Seagrass Ecology

What are the causes and mechanisms for the observed changes in seagrass community of Florida Bay? What is the effect of changing salinity, light and nutrient regimes on these communities?

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About this report

This report draws its material directly from syntheses compiled for the 2001 Florida Bay Science Conference. The Florida Bay Science Program organizes itself around five central research questions. Topical teams associated with each question consist of modelers and researchers working in the Bay and adjacent marine systems. These teams compiled the original synthesis documents.

In preparation for the 2003 Florida Bay Science Conference, the research teams have modified the existing synthesis documents to bring them up to date and implement a more uniform, common format. In some cases, entirely new documents have been drafted, such as the information here on ecosystem history and on nutrient dynamics. The present report compiles these separate documents into one and provides the reader with summary material as a guide to the contents.

Team Leaders:
Michael Durako (University of North Carolina at Wilmington), Joseph Zieman (University of Virginia), Michael Robblee (USGS, PMC)

Contributors:

Editor:
William Nuttle (consultant)

Introduction

Seagrass beds are an important component in many coastal marine environments; however, there are few locations in the world where seagrasses are as dominant in the hydroscape as south Florida (Fourqurean et al., 2001). Seagrasses are the dominant biological community in Florida Bay, historically covering over 90% of the 180,000 ha of subtidal mudbanks and basins within the Bay (Zieman et al. 1989). By comparison, mangrove islands cover only about 7% of Florida Bay. Because of the shallow nature of Florida Bay, (mean depth < 2 m, Schomer and Drew 1982), seagrasses are also the dominant physical feature of the Bay, and their presence greatly affects physical, chemical, geological as well as biological processes in this system (Zieman, 1982). Seagrass communities are also important to the economy of south Florida because they provide food and shelter to numerous fish and invertebrate species, many of commercial importance within the region (Powell et al. 1989; Thayer and Chester 1989; Tilmant 1989; Chester and Thayer 1990).

In addition, the waters of western Florida Bay form a hydrodynamic link between the Everglades and the coastal waters of the southwestern Florida peninsula/eastern Gulf of Mexico, to the north, and the Florida Keys reef tract and the Atlantic Ocean to the south (Schomer and Drew 1982). The seagrass communities of this region form an important buffer by intercepting the flow of water along this region and reducing nutrient and particulate loads in the waters reaching the reef tract (Kenworthy et al. 1998). Continued losses of seagrasses along this margin, coupled with the proposed increase in water flows out of the Everglades could result in greater fluxes of material out of Florida Bay and onto the reef tract (Kenworthy et al. 1998). Resource managers will need to consider actions that might aid in the reestablishment of continuous seagrass cover along western Florida Bay. This would be an important step in reducing sediment-resuspension induced turbidity along this boundary that could reverse the cascading declines that characterize the present system.

Seagrasses act as integrators of *net* changes in water quality variables which tend to exhibit rapid and wide fluctuations when measured directly. The shallow distribution of seagrasses places them in close proximity to the land/sea interface, a region experiencing rapid growth of human populations. This coastal distribution also places seagrass communities at the end of the watershed pipe, thus, their status reflects not only direct coastal influences, but larger, landscape-to-regional scale influences as well. Because most seagrasses are benthic-perennial plants, they are continuously subject to stresses and disturbances that are associated with changes in water quality along the land/sea interface. Seagrass abundance to a large extent determines public perception regarding the “health” of the coastal waters of Florida (Goerte 1994; Boesch et al. 1995). Thus, the recent changes in the distribution and abundance of seagrasses within Florida Bay have been perceived as a change in the health of the Bay. For these reasons, seagrasses may be the best indicators of changes in the Florida Bay ecosystem (Fourqurean et al, 1992.).

Although the initial die-off initiated in the interior basins of the Bay (Robblee et al. 1991), the greatest changes in seagrass abundance in the present system are occurring far from the Everglades/Florida Bay land/sea interface (Durako et al. 2001). The spatial patterns of abundance changes from 1995-2000 suggest that, presently, the most perturbed environment in Florida Bay with respect to seagrasses is along the western and southern Bay margins. Much of the focus of management and restoration efforts in South Florida have been directed toward landscape-scale modifications to an extensive flood-control system to increase the quantity of freshwater delivered to northeast Florida Bay, and more recently, Shark River slough.

Seagrass Communities in Florida Bay

Seagrasses continue to be the dominant biological community in Florida Bay. Of the more than 14,000 Braun-Blanquet samples (0.25 m^2) taken in the Bay from 1995 to 2000 by the Fish Habitat Assessment Program (FHAP, Durako et al. 2001), approximately 97% contained seagrass. In northeastern Florida Bay, *Thalassia* was present at 75.9% and *Halodule* was present at 69.0% of the 762 randomly selected stations sampled from May 1999 to May 2000 (Bacon et al.). The entire South Florida coastal zone, including the areas west of Florida Bay and within the Florida Keys National Marine Sanctuary, is dominated by seagrass habitats. Fourqurean et al. (2001) assessed seagrass species composition and density at 1207 sites distributed across 19,402 km^2 of nearshore marine and estuarine environments in south Florida. At these sites, a total of 8434 quadrats (0.25 m^2) were sampled from 1996 to 1998, covering an area of 2108.5 m^2. At least one species of seagrass was observed at 1056 of the 1207 sites, or 87.5 percent of all sampling sites. *Thalassia testudinum* (Turtle Grass) was the most commonly encountered species, being found at 898 sites. *Halodule wrightii* (Shoal Grass) was the second most commonly encountered species, occurring at 459 sites; followed by *Syringodium filiforme* (Manatee Grass, 239 sites), *Halophila decipiens* (Paddle Grass, 96 sites), *Ruppia maritima* (Widgeon Grass, 41 sites) and *Halophila engelmannii* (Star Grass, 28 sites).

Recent and Historical Changes

A widespread die-off of seagrasses within Florida Bay began in 1987 (Robblee *et al.*, 1991, Table 7.1). This event was first observed by backcountry fishing guides who reported the occurrence of “potholes” in the seagrass beds of the bights along the north-central part of Florida Bay. Extensive areas of *Thalassia* began dying rapidly in central and western basins, and by 1990, 4,000 ha were completely lost and 24,000 ha were affected by the die-off (Robblee *et al.*, 1991).

The patterns of changes in seagrass abundance in Florida Bay have recently undergone four phases: 1) primary die-off, 2) secondary mortality, with mortality primarily due to light attenuation, 3) seagrass recovery associated with improving water clarity, and 4) renewed primary die-off in areas where die-off has not been previously observed. The initial phase of primary seagrass dieoff occurred only in Florida Bay, which is the most continentally influenced and least oceanically flushed of all of the extensive south Florida seagrass beds, and it occurred only in the most densely developed beds within the bay. To this day, no occurrence of primary seagrass dieoff has been found outside of the densest seagrasses within Florida Bay, and no primary seagrass dieoff occurred in sparse or medium density beds within the bay.

Table 7.1: Chronology of seagrass dieoff in Florida Bay and related research

Florida Bay Seagrass Die-off Milestones

Event or Observation	Month Year	Significant Publication or Research Program Initiated (Study funding source and Title)
SPOT image shows no die-off patch in Rabbit Key Basin. No die-off observable in Johnson Key Basin or Rankin Lake.	February 2, 1987	
"Potholes" observed in *Thalassia* beds in Rankin Lake and near Cross Bank by Backcountry fishing guides	Summer 1987	Jones SERP water quality monitoring - (Boyer/Fourqurean - later)
Tagged conch observed to die in Hawk Channel due to heat stress, Carl Berg - FMRI; coral bleaching predicted and observed at Looe Key, Billy Causey; fish dying on Cross Bank – Jeff Holmquist, Robblee.	July, 1987	
Robblee observed die-off patches along north shore of Johnson Key.	November, December 1987	
Guides contact Susan Bell (USF) regarding dying seagrasses	March 1988	
Guides meet Mike Robblee and Jim Tilmant at Little Rabbit Key and observe rotting rhizomes and extensive die-off. The eastern Rabbit Key Basin die-off patch.	April 1988	
	April 1988	Everglades National Park consults with Jay Zieman. Robblee and Zieman visit Rankin Lake and Johnson Key Basin.
	May 1988	Zieman provides Everglades NP a trip report discussing die-off indicating its uniqueness and stressing need to monitor and conduct research.
	May 1988	Carlson/Durako survey Johnson Key Basin
Zieman observes that lesions were not apparent (Johnson and Rankin?)	Late Spring and Summer 1988	
Robblee and Jeff Holmquist observe extensive and persistent phytoplankton bloom (no sediment) in area NE of Long Key, approximate area of Sprigger Bank, Pontoon Bank to Old Dan Bank. The bloom persisted weeks at a time.	Late Spring, Summer 1988?	
SPOT imagery shows large die-off patch in Rabbit Key Basin	June 1988	

