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Florida Bay Science Program: A Synthesis of Research on Florida Bay

John Hunt and William Nuttle
Editors

Florida Fish and Wildlife
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John H. Hunt
Editor

Florida Fish and Wildlife Conservation Commission
Fish and Wildlife Research Institute
South Florida Regional Laboratory
2796 Overseas Highway, Suite 119
Marathon, Florida 33050 USA

William Nuttle
Editor

Eco-hydrology.com
Ottawa, Ontario
Canada K1S 4B6

Florida Fish and Wildlife Conservation Commission
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Cover Photographs

Center: The Crocodile Dragover pass, below Terrapin Bay and Madeira Bay *(Bill Perry, Everglades National Park). Clockwise from upper left:* Sampling in seagrass *(Florida Fish and Wildlife Conservation Commission);* Anhinga with spotted sea trout, Florida Bay *(Bill Perry, Everglades National Park);* Florida Bay hardbottom habitat (*Florida Fish and Wildlife Conservation Commission);* White Pelicans and Black Skimmers at low tide, Flamingo, Florida Bay *(Bill Perry, Everglades National Park).*

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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 strategic 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

Ecosystem History
G. Lynn Wingard (USGS, Reston)

Physical Processes
Thomas Lee (University of Miami), Elizabeth Johns (NOAA/AOML), Peter Ortner and Dawn Boyer (NOAA/AOML, PMC)

Nutrient Dynamics
Joseph Boyer (Florida International University), Brian Keller (Florida Keys National Marine Sanctuary, PMC)

Algal Blooms
Gary Hitchcock (University of Miami), Ed Phlips (University of Florida), Larry Brand (University of Miami), Douglas Morrison (ENP, PMC)

Seagrass Ecology
Michael Durako (University of North Carolina at Wilmington), Joseph Zieman (University of Virginia), Michael Robblee (USGS, PMC)

Higher-Trophic-Level Species
Joan Browder (NOAA/NMFS), John Lamkin (NOAA/NMFS, PMC)

Editors

William Nuttle (Eco-hydrology.com) and John Hunt (Florida FWC, PMC)

Chapter 1

Florida Bay Science

Florida Bay lies between the southern tip of the Florida mainland and the island chain known as the Florida Keys. More than 85% of the bay's 2,200-km^2 area lies within Everglades National Park, and the Florida Keys National Marine Sanctuary contains much of the rest. The bay includes more than 200 small islands, many of which are rimmed with mangroves. Florida Bay supports numerous protected species, including the Roseate Spoonbill, the bottlenose dolphin, the American crocodile, the West Indian manatee, and several species of sea turtles. Moreover, Florida Bay provides critical habitat for commercially important species, such as spiny lobsters, stone crabs, and many important finfish species. It also serves as the principal nursery for the offshore Tortugas pink shrimp, which supports an important fishery.

Florida Bay is an important component of the much larger south Florida region that is the focus of the Comprehensive Everglades Restoration Plan (CERP). The bay receives freshwater runoff from the Everglades, a large portion of which is managed discharge from canals in the region. Decisions guiding the restoration of the Everglades carry implications for future conditions in Florida Bay, just as the development of the regional water management system over the past fifty years influences present conditions. Although a specific restoration target has not yet been defined for Florida Bay, many expect that restoration of more natural hydrologic conditions in the Everglades will move the bay toward an ecological state more typical of the period prior to the time of engineered changes imposed on the regional south Florida system.

Rapid ecological changes occurred in Florida Bay between 1987 and 1991. These changes came at the end of a multiyear drought that had elevated salinity values in the central portion of the bay to nearly 70 practical salinity units (psu), almost double the typical salinity of seawater. Large areas of seagrasses began to die late in 1987. Concurrently, the shrimp harvest on the Tortugas Grounds declined to record lows. In 1991, turbidity and plankton concentrations increased dramatically, reducing the supply of light to the remaining seagrass beds through the previously "gin-clear" bay waters. Mass mortality of sponges, which help to filter the bay's waters and provide habitat for juvenile lobster, followed in the path of the plankton blooms. By the end of 1991, there was widespread concern among the public for the health of the Florida Bay ecosystem, yet very little scientific information existed that resource managers could use in response to this concern.

The Florida Bay Science Program emerged in 1994 as a coordinated effort by state and federal agencies to identify the mechanisms and underlying causes responsible for the recent ecological changes. Its objectives were to implement an interagency program of research aimed at developing the knowledge needed to guide ecosystem restoration and to communicate this scientific knowledge to restoration managers, scientists, policy makers, and the informed public. Currently 11 state and federal agencies participate in the program through representatives on the Program Management Committee. This committee formulated a Strategic Plan, which was revised in 1997, to coordinate the research supported independently by the separate agencies. The committee also provides for occasional review of the program by the independent Science Oversight Panel and for dissemination of its findings through a series of science conferences. This report is part of the Strategic Plan's effort.

The CERP was established in 2000 with the overarching goal of restoring and preserving the ecosystems of south Florida, including Florida Bay. This plan relies on scientific information to document the condition of south Florida's ecosystems and evaluate the effects of human activities on them. Human activities influence the structure and function of ecosystems both directly, by altering the ecosystems themselves, and indirectly, by altering the climatic, hydrologic, and geologic processes that drive the ecosystems and maintain their structure. This has probably occurred throughout history. However, the extent and intensity of human activities and their influence on ecosystems has increased greatly with the expansion of agriculture and urban development in the past 100 years. In order to guide restoration efforts, resource managers now require scientific information on the bay's ecosystem, how it has changed during the past 100 years, how it works, and how it likely will respond to planned restoration activities. Since its inception, the Florida Bay Science Program has pursued the goal of developing this information and providing it to resource managers.

Chapter 2

Executive Summary

Purpose of This Report

This report documents the progress made toward the objectives established in the Strategic Plan revised in 1997 for the agencies cooperating in the program. These objectives are expressed as five questions (see box below) that organized the research on the Florida Bay ecosystem. Each question examines different characteristics of the Florida Bay ecosystem and the relation of these to the geomorphological setting of the bay and to processes linking the bay with adjacent systems and driving change. This report also examines the additional question of what changes have occurred in Florida Bay over the past 150 years.

Preparation of this report coincided with the reevaluation of the strategy for organizing ecosystem research in Florida Bay around these five central questions. This strategy originated in response to the need by resource managers for basic information about startling changes in the ecosystem that occurred in the late 1980s and early 1990s. Since 1994, the program, focused by the central questions, has sought to identify the underlying mechanisms and causes of these decade-old events. Resource managers now ask a different set of questions. The inception of the Comprehensive Everglades Restoration Plan (CERP) in 2000 signals a shift in resource management away from the reactive stance of protecting natural resources toward the proactive pursuit of restoring south Florida's ecosystems. In general, ecosystem restoration challenges us to look ahead.

Can we predict future conditions in the Florida Bay ecosystem that will follow from resource-management decisions made today? The 1997 Strategic Plan describes a set of interrelated predictive models for this purpose, *i.e.,* for circulation, water quality, and ecological models. This activity has been pursued at several levels. The most visible has been the ongoing effort to identify and implement an appropriate set of numerical simulation models to describe circulation and water quality within the bay and the interaction of the bay with the Everglades, the Florida Shelf, the reef tract, and waters of the Florida Keys. Research has spawned the development of other types of predictive models, *i.e.,* historical analogs, correlative models, and mechanistically based empirical models. Some of these models can be used to peer into the future, albeit through somewhat narrow windows focused on specific elements of the bay.

The concluding chapter examines progress toward answering the original central questions and explores some of the new challenges for research on Florida Bay. By maintaining focus on the central questions to serve the programmatic purposes described above, this report addresses most directly past concerns of resource managers. However, scientific information developed by the Florida Bay Science Program is also relevant to the present management goal of restoring the ecosys-

Ecosystem History What was the Florida Bay ecosystem like 50, 100, and 150 years ago?

Question 1—Physical Processes How and at what rates do storms, changing freshwater flows, sea level rise, and local evaporation and precipitation influence circulation and salinity patterns within Florida Bay and exchange between the bay and adjacent waters?

Question 2—Nutrient Dynamics What is the relative importance of the influx of external nutrients and of internal nutrient cycling in determining the nutrient budget for Florida Bay? What mechanisms control the sources and sinks of the bay's nutrients?

Question 3—Plankton Blooms What regulates the onset, persistence, and fate of planktonic algal blooms in Florida Bay?

Question 4—Seagrass Ecology What are the causes and mechanisms for the observed changes in the seagrass community of Florida Bay? What is the effect of changing salinity, light, and nutrient regimes on these communities?

Question 5—Higher Trophic Levels What is the relationship between environmental and habitat change and the recruitment, growth, and survivorship of animals in Florida Bay?

tems of south Florida. For both the program and for efforts to restore Florida Bay, knowledge of the past offers the best perspective for looking ahead.

Ecosystem History

The alarming ecological changes witnessed in Florida Bay during the late 1980s and early 1990s precipitated a shift in natural-resource management in south Florida that culminated in the CERP. For many in the public-at-large, and among scientists as well, the restoration of Florida Bay will mean a return to conditions remembered from immediately prior to these changes—clear water, lush beds of seagrass, and good fishing. Resource managers must be concerned with whether these conditions can be sustained by the ecosystem given the variety of processes driving change in the ecosystem. Perhaps if viewed over a time span longer than only the past twenty years, the natural state of Florida Bay will be revealed as something quite different from what is remembered.

An objective of the program shared across the five central questions has been to construct a history of past conditions in the bay based principally on objective, quantitative data. Quantitative observations on the state of the Florida Bay ecosystem date back to the 1950s, when systematic surveys were conducted by Finucane, Dragovich, and Tabb. Although invaluable, these observations provide an incomplete and biased representation of the bay's natural state. Major changes had already occurred in the hydrology of the Everglades by the time these studies took place. Fortunately, through analysis of coral and sediment cores we can read the history of the Florida Bay ecosystem recorded in the skeletons of organisms that resided here during the past 150 years. This work leads to the following conclusions:

- Salinity in Florida Bay is more strongly correlated to rainfall than any other single factor. A periodicity in salinity and rainfall data suggests linkages to the El Niño/Southern Oscillation climatic patterns. Although anthropogenic influences play a secondary role to rainfall in determining salinity for Florida Bay as a whole, they may be a factor in the magnitude of salinity variations seen in recent times. Additionally, anthropogenic factors may act on a local basis to influence salinity patterns.
- Seagrass has been more abundant in the past 50 years than in the first half of the 20th century. Prior to the mid-20th century, epiphytal ostracodes were relatively rare at sites in central and northeastern Florida Bay, suggesting a greater abundance and/or density of seagrass over the past 50 years than in the first half of the century. Epiphytal mollusks, although not rare, increased significantly at most sites from approximately 1940 on. These data suggest that dense and abundant seagrass beds may not have been the long-term normal state of the ecosystem, and they carry implications for restoration.
- Downcore profiles of dated cores from central Florida Bay show that productivity events (*i.e.*, blooms) have occurred historically in Florida Bay. A large multidecadal productivity event characterized by greatly elevated levels of organic carbon and nitrogen, dated to about the mid 1700s, was observed in two cores from Whipray Basin. Interestingly, total phosphorus was not elevated during this time span. This time period (the Little Ice Age) may correspond to a period of higher rainfall in the Everglades and more extensive land runoff into Florida Bay, which may have triggered the productivity event.
- Sediments from northeastern Florida Bay (especially from sites near Pass Key and Russell Key banks) show indications of recent nutrient (carbon, nitrogen, and phosphorous) enrichment (1980 to present). This nutrient enrichment could be related to recent microalgal blooms and seagrass die-off within Florida Bay.
- Northeastern Florida Bay appears to be a source of nutrients to the mangrove zone at the southern end of Taylor Slough. Uranium-isotope studies indicate that the phosphorus contamination at the northern end of Taylor Slough appears to be fertilizer-derived. However, phosphorus contamination in Taylor Slough diminishes to background by midslough; therefore, Taylor Slough does not appear to be a source of nutrients to northeastern Florida Bay.
- Macroalgae have increased. Relative abundance of mollusks with a strong preference for *Thalassia* has declined since approximately 1970 in northeastern Florida Bay and since 1910 in Whipray, whereas more generally epiphytic organisms have generally increased. This may indicate an increase in the amount of macrobenthic algae relative to *Thalassia.*
- At Bob Allen, seagrass abundance appears to have been increasing since a recent minimum around 1960. Downcore profiles of lignin phenols from Pass Key core show large variations in lignin-phenol distributions over short time intervals, reflecting the proximity of this site to the mangrove zone along the coast and the outlet of Taylor Creek.
- Changes also occurred in circulation and exchange with adjacent waters during the early part of the 20th century. Geochemical changes recorded in coral bands suggest that construction of the overseas railroad altered exchange by blocking passes between the Keys. Other changes appear to be the result of

decreased freshwater inflow from the Everglades that resulted from "reclamation" activities on the mainland.

Physical Processes

Research on physical processes aims to identify the main external factors that control the movement of water and solutes within Florida Bay and their exchange with the Everglades and adjacent marine systems. The difficulty is estimating the relative influence of the various physical driving processes, even though the identities of the physical processes themselves are known from the study of other estuaries. The two physical characteristics of Florida Bay that distinguish it from most other estuaries in the U.S. are the restricted exchange across the shallow but otherwise open boundary with the Florida Shelf and the relatively small amount of terrestrial freshwater discharge to the bay.

- Historical data from the salinity-synthesis database (Robblee *et al.,* 2001) show that Florida Bay has behaved as a marine lagoon for the past several decades. Salinity has reached as high as 70 in the central bay on a few occasions and typically exceeded 40 during drought years like 1989–1990. For example, following the wet period of 1994–1995, salinity increased, tropical storms in 1999 induced a decrease, and data from the drought years of 2000 and 2001 indicated another increase. More recent data from 2002 and early 2003 indicate another general freshening trend.
- The south Florida coastal region is surrounded by an intense, large-scale, oceanic boundary current (the Loop Current–Florida Current system) and its evolving eddies that link local coastal waters to remote river discharges upstream in the Gulf of Mexico.
- Seasonal cycles in local wind-forcing produce seasonal patterns in circulation pathways, connecting south Florida coastal waters through western Florida Bay and transporting Everglades freshwater discharges. Southward flows through the Keys passages predominate in winter and spring, north-northwest flows in summer, and southwest flow toward the Tortugas in the fall. Large-volume, wind-forced flows through the Keys passages provide linkage for gulf-to-Atlantic exchange through the southwestern shelf region adjacent to western Florida Bay.
- Seasonal cycles in south Florida coastal current systems provide seasonal pathways for local larval recruitment. They also furnish opportunities for recruitment from remote sources.
- Shallow bank configurations that restrict water exchange tend to separate the bay's interior into three distinct regions with different salinity regimes. The northeastern region is the most isolated from oceanic influences, receives most of the surface runoff, and has the largest seasonal cycle of salinity. The central region receives little runoff and has the maximum salinity. The basins in the western region have the greatest oceanic exchange and the smallest seasonal change in salinity.
- Variability of Florida Bay average salinity is directly related to the net flux of fresh water from the combined influence of evaporation, precipitation, and runoff. For the bay as a whole, on seasonal or annual time scales, evaporation is approximately equal to precipitation, and runoff is roughly 10% of either. Historical salinity data and salinity proxy data show that Florida Bay salinity has commonly undergone large changes on time scales of seasonal, interannual (ENSO), decadal (NAO), and even longer periods that are not understood.
- Stable-isotopic markers indicate that runoff from the Everglades is the dominant source of fresh water to the northeastern region of Florida Bay, whereas for the western region, precipitation shows a strong signal. In the central region, a mixture of runoff and precipitation provides the fresh water.
- Since 1985, freshwater discharge from Taylor Slough and the C-111 canal have increased as a consequence of changes in water management. Trout Creek conveys the largest volume of fresh water to northeastern Florida Bay, varying from –6 to 32 m^3/s. By contrast, the flow from each of another eight creeks where discharge is metered ranges from –1.4 to 6 m^3/s. Negative flows can occur during the dry season and during storm events.
- Low-salinity Shark River plume waters are advected southward around Cape Sable to western Florida Bay and the Keys reef tract by seasonal, wind-driven coastal flows. For the Ten Thousand Island region of the western Everglades, the mean annual river discharge is estimated to be 13.3 m^3/s for Harney River, 11 m^3/s for Broad River, and 12.4 m^3/s for Shark River.
- Groundwater inflows are believed to be most influential along the northern boundary of the bay. However, estimates for the rate of groundwater discharge are highly uncertain, ranging over four orders of magnitude.

Nutrient Dynamics

In contrast to water movement and salinity, which reflect the influence of outside processes, both external and internal processes combine to determine characteristics of water quality. Research on this question has concentrated on quantifying external sources and sinks of nitrogen and phosphorus. More recently, the focus has been on internal exchanges between the sediment and the water column. The major external sources of nutrients have proven difficult to quantify. As a result it has been challenging to resolve the question of whether the seagrass die-off and subsequent plankton blooms were triggered by the onset of eutrophication of Florida Bay.

- Over a thirteen-year period of record, temporal trends have shown bay-wide declines in total phosphorus (P), total nitrogen (N), and chlorophyll *a* (CHLA), with an overall increase in turbidity.
- Objective analysis shows that there are three zones in Florida Bay that exhibit significant differences in water-quality characteristics due to nutrient inputs, tidal advection, and water residence time. These zones correspond generally to the northeast, central, and west regions, which are defined by variation in other ecosystem characteristics. In general, dissolved phosphorus concentrations increase and nitrogen concentrations decrease from east to west, resulting in a shift from phosphorous limitation to nitrogen limitation. Central bay waters have high ammonium concentrations, which may indicate a bottleneck in the process of nitrification.
- Atmospheric input of nutrients is large relative to other sources.
- There is a measurable effect of water management on nutrient loading in the Taylor Slough system. Terrestrial nutrient loading fluctuates in phase with freshwater flow; however, flow-weighted concentrations decrease with increasing flow. A serious disconnect exists between upland/canal loading estimates and actual input to the bay because of unmeasured nutrient processing in the intervening wetland/mangrove areas.
- High rates of organic carbon and nitrogen fluxes occur, both into and out of sediments, over diel cycles. Benthic denitrification is higher than predicted from nitrogen-loading rates. There are times when benthic N_2 fixation in Florida Bay balances denitrification but the system overall shows a net loss of nitrogen.
- Sediment flux of ammonium decreases with an increase in sediment chlorophyll *a* concentration, which indicates that the microphytobenthos is important in regulating water column nitrogen concentrations.
- There is very little, if any, inorganic phosphorous flux out of the sediments with the exception of the western bay/shelf area.

Plankton Blooms

For Florida Bay as a whole, plankton blooms can be viewed as a distinct mode of variation in the ecosystem that arises from a consequence of external drivers and internal processes. On a mechanistic level, plankton blooms form whenever plankton growth exceeds the combined effect of grazing and dispersion (the processes that reduce plankton concentrations). Studies of other estuaries link plankton blooms to increased nutrient loads in runoff. Research on plankton blooms in Florida Bay has been directed at describing the combination of internal and external conditions associated with the onset, persistence and fate of blooms in this ecosystem. Research to date indicates that there are three ecologically distinct regions within the bay from the standpoint of algal blooms: the Northeast Region, the Central Region, and the West Region. The nature and causes of blooms can be most appropriately summarized within the context of these three regions.

Northeast Region

- Algal blooms are largely absent from the Northeast Region of Florida Bay. The phytoplankton community of the Northeast Region is a diverse mixture of cyanobacteria, dinoflagellates, diatoms, and microflagellates, none of which form blooms.
- The lack of algal blooms in the Northeast Region of Florida Bay is largely attributable to the severe phosphorus limitation characteristic of the region. Despite significant water inflows to the region from the Everglades, the very low phosphorus levels in these inputs combined with the calcium carbonate-rich waters of the region result in nutrient-limited conditions.

Central Region

- Large algal blooms have been a common feature of the central region since at least 1992. The focal point for blooms is in the north-central part of the region, extending from Rankin Basin and into Whipray Basin. The greatest bloom activity is generally in the summer and early fall, although blooms have been observed in other seasons. In the fall and early summer, blooms originating in the north-central part of the Central Region are pushed southward by the prevailing, wind-driven circulation into the southern part of the Central region, where they can spread out into the Atlantic reef tract through cuts in the Florida Keys. The dominant bloom-forming alga in the central region is the picoplanktonic cyanobacterium *Synechococcus elongatus,* although several species of diatom and dinoflagellate do occasionally occur in bloom proportions.

- Nutrient limitation of phytoplankton growth in the central region appears to switch back and forth from phosphorus to nitrogen. The nature of the sources of nutrients for blooms in the central region has been a subject of considerable debate, yielding several hypotheses:
  - A significant supply of nutrients for algal production is available from the flocculent muddy sediments within the region;
  - A groundwater source of phosphorus is present within the region that, in combination with nitrogen from the northeast region, feeds algal blooms;
  - Nutrients from the shelf region west of the bay are available to blooms in the central region via tidal exchange;
  - Atmospheric deposition is a significant source of nutrients (particularly N) for algal primary production.

  These hypotheses are not mutually exclusive, and several mechanisms may be operational at the same time.
- The domination of blooms in the Central Region by *Synechococcus elongatus* is attributable to the unique ecophysiological characteristics of this species of cyanobacterium. These characteristics include
  - wide tolerance to salinity,
  - superior ability to compete for phosphorus at low concentrations,
  - ability to regulate buoyancy and thereby take advantage of nutrients available in the sediments, and
  - lower susceptibility to grazing losses.

West Region

- Algal blooms are also a common feature of the West Region of Florida Bay. The West Region, in contrast to the cyanobacterial blooms in the Central Region, is dominated by diatoms. The blooms in the West Region are mainly *Rhizosolenia* spp., *Chaetoceros* spp., and pinnate diatoms, which dominate in terms of cellular biomass. Diatom blooms in the west region begin in late summer and are advected into the bay from shallow coastal waters off Cape Sable.
- The diatom-dominated blooms in western Florida Bay are mainly limited in their growth by nitrogen, either singly or in combination with phosphorus and/or silicon supply. Temperature, salinity, and light do not appear to be important factors in the initiation or maintenance of diatom blooms. Maximum growth rates of the diatom community during bloom initiation in the West Region range from 1 to 2 day^{-1} (first-order rate constant), based on increases in netplankton (>5 µm size fraction), chlorophyll *a*, or biogenic silica. The onset of diatom blooms on the western Florida Shelf appears to be associated with enhanced riverine outflow, predominantly from the Shark River. The onset of increased diatom biomass occurs within the riverine, low-salinity plume near Cape Sable.

Seagrass Ecology

Seagrasses account for a major portion of the primary production in the Florida Bay ecosystem. Therefore, it is particularly important to understand the mechanism for the die-off observed in the late 1980s and the relation of this event to the algal blooms that occurred subsequently. The loss of seagrass observed in other estuaries has been explained as a consequence of eutrophication increasing algal growth and reducing the amount of light available to the seagrasses. The seagrass die-off in Florida Bay did not follow this pattern, and its cause may be unique to Florida Bay. Research on this topic has focused on the influence of both internal conditions and external driving factors on plant growth and metabolism and on documenting the sequence and patterns of seagrass die-off and recovery 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. Determining the relative contributions of these factors to die-off versus secondary mortality has been problematic.
- 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 mmol), self-shading of shoots, nighttime or early morning anoxia/hypoxia in meristems, and increased susceptibility for leaf-to-leaf transmission of the *Labyrinthula* disease organism. Recent die-off in the Barnes Key area occurred where *Thalassia* densities and standing crop were among the highest in Florida Bay.
- 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,* which is associated with areas of chronic turbidity (since 1994) in the West Region. These changes are most likely due to light limitation as indicated by stand-thinning in *Thalassia* beds and 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 known to be currently occurring (initiated in 1999) only 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.

- In central basins that periodically have low salinities, shallow sediments and low overall densities of *Thalassia,* there has been little net change in seagrass distribution since 1995. 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 practical salinity units (psu).
- 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 terrestrial influence.
- A statistical, discriminant-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 Northeast Region and a concomitant loss of *Thalassia* in this region.

Higher-Trophic-Level Species

The value placed on Florida Bay derives largely from its role supporting ecologically and commercially important animal species. These species and the communities they create depend on and integrate the net ecosystem metabolism at lower trophic levels. As well, the structure of the ecosystem at higher trophic levels can feed back to influence the structure and function at lower levels, *i.e.,* top-down control. Research in this area focuses on the influence of internal conditions of water quality and benthic habitat on both the growth and survival of individual organisms and on whole populations and communities. A key objective in this work has been to formulate models that can predict how valued species can be expected to respond to changes in the supply of fresh water and water quality.

- Salinity patterns and variability directly affect recruitment, survival, and growth of many animals that live in Florida Bay and that use Florida Bay as a nursery ground. We have sufficient information on about a dozen key species to predict how they will respond to future salinity conditions that might arise from altered freshwater inflow into Florida Bay.
- Habitat, tidal amplitude, freshwater inflow to Florida Bay, and salinity were the most widely influential variables explaining density in 11 forage species in a meta-analysis of data from historical surveys. Seagrass density and tidal amplitude were significant for 10 species, seagrass type and freshwater inflow were significant for nine species, and salinity was significant for seven species.
- Analysis of historical data indicates that water management affects the productive capacity of Florida Bay. This information has been used to predict the annual catch of pink shrimp in the Dry Tortugas fishery based on upstream hydrologic conditions in the Everglades.
- Recent findings discount earlier concerns that seagrass die-off and subsequent plankton blooms signaled a fundamental change in the food web. The abundance of bay anchovy in the West Region, one signal of a possible shift, has fluctuated since it reached a maximum in 1995. The diversity and overall abundance of canopy-dwelling fauna has increased since 1995 without a return to the original *Thalassia*-dominated seagrass canopy.
- Seagrass diversity may determine faunal density. A principal components analysis suggested that faunal species have affinities to certain seagrass types—*Thalassia, Halodule, Syringodium,* or macroalgae. Seagrass type was significant in explaining a meta-analysis of faunal density in Florida Bay. Faunal density in relation to seagrass type varied differently depending on faunal species. No species favored pure *Thalassia.*
- Characteristics of the bottom and shoreline habitats affect abundance and community composition. Mangrove prop root habitats in northeastern Florida Bay have significantly more fish larvae than nearby, open-water sites or nearshore areas without mangroves.
- Fishing affects fish populations. According to a comparison of the length-frequency distribution inside and outside of an area in Everglades National Park protected from recreational fishing affects the size structure of gray snapper. Evidence of overfishing is seen in gray snapper and other species on the reef tract.

- Spatial variation in influencing factors (*e.g.,* freshwater inflow, tidal mixing) is reflected in distinct regional patterns of species distributions, community composition, and trophic composition. Postlarval shrimp enter the bay preferentially where tidal flows are greatest. Peak concentrations of postlarval pink shrimp are roughly an order of magnitude greater in passes leading into the West Region from the Gulf of Mexico than in channels to Florida Bay through the Florida Keys.
- The food web shows the same regional structure as seen in the variation of circulation, salinity, and water quality. Based on stable isotope analyses, the central region has a strongly seagrass-based trophic structure, whereas the northwestern bay has a more plankton-dominated trophic structure. The Northeast Region has a non-seagrass-based diet (more likely water-column based). The trophic structure of the southwestern bay is supported by macroalgae.
- Temporal variation in recruitment strength of spiny lobster, snapper, and pink shrimp is related to regional oceanographic processes, especially the Tortugas gyres.
- High methylmercury in Florida Bay and its biota may have a local source in the bay. Sources of elevated mercury concentrations in fish from northeastern Florida Bay include (1) methylmercury in runoff from the Everglades and (2) *in situ* mercury methylation in sediments from both the mangrove transition zone and the open bay itself. Mercury concentrations seem to be higher along a Taylor River–Little Madeira Bay sampling transect than along a C-111 canal–Joe Bay transect. These data suggest that the urban and agricultural runoff that more strongly influences the C-111 canal–Joe Bay transect is not the most important source of mercury to the bay and its biota.

Loss of sponges may have reduced water clarity and affected seagrass recovery. Recovery of the largest and most abundant species has been extremely slow following a die-off in the early 1990s. Sponges are efficient filters of small (<5 µm) planktonic particles. At pre-die-off (pre-1992) densities, sponges in Florida Bay may have been capable of filtering the entire water column in one day. At present densities, filtering takes an estimated four days.

Chapter 3

Ecosystem History

Lead Author G. Lynn Wingard (USGS, Reston)
Contributors Tom Cronin (USGS) and William Orem (USGS)

Introduction

Question*—What was the Florida Bay ecosystem like 50, 100, and 150 years ago?*

A critical part of understanding an ecosystem as a whole is to understand the natural patterns and cycles of change. However, changes in ecosystems take place at many time scales, from diurnal to millennial, and it is not practical or even possible to directly observe change at the longer time scales. The ability to accurately understand natural conditions and cycles of change within Florida Bay is crucial to successfully restore and preserve the bay and to meet the goals of the Comprehensive Everglades Restoration Plan (CERP). Information on the historical and current natural system allows restoration planners to establish realistic baseline conditions, restoration goals, and performance measures; create predictive models; and monitor the success of restoration efforts. Understanding past conditions and cycles of change also allows for better-informed planning, project implementation, and land-management decisions.

Although the ecosystem history and paleoecology of Florida Bay was not specifically identified by the Florida Bay Science Program as a strategic research question, these types of studies contribute to all five strategic questions. By their very nature, these studies are multidisciplinary and integrate data to provide a holistic picture of the environment over biologically significant time scales. This chapter summarizes ecosystem history research that has contributed to the Florida Bay Science Program.

Methodology

The history of an ecosystem may be recorded in two distinct modes: (1) human records, in the form of historical accounts, reports, or archived data; and (2) natural records preserved in the sediments. Both methods can provide valuable information, but the sediment record and associated paleoecologic data can be especially important because few monitoring programs have been in place long enough to provide sufficient data to establish the range of variability in ecosystem parameters over a significant period of time. Furthermore, monitoring or experimental data are absent prior to human influence on the environment. Ideally, both human records and natural records are retrieved, compiled, and compared to develop the most complete picture possible of the configuration of an ecosystem over time and of the spatial and temporal scale of changes to the system.

HUMAN RECORDS

Significant efforts have been made by a number of individuals and groups to compile data sets and historical records for the south Florida ecosystem and Florida Bay. It is not the purpose of this summary to list all of these compilations, but the following illustrate the variety of records available:

Robblee, M. B., et al. *(2000, 2001)*—A compilation of more than 34,000 historical salinity measurements from Florida Bay, beginning in 1947 and extending through 1995.

DeMaria, K. (1996)—Changes in the Florida Keys Marine Ecosystem Based upon Interviews with Experienced Residents—A compilation of "eyewitness" accounts of 75 individuals with more than 10 years' experience on Florida Keys and Florida Bay waters.

Smith, T. J. (2002a and unpublished data)—Historical reconstruction of vegetation from aerial photographs of selected islands within Florida Bay, dating from 1927. Areas of interest include the entirety of Everglades NP, Big Cypress NP, and the Water Conservation Areas.

Smith, T. J., et al. *(2002b)*—Digitally compiled set of scanned historical topographic sheets from the Everglades and south Florida available on CD–ROM.

SEDIMENT RECORDS

Retrieving historical information recorded in sediments involves basic principals of geology (principally the laws of superposition and "the present is the key to the past") and using a number of paleoecological and geochemical tools:

Assemblage analyses—the faunal and floral remains found in a sediment core allow inferences to be made about past environments, including salinity, substrate, and water quality, based on analoguous data from the present.

Biochemical analyses—organisms with calcareous skeletons record information about the water in which they secrete their skeletons. Stable isotope analyses and metal:calcium ratios in shells or coral skeletons can provide information on salinities and sources of water.

Geochemical analyses—radiogenic isotopes are used to determine the chronology of cores, and analyses of the geochemistry of the sediments (carbon, nitrogen, sulfur, and phosphorus, for example) provide data on changes in nutrient supply and sediment influx over time.

Each of these methods is limited by the resolution of the age model for sediment deposition. Typical geochronologic methods used on late Holocene sediments involve analyses of ^{210}Pb (lead), ^{137}Cs (cesium), ^{7}Be (beryllium), and ^{14}C (carbon) (see Holmes *et al.,* 2001, for explanation). The error term increases down-core, so that a typical core from eastern Florida Bay with a sedimentation rate of 1.0 cm/year and an error of ±0.08 cm/year will have an average age of 1900 years (±8 years) at a depth of one meter. Because of the error associated with increasingly older sediments, the annual banding of corals provides the most accurate age control, but only a few large corals have been found within Florida Bay that can be used to reconstruct past conditions.

Analyses of sediment cores from Florida Bay have been conducted principally by two different groups of researchers during the past ten years (Table 3.1): (1) the University of Miami/NOAA group (C. A. Alvarez Zarikian, P. L. Blackwelder, T. Hood, T. A. Nelson, P. K. Swart, L. P. Tedesco, H. R. Wanless, *et al.*) and (2) the USGS group (T. M. Cronin, G. S. Dwyer, R. B. Halley, C. W. Holmes, J. K. Huvane, S. E. Ishman, W. Orem, E. Shinn, D. A. Willard, G. L. Wingard, *et al.*). Both groups have sought out areas of sediment accretion with minimal sediment disturbance; however, they diverge in terms of benthic habitats (Holmes *et al.,* 2001; Nelsen *et al.,* 2002). The University of Miami/NOAA group has sought out cores from bare-bottom habitats in order to ensure the presence of well-laminated sediments undisturbed by roots. The USGS group has collected cores from banks stabilized by seagrass beds because these areas are subjected to minimal erosion during storms, so that the organisms being analyzed are trapped *in situ.* Both groups X-ray and physically examine the cores for signs of sediment disruption and use the radiogenic isotope profiles as assurance of minimal disturbance. These two divergent strategies have been beneficial by providing data from different regions and different environmental settings within Florida Bay. A comparison of the findings and results will be discussed below.

Previous Work

Prior to 1990, few paleoecological analyses of sediment cores had been conducted in Florida Bay. The Holocene core studies that had been done focused on the sediments themselves and the diagenesis of the sediments (Fleece, 1962), the mineralogy of the sediments (Taft and Harbaugh, 1964), and the origins of the material composing the sediments (Enos, 1977). In their study of the molluscan fauna of Florida Bay, Turney and Perkins (1972) examined cores to determine the persistence of subenvironments over time. They discuss the growth and migration of mudbanks based on their analyses. Wanless and Tagett (1989) performed an extensive study of cores to determine the depositional history of the mudbanks within Florida Bay. All of these studies provide important information on the sedimentation and geologic history of Florida Bay and allow the history of the late Holocene ecosystem to be more accurately interpreted.

Two studies were done in the 1980s on a coral from Lignumvitae Basin. Hudson *et al.* (1989) compared the growth of a 1-m-diameter *Solenastrea* to rainfall, temperature records, and human perturbations. They found a significant correlation between poor coral growth and construction of the Flagler Railroad. Smith *et al.* (1989) investigated the relationship between the fluorescent banding (a result of terrestrial runoff) of the same Lignumvitae Basin coral and the flow of water in Shark River and Taylor sloughs. A decline in freshwater flow (as indicated by the fluorescence) began around 1912, a date that corresponds to the construction of drainage canals carrying water from Lake Okeechobee to the Atlantic. Smith *et al.* (1989) found a statistically significant difference between mean fluorescence in the pre-canal segment (pre-1932) of the coral and in the post-canal segment (post-1932) of the coral. In addition, Smith *et al.* (1989) found evidence for a 4- to 6-year periodicity in the historical annual flow regimes that was no longer apparent in the Shark River Slough flow record. This periodicity corresponds to south Florida rainfall records. They concluded that prior to canal construction, the flow of fresh water in Shark River Slough was controlled by rainfall, but that as early as 1940, flow through the slough was reduced substantially and that the natural periodicity in flow regimes had been lost.

