x		
Polysiphonia ramentacea				x		
P. subtilissima			x			
Solieria filiformis (as *Agardhiella tenera*)		x	x	x	x	x
Spyridia filamentosa		x	x	x	x	x

seagrass beds. Average drift rate was 0.5 km d^{-1}, indicating that drift algae are an effective mode of transport for animals. Ballantine *et al.* (1994) reported that balls of algae in Venezuela contained 12 species of invertebrates. The numbers of amphipods, isopods, and tanaeids in Venezuela were significantly higher on two species of red algae than were associated with blades of *S. fili-forme,* as similarly found in other previous studies (Knowles and Bell 1998). Virnstein and Howard (1987) noted that drift algae serve as habitat and food sources for gammaridean amphipods. Brooks and Bell (2001) found that drift clumps of the red alga *Hypnea cervicornis,* as they moved through seagrasses and into sandy areas, had significantly higher amphipod densities; they concluded that drift algae clumps provide a mobile corridor for animals. In Tampa Bay, drift algae form an important alternative habitat for 12 of the 20 most abundant juvenile and small adult fish (Rydene and Matheson 2003). However, drift algae deposited in seagrass beds can also affect these habitats by causing a seagrass die-back as a consequence of light and oxygen reduction (Norkko *et al.* 2000). A

combination of algae deposition and sea-urchin grazing increased the die-back of *T. testudinum* in Florida Bay (Maciá 1999). The amount of drift-algae biomass can also have a negative correlation with seagrass bed expansion if dissolved nutrients are high, as shown for Hillsborough Bay (Avery 1997). In a 10-year study, Avery (2000) found that with improved water quality the 18 species of dominant drift algae declined in average biomass from 164 g dry wt m^{-2} in 1987 to 0.0029 g dry wt m^{-2} in 1998 in Tampa Bay. The green coenocytic alga *Caulerpa prolifera* had colonized Hillsborough Bay in 1986 with an initial coverage of almost 220 ha (543 acres) but had declined to zero in 1997. In contrast, *H. wrightii* coverage increased from 0.2 ha (0.5 acres) in 1986 to nearly 57 ha (141 acres) in 1998 (Avery 2000).

A few studies exist concerning competition between seagrasses or between seagrasses and attached macroalgae, with two reports on *T. testudinum, S. filiforme,* and *H. wrightii* and rhizophytic algae in the Caribbean (Williams 1987, 1990). Williams (1987) removed the leaf canopy of *T. testudinum* in St. Croix, resulting in increased irradiance reaching the *S. filiforme* understory, and its biomass doubled within nine months. A study in Tampa Bay indicated that competition occurred between *T. testudinum* and *H. wrightii* (Rose and Dawes 1999), where *T. testudinum* had a lower biomass when growing with *H. wrightii,* suggesting interspecific competition. Further, leaf biomass and growth were significantly lower in dense, monotypic beds of *T. testudinum* compared to less dense beds, suggesting light was reduced via shading in dense beds (Rose and Dawes 1999). There are also reports regarding competition between *H. wrightii* and the coenocytic green macroalga *C. prolifera* (Bottone and Mattson 1987; Bottone and Savercool 1993). Although the data are not conclusive, *C. prolifera* may act as a weak competitor for space with *H. wrightii,* coexisting with it as an opportunistic species under stable environmental conditions in Tampa Bay (Bottone and Savercool 1993). This result is similar to those found in studies in the Indian River Lagoon (White and Snodgrass 1990). Further, *C. prolifera,* although susceptible to sudden environmental changes (*e.g.,* low salinity), can rapidly colonize areas devoid of vegetation that may occur following seagrass die-back (Bottone and Mattson 1987).

Overgrazing of seagrass beds is a rarity but has occurred on the Florida Gulf coast. Overgrazing by *Lytechinus variegatus* (purple sea urchin) resulted in large-scale denudation of seagrass beds. Over 20% of an area 26 km by up to 9.5 km were consumed near the Pepperfish Keys south of the Steinhatchee River in the northern peninsula (Camp *et al.* 1973). Density at the front of a single aggregate averaged 636 sea urchins m^{-2}, with individuals piled upon one another 2–8 individuals deep that covered the substrate. Dense aggregations of the same urchin species overgrazed about 0.81 km^2 of *T. testudinum* in outer Florida Bay; mean densities ranged from 364 to <1 individual m^{-2} (Rose *et al.* 1999). The origins of the urchin feeding fronts are not understood. In Florida Bay, high urchin densities may reflect unusually high recruitment or a release from predation pressure because of over-harvesting of spiny lobsters and stone crabs (Rose *et al.* 1999).

Moderate grazing pressures on *T. testudinum* blades were correlated with specific leaf growth rates (0.024 mg dry wt. d^{-1}) in the Yucatán, Mexico; this showed that sporadic grazing had little detrimental effect on *T. testudinum* (Cebrián *et al.* 1998). Studies on *T. testudinum* beds in northwest Florida and a review of the literature indicated that herbivory plays a major role in stimulating seagrass growth by removing macroalgae (Heck and Valentine 1995; Valentine and Heck 1999). Also, long-term effects of grazers have been shown in a relationship between *L. variegatus* and *T. testudinum* in the Gulf of Mexico (Heck and Valentine 1995), where urchins and seagrass coexist in balance. In these cases, a balance developed among intensive grazing, loss of habitat, and predation by fish on the urchins. In the 1995 experiment, protection from predator fish by enclosures resulted in intense grazing by the urchins, which became most destructive in winter when *T. testudinum* could not recover as rapidly. The more intensively grazed beds showed significant reductions in above- and below-ground biomass, which was apparent even 3.5 years after grazing had ceased. Varying the number of *L. variegatus* in experimental plots in St. Joseph Bay, Valentine *et al.* (1997) found an increase in shoot density and productivity of *T. testudinum* under moderate grazing pressure. In a later study, Valentine *et al.* (2000) demonstrated that the effect of grazing in Florida Bay was related

Table 4.5 $\delta^{15}N$ and $\delta^{13}C$ values of seagrasses and marine macroalgae from various locations.

Plants	$\delta^{15}N$	$\delta^{13}C$
Seagrasses		
Thalassodendron ciliatum (Australia)	+3.5	−9.3
Syringodium isoetifolium (Australia)	+5.0	−4.0
Thalassia testudinum (Nicaragua)	+3.5	−13.2
Halodule wrightii (Texas)	+3.9	−10.3
Ruppia maritima (Texas)	+3.6	−7.9
Halophila engelmannii (Texas)	+3.8	−7.9
Thalassia testudinum (Texas)	+3.9	−8.9
Thalassia testudinum (Jamaica)	+4.3	−11.1
	$\bar{x} = 3.9 \pm 0.5$	−9.1 ± 2.7
Marine Macroalgae		
Ulva fasciata (Texas)	+8.1	−14.6
Ulva lactuca (Texas)	+8.1	−14.6
Gelidium crinale (Texas)	+7.9	−14.3
Ascophyllum nodosum (Maine)	+8.0	−16.9
Fucus vesiculosis (Maine)	+8.1	−16.5
Acetabularia kilnori (Australia)	+6.5	−9.5
	$\bar{x} = 7.8 \pm 0.6$	−14.4 ± 2.6

Macko (1981) cited in Fry *et al.* (1987).

to season and water depth, with grazing having a stronger effect in the winter or in seagrass beds at greater depths. Thus, repeating experiments in environments with differing physical conditions and in different seasons is critical in order to determine the effects of blade loss and seagrass bed maintenance.

Few studies have been carried out on predation within seagrass beds since the reviews by Orth *et al.* (1984) and Zieman and Zieman (1989). Based on feeding and caging studies, predation, especially by pinfish and pink shrimp, is probably a major biological interaction influencing invertebrate community structure (Virnstein 1987). In a study in St. Joseph Bay, increased biomass of a mussel (*Modiolus americanus*) in *T. testudinum* beds resulted in greater abundance, biomass, and annual production of other invertebrates (Valentine and Heck 1993).

TROPHIC DYNAMICS

The ultimate fate of plant biomass is mineralization to simple inorganic compounds, with a portion of seagrass leaf decomposition occurring while it is still attached to the plant. Nevertheless, most biomass decomposition occurs on and in the sediment of seagrass meadows (Hemminga and Duarte 2000).

A long-term study (419 days) in Laguna Madre, Texas of *H. wrightii* senescent blades suspended in the water column revealed that decomposition resulted in a loss of 36% of the organic matter within the first 24 days (Opsahl and Benner 1993). By the end of the study, decomposition had resulted in a 76% loss of the organic matter. Neutral sugars were the most abundant in the starting material and also the most rapidly lost. In contrast, the most persistent sugars in the senescent blades were xylose and glucose, reflecting the more stable polymers of cellulose and xylan from which the sugars are derived. Near St. Croix, at depths between 14 and 32 m, the decomposition rates of a more delicate seagrass, *H. decipiens,* differed between litter bags that were buried in the sediment and those tethered at the surface of the sediment (Kenworthy *et al.* 1989). After 6.5 days, buried leaves lost 56% of the original ash-free dry weight compared to only 28% lost by those left on the surface. These findings were similar to two 7-day studies made in two consecutive years that included photosynthetic measurements in the same area and using the same species (Josselyn *et al.* 1986), this earlier

Table 4.6 δ^{34}S values for sulfur sources and plants, Redfish Bay, Texas, November 1980–February 1981 (from Fry, 1981).