	September 1988	Robblee provides Superintendent Finley with memo summarizing seagrass die-off as understood at that time. On this basis Finley provides funds to gather researchers to evaluate die-off
	November 1988	NPS sponsors field trip to Florida Bay. Robblee, Carlson, Durako, Fourqurean, Muehlstein, Porter, and Zieman visit die-off areas. Porter/Meuhlstein – *Labyrinthula* detected - assoc with die-off areas
	April 1989	Durako - initiates studies on morphometric changes, Braun-Blanquet abundance, and demography. Carlson - initiates studies on hypoxia/sulfide - ADH, ethylene, H2S, conducts bucket experiments. (Everglades National Park: Evaluation of seagrass die-off in Florida Bay) (United States Fish and Wildlife Service -Florida marine animal health and contamination assessment - Study III. Studies on seagrass die-back in Florida Bay) (Office of Coastal Zone Management: Investigations on the causes, extent, and characteristics of a seagrass die-back in Everglades National Park/Florida Bay, CM-257 & CM-283)
	June 1989	Zieman completes version 1 of his conceptual model of seagrass die-off.
	June 1989	Zieman - initiates long-term *Thalassia* productivity measurements near four core die-off areas.
	May 1989	Robblee initiates studies of seagrass associated animal responses to seagrass die-off in Rankin Lake, Johnson and Rabbit Key basins. Monitoring of plant community response to *Thalassia* die-off was initiated.
	July 1990	Thayer et al. - investigate responses of plant communities to die-off in Johnson and Rabbit Key basins
Earliest observation of persistent turbidity caused by tidally resuspended sediments observed in Johnson Key Basin. Kuss, DiDomenico, Robblee observers.	April 1991	
	April 1991	Robblee et al. 1991- Marine Ecology Progress Series 71:297-299. First published observations of the die-off: clear, warm, hypersaline conditions
Early conceptual models of die-off developed- Zieman, Carlson-Durako	Fall 1991	Durako/Kuss - *Labyrinthula* effects on *Thalassia* photosynthesis. (Everglades National Park: Photosynthetic capacity as a correlate of Thalassia testudinum die-back in Florida Bay, CA5280-1-9008)
1990-91 colonization of many die-off patches by Halodule		

Initiation of algal blooms - cyanobacteria (*Synecoccus* sp. in Rabbit Key basin)	November 1991	
Hurricane Andrew passes over south Florida. Andrew has little direct impact on Florida Bay.	August 24 1992	
High rainfall occurring the week after Andrew washed mangrove "rot" into Florida Bay. Zieman observed that this event began the severe turbidity events in the bay.	Approx. September 1, 1992	
Major turbidity plume from western Florida Bay reaches Big Pine Key.	December 22, 1992	
Widespread turbidity 91-95 - much speculation on how much seagrass loss - one report states 100,000 acres have been lost		
	April 1993	Zieman et al. - looked at light-reduction effect on *Thalassia* in Rabbit Key basin and Sunset Cove. (Environmental Protection Agency: Effects of chronic light reduction on *Thalassia)*
	October 1993	Hefty et al. - DERM initiates seagrass monitoring of northeastern basins in response to Taylor Slough and C-111 concerns (South Florida Water Management District: C-11/Taylor Slough Water Quality and Biological Monitoring)
	June 1994	Hall and Durako - 107 stations previously sampled in 1983/84 are resampled for decadal comparison of seagrass abundance. (Florida Department of Environmental Protection, Pollution Recovery Trust Fund: Biological Resource Assessment of Florida Bay, Study 2 Macrophytes and Mangroves)
	October 1994	A series faunal studies conducted in the mid-1980's are repeated as a part of the decadal comparison program: Thayer/NMFS, Matheson and Camp/FMRI, Robblee/NBS.
	November 1994	Durako and Hall - Preliminary test of EMAP-based Braun-Blanquet sampling
Spring 1995 - very wet spring and summer – true estuarine conditions exist throughout Florida Bay	April 1995	Durako and Hall - Fish Habitat Assessment Program (FHAP) initiated. Landsberg and Blakesley - *Labyrinthula* spatial and temporal dynamics. (US Geological Survey: Fisheries Habitat Assessment Program - Florida Bay)
	October 1995	Montague - initiates field studies along northern Florida Bay starts construction of a mesocosm system in Key Largo to look at salinity fluctuation effects. (South Florida Water Management District: Responses of submersed macrophytes to fresh water inflow to Florida Bay)

Halophila engelmannii first observed in Johnson Key basin - suggests a shade adapted community	October 1996	
	August 1997	Stumpf - Examines satellite imagery to detect changes in seagrass abundance from 1986-1997 (USGS South Florida Ecosystem Program NOAA Coastal Ocean Program)
Rudnick - Conceptual model of Florida Bay ecosystems	1997	
95-99 Tt loss in turbid west gains in middle – overall small changes; Hw up 400% in JKB, up 200% baywide.		
97-99 – Water clarity improves - Tt, Hw, and He all generally increasing		
	October 1997	Carlson and Blakesley - Banktop die-off studies initiated
	November 1997	Fourqurean et al.- Sample two areas in Rabbit Key basin to examine scale-based variability in potential *Thalassia* ecoindicators. (Environmental Protection Agency: Multiscale Assessment of the Population Status of Thalassia testudinum: A New Approach to Ecosystem Assessment)
Flowering in *Thalassia* and *Halodule* widespread (the latter is unprecedented) - Let the good times role	May 1998	
Hurricane Georges passes west of Florida Bay	September 25, 1998	
Barnes Key eastern bank and basin had no die-off, extremely dense *Thalassia*, crystal clear water. "Classic" die-off patches present on the bank edge east of Big Rabbit Key.	October 1998	
		Koch - Sulfide phytotoxicity studies on *Thalassia*
New "classic" die-off observed in Barnes Key area. Also in Sunset Cove. History repeats itself	January 1999	Hall and Blakesley - Establish transects and permanent plots to monitor changes in *Thalassia* characteristics and *Labyrinthula* abundance
Die-off patches present on bank to east of Barnes Key and in basin north of key.	April 1999	
Flowering in *Thalassia* and *Halodule* observed in core samples from several stations, again.	May 1999	
Hurricane Irene passes west of Florida Bay	October 1999	
Flowering of *Thalassia* observed in field, recruiting seedlings observed in cores.	May 2000	

Primary Seagrass Dieoff

The first phase of primary seagrass dieoff occurred during the relatively dry and clear period of 1987 to early 1991. During this period density, standing crop and areal productivity of *Thalassia* were high, but then declined as die-off progressed (Durako 1995, Zieman et al. 1999). Some stations had shown large increases in seagrass standing crop in the period prior to the dieoff (Zieman et al. 1999). In addition, there was rapid spread of *Batophora oerstedi* and *Halodule* into die-off patches (Thayer et al., 1994). At this time, Florida Bay waters as a whole remained as clear as in the years just prior to the dieoff, with limited turbidity from suspended sediments in the immediate vicinity of the denuded dieoff patches.

Secondary Mortality

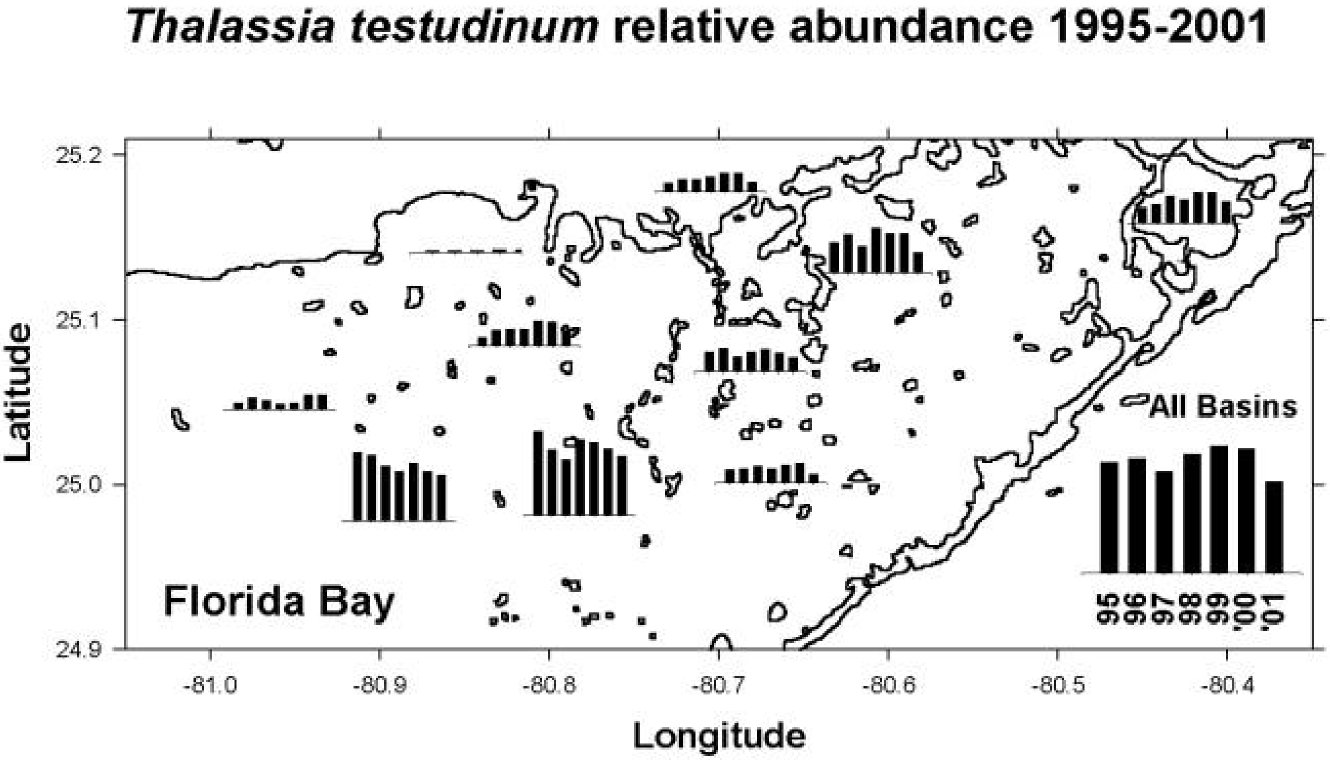
Several years after the initiation of the seagrass die-off, Florida Bay began exhibiting widespread and chronic turbidity with a concomitant decline in *Thalassia* and *Halodule* in Johnson Key Basin and Rankin Lake (Stumpf *et al.*, 1999). The increase in turbidity, which began during the fall of 1991, was principally due to cyanobacteria-dominated microalgal blooms and resuspended sediments associated with the loss of seagrasses on the western banks, and was most severe in the western and central Bay (Phlips and Badylak, 1996). The blooms may have been initiated by the nutrients liberated from the die-off of seagrasses (Butler et al. 1995). Loss of seagrass cover was the major factor in the increases in sediment resuspension in the Bay (Prager, 1998). This resulted in a negative feedback loop in which loss of seagrass cover from die-off led to exposed, easily resuspended sediments, and more, widespread loss of seagrasses due to turbidity. Sponge mortality, changes in juvenile lobster population dynamics (Butler et al. 1995) and indications of cascading effects on plant and animal communities in adjacent systems (e.g., sea urchin population explosions and unbalanced growth of *Syringodium filiforme* in the waters of the Florida Keys National Marine Sanctuary southwest of Florida Bay, Rose at al. 2000; Kenworthy et al. 1998) were also observed. From 1992 to 1995, salinities showed a progressive decline throughout the bay (Boyer et al. 1999).