Table 3.1A *List of sediment cores analyzed in Florida Bay between 1990 and present. Abbreviations in square brackets following core location correspond to abbreviations on Figure 3.1 and were used by the original authors.*

General Core Location (Core ID)	Researchers	Analyses Done	Status/References
1 Joe Bay [JB]	Holmes Willard Wingard Ishman	^{210}Pb Geochronology Pollen Assemblages Molluscan Assemblages Foraminferal Assemblages	Holmes *et al.*, 1999; Willard *et al.*, 1997
2 Taylor Creek [TC] (T24) (TC-1, TC-1a, TC-2, TC2br)	Ishman Wingard Cronin Holmes Dwyer Willard Edwards Orem	Foraminferal Assemblages Molluscan Assemblages Ostracode Assemblages ^{210}Pb Geochronology Ostracode Biochemistry Pollen Assemblages Dinoflagellate Assemblages Sediment Geochemistry	Brewster-Wingard *et al.*, 2001; Cronin *et al.*, 2001; Dwyer and Cronin, 2001; Holmes *et al.*, 2001; Ishman *et al.*, 1996
3 Pass Key [PAK] (PK17D, PK37) (FB-1 Pass Key)	Wingard Cronin Ishman Halley Holmes Huvane Willard Edwards Orem	Molluscan Assemblages Ostracode Assemblages Foraminferal Assemblages Molluscan Biochemistry ^{210}Pb Geochronology Diatom Assemblages Pollen Assemblages Dinoflagellate Assemblages Sediment Geochemistry	Brewster-Wingard *et al.*, 1998a; Brewster-Wingard *et al.*, 2001; Cronin *et al.*, 2001; Halley and Roulier, 1999; Huvane and Cooper, 2001; Orem *et al.*, 1999a
4 Russel Bank [RB] (RB19A, RB19B) (RB19C) (FB-2)	Wingard Cronin Ishman Holmes Dwyer Willard Halley Edwards Orem	Molluscan Assemblages Ostracode Assemblages Foraminferal Assemblages ^{210}Pb Geochronology Ostracode Biochemistry Pollen Assemblages Molluscan Biochemistry Dinoflagellate Assemblages Sediment Geochemistry	Brewster-Wingard and Ishman, 1999; Brewster-Wingard *et al.*, 2001; Cronin *et al.*, 2001; Cronin *et al.*, 2002; Dwyer and Cronin, 2001; Halley and Roulier, 1999; Holmes *et al.*, 2001; Huvane and Cooper, 2001; Brewster-Wingard *et al.*, 1997; Orem *et al.*, 1999a
5 Park Key [PKK] (PKK23A)	Cronin, Dwyer Holmes	Ostracode Biochemistry ^{210}Pb Geochronolgy	Cronin *et al.*, 2001 Dwyer and Cronin, 2001; Holmes *et al.*, 2001
6 Bob Allen [BA] (BA6A) (FB-3)	Wingard Cronin Ishman Holmes Halley Willard Edwards Orem	Molluscan Assemblages Ostracode Assemblages Foraminferal Assemblages ^{210}Pb Geochronology Molluscan Biochemistry Pollen Assemblages Dinoflagellate Assemblages Sediment Geochemistry	Brewster-Wingard and Ishman, 1999; Brewster-Wingard *et al.*, 2001; Cronin *et al.*, 2001; Dwyer and Cronin, 2001; Halley and Roulier, 1999; Wingard *et al.*, 1995; Orem *et al.*, 1999a

Table 3.1A *List of sediment cores analyzed in Florida Bay between 1990 and present. Abbreviations in square brackets following core location correspond to abbreviations on Figure 3.1 and were used by the original authors. (continued)*

General Core Location (Core ID)	Researchers	Analyses Done	Status/References
7 Whipray [WH] (25B) (FB-4, FB-5)	Wingard Cronin, Dwyer Holmes Orem	Molluscan Assemblages Ostracode Geochemistry ^{210}Pb Geochronology Sediment Geochemistry	Trappe and Wingard, 2001; Cronin *et al.*, 2001; Holmes *et al.*, 2001; Orem *et al.*, 1999a
8 Rankin [RA]	Wingard Cronin, Dwyer Holmes Orem Shinn, Reich	Molluscan Assemblages Ostracode Geochemistry ^{210}Pb Geochronology Sediment Geochemistry, Lignin Phenols Sediment Trace Element Geochemistry	Unpublished data; report in progress
9 Jimmy Key [JK]	Wanless, Nelsen	Sedimentology, Geochronology	Nelsen *et al.*, 2002
(JK)	Hood Zarikian Swart Trefry and Metz Blackwelder, Capps O'Neal, Garte, Featherstone, Kang, Ellis	Foraminferal Assemblages Ostracode Assemblages, Ostracode Geochemistry Stable Isotope Geochemistry Geochemistry	
10 Oyster Bay [OB]	Wanless, Nelsen	Sedimentology, Geochronology	Alvarez Zarikian *et al.*, 2001; Nelsen *et al.*, 2002
(OB)	Hood Zarikian Swart Tedesco Trefry and Metz Blackwelder, Capps O'Neal, Garte, Featherstone, Kang, Ellis	Foraminferal Assemblages Ostracode Assemblages, Ostracode Geochemistry Stable Isotope Geochemistry Pollen Assemblages Geochemistry	
11 Coot Bay [CB]	Wanless, Nelsen Trefry and Metz Blackwelder, Capps O'Neal, Garte	Sedimentology, Geochronology Geochemistry	Nelsen *et al.*, 2002

Summary of Ecosystem History and Paleoecology Research

Following are the significant research findings to date of the Ecosystem History-Paleoecology research groups, organized into the five principal Florida Bay research questions (Table 3.2).

Question 1*—How and at what rates do storms, changing freshwater flows, sea level rise, and local evaporation and*

Table 3.1B *List of corals analyzed in Florida Bay between 1990 and present. Numbers in parentheses following the location are shown in Figure 3.1 and were used by the original authors.*

Location	**Researchers**	**Analyses Done**	**References**
Lignumvitae (SFB-5)	Swart, Healy, *et al.*	Stable isotopes (C and O) Fluorescence, trace elements (Ba)	Swart *et al.*, 1996; Swart *et al.*, 1999
Lignumvitae Basin (referred to as Peterson Key Basin by Smith *et al.*) (SFB-6)	Smith, Hudson	Fluorescence, growth bands	Smith *et al.*, 1989; Hudson *et al.*, 1989
Blackwater Sound (SFB-3)	Swart, Healy, *et al.*	Stable isotopes (C and O)	Swart *et al.*, 1999
Arsenicker Keys (SFB-7)	Swart, Healy, *et al.*	Stable isotopes (C and O)	Swart *et al.*, 1999
Rabbit Key (SFB-14)	Swart, Healy, *et al.*	Stable isotopes (C and O)	Swart *et al.*, 1999
Bob Allen Key Basin/ Calusa Key (SFB-16)	Swart, Healy, *et al.*	Stable isotopes (C and O)	Swart *et al.*, 1999
Duck Key Basin/The Bogies (SFB-23)	Swart, Healy, *et al.*	Stable isotopes (C and O)	Swart *et al.*, 1999
Lignumvitae Basin (SFB-40)	Swart, Healy, *et al.*	Stable isotopes (C and O)	Swart *et al.*, 1999
Lignumvitae Basin (SFB-42)	Swart, Healy, *et al.*	Stable isotopes (C and O)	Swart *et al.*, 1999
Manatee Key (SFB-45)	Swart, Healy, *et al.*	Stable isotopes (C and O)	Swart *et al.*, 1999

precipitation influence circulation and salinity patterns within Florida Bay and outflows from the bay to adjacent waters?

- Salinity in Florida Bay is more strongly correlated with rainfall than with any other single factor, and the periodicity in salinity and rainfall data suggests linkages to El Niño/Southern Oscillation (ENSO) climatic patterns.
- Anthropogenic influences play a secondary role to rainfall in determining salinity for Florida Bay as a whole, but they may be a factor in the magnitudes of salinity variations seen in recent times. Additionally, anthropogenic factors may act on a local basis to influence salinity patterns.
- Declines in diversity and increases in dominance of salinity-tolerant species have occurred since the 1980s in several benthic invertebrate groups in different regions of Florida Bay.

Question 2*—What is the relative importance of the influx of external nutrients and of internal nutrient cycling in determining the nutrient budget for Florida Bay? What mechanisms control the sources and sinks of the bay's nutrients?*

- Uranium isotope studies indicate that the phosphorus contamination at the northern end of Taylor Slough appears to be fertilizer-derived. However, phosphorus contamination in Taylor Slough diminishes to background by mid slough; therefore, Taylor Slough does not appear to be a source of nutrients to eastern Florida Bay.
- Eastern Florida Bay does appear to be a source of nutrients to the mangrove zone at the southern end of Taylor Slough.
- Sediments from eastern Florida Bay (especially from sites near Pass Key and Russell Key banks) show indications of recent nutrient (carbon [C], nitrogen [N], and phosphorus [P]) enrichment (1980 to present). This nutrient enrichment could be related to recent microalgal blooms and seagrass die-off within Florida Bay.
- Downcore profiles of dated cores from central Florida Bay (Whipray Basin) show that productivity events have occurred historically in Florida Bay.
- A large, multidecadal productivity event in the

Table 3.2 *Summary of research on ecosystem history by topic.*

Research Questions	**Type of Analysis** **Faunal and Floral Assemblage Analysis**	**Biochemical Analysis**	**Geochemical Analysis**
1 How and at what rates do storms, changing freshwater flows, sea levels, and local evaporation/precipitation influence circulation and salinity patterns within Florida Bay and outflows from the bay to adjacent waters?	Wingard *et al.*, 1995; Ishman *et al.*, 1996; Brewster-Wingard *et al.*, 1997; Brewster-Wingard *et al.*, 1998a,b; Brewster-Wingard and Ishman, 1999; Alvarez Zarikian *et al.*, 2001; Brewster-Wingard *et al.*, 2001; Cronin *et al.*, 2001; Huvane and Cooper, 2001; Trappe and Wingard, 2001; Cronin *et al.*, 2002; Nelsen *et al.*, 2002	Smith *et al.*, 1989; Halley *et al.*, 1994; Healy, 1996; Swart *et al.*, 1996; Halley and Roulier, 1999; Swart *et al.*, 1999; Alvarez Zarikian *et al.*, 2001; Dwyer and Cronin, 2001; Cronin *et al.*, 2002; Nelsen *et al.*, 2002	Holmes *et al.*, 2001; Nelsen *et al.*, 2002
2 What is the relative importance of the influx of external nutrients and of internal nutrient cycling in determining the nutrient budget for Florida Bay? What mechanisms control the sources and sinks of the bay's nutrients?		Swart *et al.*, 1999	Orem *et al.*, 1997; Orem, 1998; Orem *et al.*, 1999a; Gough *et al.*, 2000; Nelsen *et al.*, 2002
3 What regulates the onset, persistence, and fate of planktonic algal blooms in Florida Bay?	Huvane and Cooper, 2001	Swart *et al.*, 1999	Orem *et al.*, 1999a Holmes *et al.*, 2001
4 What are the causes and mechanisms for the observed changes in seagrass communities of Florida Bay? What are the effects of changing salinity, light, and nutrient regimes on these communities?	Brewster-Wingard *et al.*, 1998b; Brewster-Wingard and Ishman, 1999; Brewster-Wingard *et al.*, 2001; Cronin *et al.*, 2001; Trappe and Brewster-Wingard, 2001	Dwyer and Cronin, 2001	Orem *et al.*, 1999a, b; Holmes *et al.*, 2001
5 What are the relationships between environmental and habitat changes and the recruitment, growth, and survivorship of animals in Florida Bay?	Brewster-Wingard *et al.*, 2001 (mollusks only)		Holmes *et al.*, 2001

mid-1700s, which was characterized by greatly elevated levels of organic carbon and nitrogen, was observed in two cores from Whipray Basin. Interestingly, although organic carbon and total nitrogen were high, total phosphorus was not elevated during this time span. This time period (the Little Ice Age) may correspond to a period of higher rainfall in the Everglades and more extensive land runoff into Florida Bay, which may have triggered the productivity event.
- Organic carbon records from Jimmy Key indicate that hurricanes help flush organic carbon out of Florida Bay.

Question 3*—What regulates the onset, persistence, and fate of planktonic algal blooms in Florida Bay?*
- Surface sediments from eastern Florida Bay show indications of nutrient (carbon, nitrogen, and phosphorus) enrichment from 1980 to the present, which could be related to recent microalgal blooms within Florida Bay.
- The multidecadal productivity event of the 1700s noted in sediment geochemical analyses from Whipray Basin cores may represent a period of extensive algal blooms.
- Downcore changes in abundance and assemblages of dinoflagellates and diatoms have been examined at some sites in Florida Bay. Additional studies of the ecology of dinoflagellates and diatoms are needed to interpret the findings in terms of bloom conditions.

Question 4*—What are the causes and mechanisms for the observed changes in seagrass community of Florida Bay? What are the effects of changing salinity, light, and nutrient regimes on these communities?*
- Frequent changes have occurred in the relative abundance of epiphytal species of ostracodes and mollusks over the past century.
- Prior to mid-20th century, epiphytal ostracodes were relatively rare at sites in central and eastern Florida Bay, suggesting a greater abundance and/or density of subaquatic vegetation (SAV) over the past 50 years than in the first half of the 20th century. Epiphytal mollusks, although not rare, increased significantly in relative abundance from approximately 1940 onward at most sites. These data raise the question of whether dense and abundant seagrass beds are natural in Florida Bay; if the answer is no, these results have very significant implications for restoration.
- A decline occurred in SAV-dwelling ostracodes and mollusks in cores from Whipray, Russell, Bob Allen, and Pass keys between the 1970s and 1980s.
- The relative abundance of mollusks with a strong preference for *Thalassia* has declined since approximately 1970 in eastern Florida Bay and since 1910 in Whipray, whereas SAV generalists have increased. These findings may indicate an increase in the amount of macrobenthic algae relative to *Thalassia.*
- Downcore profiles of lignin phenols from a Pass Key core show large variations in lignin phenol distributions over short time intervals. These variations reflect the proximity of this site to the mangrove zone along the coast and the outlet of Taylor Creek.
- At Bob Allen Keys, the lignin-phenol distributions show downcore variations in the abundance of seagrass over time. At Bob Allen, seagrass abundance appears to have been increasing since a recent minimum around 1960.

Question 5*—What are the relationships between environmental and habitat changes and the recruitment, growth, and survivorship of animals in Florida Bay?*
- Declines in molluscan faunal diversity have occurred during the latter half of the 20th century.

Salinity Patterns and Trends

The majority of the ecosystem history-paleoecology research since 1994 has been focused on addressing the question of salinity patterns and influx of fresh water into Florida Bay. The most critical issue in the CERP is to restore more natural patterns of freshwater flow through the terrestrial ecosystem and into the estuaries and coastal areas. Restoring natural flow to Florida Bay includes restoring the timing, delivery, quantity, and quality of the water to the bay. In order to re-create natural freshwater flow patterns, it is essential to understand both the natural patterns of freshwater flow and the natural sources of water prior to significant human alteration of the system. Changing salinity patterns, whether natural or anthropogenically induced, affect the fauna and flora of the bay. The first step in restoration is to understand the natural patterns and be able to set targets and performance measures for restoration.

An important tool in the restoration effort is modeling the freshwater flow from the Everglades to Florida Bay under different restoration scenarios. The "Natural System Model" (NSM) of the South Florida Water Management District (SFWMD) was developed in part to meet these needs. The NSM is driven by rainfall. Efforts to calibrate model-simulated freshwater flow in the Everglades using historical rainfall records have only been partially successful due to the lack of historical data on natural conditions prior to water-diversion activities. A similar lack of long-term instrumental records of salinity in adjacent Florida Bay has limited our ability to set restoration targets for aquatic ecosystems.

The research projects summarized below have addressed the lack of historical data on Florida Bay salinity and freshwater influx. One goal of these studies has been to determine the natural patterns of salinity change and freshwater influx. A second goal has been to distinguish the natural patterns of change from changes in the salinity regime caused by water diversion in the Everglades during the 20th century. This section summarizes the methodology applied and the progress made towards these goals.

Methods

Both the University of Miami/NOAA and USGS research groups have used basic assemblage analyses and biochemical analyses. They use these forms of analysis to extract salinity information from sediment cores dated using ^{210}Pb and other methods of establishing chronology (Table 3.1). Interpretations of faunal and floral assemblages are based on observations of the modern ecology of the organisms being studied. These assemblages represent a death assemblage and are therefore time-averaged. However, decadal-scale resolution can be obtained from the assemblages because the Florida Bay environment has relatively rapid sedimentation rates, little erosion, and low transport of silt and sand-sized sediments (Turney and Perkins, 1972; Halley *et al.,* 1997). Additional support that a death assemblage accurately represents a life assemblage, and therefore a discrete environment, is obtained when several faunal groups are analyzed and compared from a single sample and the condition of the shell material is considered.

Biochemical methods are based on the analyses of individual shells and therefore capture the salinity record of the time during which that shell was secreted. Although these analyses can provide an almost instantaneous record, the data are still limited by the temporal resolution of the dating-method for the sample from which the shell was extracted.

Dwyer and Cronin (2001) and Cronin *et al.* (2001, 2002) have used the ratio of magnesium to calcium (Mg:Ca) ions in ostracode shells to reconstruct salinity from Florida Bay cores. They have examined the ecology and shell chemistry of modern ostracodes in Florida Bay and have demonstrated that the Mg:Ca ratios in the calcium carbonate shells of ostracodes are strongly influenced by the salinity and temperature in which the organism secretes its shell. They have focused the shell biochemical studies on the epiphytal species *Loxoconcha matagordensis,* although in some cores, *Peratocytheridea setipunctata* is analyzed. Based on their ecological studies, it appears that adult *L. matagordensis* secrete their shells principally during spring or summer seasons (Cronin *et al.,* 2001). In Florida Bay, warm-season temperatures vary little over interannual timescales, so temperature is considered less important than salinity in influencing ostracode Mg/Ca. However, additional research is warranted.

Alvarez Zarikian *et al.* (2001) and Nelsen *et al.* (2002) have conducted stable isotopic analyses (δ^{18}O and δ^{13}C) on ostracodes and benthic foraminifera to extract information on rainfall, freshwater influx, and evaporation to infer salinity conditions. Changes in δ^{18}O can be correlated to changes in salinity, and those in δ^{13}C can indicate changes in the influx of organic material. Evaporation of marine and brackish water preferentially removes the lighter isotopes (^{16}O) and enriches the water with heavier isotopes (^{18}O). An increase in δ^{18}O indicates increased evaporation and therefore, increased salinity. In Florida Bay, however, interpretation of the δ^{18}O value is complicated by the influx of fresh water from the terrestrial Everglades. Interpretation of δ^{13}C is also complicated in coastal waters. Under normal marine conditions, the δ^{13}C of calcareous organisms is principally controlled by physiological processes However, in areas where fresh and marine waters mix, variations in the dissolved inorganic carbon are probably the dominant factor. Freshwater from the Everglades is typically isotopically depleted in δ^{18}O and δ^{13}C, whereas the marine waters from the gulf or Atlantic are enriched in δ^{18}O and δ^{13}C. By comparing and correlating δ^{18}O to δ^{13}C, researchers can interpret the relative influence of fresh and marine waters at the core site. (See Halley *et al.,* 1994; Swart *et al.,* 1996, 1999; and Alvarez Zarikian *et al.,* 2001, for a detailed explanation of the environmental factors that influence δ^{18}O and δ^{13}C.)

Stable isotopic analyses have also been used to analyze corals within Florida Bay (Healy, 1996; Swart *et al.,* 1996, 1999) and on a reef affected by Florida Bay waters (Halley *et al.,* 1994). The annual banding of corals provides a very accurate means of determining the age of the isotopic samples being analyzed. Halley and Roulier (1999) used whole mollusk shells (*Brachidontes exustus* and *Transennella* spp.) from radiometrically dated cores for δ^{18}O and δ^{13}C analyses.

Findings

The following summary is intended to synthesize briefly the key results from paleoecologic studies completed in the past 10 years. The reader is referred to the original papers for detailed results, methods, and evidence supporting the conclusions.

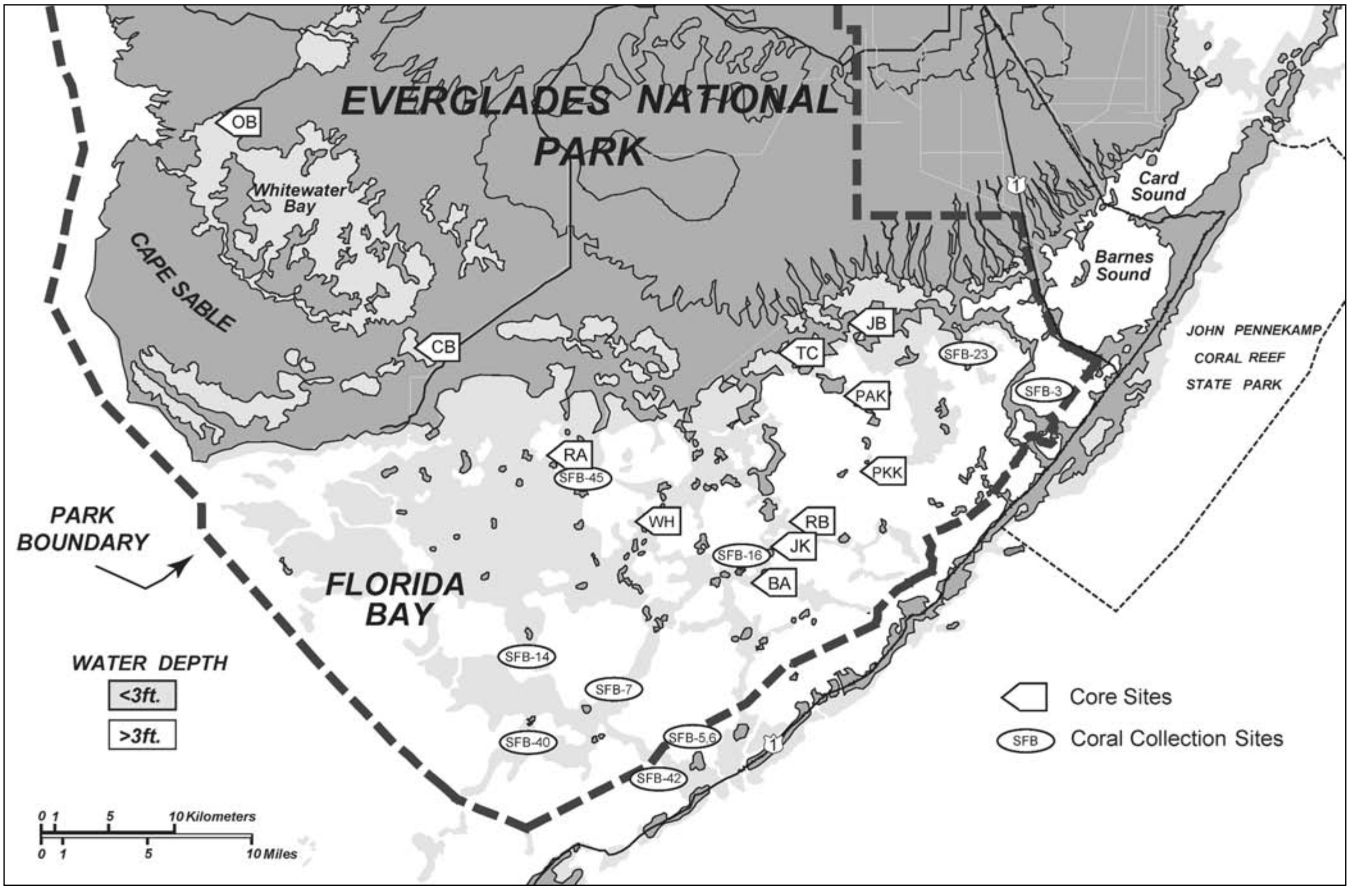

Figure 3.1 *Location of sites within Florida Bay where cores and corals have been analyzed for paleoecologic information. Table 3.1 lists details about the investigations. Sediment cores listed in Table 3.1A are identified as follows on the map: Bob Allen = BA; Coot Bay = CB; Jimmy Key = JK; Joe Bay = JB; Oyster Bay = OB; Park Key = PKK; Pass Key = PAK; Rankin Basin = RA; Russell Bank = RB; Taylor Creek = TC; Whipray Basin = WH. Coral collection sites (SFB) are listed in Table 3.1B.*

- Salinity in Florida Bay is more strongly correlated with rainfall than with any other single factor, and a periodicity in salinity and rainfall data suggests linkages to El Niño/Southern Oscillation climatic patterns.

Nelsen *et al.* (2002) and Alvarez Zarikian *et al.* (2001) concluded on the basis of multidisciplinary studies of cores from Oyster Bay and Jimmy Key (Table 3.1, Figure 3.1) that "anthropogenic influences play a secondary role to natural influences such as regional rainfall" (Nelsen *et al.*, 2002: 445). Their analyses showed that salinity responded directly to regional rainfall and that "microfaunal data also indicate direct correlation to rainfall patterns for temporal scales ranging from decadal down to the limit-of-resolution of geochronology" (Nelsen *et al.*, 2002). Even at the mouth of Shark River Slough they found rainfall to be the dominant driver.

Dwyer and Cronin (2001) compared downcore salinity trends derived from Mg:Ca ratios from Russell Bank, Park Key, and Bob Allen Key mudbank (Table 3.1; Figure 3.1) to historical rainfall records. They found good correspondence between rainfall and the paleosalinity data. In addition, they found four extreme low-salinity periods that corresponded to strongly negative values in the El Niño/Southern Oscillation (ENSO) index.

Cronin *et al.* (2002) conducted time-series analyses on ostracode Mg:Ca ratios and ostracode abundance data from the Russell Bank core (Table 3.1, Figure 3.1). They determined that based on the Mg:Ca ratio, a 5.6-year salinity periodicity existed and that all salinity proxy data analyzed showed 6- to 7-year, 8- to 9-year, and 13- to 14-year periods of variability. They compared the paleosalinity data to climatic factors and conducted a time-series analysis on south Florida winter rainfall and the Southern Oscillation Index (SOI), which suggested ~5-, 6- to 7-, 8- to 9-, and 13- to 14-year cycles. Paleoproxies and climate data were compared using cross-spectral analyses. The results suggest "that regional rainfall variability influences Florida Bay salinity over interannual and decadal timescales and that much of this variability may have its origin in climate variability in the Pacific Ocean/atmosphere system." It may also be related to ENSO (Cronin *et al.,* 2002).

Swart *et al.* (1999), in an analysis of coral records from Florida Bay (Table 3.1), mentioned that "a superficial comparison between precipitation from the lower east coastal region of south Florida appears to indicate that periods of lowest rainfall relate to times when the salinity was highest." However, a comparison of the $\delta^{18}O$ of the coral skeleton from Lignumvitae Basin indicates no statistically significant correlation. Perhaps this is due to miscalculations in the age of the coral bands or to the lack of accurate rainfall data for that basin. They conducted spectral analyses on the salinity values calculated from the corals and found three statistically significant signals at 4–7 years, 28 years, and 12–14 years. They pointed out that the most significant periodicity, the 4–7-year cycle, which accounts for greater than 20% of the variance, may be related to ENSO cycles (Swart *et al.,* 1999: 392–393).

These short-term cycles in salinity that have been found in recent research are consistent with the findings of Smith *et al.* (1989) in their examination of fluorescent banding in the Lignumvitae Basin coral. They found "strong evidence for a regular 4- to 6-year periodicity in the historical annual flow regimes: years of low flow alternated with years of high flow." (Smith *et al.,* 1989: 280)

- Anthropogenic influences play a secondary role to rainfall in determining salinity for Florida Bay as a whole, but they may be a factor in the magnitude of salinity variations seen in recent times. Additionally, anthropogenic factors may act on a local basis to influence salinity patterns.

Dwyer and Cronin (2001) noted a shift to high-amplitude salinity oscillations after 1950 as indicated by the Mg:Ca ratio from cores in eastern Florida Bay (Table 3.1, Figure 3.1). These high-amplitude oscillations corresponded to a period of increased variability in rainfall, but human alteration of freshwater flow may also have been a factor.

Brewster-Wingard and Ishman (1999) noted similar increases in the amplitude of salinity oscillations after ~1940, as indicated by foraminiferal and molluscan assemblages in cores from Bob Allen and Russell banks (also examined by Dwyer and Cronin; Table 3.1, Figure 3.1). They did not conduct any statistical comparisons but they did note that the cause could be meteorological patterns, anthropogenic changes to freshwater flow, or a combination of factors.

Clear evidence of decreasing freshwater influence during the 20th century was found in the northern transition zone at the mouth of Taylor Creek and at Mud Creek near Joe Bay by Holmes *et al.* (1999) and Willard *et al.* (1997) (Table 3.1, Figure 3.1). The changes in the molluscan assemblage from an oligohaline-mesohaline fauna to a predominantly polyhaline fauna could be explained by the local alteration of flow through Taylor Slough, by changes in rainfall that ultimately affected the flow, or by a combination of both.

Alvarez Zarikian *et al.* (2001) and Nelsen *et al.* (2002) presented evidence of the local effects of water-management practices in their detailed analyses of the Oyster Bay core (Table 3.1, Figure 3.1). Several anthropogenic factors affected Oyster and Whitewater bays during the 1980s: the beginning of SFWMD's "Rainfall Plan" for managing flow, the shift of water from Shark River Slough basin into Taylor Slough basin, and the closing of Buttonwood Canal. Alvarez Zarikian *et al.* (2001) noted that a significant decline in ostracode diversity and abundance occurred around 1980, which could have been linked to these anthropogenic changes or could have been due to the mid-1980s drought. Nelsen *et al.* (2002) illustrated that regardless of the cause of the faunal changes in Oyster Bay, a comparison of rainfall and flow records showed that the most significant correlations were prior to 1960, during the "pre-management period," and after 1983, during implementation of the Rainfall Plan.

- Declines in diversity and increases in dominance of salinity-tolerant species have occurred since the 1980s in several benthic invertebrate groups in different regions of Florida Bay.

Alvarez Zarikian *et al.* (2001) and Nelsen *et al.* (2002) saw two periods of reduced diversity in the benthic microfauna at Oyster Bay: mid-1930s to late 1940s and late 1970s to the time of core recovery in 1994. Nelsen *et al.* (2002: 444) related the faunal changes to "the changing nature of the salinity field at Oyster Bay after ~1980." At Jimmy Key, the periods of reduced diversity were from the mid to late 1930s and late 1970s to core recovery in 1997, which they also related to changes in the salinity field. Prior to 1950, declines in ostracode abundance and diversity were followed by rapid recovery. Following the crash in the late 1970s, the population has not recovered. The ostracode and foraminiferal faunas in the period from the late 1970s on are dominated by individual species (*Peratocytheridea setipunctata* and *Ammonia parkinsoniana typica*), interpreted as showing survivor-type dominance. *Peratocytheridea setipunctata* is known to tolerate extreme salinity fluctuations from less than 5 practical salinity units (psu) to 42 psu (Alvarez Zarikian *et al.,* 2001: 140).

Brewster-Wingard *et al.* (2001) and Trappe and

Brewster-Wingard (2001) noted similar patterns in the molluscan assemblages from cores in eastern and central Florida Bay. In every core examined, *Brachidontes exustus*, a mollusk known to tolerate large salinity variations (10–44 psu measured in the field) and reduced water quality, became the dominant species in the upper portions of the cores from approximately 1980 on. The exception was in Whipray Key, where *Brachidontes* reached its peak in the late 1970s and then declined. In almost every core, with the exception of the Taylor Creek core, increases in the relative abundance of *Brachidontes* corresponded to declines in molluscan diversity. Brewster-Wingard *et al.* (2001) interpreted this as opportunistic dominance.

Status of Research

ACCOMPLISHMENTS AND QUESTIONS RESOLVED

- Most researchers have reached the consensus that rainfall and climatic patterns are the strongest driving factor in determining Florida Bay salinity patterns. Anthropogenic influences play a secondary role.
- An indication of an increasingly stressed system is the dominance of species that tolerate extreme fluctuations in salinity. This pattern of dominance is unprecedented in cores prior to the latter quarter of the 20th century.
- Careful comparison of faunal data and biochemical data to instrumental salinity records for the past 50 years has demonstrated the validity of using paleoecologic techniques to interpret downcore salinity patterns that extend beyond instrumental data records.
- Increasing the coverage of Florida Bay by adding new cores will elucidate bay-wide trends.
- Increased refinement of proxy data has allowed more accurate interpretation of downcore results.

RECENT ACCOMPLISHMENTS

- Ground-truthing of ostracode Mg:Ca-ratio-based paleosalinity reconstruction with instrumental salinity records (1950–present) confirms that the Mg:Ca method yields salinity values within 1–4 psu of salinity maxima and minima over the past 50 years.
- A method of reducing molluscan-assemblage data to a single salinity value has been developed.
- The hypothesis that decadal patterns of salinity are driven by climatological factors, including rainfall, was supported by analyses of the sediment-core paleosalinity record from Rankin Lake. The Rankin Lake paleosalinity record matches records obtained in earlier studies of Russell Key and Bob Allen Key.

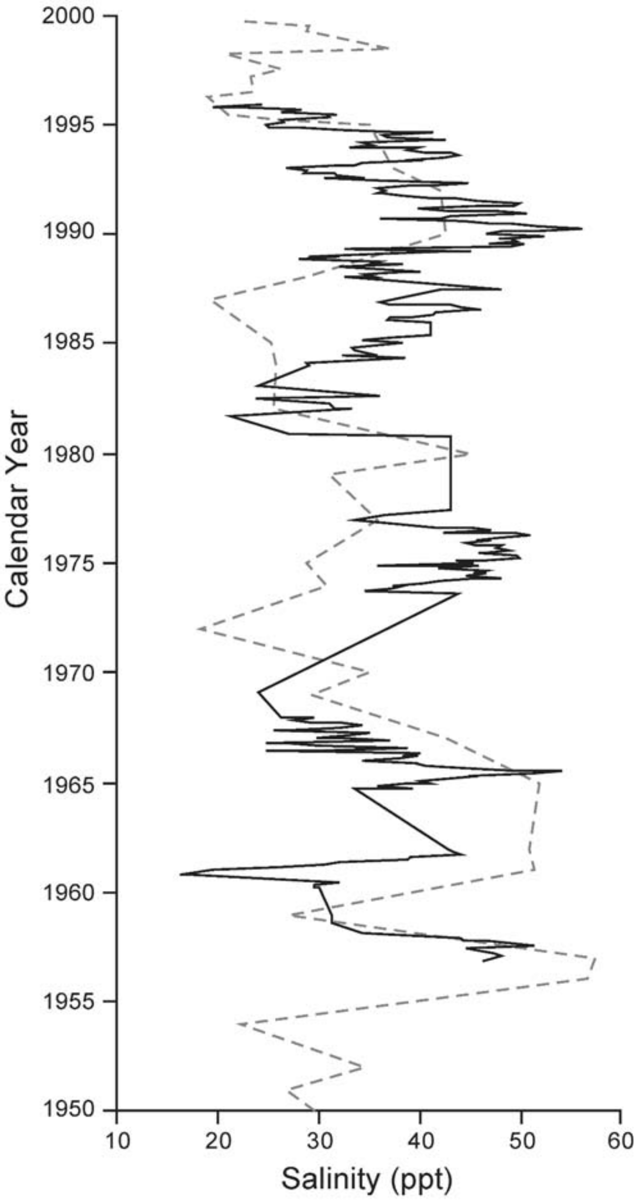

Figure 3.2 *Comparison between instrumental salinity (black line) and salinity calculated from Mg/Ca ratios of ostracodes in Russell Bank core 19B (dashed gray line). Instrumental data from Robblee* et al. *(2000, 2001). The measured instrumental salinity curve was constructed by computing monthly mean values for Whipray, Rankin, and Bob Allen Basins and then obtaining a grand mean for the central region.*

- The Rankin Lake core indicates the strong influence of freshwater at the site near the bottom of the core.