Sources	δ^{34}S
Seawater Sulfate	+19.7 to +20.0
Sediment Sulfide	−23.4
Porewater Sulfate	+15.0 to +17.0
Rain Sulfate	+6.3[a]

	Leaves			Roots	
	Total	After Washing		Total	After Washing
Algae, Submerged Plants					
Digenia simplex	+18.7	+17.2			
Gracilaria verrucosa	+18.6				
Gracilaria debilis	+18.9	+17.5			
Thalassia epiphytes[b]	+17.4	+15.2			
Seagrasses, Submerged Plants					
Thalassia testudinum					
Sample 1 (November 29)[c]	+15.2			−12.3	−15.9
Sample 2 (November 29)	+12.9[d]				
Sample 3 (January 3)		6.9[d]			−17.3
Halodule wrightii	+10.4			−9.3	
Syringodium filiforme[c]	+11.5			−3.3	
Halophila engelmannii	+11.2			+11.5	
Intertidal, Emergent Plants					
Spartina alterniflora[e]	+3.5			−9.4	
Avicennia germinans[e] (as *A. nitida*)	−0.2			−3.2	

[a]From Jensen and Nakai (1961).
[b]Epiphytic community collected after freeze drying. Contained some small animals and mud.
[c,e]Plants marked with the same letter were growing intertwined in the same sediments.
[d]Epiphyte-free seagrass.

study reporting greater than 50% decomposition of all buried seagrass material.

Seagrass epiphytes appear to be a more significant source of direct food for many invertebrates than are seagrass detritus or living tissue. Virnstein (1987) has proposed the following sequence for a south Florida seagrass food web: (1) the important primary producers are epiphytic algae, which have rapid turnover rates; (2) epiphytic algae are preferentially grazed by most species of small invertebrates associated with seagrass blades; (3) small invertebrates are preyed upon by decapod crustaceans or small fishes that include resident adults and juvenile seasonal visitors; and (4) decapods and small fishes are preyed on by larger, mostly nonresident fishes. Of the 154 grazers listed by McRoy and Helfferich (1980) that directly feed on seagrass blades, the most important invertebrates are echinoderms, molluscs, and crustaceans. For

example, seagrass blades constitute up to 50% of the total diet for crustaceans (Klumpp *et al.* 1989). Crabs, isopods, and sea urchins are the principal direct grazers on seagrasses, whereas other invertebrates consume seagrass detritus and various algal epiphytes. Fry and Parker (1979) and Fry (1984), using stable carbon isotopes (δ^{13}C), showed that microalgae on the sediment and seagrass blades are a major source of carbon for grazers. In some seagrass meadows, micro- and macroalgae predominate in food webs (Virnstein 1987). In a review of stable-isotope studies, Fry *et al.* (1987) concluded that algae are nutritionally more important for consumers than are seagrasses but that δ^{13}C data alone can be misleading because benthic algae have values similar to those of seagrasses. Thus, they recommended using other elements with stable isotopes, including nitrogen and sulfur (Tables 4.5 and 4.6).

RELATIONSHIPS with OTHER COMMUNITIES

Because seagrass beds are mostly found in areas of low wave energy, they often occur next to tidal-flat, salt-marsh, and mangrove communities along Florida's Gulf coast and are influenced by these intertidal communities. Salt marshes are estimated to cover about 170,000 ha (419,900 acres) of Florida's coasts; about half of the marsh area extends from Tampa Bay north to the Alabama border on the Gulf coast (Montague and Wiegert 1990). The estimated salt-marsh area is substantially less than the estimate of McNulty *et al.* (1972) of 214,000 ha (528,580 acres) for the Gulf coast of Florida. The largest salt marshes on the Gulf coast of Florida are in the Big Bend area, from Aripeka to Apalachicola Bay, a coast with low wave energy and extensive seagrass beds. About 60% of northwest Florida salt marshes are monotypic stands of *Juncus roemerianus* Scheele (Needle Rush), which often extend down to 0.2 to 0.5 m above MLW and thus are adjacent to near-shore seagrass beds. Above-ground primary production ranges from 250 to 950 g dry wt m^{-2} yr^{-1} for *J. roemerianus* and 130 to 700 g dry wt m^{-2} yr^{-1} for *Spartina alterniflora* Loisel. (Smooth Cordgrass). (Montague and Wiegert 1990), the difference probably due to the higher density of *J. roemerianus* culms. The large biomass of salt-marsh plants and low direct consumption by herbivores (10%) means that most of the biomass decomposes and becomes part of the salt-marsh detritus (Montague *et al.* 1987). Apparently little of the detritus is exported to near-shore seagrass beds because of the relatively high elevation of Florida's salt marshes and often the presence of a berm that retains the detritus within the salt marsh (Montague *et al.* 1987).

In contrast to the low level of detrital export, a diverse fauna is shared between salt marshes and adjacent seagrass beds, for example, mullet, spot, blue crabs, oysters, and penaeid shrimps (Montague and Wiegert 1990). In addition, tarpon (*Megalops atlanticus*), snook (*Centropomus undecimalis*), red drum (*Sciaenops ocellatus*), seatrout (*Cynoscion* spp.), and kingfish (*Menticirrhus* spp.) move from near-shore seagrass beds into salt-marsh tidal streams (Lewis *et al.* 1985b).

The three Caribbean mangrove species, *Rhizophora mangle* L. (Red Mangrove), *Avicennia germinans* (L.) L. (Black Mangrove), and *Laguncularia racemosa* (L.) C. F. Gaertn. (White Mangrove) are estimated to cover 189,725 ha (468,620 acres) along Florida's coasts (Lewis *et al.* 1985b). About 90% of mangrove forests (or mangals) occur in the most southern four counties of Florida (Lee: 14,275 ha, Collier: 29,126 ha, Monroe: 94,810 ha; Dade: 32,931 ha), a region of low wave energy and consequently abundant seagrass beds. Because of the lack of severe freezing temperatures since 1989, mangroves extend intermittently northward of Tampa Bay to the western panhandle on the Gulf coast and north to the Tomoka River on the Atlantic coast (Odum and McIvor 1990; D. Crewz *pers. obs.*). Export of mangrove-leaf detritus is highest in riverine (1.2–2.7 g carbon m^{-2} d^{-1}) and fringing forests (0.5–0.7 g carbon m^{-2} d^{-1}), and these contribute to detrital-based food webs in near-shore seagrass beds (Odum and McIvor 1990). Stable carbon isotope levels (δ^{13}C) of seagrass blades and mollusk shells taken from seagrass beds near south Florida mangrove forests had significantly lower mean values (–12.8 and –2.3 ppt, respectively) than did blades and shells far from the coastal forests (–8.3 and +0.6). The lower δ^{13}C values near mangrove forests indicate release of carbon dioxide by mangrove-detritus mineralization, conversion to bicarbonate, and subsequent uptake of bicarbonate by the adjacent seagrass beds (Lin *et al.* 1991).

The habitat values of mangals, adjacent seagrass beds, and nonvegetated open water were compared for densities of fish, shrimp, and crabs in Rookery Bay near Naples (Sheridan 1992). Fish densities were highest in nonvegetated areas (74% of the total caught), while shrimp and crab densities were highest in seagrass beds (74% and 47% of the total capture respectively). However, flooded *R. mangle* forests had resident and transient fish and crab numbers equal to those of other areas on some occasions. The data suggest that seagrass beds are a principal habitat for shrimp and crabs, whereas mangrove prop roots and pneumatophores may serve an ancillary role for a variety of fish and invertebrates, contrary to the conclusion drawn in earlier studies (*e.g.,* Thayer *et al.* 1978, 1987).

South Florida's shallow-water coral reefs are unique in North America. Florida's reefs are simi-

lar in species composition and physiographic features to those in the Caribbean Sea and Bahama Islands (Dawes 1998a). Occasionally, hard corals occur as far north as Jupiter Island on the Atlantic coast (27°N lat.). Coral reefs form extensive three-dimensional structures south and west of Cape Florida and along the Florida Keys archipelago (Jaap and Hallock 1990). Seagrass beds cover 80% of the sea bottom between Cape Sable and throughout Florida Bay, along the Florida Keys, extending westward to the Dry Tortugas, and north on the Atlantic coast into Biscayne Bay, thus co-occurring with the Florida reef tract (Jaap and Hallock 1990). Aerial photography of Biscayne National Park showed that moderately dense to highly dense seagrass beds covered 25,445 ha (62,849 acres) of the 55,000 ha (135,850 acres) in the park (Lewis *et al.* 2002) and were closely associated with coral patch reefs.

The relationship of seagrass beds to patch and tract reefs is considered to be in danger due to nutrient-rich runoff from canals in Biscayne Bay (Lewis *et al.* 2002) and from septic tanks in the Florida Keys (Jaap and Hallock 1990). A key feature of coral-reef dependence on adjacent seagrass beds is their sensitivity to nutrient enrichment, which enhances macroalgae overgrowth on the coral structures (Dawes 1998a). Thus, nutrient removal from the water column by adjacent seagrass beds may play a major role in protecting coral reefs. In addition, the ecological role of seagrasses as habitat and nursery in the life cycle of the spiny lobster (*Panulirus argus*), whose juveniles settle in algae associated with seagrass beds, has been noted (Marx and Herrnkind 1985).