During this time, there was much speculation regarding how much seagrass had been lost, with estimates as high as 100,000 acres (40,000 ha) of loss being stated with no data support. With the decline in water clarity, aerial photography became useless in determining seagrass distribution over much of Florida Bay. Because of the continuing concern regarding the extent of seagrass changes within Florida Bay, and the need to monitor the effects on seagrass communities of proposed water management alterations for the restoration of the Everglades/Florida Bay ecosystem, the Fisheries Habitat Assessment Program (FHAP) was initiated during spring 1995. The turbid conditions in western Florida Bay from 1995-1997 complicated measurements and interpretations of seagrass losses and changes in species' distributions due to primary die-off versus secondary effects attributable to light limitation. Early FHAP data (1995-1997) indicated that seagrass decline in the western basins was primarily due to deteriorated water quality because mortality was evident as a general shoot thinning, rather than the occurrence of distinct die-off patches surrounded by dense beds. A comparison of seagrass distributions in Florida Bay between 1984 and 1994 (Hall et al., 1999) and between 1995 and 1998 (Durako et al., 2001) also indicated that the chronically turbid regions had exhibited the most significant losses of *T. testudinum*.

Stabilization and Recovery

Following the initial die-off and period of widespread turbidity, seagrass abundance has shown three distinct phases (Zieman et al. 1999; Zieman et al). At stations associated with primary seagrass dieoff, standing crop declined from 1989 to 1995. It remained stable from 1995 through 1997, and has increased during the past several years (1998-2001). *Thalassia* has shown little net change in abundance (" 8% of the mean) at the Bay scale from 1995-1999 (Figure 7.1),

Figure 7.1: Changes in relative abundance, as determined by Braun-Blanquet sampling, of *Thalassia* from spring 1995 to spring 2001.



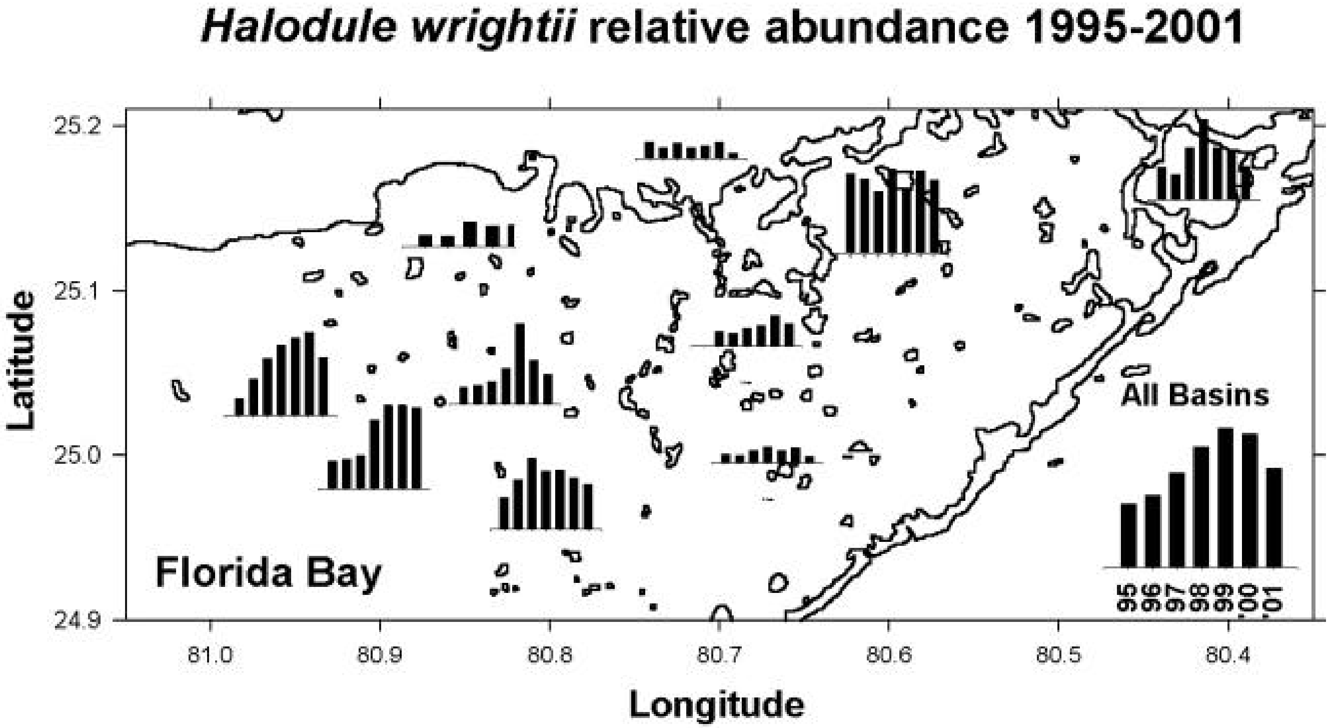
although at the basin scale abundance has varied by an average of " 30% (losses then gains in the west, contrasted with stability or gains in the middle and east basins). Most of the increase in seagrass abundance has resulted from expanding coverage by *Halodule* (Figure 7.2, + 200% Baywide, + 450% in Johnson Key and Rabbit Key Basins, Durako and Hall 2000). Thus, the dominance of *Thalassia* is declining and mixed turtlegrass and shoalgrass beds are becoming more common. In the past 5 years, relative *Thalassia* abundance has dropped from being over 5 times that of *Halodule* to being less than three times more abundant; in spring 1997 *Halodule* replaced *Thalassia* as the most abundant seagrass in Johnson Key Basin (JKB, Durako et al. 2001). During fall 1996, the small-bodied, low-light adapted seagrass *Halophila engelmannii* was observed at one station in JKB. By spring 1998 this species was present at 15 of the 32 stations in this basin.

The passage of hurricane Georges west of the Bay in Fall 1998 uprooted much of the *Halophila* in JKB (it was only observed at 5 stations nine days after the storm), reduced the cover of *Thalassia*, especially in areas where it had been sparse, and it removed much of the litter layer on the bottom. However, by spring 1999 *Halophila* cover increased in JKB and this species was observed in Rankin Lake (RAN), Whipray Basin (WHP) and Twin Key Basin (TWN). This rapid increase in spatial distribution suggests the hurricane may have played a role in distributing propagules (Durako et al. 2001). Sediments were also resuspended by Georges (longer internodes of Barnes Key SS suggests recent sediment deposition- meristems still relatively deep). Hurricane Irene also reduced cover in areas of sparse *Thalassia* and reduced *Halophila* distribution as determined by before and after sampling by FHAP.