Cronin and Dwyer (Cronin *et al.*, 2003) have tested the accuracy of their downcore salinity estimates based on a comparison of the Mg:Ca ratios in ostracode shells to historical instrumental salinity records from the Russell Bank. These historical records date back to

1947 and have been compiled by Robblee *et al.* (2000, 2001). Figure 3.2 compares the Mg:Ca paleosalinity curve against the instrumental record of salinity for the past 50 years. Both the instrumental records and the paleosalinity curve show large decadal swings in salinity in central Florida Bay from salinities exceeding 50 psu to those in the low 20s. For salinity maxima during the early 1990s, late 1970s, and mid-1960s, the difference between paleosalinity and instrumental salinity was approximately –1.1., 0.9, and 3 psu, respectively. The differences in the four periods of Florida Bay salinity mimima (1993–1995, the 1980s, the late 1960s to early 1970s, and near 1960) were 0.3 psu, 3.6 psu, 1.9 psu, and 0.8 psu, respectively. Given the temporal gaps in the instrumental record, the error on the sediment core age estimates, and the spatial and temporal averaging used for both records, these comparisons provide a remarkable confirmation that the Mg:Ca-based shell chemistry method yields accurate estimates of past salinity to within less than 1–4 psu.

Wingard (unpublished report) has developed a method to reduce the core samples to a single averaged salinity value for molluscan faunal assemblage data. Presence and absence data for live mollusks and for numerous environmental parameters, including salinity, have been recorded in Florida Bay since 1995 (http://sofia.usgs.gov/exchange/flaecohist/). These salinity data have been compiled and examined statistically to determine the mean, median, minimum, maximum, standard deviation, and confidence interval for each mollusk species observed live. Any species with a confidence level above 5 or number of observations less than 15 were deleted from the modern database. The modern salinity information was then combined with data from a core sample. It was then weighted based on the percent abundance of each species present in the sample core assemblage, and a cumulative average salinity value was produced for the entire sample. This method has allowed the average salinity value to be directly compared to instrumental records of salinity and can be used by modelers.

A preliminary comparison (Wingard, unpublished report) of the cumulative, weighted-average salinity data from three cores and the instrumental records of salinity compiled by Robblee *et al.* (2000, 2001) has been completed. It is important to note that this method is only as good as the modern data upon which it is based. During the period of observations between 1995 and 2000, salinity values in excess of 48 psu were never recorded, and only four site surveys were conducted in water exceeding 40 psu during the course of the study (Brewster-Wingard *et al.,* 2001, and unpublished data). This lack of high-salinity observations means that the modern database is skewed toward lower salinities. Despite this problem, the cumulative weighted averages show downcore trends and can be compared with the instrumental records because they give a precise numerical value, unlike standard analyses of assemblage data.

ONGOING RESEARCH

- Dwyer and Cronin are continuing to examine the ecology of the ostracode *Loxoconcha matagordensis* in order to refine their understanding of the role of temperature versus salinity in the Mg:Ca ratios in the shells. They also plan to examine the different magnesium ionic concentrations of fresh versus marine waters. These studies may provide another way to determine past freshwater influx into Florida Bay.
- Wingard, Stamm, and Murray are conducting growth experiments and calibrating water chemistry to shell chemistry for the molluscan species *Chione cancellata.* These experiments should allow them to be able to extract salinity data from the metal:Ca ratios and stable isotopic ratios (^{18}O and δ^{13}C) in the individual growth increments of the shell.
- Wingard, Cronin, Dwyer, Orem, Holmes, and others are completing analyses on cores from Rankin Lake. Results will help determine whether hypersalinity bull's-eyes noted in this area over the past 15 years are a recent phenomenon or if they existed under natural flow conditions.
- Wingard, Stamm, and Murray are conducting salinity-stress tests on common molluscan species found within modern Florida Bay. They are also testing sediment cores in order to refine the average salinity values for each molluscan species used in the cumulative, weighted-sample, average-salinity method discussed above.

UNRESOLVED QUESTIONS AND NEEDED RESEARCH

- How did salinity change in Florida Bay on a seasonal basis prior to significant alteration of freshwater flow into the bay? What were the extremes in seasonal change?
  - Wingard and others are researching the biochemistry of individual molluscan growth increments to address this question.
- Did hypersalinity zones form in Florida Bay prior to instrumental data recordings in the past two decades? If so, how often, what was the duration, and were these linked to natural climatic patterns or to anthropogenic change?
  - Examination of Rankin Core by USGS groups is beginning to address these questions.
- Additional cores are needed from critical areas within the bay, such as from transects along the

margins of northern and eastern Florida Bay and the Cape Sable–Ten Thousand Islands area, where short-term salinity oscillations are large.

- Attempts should be made to locate areas with records extending back into the early 1800s in order to examine 50–100 years of salinity patterns prior to any alteration of the environment.
- A better understanding of the controls on shell biochemistry should be developed, especially in coastal areas where fresh and marine waters mix. This effort should include refining our understanding of the salinity and temperature effects on shell chemistry by integrating trace elemental (principally Mg-Ca, but also strontium [Sr] and barium [Ba]) analyses with stable isotopic analyses.
  - Zarikian and Swart plan to continue their stable isotopic studies of water, ostracodes, and corals.
  - Dwyer and Cronin are continuing their studies of Mg-Ca in water and ostracodes.
  - Swart, Zarikian, Dwyer, and Cronin hope to work together on the same cores, examining both isotopic and trace elements in ostracode and foraminifer shells.
- Knowledge of modern ecology of organisms being used in downcore studies should be refined.
  - Wingard and others are continuing tests *in situ* and in the laboratory on mollusks to determine tolerance to salinity extremes.
- Examine modern data (Montague and Ley, 1993. See discussion in Nelsen *et al.* (2002) to determine whether mean salinity or standard deviation in salinity exerts more control over benthic fauna and flora.
- A carbon budget for Florida Bay should be developed in order to contribute to a better understanding of the carbon isotope record of the cores and provide a better means for interpreting historical freshwater influx into the bay (Halley and Roulier, 1999).
- We need to perform additional "groundtruthing" of paleosalinity methods (Mg:Ca in ostracodes; cumulative, weighted-sample average of mollusks) by comparing the results of these methods on new, short sediment cores from key sites with the fairly continuous instrumental salinity record available since 1985.
- Calibrate Mg:Ca ratios in other ostracode species and apply them to new areas of study within the bay.
- Measured and reconstructed salinity and forcing factors (rainfall, evaporation, groundwater, and discharge from sloughs) should undergo more rigorous statistical analyses.
- Apply paleosalinity data to Natural System Model simulations to test the model's accuracy in predicting the trends determined from the paleorecord. Begin with paleosalinity data that has been "groundtruthed" by comparison with instrumental records of Robblee *et al.* (2000, 2001).

Nutrient Patterns and Trends

Restoration efforts to reestablish natural rates of freshwater discharge into Florida Bay potentially could cause additional harm to the bay if the quality of the water entering the system is not considered. It is essential to understand the prealteration patterns of nutrient influx into the bay and nutrient cycling within the bay in order to provide the baseline information for nutrient modeling.

Methods

Sediments have been geochemically analyzed by both research groups (University of Miami/NOAA and USGS) to extract information from sediment cores dated using ^{210}Pb and other methods of dating (Table 3.1). Orem *et al.* (1999a) typically analyzed the sediments for organic carbon, total nitrogen, and total phosphorus. Nelsen *et al.* (2002) analyzed organic carbon, total aluminum, and lead. Swart *et al.* (1999) discussed the possible use of trace elements in calcareous organisms as a proxy for nutrients.

Findings

LOWER TAYLOR SLOUGH AND MANGROVE FRINGE

- Uranium isotope studies indicate that phosphorus contamination at the northern end of Taylor Slough appears to be fertilizer-derived. However, phosphorus contamination in Taylor Slough diminishes to background by mid slough; therefore, Taylor Slough does not appear to be a source of nutrients to eastern Florida Bay.
- Eastern Florida Bay does appear to be a source of nutrients to the mangrove zone at the southern end of Taylor Slough.

Orem *et al.* (1997, 1999a), Orem (1998), and Gough *et al.* (2000) conducted detailed surveys of nutrients, metals, and major ion geochemistries in Taylor Slough and in eastern and central Florida Bay from 1996 to present. The study involved analyses of surface water, sediment porewater, and solid phase sediments from cores (Table 3.1, Figure 3.1; Taylor Slough cores are not included because they are not within Florida Bay). Cores were dated using ^{210}Pb, ^{137}Cs, and ^{14}C. Results from Taylor Slough showed that there is some degree of nutrient contamination (phosphorus) at the head of the slough. Uranium isotope studies indicated that this phosphorus contamination appeared to be fertilizer-derived. The phosphorus contamination in Taylor Slough diminished to background levels by mid-slough, so Taylor Slough does not appear to be a source of nutrients to eastern Florida Bay. Rather, Florida Bay appears to be a source of nutrients to the mangrove zone at the southern end of Taylor Slough.

EASTERN AND CENTRAL FLORIDA BAY

- Beginning in the mid 1980s, nutrification (increases in nitrogen and phosphorus) has occurred in portions of eastern and central Florida Bay as indicated by abrupt shifts in organic carbon, total nitrogen, and total phosphorus. Pass Key, located closest to terrestrial influx, showed the most pronounced shifts, and Bob Allen Key, the most southerly site, showed the least pronounced shifts.
- A large multidecadal-productivity event in the mid-1700s, which was characterized by greatly elevated levels of organic carbon and nitrogen, was observed in two cores from Whipray Basin.

Orem *et al.* (1999a) conducted analyses on organic carbon, total nitrogen, and total phosphorus from five sites in eastern Florida Bay (Table 3. 1, Figure 3.1). They found "sudden and dramatic shifts" indicating increased nutrification that could not be explained by diagenetic processes. The sediments at Pass Key showed two episodes of increased nutrification in the mid-1970s and after 1985. Nutrification at Bob Allen and Russell banks began in the early 1980s. The shifts in nitrogen and phosphorus occurred just prior to the reported microalgal blooms and seagrass die-off events in 1987.

Two cores from Whipray Basin, which preserve a long record dating back into the 1700s, were analyzed by Orem *et al.* (1999a). Downcore profiles at these sites illustrated a large productivity event that occurred in the mid-1700s. This event was multidecadal and characterized by greatly elevated levels of organic carbon and nitrogen, probably representing a period of extensive algal blooms. Interestingly, total phosphorus was not elevated during this time span. This productivity event occurred during the Little Ice Age and may correspond to a period of higher rainfall in the Everglades. Higher rainfall would contribute to more extensive land runoff into Florida Bay, which may have triggered the productivity event.

WESTERN FLORIDA BAY–WHITEWATER BAY AREA

- Organic carbon records from Jimmy Key indicate that hurricanes help to flush organic carbon out of the bay.

Nelsen *et al.* (2002) analyzed and contrasted organic carbon content in Oyster Bay, Jimmy Key, and Coot Bay cores (Table 3.1; Figure 3.1). They found that organic carbon decreased by a factor of two from Oyster Bay to Coot Bay and by a factor of four from Oyster Bay to Jimmy Key. Aluminum was closely correlated to organic carbon at Oyster Bay and Coot Bay because of erosion and mixing of the mangrove peats, which contribute the organic carbon and the associated clay and quartz, which in turn contributes the aluminum. Storm deposits and subsequent dissolution then concentrate the aluminum and organic carbon. Large organic carbon excursions at Oyster Bay correspond to hurricane events because of an increase in organic detritus. The trend in organic carbon at Oyster Bay is towards a decline from the first to the second half of the 20th century. At Coot Bay, organic carbon increases upcore, but at Jimmy Key it is segmented. The periods of organic carbon increase at Jimmy Key (1900 to mid 1930s and after mid-1970) correspond to periods of decreased hurricane activity, whereas the period of declining organic carbon (mid-1930s to mid-1970s) took place during a period of increased hurricane activity. These data support the hypothesis that hurricanes contribute to flushing of organic carbon from the bay (Nelsen *et al.*, 2002: 424, 442).

TRACE–ELEMENT ANALYSES OF CORAL

Swart *et al.* (1999) tested the use of barium (Ba) as a proxy for nutrient enrichment. They found that Ba increased when salinity decreased, but they concluded that the controls on barium were "enigmatic" and that more research was necessary to understand the distribution of barium within the bay.

Status of Research

ACCOMPLISHMENTS AND QUESTIONS RESOLVED

- Multidecadal shifts in nitrogen and phosphorus have been documented in sediments deposited prior to anthropogenic change, illustrating that these shifts occur naturally and can be of long duration.
- Recent dramatic increases in nitrogen, phosphorus, and total carbon have occurred in eastern Florida Bay and show decreasing amplitude with increasing distance from Taylor Slough.

ONGOING RESEARCH

- Orem *et al.* are currently working on analyses of carbon, nitrogen, and phosphorus from a Rankin Lake core.

UNRESOLVED QUESTIONS AND NEEDED RESEARCH

- Certain trace elements within calcareous skeletons (cadmium [Cd], barium, and manganese [Mn]) may be proxies for nutrient enrichment (see Swart *et* al., 1999, for discussion of previous research on this method). This method could be tested and used on downcore specimens.

- The use of $\delta^{13}C$ as a proxy for nutrient fluxes, in combination with other analyses, should be explored.
- Additional analyses from critical areas within the bay should be conducted in order to increase our understanding of past changes in nutrients.

Occurrence and Pattern of Algal Blooms

Only minimal ecosystem-history research has been done to contribute information on past algal blooms, and little of this work provides direct evidence. However, this is an area where there is the potential to obtain significant new information.

Methods

Huvane and Cooper (2001) have conducted assemblage analyses of diatoms, microscopic "algae" whose siliceous shell, or frustule, is well preserved in the sediments (Table 3. 1, Figure 3.1). Diatoms can be planktonic or epiphytic and can be indicative of many environmental factors. Edwards (Wingard *et al.*, 1995; Ishman *et al.*, 1996; Brewster-Wingard *et al.*, 1997, 1998b) examined dinoflagellate cysts, a stage in the life cycle of dinoflagellates, preserved in the sediments (Table 3.1, Figure 3.1).

Orem *et al.* (1999a) inferred bloom conditions based on analyses of organic carbon, total nitrogen, and total phosphorus. Swart *et al.* (1999) inferred bloom conditions based on a shift in $\delta^{13}C$ in small *Siderastrea radians* corals collected throughout Florida Bay.

Findings

- Surface sediments from eastern Florida Bay show indications of nutrient (C, N, and P) enrichment from 1980 to the present, which could be related to known microalgal blooms within Florida Bay.
- The multidecadal-productivity event noted in sediment geochemistry from Whipray Basin cores may represent a period of extensive algal blooms.

Orem *et al.* (1997) analyzed surface sediments from eastern Florida Bay, including sites near Pass Key and Russell Key banks. These analyses show indications of nutrient (C, N, and P) enrichment over the past two decades. This nutrient enrichment could be related to recent microalgal blooms and/or seagrass die-off within Florida Bay. The analyses of two cores from Whipray basin (Orem *et al.*, 1999a) may highlight a period of extensive, multidecadal bloom conditions during the mid-1700s.

- Downcore changes in abundance and assemblages of dinoflagellates and diatoms have been examined at some sites in Florida Bay. Additional studies of the ecology of dinoflagellates and diatoms are needed to interpret the findings in terms of bloom conditions.

The findings on diatoms (Huvane and Cooper, 2001) and on dinoflagellate cysts (Wingard *et al.*, 1995; Ishman *et al.*, 1996; Brewster-Wingard *et al.*, 1997, 1998b) have been inconclusive to date. Additionally, detailed studies of the biology and ecology of diatoms and dinoflagellate cysts are needed to accurately interpret the findings. In addition, because these phytoplankton are found in the less than 63-µm fraction of the sediments, they are more susceptible than the benthic microfauna (greater than 63 µm) to transport, redeposition, and reworking processes.

- Increases in heavy excursions of $\delta^{13}C$ may indicate the occurrence of algal blooms.

Swart *et al.* (1999) analyzed $\delta^{13}C$ in small *Siderastrea radians* corals collected throughout Florida Bay (Table 3.1, Figure 3.1). They separated the corals into two groups—those with $\delta^{13}C$ enrichment from approximately 1989 to 1993 and those with $\delta^{13}C$ depletion over the same time period. Corals showing the maximum $\delta^{13}C$ depletion, including the coral with the long record from Lignumvitae Key, occurred around 1984. Two possible causes for $\delta^{13}C$ increases seen in the first group of corals: (1) either a relative decrease in the influence of carbon derived from marine sources or (2) an increase in photosynthesis, which may indicate algal blooms. They discussed the contradictory evidence of the $\delta^{13}C$ patterns seen in the two groups of corals. They concluded that "the most probable cause is increased oxidation of organic material in the northeastern portion of Florida Bay and an increase in algal blooms in the western part of the bay."

Status of Research

ONGOING RESEARCH

- No known research on downcore phytoplankton remains is currently being conducted.
- Continued analyses of $\delta^{13}C$ in ostracodes, foraminifera, mollusks, and corals are part of several ongoing studies, but the primary intent of these analyses is to address Question 1.

UNRESOLVED QUESTIONS AND NEEDED RESEARCH

The potential exists to extract information from sediment cores about phytoplankton blooms via analyses of the remains in the core and through inferences based on changes in sediment geochemistry, carbon isotopes, and faunal assemblages. However, a great deal of work needs to be done to understand the ecology of the living phytoplankton and to understand the signature left in sediments following a bloom. In addition, the relationship between $\delta^{13}C$ and blooms needs to be tested and calibrated in the modern environment before information can be accurately applied to paleoanalyses. The questions that could be addressed include the following:

- Prior to human alteration of flow and circulation in Florida Bay, did planktonic blooms occur? If yes, what was their timing and duration? What natural events may have triggered blooms?
- Did the frequency and duration of blooms change after the construction of the Flagler Railroad or after the alteration of freshwater flow into Florida Bay?
- Can algal blooms be recognized in the sedimentary record? If so, can they be characterized and quantified?

Seagrass Trends and Patterns

A significant amount of ecosystem history research has addressed changes in seagrasses specifically and subaquatic vegetation (SAV) in general over time and the effects of changes in environmental components (salinity, nutrients, water quality) on the vegetation. These questions are critical to restoration. The massive die-off in 1987–1988 focused public attention on the plight of Florida Bay and the changes that were occurring in the ecosystem. It is important to place these changes in historical context over decadal and even centennial time scales to determine if die-offs and fluctuations in seagrass abundance are natural, cyclical events. In addition, ecosystem history data from sediment cores can provide insights into long-term sequences of change preceding die-offs.

Methods

Basic assemblage analyses and geochemical analyses have been used to detect downcore trends and patterns in subaquatic vegetation (SAV) from sediment cores dated using ^{210}Pb and other methods of dating (Table 3.1). Cronin (Cronin e*t al.*, 2001) and Wingard (Brewster-Wingard *et al.*, 1998a, 2001; Brewster-Wingard and Ishman, 1999) have used ostracodes and mollusks in their downcore analyses of SAV trends by applying data gathered in Florida Bay. Modern studies have established that some ostracode and mollusk species prefer living as epiphytes on *Thalassia* or *Halodule* (two common true seagrasses in Florida Bay), some prefer macrobenthic algae (such as *Chondria* or *Laurencia*), and some are SAV generalists that do not have a preference for a particular species of grass or algae. The modern data were gathered through field observations and samples collected from 1995 to the present (field data available via http://sofia.usgs.gov/flaecohist/). (See Salinity Trends and Patterns methods section for a discussion of taphonomic and sediment transport considerations in assemblage analyses.)

Geochemical analyses of sediments can provide information on the presence and distribution of seagrasses (Orem *et al.*, 1999b). The concentration of lignin phenols in sediments is a potential marker for historical seagrass abundance in Florida Bay. Seagrasses in Florida Bay, although angiosperms, have a lignin phenol distribution similar to that of gymnosperms (*i.e.*, little or no syringyl phenols present). Apparently the syringyl phenol content of the lignin in the seagrasses has been lost evolutionarily in the transition of these angiosperms back to the aquatic realm. This characteristic allows seagrass lignin (syringyl-phenol poor) to be differentiated from the other dominant lignin source in Florida Bay (mangroves; syringyl-phenol rich). Analyses of organic carbon and total nitrogen (Orem *et al.*, 1999a) may also provide information about seagrass die-offs, especially when combined with faunal assemblage and/or lignin phenol data.

Findings

- Frequent changes have occurred in the relative abundance of epiphytal species of ostracodes and mollusks over the past century.
- Prior to the mid-20th century, epiphytal ostracodes were relatively rare at sites in central and eastern Florida Bay, suggesting a greater abundance and/or density of SAV over the past 50 years than in the first half of the century. Epiphytal mollusks, although not rare, increased significantly in relative abundance from approximately 1940 to the 1970s at most sites. These data raise the possibility that dense and abundant seagrass beds may not be natural; if this finding is true, it will have great implications for restoration.
- A decline in SAV-dwelling ostracodes and mollusks occurred in cores from Whipray, Russell, Bob Allen, and Pass keys during the 1970s and 1980s.
- Relative abundances of mollusks with a strong preference for *Thalassia* have declined since approximately 1970 in eastern Florida Bay and since 1910 at Whipray Key, whereas SAV generalists have increased. These findings may indicate that the amount of macrobenthic algae has increased more than *Thalassia* has.

Cronin *et al.* (2001) found that ostracode assemblages during 1900–1940 at Whipray Basin, Bob Allen

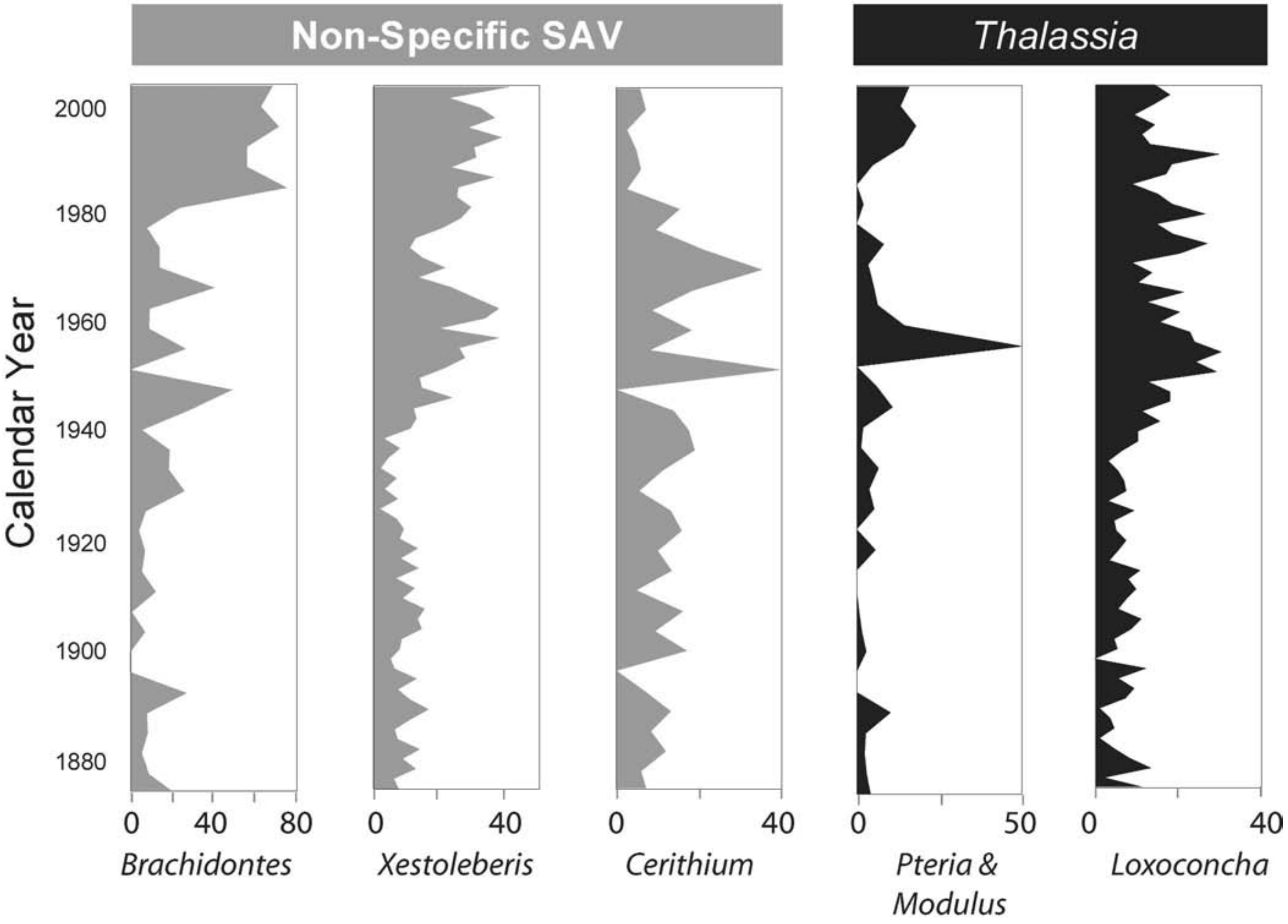

Figure 3.3 *Percentage of abundance of select mollusk and ostracode species that are indicators of sub-aquatic vegetation, plotted against estimated age for Russell Bank core 19B. Light gray are species indicative of any type of sub-aquatic vegetation (generalists). Black are species primarily indicative of* Thalassia *(specialists). Note different percent abundance scales.*

Key mudbank, Russell Key Bank, and Park Key were characterized by moderate to large proportions of *Peratocytheridea,* which is typically found associated with mud and *Halodule* substrates. Ostracode species associated with *Thalassia* and macroalgae were less common during this period. From approximately 1930 to 1950, *Peratocytheridea* declined significantly, whereas *Loxoconcha* (a *Thalassia* indicator) and *Xestoleberis* (an SAV generalist) increased (Figure 3.3). This pattern of long-term decline in *Peratocytheridea,* coincident with an increase in species associated with *Thalassia* and macrobenthic algae, was seen in cores from central, eastern, and northern Florida Bay. This shift suggests greater abundance and/or density of SAV in central Florida Bay during the past 50 years than in the first half of the century. A second shift occurred in the 1970s and 1980s, when a decline in *Thalassia*- and algal-dwelling species occurred in most cores. Cronin *et al.* (2001: 176) stated that "although the strength of the decline varied by species and by site, the stark contrast between the abundance of epiphytal species during the 1950s and 1960s and the very low abundance at times during the following two decades suggests a broad regional shift occurred at this time." These shifts in the 1970s and 1980s may be related to large-scale seagrass die-offs (principally *Thalassia*).

Brewster-Wingard *et al.* (1998a), Brewster-Wingard and Ishman (1999), and Trappe and Brewster-Wingard (2001) noted frequent and relatively dramatic shifts in the populations of the epiphytal species of mollusks. Cores from Whipray Key, Russell Key Bank, and Taylor Creek all show increases in epiphytal mollusks beginning around 1940, so the molluscan data agree with the ostracode data (Figure 3.3). There was a general increase in epiphytal organisms during the latter half of the 20th century, indicating a greater SAV coverage during this period than in the first half of the century. The molluscan epiphytal species were split into two groups based on modern field observations (Figure 3.3): (1) species that have a strong preference for *Thalassia* and (2) nonspecific SAV dwellers that may be found on either *Thalassia* or macrobenthic algae. These data illustrate an interesting trend—the relative abundance of *Thalassia* dwellers has declined since approximately 1970 at Bob Allen and Russell keys and since 1910 at Whipray Key, whereas the nonspecific SAV dwellers have increased. The ostracode *Xestoleberis* is a nonspecific SAV dweller, and its trends in abundance agree with the molluscan data.

- Downcore profiles of lignin phenols from a Pass Key core show large variations in lignin-phenol distributions over short time intervals, therefore reflecting the proximity of this site to the mangrove zone along the coast and to the outlet of Taylor Creek and thus to the influence of decaying mangrove and terrestrial plant detritus.
- At Bob Allen Keys, the lignin-phenol distributions show downcore variations in the abundance of seagrass over time. Seagrass abundance appears to have been increasing since a recent minimum around 1960.

Downcore profiles of lignin phenols were analyzed from Pass Key and Bob Allen Keys (Orem *et al.*, 1999b). The Pass Key core shows large variations in lignin phenol distributions over short time intervals. These variations are consistent with the proximity of this site to the mangrove zone along the coast and to the outlet of Taylor Creek and the influence of decaying mangrove vegetation and influx of terrestrial plant detritus. At Bob Allen Keys, the lignin distributions show downcore variations in the abundance of seagrass over time. At Bob Allen, seagrass abundance appears to have been increasing since a recent minimum around 1960.

- Surface sediments from eastern Florida Bay show indications of nutrient (C, N, and P) enrichment from 1980 to the present; which could be related to recent seagrass die-off within Florida Bay.

The analyses conducted by Orem *et al.* (1999a) (discussed under Question 3 above) at sites near Pass Key and Russell Key banks indicated that nutrient (C, N, and P) enrichment from 1980 to the present could be related to recent seagrass die-off within Florida Bay.

Status of Research

ACCOMPLISHMENTS AND QUESTIONS RESOLVED

- Common trends in mollusk and ostracode epiphytal species across basins and regions of Florida Bay indicate that while substrate and seagrass coverage may be patchy, it appears that there are bay-wide forcing factors affecting the abundance and distribution of the beds.
- Frequent and relatively rapid changes occur in the epiphytal indicator species, implying that the SAV itself goes through frequent and significant changes.
- There is evidence of increasing macrobenthic algae abundance in Florida Bay.
- Trends in SAV distribution throughout the 20th century imply that dense and abundant seagrass beds occurred in an already altered system. This finding has important implications for restoration.

ONGOING RESEARCH

- Current USGS work is focused on completing analyses of a core from Rankin Lake. This core was from an area of documented seagrass die-off (P. Carlson, personal communication) and was collected to examine the long-term (decadal-scale) sequences of change in a number of variables prior to the die-off event in 1987–1988. Ostracode and molluscan assemblages, ostracode geochemistry (Mg:Ca ratio), sediment geochemistry, and lignin phenols are being analyzed downcore.
- An additional core from the site of seagrass die-off at Barnes Sound is currently being processed and will be analyzed by the USGS group for faunal assemblage data and Mg:Ca ratios. A core from Whipray Basin will be analyzed for lignin phenols.
- Samples have been collected and processed to begin to quantify the relationships between molluscan species and SAV species.

UNRESOLVED QUESTIONS AND NEEDED RESEARCH

- The causes of seagrass die-off are still poorly understood. Detailed studies of sediment cores from sites of known die-off should help researchers examine the decadal-scale sequences of change that have led to the recent die-off events. Multiple forcing factors are undoubtedly at play in massive die-off events, and long-term data may allow researchers to better understand the interaction of these factors prior to die-offs.
- The potential influence of climate variability and its role in factors that directly affect sea-grasses, such as light attenuation, disease, and salinity fluctuations, need additional study.
- A quantitative analysis of modern vegetation and epiphytic species would allow more refined interpretations of the downcore assemblages.

Higher-Trophic-Level Species

Ecosystem history research and analyses of sediment cores have contributed very little to Question 5, in large part because Question 5 has been focused on the higher-trophic-level species, which are generally absent or not well represented in the cores. The only exception is the molluscan fauna. As Brewster-Wingard *et al.* (2001) pointed out, mollusks are well preserved in the cores, and they represent a number of trophic categories (filter feeding, grazing, scavenging, and carnivory). Simple measures of molluscan faunal diversity in cores from eastern and central Florida Bay have illustrated patterns of change over time (Brewster-Wingard *et al.*, 2001; Trappe and Brewster-Wingard, 2001), but these measures have not been rigorously tested. An apparent trend toward decreasing diversity has been observed in the upper portions of most of the cores beginning between 1960 and 1980.

If Question 5 were to expand and examine the lower invertebrates, paleoecologic data could contribute more valuable data from the benthic microfauna. Some of these trends are discussed under Question 1 and Question 4 above.

Status of Research

ONGOING RESEARCH

- No active research on higher trophic levels, other than molluscan faunal assemblage analyses, is currently being done. The current focus of the molluscan studies is to address Question 1 and Question 4, but molluscan faunal changes in response to salinity and benthic habitat will provide secondary information to address Question 5.
- Benthic microfaunal assemblage analyses are also contributing data about changes in the Florida Bay benthic habitat over time.

UNRESOLVED QUESTIONS AND NEEDED RESEARCH

- There are significant questions about changes in benthic habitat that could be addressed (and in part are being addressed) by expanding Question 5 to include lower invertebrates. These organisms form the bottom of the food chain and are therefore essential to the survival of the higher-trophic-level organisms. Because the lower invertebrates are more readily preserved in sediment cores, decadal- to centennial-scale analyses of environmental change and its effect on animals in Florida Bay would be possible.
- More rigorous analyses of the molluscan faunal diversity data should be conducted.
- The use of mollusks as proxies for higher-trophic-level diversity should be explored.

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Chapter 4
Physical Processes

Lead Authors Dr. Thomas Lee (University of Miami),
Dr. Elizabeth Johns (NOAA/AOML), and Dr. Peter Ortner (NOAA/AOML)
Contributors Joseph Boyer, Jeff Chanton, Shuyi Chen, John Hammrick, Clinton Hittle, Villy Kourafalou ,
Chris Langevin, Victor Levesque, Frank Marshall , Zaki Moustafa, William Nuttle, Eduardo Patino,
Joseph Pica, Rene Price, Michael Robblee, David Rudnick, Ray Schaffranek, DeWitt Smith, Ned Smith,
Eric Swain, Peter Swart, Zafer Top, Paul Trimble, Sandra Vargo, John Wang, Paul Willis

Introduction

Question 1*—How and at what rates do storms, changing freshwater flows, sea level rise, and local evaporation-precipitation patterns influence circulation and salinity patterns within Florida Bay and exchanges between the bay and adjacent waters?*

The research conducted addressing Question 1 was intended to produce quantitative predictions of circulation and salinity responses within Florida Bay. Exchange between the bay and the Gulf of Mexico, exchange between the bay and the coastal zone of the Florida Keys, and oceanographic, climatic, and hydrological driving processes were also areas that were to be addressed. Table 4.1 includes relevant representative references to research addressing driving forces, system characteristics, and their intersection. The Research Summary highlights major findings to date.

Background

The south Florida coastal system surrounding and interacting with the interior waters of Florida Bay (made up of the gulf and Atlantic waters of the Florida Keys, the Dry Tortugas, and the southwestern Florida shelf) is highly coupled by the combined influence of coastal and oceanic currents (Lee *et al.,* 2002). The bay itself is a lagoonal system; a complex network of shallow, often intertidal, banks isolate the interior portions of Florida Bay from the direct influence of regional or larger-scale oceanographic processes (Figure 4.1). As a result, local and direct climatic processes, such as the inflows of surface and groundwater, rainfall, evaporation, and wind-driven flow, greatly affect salinity, circulation, and exchange processes.

The climate of south Florida is subtropical, with a comparatively small annual temperature range but distinct wet (summer-fall) and dry (winter-spring) seasons. During the wet season, showers associated with the afternoon sea breeze occur almost daily, and tropical storms are transient occurrences. During the dry season, cold fronts pass through the region on an approximately weekly basis, accompanied by increased wind speeds and clockwise-rotating wind directions.