Seagrass detritus and vegetative parts are exported into deep-water habitats, especially on the Atlantic coast. Deep water (>200 m) is farther offshore on the Gulf coast of Florida than along the Atlantic, but seagrass beds are more developed in the Gulf. The larger-stature seagrass species extend to about 9 m (Dawes 1974; Iverson and Bittaker 1986). In contrast, the smaller-stature *Halophila engelmannii* grows in 1–5 m in Tampa Bay (Dawes 1967), in 1.4 m off Tarpon Springs (Phillips 1960b), and to 73 m off the Gulf coast (Dawes and van Breedveld 1969; Dawes and Lawrence 1990) and the Dry Tortugas (Taylor 1928). The more diminutive *H. decipiens* appears to be limited to deep water on the Gulf coast and occurs in 20 to 90 m (Dawes and van Breedveld 1969; Zieman 1982; Dawes and Lawrence 1990; Fonseca *et al.* 2001; see also Chapter 4). In the summer and early fall on the Gulf coast, *H. decipiens* often forms extensive beds in 20–30 m of water (Dawes and Lawrence 1990). However, no information currently exists regarding the export or role of detritus from inshore seagrass beds to the 200-m deep continental shelf west of Florida (Florida Institute of Oceanography 1994).

Natural and ANTHROPOGENIC EFFECTS

⤷ Seagrass regression and die-off observed in Florida Bay in the late 1980s resulted from a combination of natural and human causes, including overproduction of seagrasses that resulted in dense shoots; anoxia that increased sediment sulfide levels; nutrient inputs that caused algal blooms, reducing light levels; lack of freshwater inputs that resulted in hypersalinity; and infection by *Labyrinthula,* a pathogen of *Thalassia testudinum.*

⤷ The relationship between *Labyrinthula* infection and die-off of *T. testudinum* is not clear, as the pathogen has been found in a number of Florida Gulf-coast estuaries in seagrass beds that have not experienced die-off.

⤷ Storms appear to have little direct impact on most seagrass communities, except for erosion and deposition of sediment in some areas, as found following Hurricane Andrew.

⤷ The 1997–1998 *El Niño* event caused a general die-back of seagrass communities because of low salinities and increased nutrient loads and turbidity from runoff.

⤷ The importance of long-shore sand bars is not adequately understood, but they may protect seagrass beds from waves and erosion in some locations.

⤷ Mechanical damage to seagrass beds continues, with propeller scarring being common in shallow-water communities.

⤷ The effects of small-scale seagrass-bed damage on local animal populations is not adequately understood; for example, moderately scarred beds show little change in shrimp and pinfish densities.

⤷ Nutrient pollution continues to be a serious problem, with 8 of the 15 Florida Gulf-coast estuaries regarded as being eutrophic.

⤷ Nutrient enrichment from natural or human sources results in increased phytoplankton density and resultant chlorophyll levels, reduction in light penetration, increased seagrass loss, increased epiphytism, increased sediment hypoxia, and shifts in seagrass species dominance.

⤷ The effects of sediment contaminants on seagrass communities are not clear. The highest contaminant levels of metals and pesticides are associated with fine muds, limited PAR, and low salinities.

Stargrass, *Halophila engelmannii*
Ron Phillips photo

*M*any studies, including those by resource management programs of the National Estuary Programs for Tampa Bay, Sarasota Bay, and Charlotte Harbor and by the National Estuarine Research Reserves at Apalachicola and Rookery bays, have emphasized the importance of Florida's Gulf-coast seagrass communities. Understanding of natural- and human-induced seagrass disturbances has increased substantially, as shown in a review by Durako (1988), Short and Wyllie-Echeverria (1996) and Duarte (2002). Since 1989, many publications have examined the condition of seagrass communities on Florida's Gulf coast. These include studies of the north-central Gulf coast (Mattson 1995, 2000), Tampa Bay (Lewis *et al.* 1991, 1998; Johansson and Ries 1997; Kurz *et al.* 1999; Pribble *et al.* 1999; Greening 2002a; Johansson 2002a), and Sarasota Bay, Lemon Bay, and Charlotte Harbor (Kurz *et al.* 1999; Staugler and Ott 2000; Tomasko *et al.* 2001). Declines in seagrass coverage in various estuaries on the Gulf coast (including Florida Bay) have often been attributed to interactions between natural and anthropogenic factors.

In Florida Bay, *T. testudinum* die-off was noted in late 1987 by Robblee *et al.* (1991) and has been studied by many others since then (Carlson *et al.* 1994; Durako 1994; Durako and Kuss 1994; Thayer *et al.* 1994; Carlson and Yarbro 2001; Fourqurean and Robblee 1999; Hall *et al.* 1999; Zieman *et al.* 1999). Often, natural processes can result in increased damage to seagrass beds if they had been previously stressed by anthropogenic impacts, as appears to have happened regarding the seagrass die-off in Florida Bay. Despite the acknowledged interactions of natural and anthropogenic influences in these and many other systems, however, these categories are addressed separately below.

NATURAL PROCESSES

Natural processes have biological and nonbiological sources and include such influences as storms, sea urchin population increases, phytoplankton blooms, and macroalgae overgrowth. Such sources can cause direct or indirect damage that include shading, overgrazing, or disease.

Although moderate grazing is common and may even affect seagrass communities positively, overgrazing by urchins, and to a lesser extent by manatees or sea turtles, can result in complete denudation in some areas. For example, overgrazing by *Lytechinus variegatus* (purple sea urchin) resulted in severe seagrass denudation near the Pepperfish Keys (Camp *et al.* 1973) and in outer Florida Bay (Maciá and Lirman 1999; Rose *et al.* 1999).

As summarized in Chapter 4, epiphytes on seagrass blades have both positive and negative effects, with most damage being linked to shading and reductions in photosynthesis. In Tampa Bay, shading by epiphytes of *T. testudinum* blades is an important controlling factor in its depth distribution (Dixon and Leverone 1997).

High levels of drift algal biomass suppress seagrass-bed expansion and, similar to seagrass epiphytism, are usually linked to nutrient enrichment. In Hillsborough Bay, Avery (2000) reported in a 10-year study (1986–1994) that the 18 species of dominant drift algae (see Table 4.6 and Chapter 4) declined from an average biomass of 930 to 80 g dry wt m^{-2} and continued to decline through 1997. In contrast, due to reductions of water-column nutrients in Hillsborough Bay, *H. wrightii* beds expanded from 0.2 ha to 40 ha (Avery 2000). On the positive side, drift and epiphytic algae probably serve as nutrient sinks and as food for a variety of invertebrates and fish (Kharlamenko *et al.* 2001; Moncreiff and Sullivan 2001).

The decline in the past 20 years of seagrass communities in Florida Bay is a conspicuous example of the effects of natural and possibly human influences on seagrass populations on the Gulf coast. In 1987, vast areas of *T. testudinum* began dying rapidly. Short-shoot densities dropped by 22% and standing crop by 28% at 107 sampling stations (Figure 5.1) between 1984 and 1994 (Hall *et al.* 1999). Losses were highest in western Florida Bay in areas with high standing crops. Similar or greater declines in standing crops were evident for *H. wrightii* (92%) and *S. filiforme* (93%) between 1984 and 1994. Hall *et al.* (1999) suggested that the most likely cause was chronic light reduction due to increased water turbidity.

A pathogen, *Labyrinthula,* was also suggested as being involved in the die-off of *T. testudinum* in Florida Bay (Porter and Muehlstein 1989; Robblee *et al.* 1991). It is similar to one that was implicated in the wasting disease of *Z. marina* over the past 50 years in the Atlantic (Burdick *et al.* 1993). Porter
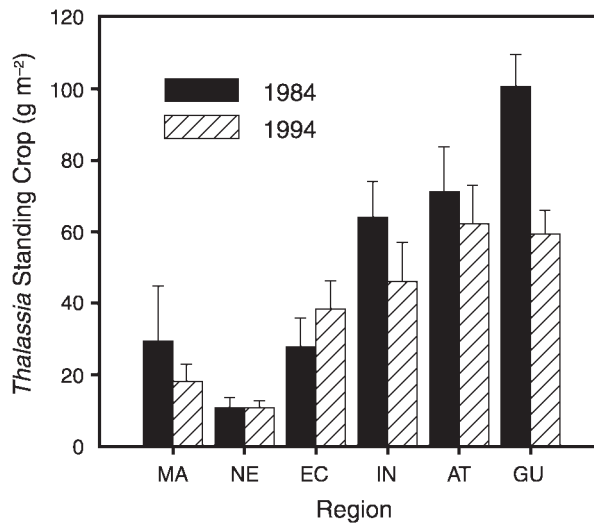
Fig 5.1 *Standing crop (±SD) of* Thalassia testudinum *in six ecological regions of Florida Bay 1984 and 1994 (Hall* et al. *1999). MA = Mainland, NE = Northeast, EC = East Central, IN = Interior, AT = Atlantic, GU = Gulf.*

and Muehlstein (1989) reported the presence of an undescribed species of *Labyrinthula* in blackened, necrotic lesions on the leaves of *T. testudinum* collected in seagrass die-off areas of Florida Bay. Durako and Kuss (1994) found that photosynthesis in necrotic lesions on *T. testudium* blades was impaired. They suggested that this may have reduced oxygen available for transport via the blade lacunae to belowground organs, resulting in increased sediment hypoxia and leading to sulfide toxicity. The pathogen has also been found to be infecting from 0% to 100% of *T. testudinum* blades in at least 10 sites on the Gulf coast (Figure 5.2) from the Chandeleur Islands (LA) to Florida Bay (Blakesley *et al.* 2002). The authors found that 60% to 90% of the sites sampled in Tampa Bay had infected short shoots of *T. testudinum.*

Thayer *et al.* (1994) ascribed the die-off in Florida Bay to "as yet unknown environmental stresses." Studies now suggest that the die-off arises from a combination of human-derived and natural factors that may collectively stress *T. testudinum* and thereby enhance infectivity by the pathogen (Blakesley *et al.* 2002). The factors involved include hypersalinity (Fourqurean and Robblee 1999); persistent microalgal and cyanobacterial blooms and resuspended sediments that reduced illumination (Hall *et al.* 1999); anoxia that increased levels of sediment sulfide (Carlson *et al.* 1994, 2002; Carlson and Yarbro 2001); and enhanced growth that resulted in high biomass (Zieman *et al.* 1999).