Another recent dramatic change in the ecology of seagrasses in Florida Bay is the widespread occurrence of flowering, in both *Thalassia* and *Halodule*. In spring 1999, reproductive short-shoots of *Thalassia* were present at 19 sites in 7 basins across the Bay; reproductive short-shoots of *Halodule* were present at 24 sites in 4 basins in the western part of the Bay (Durako et al 2001). In spring 2000, flowering *Thalassia* was observed at 19 sites in 6 basins. The recent increases in seagrass cover and the dramatic increase in flowering may reflect improvements in water quality, although shifts from turtlegrass to shoalgrass often are associated with declining light availability, as is the appearance and spread of *Halophila engelmannii*.

Since 1998, there has been an upturn in abundance, productivity, standing crop, and flowering of *Thalassia* and *Halodule* that seems to be associated with improving water clarity (Durako et al. 2001, Zieman et al.). Some of this improvement in water clarity may be due to a decrease in unvegetated bottom (Durako et al. 2001). However as recovery begins to occur at the original die-off sites, a new instance of primary seagrass die-off has been observed north of Barnes Key beginning in January 1999. This new primary die-off is occurring in an area where die-off has not been previously observed, but it has some characteristics very similar to those observed during the initial seagrass die-off in 1987. The area has excessively dense beds of *T. testudinum* with die-off patches interspersed among the dense beds, and the same unusual seagrass morphologies (‘twinning’) have been observed in surviving shoots (Zieman et al). Seagrasses affected by the new die-off exhibit symptoms like those of the 1987 event, i.e. the short-shoot meristem tissue appeared to be the tissue most immediately affected. Meristems seemed mushy and smelled like “mustard” while the rest of the blade looked green and healthy (Carlson).

Figure 7.2: Changes in relative abundance, as determined by Braun-Blanquet sampling, of *Halodule* from spring 1995 to spring 2001.



Paleoecological Investigations

While not part of the seagrass research program, the paleoecological investigations add relevant information for the understanding of how recent seagrass changes fit into the matrix of historical expansion and contractions of seagrass cover. At present it appears that seagrass coverage, as estimated both by the abundance of seagrass-associated microfossils and by chemical signatures in the sediments, has shown repeated cycles of presence and absence at the core sites. Thus, the recent changes in seagrass cover apparently are not unprecedented. However, the paleoecological data come from only a few selected locations, limiting the confidence that can be placed in their general applicability. Therefore, it would be extremely valuable to have additional paleoecological information from more sites throughout the Bay.

Conceptual Models for Seagrass Dieoff

Early in the dieoff studies conceptual models were developed of hypothesized dieoff mechanisms and the conditions and processes leading up to the dieoff. Initially the model developed by Zieman, Fourqurean, and Robblee was a more process-oriented model, and placed strong emphasis on the historic conditions leading up to the dieoff. The other conceptual model was developed by Carlson and Durako and was a more mechanistic conceptual model with more emphasis on the dieoff process. These conceptual models are shown in the accompanying figures.

The Zieman et al model has three major phases, Figure 7.3. A *Developmental Phase* (A-C), where a combination of natural and anthropogenic processes contributed to an extensively developed (overdeveloped actually) *Thalassia* ecosystem. An *Initiation Phase* ((D-G) where the heavily developed system interacted with a suite of environmental stresses to produce the initial dieoff episodes, and a *Maintenance Phase* (G-L-G and repeat) where the process became self-sustaining. Here interactions of the dense *Thalassia* and the environmental stresses formed the primary trigger to the initial dieoff episodes.

The Carlson and Durako model, Figure 7.4, included over-developed *Thalassia* as a component, but focused more on the role of physiological stress, especially hypoxia and sulfide toxicity as major drivers. In addition, this model gives a much larger role to the effects of the slime mold, *Labyrinthula* as a causative element. Although both of these models have matured as research has progressed, the process has been one of small refinements, as both are little changed in the past decade.

Figure 7.3: Zieman et al. model for seagrass dieoff

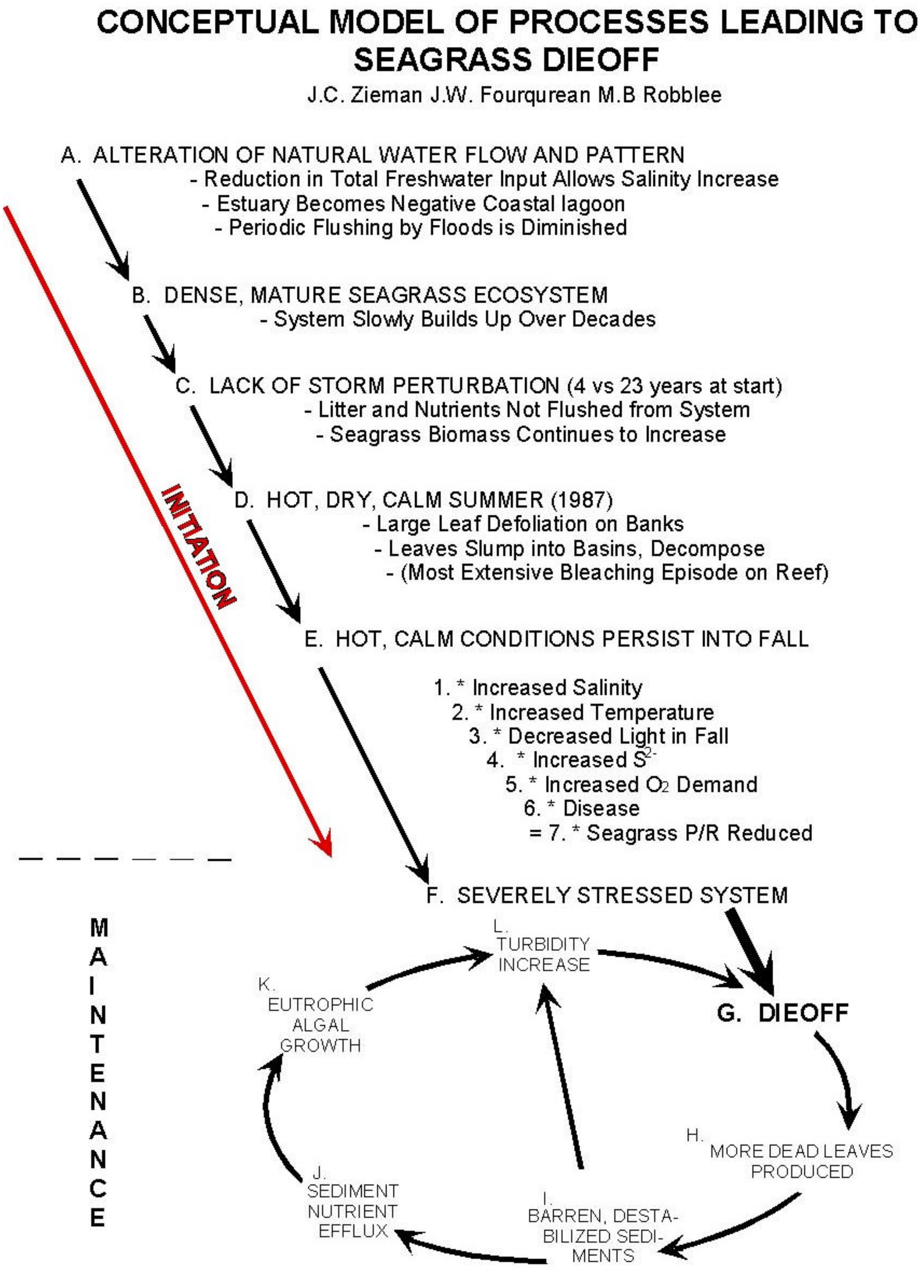
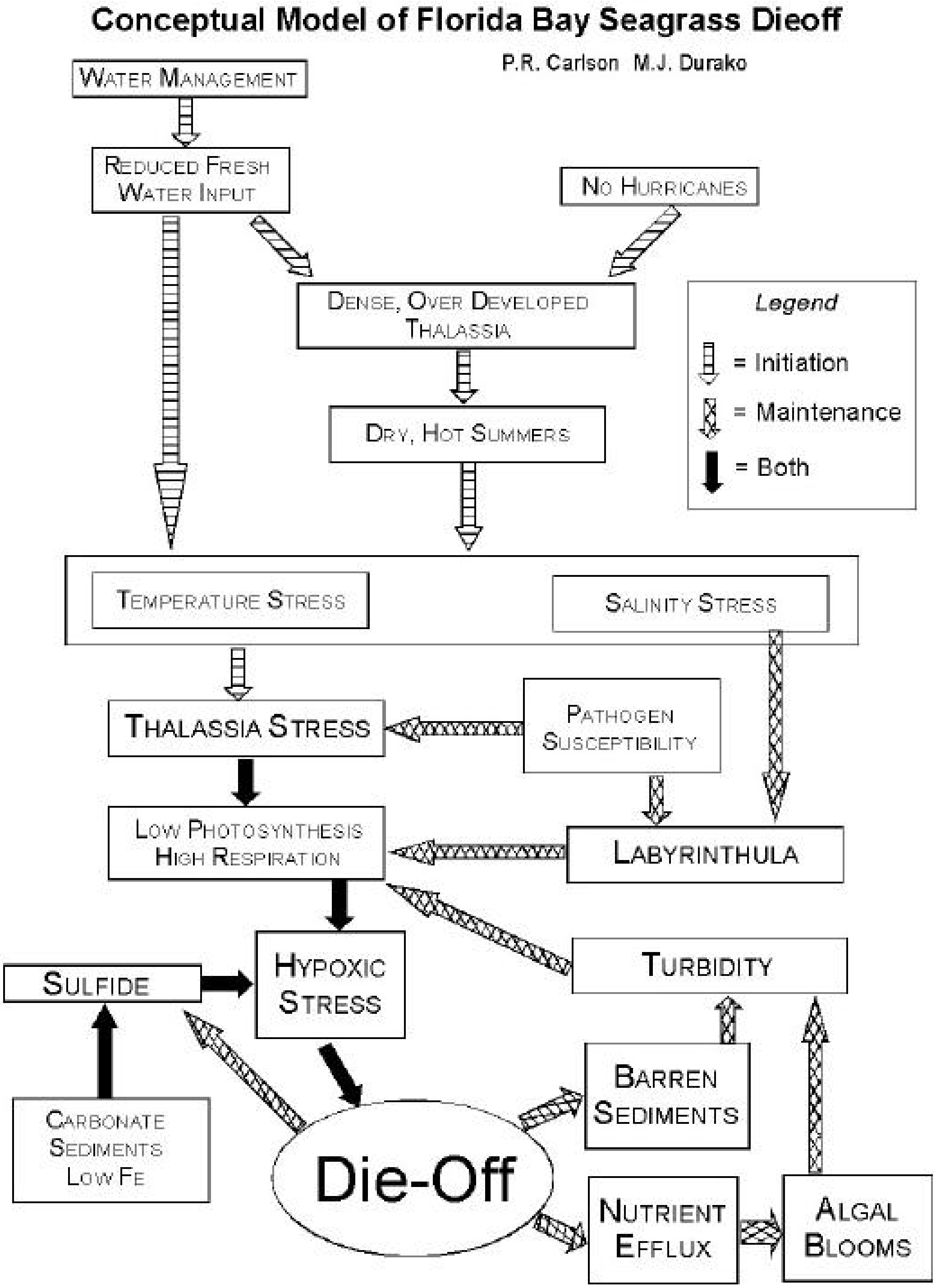