Spatially, the bay can be thought of as four distinct regions subject to different geophysical forcings, topographic constraints, and freshwater inputs. The northeastern region of Florida Bay is not significantly affected by tides or directly influenced by the surrounding marine waters of the Atlantic and Gulf of Mexico. This region is the direct recipient of freshwater flows from Taylor Slough and the C-111 canal system. Upstream water-management practices influence the quantity, timing, and distribution of fresh water entering this region. Runoff varies spatially across the northern boundary, with the greatest flow through Trout Creek. Wind events often determine the timing of freshwater discharges on hourly to daily time scales, and regional rainfall cycles (*e.g.,* seasonal and El Niño/La Niña-driven) influence discharges on annual to multiyear time scales. Salinity along the northern boundary of the bay responds very rapidly to rainfall and/or discharge events. High flow causes dramatic freshening in the small bays along the northern boundary. Subsequently, fresh water slowly mixes with the more saline Florida Bay waters to the south and southwest over a period of weeks to months (Johns *et al.,* 2001a).

The central region of Florida Bay receives less direct freshwater inflow, but fresh water can move into central Florida Bay through McCormick Creek into Terrapin Bay, through Alligator Creek into Garfield Bight, as well as over the Buttonwood Embankment. Groundwater inputs have also been hypothesized. Under historically higher water levels, these surface and groundwater inputs were presumably more significant throughout the southern Everglades. During times of reduced precipitation and high evaporation, this central area can become hypersaline, with salin-

Table 4.1 *Research categories defined by Question 1 and representative references to relevant research.*

	System Characteristics		
Driving Process	**Salinity Patterns**	**Circulation Patterns**	**Exchange with Adjacent Waters**
General Characteristics	Robblee *et al.* (2001), Boyer *et al.* (1997), Boyer and Jones (2001), Lee *et al.* (2002), Johns *et al.* (2001a), D. Smith (2001)	Lee and Williams (1999), Lee *et al.* (1999), Lee *et al.* (2002), D. Smith (2001)	N. Smith (2002), Smith and Pitts (2002), Lee and Smith (2002), Yang (1999), Lee and Williams (1999), Lee *et al.* (1999, 2002)
Winds and Storms Goldenberg *et al.* (2001), Albrecht *et al.* (2003)	Johns *et al.* (2001b), D. Smith (2001), R. Smith *et al.* (2001)	Lee and Williams (1999), Lee *et al.* (2002), Smith and Pitts (2002), Wang *et al.* (1994), N. Smith (2001)	Lee and Smith (2002), Smith and Pitts (2002), N. Smith (2001), Johns *et al.* (2001b)
Precipitation Willis (1999), Trimble *et al.* (2001), Mattocks (pers. com.), Pielke *et al.* (1999)	Swart and Price (2001), Nuttle *et al.* (2000, 2001) Johns *et al.* (2001a)	No observed effect of precipitation on circulation has been reported.	No observed effect of precipitation on exchanges with adjacent waters has been reported.
Evaporation Pratt and Smith (1999), N. Smith (2000), Price *et al.* (2001), Mattocks (pers. com.)	Swart and Price (2001), Nuttle *et al.* (2000, 2001)	No observed effect of evaporation on circulation has been reported.	No observed effect of evaporation on exchanges with adjacent waters has been reported.
Surface Water Hittle *et al.* (2001), Vosburg *et al.* (2001), Cable *et al.* (2001) Swart and Price (2001), Levesque and Patino (2001), Trimble *et al.*(2001)	Lee *et al.* (2002) Ortner *et al.* (1995), Nuttle *et al.* (2000, 2001), Swart and Price (2001), Johns *et al.* (2001a), Langevin *et al.* (2002a), Schaffranek *et al.* (2002), Hurricane Georges Workshop	Lee *et al.* (2002), Langevin *et al.* (2002a)	No observed effect of surface water on exchanges with adjacent waters has been
Groundwater Price and Swart (2001), Fitterman and Deszcz-Pan (2000, 2002), Vosburg *et al.* (2001), Top and Brand (2001)	Fitterman *et al.* (1999), Fitterman and Deszcz-Pan (2001), Langevin *et al.* (2002a)	Langevin *et al.* (2002a)	No observed effect of groundwater on exchanges with adjacent waters has been reported
Sea Level and Tides Maul and Martin (1993), Smith (1997), Frederick *et al.* (1994)	Lee *et al.* (2001, 2002), Johns *et al.* (2001a)	Lee and Smith (2002), Smith (1998), Wang *et al.* (1994)	N. Smith (1998), Smith and Lee (2003), Lee and Smith (2002), Smith and Pitts (2002), N. Smith (2001)
Boundary Currents Lee and Williams (1999), Lee and Smith (2002)	Ortner *et al.* (1995), Lee *et al.* (2001, 2002)	Lee *et al.* (2002), Yang *et al.* (1999)	Lee *et al.* (2001, 2002), Yang *et al.* (1999)
Prediction	Nuttle *et al.* (2000, 2001), Cosby *et al.* (1999), Wang *et al.* (1994), Marshall (2001), Walker (1998), Kim *et al.* (1999)	Wang *et al.* (1994), Kim *et al.* (1999)	HYCOM model group

ity often exceeding 40 practical salinity units (psu) and historically as high as 70 psu (Boyer and Jones, 2001; Robblee *et al.*, 2001). High salinity persists over periods of weeks to months, indicating that like waters of the northeastern region, those of the central region have a relatively long residence time.

The western region of Florida Bay is the least topographically isolated, sharing an open boundary with the Gulf of Mexico and exchanging water with the central region of Florida Bay through the main Flamingo channel and with the Atlantic Ocean through passages in the middle Keys. This western region is also subject to robust tidal mixing. Therefore, residence times in the western region are shorter than in the central and northeastern regions, and salinity can show a relatively rapid response to meteorological events such as tropical storms and cold fronts. Oceanographically, the entire coastal region of south Florida is one integrated system (Figure 4.2). Florida Bay is connected to the southwestern Florida shelf and, on occasion, to

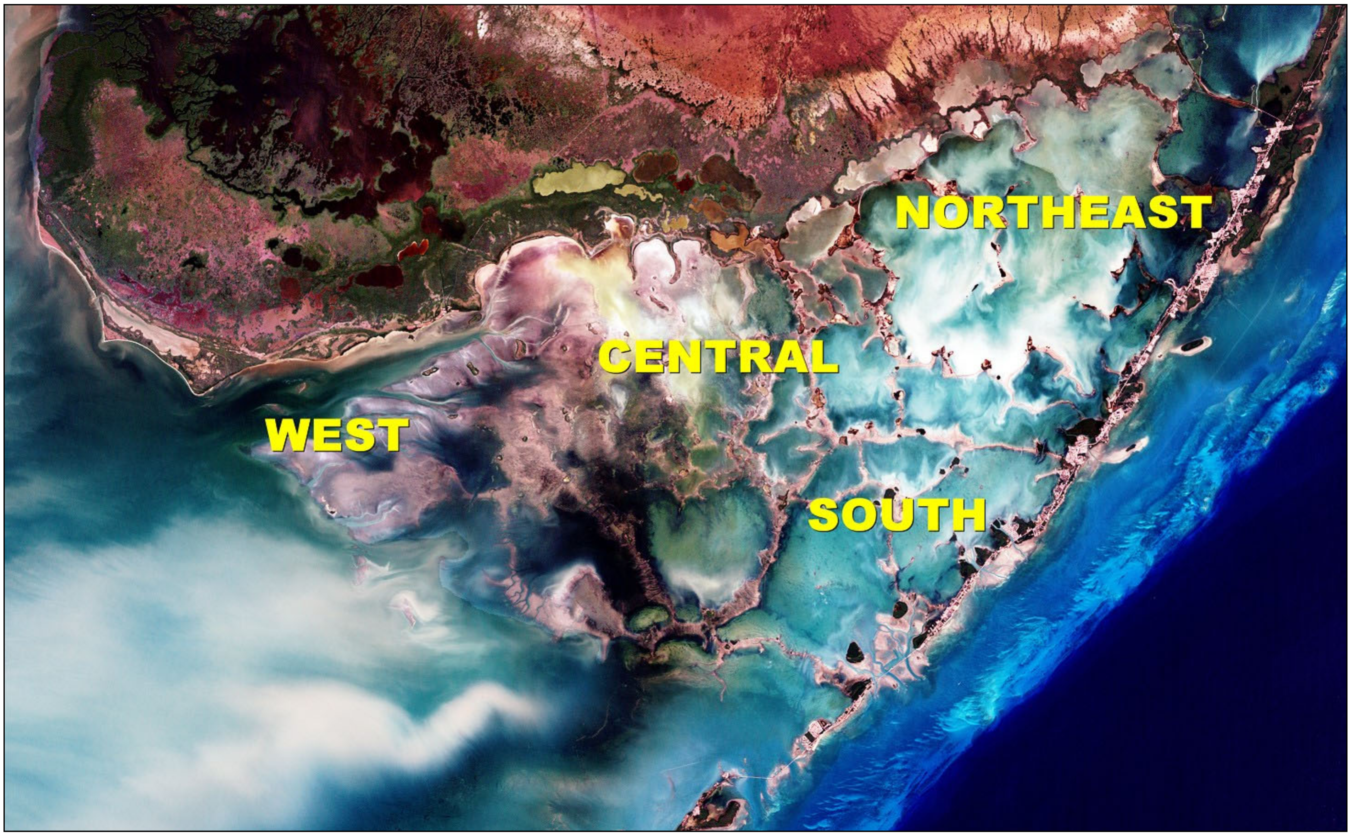

Figure 4.1 *LANDSAT–7 extended thematic mapper image of Florida Bay, showing its shallow bank bathymetry and four principal subregions.*

more remote regions of the Gulf of Mexico. As a result, western Florida Bay can be influenced by the delivery of fresh water from rivers discharging into the Ten Thousand Islands region and along the west coast of Florida (the Shark, Broad, Harney, and Lostmans rivers). These river waters are carried southward along the southwestern Florida coastline and around Cape Sable in a general pattern of outflow through the Keys to the reef tract (Lee *et al.,* 2001, 2002). Freshwater inflow from remote gulf regions is more likely during summer and fall and has been shown to include that from Mississippi River floods (Ortner *et al.,* 1995). Subsequent transport of this water to Florida Bay and the Keys is aided by the Loop Current and the Florida Current.

Finally, the southern region of Florida Bay differs from the central region because it has an open connection through the middle Keys passages and at times can receive an influx of Atlantic Ocean water. The southern region may also be a source of bay waters to the coral reef areas of the Florida Keys National Marine Sanctuary (FKNMS).

Circulation of water in western Florida Bay and adjacent coastal regions on subtidal time scales is strongly influenced by local wind forcing that results in seasonal flow patterns: southward toward the Keys in winter and spring, northwestward into the gulf in summer, and southwestward toward the Tortugas in the fall. Episodic transport processes can deliver warm, salty water to the reef tract from Florida Bay in the spring and early summer. During the winter, cold, turbid water intrusions from Florida Bay can occur.

Research Summary

To date, researchers have documented regional oceanographic and hydrological driving processes. Circulation in the outer portion of Florida Bay, the adjacent southwestern Florida shelf, and Florida Keys; exchange between Florida Bay and the Keys coastal zone; the potential pathway for exchange across the western boundary; and the patterns of salinity variation throughout the bay and adjacent marine systems are among those processes. These results were derived from several extensive observational programs that have now collected almost 10 years of data on regional water properties, meteorology, and flow.

By comparison, major uncertainties remain about circulation within the interior basins, interbasin exchange, flow across the bank tops, the effect of evaporative processes upon bank-top waters, groundwater

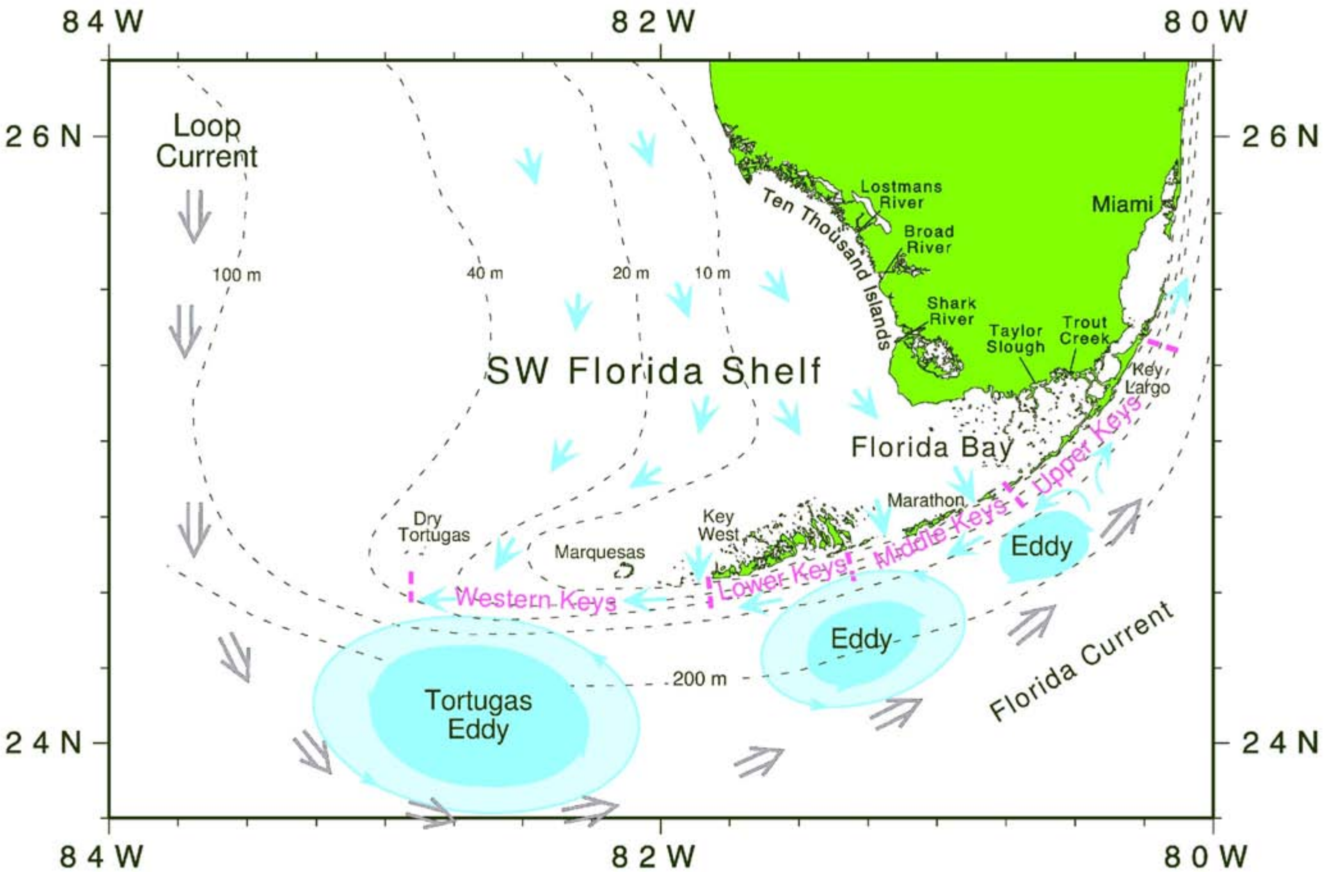

Figure 4.2 *Schematic representation of the average flow patterns in the interconnected south Florida coastal circulation system. The single arrows represent mean current directions, whereas the double arrows represent the Loop Current and the Florida Current.*

entering the bay across its northern boundary, and the quantitative details of exchange across the bay's extensive and complex western boundary. The hydrological model of surface waters entering northeastern Florida Bay has been improved over the past few years, and progress has been made on expanding the model to the entire northern boundary and the lower southwestern shelf including the Shark River slough. However, we still do not have an adequate hydrodynamic model of the interior of Florida Bay.

As a result, our ability to rigorously forecast changes in salinity within the bay resulting from planned modifications in upstream water management is inadequate. Nonetheless, a water budget has been developed for Florida Bay based upon long-term (31 years) salinity data. The budget takes into account seasonal and interannual variations in the supply of fresh water (Nuttle *et al.,* 2000). A depiction of the climatic cycle of surface runoff, evaporation, and precipitation over the 31-year period is shown in Figure 4.3. Across the whole bay, discharge from the estuarine creeks amounts to about 2 cm/year, or about 20% of the annual rainfall. In the northeast region, where the majority (98%) of the creek discharge enters the bay, creek discharges amount to about 67% of the annual rainfall. Similar to the 31-year average, the majority of the freshwater inflow is now concentrated in the northeastern part of the bay and has a major influence on salinity variations therein, effectively inhibiting hypersalinity. Conversely, the lack of freshwater flow to the central bay exacerbates hypersalinity.

Higher discharges through the Shark River slough and higher water levels in the southern Everglades could redistribute freshwater input to the bay and could provide greater input to the central basins in particular. Integrated hydrological/hydrodynamic models incorporating the most recent observational data and process-study results linked to appropriate regional/boundary hydrodynamic and atmospheric models are required to rigorously address the most central management concern: what salinity distributions will result from various upstream water-management alternatives. This has become a principal objective of the Florida Bay and Florida Keys Feasibility Study (FBFKFS).

The principal findings are summarized below and relevant citations are enumerated in Table 4.1.

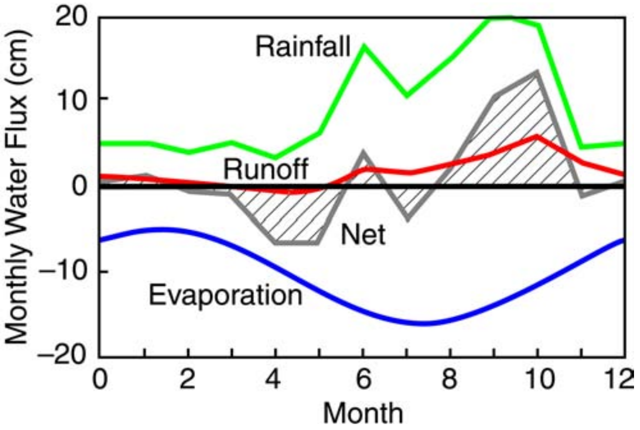

Figure 4.3 *Average seasonal rainfall, runoff, evaporation, and net freshwater gain/loss in Florida Bay (Nuttle, personal communication).*

SALINITY

- Historical salinity data and salinity proxy data show that large salinity changes are not yet understood. Those changes have commonly taken place in Florida Bay seasonally, interannually (the El Niño/Southern Oscillation, ENSO), decadally (the North Atlantic Oscillation, NAO), and for even longer periods.
- Historical data from the salinity synthesis database (Robblee *et al.*, 2001) show that Florida Bay has behaved as a marine lagoon for the past several decades. Salinities have reached as high as 70 psu in the central bay on a few occasions and typically exceeded 40 psu during drought years such as 1989–1990. For example, following the wet period of 1994–1995, salinity increased until tropical storms in 1999 induced a decrease, which was followed by another increase during the drought years of 2000 and 2001. Recent data from 2000–2002 indicate that Florida Bay salinity may again be on the rise.
- Variability of Florida Bay average salinity is directly related to the net flux of fresh water from the combined influence of evaporation, precipitation, and runoff. For the bay as a whole on seasonal or annual time scales, evaporation is approximately equal to precipitation, while runoff is roughly 20% of either.
- Recent studies have narrowed the range of evaporation to around 75–180 cm/year.
- Shallow banks, which restrict water exchange, tend to separate the bay's interior into three regions with distinct salinity variations. The northeastern basin is the most isolated from oceanic influences, receives most of the surface runoff, and has the largest seasonal cycle of salinity. The central basin receives little runoff and has the highest salinity. The western basins have the greatest oceanic exchange and the smallest seasonal change in salinity.
- Continuous surveys of the bay's salinity patterns show large spatial gradients coinciding with the wide, shallow banks that tend to inhibit interbasin exchanges.

FRESHWATER INPUT

- Stable isotopic markers indicate that the dominant source of fresh water for northeastern Florida Bay is Everglades runoff, whereas for the western region, precipitation has a stronger influence. In the central region, a mixture of runoff and precipitation provides the fresh water.
- Measurements and modeling (both hydraulic and regression) of surface inflows to the bay from the Everglades continue to improve. These analyses show that there have been increasing inflows to Taylor Slough and the C-111 canal since 1985 as a result of management activity.
- Trout Creek contributes the largest volume of fresh water to northeastern Florida Bay, varying from –6 to 32 m^3/s. By contrast, the flow from each of the other eight creeks ranges from –1.4 to 6 m^3/s. Negative flows can occur during the dry season and storm events.
- For the Ten Thousand Island region of the western Everglades, the mean annual river discharge is estimated at 13.3 m^3/s for Harney River, 11.0 m^3/s for Broad River, and 12.4 m^3/s for Shark River.
- Shark River's low-salinity plume waters are commonly advected southward around Cape Sable to western Florida Bay and the Keys reef tract by wind-driven coastal flows.
- Groundwater inflows are believed to be most influential along the northern boundary of the bay; however, estimates of the volume of this flow range over four orders of magnitude. New measurements and hydraulic modeling should help to put bounds on the inflow estimates.

CIRCULATION AND EXCHANGE

- The entire south Florida coastal system, consisting of the southwestern Florida shelf, the Florida Keys reef tract, and western Florida Bay, is highly connected by local and oceanic circulation patterns responding to wind and boundary-current forcing.
- Large-volume, wind-forced flows through the Keys passages provide linkage for gulf-to-Atlantic exchange through the open western region of Florida Bay.
- Measurement of sea level slopes across the Florida Keys provides a tool for monitoring gulf-to-Atlantic transports of heat, salt, nutrients, and toxic algae toward the reef tract.

- Seasonal cycles in local wind forcing produce seasonal patterns in circulation pathways, connecting south Florida coastal waters through western Florida Bay and transporting Everglades freshwater discharges. Southward flows through the Keys passages predominate in winter and spring, north-northwestward flows in summer, and southwestward flows toward the Tortugas in the fall.
- Seasonal cycles in south Florida coastal current systems provide seasonal pathways for local larval recruitment and opportunities for recruitment from remote sources.
- The south Florida coastal region is surrounded by an intense, large-scale oceanic boundary current (the Loop Current–Florida Current system) and its evolving eddies that link local coastal waters to remote upstream river sources in the Gulf of Mexico.

PREDICTION

Steady progress has been made toward developing a predictive capability for salinity and circulation changes in Florida Bay and connecting coastal waters.

- Two-dimensional hydrodynamic models with coarse grids have been developed for Florida Bay as pilot projects by J. Wang (finite element) and J. Hammerick (finite difference). The results are encouraging because the model outputs of salinity fields are similar to observed salinity patterns.
- Better estimates of surface and groundwater inflows are available from recent measurements and hydraulic-model results of the United States Geological Survey (USGS) and the South Florida Water Management District (SFWMD).
- Improved estimates of evaporation are available from recent studies by R. Price, P. Swart, W. Nuttle, and N. Smith.
- Improved estimates of precipitation patterns and quantities are available from calibrated Next Generation Radar (NEXRAD) measurements (P. Willis).
- Measurements of interior-basin circulation and exchange processes are available to improve understanding of bay dynamics, quantify residence times, and help to validate and improve hydrodynamic models (T. Lee, E. Johns, V. Kourafalou, and N. Smith).
- Modeling Terms of Reference (MTR) were established by the Physical Science Team (PST) and approved by the Program Management Committee (PMC).
- A Standard Data Set has been established for model use (J. Pica).
- An interagency, nested-model program has been formulated using regional hydrodynamic and hydrological models to provide boundary conditions for the Florida Bay model (SFWMD, USGS, and the National Oceanic and Atmospheric Administration [NOAA]).

Driving Processes

Winds and Storms

Winds in south Florida, including Florida Bay, follow a regular seasonal pattern: weak southeasterly winds and daily sea breezes in summer, persistent northeasterly winds in fall, and the regular passage of cold fronts causing moderate increases in wind speed and a clockwise rotation of wind direction during the winter. During hurricane season (summer–early fall), the persistent southeasterly tradewind and sea breeze pattern can be interrupted by the passage of tropical storms, often resulting in substantial increases in wind speed, precipitation, and runoff, which can flow directly into the central basin. Due to the absence of significant topography in south Florida, winds overall are highly coherent across the bay, with the exception of locally intense convective events. Low-frequency wind stress varies seasonally (Smith, 2002). Because low-frequency scatter about the monthly mean is an important measure of wind forcing, this seasonal variability is significant.

Recent measurements indicate that there is a significant response of the salinity patterns, sea level, currents, and turbidity of Florida Bay and adjacent coastal waters to wind forcing associated with the passage of even relatively weak tropical cyclones (Johns *et al.,* 2001b; Hurricane Georges Workshop report, http://www.aoml.noaa.gov/flbay/hurgeocoverpage.html). Based on results from several research efforts at different locations, the effect of storms on water levels in the Everglades and in Florida Bay and the freshwater flow response after storms pass has been characterized (D. Smith, 2001; Johns *et al.,* 2001b; Smith *et al.,* 2001).

Mattocks (personal communication) used a version of the Advanced Regional Prediction System (ARPS) mesoscale atmospheric weather prediction model reconfigured to match South Florida Water Management District (SFWMD) models at a 3.2-km resolution and included land use and soil types. His model shows mesoscale structures in wind, evaporation, and precipitation fields that are associated with land use and land-sea interactions, including the sea breeze. Strong, divergent downdraft outflows that occur beneath thunderstorms and over the Florida Keys appear to produce their own sea-breeze convergence fronts. The different soil types and land uses, together with the spatial patterns in the wind fields, determine spatial patterns in the evaporation and precipitation fields over south Florida and the surrounding waters, including Florida Bay.

Indications are that we are entering a period of enhanced Atlantic hurricane activity (Goldenberg *et al.,* 2001) and that the prior two or three decades represented a period of diminished activity. The difference apparently reflects a multidecadal climatic oscillation. If the assumption is made that the probability of a tropical storm affecting south Florida is directly related to overall activity, then Florida Bay is more likely to be affected by a storm than it has been for several previous decades. Goldenberg *et al.* (2001) suggested that this pattern is likely to continue for an additional 10 to 40 years.

Precipitation

South Florida in general, including Florida Bay, has pronounced dry (winter-spring) and wet (summer-fall) seasons. Nuttle *et al.* (2000) used 31 years of historical data to show that the seasonal rainfall pattern for the bay as a whole is nearly balanced by bay-wide evaporation. The distribution of rainfall is highly heterogeneous due to the dominance of local convective events, sea-breeze convergence, and to variations caused by urban development effects known as "desertification" (Pielke *et al.,* 1999). However, significant climatic variability is possible and has been documented within the period of record of the ongoing monitoring.

Trimble *et al.* (2001) indicated that low-frequency meteorological modes associated with ENSO and the Pacific Decadal Oscillation can also have significant effects on south Florida rainfall and freshwater supply variability. For example, Johns *et al.* (2001a) have shown that the El Niño of 1998 reversed the seasonal rainfall pattern over south Florida, causing a winter-spring wet season and a summer-fall dry season.

There is excellent agreement between independent data set tests that used NEXRAD radar and rain gauges (Willis, 1999). Cumulative rainfall distributions are nearly identical except for the highest rainfall rates. Radar-estimated rainfall distributions provide the high resolution needed to resolve spatial patterns over south Florida and Florida Bay. This NEXRAD precipitation product, done on a research basis for two years, has now been mapped to the SFWMD grid and is archived at SFWMD. These efforts have paved the way for an operational rainfall-distribution product that can be input to atmospheric models.

Evaporation

Evaporation in marine systems is a function of air and water temperature differences, specific humidity, and wind speed. Although winds are highly coherent across the bay, ongoing studies suggest that there are significant spatial differences in evaporation minus precipitation (E – P) (Price *et al.,* 2001). Recent estimates of evaporation in Florida Bay were derived using a variety of independent methods and the comparison of those results is encouraging.

Nuttle *et al.* (2000, 2001) estimated that bay-wide annual evaporation, based on calibration of steady-state box models that used historical salinity data for each of four regions in the bay, was 110 cm. Pratt and Smith (1999) estimated annual evaporation to be 73 cm by using a Dalton Law formula. Subsequent to this study, Smith (2000) refined the application of the Dalton Law approach by including the effect of increasing estimated annual evaporation. On the other hand, estimates based on surrogate data differ by up to a factor of three. Evaporation-pan data are available for several years from Flamingo, a site located on the northern shore of the bay. The average of these data is 210 cm/year (National Climatic Data Center, http://www.ncdc.noaa.gov), which appears to be too high to accept directly as an estimate of evaporation in the bay.

A distinct seasonal cycle underlies the mean annual water loss, with a maximum in late summer and a minimum in mid winter. Calculations using the Long Key C-MAN data in bulk aerodynamic formulas indicate average evaporative water losses of approximately 0.7 cm/day in September and October and approximately 0.3 cm/day in December and January. Unpublished data from this 15-month study (N. Smith, personal communication) indicate a mean daily evaporative water loss of 0.5 cm and a total annual water loss of approximately 180 cm. Therefore, reliable evaporation estimates appear to be converging upon the 75–180 cm/year range, but more research is required to confirm this amount.

Surface-Water Input

A significant amount of surface water enters Florida Bay directly only along its northern boundary with the southern Everglades and is concentrated at present in the northeastern region. Fresh water occasionally enters the central bay directly if there is enough rain. For example, during and after Hurricane Irene, fresh water from the Everglades was able to flow over the Buttonwood Embankment (Johns *et al.,* 2001a).

Freshwater runoff enters principally through natural channels cut through the mangrove and buttonwood-confining berms (Hittle, 2001; Hittle *et al.,* 2001). USGS measurements indicate that Trout Creek contributes the largest annual discharge of fresh water into northeastern Florida Bay, varying from about 110,000 to 190,000 acre-ft/yr (4.3 m^3/s to 7.4 m^3/s). By contrast, the annual discharge from each of the other eight creeks varies between 10,000 and 45,000 acre-ft/yr (0.4 m^3/s to 1.8 m^3/s). Negative flows over the mangrove embankments can be caused by storm events, and net negative monthly average flow, which usually lasts for several months, occurs in all creeks during every dry season represented by the data.

Cable *et al.* (2001) reported on the relationship between precipitation and inflow into Florida Bay, finding that fall and winter storms cause pulses of freshwater inflow, with the flow in Taylor Creek showing a marked response to the storms. Typically, water levels in the Everglades were found to be highest in early fall and lowest in the winter. Tropical storms cause the water levels in the Everglades and Taylor Slough to rise relatively rapidly and then recede slowly after the storms pass. The water level's rise is on the order of hours, whereas the fall is on the order of weeks. During the winter, northeasterly winds drive water out of Taylor Creek into Florida Bay.

Stable isotopic markers have identified the principal sources of fresh water in various regions of the bay (Swart and Price, 2001). Freshwater inputs to northeastern Florida Bay are dominated by contributions from Everglades runoff. Rainfall has a strong signal in the west, and both rainfall and runoff provide fresh water to the central portion of the bay.

Surface freshwater inputs from the rivers of the southwestern coast of Florida (primarily the Broad, Harney, and Shark rivers) may also be significant to Florida Bay, particularly in its western region. Levesque and Patino (2001) reported measurements of water level, velocity, specific conductance, and temperature in each of these three rivers during the calendar year 1999. Discharges from the three rivers are influenced by the semidiurnal tides, wind, and freshwater flows from the watershed. All three rivers are well mixed, with very little vertical gradient except near the coastal front. The only evidence of stratified, bidirectional flow is around the time of slack tide. Instantaneous discharges ranged from –2,400 to +3,500 cfs (–68 to +99 m^3/s) in the Broad River, –15,600 to +12,900 cfs (–442 to +365 m^3/s) in the Harney River, and –10,100 to +10,500 (–286 to +247 m^3/s) in the Shark River. When tidal effects have been filtered from the data, the residual flows ranged from –900 to +2,500 cfs (–25 to +71 m^3/s), –3,600 to +5,700 cfs (–102 to 161 m^3/s), and –2,300 to +4,400 cfs (–65 to +124 m^3/s) for the Broad, Harney, and Shark rivers, respectively. Mean annual residual discharge values have been reported to be 400 cfs (11 m^3/s or 284,000 acre ft/year) for Broad River, 440 cfs (12.4 m^3/s or 320,000 acre ft/year) for Shark River, and 470 cfs (13.3 m^3/s or 343,000 acre ft/year) for Harney River (Levesque and Patino, 2001).

Groundwater Input

Anecdotal or historical information suggests that prior to water management, groundwater inputs to south Florida estuaries like Biscayne Bay and Florida Bay were significant. At present, because of lowered water tables and the intrusion of seawater into the coastal aquifer, fresh groundwater may be prevented from discharging directly into Florida Bay. However, groundwater may be passing from the Floridan aquifer into the surficial aquifer and then into Florida Bay. Because the Floridan aquifer is saline, the discharging groundwater would be saline, not fresh. This hypothesis is supported by geophysical measurements in the southern portions of Everglades National Park (ENP) between Flamingo and U.S. 1 that indicate that the aquifer is saltwater-saturated from the surface to a depth of at least 15 m (Fitterman *et al.,* 1999; Fitterman and Deszcz-Pan, 2000, 2002). Results from the integrated surface-groundwater model of the southern Everglades suggest that groundwater seepage beneath the Buttonwood Embankment may be allowing brackish water from the Everglades to discharge into northeastern Florida Bay (Langevin *et al.,* 2002). Model results suggest that surface water can be impounded on the north side of the embankment, creating a hydraulic drive for groundwater discharge into Florida Bay. However, data are lacking to support these model results.

Vosburg *et al.* (2001) reported on surface water and groundwater measurements taken at two locations in the dwarf mangrove wetlands along Taylor Creek near its mouth at Florida Bay. The water level of surface water and groundwater were measured at both sites. Surface-water levels demonstrated a relatively rapid response to rainfall, runoff, tide, and wind, whereas the groundwater response was less rapid. However, groundwater response times were different at each site, which was attributed by the authors to the differences in sediment type.

Price and Swart (2001) provided recent additional information about the role of groundwater in the hydrologic regime of Florida Bay and the adjacent areas of the Everglades. The extent of saltwater intrusion into the surficial aquifer increases from east to west, extending about 6 km inland along the C-111 canal basin to about 20–28 km inland at Shark River Slough (Fitterman and Deszcz-Pan, 2000, 2001). Groundwater may be discharged into the overlying surface waters of the Everglades within this strip, which more or less parallels the coastline. An empirical calculation of groundwater discharge yields values of about 0.04–0.175 cm^3/day.

Top and Brand (2001) also recently studied groundwater in Florida Bay. They used anomalies in the dissolved helium concentrations in groundwater to estimate groundwater inputs to Florida Bay. These authors used a box model to estimate that the input of groundwater to Florida Bay was 2.5–4.0 cm/day in the summer and 10–16 cm/day in the winter. Radon-data estimates yielded a groundwater flux of 0.8–1.7 cm/day. According to Top and Brand (2001), saline water from the Florida aquifer is under artesian pressure and is rising through breaks in the confining layer, where it mixes with the shallow aquifer before entering Florida Bay. This two-layer structure of the aquifer system explains the difference between the helium and radon flux estimates.

Note that the radio-isotope values convert to hypothesized groundwater inflows of 575 to 3,680 m^3/s. Based on these results, if true, groundwater would appear to be a significant source of saline water to Florida Bay. However, these estimates have large differences and appear to conflict with mass-balance water-budget estimates and the observed large seasonal salinity variations.