Hypersaline areas of Florida Bay probably resulted in part from a lack of flushing in the absence of periodic hurricanes. This condition may also be exacerbated by a reduction in freshwater flow from the Everglades because of surface-water diversion. Nevertheless, data covering 1989–1995 suggest that seagrasses were once again growing rapidly in Florida Bay and that the loss of *T. testudinum* appeared to be slowing (Zieman *et al.* 1999).

Little information is available regarding the effects of storms on Florida's Gulf-coast seagrass communities, except for that following Hurricane Andrew, which swept across southern Florida on August 24, 1992, and exited into Florida Bay at Lostmans River (Ogden 1992; Dawes *et al.* 1995). Although coastal mangrove forests were destroyed, seagrass beds in Lostmans Bay showed no signs of alteration or depletion of the meiofauna when sampled two and nine months after the storm (Dawes *et al.* 1995). To be sure, during hurricanes large volumes of water fall simultaneously upon broad landscapes, leaching large amounts of nutrients and other compounds from soils. Together with the lowering of salinities, this short-term pulse of pollutants may alter community dynamics in seagrass beds.

Also, excessive rainfall over an extended period can damage seagrass communities. An *El Niño* event between December 1997 and March 1998 resulted in over 52 cm (approximately 20 inches) of rain, which triggered widespread, persistent phytoplankton blooms, decreasing the light available to seagrasses, along the Gulf coast of Florida (Carlson *et al.* 2003). In 1997, 1998, and 1999, sampling near the Homosassa and Anclote rivers and in Tampa Bay and Charlotte Harbor found that short-shoot densities, blade widths and numbers, leaf-area indices, rhizome-apex densities, and stored carbohydrates of *T. testudinum* declined (Carlson *et al.* 2003) in response to the 1997–1998 *El Niño.*

Long-shore sand bars often occur seaward of seagrass communities and have been suggested to play a role in protecting seagrasses from strong waves and currents (Lewis 2002). Thus, reductions in seagrass coverage in some areas of Tampa Bay may reflect historical loss of these bars, similar to those in North Carolina (Fonseca and Bell 1998). In this regard to this idea, Fonseca *et al.* (2002) employed a wave-exposure model (Relative Expo-
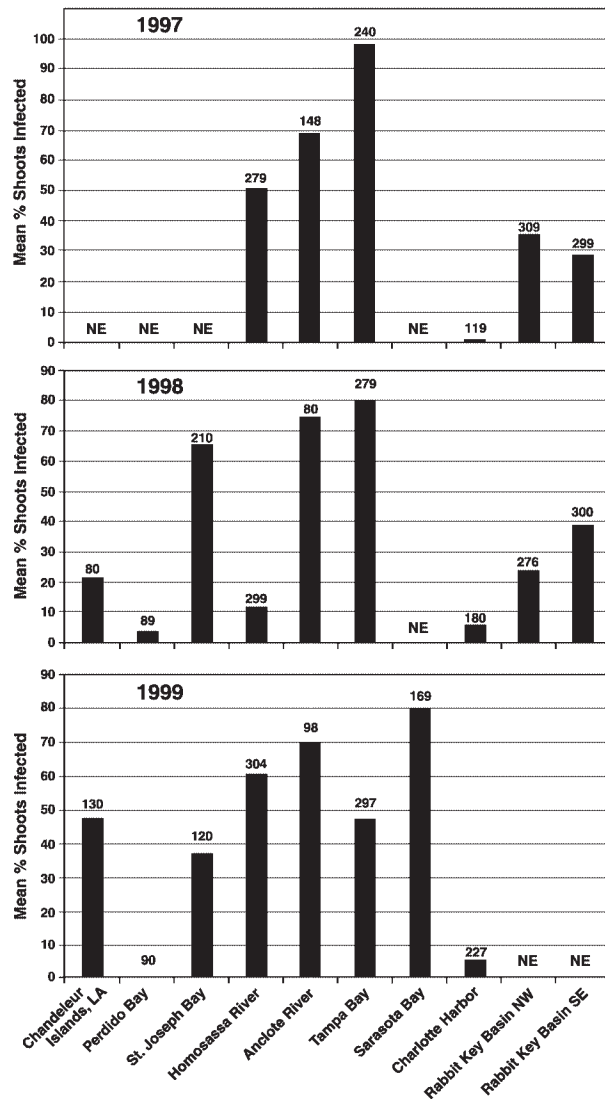
Figure 5.2 *Mean percentage of* Thalassia testudinum *short-shoots infected with a pathogenic species of* Labyrinthula *at ten sites along the Gulf coast. Numbers over bars are sample sizes. NE = not examined. (modified from Blakesley* et al. *2002).*

(human-derived) effects on seagrass meadows (Table also presented in Zieman and Zieman 1989), including direct physical damage and pollution, with an emphasis on nutrient enrichment. Since that review, various studies have described anthropogenic effects and also include estimates of seagrass losses (see Chapter 4). Nutrification and sediment loading from maintenance dredging of shipping channels and vessel-generated resuspension are cited as important causes of seagrass declines (Schoellhamer 1991; Tomasko and Lapointe 1991; Culter and Leverone 1993; Quammen and Onuf 1993; Lapointe *et al.* 1994). Dredging, although now generally restricted, continues in all estuaries on the Gulf coast to maintain channels and create new harbors. Certainly, such activities cause temporary resuspension of contaminated sediments and contribute to reduction of water transparency (Godcharles 1971; Schoellhamer 1991; Ailstock *et al.* 2002).

Mechanical damage is also done to seagrass beds by erosive effects following boat (and ship) groundings, by propeller wash, and by ship and boat wakes in shallow waters. Kenworthy *et al.* (1988a) found that boat wakes substantially increased bottom shear stress along edges of shallow seagrass beds. Even though nets used for bait-shrimp trawling in Tampa Bay do not appear to cause much direct damage to seagrass beds (Meyer *et al.* 1999) a large diversity of animals are killed as by-catch, plus trawling may suspend sediments which decreases water clarity.

Propeller scarring is another type of physical damage to seagrass beds (Figures 5.3, 5.4) that continues to increase in all areas of coastal Florida (Sargent *et al.* 1995). Many shallow flats and mud banks are now severely eroded due to constant scarring, ship groundings, chronic wave action from boats, and water-current scouring (Kruer 1994). Culter and Leverone (1993) stated that prop scarring was visible in almost all seagrass beds in Sarasota Bay. Sargent *et al.* (1995) determined that 6.2% (over 70,000 ha or 183,000 acres) of Florida's 1.1 million ha (2.7 million acres) of seagrass beds have been scarred by boat propellers (prop-dredging, prop cuts) and by similar causes, principally in coastal waters less than 2 m deep. They concluded that scarring in seagrass beds has become acute because of increasing human population densities, increasing popularies of boating, fish-

sure Index—REI) to evaluate the influence of long-shore sandbars on seagrass coverage in Tampa Bay. Their results hindcasted that erosion or loss of long-shore sand bars on the southeastern shore of the bay, where wave exposure is relatively high, had caused the loss of seagrass originally located between the shore and the historical sand bars. They recommended that no restoration efforts be conducted in areas of strong wave exposure without including engineering to reduce REIs.
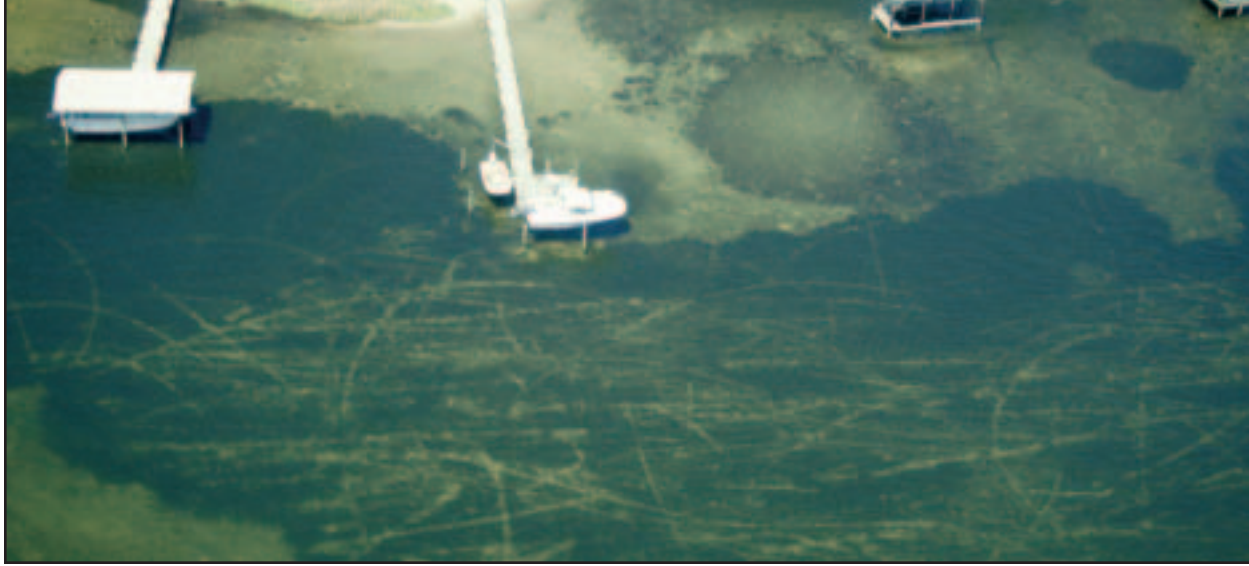
ANTHROPOGENIC EFFECTS