Figure 7.4: Carlson and Durako model for seagrass dieoff



As research progressed and the conceptual models matured, seagrass researchers found much common ground on which to agree. Among these points of agreement are:

1. Primary seagrass dieoff is species specific – *Thalassia testudinum*.
2. Primary dieoff only occurs in very dense beds, sparse and medium density beds have never been shown to have primary dieoff.
3. Primary dieoff has occurred in Florida Bay only. It has occurred in continentally influenced regions with reduced circulation, reduced flushing.
4. Primary dieoff occurs primarily from late summer-fall or fall-early winter. Both the Sunset Cove and Barnes Key die-off events were first observed during January-February. Most significantly, it does not occur in the hottest months of summer
5. Researchers with experience in Florida Bay prior to the initial primary dieoff found the waters to be clear and the seagrasses mostly free from epiphytes from 1987-89. Reduced water clarity and epiphytic growth followed seagrass dieoff by several years.

Factors such as elevated water temperature, prolonged hypersalinity, and excessive seagrass biomass (due to lack of recent disturbances, including hurricanes and reduced salinities), leading to increased respiratory demands, hypoxia and sulfide toxicity are some of the physiological stressors thought to have contributed to *Thalassia* die-off (Robblee *et al.*, 1991; Carlson *et al.*, 1994). Observations indicated the waters of Florida Bay were generally clear, warm and hypersaline in most areas exhibiting die-off. High water column light attenuation from suspended sediments or eutrophic phytoplankton growth was not present at the initiation of the dieoff or for the first several years (Boyer et al, 1999).

Blade lesions were frequently observed on *Thalassia* in areas affected by die-off, although they were not universally present during the earliest phases. An undescribed species of marine slime mold in the genus *Labyrinthula* was the most common microorganism isolated from die-off affected short-shoots (Porter and Muehlstein, 1989). Physiological stress and a negative carbon balance are associated with infection of *Thalassia* by *Labyrinthula* (Durako and Kuss, 1994). Based on these early observations and data, the two conceptual models were formulated (the Zieman Model and the Carlson and Durako Model) incorporating distal and proximal elements thought to have contributed to die-off. These models also included predictions of negative cascades following die-off.

Establishing the relative contribution of (*primary)* dieoff versus light-stress induced mortality to the recent losses of *Thalassia* in western Florida Bay is problematic. There is a high spatial coincidence among the distribution patterns of seagrass loss, *Labyrinthula* abundance (Blakesley et al. 1998), high sediment sulfide levels (Carlson et al., 1994), and turbidity (Phlips et al. 1995; Stumpf et al. 1999). Increases in *Halodule* in the Bay may reflect its lower light requirements (Williams and McRoy 1982; Dunton and Tomasko 1994), ability to rapidly spread into areas where the *Thalassia* canopy has been removed (Thayer et al. 1994), or resistance to disease. There has been little change in *Thalassia* and *Halodule* abundances in basins that are periodically subjected to low salinities. This may reflect the effects of intermediate disturbance (*sensu* Connell's Intermediate Disturbance Hypothesis) in maintaining a mixed-species subclimax (Zieman 1982, fig. 13), as well as offering a low-salinity refugia from disease since *Labyrinthula* has never been found in Florida Bay at salinities below 15 ppt (Blakesley et al. 1998).

Summary of Research

Research on seagrass dynamics has focused on the influence on plant growth and metabolism of both internal conditions in the ecosystem and external driving factors and on documenting the sequence and pattern of seagrass dieoff and recovery in Florida Bay, Table 7.2. The principal findings of this work follow:

- Primary die-off is associated with high-density *Thalassia* beds. High-density beds result in conditions that increase stress on *Thalassia*: high sediment sulfide levels (>2-4 mM); self-shading of shoots; night-time/early morning anoxia/hypoxia in meristems; and increased susceptibility for leaf-to-leaf transmission of *Labyrinthula*. Recent die-off in the Barnes Key area occurred where *Thalassia* densities and standing crop are among the highest in Florida Bay.

- Geographic variation in patterns of seagrass loss suggests multiple causes and a distinction between primary die-off and secondary mortality. There is a high spatial coincidence among the distribution of *Thalassia* loss, *Labyrinthula* abundance, high sediment sulfide levels, and turbidity, but determining the relative contributions of these factors to die-off versus secondary mortality has been problematic.

- Recent bay-scale changes in seagrass distribution and abundance following the region-scale primary seagrass die-off (1987-1991) are largely due to secondary mortality of *Thalassia* associated with areas of chronic turbidity (since 1994) in western Florida Bay. These changes are most likely due to light limitation as indicated by stand-thinning in *Thalassia* beds with concommitant increases in low light adapted species such as *Halodule wrightii* and *Halophila engelmanii*. There has also been a loss of *Thalassia* in northern Little Madeira Bay, near the mouth of the Taylor River, followed by recolonization by *Halodule* and *Ruppia*. The cause of this loss is unknown. Primary acute die-off (rapidly developing dead patches within dense beds) is only known to be currently occurring (initiated in 1999) in the high-density *Thalassia* beds of the Barnes Key area. A chronic die-off is occurring in dense beds in Sunset Cove. However, the etiologies of these two sites are different.

- The boom and bust pattern of *Halodule* and *Ruppia* characteristic of the Joe Bay and Highway Creek areas of northeastern Florida Bay prior to 1991 has stabilized with the occurrence of relatively constant estuarine/marine salinities and the lack of periodic intense hypersaline conditions.

- There has been little net change in seagrass distribution and abundance since 1995 in central basins that are periodically subjected to low salinities or have shallow sediments and lower overall densities of *Thalassia*. These conditions may reduce density-related stresses and allow for development of robust species communities; low-salinity may also provide refugia from disease since *Labyrinthula* has never been observed in Florida Bay in salinities below 15 psu.

- The variable abundances of seagrass-associated microfossils in cores suggest repeated cycles of seagrass presence and absence at core locations over the past 200 years. Thus, the recent changes in seagrass abundance may not be unprecedented.

- A statistical, disciminant-function model of seagrass species occurrence has been developed. The model predicts that an increase in freshwater delivery to Florida Bay will result in an expansion of *Ruppia maritima* and *Halodule wrightii* distribution into the northeastern bay with a concomitant loss of *Thalassia* in this region.

Why did seagrass die-off occur only in Florida Bay?

Unique characteristics of the Florida Bay ecosystem make it susceptible to conditions that contribute to primary die-off. Other marine areas with high *Thalassia* densities and carbonate sediments, such as the Lakes Region of the lower Keys, did not experience extensive die-off in the late 1980s. Relative to these other areas, the central basins in Florida Bay are isolated from tidal influences and are subject to relatively high continental influence.

Table 7.2: Research topics defined by Question 4 (cells in the matrix) and key references to the associated research.