Sea Level and Tides

Sea level variability in Florida Bay is controlled by wind and tidal forcing, strongly modified by topography and coastline (Wang *et al.,* 1994). Regional sea level is thought to have risen rapidly in the last century (Maul and Martin, 1993; see also the Key West sea level record from 1913 to present, available from the National Climatic Data Center [NCDC]), but the implications of that observation are not addressed here. Differences in sea level between basins and across tidal passages can be a dominant factor controlling flow and renewal of bay waters. The diurnal tide of the Gulf of Mexico combined with the semidiurnal tide of the Atlantic results in a mixed tide. This results in the largest tidal ranges south of Savannah, Georgia, for the region near the mouth of the Shark River (>2 m at spring tide). Measurements at East Cape indicate a mean tidal range of only 75 cm. The mean range is half that at the southern end of the western boundary, just north of Marathon. However, the tide entering the interior part of the bay is strongly damped by the shoals and mud flats, decreasing the range to just a few cm in the northeast (Smith, 1997).

Smith (1997) also reported upon spatial patterns of tidal water-level fluctuations in the interior portion of Florida Bay and the seasonal pattern of water-level fluctuations at subtidal frequencies. Wind set-ups of 10–30 cm are observed inside the bay, but the basin-to-basin variations in wind forcing are not well understood at present. An annual change in sea level of about 30 cm is widespread over the western North Atlantic and extends into the interior of the bay as well.

Boundary Currents

The Loop Current in the Gulf of Mexico and its extension, the Florida Current in the Atlantic, surround the south Florida coastal waters and the Keys. Both are part of the Gulf Stream system, which is one of the strongest and best-studied western boundary currents. Both currents are complex and can generate eddies and meanders that can affect how the currents interact with Florida Bay. Together these oceanic currents cause sea level differences across the Keys that can drive flows through western Florida Bay. Lee and Smith (2002) recently showed that changes in sea-level slopes across the Keys are a direct response to tide and wind forcing. They have suggested a longer period response to Loop Current extensions into the Gulf of Mexico. Wind forcing affects sea level differently on the Atlantic and gulf sides of the Keys, causing sea-level slopes that can enhance the exchanges of bay waters with the surrounding regions. The boundary currents and their induced flows along western Florida Bay can transport river waters and/or algal blooms from remote regions to interact with the bay (Lee *et al.,* 2001, 2002).

Influence of Driving Processes

Salinity

Florida Bay's salinity varies with time on a wide range of scales. Bay salinity normally reflects the annual wet and dry seasons driven by regional precipitation and temperature patterns but also responds to episodic meteorological events such as tropical storms and cold fronts. In addition, Florida Bay salinities are influenced by interannual El Niño/La Niña cycles and by decadal variability in precipitation driven by Atlantic Ocean multidecadal forcing. Variability on all of these time scales (and even longer scales, the causes of which are completely unknown) can be seen in historical salinity and "salinity proxy" (*i.e.,* paleoecological) data.

A preliminary analysis of historical data from the Salinity Synthesis database (Robblee *et al.,* 2001) shows that for the past few decades, the bay has behaved as a marine lagoon, with salinities as high as 70 psu reported on a few occasions in central Florida Bay. During drought years, salinity typically exceeds 40 psu over most of the bay. Estuarine (*i.e.,* mesohaline) conditions are rare in recent history and are associated with episodic events such as hurricanes and tropical storms or with other periods of above-average rainfall (*e.g.,* 1994–1995). Increased water releases from the C-111 canal can also lower salinities across the bay during relatively dry years (*e.g.,* 1983–1985).

Salinity variability is greatest in the northeast and decreases to the west. Boyer *et al.* (1997) and Boyer and Jones (2001) have described a decadal trend in monthly salinity values collected by Florida International University's (FIU) Southeast Environmental Research Center (SERC) in Florida Bay from 1989 to 1999. During that decade, salinity in the eastern, central, and western regions declined by 13.6, 11.6, and 5.6 psu, respectively. This "trend" was due largely to very high salinities during the 1989–1990 drought and is not descriptive of the substantial interannual variability of salinities in the bay. For example, following the wet period of 1994–1995, salinity increased until tropical storms in 1999 induced a decrease, and data from the drought years of 2000 and 2001 indicated that salinities increased again. More recent data from 2002 and early 2003 indicate another general freshening trend (see South Florida Program (SFP) Web site at www.aoml.noaa.gov/SFP for monthly survey maps of salinity posted by NOAA's Atlantic Oceanographic and Meteorological Laboratory [AOML] and the University of Miami's [UM] Rosenstiel School of Marine and Atmospheric Science [RSMAS]).

WINDS AND STORMS

In combination with upstream water-management releases (that are due to flood-control restrictions), storms can affect salinity by causing pulsed freshwater inflows even in the "dry" season. Tropical storms can cause Everglades water levels to rise rapidly and then recede slowly as fresh water seeps down into northeastern Florida Bay. Northeasterly winds drive fresh water out of the Everglades into Florida Bay. Biogeochemical materials in these freshwater flows follow similar input patterns (Cable *et al.,* 2001). Higher-salinity water moves from Florida Bay into the mangrove fringe area for several months during the dry season in typical years.

Along the southwestern coast of the Everglades, river discharge is affected by tidal forces, but tidal-forcing effects can be masked by storm events (Levesque and Patino, 2001). Wind-driven flows can redirect low-salinity plumes from discharges in the western Everglades into western Florida Bay and the Keys. Wind-driven currents tend to advect water masses and realign salinity patterns in the direction of the flow, causing low-salinity bands of river discharge and subsequent transport to connecting regions (Johns *et al.,* 2001b). At present, the extent to which these plumes exchange with the interior waters of Florida Bay is unclear.

During the past several years, a number of tropical cyclones have influenced the south Florida region through intense wind forcing, rainfall, or both. Johns *et al.* (2001b), D. Smith (2001), and R. Smith *et al.* (2001) recently showed that, although not as intense as in past periods of cyclone activity, these events caused significant and long-lasting (~months) changes in salinity patterns and turbidity in Florida Bay.

PRECIPITATION AND EVAPORATION

Florida Bay salinity patterns are a function of spatial and temporal patterns in precipitation, evaporation, runoff, and exchange with the gulf and Atlantic. Evaporation and precipitation are the two largest components of the Florida Bay water budget, but we lack good spatial resolution for them. Their respective positive and negative effects upon salinity are addressed under Driving Processes, above. Interannual variations in salinity appeared to be affected primarily by fluctuations in rainfall, which not only falls directly into the bay but also results in variations in the volume of surface water discharged into Florida Bay from the southern Everglades.

An annual water budget for Florida Bay has been constructed using 31 years of salinity, hydrological, and climate data (Nuttle *et al.,* 2000, 2001). A simulation using a calibrated box model in which runoff was doubled decreased salinity in the eastern bay, increased variability in the southern bay, but had no effect in the central or western regions of the bay. During 1965–1995, annual runoff from the Everglades was one fifth of the annual direct rainfall into the bay, and annual evaporation slightly exceeded annual rainfall. On a seasonal basis, rainfall, evaporation, and runoff were not in phase, leading to a strong seasonal pattern of salinity in the bay.

SURFACE–WATER INPUTS

Surface discharges from Trout Creek and Taylor Slough significantly affect salinity patterns and variability in northeastern Florida Bay, where minimum salinity occurs near river mouths and strong gradients occur in the basin. In the fall, when sea level is relatively high, interbasin exchange is enhanced, resulting in more surface fresh water reaching the central basin. The same can occur directly during tropical storms if the water table is sufficiently high (see Hurricane Georges Workshop report available at http://www.aoml.noaa.gov/flbay/hurgeocoverpage.html). Enhanced exchange and tropical storms help reduce hypersalinity in the bay's interior. River discharges, from sources both remote from and local to Florida Bay can be transported by coastal and boundary currents to different parts of the south Florida ecosystem for mixing and exchange. Under appropriate wind conditions, flow from rivers along the southwestern Florida coastline can reduce salinities along the perimeter of the interior bay and perhaps into its westernmost basins. Clear examples are the transport of the Shark River plume to western Florida Bay to help buffer salinity in that region (Lee *et al.,* 2001, 2002) and the transport of Mississippi River waters to the Florida Keys (Ortner *et al.,* 1995). Exchange of surface water discharged into the western bay with adjacent interior basins is not well understood at present, and new observations are underway to better resolve these processes.

GROUNDWATER INPUTS

No large-scale effects of groundwater on salinity have been observed. Observing this input is made more difficult by the fact that the primary groundwater input is thought to be saline. However, anecdotal evidence indicates the existence of local springs, and scientists in nearby Biscayne Bay have observed similar springs, at least within a few hundred meters of the shoreline (J. Proni, personal communication).

SEA LEVEL AND TIDES

At times of high sea level in the fall, especially during and after tropical storms, overland flow can occur directly into the central basin, thereby reducing hypersalinity (see above). On the other hand, low sea level can restrict exchange between adjacent basins by minimizing overbank exchange. Runoff to central Florida Bay is probably more common in the fall tropical storm season, when annual water levels are relatively high, but could occur at any time of the year. Higher water levels may facilitate movement of this fresh water across banks to the south and west. However, seasonal or wind-induced high water along the northern boundary may also hinder freshwater flow to the bay by reducing the head gradient.

BOUNDARY CURRENTS

Ortner *et al.* (1995) and Lee *et al.* (2001, 2002) have clearly shown that fresh water from remote sources in the eastern Gulf of Mexico, transported by boundary currents, can have a significant effect on the salinity patterns in south Florida coastal waters, including the westernmost regions of Florida Bay. Boundary currents surrounding south Florida coastal waters can also change sea-level slopes and gulf-Atlantic flows through western Florida Bay that enhance bay-water exchange with adjacent waters.

Circulation

The interior portion of Florida Bay is made up of a complex maze of shallow basins separated by mud banks and mangrove islands. The bay is openly connected to the southwestern Florida shelf along its wide western boundary, but exchange with the Atlantic coastal zone of the Keys is restricted to a few narrow tidal channels through the Keys island chain. The northern boundary is mangrove fringed, with freshwater input in the northeastern region through Taylor Slough and Trout River. The rapid fall-off of tidal range with distance from the western boundary and the dramatic increases in salinities observed in the interior basins indicate poor water exchange between the northeastern and central portions of the bay with adjacent subregions.

The entire south Florida coastal ecosystem, except for the interior of Florida Bay, is highly connected by a regional recirculation system. This regional circulation is driven by the combined forcing of winds, sea-level slopes, oceanic currents such as the Florida Current and Loop Current, and eddies at the offshore boundaries (Lee and Williams, 1999; Lee *et al.,* 1999, 2002). Seasonal patterns in wind forcing result in seasonal shifts in the regional circulation system and preferred pathways of exchange between waters of the southwestern Florida shelf (including the nearshore waters of the southwestern Everglades and western Florida Bay) and the waters of the Keys Atlantic coastal zone. Everglades discharges are typically advected southeastward along the western boundary of Florida Bay's interior and through the channels of the middle Keys to the reef tract in the winter and spring. They move toward the Dry Tortugas in the fall and northwestward to the west Florida shelf in the summer, followed by entrainment by the Loop Current and return to the Keys coastal zone (Lee *et al.,* 2002). Advective time scales to reach the Keys Atlantic coastal waters range from one to two months in winter, spring, and fall to as much as six months in the summer.

WINDS AND STORMS

Coherent mesoscale and synoptic-scale wind forcing causes alongshore barotropic currents, which are geostrophically balanced by coastal sea level on either side of the Keys, and cross-Key sea-level slopes that drive exchange of Atlantic water with Florida Bay water on daily to weekly time scales. A strong alongshore-current response to alongshore wind forcing was found for the Keys Atlantic coastal zone (Lee and Williams, 1999) and for the southwestern Florida shelf (Lee *et al.,* 2002) for synoptic-scale and seasonal-scale winds. The seasonal pattern of the wind forcing results in seasonal circulation patterns that link the south Florida coastal waters along the western boundary of interior Florida Bay (Lee *et al.,* 2002): southward gulf-to-At-

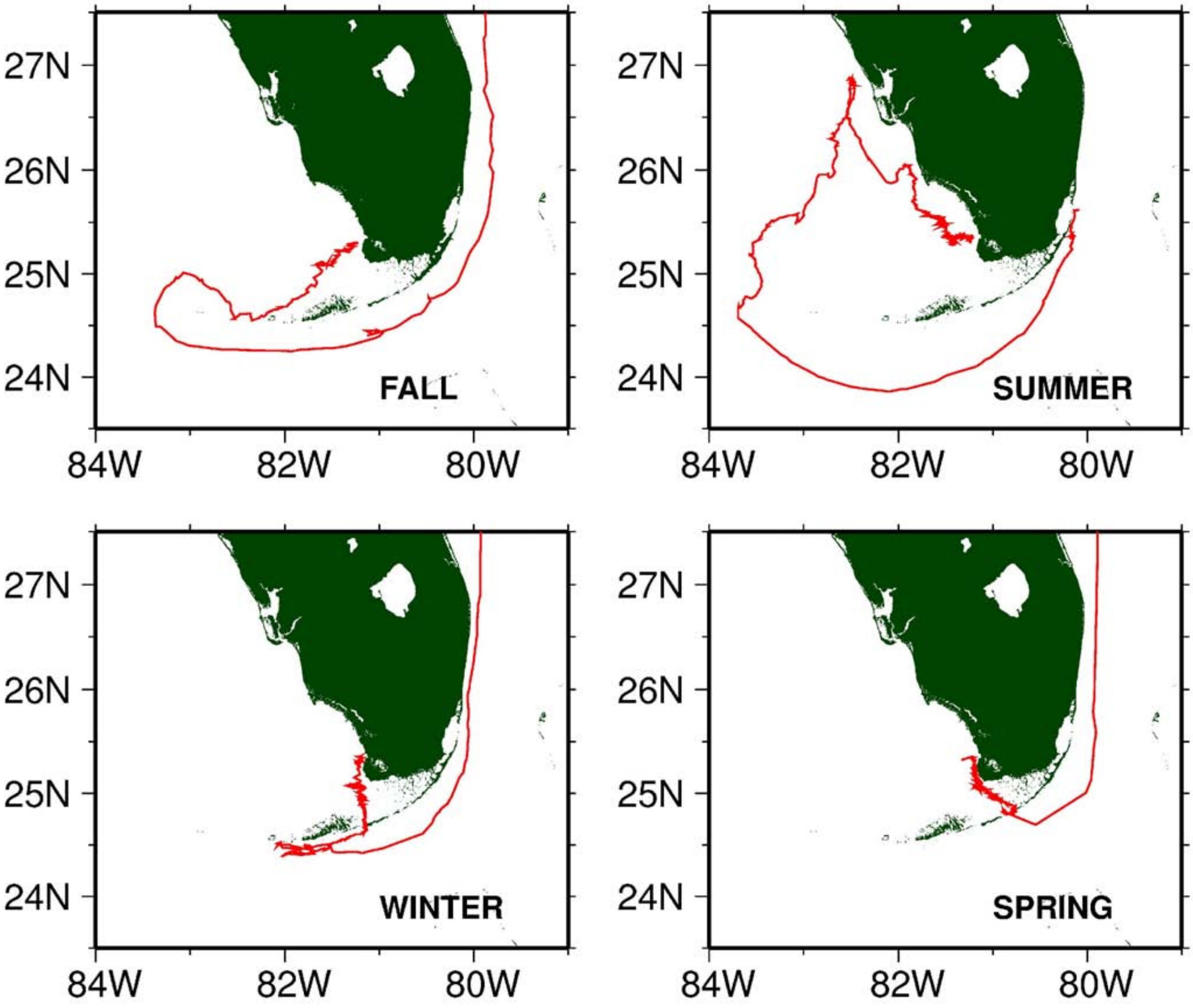

Figure 4.4 *Representative seasonal trajectories of satellite-tracked surface drifters (Lee* et al.*, 2002).*

lantic flows in winter and spring, northwestward flows to the gulf in summer, and southwestward flows toward the Dry Tortugas in fall. This pattern is clearly demonstrated in the trajectory pathways of Lagrangian drifters that have been regularly released over the past few years (Figure 4.4).

Mean cross-shelf flows on the southwestern shelf and along the western boundary of interior Florida Bay indicate an estuarine-like circulation. Estuarine-like circulation has offshore flow in the upper layer and onshore flow in the lower layer, suggesting a response to prevailing eastward winds and buoyancy-forcing from freshwater discharges through the western Everglades.

The transient effect that storms have on circulation depends upon wind strength, direction, and duration. Large increases in current speeds have been observed in western Florida Bay and along the southwestern Florida shelf and the Keys coastal zone with the passage of tropical storms (Johns *et al.,* 2001b).

PRECIPITATION

Precipitation has not been observed to have any direct effects upon circulation.

EVAPORATION

Evaporation has also not been observed to have any direct effects upon circulation. However, some anti-estuarine flow (flow toward areas with high rates of evaporation) presumably results from net evaporation during the dry season.

SURFACE–WATER INPUTS

Surface-water inputs through the small rivers of the western Everglades tend to form a low-salinity band in the nearshore waters that is entrained by coastal currents and transported to western Florida Bay and the Keys (Johns *et al.*, 2001a). This is a passive response to existing circulation. The amount of buoyancy-forcing from these small rivers (5–30 m^3/s) appears to be insufficient to produce a dynamic coastal current within the low-salinity plume. Salinity observations do indicate that freshwater discharges to the northeastern bay tend to move slowly to the south and west and can serve as a passive tracer of the bay's interior circulation.

GROUNDWATER INPUTS

Isotope-derived estimates of groundwater inputs to Florida Bay vary by several orders of magnitude (see above under Driving Processes). Efforts are underway by USGS and SFWMD to resolve this discrepancy by applying improved hydrological models. Groundwater-forcing is not included in present bay hydrodynamic or water-budget models. It does not appear necessary for conservation of mass or for simulation of large seasonal salinity cycles. The between-basin flows that would result from the higher estimates are also inconsistent with available intrabasin flow observations.

SEA LEVEL AND TIDES

Water movements occur on time scales ranging from minutes to seasons to years. Tidal currents often account for a large part of the variation in coastal currents and are important for local mixing and dispersion of materials. However, because of the regular reversal of tidal currents, they are not efficient transport mechanisms over distances larger than a few kilometers. In the interior of the bay, cross-bank sea-level slopes are believed to have an important influence on driving flows between basins and ultimately on residence times. Subtidal or low-frequency currents, driven by sea-level slopes caused by wind or offshore boundary currents, are principally responsible for linking adjacent as well as remote regions to south Florida ecosystems. Cross-Key sea-level slopes drive flows through the Keys tidal passages at tidal and subtidal frequencies that couple the gulf and Atlantic coastal regions of south Florida (Lee and Smith, 2002).

BOUNDARY CURRENTS

Although boundary currents are the dominant feature of the regional circulation, their effect is indirect within Florida Bay. Long-term moored current observations indicate a mean southward flow on the southwestern Florida shelf that can transport eastern gulf waters, including river discharges from the west Florida shelf and Mississippi River to the Dry Tortugas and through western Florida Bay to the Keys coastal zone (Lee *et al.*, 2002). The origin of the mean flow is not clear, but the position of the Loop Current appears to influence mean flow magnitude and may be the driving force. To more fully understand the relevant processes will depend upon rigorous, calibrated regional model simulations incorporating field observations and satellite data.

Exchanges with Adjacent Waters

Exchanges with adjacent waters are related to three of the driving forces that have been discussed above, specifically winds and storms, sea level, and boundary currents. Waters of the interior portion of Florida Bay interact with waters from two very different continental shelves: the wide, north-south-oriented southwestern Florida shelf to the west and the narrow, curving Keys coastal zone and its shallow, reef-tract topography to the east and south. These two shelf regions exchange waters with each other through the tidal channels between the Keys and with the strong oceanic currents at their outer edges: the Loop Current in the Gulf of Mexico and the Florida Current on the Atlantic side of the Keys. There is strong interaction with the Florida Current by way of eddy processes throughout the Keys shelf domain. It is apparent by looking at satellite imagery, water-property distributions, and model results that a similar process occurs along the outer edge of the southwestern Florida shelf. Recent drifter trajectories (Yang, 1999) indicate that there is a discontinuity between midshelf waters in the region offshore of Tampa Bay that is possibly related to the amplitude of river discharge.

Current measurements by N. Smith (2002) in several channels connecting interior subbasins of Florida Bay, suggest a generally southward motion of waters from the north-central region of the bay that seem to diverge toward the Atlantic and gulf in the southeastern region of the bay. Exchange between basins appears to be strongly influenced by wind direction as well as magnitude. Little is known about the physical processes that regulate water renewal in the bay's interior or about the preferred pathways of circulation.

Mean flows through the western boundary of interior Florida Bay (between East Cape and Marathon) have been roughly estimated from long-term current observations to indicate an inflow (eastward) of about 1,300 m^3/s in the northern portion and an outflow (westward) of about 300 m^3/s in the southern region, giving a net inflow across the section of about 1,000 m^3/s (Smith and Pitts, 2002; N. Smith, 2002). Because 400–500 m^3/s of this inflow exits southward through the middle Keys passages, approximately 500–600 m^3/s are available for transport into interior regions of Florida Bay. Tidal, subtidal, and long-term transports into Florida Bay are neither well resolved nor understood. It is also unclear what portion of the net inflows to the Florida Bay interior are used to balance mean sea level rise, account for evaporative water losses, or drive residual circulation. Observations have also quantified tidal-period transports (N. Smith, 2002). To some degree, mixing during tidal exchanges must import gulf and Atlantic water into Florida Bay and export bay water to the gulf and to Hawk Channel. Further observations and calibrated model simulations are needed before the net exchange resulting from this process can be quantified.

WINDS AND STORMS

Wind forcing was found to set up cross-Key sea-level slopes that can drive large flows into or out of western Florida Bay (Lee and Smith, 2002). Strong easterly and northeasterly winds during the fall cause a positive cross-Key slope and consequently inflow to the bay from the Atlantic. Gulf-to-Atlantic outflows from the bay are associated with negative cross-Key sea-level slopes from southeasterly (summer), westerly (winter), and northerly (spring) winds. Wind-driven exchanges through the middle Keys can produce net flows of 1,000–2,000 m^3/s over the duration of the event (typically 1–10 days) for Long Key Channel alone and possibly two to four times this amount of net flow for all of the middle Keys channels.

Recent current measurements in the main shipping channel at Key West indicate a net northward flow into the gulf that appears to be related to the prevailing westward winds and suggests an Ekman response in the Keys coastal zone (Smith and Pitts, 2002). The magnitude of this flow has not yet been determined. However, when combined with the gulf-to-Atlantic flows in the middle Keys, this information provides an indication of a possible clockwise recirculation around the lower Keys.

Subtidal transports through passages in the upper Keys are much weaker than the middle Keys and appear to be highly influenced by onshore or offshore winds that may cause a set-down or set-up of water level in northeastern Florida Bay (N. Smith, 2001).

SEA LEVEL AND TIDES

It is clear that the volume transports through the Keys passages are produced by cross-Key sea-level slopes and that low-frequency changes are strongly dependent on wind forcing over the dynamically different shelf regimes on either side of the Keys. The strongest flows occur in the middle Keys channels, where the combined subtidal outflows toward the reef tract can be as high as 7,000 m^3/s during winter cold-front passages, and inflows to western Florida Bay can reach 2,800 m^3/s during fall northeast-wind events. The magnitude of these flows is 100–200 times larger than the total freshwater inflows to Florida Bay. The mean flow through the middle Keys passages is estimated to be approximately 800 ± 100 m^3/s toward the reef tract (Figure 4.5). The cause of the mean flow is uncertain but appears to be related to the mean sea level difference between the gulf and Atlantic and may be influenced by the Loop Current position. A series of investigations by N. Smith (1998), Smith and Lee (2003), Lee and Smith (2002), Smith and Pitts (2002), and N. Smith (2001) have quantified the magnitudes and variability of the inflows and outflows of Florida Bay through the Keys tidal passes and across the western boundary in the gulf transition region.

BOUNDARY CURRENTS

Boundary currents provide the coupling of the gulf and Atlantic through western Florida Bay via sea level differences and along the seaward edges of the gulf and Atlantic shelves through eddy and wind-driven exchanges (Lee *et al.*, 2001, 2002). Boundary currents can transport remote waters, including river discharges, to near the bay. Eddies shed by these currents and related dynamic mesoscale features can enhance exchange between the currents and adjacent shelf regions. Continued monitoring and modeling of boundary currents and their relationship to local circulation and exchange processes is essential.

Prediction

Observational data alone are not sufficient to predict salinity patterns, circulation, freshwater input, and exchanges with adjacent waters under different restoration and climatic scenarios. Because of the physical complexities of the bay, these data need to be complemented by calibrated models, a number of which are listed below.

Fresh Water Inflow

To predict salinity, hydrological models that can provide estimated runoff at the hydrodynamic model's terrestrial boundary are essential. The freshwater-discharge model must also be able to estimate runoff under various Comprehensive Everglades Restoration Plan (CERP) alternatives. The USGS has developed a hydrodynamic transport model to simulate water flow and salt fluxes through connected surface and groundwater systems. An algorithm has been developed that synchronizes surface-water tidal-compati-

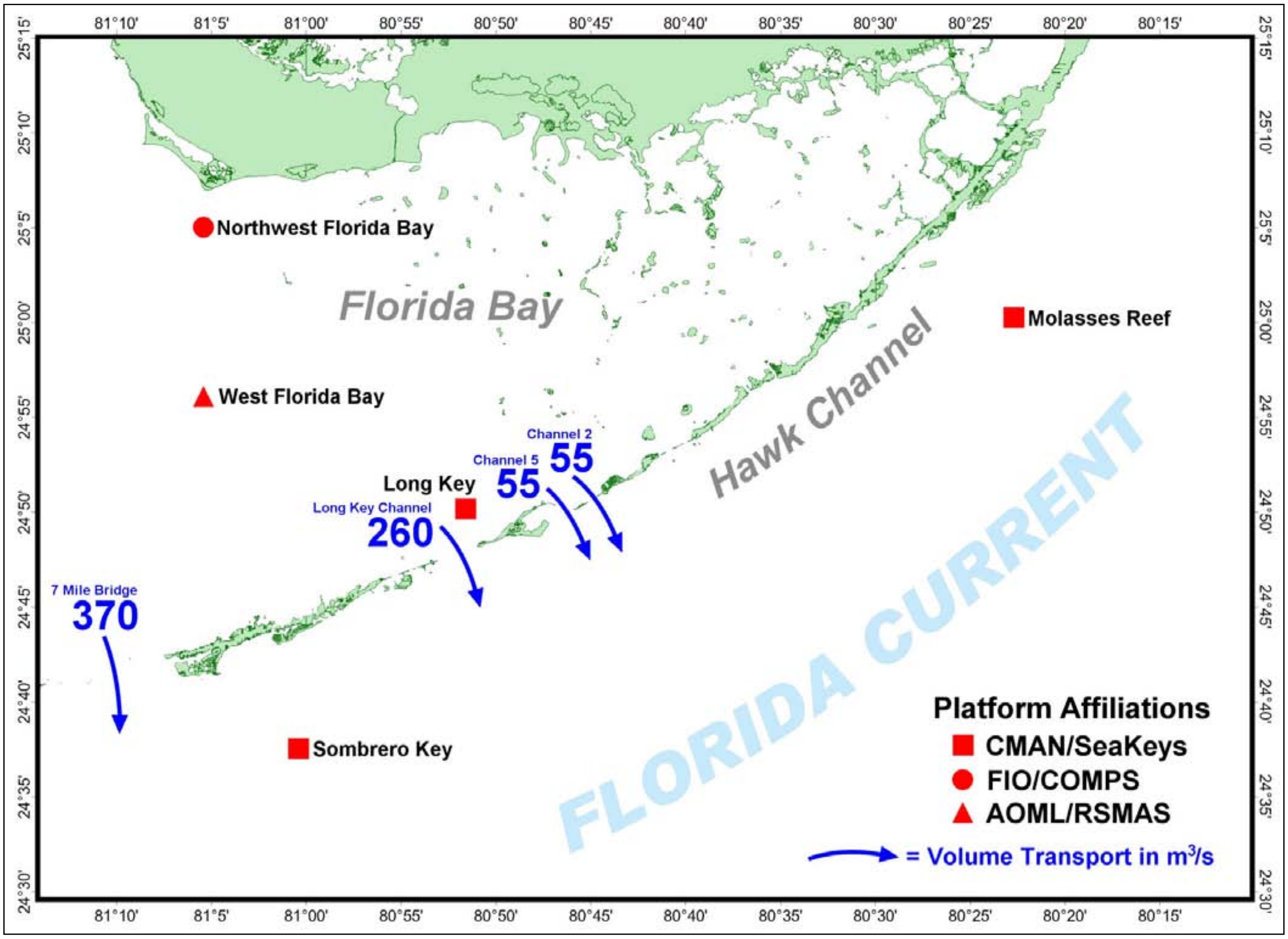

Figure 4.5 *Average sub-tidal flow through the middle Keys passages (Lee and Smith, 2002).*

ble time steps with groundwater stress periods and that assures mass conservation of simulated flux quantities across the surface-groundwater interface and land-surface boundary in the coupled model (Swain and Langevin, 2001; Swain *et al.,* 2002). Hydraulic expressions derived from studies of hydrologic processes in the Everglades have been formulated to link flow resistance, wind stress, and evapotranspiration processes to the vegetation properties and shallow flows typical of these low-gradient wetlands. Two applications of the coupled model have been made that are largely within the confines of ENP (Figure 4.6). The Southern Inland and Coastal Systems (SICS) model encompasses the Taylor Slough wetlands, part of the C-111 drainage basin, and subtidal embayments along the northern coastline of Florida Bay. The Tides and Inflows in the Mangrove Ecotone (TIME) model encompasses the SICS model domain, Shark River Slough, other western sloughs, and subtidal embayments and tidal creeks along the southwestern gulf coast. Measured surface-water discharges, water levels, and salt concentrations in tidal creeks; wetland water levels and flow velocities; groundwater heads and salinities supplemented by subsurface salinity maps; and soil properties are used for model calibration and verification. Tide levels and salt concentrations along the coast and discharges and water levels at hydraulic control structures, bridges, and culverts are used to drive the SICS and TIME simulations. The models simulate flow exchanges and saltwater fluxes between the surface and groundwater systems in response to these multiple driving forces, which could be altered based on proposed changes to the system. Insight into flow patterns and salt fluxes, which can be obtained only through hydrodynamic transport models, is needed to fully evaluate the potential effect of restoration decisions for the greater Everglades on ecologically sensitive, land-margin ecosystems bordering the northern coastline of Florida Bay and the southwestern gulf coast of Everglades National Park.

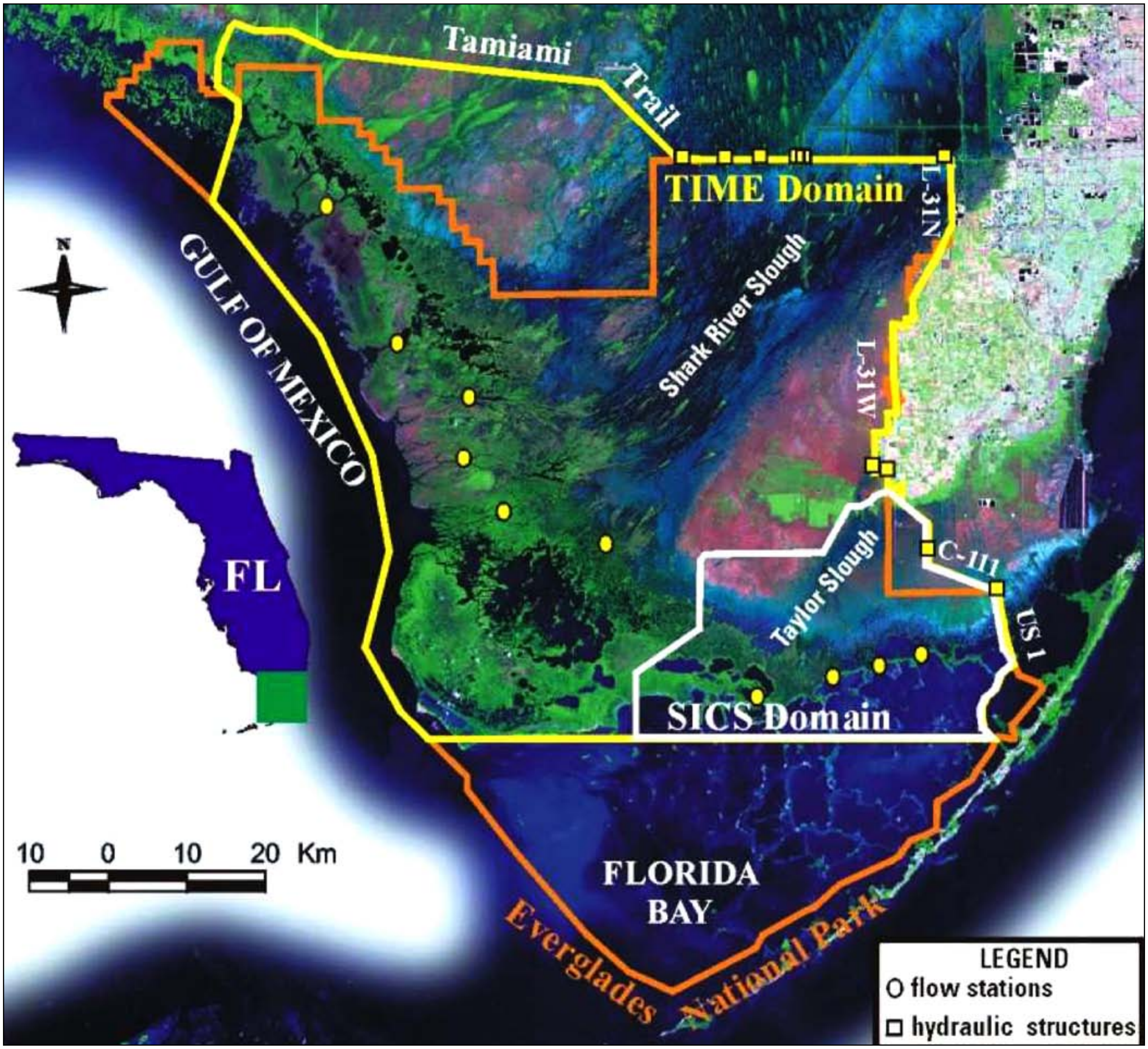

Figure 4.6 *South Florida satellite image showing SICS and TIME model domains (USGS).*

Exchanges with Adjacent Waters

The predictions needed from Florida Bay numerical circulation models can be carried out only with suitable inputs along their boundaries. These inputs are necessary to introduce the complex interactions that dominate circulation and water exchange between the shallow bay interior and the adjacent shelf and oceanic flows. The boundary conditions must cover a range of time scales to accommodate different types of simulations planned by the inner Florida Bay modeling teams (interannual, seasonal, and event-oriented simulations). Existing global models are not suitable for this task because of their coarse resolution and the lack of flexibility in performing simulations that match currently planned and future Florida Bay modeling activities. Therefore, it is necessary to develop a regional-scale model that will perform simulations that are closely linked to interior Florida Bay modeling needs. The regional model must be dedicated to the computation of the required hydrodynamic fields surrounding the Florida Bay model domain and to the calibration of these fields with observational data. Such a model, currently under development, applies the three-dimensional, finite-difference community hydrodynamic model HYCOM (Hybrid Coordinate

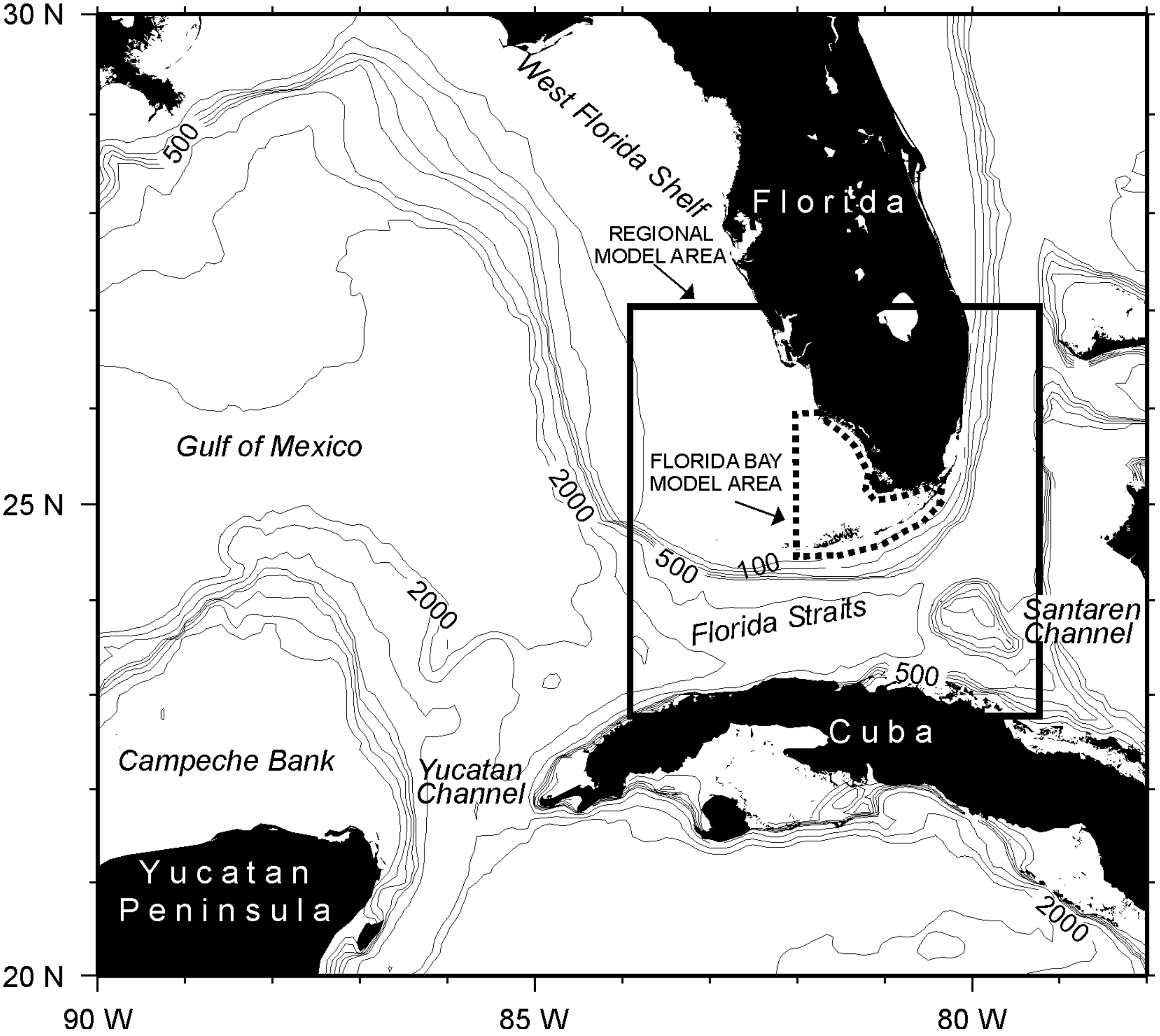

Figure 4.7 *A nested-model approach. Planned regional south Florida model area (thick solid line). Thick dashed line marks the Florida Bay and Florida Keys model area. The oceanic waters surrounding the regional model domain are included within the University of Miami's large-scale North Atlantic, Caribbean, and Gulf of Mexico model (HYCOM).*

Ocean Model, http://oceanmodeling.rsmas.miami.edu/hycom/) to the coastal waters adjacent to Florida Bay and the Florida Keys, including the Florida Straits, the western Gulf of Mexico and the southwestern Florida Shelf (Figure 4.7). This model is being coupled with an existing large-scale, coarse-resolution application of HYCOM that includes the North Atlantic, the Gulf of Mexico, and the Caribbean. This nested approach ensures the interaction of Florida Bay models with the Loop Current, Florida Current and related eddies, and remote sources of river-induced low salinity.