Livingston (1987) summarized anthropogenic

Figure 5.3 *Propeller scarring from recreational boating in a* Thalassia testudinum *bed near Panama City, Florida.*

ing, diving, and other water sports, and increasing tourism. Scarring level was divided among three categories: 1) light scarring, in which less than 5% of the seagrasses in a particular map polygon were scarred; 2) moderate scarring, in which 5% to 20% of the seagrasses within the polygon were scarred; and 3) severe scarring, in which more than 20% of the seagrasses in the polygon were scarred (Sargent *et al.* 1995). The highest level of scarring was found in Monroe and Citrus counties, which also contained the highest amount of seagrass coverage (688,259 ha; 1.6 million acres). Of this total, they calculated that 23,332 ha (57,630 acres) were scarred with 17.3% of the seagrasses being in Monroe County and 15.8% in Citrus County.

The influences of prop scars on seagrass community production have been studied in Tampa Bay and Charlotte Harbor (Durako *et al.* 1992; Clark 1995; Dawes *et al.* 1997; Bell *et al.* 2002), Sarasota Bay (Folit and Morris 1992), and the Florida Keys (Matthews *et al.* 1991). Fragmentation of seagrass beds in Tampa Bay due to propeller cuts did not appear to have any consistent effects on some animal populations over a one-year period, as long as seagrass patch sizes were greater than 1 m^2 (Bell *et al.* 2002). The numbers of pinfish (*L. rhomboides*), pipefish (*Syngnathus scovelli*), and eight species of epibenthic shrimp were similar in moderately scarred (6% to 31% loss of the beds) and nonscarred seagrass beds in Tampa Bay. The results of these studies suggest that propeller scars that fragment seagrass beds may enhance certain faunal development caused by edge effects along the cuts as long as they are not too severe. Nevertheless, a recent study of scarring in a *T. testudinum* bed in Puerto Rico revealed a negative effect of scarring on crabs and molluscs

up to 5 m from the scar. Also, shrimp species within the scar differed from those in the non-scarred seagrasses. Fish populations did not show an effect from the scarring. Further studies are clearly needed to define the effects of moderate scarring compared to those of severe scarring on seagrass productivity.

More recent studies have confirmed previous observations by Jones (1968), Godcharles (1971), and Zieman (1976) for the long time period required for scars to heal (Eleuterius 1987; Durako *et al.* 1992; Dawes *et al.* 1997). When seagrass rhizomes and roots are completely removed by scarring, sediment is destabilized and resuspension occurs, thereby lowering water transparency and retarding seagrass regrowth into the scar. Regrowth of *T. testudinum* into prop scars in Tampa Bay was estimated to require an average of 3.5 to 4.1 years for existing propeller scars and up to 7.6 years in newly made ones (Dawes *et al.* 1997). Shorter recovery periods in existing scars probably reflect their older ages and shallower depths. Based on studies at Weedon Island (Durako *et al.* 1992) and Cockroach Bay (Dawes *et al.* 1997) in Tampa Bay, the authors recommended that shallow-water seagrass beds be protected from propeller scaring. Criteria for the protection of seagrass beds have been proposed and adopted for Tampa Bay (Clark 1995; Stowers *et al.* 2002).

Another source of physical impacts that degrade seagrass communities is docks, which shade seagrass beds, as shown in Perdido Bay (Shafer 1999), Charlotte Harbor (Loflin 1995), and the Indian River Lagoon (Beal and Schmit 2000). Smith and Mezich (1999) surveyed 200 out of the 3,592 permit-exempt single- and multi-family docks that were deemed to have the potential to

FWC–FWRI photo

Figure 5.4 *Propeller scarring from commercial fishing in a seagrass bed in Pine Island Sound, Florida.*

damage seagrass beds in Palm Beach County. They found that 16% of the docks were larger than regulations allowed, owing to additions, and that approximately 1,491 single-family docks in the county had affected seagrass negatively. They estimated that, in total, docks eliminated 20.4 ha (50.4 acres) of seagrass beds, which is equal to 2.1% of the seagrass extents in Palm Beach County. Their recommendations were that all docks in Florida be considered within the jurisdiction of FDEP permitting programs. Currently, environmental resource permits are not required within designated Aquatic Preserves if the docks are less than 46.5 m² (500 ft²) or if they are less than 92.9 m² (1,000 ft.²) when outside Aquatic Preserves. Smith (1998) concluded that strong enforcement of the regulations protecting sovereign submerged lands (253.04–05, 380.05, F.S. and Chapter 18-14, F.A.C.) would act as a powerful deterrent against boat and dock damage to seagrass systems.

Direct physical damage of seagrasses can result from changes in freshwater inputs. The importance to watershed management and reduction of freshwater removal from tributaries flowing into Gulf-coast estuaries has been reviewed for Tampa Bay (Zarbock 1991) and for Charlotte Harbor (Kurz *et al.* 1999). Estevez (2000) found that changes in the amount, timing, and location of freshwater inflow are primary stressors to estuarine and oceanic seagrass communities, with salinity changes often being a first-order stressor (Montague and Ley 1993). The present estimated daily freshwater inflows into Tampa Bay (Zarbock 1991) range from 152.0 to 214.6 m³ s⁻¹ (1,792 to 2,530 ft³ s⁻¹) compared to historical estimates of 193.4 m³ s⁻¹ (2,280 ft³ s⁻¹). Although timing and duration of riverine inflow, along with nutrient

loading and changes in water color, clearly affect seagrass communities in Charlotte Harbor, the relationships between these factors is more complex in Tampa Bay and Sarasota Bay (Kurz *et al.* 1999). Similarly, diversion of fresh water before it enters the Everglades, coupled with a decrease in hurricane-induced flushing (Thayer *et al.* 1994) and rising salinities and sediment anoxia (Zieman *et al.* 1999), has been proposed as influencing factors in the precipitous decline of Florida Bay seagrasses.

Short and Neckles (1999) hypothesized that global warming will probably influence seagrass distribution by causing increases in sea level, in storm frequency and intensity, in disease from higher water temperatures, and in turbidity from eutrophication. The authors also predicted an increase in ultraviolet radiation that will damage seagrasses, as has been shown for macroalgae (Larkum and Wood 1993) and terrestrial plants (Caldwell *et al.* 1989). In addition, the shallow coastal and estuarine waters and low elevations on the Gulf coast of Florida will certainly be affected by any eustatic sea-level rise. A potential positive effect on seagrass distribution may occur from an increase in dissolved inorganic carbon (C_i) composition in seawater, as seagrasses are presently CO_2 limited and have an affinity for C_i (Beer and Koch 1996).

Nutrient enrichment, probably the most common human effect in Gulf-coast estuaries, can result in a variety of changes in seagrass communities. A number of these changes have been presented in Chapter 4. These include an increase in water-column chlorophyll levels (Johansson 1991; Janicki *et al.* 1999; Tomasko *et al.* 1996, 2001; Morrison *et al.* 1997), in algal epiphytism and shading

of seagrass blades (Tomasko and Lapointe 1991; Tomasko *et al.* 1996; Dixon 2002), in shifts in dominant seagrass species (Duarte 1995; Fourqurean *et al.* 1995), and in sediment hypoxia (Carlson *et al.* 2002).

A review of U.S. estuaries (Bricker *et al.* 1999) cited 15 estuaries on the Gulf coast of Florida that had various levels of eutrophic conditions. Eight of these estuaries (Florida Bay, the southern Ten Thousand Islands, Caloosahatchee River, Charlotte Harbor, Sarasota Bay, Tampa Bay, Choctawhatchee Bay, and Perdido Bay) had high levels of eutrophic symptoms. More detailed data are available regarding nutrient loadings and damage to seagrasses in Tampa Bay (Treat and Clark 1991; Zarbock *et al.* 1994, 1996; Treat 1997; Lewis *et al.* 1998; Pribble *et al.* 1999; Greening 2002b), Sarasota Bay (Haddad 1989; Tomasko *et al.* 1992, 1996), and Lemon Bay (Tomasko *et al.* 2001). Tampa Bay has been the subject of several reviews (Treat and Clark 1991; Treat 1997; Greening 2002a) that include data regarding point- and nonpoint-source pollution, domestic and industrial effluents, accumulation of toxic substances in the sediment, and potential brine damage from desalination facilities.