	Plant Growth and Metabolism	**Seagrass Dieoff and Recovery** Stumpf et al. 1999, Bacon et al., Hall et al. 1999, Durako et al. in press, Durako and Hall 2000, Zieman et al. 1999, Thayer et al. 1994, Durako et al. Fourqurean et al. 1992, Robblee et al. 1991
Temperature and Salinity *(see research under Question 1)*	Chesnes et al., Montague et al. 1999	Blakesley et al. 1999 (low salinity refugia from Laby) Boyer et al. 1999 Fourqurean et al in press
Light Attenuation *(see research under Question 3)*	Williams and McRoy 1982,Dunton and Tomasko 1994, Thayer et al. 1994, Frankovich and Zieman, Holmquist	Prager 1998, Stumpf et al. 1999 Fourqurean et al in press
Nutrients *(see research under Question 2)*	Forqurean C:N:P papers Short P papers	Butler et al. 1995 Fourqurean et al in press
Anoxia and Sulfide	Erskine and Koch 2000	Barber and Carlson 1993 Carlson et al. 1994 Erskine and Koch 2000
Disease	Durako and Kuss 1994 Durako and Kunzelman 2002	Muehlstein 1992, Porter and Muehlstien 1989, Blakesley et al. 1998, 1999a, 1999b
Dense Grass Beds	Durako 1995 Hall et al. 1999	Durako 1994, Durako 1995 Durako et al. 2001 – flowering
Sediment Characteristics		Carlson et al. 1994
Climate *(see research under Question 1)*		
Freshwater Inflow *(see research under Question 1)*		Fourqurean et al in press

Effect of Ecosystem Characteristics on Growth and Survival

"Physiological stressors such as elevated water temperature, prolonged hypersalinity, excessive seagrass biomass leading to increased respiratory demands, hypoxia and sulfide toxicity, and disease are some of the factors thought to have contributed to Thalassia dieoff. However the causative mechanisms responsible for initiating the dieoff remain incompletely understood (Robblee et al. 1991; Carlson et al., 1994; Durako, 1994; Durako and Kuss, 1994)."
- from Durako, Hall and Merello, 2002

Changes in plant morphology and metabolism measured in the field provide indicators of response of seagrasses to environmental stressors in advance of dieoff. Zieman et al. (1999) report results of long-term monitoring at sites of pre-existing die-off and at sites not yet affected by die-off. "Measurements were made of short-shoot density, standing crop, leaf morphology and productivity of *Thalassia testudinum*. Seagrass beds in Florida Bay have continued to decline in density and biomass since the die-off event began in 1987. [...] In contrast to the loss of seagrass density and standing crop, we found that mass-specific productivity increased markedly from 1989 to 1995 at the die-off sites. [...] The increases in mass-specific productivity of seagrasses in Florida Bay occurred at the same time that transmission of light to the bottom was decreasing dramatically. [...] Despite increasing productivity on a mass-specific basis over the period 1989-1995, area productivity of *Thalassia testudinum* decreased at three of the five die-off sites. This can be explained by a change in shoot density and size."

Seagrasses in Florida Bay are meristem dependent and depend on rhizome growth and branching to maintain or increase their populations. Excess carbon from photosynthesis is needed for production and growth of apical meristems to allow lateral growth and spread of populations. Core samples (15cm diameter) obtained during spring 1998 and 1999 FHAP sampling indicated that the mean branching frequency was 0.24 during this period, or one rhizome apical branch produced for every four short-shoots (Paxson and Durako). This is very similar to the branch frequency of 0.28 observed during the early die-off from 1989-1990 (Durako, 1994). The relationship between rhizome branching in 1998 and shoot density changes from 1998 to 1999 was significant ($p< .0001$), however, the r^2 value of .12 was low.

Carlson et al. have reported that alcohol dehydrogenase (ADH) increases in *Thalassia* under hypoxic conditions, exacerbating the carbon drain on belowground tissues. Apical meristem density and branch frequency (rhizome apical density normalized to short-shoot density) may act as "ecoindicators" of the potential for loss or gain of seagrass density.

Temperature

The large-scale distribution of marine plants is largely controlled by temperature. The effects of temperature on seagrasses have been extensively investigated and are well known. The range of thermal tolerance in tropical species is about half that of temperate species; upper thermal limits are similar for both groups, but tropical species are less tolerant of low temperatures (Zieman et al. 1989). Because tropical species are growing near the upper temperature limits, thermal impacts such as discharge of cooling waters from electrical power plants can result in mortality during the warm summer months, although productivity may actually enhanced during the winter

(Barber and Behrens 1985). *Thalassia* may exhibit defoliation or reductions in leaf length when temperatures fall below 15 C or exceed 30 C (Phillips, 1960; Zimmerman and Livingstone, 1976; Durako and Moffler, 1985). Temperatures exceeding these extremes have been observed on bank tops in Florida Bay. *Syringodium* seems to be more tolerant of low temperatures than *Thalassia* (no defoliation at temperatures just below 15 C); the former species exhibits maximal growth between 23-29 C while the latter species maximal growth occurs between 23-31 C (Zimmerman and Livingstone 1976). In shallow bays with widely fluctuating temperatures, *Thalassia, Syringodium,* and *Halodule* exhibit narrower leaf widths, suggesting increased stress (McMillan 1978). *Ruppia* exhibits a wide tolerance to temperatures (7-35 C) and exhibits highest growth rates during the cooler spring months (Phillips, 1960; Pulich, 1985). Water temperatures are not expected to be significantly affected by altered water management.

Salinity

Salinity plays a very important role in controlling benthic plant communities in the upper estuaries of Florida Bay; areas of high variability in salinity have low biomass of submerged plants (Montague and Ley, 1993). The mesocosm studies (Chesnes et al., Montague et al., 1999) have produced data on how fluctuating salinities may affect turtlegrass, shoalgrass and widgeon grass. Unfortunately, operational difficulties plagued the mesocosm facility, which slowed progress and resulted in problems with maintaining proper controls.

The role of hypersalinity in seagrass dieoff still remains unclear. Salinities during the initial dieoff episodes in 1987-89 were accompanied by hypersalinities ranging from 45 to 70 ppt in addition to the other environmental stresses. The Barnes Key dieoff clearly did not correlate with this level of salinity but exhibited many of the other stresses that accompanied the original primary dieoff. While the role of hypersalinity may vary relative to other stresses, what is clear is that low salinity does provide refugia from *Labyrinthula*, as infection does not occur at < 15 ppt (Blakesley et al., 1999).

Light

Light penetration to the leaf blades, which sets the limits for seagrass photosynthesis, varies as a function of depth, turbidity, and epiphyte cover.

Turbidity

To assess the relationship between water clarity and seagrass recovery in Florida Bay, Carlson et al. have continuously measured subsurface and bottom PAR at seven stations in Florida Bay since fall 1998. In addition to continuous light data, discrete water samples for analysis of turbidity, color, chlorophyll and total suspended solids and plant samples for epiphyte light attenuation measurement have been collected monthly. Diffuse attenuation coefficients vary seasonally and among basins within Florida Bay: attenuation is higher in winter than in summer and generally higher in the basins which lost large amounts of seagrass in die-off episodes between 1987 and 1991. Persistent phytoplankton blooms in the north-central region of the Bay are associated with high (>3) Kd values, but water clarity at most sites was higher in 2000 than in 1999.

Epiphytes

There are spatial and temporal gradients in species composition of epiphytes with coralline reds being more dominant in western high-flow areas of the Bay (Frankovich 1999). Fleshy epiphytes have restricted distributions only occurring near bird islands and near the Keys. The cyanobacteria *Lynbya* is very common in the *Syringodium filiforme* beds in the west (Frankovich and Zieman). Epiphyte attenuation is higher in winter and spring (30-50%) than in summer and fall (15-30%), and values are higher in the eastern region of the Bay (>40%) than in the west (ca. 20%). Calcium carbonate derived from calcareous algae and resuspended sediment comprises more than half of the epiphyte load.

Epiphytic light attenuation has also been measured using Mylar strips and a light attenuation measurement apparatus that has been successfully employed by investigators in Australia and Chesapeake Bay (Frankovich and Zieman). The Mylar strips have been set out within various seagrass meadows across the Bay for a sufficient time period to allow for the accumulation of epiphytic organisms. Distinct epiphytic communities consisting of benthic diatoms, coralline red algae (*Melobesia membranacea, Hydrolithon farinosum*), and filamentous red and brown algae occur seasonally in various regions across Florida Bay. These various epiphyte functional forms, and combinations thereof, result in differing levels of light attenuation at the leaf surface relative to the amount of epiphyte loading. Epiphyte loads at Barnes Key are at lower 5% of bay wide averages (Frankovich and Zieman). Highest epiphyte loads area in areas of highest seagrass productivity, so epiphytes are not reducing production (Frankovich and Zieman).

Grazers may have an important role in controlling epiphyte abundance. Snails (50/m^2) and hermit crabs are conspicuous at Rabbit Key Basin (Frankovich). Baywide, *Bittium* occurs at densities of 3/m^2, versus in Indian River Lagoon were densities of 20/*Halodule* short-shoot or 1000's/m^2 have been observed.