Circulation Models

To understand circulation and exchange within the interior of Florida Bay, a fully calibrated and verified circulation model is needed. The growing database of salinity, currents, volume transports, surface and groundwater inputs, and atmospheric forcing is rapidly becoming sufficient to provide comprehensive evaluation and validation of circulation models. To this end, a Standard Data Set has been agreed upon and is under development (J. Pica, personal communication).

Indeed, the complexities of Florida Bay demand a suitable modeling approach to properly evaluate possible future water delivery schemes to the bay. Expertise and modeling resources are available that can be applied to this problem in a reasonable time frame. However, two particular problems need to be addressed urgently: (1) the bathymetry, which is not currently available at the detail needed by the models; and (2) the appropriate inputs at the boundaries of Florida Bay models need to incorporate the complex interactions between the shallow coastal areas within Florida Bay and the adjacent oceanic flows.

Both the bathymetry and the boundary conditions must be part of an integrated modeling approach that includes parallel, coupled numerical simulations in Florida Bay and the adjacent seas. This comprehensive modeling tool must get underway soon to correspond with the observational programs and to advise management in a timely manner.

Salinity Models

To understand and predict salinity variability in Florida Bay, three types of models have been applied: statistical (regression analyses), mass-balance, and mechanistic, the last of which will be discussed below under Unresolved Questions and Ongoing Research, Hydrodynamic Models.

STATISTICAL MODELS

The PST subgroup evaluating salinity performance measures recommended a two-phase plan to develop updated salinity performance measures to predict freshwater runoff. First, a multivariable linear regression model that uses lagged terms should be constructed. Second, a time-series model relating the freshwater flows from the operation of the C-111 canal to the salinity of the nearshore embayments should be prepared for use in management decisions. A follow-up meeting of the group recommended that the use of Seasonal, Autoregressive, Integrated Moving Average (SARIMA) models be explored. A preliminary evaluation of current salinity performance measures relating water levels in the Everglades to the salinity in northeastern Florida Bay has been reported on (Marshall, 2001). Problems with the use of linear regression models for this data set were identified, particularly seasonality, cross correlation, and autocorrelation of hydrologic parameters. At that time, models and modeling techniques were not capable of adequately simulating the effect of changes in operations of the C-111 canal.

A subsequent project for Everglades National Park evaluated the use of SARIMA models to simulate salinity in the nearshore embayments of Florida Bay using the Park's Physical Monitoring Network daily data set (Marshall *et al.,* 2003). The purpose of the evaluation was to determine the appropriate statistical models that could be coupled with the SFWMD South Florida Water Management Model, also known as the 2x2 ("2 by 2") model. It was found that multivariable linear regression models were much easier than SARIMA models for coupling with the 2x2 model output. Statistical models have been developed that were capable of reasonably simulating salinity in the nearshore areas. Simulated salinities were functions of water levels in the Everglades and other areas upstream of Florida Bay, Taylor Slough, and C-111 canal flows; wind; tide; and rainfall. Improvements to the models are currently being incorporated, including the potential inclusion of a term in the model to simulate evaporation.

MASS–BALANCE MODELS

Box models by Walker (1998), Nuttle *et al.* (2000, 2001), Cosby *et al.* (1999), and Twilley (http://www.ucs.louisiana.edu/~rrt4630/mangrove-restudy.htm) applied mass-balance calculations to the analyses of wetland hydrology, Florida Bay salinity, and the salinity of Shark River. In each case, these models incorporated simplified representations of water flow that are parameterized by matching model prediction to observed hydrology and salinity.

Walker (1998) implemented a set of watershed hydrology models in Everglades National Park. These were used to estimate water and nutrient fluxes into the coastal mangroves. The models constructed monthly water budgets for several wetland basins based on data provided by the 2x2 hydrology model. The aggregated discharge from each basin was related to mean water depth by a generalized power law. The parameters of this power law were estimated by fitting simulated water depths to observations. Over the long term, the mean outflow from the basins must be correct if the data on other terms in the water balance are accurate. The parameters of the flow model control the variation of estimated flows around the long-term mean value. Walker (1998) lacked the outflow data necessary to validate his watershed models but did find that predicted outflows were correlated with salinity in the coastal bays in the Taylor Slough–C111 area.

Nuttle *et al.* (2001) implemented a mass-balance model for estimating evaporation in Florida Bay. This model calculates salinity, using monthly time steps, from variation in the net supply of fresh water to and water exchange between each of four regions in the bay, and water exchange with the Gulf of Mexico. The regions used in this model correspond to the regions defined from similarities in water quality (Boyer *et al.,* 1997) and other attributes of the Florida Bay ecosystem.

Rainfall and salinity data used to drive the model were measured in the bay. Freshwater runoff was estimated from measured flows in Taylor Slough and the C111 canal that discharge into the mangrove wetlands north of Florida Bay. The four-box model by Nuttle *et al.* (2001) has been calibrated against salinity data for the period 1993 through 1995 and validated by comparison with salinity data for the period 1996 through 1998. The standard error of prediction is about 2 psu across all four regions. Calibration of the model produces estimates for the unknown seasonal evaporation rates and the exchange rates between basins and with the Gulf of Mexico. These exchange rates can be used to investigate residence times in the bay, information that is needed to understand the processes that control nutrient concentrations and plankton blooms.

Nuttle *et al.* (2000) employed two different box models. One was essentially the annual averaged version of the four-box model described above, which they used to estimate mean annual evaporation from Florida Bay. The other, FATHOM (Cosby *et al.*, 1999), divided the bay into approximately 40 basins, based on morphology, and estimated exchanges between basins based on tide-driven hydraulic calculations. FATHOM has been used to analyze the influence of changing runoff into Florida Bay (Nuttle *et al.*, 2000), but the calculated exchange rates and resulting residence times have yet to be validated by comparison with observation.

Twilley (http://www.ucs.louisiana.edu/~rrt4630/mangrove-restudy.htm) modeled salinity in the Shark River by using boxes representing upper and lower reaches along the channel. The model included the effects of advection, estimated from long-term records of freshwater flow and dispersion, determined by calibration. This is one of a set of models under development as part of a study of mangrove-forest dynamics.

Unresolved Questions and Ongoing Research

Driving Processes

WINDS AND STORMS

Although the synoptic-scale and seasonal winds over south Florida coastal waters appear to be highly coherent over the whole region, there is now evidence from high-resolution numerical atmospheric models (Mattocks, personal communication; Albrecht *et al.*, 2003) that indicates considerable spatial variability as a result of mesoscale activity associated with convective systems and sea breeze development. A number of questions remain: What are the long-term effects of the daily development of convergent wind patterns over the bay? What are the magnitudes, spatial, and temporal scales of this mesoscale wind forcing? How does it influence the south Florida seascape in terms of water levels, evaporation and precipitation patterns, circulation and exchange between water bodies, and surface and groundwater inflows to the bay? What is the effect of winds on residence times of the interior waters of the bay? It is not clear what changes may occur from intense cyclones, nor how long these changes may persist. Predictive modeling of different classes of tropical cyclones is needed to anticipate these impacts.

PRECIPITATION

Considerable progress has been made with regard to the process of making precipitation observations into an operational product. Applicable NEXRAD data fields have been mapped onto the SFWMD hydrological (2x2) grid and are now archived at the SFWMD. Locally generated statistical functions relating radar reflectance to tropical convective rainfall are now being used (Willis, 1999). As a result, we are now ready to address a number of unresolved questions in regard to precipitation such as: Do the spatial patterns of bay surface salinities measurably change as a result of the heterogeneity of precipitation? To what degree has precipitation over the bay been changing because of land-use changes on the peninsula?

EVAPORATION

Price *et al.* (2001) described an investigation that is designed to provide mean rates of evaporation and its variation both spatially and temporally in Florida Bay. This investigation will be the first systematic attempt at determining evaporation in Florida Bay and tying mean estimates of evaporation to longer-term monitoring efforts ongoing in the bay. Questions to be answered by this project include these: What is the mean rate of evaporation in Florida Bay? What is the spatial and temporal variation of evaporation? How reliable are long-term estimates of evaporation? How much additional precision can be gained by refinement of stable isotope methods?

Other questions regarding evaporation include

- To what degree does the seasonality of evaporation need to be considered in evaluating the effect that different salinity patterns have upon water-management scenarios?
- What is the effect of the bay's bank-and-basin topography upon evaporation?

The rate of evaporation over the extensive, shallow banks may be different from the average estimates used to date. Neither instrumented-platform meteorological data nor synoptic radiation surveys have characterized conditions over shallow, seasonally exposed banks. Although the radiation-forcing over the banks will be the same as elsewhere, the different characteristics of the water column (shallow) and bottom (dense sea grass) are expected to affect how outgoing heat flux is partitioned, which in turn could significantly change local evaporation rates.

SURFACE-WATER INPUTS

Simulation models under construction by USGS and SFWMD in conjunction with their ongoing measurement programs are expected to resolve any remaining uncertainty concerning surface-water discharges into Florida Bay. Hydrodynamic transport models have been developed that are capable of being linked to upland-management models to address the effect of freshwater inflows on tempering salinities and conveying nutrients and contaminants to Florida Bay and southwest coastal estuaries. Langevin *et al.* (2002) of USGS have developed a coupled surface-groundwater model of the southern Everglades that is capable of simulating flow and salinity patterns in coastal embayments of northern Florida Bay in response to naturally occurring hydrologic events in the wetlands and the effects of upland-management practices on freshwater releases. The model provides the ability to evaluate the complex exchange and interaction of water and dissolved salt between the Everglades wetlands, the Florida Bay estuaries, and the underlying Biscayne Aquifer. Further enhancements of the model are ongoing, and its computational domain is being extended to include Shark River, Lostmans River, and other western sloughs within Everglades National Park south of Tamiami Trail (Schaffranek *et al.,* 2002). Both models are being developed at temporal and spatial resolutions that are facilitating the formulation of new estuarine species models (Cline and Swain, 2002) in the Across Trophic Level Simulation System (ATLSS). These models will allow researchers and managers to assess the ecological health of the total ecosystem and to develop and evaluate performance measures within CERP (DeAngelis *et al.,* 2002).

GROUNDWATER INPUTS

The discrepancy between isotope-derived estimates and the more traditional hydrological approaches (well heads and models) has been discussed above, as has the discrepancy between mass-balance and flow observations and isotope estimates. Clearly, many unresolved questions remain concerning not only the absolute amount of groundwater input to Florida Bay but also its temporal and spatial variability and the resulting salt and nutrient fluxes. The consensus at present is that the water-quality implications of groundwater input from either the southern Everglades or Florida Keys may be more significant than its physical consequences unless the larger estimates prove to be correct.

SEA LEVEL AND TIDES

No major unresolved issues remain concerning tides. Studies are underway concerning the effects of sea level differences on interbasin exchange and upon flow through the passages between the Florida Keys. It is also not clear how long-term sea level differences between the gulf and Atlantic affect the observed mean southeastward flow that transports water to the Florida Keys reef tract.

However, Frederick *et al.* (1994) and others have noted an acceleration in local sea level rise over the past century. The extent of this is not entirely clear nor is there yet an adequate geophysical explanation. Such a sea level rise would certainly have implications concerning bay restoration targets. A SFWMD study has concluded, however, that the currently projected sea level rise does not substantially affect CERP project water deliveries. While not precisely a "research issue," additional tide gauge benchmarks are needed near each water-level recorder in Florida Bay and all the gulf-coast stations to obtain absolute sea level measurements. Multiple stations are in place, but many others remain to be installed. The USGS mapping division and the USGS St. Petersburg laboratory are currently working to establish elevations at many gulf-coast platforms.

BOUNDARY CURRENTS

Questions concerning the effects of boundary currents are given below under System Characteristics. Modeling and observational studies are continuing to address how boundary currents are influencing the variability of flow through Florida Bay and the exchanges that take place between boundary currents and adjacent shelf waters.

System Characteristics

SALINITY

Although the spatial and temporal variability of salinity in Florida Bay is well documented and continues to be monitored both with field surveys and fixed instruments, a number of unresolved questions remain, including the following:

- How is the salinity of Florida Bay influenced by atmospheric forcing on time scales from daily to interdecadal, including significant transient meteorological events such as hurricanes and tropical storms?
- How do the spatial patterns of evaporation, precip-

itation, and basin residence time affect bay salinity distributions?
- For example, does hypersalinity occur where it does because evaporation is greater over broad shallow banks than in the rest of the bay or because exchange with lower-salinity water is restricted?
- How do the salinity records inferred from paleoecological data compare with salinity values measured over the past 45 years?
- Is there a statistical transfer function sufficient to adequately describe the effect of freshwater flows on salinity for the purposes of predicting the effect of restoration scenarios upon bay salinities?
- If so, over what spatial domain does it apply?

CIRCULATION

Circulation and exchange between isolated basins in the interior of the bay is the subject of several ongoing field research projects and will be a focus of the forthcoming interior Florida Bay model. Scientists from RSMAS, AOML, Harbor Branch Oceanographic Institute, ENP, and USGS have at various times been maintaining arrays of current, temperature, salinity, and water-level recorders within basins and channels during wet and dry seasons. Additional observations include shipboard Acoustic Doppler Current Profiler (ADCP) observations, salinity surveys, and surface drifter trajectories. These data will be used to directly compute salt transports, water exchange, and interior circulation. In contrast, the exchange between the Gulf of Mexico and western areas of the bay has yet to be quantified and is one of the principal unresolved questions concerning circulation.

A better understanding of flow across banks, and bank characteristics in general (*e.g.,* cover, elevation, salinity, and temperature), will be necessary for successful hydrodynamic and ecological modeling of the bay's interior. The bathymetry of Florida Bay, particularly with respect to the shallow banks, needs to be more adequately described for use by modelers. It is not clear to what degree remote sensing (*e.g.,* LIDAR) can be used to address this deficiency, given the density of seagrass. The depth over many of the banks is approximately equal to or less than the range of seasonal fluctuations in mean sea level. What consequences might this have for rates and patterns of interbasin water exchange in the interior portion of the bay? What are the rates and pathways of exchange between the interior basins and across the banks in the western, central, and eastern regions of Florida Bay and with the southwestern Florida shelf?

On a regional scale, very little is known about the cause of the net southward flow that couples the eastern gulf and Atlantic coastal region of the Keys and its long-period variations. This flow transports low-salinity discharges from rivers emptying into the southeastern gulf around Cape Sable to western Florida Bay, where they can interact with interior waters of the bay as well as with the Atlantic coastal waters of the Keys. It is essential to better describe and understand this flow in order to aid future model development and facilitate informed management decisions. What is the influence of the Loop Current or synoptic winds over the west Florida shelf on driving this flow? Are topographic constraints on the southwestern Florida shelf important? How is the flow related to observed southward flows farther north on the west Florida shelf that appear to diverge from the coast before reaching the southwest shelf (Yang *et al.,* 1999)?

EXCHANGES WITH ADJACENT WATERS

During the dry season, high-salinity waters from western Florida Bay and the gulf transition region are transported southward toward the Florida Keys National Marine Sanctuary. There is evidence from the large-scale hydrographic surveys that at times these high-salinity waters can form a near-bottom, salty layer in the Hawk Channel region. However, very little is known about this process. How are the salty bottom layers formed? What are their spatial extent and transport pathways? What are their durations?

Analysis of current records taken in different years suggest that up to 500–600 m^3/s could be available for exchange with the interior of Florida Bay. Transports across the western boundary are very uncertain at this time; however, field research is planned to improve understanding of transport processes and help quantify this exchange. There are also unresolved questions regarding the bank "overtopping" process and whether this could explain the observed net outflow from the central part of the bay.

Mean gulf-to-Atlantic flows through western Florida Bay to the Keys coastal zone and reef tract have been estimated from observations and are believed to be connected to the boundary currents (Loop Current and Florida Current) surrounding south Florida (Lee and Smith, 2002). More effort is needed to quantify and monitor this mean flow to better understand the physical processes involved. Is it related to the position and configuration of the Loop Current as gulf models and satellite observations suggest? Coupling of a large-scale model that includes the gulf and Straits of Florida to a finer-scale Florida Bay model is needed to address this issue.

Hydrodynamic Models

Researchers developing and applying mechanistic models have pursued two radically different approaches: the aggregated representation of hydrology and salinity in mass-balance models, described above, and the detailed representation of tide and wind-driven water movements in wetland hydraulic and estuarine hydrodynamic models, for example, the RMA-10 model (Kim *et al.,* 1999). The PST reviewed the RMA-10 some time ago, but little work has proceeded on it since that time. The review raised fundamental concerns both in regard to the degree to which the model was calibrated and verified and also in regard to more basic issues such as boundary conditions and transport processes within the bay's interior (http://www.aoml.noaa.gov/flbay/pmcphysci.html). J. Wang (personal communication) recently applied the finite-element model CAFE3D in 2-D mode with realistic winds and tides to estimate salinity fields in Florida Bay resulting from a "climatological" run-off hydrography. Multi-year simulations have been made and show patterns similar to observations (http://anole.rsmas.miami.edu/people/jwang/Florida_Bay_Model.html).

The FBFKFS of CERP convened a Hydrodynamic Model Review Workshop in June 2002, and a Review Panel was assigned to assess prospects for the successful modeling of Florida Bay hydrodynamics to be used as a management tool. This panel provided strong support for the development of a numerical hydrodynamic model because of the need to support water-quality and seagrass modeling of the bay. The panel also firmly recommended not combining different numerical modeling frameworks (specifically, hybrid mixing of finite-element and finite-difference numerical grid solutions for hydrodynamic and water-quality modeling). The panel's recommendations were generally consistent with the Physical Sciences Team's previously issued Modeling Terms of Reference.

During this workshop, the SFWMD described their exploratory analysis for determining the feasibility and applicability of a finite-difference model based on the Environmental Fluid Dynamic Code for Florida Bay. SFWMD's Phase I of model evaluation was completed in 2002 and was intended to help provide a basis for further development and application of a hydrodynamic model for the FBFKFS and other projects. Phase I was done under contract by J. Hammrick, of Tetra Tech, Inc. Numerical-model grids were generated, a five-year calibration data set was synthesized (and incorporated into the Physical Sciences Team's Standard Data Set), and the performance of the model was evaluated. Simulations of water-surface elevation, currents, and temperature were judged to be more than adequate for confidence in long-term prediction of these quantities. Using the observationally defined inflows and their associated observed salinities, the model tended to overpredict salinity, particularly in the northeastern portion of Florida Bay. This overprediction seemed likely to be due to uncertainties in estimates of freshwater discharge, evaporation, or other boundary exchanges.

The Phase I final report is currently under review at the SFWMD. Based on past comments from the Physical Science Team, the Florida Bay Science Program Science Oversight Panel, the Feasibility Study's workshop Review Panel, and information gained from Phase I, a detailed work plan for Phase II is being written. This phase will consist of the completion of a validated circulation model for the interior bay that will enable the SFWMD, the United States Army Corps of Engineers (USACE), and other partner agencies to evaluate potential restoration alternatives as part of the FBFKFS. The success of this model development and application will be highly dependent upon inputs from boundary models, including a regional, oceanic hydrodynamic model for the Gulf of Mexico and Atlantic boundaries and a regional hydrologic model at the Everglades boundary.

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Chapter 5

Nutrient Dynamics

Team Leaders Joseph N. Boyer (Florida International University),
Brian Keller (Florida Keys National Marine Sanctuary, PMC)
Contributors Joe Boyer, Larry Brand, Bill Burnett, Jaye Cable, Paul Carlson, Carl Cerco, Randy Chambers,
Jeff Chanton, Dan Childers, Reide Corbett, Jeff Cornwell, Susan Dailey, Cynthia Heil, Gary Hitchcock,
John Hunt, Ron Jones, Jennifer Jurado, Chris Kelble, Brian Keller, Steve Kelly, Mike Kemp, Gary Kleppel,
Margurite Koch-Rose, Bill Kruczynski, Brian Lapointe, Chris Madden, Bill Mcpherson, Frank Millero,
Bill Nuttle, William Orem, Ed Phlips, Rene Price, Enrique Reyes, Dave Rudnick, Eugene Shinn,
Fred Sklar, DeWitt Smith, Richard Stumpf, Peter Swart, Zafer Top, Gabe Vargo,
Cecilia Weaver, Laura Yarbro, Jia-Zhong Zhang

Introduction

Question 2*—What is the relative importance of the influx of external nutrients and of internal nutrient cycling in determining the nutrient budget of Florida Bay? What mechanisms control the sources and sinks of the bay's nutrients?*

Ecological changes within Florida Bay, including *Thalassia testudinum* mass mortality and algal blooms, which have been evident during the past two decades, have commonly been attributed to many of the same human activities that have changed the Everglades. The diversion of freshwater to the Atlantic coast by canals has increased the salinity of the bay. Freshwater discharges from canals to the Atlantic Ocean were roughly four times larger than discharges to sloughs that flowed toward Florida Bay during the 1980s. Additionally, anthropogenic nutrient inputs from the Florida Keys, Gulf of Mexico, the atmosphere, and the Everglades may have increased. Inputs from the gulf may include phosphorus, which is transported by longshore currents from the central Florida coast, and nitrogen (N), which originates in the Everglades and flows into the gulf through Shark River Slough.

The main informational needs relative to nutrient cycles in Florida Bay is an understanding of the factors that triggered and maintain the mass mortality of seagrasses and the episodic phytoplankton blooms. Also critical is sufficient understanding to enable us to assess the effects of various environmental management strategies being considered for bay restoration. In particular, we need to accurately predict the sensitivity of the bay's nutrient cycles to changing freshwater flow into the bay and to the resultant change in the bay's salinity regime. For much of the bay, any factor that increases phosphorus (P) availability either by increasing input or decreasing removal is likely to exacerbate the current problems of the bay. Recent evidence also indicates that algal blooms in the central and western bay are sometimes stimulated by nitrogen (N) enrichment. Thus we need a thorough understanding of the bay's nutrient cycles. Questions that the current monitoring and research program must address in order to meet these needs follow.

The water column in Florida Bay is generally oligotrophic, and phytoplankton biomass has historically been quite low throughout the system. Although phytoplankton in Florida Bay are generally phosphorous limited (Fourqurean *et al.*, 1993; Phlips and Badylak, 1996; Lavrentyev *et al.*, 1998), other resources (*e.g.*, light, nitrogen, silicon) may also be important in controlling plankton biomass in some areas of the bay (Lavrentyev *et al.*, 1998). Dissolved inorganic phosphorous (DIP) concentrations are near detection limits (20 nmol), but concentrations of dissolved inorganic nitrogen (DIN) can be relatively high (median value 3.3 µmol, but concentrations >10 µmol are not uncommon) and dominated by ammonium (Fourqurean *et al.*, 1993; Boyer *et al.*, 1997; as summarized in Fourqurean and Robblee [1999]).

A spatial analysis of data from the monitoring program conducted by Boyer *et al.* (1997) resulted in the delineation of three groups of stations (eastern, central, and western) that have robust similarities in water quality (Figure 5.1). We deem these spatially contiguous groups of stations to be the result of similar hydrodynamic forcing and processing of materials; hence, we call them "zones of similar influence." The eastern bay zone acts most like a 'conventional' estuary in that it has a quasi-longitudinal salinity gradient caused by the mixing of freshwater runoff with seawater. In contrast, the central bay zone is a hydrographically isolated area with low and infrequent terrestrial freshwater input, a long water residence time, and high evapora-

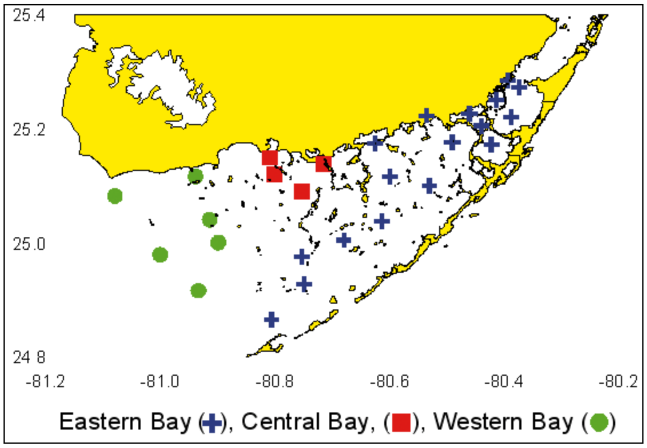

Figure 5.1 *Zones of similar water quality in Florida Bay.*

tive potential. The western bay zone is the most influenced by the Gulf of Mexico tides and is also isolated from direct overland freshwater sources.

Summary of Knowledge

Research on nutrient dynamics in Florida Bay focuses on the exchange of nutrients with adjacent regions ("external" dynamics), the cycling of nutrients within Florida Bay ("internal" dynamics), and the influence of these processes on ecosystem structure and function, *i.e.,* on spatial and temporal variation (Table 5.1). A continuing program of monitoring and research, including computer modeling, addresses the question of how human activity is affecting the nutrient dynamics of Florida Bay and how future restoration actions will alter these dynamics.

- What do we know about status and trends in water quality over space and time?
    - Objective analysis shows that there are three zones (eastern, central, and western) in the bay that exhibit significant differences in water-quality characteristics due to nutrient inputs, tidal advection, and water residence time.
    - In general, DIP concentrations increase and DIN decreases from east to west, resulting in a shift from P limitation to N limitation.
    - Central bay waters have high ammonium concentrations, which may indicate a bottleneck in the process of nitrification.
    - Temporal trends over a 13-year period of record show bay-wide declines in total phosphorus (TP), total nitrogen (TN), and chlorophyll *a* and an overall increase in turbidity (cloudiness of the water).
- What do we know about sources and amounts of external nutrient loading to Florida Bay?
    - Terrestrial nutrient loading fluctuates with freshwater flow, but flow-weighted concentrations decrease with increasing flow.
    - Phosphorus loading from the Everglades is a small proportion of the Florida Bay nutrient budget. Most phosphorus (P) appears to be derived from the Gulf of Mexico.
    - Nitrogen output from the southern Everglades (including Shark River Slough) is a significant proportion of the Florida Bay nutrient budget (similar in magnitude to atmospheric loading). Most nitrogen flowing from the wetlands is in the form of dissolved organic compounds. Studies on the bioavailability of dissolved organic nitrogen (DON) are currently underway.
    - The atmospheric input of nutrients is large, and most atmospheric nitrogen is inorganic.
    - Knowledge of the bay's nutrient budget is coarse over time and space (annual averaging for entire bay). Large uncertainty exists regarding the magnitude of nutrient exchange at the Gulf of Mexico boundary and regarding saline groundwater sources.
    - There is a measurable effect of water management on the quantity and distribution of water and nutrients through the length of the Taylor Slough–C-111 basin system, influencing inputs to Florida Bay.
    - A serious disconnect exists between upland/canal loading estimates and actual input to the bay because of unmeasured nutrient processing in the intervening wetland/mangrove areas.
- What do we know about internal nutrient-cycling processes?
    - Benthic denitrification is higher than expected based on denitrification: N-loading relationships in other estuaries.
    - The balance of N_2 fixation and denitrification in the bay is highly variable, but there appears to be a net loss of N in the overall system.
    - Sediment regeneration of ammonium under dark conditions is low relative to benthic dissolved oxygen demand.
    - Sediment regeneration of ammonium decreases with increases in sediment chlorophyll *a* concentration, indicating that the microphytobenthos is important in regulating water column N concentrations.
    - There is very little, if any, P flux out of the sediments, with the exception of the western bay-shelf area.
    - High rates of organic carbon (C) and N fluxes occur, both into and out of sediments over diel cycles (particularly in the central and western bay).
    - Phosphorus sorption-desorption varies strongly as

Table 5.1 *Research topics defined by Question 2 (cells in the matrix) and key references to the associated research.*

Research Topics	Spatial Variation	Temporal Variation
Water-Quality Patterns and Trends	Fourqurean *et al.*, 1993; Boyer *et al.*, 1997; Burd and Jackson 2002	Boyer *et al.*, 1999; Burd and Jackson, 2002
Overall Nutrient Budget	Boyer and Jones, 1999; Rudnick *et al.*, 1999; Cerco *et al.*, 2000	Boyer and Jones, 1999; Rudnick *et al.*, 1999; Cerco *et al.*, 2000
External Nutrient Loading		
Terrestrial Inputs		
Everglades	Walker, 1998; Rudnick *et al.*, 1999	Walker, 1998; Rudnick *et al.*, 1999
Mangroves	Childers *et al.*, 1999a,b; Davis *et al.*, 2001; Sutula *et al.*, 2001, 2003	Childers *et al.*, 1999a,b; Davis *et al.*, 2001a,b; Cable *et al.*, 2001; Sutula *et al.*, 2001, 2003
Keys	Kruczynski and McManus, 2002	
Atmospheric Inputs	Nuttle *et al.*, 2000	
Groundwater Inputs	Shinn *et al.*, 1994; Corbett *et al.*, 1999, 2000a,b; Price and Swart 2001	
Gulf of Mexico	Rudnick *et al.*, 1999	
Atlantic Ocean	Szmant and Forrester, 1996	
Internal Nutrient Cycling		
N_2 Fixation	Cornwell, 2001; Owens and Cornwell, 2001	
Benthic Flux	Rudnick, 1999; Carlson and Yarbro, 1999; Yarbro and Carlson, 1999; Chambers *et al.*, 2001; Yarbro and Carlson, unpublished	
Nitrification/Denitrification	Kemp and Cornwell, 2001	Kemp and Cornwell, 2001
Microbial Loop	Cotner *et al.*, 2000; Boyer *et al.*, 2006	Boyer *et al.*, 2006
DOM Remineralization	Boyer *et al.*, 2006	Boyer *et al.*, 2006
Seagrass Effects on Water Quality	Madden and McDonald, 2006; Madden *et al.*, 2003; McDonald *et al.*, 2003; Gras *et al.*, 2003; Nielson *et al.*, 2006	Madden and McDonald, 2006; Madden *et al.*, 2003; McDonald *et al.*, 2003; Gras *et al.*, 2003; Nielson *et al.*, 2006
Higher-Trophic-Level Effects on Water Quality		
Water Quality Modeling	Cerco *et al.*, 2000	

a function of temperature and salinity.

- The decreasing bayward gradient in iron content of sediments has implications in P availability, sulfide toxicity, and primary production in the benthos.
- The seagrass community is a major sink for nutrients from either the water column or sediment pore waters in the bay.

Patterns and Trends in Water Quality

A network of water-quality monitoring stations was established in 1989 (and funded by SFWMD in 1991) to investigate both spatial patterns and temporal trends in water quality in an effort to elucidate mechanisms behind the recent ecological change. One of the primary

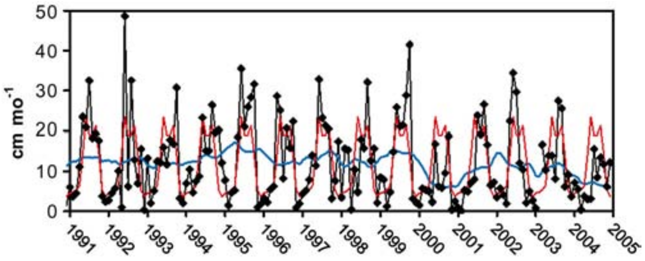

Figure 5.2 *Monthly average rainfall in the Florida Bay area, 1991–2005.*

purposes for conducting long-term monitoring projects is to be able to detect trends in the measured variables over time. These programs are usually initiated as a response to public perception (and possibly some scientific data) that 'the river-bay-prairie-forest-etc. is dying.' In the case of Florida Bay, during 1987, the impetus was the combination of a seagrass die-off, increased phytoplankton abundance, sponge mortality, and a perceived decline in fisheries.