Many studies worldwide support the contention that seagrass distribution, survival, and growth are principally determined by water clarity (Batiuk *et al.* 1992; Dennison *et al.* 1993; Duarte 1991; Kenworthy and Haunert 1991; Kenworthy 1993; Koch and Beer 1996; Morris and Tomasko 1993; and Tomasko *et al.* 2001; also individual papers contained in the publications of Bortone 2000 and Greening 2002a). However, other factors such as waves and water currents can affect seagrass distribution as well (Koch 2001; see Chapter 2). Water clarity is influenced by nutrient inputs, which stimulate the growth of phytoplankton (particularly by nitrogen), and by total dissolved and suspended solids. An overabundance of nutrients leads to eutrophication that supports increased levels of phytoplankton, drift algae biomass, and coverage by epiphytes on seagrass blades, all of which result in shading of seagrass leaves (Sand-Jensen 1977, 1990; Cambridge *et al.* 1986). In all cases a decrease in water clarity over seagrass beds was correlated with a decline in seagrass standing stock (Orth and Moore 1983; Short *et al.* 1996; Short and Wyllie-Echeverria 1996; Fitz-patrick and Kirkman 1995; Lewis *et al.* 1985a).
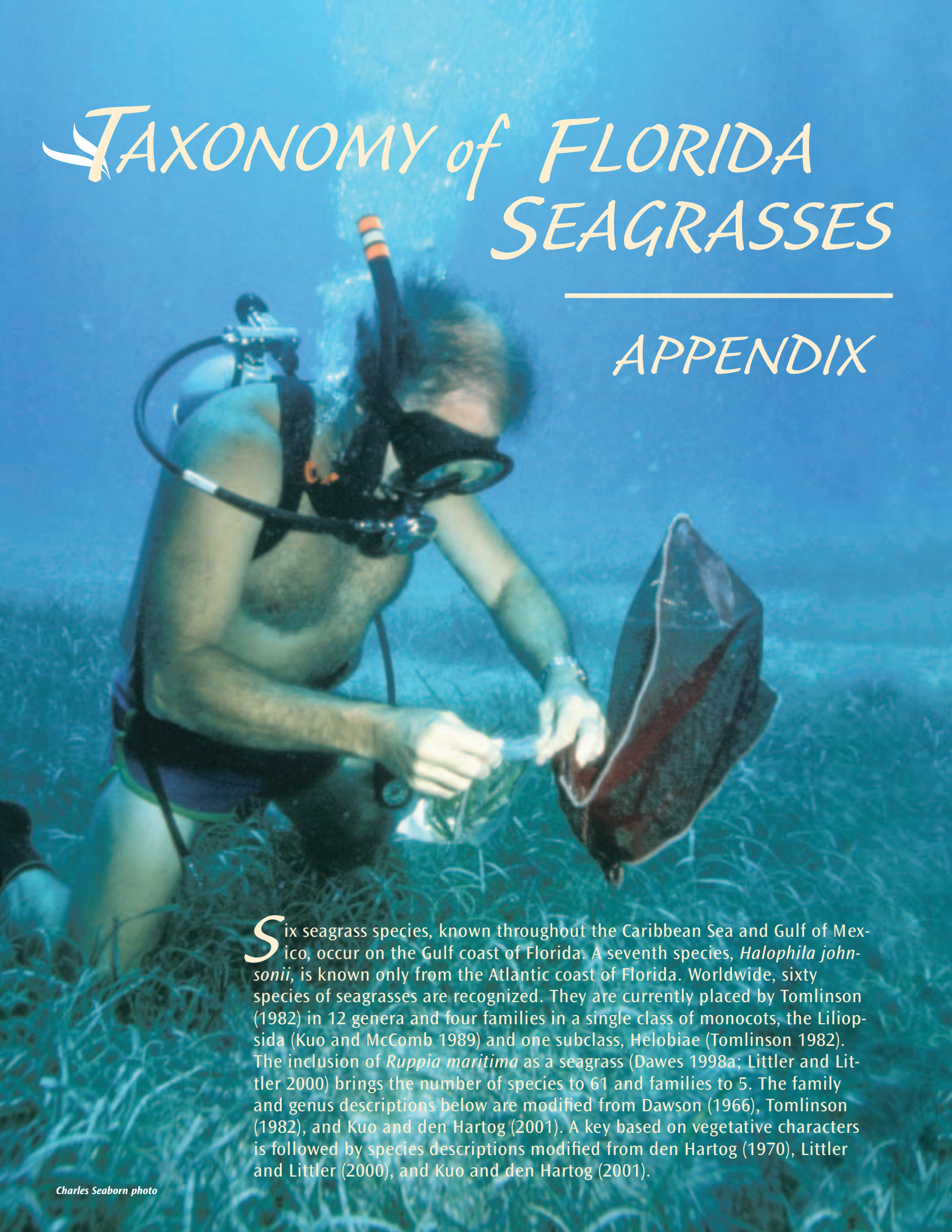
The influence of possible sediment contaminants on seagrass beds is not understood. The concentration of metals, nutrients, petroleum, chlorinated hydrocarbons, and radionuclides correlate with the smaller particle-size sediments (muds; <63μm in diam.) in Tampa Bay (Brooks and Doyle 1991) and with sediment-quality factors (Zarbock *et al.* 1997). Thus, concentrations of all contaminants are highest in west-central Hillsborough Bay and Old Tampa Bay (Brooks and Doyle 1991) for total organic matter (to 16%), total hydrocarbons (>40 μg g^{-1}), total organic nitrogen (0.1%), and total phosphorus (0.4%). Using the triad method of weighting sediment chemistry, toxicity, and benthic samples, Zarbock *et al.* (1997) determined that upper and middle Hillsborough Bay, parts of Old Tampa Bay, Boca Ciega Bay, and western Middle Tampa Bay had the most contaminated sediments. In a review of sediment quality in Tampa Bay, Grabe (1999) found that approximately 1% of its sediments were subnominal and had a high probability of being toxic. However, at the levels known for Tampa Bay, evidence that the heavy metals and pesticides directly affect seagrasses does not exist.

In conclusion, it is apparent that a mix of natural and human-induced events has negatively influenced the seagrass meadows on the Gulf coast of Florida. Because of limited historical data, determining the extent of seagrass decline is often difficult, although detailed historical analyses are possible in some areas, such as for Tampa Bay (Greening 2002a). Anthropogenic influences, particularly those that result in a decline in water quality, are considered the principal causes of seagrass losses throughout the world (Short and Wyllie-Echeverria 1996) and in the estuaries of Florida's Gulf coast (Lewis *et al.* 1985a). The loss of seagrass communities continues worldwide (Duarte 2002) as well as on Florida's Gulf coast (see Chapter 2). However, restoration management can result in the expansion and enhancement of seagrass meadows, as seen in Tampa Bay and Sarasota Bay (Greening 2002b). Future studies are needed to distinguish secondary and primary stressors that result in seagrass declines, such as the modification of watershed-level stormwater runoff and direct nutrient input.

Taxonomy of Florida Seagrasses

APPENDIX

*S*ix seagrass species, known throughout the Caribbean Sea and Gulf of Mexico, occur on the Gulf coast of Florida. A seventh species, *Halophila johnsonii,* is known only from the Atlantic coast of Florida. Worldwide, sixty species of seagrasses are recognized. They are currently placed by Tomlinson (1982) in 12 genera and four families in a single class of monocots, the Liliopsida (Kuo and McComb 1989) and one subclass, Helobiae (Tomlinson 1982). The inclusion of *Ruppia maritima* as a seagrass (Dawes 1998a; Littler and Littler 2000) brings the number of species to 61 and families to 5. The family and genus descriptions below are modified from Dawson (1966), Tomlinson (1982), and Kuo and den Hartog (2001). A key based on vegetative characters is followed by species descriptions modified from den Hartog (1970), Littler and Littler (2000), and Kuo and den Hartog (2001).

ARTIFICIAL KEY to SPECIES, BASED on VEGETATIVE FEATURES

(see also Florida Department of Environmental Protection: http://www.fiu.edu/~seagrass/key/seagrasskey.html)

1. Leaf blades cylindrical; terete in cross section . . . .*Syringodium filiforme.*
1. Leaf blades flat . . . . .2.

2. Leaves paddle-shaped, associated with scale-like leaves . . . . .3.
2. Leaves strap-like or linear . . . . .5.

3. Leaves in a pseudo-whorl; each shoot with 2 scales at the base and 2 scales halfway up the shoot . . . .
. . . .*Halophila engelmannii.*
3. Leaves paired, with 2 scales at their base . . . . .4.

4. Leaves linear-elliptical, margins entire . . . .*Halophila johnsonii.*
4. Leaves oblong to elliptical, margins minutely serrate . . . .*Halophila decipiens.*

5. Leaves greater than 3 mm wide; rhizomes scaley . . . .*Thalassia testudinum.*
5. Leaves usually less than 3 mm wide . . . . .6.

6. Leaf tips blunt with dentate points; rhizomes usually straight . . . .*Halodule wrightii.*
6. Leaf tips with fine points; rhizomes often in a zig-zag pattern . . . .*Ruppia maritima.*

HYDROCHARITACEAE *Jussieu*

Family of 15 genera, diverse and cosmopolitan, of which 3 are seagrasses (*Enhalus, Halophila, Thalassia*). Plants aquatic herbs, leaves either large, linear to strap-shaped and with sheathing base (*Thalassia*) or small, usually nonlinear, with distinct petiole and without sheathing base (*Halophila*). Rhizomes with scale-like leaves, and branching via apical bifurcation. Flowers unisexual and anthers either sessile or on long slender filaments. Female flowers usually with long hypanthium and inferior ovary. Fruits fleshy and often indehiscent.