Macroalgae such as *Laurencia* are patchy in abundance. It is unknown at present whether its abundance has changed in response to the changes in seagrass abundance (although these date are in the FHAP dataset). Jeff Holmquist found that Laurencia accumulation did not kill underlying *Thalassia*.

Nutrients

Worldwide, many estuaries have exhibited loss of seagrasses as a result of eutrophication. However, the mechanism for nutrient-enrichment induced seagrass losses is that increased nutrients lead to increased epiphyte loads and consequent shading and deterioration of the seagrasses (Cambridge et al. 1986). Phytoplankton blooms are usually subsequent rather than causative. As stated above epiphyte loads on seagrasses are relatively low in Florida Bay and do not seem to be reducing production.

Sulfide

The potential links between elevated sediment sulfide concentrations and seagrass mortality (an hypothesis long proposed to account for seagrass die-off) have been explored by Carlson et al. and Erskine and Koch. Hydrogen sulfide is a known plant toxin. High sulfide levels in sediments have been observed during, and after, die-off episodes (Carlson et al. 1994). Sulfide concentrations > 2-4 mM have been measured in die-off sites, but it is not known if this is a cause or an effect of die-off. If sulfide concentrations are < 2 mM, no die-off has been observed. However, photosynthetic rates in *Thalassia* increase as a function of increasing sulfide up to 6 mM, and sulfide levels up to 10 mM have failed to produce visual signs of acute sulfide toxicity, although high sulfide levels have been shown to result in reduced leaf elongation rates (Erskine and Koch, 2000).

A series of field experiments has been undertaken to help understand how sulfide concentrations may influence seagrass growth and abundance and clear up uncertainties between the two conflicting sets of results. A submersible pulse amplitude modulated fluorometer (Diving-PAM) was used to investigate photosynthetic yields of *Thalassia testudinum* leaf material *in situ* within bucket experiments established by Carlson. Photosynthetic yields were significantly lower in buckets with added glucose and acetate (Figure 7.5), both treatments that should have increased sediment sulfide levels.

Labyrinthula Infection

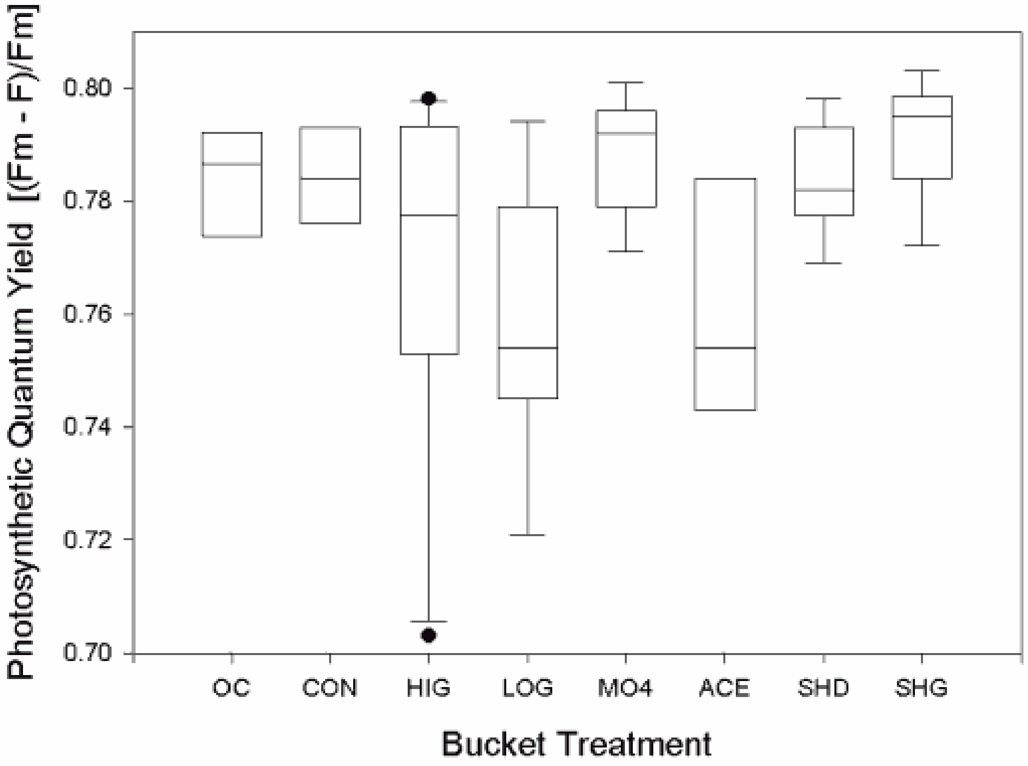
A theoretical model for die-off as a disease (Blakesley et al.1999) has suggested 3 different roles that *Labyrinthula* might play in Florida Bay under different environmental conditions. These included: (1) a nonpathogenic parasite; (2) an opportunistic secondary pathogen; and (3) a primary pathogen. Five different factors were discussed as critical elements in determining the role(s) of *Labyrinthula* in seagrass health at a particular site in Florida Bay (Blakesley et al., 1999b).

Salinity controls infection (infection does not occur at < 15 ppt). Seagrass density determines the extent to which *Labyrinthula* infection spreads because the slime mold transmission is thought to depend on blade-to-blade contact (Muehlstein, 1992). Pathogenicity of a particular strain of *Labyrinthula* will determine severity of infection. Environmental stressors (abiotic factors) such as low light or high temperatures may weaken *Thalassia* and, in combination with the infection by pathogenic *Labyrinthula,* cause seagrass die-off. Resistance to disease due to genetic factors or production of phenolic compounds may be important in determining the health of *Thalassia* in Florida Bay.

The model predicted that in areas with high seagrass density, high salinity, “suboptimal seagrass conditions (environmental stress)”, and presence of pathogenic *Labyrinthula*, the slime mold could contribute to either chronic or acute die-off acting as an opportunistic secondary pathogen. With the same conditions, but without environmental stress, it was suggested that *Labyrinthula* could still cause “thinning” or patchy die-off acting as a primary pathogen (Blakesley et al., 1999). *Labyrinthula* occurrence was found to have significant negative influences on branching frequency (p= .03), shoot density (p= .004), and apical density (p= .033, Paxson and Durako, unpublished data) suggesting this microorganism has a negative influence on seagrass growth and carbon balance (sensu Durako and Kuss, 1994).

The occurrence of the marine slime mold *Labyrinthula* has also been shown to affect photosynthetic characteristics of *T. testudinum* (Durako and Kuss 1994). Durako and Kuss (1994) demonstrated that *Labyrinthula* infection reduces oxygen production and may increase susceptibility to sulfide. These results indicate that reduced photosynthetic capacity, may be caused by *Labyrinthula*-induced lesions or elevated sulfide. This may make *Thalassia* more

Figure 7.5: Photosynthetic quantum yields of Thalassia in Carlson buckets exposed to high glucose (HIG), low glucose (LOG), molybdate (MO4), acetate (ACE), shaded (SHD), and shaded with glucose (SHG) relative to controls inside (CON) and outside (OC)plots.



susceptible to sulfide toxicity, hypoxia, or disease by imposing a negative carbon drain on belowground tissues.

Photosynthetic yields of *Thalassia testudinum* leaf material measured *in situ* at Sunset Cove and Cross Bank, using a submersible pulse amplitude modulated fluorometer (Diving-PAM), were significantly lower for regions of *Thalassia* leaves that had visible lesions. These patterns agree with those previously reported by Durako and Kuss (1994). However, close interval PAM fluorescence measurements along an individual leaf with several visible lesions indicated the reductions in photosynthesis were restricted to the immediate area of the lesion. Quantum yields of lesion-free leaf regions of short-shoots also declined along transects from dense, apparently healthy beds to recent die-off patches at both Barnes Key and Cross Bank. The photosynthetic characteristics of solitary short shoots within the die-off patches were significantly lower than those of shoots along the ecotones and shoots 1 m inside the bed. This indicates that photosynthesis may be reduced even in the absence of visible lesions. The PAM data also reveal that the severity of stress imposed by the leaf lesions will be a function of the proportion of total leaf surface that is necrotic and it remains to be determined what is the lethal threshold for lesion coverage.

Sediment Characteristics

Carlson (unpublished data) has observed that high porosity sediments correlate with high hydrogen sulfide because of low permeability. Barnes Key surface sediments have very high porosity (lots of water and fine sediments).

Die-off has only been observed in biogenic carbonate sediments. This sediment type is usually low in iron. However, Florida Bay carbonate sediments have relatively high iron levels for carbonate sediments (Carlson et al). Spatially, iron is high near mainland and high toward west. Atmospheric deposition, as proposed by Shinn et al. is still not known. Addition of iron to sediments decreases the flux of sulfide to *Thalassia* (Carlson bucket experiments) and results in a significant but small increase in growth. Iron distribution may also have a role in controlling phytoplankton blooms in the Bay.