Period of Study

Climactic changes occurring over the data-collection period of record had major effects on the health of the bay. Precipitation rebounded from the drought during the late 1980s and has been greater than the long-term average (9.2 cm mo^{-1}) for 9 of the past 12 years (Figure 5.2). Early in the record, salinity and total phosphorus (TP) concentrations declined baywide, while turbidity increased dramatically. The salinity decline in eastern and central Florida Bay was dramatic early on but has since stabilized into a regular seasonal cycle (Figure 5.3). Some of the decrease in the eastern bay could be accounted for by increased freshwater flows from the Everglades, but declines in other areas point to the climactic effect of increased rainfall during this period. The central bay continues to experience hypersaline conditions (greater than 35 practical salinity units [psu]) during the summer, but the extent and duration of the events are much smaller.

Chlorophyll *a* concentrations (CHLA), a proxy for phytoplankton biomass, were particularly dynamic and spatially heterogeneous (Figure 5.4). The eastern bay generally has the lowest CHLA, and the central bay has the highest. In the eastern bay, which makes up roughly half of the surface area of Florida Bay, CHLA have declined by 0.9 $\mu g\ l^{-1}$ or 63%. Most of this decline occurred over a few months in the spring-summer of 1994 and has remained relatively stable. The isolated central bay zone underwent a fivefold increase in CHLA from 1989 to 1994, and then rapidly declined to previous levels by 1996. In western Florida Bay, there was a significant increase in CHLA, but median concentrations remained modest (2 $\mu g\ l^{-1}$) by most estuarine standards. There were significant blooms in the central and western bay immediately following Hurricane Georges (November 1998), but it was Hurricane Irene's large rainfall input (October 1999) that induced a large bloom throughout the bay. It is important to note that these changes in CHLA (and turbidity) happened years after the poorly understood seagrass die-off in 1987. It is possible that the death and decomposition of large amounts of seagrass biomass might partially explain some of the changes in water quality of Florida Bay, but the connections are temporally disjunct and the processes are indirect and not well understood.

As mentioned previously, TP concentrations have declined baywide over the 12-year study period (Figure 5.5). As with salinity, most of these declines occurred during the early part of the study. Unlike most other estuaries, increased terrestrial runoff may have been partially responsible for the decrease in TP concentrations in the eastern bay because the TP concentrations of the runoff were at or below ambient levels in the bay. The elevated TP in the central bay was mostly due to high evaporation. It is important to understand that almost all the phosphorus measured as TP is in the form of organic matter, which is less accessible to plants and algae than inorganic phosphate.

The DIN pool is made up of three components: ammonium (NH_4^+), nitrate (NO_3^-), and nitrate (NO_2^-). The western bay is lowest in DIN; phytoplankton in this region may be limited by N availability on a regular basis (Figure 5.6). DIN in the eastern bay is a little higher and is mostly in the form of NO_3^-, and highest levels are found in the central bay as NH_4^+.

Turbidities in the central and western bay have increased tremendously since 1991 (Figure 5.7). Turbidity in the eastern bay increased twofold from 1991 to 1993, whereas those in the central and western bays increased by factors of 20 and 4, respectively. Generally, the eastern bay has the clearest water, which is due to a combination of factors such as high seagrass cover, more protected basins, low tidal energy, and shallow sediments. We are unsure what caused it, but the loss of seagrass coverage may have destabilized the bottom so that it is more easily disturbed by winds.

An extensive set of contour maps of water-quality parameters for Florida Bay is available at http://serc.fiu.edu/wqmnetwork/.

Recent Conditions

Most water-quality variables during 2001 generally followed typical annual trends, with one prominent exception. All regions of the bay experienced a pro-

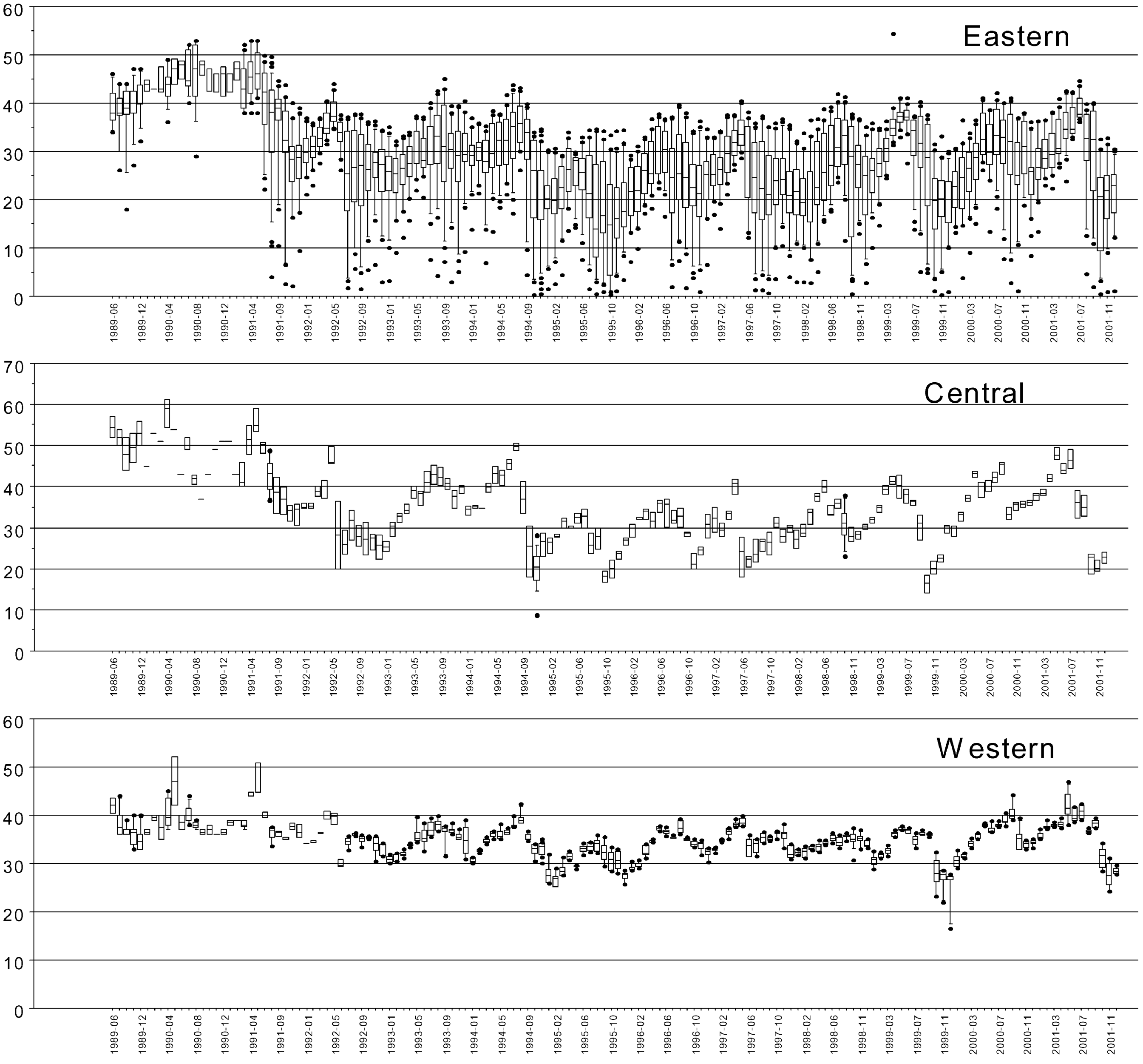

Figure 5.3 *Monthly median salinity in the three Florida Bay zones.*

longed period of hypersalinity during the summer months. Most of this was due to the previous dry year, which set up the system for this occurrence. The annual pattern in CHLA was unremarkable—no blooms reported. Total phosphorus values declined from very high levels in the fall of 2000 to normal levels in 2001. The western bay showed elevated DIN during the early part of 2001 but was not excessive compared with other years. Turbidity continued to fluctuate above post-1993 levels. Note that the high turbidities observed in the western bay during the winter also correlated with elevated TP.

NOAA/AOML also has a water-quality monitoring program in Florida Bay. Its primary purpose is to measure physical aspects of the system (see Question 1), but there is also a nutrient component to the sampling. An example of this is the analysis of phosphorus (Figure 5.8) using long-path-length liquid waveguide technology from Zhang and Chi (2002).

Exogenous Sources of Nutrients

A budget of Florida Bay's exogenous nutrient sources, which was estimated for the 2001 Florida Bay Confer-

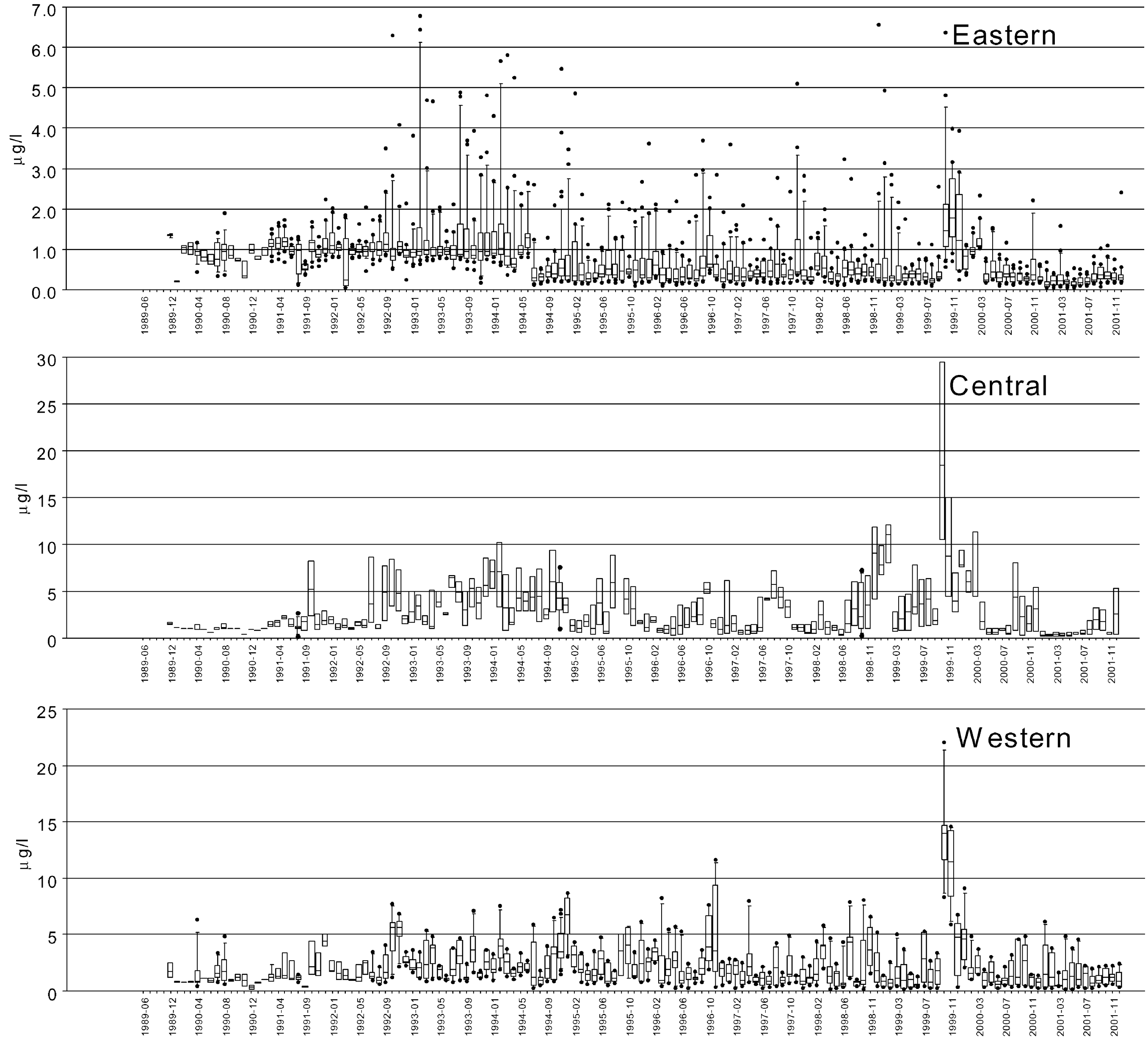

Figure 5.4 *Monthly median chlorophyll* a *in the three Florida Bay zones.*

ence, included inputs from the Everglades, wastewater and storm water from the Florida Keys, saline groundwater, the Gulf of Mexico, the Atlantic Ocean, and the atmosphere. Results from this exercise, with revision of the estimated saline groundwater source, are presented in Figures 5.9–5.11.

Nutrient Inputs from the Everglades: Taylor Slough–C-111 and Shark River

Nutrient outputs from the Everglades in this budget have been estimated from inputs to Everglades National Park wetlands from canals as reported by Rudnick *et al.* (1999). This approach can only be considered a rough estimate because of nutrient-processing during transport through the southern Everglades. However, these estimates are more likely to be correct than estimates of most other components of the bay's nutrient budget. The accuracy of estimates for the southeastern Everglades nutrient outputs is indicated by results of Sutula *et al.* (2003). This study found that TN and TP inputs from the mouths of mangrove creeks into Florida Bay in 1997 were similar to estimated inputs to the wetland that year (TN loads differed by 7%, and TP loads differed by one metric ton per year).

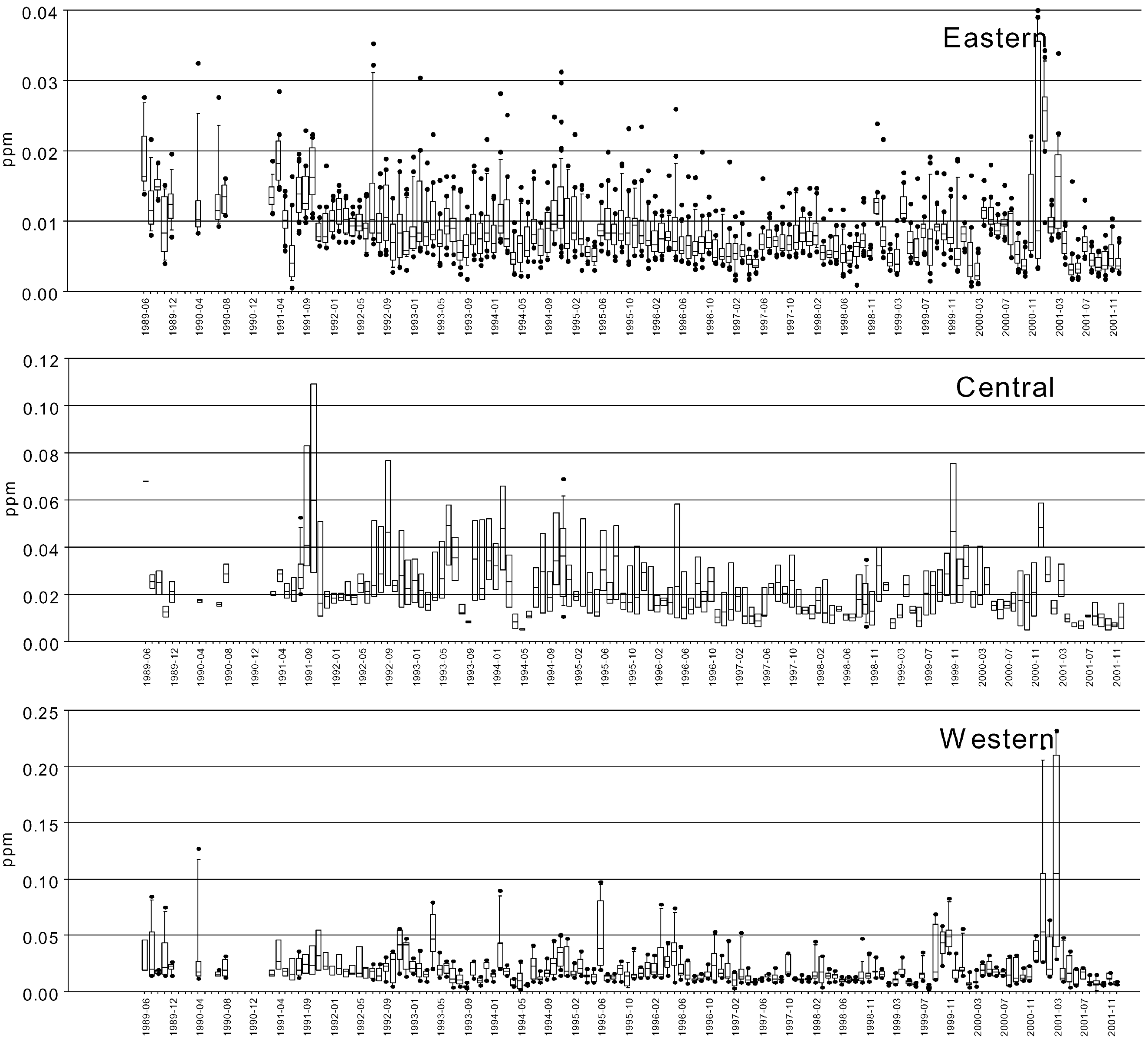

Figure 5.5 *Monthly median total phosphorus in the three Florida Bay zones.*

Studies of nutrient export from Taylor River, Trout Creek, and McCormick Creek (Sutula *et al.,* 2003; Davis *et al.,* 2003) have provided insights into the relationship between patterns of freshwater discharge and those of nutrient dynamics and output into Florida Bay. Nutrient outputs have been found to increase with increasing water discharge. As observed for inflows to Everglades National Park wetlands from canals, this increase is not linear; flow-weighted mean nutrient concentrations decrease with increasing discharge (Rudnick *et al.,* 1999; Figure 5.12). Output of phosphorus to Florida Bay is mostly as dissolved organic phosphorus, but it is very low in magnitude. During the dry season, both suspended solids and phosphorus are imported into the mangrove ecotone from the northeastern region of the bay. Output of nitrogen is also largely as dissolved organic nitrogen, but this quantity is high, resulting in a very high TN:TP ratio in creek outputs (molar ratio average near 200).

During the next year, RECOVER (the monitoring and assessment program of the Comprehensive Everglades Restoration Plan [CERP]) will expand the network of creek discharge and nutrient-sampling stations to include new sites along Florida Bay's coastline and the western Everglades rivers. A total of eight paired (upstream-downstream) stations are planned, includ-

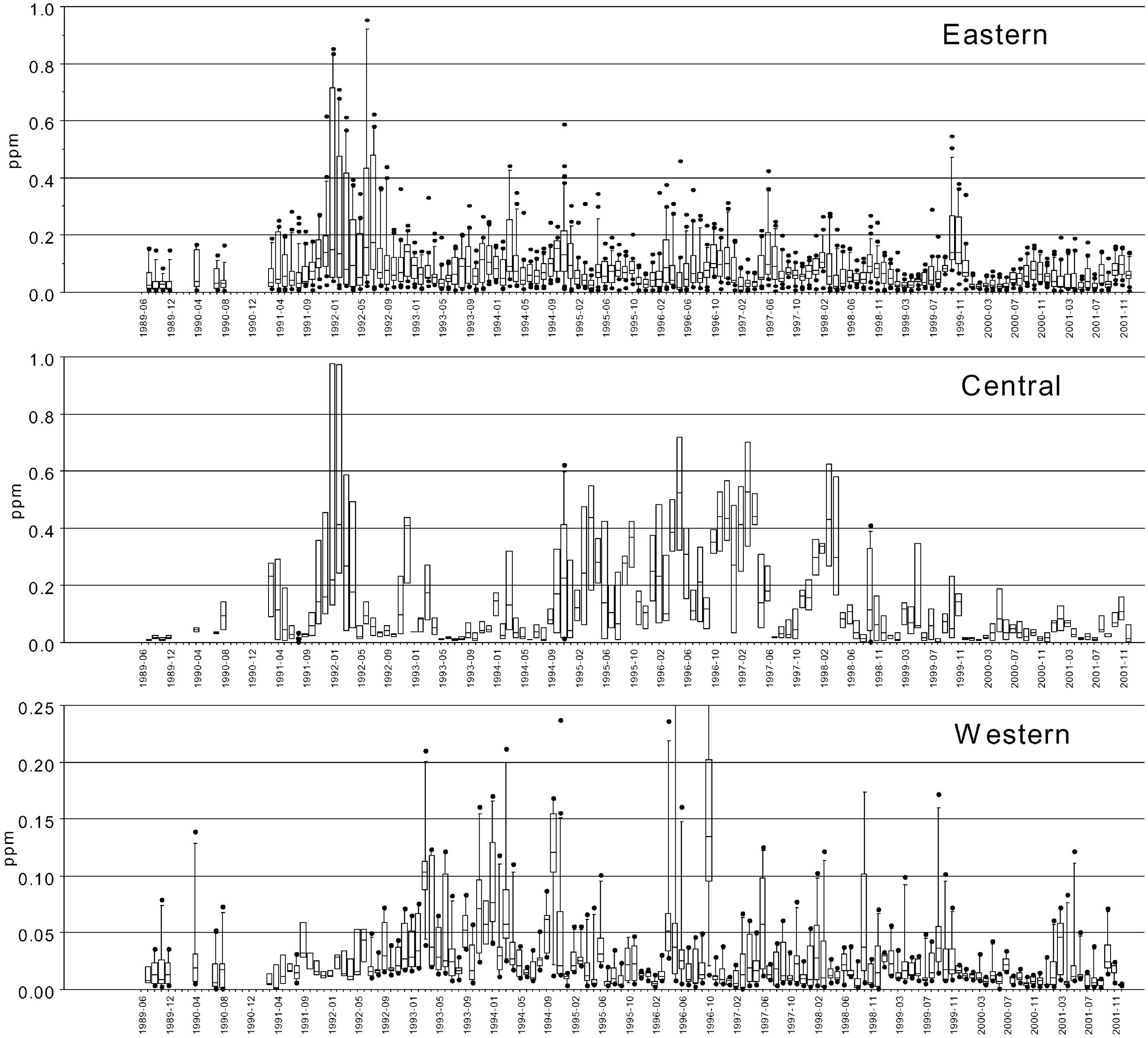

Figure 5.6 *Monthly median dissolved inorganic nitrogen in the three Florida Bay zones.*

ing four creeks entering Florida Bay and four rivers entering the Gulf of Mexico. It should also be noted that the Florida Coastal Everglades Long Term Ecological Research (LTER) is providing information on nutrient processing in the southern Everglades and mangrove zone, with particular emphasis on the formation, transport, and decomposition of dissolved organic matter.

Ground Water

The input of nutrients to Florida Bay via ground water remains highly uncertain. No new estimates of groundwater flux have been made since the 2001 conference. At that time, it was evident that subsurface freshwater inputs are negligible. Ground water beneath Florida Bay and its mangrove ecotone along the Everglades coast is saline (Reich *et al.,* 2002; Price, 2001; C. Reich and E. Shinn, personal communication). Thus, fresh ground water beneath the Everglades that flows toward Florida Bay appears to rise toward the surface, over denser saline water, to the north of the bay boundary (Price, 2001).

In contrast to fresh ground water, significant advection of saline ground water into the bay may occur from beneath the bay itself. Based on groundwater-tracer (radon, methane) concentrations, Corbett *et al.*

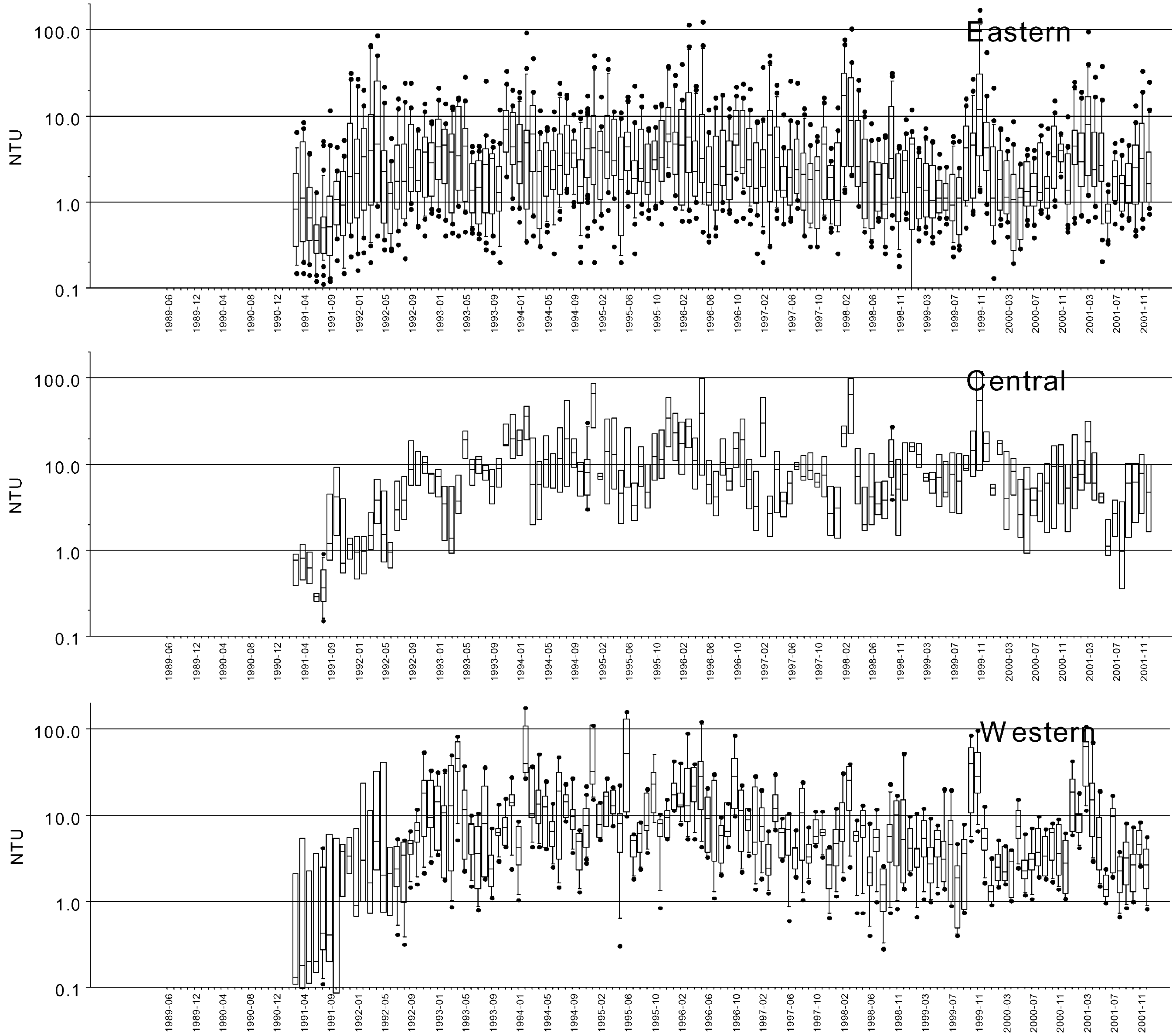

Figure 5.7 *Monthly median turbidity in the three Florida Bay zones.*

(1999, 2000a) have estimated a bay-wide vertical groundwater flow of about 1 cm/d or higher (Top *et al.*, 2001). The nutrient budget presented at the 2001 Florida Bay Conference used this value along with nutrient concentrations of 0.1 µmol TP, 1 µmol DIN, and 10 µmol TN. These concentrations are typical of wells at pristine sites in the Florida Keys (E. Shinn, personal communication). However, C. Reich and E. Shinn (personal communication) now report that these concentrations are considerably lower than those found in wells throughout Florida Bay. Over a four-year period, concentrations averaged approximately 1.5 µmol TP, 80 µmol TN, and 44 µmol NH_4. Still assuming a 1-cm/d groundwater flow, these higher concentrations would result in a groundwater nutrient input of 38 MT/y for TP, 8,800 MT/y for TN, and 5,000 MT/y for DIN. Compared to nutrient inputs from the Everglades, these estimated groundwater inputs are about 10 times higher for TP, about 6 times higher for TN, and more than 100 times higher for DIN. Some caution may be advised before applying these well-water concentrations because they may be affected by biogeochemical processes such as adsorption or denitrification prior to discharge, thus lowering their input into surface waters.

However, if this groundwater-input estimate of DIN is accurate, it would represent about 75% of all in-

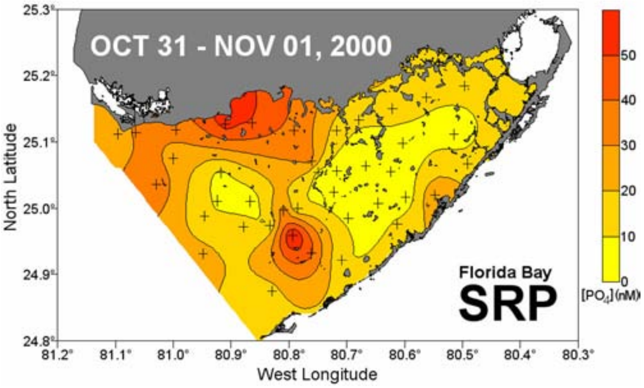

Figure 5.8 *Water column phosphate concentration in Florida Bay.*

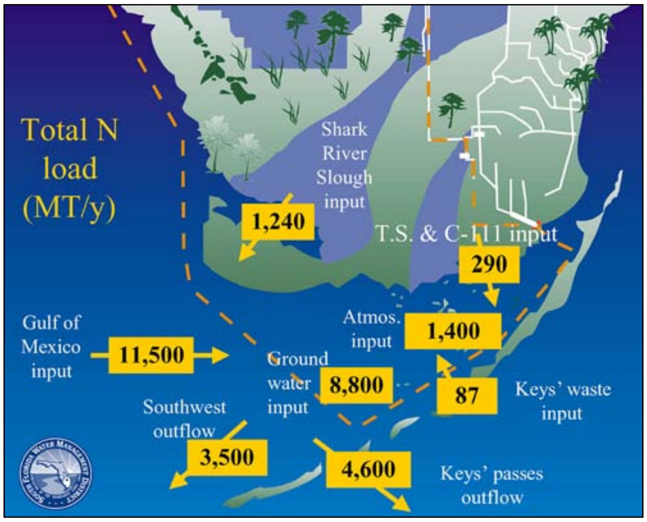

Figure 5.10 *Estimates of the annual exchange of TN at Florida Bay's boundaries. Everglades estimates are annual median inputs to wetlands from canals (since 1979 for Shark Slough and since 1984 for Taylor Slough and the C-111 basin). Note that flow-weighted mean TN concentrations have been consistently decreasing since 1985 in both systems and that medians provided here may be higher than those of recent years.*

organic nitrogen inputs to the bay. Furthermore, at such a high concentration, this inorganic nitrogen would be readily available for algal and submerged aquatic vegetation (SAV) productivity (in contrast to the low-concentration input from the Gulf of Mexico). It should be noted that this estimated groundwater DIN input is equivalent to 18 µmol m^{-2} h^{-1}, or roughly half of the median nocturnal nutrient flux across the sediment–water interface, as measured along the northern Florida Bay coast. It is also roughly equal to the median nocturnal benthic input found in the interior bay (P. Carlson, personal communication). The surprisingly high magnitude of the groundwater DIN input estimate, combined with the fact that ground water is usually hypersaline, is grounds for skepticism regarding the estimated 1 cm/d groundwater input as a rate that occurs commonly throughout the bay. This does not, however, preclude the possibility that large inputs of ground water occur at some locations in the bay, particularly near the Keys (see below).

An additional source of uncertainty in groundwater input is the depth from which the ground water is advected. For example, advective flow through surficial sediments can be caused by current-induced gradients over topographic expressions such as sand ripples (Huettel and Gust, 1992). Presumably, flow over

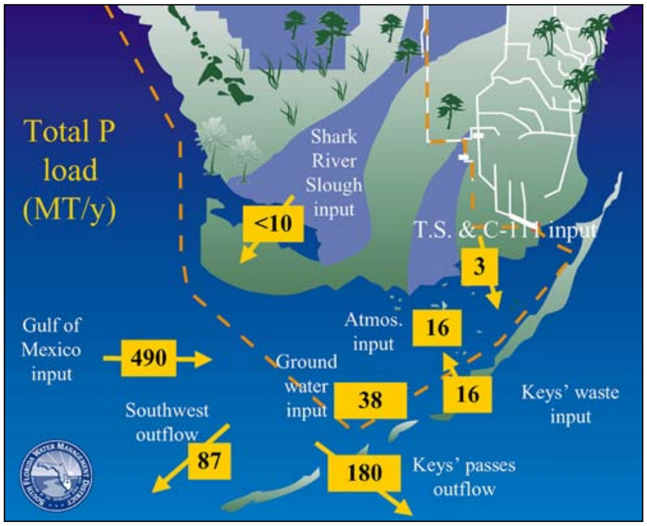

Figure 5.9 *Estimates of the annual exchange of total phosphorus at Florida Bay's boundaries. Everglades estimates are annual median inputs to wetlands from canals (since 1979 for Shark Slough and since 1984 for Taylor Slough and the C-111 basin).*

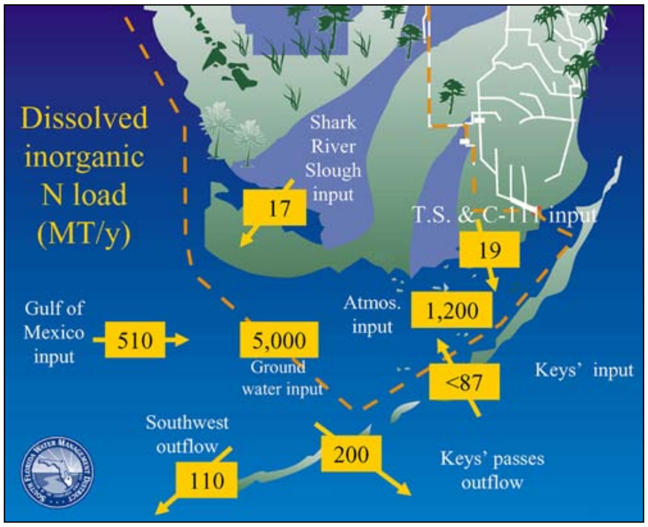

Figure 5.11 *Estimates of the annual exchange of inorganic nitrogen at Florida Bay's boundaries. Everglades estimates are annual median inputs to wetlands from canals (since 1979 for Shark Slough and since 1984 for Taylor Slough and the C-111 basin).*

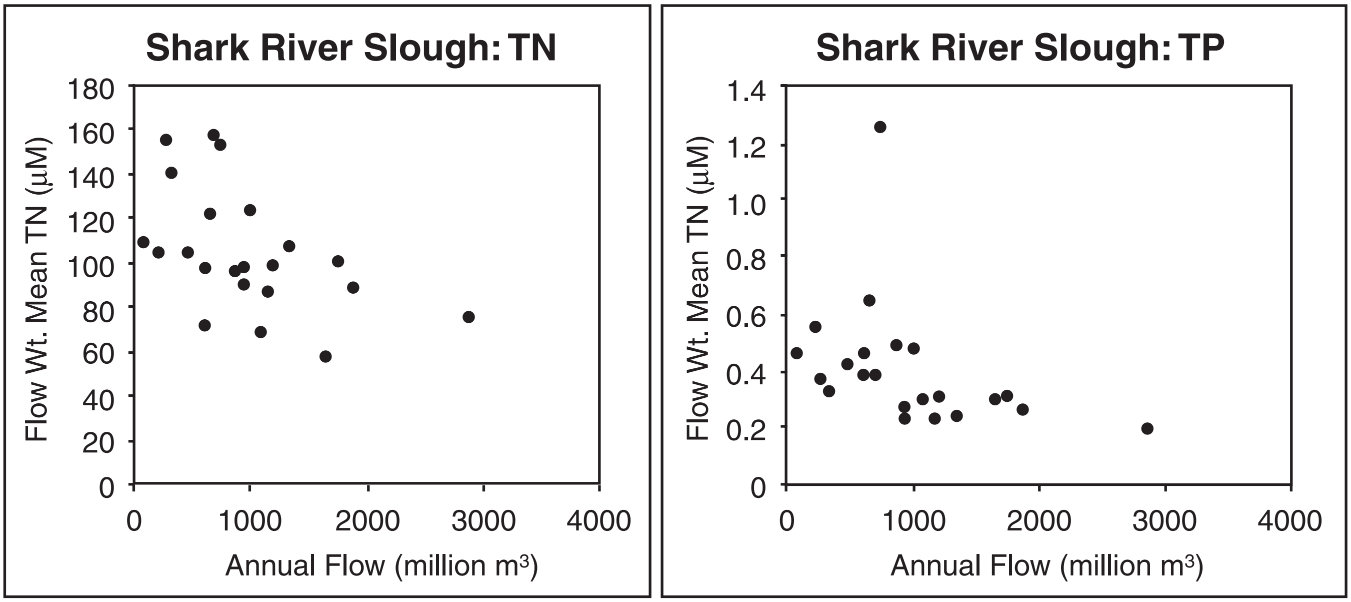

Figure 5.12 *Relationship between TN and TP concentrations (annual flow-weighted mean) in waters flowing into Shark River Slough and annual water discharge into the slough.*

banks, corals, or a host of other features could set up such shallow, subsurface flows. Flow through the seafloor caused by currents flowing over topography or waves may be responsible for the elevated tracer concentrations in the water column. The nutrient concentrations of these advected waters are probably lower than those sampled in wells and thus would lower the estimates of nutrient flux from groundwater flow.