***THALASSIA* Banks and Solander ex König.** 1805. Ann. Bot. (König *et* Sims) 2: 96 (Gr. *thalassa:* marine, of the sea).

Rhizomes creeping, horizontal, thick, fleshy, and indeterminate; bearing scale leaves and erect short-shoots (rhizomes) at irregular intervals that arise from rhizome meristem. Erect short shoots determinate, encased in leaf sheaths, producing foliate leaves and flowers. Roots unbranched, fleshy, arising at nodes of short shoots. Leaves strap-shaped, with sheathing bases, and growing from basal meristem. Short shoots with conspicuous leaf and inflorescence scars. Plants are dioecious. Male flowers on short stalks, in clusters of 1–3. Female flowers solitary. Fruits globose and opening by irregular splitting, containing several large angular "seeds" (seedlings).

***Thalassia testudinum* Banks and Solander *ex* König.** 1805. Ann. Bot. (König *et* Sims) 2: 96 (L. *testudinis:* a tortoise). Common name: Turtlegrass (Figure A.1.4).

Rhizomes creeping, 3–6 mm in diameter, 4–7 mm long between nodes, with scale leaves. Roots single, unbranched, arising at short-shoot nodes, producing delicate root hairs at tips. Erect short shoots with clusters of 3–7 leaves; leaves to 2 cm wide, with persistent colorless basal sheath, 9–17 parallel veins, and lacunae that are continuous throughout the plant. Plants dioecious. Flowers on short peduncles, with single whorl of white tepals. Male flowers with 3 to 12 stamens, pollen grains in mucilage, forming moniliform chains. Female flowers bearing one ovary with 6–8 carpels; style divided into 2 filiform stigmata. Fruits buoyant, 15–20 mm long, rough, fleshy, tips pointed, with one to few "seeds" (seedlings).

***HALOPHILA* Du Petit-Thouars.** 1806. Nova Madag. 2 (L. *halo:* salt + *philus:* loving).

Rhizomes horizontal, usually on surface and bearing two scales at each node, producing a lateral shoot and one unbranched root, short erect shoots either with paired leaves on long petioles, distichously arranged along the axes, or in a pseudo-whorl at top of shoot. Leaves oval, ellipti-

cal, lanceolate or linear, with mid and marginal veins. Plants monoecious or dioecious. Flowers covered by 2 bracts; sepals small, petals absent. Male flowers stalked, with 3 stamens having sessile anthers. Female flowers sessile, with 3–6 styles. Fruits ovoid capsules, bearing many seeds.

Halophila decipiens **Ostenfeld.** 1902. Bot. Tildsskr. 24: 260 (L. *decipio:* beguiling, deceptive). Common name: Paddlegrass (Figure A.1.1).

Rhizomes thin, with transparent, hairy scales, internodes 1.0–4.5 cm long. Petioles 3–15 mm long, bearing one pair of leaves; leaves oblong to elliptical, 10–25 mm long, 3–6 mm wide, with short rigid unicellular hairs on one or both sides of blades, margins finely serrate. Plants monoecious, male and female flowers on same stalk, covered by spathe, stalks to 1.5 mm long. Male flowers with 2 anthers to 1 mm long. Female flowers with 3 styles 1.5–2.5 mm long; single ovary to 1 mm long. Fruits 2.5 mm long, 1.5 mm wide, elliptical, bearing up to 30 seeds; seeds oval, to 0.2 mm long.

Halophila engelmannii **Ascherson in Neumayer.** 1875. Anl. Wiss. Beobeibet Reiser. p. 368 (Named for George Engelmann [1809–1885], an American physician and German botanist who settled in St. Louis). Common name: Stargrass (Figure A.1.3).

Rhizomes indeterminate, narrow, with internodes 2–4 cm long. Determinate, erect shoots 20–40 mm tall at each node. Leaves with petioles, 2 scales at base and another pair half-way up shoot, petioles to 2 mm long, bearing 2–4 pairs of leaves in pseudo-whorls. Blades oblong to linear-oblong, 10–30 mm long, 3–6 mm wide, tips pointed and margins serrate. Plants dioecious. Male flowers with 3 imbricate tepals and 3 stamens. Female flowers with one sessile, inferior ovary, ovaries 3–4 mm long, ovoid, with 1–3 styles; styles to 30 mm long. Fruit globose, fleshy capsule, 3–4 mm in diam. with several minute subspherical seeds.

Halophila johnsonii **Eiseman.** 1980. In Eiseman and McMillan, Aquatic Bot. 9: 16 (Named for J. Seward Johnson, cofounder of Harbor Branch Oceanographic Institute, where N. Eiseman studied). Common Name: Johnson's Seagrass. (Figure A.1.2).

Rhizomes thin, 1 mm in diam., nodes bearing scale leaves on upper and lower surfaces, internodes 1–2 cm long. Petioles 10–20 mm long, bear-

ing pair of linear to spatulate leaves; leaves slightly asymmetrical, 5–25 mm long, 1–4 mm wide, margins entire and surfaces glabrous. Plants dioecious (?), only female plants found. Female flowers sessile, with three styles 4–6 mm long; seeds unknown. occurring only in Atlantic Florida (Sebastian Inlet to Biscayne Bay) and classified as a threatened species. May not be distinct from *H. ovalis* (R. Brown) J.D. Hooker *f.*, 1858.

CYMODOCEACEAE N. Taylor

Family of 5 morphologically distinct genera and about 20 species, all seagrasses. Plants perennial herbs. Rhizomes creeping, leafy, herbaceous or distinctly woody, scale-bearing. Leaves distichous with distinct sheath and blade; blades linear, flat or terete, leaves with numerous tannin cells. Plants dioecious. Flowers solitary or in cymose inflorescences and usually terminal. Male flowers subsessile or stalked with 2 anthers producing filiform pollen. Female flowers with 2 free carpels, each with 1 style. Fruits 1-seeded nuts, indehiscent.

HALODULE **Endlicher.** 1841. Gen. 1368 (L. *halo:* salt + *dule:* loving).

Rhizomes monopodially branched; each node producing one to several unbranched roots and erect short shoot with 1–4 leaves. Leaves narrow, linear, with 3 longitudinal veins and short basal sheaths. Plants are dioecious. Flowers solitary, terminal, enclosed by leaf. Male flowers stalked, with 2 anthers. Female flowers with 2 free carpels, with long undivided styles. Fruits oval to slightly flattened, with a stony pericarp.

Halodule wrightii **Ascherson.** 1868. Bot. Zeitung (Berlin) 26: 511 (Named for Charles Wright [1811–1885], who collected extensively in the southwest U.S. and Cuba and sent specimens to Ascherson). Common names: Shoalgrass, Cuban Shoalgrass, or Shoalweed (Figure A.2.3).

Rhizomes slender, bearing 2–4 roots and a short shoot at each node; internodes 0.75–3.5 cm long, with elliptic scale leaves 5–10 mm long. Leaf sheaths 1.5–6.0 cm long; blades 5–12 (–20) cm long, 0.50–1.5 (–2.0) mm wide, with 3 parallel veins; blade tips with 2–3 short horn-like points. Plants are dioecious. Flowers lack tepals; male flowers on peduncles 1.5–2.0 cm long, anthers slender, 3.5–5.0 mm long. Female flowers with one

oval to elliptic ovary, 1.5–2 mm wide, with 10–28 mm long style. Fruits about 1.5–2.0 mm in diam. with stony pericarp and stylar beak.

SYRINGODIUM Kützing. 1860. In Hohenacker, Alg. Marin. Sicc. 9: 426 (Gr. *Syringx:* a tube + *odium:* similar to; thus like *Syringa,* a genus of flowering plants).

Rhizomes indeterminate, with monopodial branching and scale leaves; each node bearing 1–3 branching roots and erect, unbranched, determinate short shoot. Short shoots producing 2–3 cylindrical leaves with basal sheaths. Plants dioecious. Flowers in erect cymose infloresences; male flowers stalked, with 2 anthers. Female flowers with 2 free carpels, each with short style. Fruits with stony, smooth pericarp.

Syringodium filiforme Kützing. 1860. In Hohenacker, Alg. Marin. Sicc. 9: 426 (L. *filiforme:* long and thin). Common name: Manateegrass (Figure A.2.2).

Rhizomes 2–4 mm in diameter, nodes bearing 2–4 roots with abundant root hairs, scale leaves, and erect short shoot. Short shoots with 2–3 leaves; leaves to 30 cm long, 1–2 mm in diam., cylindrical, with extensive basal sheathing, cylindrical. Plants dioecious. Male flowers on short peduncles, with 2 anthers. Female flowers sessile, with leaf sheath and 2 free carpels. Fruits oval to oblique, to 6 mm long, 3–5 mm in diam.

RUPPIACEAE Hutchins

Family of one genus and 2–3 species, all seagrasses, closely related to the Potomogetonaceae. Plants glabrous, submerged perennial herbs found in alkaline lakes and brackish to oceanic waters. Rhizomes creeping and little differentiated from erect axes, with monopodial branching. Leaves opposite or alternate, narrowly linear, with single medial vein and short basal sheath. Plants monoecious. Flowers perfect, on spikes subtended by 2 subopposite involucral leaves with slightly inflated sheaths; two flowers per spike, each with 2 stamens and few to 4 carpels with short, stout to finely attenuate styles and peltate stigmas. Fruits indehiscent achenes, the outer layers soft, decaying and inner pericarp stony.