Effect of Ecosystem Characteristics on Community Structure and Distribution

"The present distribution and species composition of seagrasses in South Florida are a result of the interaction of many factors, the most important being water depth, water clarity, and nutrient availability. Changes in the movement and quality of water in the region, whether natural or anthropogenic, are likely to cause changes in the large-scale patterns in abundance and composition of these seagrass beds. [...] It is also likely that the first symptoms of a changing coastal environment will be a change in species composition of seagrass beds, not a wholesale loss of seagrass cover (e.g. Hall et al. 1999; Durako et al., 2002). For this reason, accurate data on the species composition of the seagrass communities must be collected periodically as a measure of the status of the coastal environment."
- from Fourqurean, Durako, Hall, and Hefty, 2002

Correlation with Patterns of Water Quality

Forqurean et al. (in press) developed a discriminant function model using seagrass species occurrence and abundance data from 677 locations and water quality data from 28 monitoring stations in Florida Bay. The model predicted that the distribution of benthic habitat types in Florida Bay would likely change if water quality and water delivery were changed by changes in water delivery to the Bay. Specifically, an increase in seasonal delivery of freshwater should cause an expansion of the distribution and abundance of *Ruppia maritima* and *Halodule wrightii* at the expense of *Thalassia testudinum* along the northeast region of the Bay.

Geographic Variation in Seagrass Dieoff

The production of distribution and abundance maps of the seagrasses have proven valuable and they provide a quantitative record of distribution and abundance at both basin and Bay scales. The change maps provide clear visualization of where and how much the distribution and abundance changes, thus can point to "hot spots" that may be related to specific forcing events or conditions. The use of cover has become an assessment standard in region (FKNMS, DERM, FHAP) and cover may be a more sensitive performance measure to short-term changes than density since density changes require mortality and recruitment of short-shoots while cover can vary also in response to just changes in the leafiness of short-shoots. Short-shoot density may be a better longer-term performance measure and it is a quantitative measurement. Density is the net effect of mortality, recruitment, and life span (demographics).

The recurrence of an acute die-off in Barnes Key presented an opportunity to test a portion of the theoretical model by comparing the symptoms and progression of an acute event in the Barnes Key mud bank area with the symptoms and progression of what we believed to be chronic die-off in Sunset Cove. The hypothesis was that in Sunset Cove *Labyrinthula* acted as a primary pathogen in an environmentally unstressed site whereas in Barnes Key *Labyrinthula* more likely played the role of a secondary pathogen in an environmentally stressed site.

Comparisons of results for the Sunset Cove and Barnes Key sites revealed that although active die-off was occurring in both places, the sites were very different. At both sites the pattern of die-off was patchy, suggesting disease processes rather than a physical process as the primary cause. Both sites had high salinities (> 15 ppt) and dense *Thalassia* beds - necessary elements for *Labyrinthula* infection and transmission. However the data from the two sites revealed important differences summarized below:

Table 7.2: Characteristics of dieoff at two locations in Florida Bay

Barnes Key	Sunset Cove
• Seagrass loss is rapid • Meristem "rots" • Lesions occur *after* die-off • Water temps are high in summer • "High" sediment sulfide levels (up to 7,000 µM) Levels vary in different zones with highest values found in active die-off zones.	• Seagrass loss is slower • Meristem "healthy" • Lesions occur *before* die-off • Water temps are "normal" • "Low" sediment sulfide levels (= 1600 µM) in bare, sparse, and dense seagrass zones.

These differences strongly suggest that the mechanisms for the die-offs in Barnes Key and Sunset Cove are not the same. Blakesley et al propose that the acute die-off in Barnes Key results from a series of events beginning with heat stress and an initial infection/disease (not *Labyrinthula*-induced) that rapidly kills the infected seagrass. The resultant large amount of decaying below-ground biomass from the rapidly dying *Thalassia* roots and rhizomes promotes microbial activity that in turn elevates the sediment sulfide levels selectively in those vegetative zones where the die-off is occurring or has recently occurred. The high sediment sulfide levels do not kill seagrass outright, but instead further stress the other seagrass in the immediate area. Finally, *Labyrinthula*, acting as an opportunistic secondary pathogen, infects the already weakened remaining seagrass.

In contrast, the chronic die-off in Sunset Cove is hypothesized to be directly caused by the presence of the slime mold *Labyrinthula* acting as a primary pathogen. Sediment sulfide levels may remain relatively low in all the vegetative zones tested simply because the slowly dying *Thalassia* roots and rhizomes result in a smaller decaying below-ground biomass so that the sediment sulfide levels may remain relatively low in contrast to the Barnes Key scenario. Such chronic seagrass die-off is still ongoing in many parts of Florida Bay where the *Thalassia* beds are dense enough for transmission of the disease and the salinity is high enough for infection to occur.

Recent high-resolution in *situ* oxygen measurements show the short-shoot meristems of *Thalassia* at the Barnes Key dieoff site go anoxic during the night in November and remained anoxic for up to 5 hours (Borum et al.). In contrast, leaf meristems at Rabbit Key Basin did not go hypoxic. The Barnes Key Samples showed a more rapid decline in oxygen concentration after sunset, and slower internal oxygen concentration increases in the morning than samples from Rabbit key Basin. *Thalassia* at Barnes Key is very dense with over 1200-1500 short-shoots/m^2, has a very high biomass (SC 300 g/m^2), and low turnover rate (1.2%/ day) with a very thick litter layer. In Rabbit Key Basin densities are also high (1200-1300 short-shoots/m^2) but biomass (SC 109 g/m^2) and turnover rates (1.7% /day) are more moderate (Zieman et al). The long short-shoot stems at Barnes Key lead to increases in diffusion distance for oxygen. Long internodes may be a response to hypoxia or rapid sedimentation.

Seagrass loss has also been recently observed in the northern portion of Little Madeira Bay from the mouth of the Taylor River to the south and west (Bacon et al.). This area has shown recolonization by *Halodule* and *Ruppia*. These observations of renewed seagrass die-off led to a plan for a series of observations and experiments to test several of the remaining hypotheses that might explain seagrass die-off.

Modeling Change in Benthic Communities

Statistical modeling was commissioned by the Restudy consistent with recommendations from the 1998 Seagrass Modeling Workshop (Fourqurean et al. in press). The goal of this work is to seek relationships between water quality variables and seagrass species composition and abundance, which if sufficiently strong, can be used to predict the effects of various alterations in Florida Bay salinity regimes. The statistical models developed in this project will be used in conjunction with output from other models to predict the effects of Restudy scenarios on the benthic habitats of Florida Bay. The statistical model will not address mechanisms or degree of change in water quality that result from Restudy scenarios; other models (like the NSM, FATHOM, and the Florida Bay salinity transfer function models currently employed by the Restudy) must simulate water quality changes across Florida Bay that will provide the input to the new models developed in this project. As a consequence, it is anticipated that the benthic habitat change predictions of the statistical models will be the most reliable in the regions most closely coupled with water management practices, i.e. in the enclosed, mangrove-lined estuaries on the fringe of Florida Bay. As the fidelity of the physical water quality models to the behavior of the system declines, the reliability of the benthic changes predicted by our model will also decline. But, since the statistical relationships will be based on data from more marine areas as well as upper estuaries, the basic relationships between actual water quality (not modeled) and benthic habitats will be robust.

In addition, other seagrass modeling efforts have recently been initiated. These include the development of both seagrass unit models for *Thalassia* and *Halodule* and a landscape model that will take output from the unit models. Smith et al. is developing a hierarchical approach to modeling the interaction between plant and physical processes in the Florida Bay that involves two distinct spatial scales – the demographic unit (ca. 10 $m^{2)}$ and the landscape unit (ca km^2). Plant processes will be modeled at a spatial scale ca. 10 m^2, the spatial scale that we refer to as the demographic unit. A preliminary landscape model of *Thalassia* that explicitly relates patterns of photosynthesis, respiration and carbon allocation to environmental conditions that include salinity, temperature, PAR and nutrient availability has been developed.

Physical processes such as sedimentation, decomposition and nutrient cycling will be modeled on a spatial scale of km^2, defined as the landscape unit. The approach provides a hierarchical framework where the demographic units used to simulate plant processes exist in the context of the landscape units, which will define the underlying physical environment. The plant characteristics that are relevant to the feedbacks with the physical environment, such as primary productivity, inputs of dead organic matter, etc. are described statistically for the demographic units and used to define the biological environment for each landscape unit. In this manner, the framework functions as a dynamic, interactive GIS where each parameter and process is described and simulated at the appropriate time and space scale.

Current Research

Field Assessment

- FHAP is continuing spring and fall sampling and has incorporated (since spring 2001) measurements of photosynthetic characteristics of *Thalassia* using PAM-fluorometry at each station, in addition to the Braun-Blanquet and standing crop measurements.
- FMRI (Carlson) is continuously monitoring benthic light availability at fixed stations in several basins
- Zieman is maintaining the long-term productivity measurements

Experimental

- SFWMD is funding a new study entitled "High salinity, nutrient and multiple stressor effects on seagrass communities of NE Florida Bay" (Koch and Durako). The results of this study are intended to help parameterize the unit model with data from Florida Bay seagrasses.
- FMRI (Carlson) bucket experiments have been conducted to examine effects of multiple stressors (sulfide nitrogen and light) on seagrasses in situ.

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