RUPPIA Linnaeus. 1753. Species Plantarum, p. 127 (Named for Heinrich Reinhard Ruppius [1688–1719], a German botanist who wrote the Flora of Jena).

Genus with characters of the family.

Ruppia maritima Linnaeus. 1753. Species Plantarum, p. 127 (L. *maritima:* of the ocean, marine). Common names: Ditchgrass; Widgeongrass (Figure A.2.1).

Rhizomes thin, 1–3 mm in diameter, profusely branched, with growth forms; often geniculate. Leaves produced at nodes, sheath 6–10 mm long. Reproductive axes on erect stalks 60–90 cm long. Leaves to 1 dm long, 0.3 mm wide, 1 veined, with pointed tips and appearing to arise directly from rhizome. Plants monoecious. Flowers on short (>6 cm) peduncles elongating after anthesis, becoming loosely coiled spiral. Flowers with 2 sessile anthers 2-celled, elliptical, 0.6–0.7 mm long; carpels oval, to 2 mm long, style short and stout to attenuate. Fruitlets (nutlets) 2–3 mm long, on short stipe, often curved.
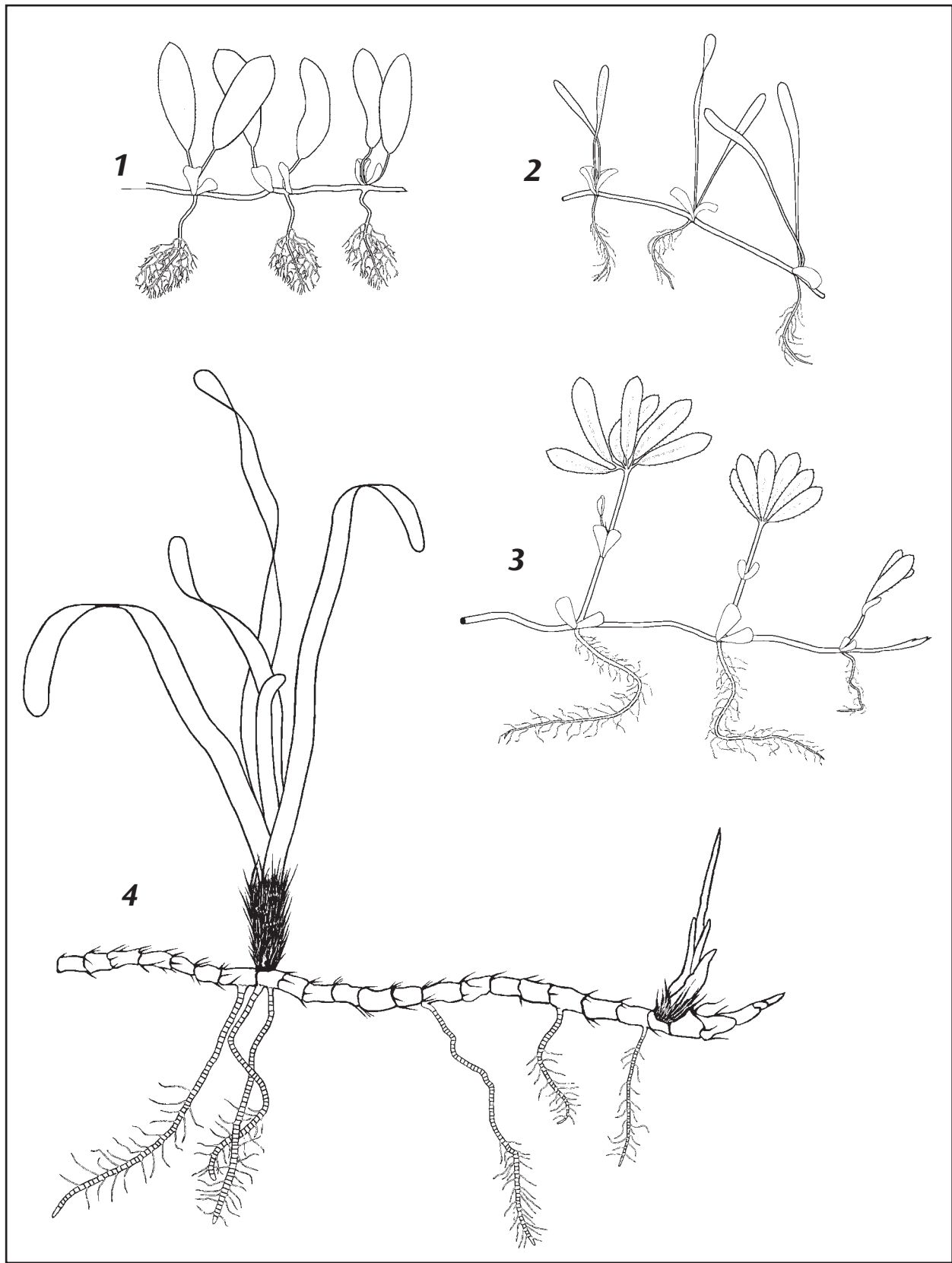
Figure A.1 *HYDROCHARITACEAE: **1** Halophila decipiens, *Paddlegrass (× 2⁄3); **2** H. johnsonii, *Johnson's Seagrass (× 3⁄4); **3** H. engelmannii, *Stargrass (× 3⁄4); **4** Thalassia testudinum, *Turtlegrass (× 1⁄3). Scale approximate. Smaller phenotypes are common.*

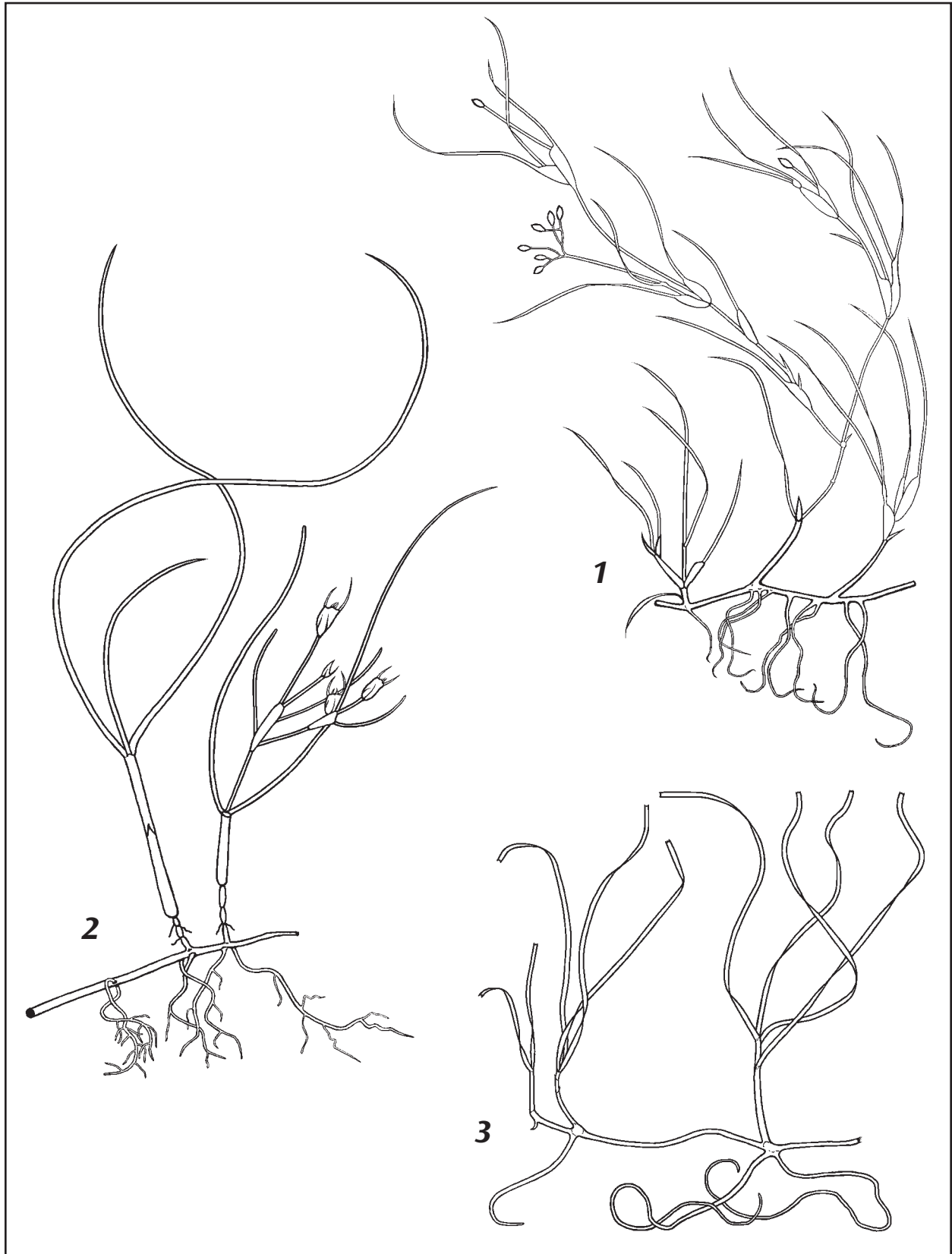**Figure A.2** *RUPPIACEAE: 1* Ruppia maritima, *Widgeongrass (× ¼). CYMODOCEACEAE: 2* Syringodium filiforme; *Manateegrass (× ¼); 3* Halodule wrightii, *Shoalgrass (× ¹⁄₃). Scale approximate. Smaller phenotypes are common.*

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