An additional mechanism that can drive groundwater flow is the difference in tidal elevations across narrow reefs or barrier islands (Bokuniewicz and Pavlik, 1990; Reich *et al.,* 2002; Chanton *et al.,* 2003). Observations of seepage in the Upper Keys are consistent with this hypothesized mechanism (Chanton *et al.,* 2003). On an annual average basis, the water level in Florida Bay is several cm higher than the water level in the Atlantic (Reich *et al.,* 2002). However, the Atlantic has a daily tidal range of roughly half a meter, whereas daily water levels in Florida Bay are relatively constant. Therefore, during a high Atlantic tide, the ocean level is higher than the bay's water surface, creating a pressure differential pushing water from the Atlantic toward Florida Bay. In contrast, when the Atlantic tide is low, the situation is reversed, and there is a pressure differential pushing ground water from Florida Bay toward the Atlantic (Reich *et al.,* 2002).

The porous nature of the Key Largo Limestone that underlies the Upper Keys is consistent with this delivery of ground water to Florida Bay by this tidal-pumping mechanism. Studies employing viral and chemical tracers have documented horizontal and vertical transport rates of meters per day for water flow in the subsurface (Dillon *et al.,* 1999, 2000, 2003; Paul *et al.,* 1995, 1997, 2000; Lapointe *et al.,* 1990; Reich *et al.,* 2002). Hydraulic conductivity in the Key Largo Limestone ranges between 1,400 and 38,000 meters per day (Dillon *et al.,* 1999; Vacher *et al.,* 1992). Dillon *et al.* (1999) followed water-table height as a function of Atlantic tide in an onshore well on Key Largo. In this well, the groundwater table oscillated with Atlantic tide with only a 1.4-hour lag between Atlantic high tide and the highest water level in the well (Dillon *et al.,* 1999). There was only a 60% dampening of the tidal amplitude as the pressure wave moved through the carbonate rock. The extremely transmissive nature of the Keys aquifer system, in conjunction with the varying head differentials, promotes the interaction of subsurface waters with surface waters.

Ground waters in the shallow subsurface of the Keys contain dissolved nutrients from organic materials disseminated within the matrix (Sansone *et al.,* 1990) and are further contaminated from on-site sewage-disposal systems. Sewage in the Florida Keys is discharged into more than 600 disposal wells that penetrate the permeable Key Largo Limestone to depths of 10–30 m. Additionally there are an estimated 24,000 septic tanks and 5,000 cesspits on the islands (Kruczynski and McManus, 2002). Recent research has demonstrated a direct interaction between waste water delivered to the subsurface via injection wells and surface waters (Corbett *et al.,* 2000b; Dillon *et al.,* 1999, 2000, 2003). Natural tracers, including ^{15}N of seagrass tissue, have indicated that the greatest impact of groundwater discharge is along the shore of the Florida Bay side of the Upper Keys (Corbett *et al.*, 1999). Nutrient inputs from Keys ground water may be dominated by wastewater inputs and so are considered in the next section. The associated nutrient load to coastal waters would be substantial without significant subsurface biogeochemical alteration. This is particularly true with respect to phosphate delivery, which has been shown to be the limiting nutrient in eastern Florida Bay. Studies of the fate of nutrients injected into Class 5 wells in the Keys suggest phosphate removal with moderate nitrate attenuation (Corbett *et al.*, 2000b; Dillon *et al.*, 2003). Although it is understood that phosphate may be removed during transport, it is not clear whether this removal will be sustained. One question of particular importance is whether the phosphate may be released at some point to the phosphorus-limited waters surrounding the Keys, thus creating a significant water-quality problem for the marine environment. If phosphate uptake is ephemeral, then long-term transport of phosphorus to coastal waters may occur through the limestone aquifers. There is some evidence that the limestone surrounding Class 5 injection wells may saturate with phosphorus (Dillon *et al.*, 2003).

Atmospheric, Keys Waste Water, Keys Storm Water, and the Gulf of Mexico Nutrient Inputs

The remaining components of the Florida Bay nutrient budget (atmospheric, Keys wastewater and storm water, and the Gulf of Mexico) have not been revised since the 2001 conference. Atmospheric deposition is certainly an important nutrient source, particularly with regard to the relatively high input of inorganic nitrogen. The estimates in Figures 5.9–5.11 are derived from a study by T. Meyers in 1999 and 2000 on Long Key (T. Meyers, personal communication). Although bulk deposition of nitrogen can be estimated from a long-term National Atmospheric Deposition Program (NADP) site in Everglades National Park, few data are available to estimate dry deposition of nitrogen or phosphorus. Furthermore, phosphorus estimates in south Florida are often suspect because of the contamination of low ambient concentrations (Redfield, 2000). Estimates of the Florida Keys and Gulf of Mexico contributions are based on methods and data described in Rudnick *et al.* (1999). The Keys estimate entails far less uncertainty than the gulf estimate. It should be noted that the gulf contribution provided here (Figures 5.9–5.11) probably overestimates inputs to interior Florida Bay because the flow meters that produced the data used in the calculation were west of Florida Bay's mud banks. A large proportion of water flow measured by these flow meters never entered the bay. It should also be noted that a large discrepancy between the estimates of Rudnick *et al.* (1999) and Cerco *et al.* (2000) exists. The latter estimate was based on flow fields derived from a hydrodynamic model (Table 5.2).

Summary

The major source of TP and TN was the Gulf of Mexico (Figures 5.9, 5.10) and the major source of DIN was ground water (Figure 5.11). The smallest source of TP was Taylor Slough–C-111 (Figure 5.9). The smallest input of TN was from the Keys (Figure 5.10), whereas the smallest inputs of DIN were from Shark River and Taylor Sough–C-111 (Figure 5.11).

Internal Nutrient Cycling

Benthic Nutrient Fluxes

In situ benthic metabolism and nutrient regeneration were measured seasonally for 3 years (1997 through 2000) at five sites near the northern Florida Bay coast (Rudnick *et al.*, 2001) and for 1.5 years (1997–1998) at six bay sites away from the northern coast (Carlson and Yarbro, 1999). Additional flux measurements have been made more recently in sediment cores (Cornwell and Owens, 2003). The most notable results of these studies have been that phosphorus fluxes are very low (typically not significantly different from zero) and that inorganic nitrogen fluxes from sediment to water are surprisingly low. Sediments consistently removed nitrates and nitrites from the water column under dark and light conditions. Compared to rates of sedimentary oxygen uptake in the dark, rates of ammonium release have been found to be very low. Median O:N (oxygen:nitrogen) molar ratios in dark chambers at northern coastal sites greatly exceeded that expected from the mineralization of algal or seagrass detritus, ranging from 51 to 124 (O uptake:N release) (Rudnick *et al.*, 2001). Given the high organic matter concentrations of central Florida Bay, the finding of consistently low (<50 μmol m^{-2} h^{-1}) ammonium fluxes from Rankin Lake sediments (Carlson and Yarbro, 1999; Kemp and Cornwell, 2001) is surprising.

Studies by Cornwell *et al.* (2000) and Kemp and Cornwell (2001) provide insights of mechanisms that explain the observed low rates of ammonium regeneration. They found that ammonium fluxes were negatively correlated with benthic chlorophyll *a* concentrations (Figure 5.13), perhaps because benthic algae stimulate coupled nitrification-denitrification.

Table 5.2 *Comparing Florida Bay nutrient budgets (positive into system) (from Cerco* et al.*, 2000).*

	Rudnick *et al.*		**Model Dry Season**		**Model Wet Season**	
System	**Total P (kg/day)**	**Total N (kg/day)**	**Total P (kg/day)**	**Total N (kg/day)**	**Total P (kg/day)**	**Total N (kg/day)**
Everglades	7.1	685	3.0	679	9.1	1,753
Atmosphere	104.1	1,945	127.0	2,393	127.0	2,393
Keys Loads	115.1	466	54.9	238	54.9	238
Western Boundary	1,112.3	21,918	192.7	3,105	-589.6	–6,217
Keys Passes	–493.2	–32,877	101.8	2,068	158.4	4,154
Net	**845.5**	**–7,863**	**479.4**	**8,483**	**–240.2**	**2,321**

These studies found that net N_2 fluxes were typically from sediment to water (dentrification exceeding nitrogen fixation). Denitrification rates (dark N_2 fluxes) at six sites averaged 127 ± 87 µmol m^{-2} h^{-1} in August and 65 ± 82 µmol m^{-2} h^{-1} in March. These fluxes greatly exceeded ammonium fluxes. Further support for the inference that low inorganic nitrogen regeneration is attributable to coupled nitrification-denitrification was provided by *in situ* hypoxia experiments (Rudnick *et al.*, 2001). Dissolved oxygen and nutrients were followed in a time series over 28 hours in dark benthic chambers. When dissolved oxygen in the water column dropped below 0.2 mg/L, ammonium fluxes increased five fold.

Yarbro and Carlson (unpublished) measured benthic fluxes of filterable reactive phosphorus (FRP), NH_4^+, silicate, TP, TN, dissolved organic phosphorus (DOP), and DON in seagrass beds in the eastern bay (Sunset Cove and Swash keys), central bay (Rankin Lake and Calusa Key), and western bay (Johnson and Rabbit Key basins). FRP fluxes ranged from uptakes of 3 µmol m^{-2} h^{-1} in Johnson Key Basin in the western bay to releases of 1–2 µmol m^{-2} h^{-1} in the eastern bay. Dissolved organic phosphorus (DOP) fluxes (2–4 µmol m^{-2} h^{-1}) were considerably higher than FRP fluxes and were more often released from the benthos, especially at central and western bay sites. These small fluxes are in sharp contrast to the large phosphorus pool in surficial sediments (1–12 µmol gDW^{-1}).

Additionally, the sharp increase in sediment phosphorus from east to west in the bay was not reflected in benthic fluxes. Keeping in mind that these fluxes represent net flux to or from the seagrass community, we estimate that ammonium and the sum of FRP and DOP fluxes can meet 20%–50% of the phytoplankton demand in the eastern and western regions of Florida Bay but only 5%–10% of the phytoplankton demand in the highly productive, *Synechococcus*-dominated north-central bay.

Internal Nutrient Cycling: Carbonate-Phosphorus-Iron Relations

A study by Chambers *et al.* (2001) documented the spatial variation in sediment phosphorus, iron, and sulfur. Total sediment phosphorus decreases on a west-east gradient across Florida Bay, similar to the pattern in which surface-water quality decreases. Mineral sulfides and extractable iron in Florida Bay sediments decrease on a north-south gradient. Most inorganic phosphorus in the sediment is associated with abundant calcium carbonate minerals and not with reactive iron oxides that occur in very low concentrations. Iron availability limits mineral sulfide formation, but dissolved sulfide concentrations in Florida Bay sediments are high. Experimental addition of reactive iron to seagrass plots in Florida Bay stimulated phosphorus retention in the sediment and buffered plants from toxic sulfide accumulation. Phosphorus availability to seagrass still appears to limit production in carbonate sediments more than sulfide toxicity. Generation of inorganic phosphorus in seagrass sediments may occur directly via mineralization of organic matter and indirectly via concomitant carbonate mineral dissolution (Ku *et al.*, 1999).

Role of Sediment Resuspension in Phosphorus Cycling

Phosphorus is retained on the surface of calcium carbonate sediments (Zhang and Fischer, 2001). Within a few minutes of sediment resuspension, phosphate that is weakly bound to particle surfaces is released to the water column, where it may be used by phytoplankton. Coprecipitation of calcium phosphate with calcium carbonate may scavenge dissolved phosphate out of the water column.

Total sedimentary phosphorus (TSP) was fractionated into five chemically defined pools (Zhang and

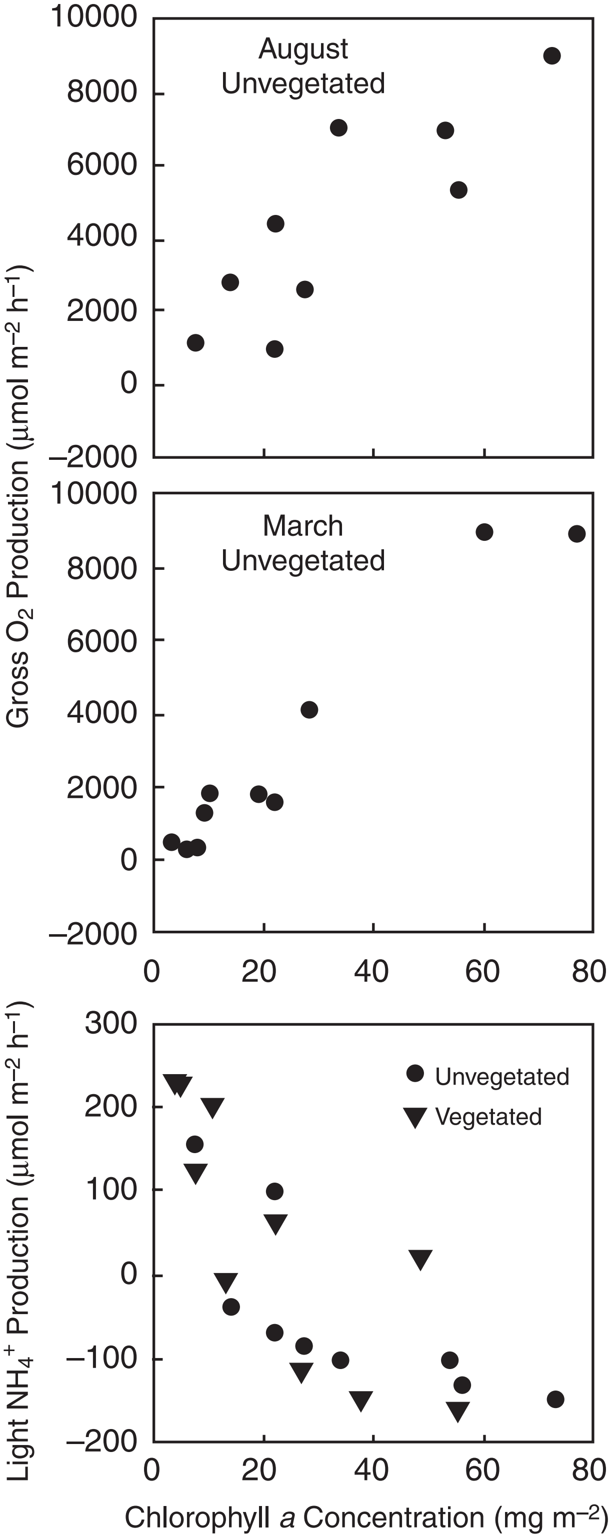

Figure 5.13 *Results from denitrification study conducted by Cornwell (2001). This figure indicates the importance of benthic microalgae in the nitrogen cycle. Ammonium uptake from the water column is associated with high chlorophyll concentrations.*

Fischer, 2001): (1) adsorbed (readily exchangeable) inorganic and organic phosphorus, (2) Fe-bound inorganic phosphorus, (3) autogenic apatite calcium carbonate-bound inorganic and organic phosphorus, (4) detrital apatite phosphorus, and (5) refractory organic phosphorus. This study observed a strong gradient of decreasing TSP from the west (14.6 µmol g^{-1}) to the east (1.2 µmol g^{-1}) across central Florida Bay (Zhang *et al.,* 2004).

Among the five pools, autogenic apatite calcium carbonate-bound phosphorus accounted for the largest fraction of phosphorus (45% of TSP; Zhang *et al.,* 2004); inorganic phosphorus dominated this pool (70%–90%). The refractory organic phosphorus (24% of TSP) and iron-bound inorganic phosphorus (19% of TSP) were the second largest pools. Adsorbed phosphorus accounted for 8% of TSP (60% organic phosphorus), and detrital apatite phosphorus composed the smallest fraction (5% of TSP). Overall, organic phosphorus accounted for 38% of TSP.

Nutrient Flux at the Sediment-Water Interface

Yarbro and Carlson (1999) measured silicate fluxes that ranged from –337 µmol m^{-2} h^{-1} at Rankin Lake, (September 1997) to 766 µmol m^{-2} h^{-1} (August 1998). Ammonium fluxes ranged from –8.3 µmol m^{-2} h^{-1} at Rankin Lake (November 1998) to 156 µmol m^{-2} h^{-1} at Sunset Cove in November 1998. Total dissolved nitrogen fluxes were highly variable between sites and sampling dates, ranging from –340 µmol m^{-2} h^{-1} at Rabbit Key Basin in August 1998 to 193 µmol m^{-2} h^{-1} at Sunset Cove in November 1998. Dissolved organic nitrogen (DON) also varied between sites and sampling dates, ranging from 5.7 µmol m^{-2} h^{-1} at Swash (May 1998) to 250 µmol m^{-2} h^{-1} at Rabbit Key Basin (August 1998). Net DON flux was always from the sediment to the water column.

Because filterable reactive phosphorus (FRP) concentrations generally were very low, flux estimates were highly variable (Yarbro and Carlson, 1999). Total dissolved phosphorus and FRP fluxes ranged from net uptakes of –6.23 to –0.02 µmol m^{-2} h^{-1} and sediment releases of 0.02 to 11.57 µmol m^{-2} h^{-1}. Most fluxes were less than 1 µmol m^{-2} h^{-1}.

Seagrass Modeling

An ecological model of the Florida Bay seagrass community, funded by USGS through the Critical Ecosystems Initiative, was conceived as a means of enhancing the ability of managers to improve health of the Florida Bay ecosystem, seagrass habitat in particular (Madden *et al.,* 2003, McDonald and Madden, 2003; Figures 5.14, 5.15). This model is a dynamic, mechanistic simulation of seagrasses, emphasizing nutrient cycling and nutrient demand related to seagrasses. It is being used as a tool for determining the causes of seagrass mortality due to environmental stress and to calculate nutrient-sink characteristics of the seagrass community.

In scenario analyses, this model was used to test the effects of individual and simultaneous multiple stressors, at levels measured to occur *in situ* on primary productivity. Application of multiple stressors involving elevated nutrients, salinities, and elevated sulfide concentrations produced dramatic results in the *Thalassia* growth profile. Biomass declined continuously from the point of application of simultaneous stressors in January throughout the growing season as *Thalassia* rapidly died off. Examination of processes underlying this model behavior revealed that photosynthesis, though operational, was impaired and functioning at such a low level that the net daily production was negative throughout the growing season.

Interaction of the above- and below-ground compartments played a strong role in the trajectory of the seasonal biomass curve in the model. Exchanges of organic carbon and nutrients between leaf and root compartments are seasonally variable and critical for survival of submerged plants. The modeled plants can mobilize below-ground resources to supplement carbon input to the above-ground compartment should autotrophic assimilation become deficient. The amount of carbon in the root/rhizome material available for growth supplementation can control the outcome of plants subjected to stress conditions. Therefore, the status of the below-ground compartment can determine the survival of the entire plant. Conversely, when conditions are unfavorable to growth and below-ground resources are depleted, the existence of above-ground plant material can mask a plant community in fragile condition. We believe that this model's conceptualization is realistic and is likely close to the physiological and community reactions that occur in the real system, emphasizing the importance of thresholds and nonlinear reactions, which can be tracked and revealed by model analysis.

A series of model runs were made to determine nutrient demand under a range of C:N ratios (15–36) and C:P (400–1800) ratios typical of the bay. On an annual basis, P supplied to sediment pore waters via organic remineralization and rock dissolution each averaged about 1–1.5 mg P m^{-2} d^{-1}, whereas P exported from the Everglades averaged 0.05 mg P d^{-1} to overlying waters in Little Madeira Bay (Rudnick *et al.,* 1999). Depending on tissue ratios of nutrients applied to the model, these rates supply from >1,000% to only 30% of P demand by *Thalassia.* Significantly, the C:P ratio estimated by inverse modeling required to use 100% of the available sediment P regenerated daily (2.3 mg^{-2} d^{-1}) is 500:1, which approaches the average C:P ratio of 800:1 that has been measured empirically in Little Madeira Bay and northeastern Florida Bay.

Influence of Florida Bay Water Quality on the Reef Tract

Nutrient Export Through Keys Passes

The rate of outflow was estimated by Lee and Smith (2002) from measurements made in Channel 5 and Channel 2 near Long Key in 1997 and 1998. The long-term mean was 370 m^3/s (11.7 × 109 m^3/y). The estimated exports (MT/y) were TP = 180; TN = 4,600; DIN = 200 (Figures 5.9–5.11). Nutrient concentrations were measured as part of FIU's monitoring (Jones and Boyer, 2002), and the flux calculation assumed median concentrations.

Based on these estimates, Florida Bay is a sink for approximately half of the inputs of TP and TN and more than 80% of the inputs of DIN. Additional export of N and P from Florida Bay may occur in the form of drift seagrasses and algae but no quantitative estimates have been made of these exports.

Water-Quality Modeling

The water-quality model (Cerco *et al.,* 2000) linked modules including water-column eutrophication, seagrass dynamics, sediment diagenesis, solids and nutrient resuspensions, and benthic algal production. To our knowledge, this is a first for Florida Bay. In fact, we know of few systems that currently have a model application to rival the current effort in Florida Bay. However, the model requires substantial upgrading to fully represent processes in the bay.

Nutrient loads from various sources to the bay and surrounding waters were calculated for the model study. Estimates indicated that the atmosphere is the largest loading source to the bay. Runoff from the mainland is the smallest source of phosphorus and second smallest source of nitrogen. Paradoxically, runoff appears to be the most intensely studied loading source. There are large degrees of uncertainty as to what the greatest loads are. Attention should be devoted to accurately quantifying atmospheric and phosphorus loads from the Keys.

No *in situ* measures of nitrogen fixation were available to us. Rates associated with seagrass beds, measured in other systems, were adapted for the model.

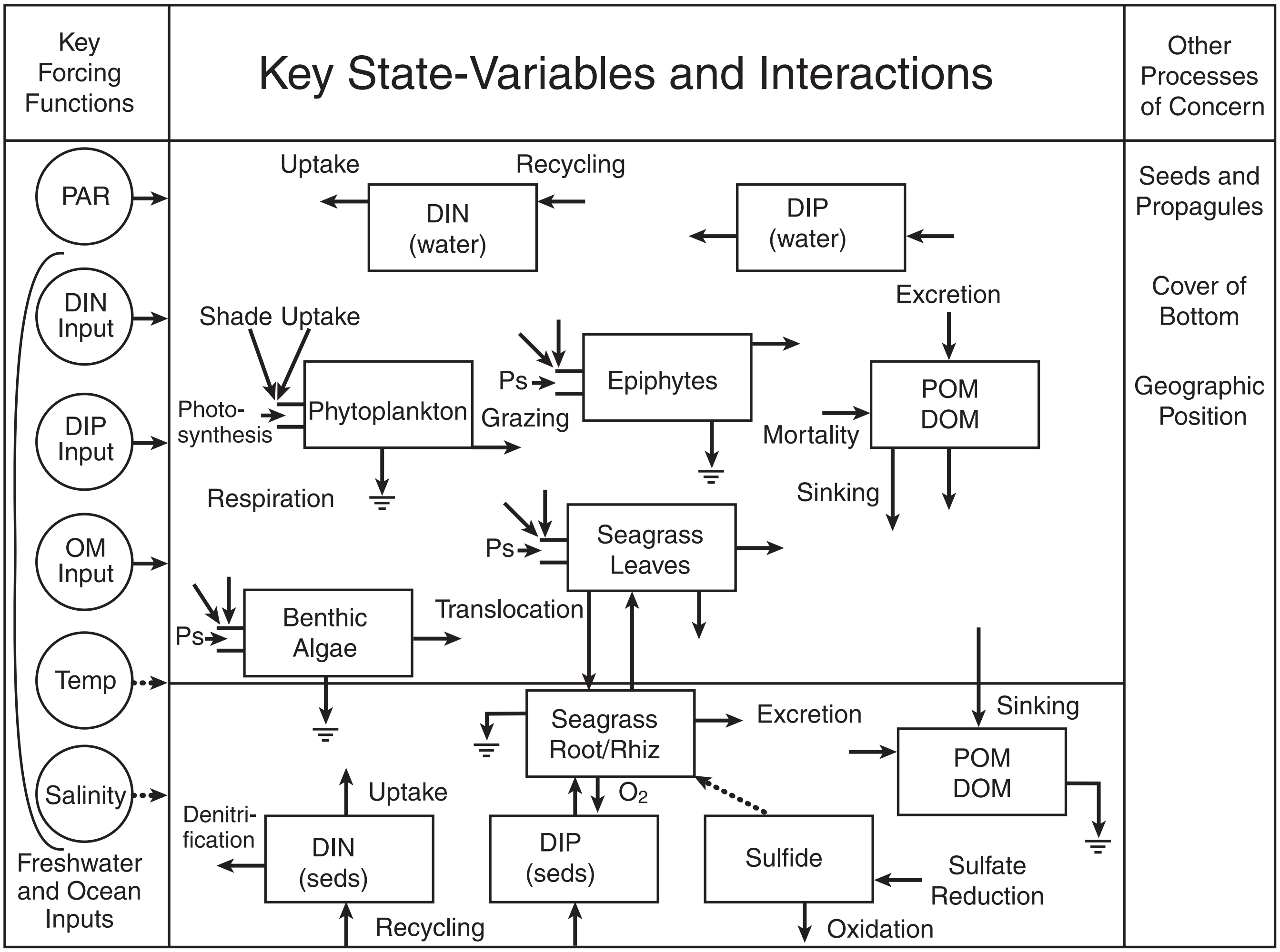

Figure 5.14 *Ecosystem process model of south Florida estuarine systems. Conceptual diagram of Florida Bay seagrass model emphasizing major nutrient cycles. (Madden* et al., *2003).*

Estimated nitrogen fixation associated with seagrass leaves equals the estimated atmospheric nitrogen load. The sum of nitrogen fixed in the leaves and roots makes nitrogen fixation the largest single source to the system. Measures of nitrogen fixation are currently being conducted and these measures should be swiftly incorporated into the model and into system nutrient budgets.

Measures of denitrification within benthic sediments were also unavailable. Rates of denitrification were calculated by the sediment diagenesis model, with values adapted from Chesapeake Bay. Calculated denitrification roughly equals total nitrogen fixation. Denitrification rates should be measured and used to verify the computations provided by the model.

The model underestimates the amount of nitrogen in both the sediments and water column. Sensitivity analysis indicates that the shortfall is unlikely to originate from the loading estimates. Either a source of nitrogen has been omitted or the estimated loads are greatly in error. Potential sources of omission or error include groundwater, nitrogen fixation, and denitrification.

The model does not indicate that material does not concentrate in the central basins. This behavior may be attributed to several factors. First, the underlying hydrodynamic calculations may not concentrate material. Second, the linkage method may introduce errors in the computed hydrodynamic field. Third, the water-quality grid and numerics may introduce artificial dispersion. Dye-tracer tests indicated that the water-quality model qualitatively tracks transport in the hydrodynamic model in Florida Bay. (Transport is not equivalent on the western shelf because of artificial dispersion and boundary-condition specification.) The tracer tests led us to the conclusion that the underlying hydrodynamics prevent computation of hypersalinity and concurrent concentration of nitrogen and other materials.

Interpretation of results from the water-quality

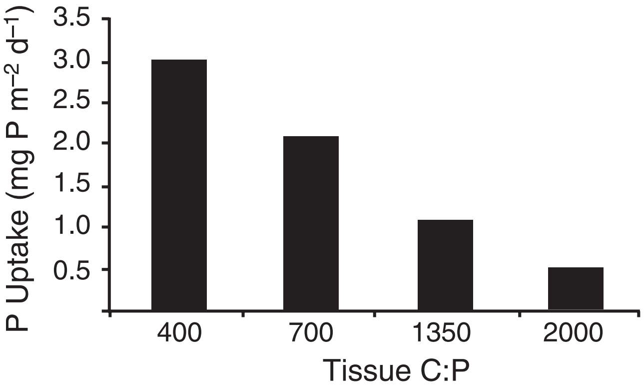

Figure 5.15 *Theoretical phosphorus demand by* Thalassia *in mg per m^2 per day as calculated by the seagrass model to satisfy seagrass primary productivity rates in northeast Florida Bay.*

model was severely compromised by the lack of a verified hydrodynamic model operable on the same time scale as the water-quality model.

Successful simulation of a ten-year sequence of water quality was virtually impossible without corresponding hydrodynamics. The highest priority should be given to applying a detailed, volume-conservative hydrodynamic model to the bay and adjoining waters. The model should simulate at least a ten-year period and provide good agreement to salinities observed within that period.

The major uncertainty in the system's nutrient budget is transport across the western boundary and through the Keys passes. This transport cannot be observed on a long-term basis. Computation via a model is the only alternative for long-term budget estimates. High priority should be given to estimating flow across system boundaries once a verified hydrodynamic model is available.

Sensitivity analysis indicated that model computations are very sensitive to the biological activity at the sediment–water interface. In the present model, this activity is represented by the benthic algal component, and as formulated, the model cannot represent all observed fluxes, especially those of dissolved organic matter. Attention should be devoted to quantifying sediment–water fluxes, to investigating the nature of the benthic community, and to process-based modeling of this community.

A great number of observations have been collected in the bay since this study commenced, and considerably more is known about the bay than was known a few years ago. Once suitable hydrodynamics are available, the water-quality model should be reapplied on a ten-year time scale and validated with the latest observations of conditions and processes in the bay. Concurrent with the reapplication, first-order improvements (*e.g.,* division of dissolved organic matter into labile and refractory components) can be incorporated into the water-quality model.

As part of the Florida Bay and Florida Keys Feasibility Study of the CERP, a new attempt is currently being made to develop, calibrate, validate, and apply a Florida Bay water-quality model.

Current and Ongoing Research

Unresolved Questions

Past informational needs relative to nutrient cycling in Florida Bay have been coupled to understanding the factors that triggered the mass mortality of seagrass and what initiated and maintained the phytoplankton blooms. Current needs have become more focused around assessing the effects of various environmental management strategies being considered for bay restoration. In particular, we need to accurately predict the sensitivity of the bay's nutrient cycles to changing freshwater flow to the bay and the resultant change in the bay's salinity regime. For much of the bay, any factor that increases phosphorus availability, either by increasing sources or decreasing removal, is likely to exacerbate the current problems of the bay. Recent evidence also indicates that algal blooms in the central and western bay are also stimulated by nitrogen enrichment. Thus we need a thorough understanding of the bay's nutrient cycles, particularly with regard to the fate and effects of dissolved organic nitrogen inputs from the Everglades. Understanding the mechanisms that have triggered and are sustaining algal blooms in the bay is fundamental to restoration decision-making. This understanding entails quantifying the nutrient demands of these algae and how these nutrients are supplied. Questions that the future program should address in order to meet these needs are as follows:

- What are the sources of nutrients that sustain algal blooms?

  Understanding the mechanisms that have triggered and are sustaining algal blooms in the bay is fundamental to restoration decision-making. This understanding entails quantifying the nutrient demands of these algae and how these nutrients are supplied.

- How will changing freshwater flow directly and indirectly alter the supply and availability of nutrients in the bay? What effect does changing salinity have on nutrient availability in the bay?
  - How will the quality and quantity of nutrient out-

  - puts from the Everglades change with restoration?
  - What is the fate and effect of dissolved organic matter from the Everglades and how will this change with restoration?
  - What effect does changing salinity have on nutrient cycling and availability in the bay?

With increased freshwater flow expected from restoration of the Everglades and Florida Bay, nutrient loading from the Everglades watershed will also probably increase. For nitrogen, most of this loading will be in the form of dissolved organic compounds. The sources, fate, and effects of DON from the Everglades watershed are unknown, and predictions of how changing freshwater flow will influence these DON dynamics are highly uncertain. Measurements of the composition and bioavailability of Everglades DON to Florida Bay's microbial communities (pelagic, epiphytic, and benthic) are essential in order to assess the functional relationship of Florida Bay and its watershed. Although the magnitude of this expected increase is unknown, this direct input may be less important than the indirect effect of an altered salinity regime caused by increased freshwater influx. Altered salinity can affect internal nutrient cycling by (1) altering community structure (such as changing seagrass-species dominance, thus changing nutrient storage and cycling), and (2) modifying specific processes, such as phosphorus surface reactions and sulfate reduction. A change in freshwater flow and salinity could also alter nutrient processing in the mangrove zone and thus alter nutrient exchange along the bay's northern boundary, the Gulf of Mexico boundary with the Everglades, and near mangrove islands in the bay.

The factors that influence the loading of nutrients into Florida Bay and the availability of nutrients within the bay are not well understood. In particular, we need to understand the effect that potential environmental-management actions, such as increasing freshwater flow and decreasing salinity, will have on the bay's nutrient transformations and fluxes. Information on suspended sediment particles and on factors that may influence the mobilization and immobilization of phosphorus in carbonate sediments is critical. Results of past experiments (Zhang *et al.*, 1999) need to be evaluated in the context of the development of a water-quality model to assess the sufficiency of current data for estimating salinity effects.

Given the unusually high ammonium concentrations of the bay and the potential for nitrogen limitation in the western bay, experiments on factors that may influence key nitrogen transformations, such as nitrification and denitrification, are also needed. Experiments that explore how nutrient cycling is altered by changes in seagrass community structure and physiological condition (particularly below-ground nutrient changes) are also important but have yet to be done.

- What effect does a change in seagrass community structure have on nutrient availability in the bay? Has seagrass mortality only increased nutrient availability by releasing nutrients from this detrital source or has seagrass mortality also caused other less direct changes, such as a decrease in the capacity of the sediments to sequester nutrients?

The lag of several years between the onset of seagrass mass mortality and the occurrence of algal blooms in the bay argues against the hypothesis that only nutrients released from dead seagrass tissue fuel the blooms. However, the increase in nutrients from this detrital source, combined with a net decreased uptake capacity associated with seagrass mortality, may explain the bloom's temporal patterns. Thus, we need estimates of net benthic nutrient uptake or release rates over a range of seagrass growth rates, mortality rates, and detrital decomposition rates for different seagrass species. The accuracy of such estimates may depend largely upon understanding sedimentary nutrient transformations, including how seagrass roots affect nutrient mobility and how such processes change with seagrass mortality. Seagrass mortality may have indirectly affected nutrient cycles in the bay. For example, sediment resuspension increases with decreasing seagrass density, and phosphorus associated with this suspended sediment may be available to phytoplankton. Finally, changing seagrass cover also influences the biomass and activity of benthic algal mats. This change in microbial mats in turn affects nitrogen availability by altering patterns of nitrification, denitrification, and nitrogen fixation. Measurements of the quantitative relationships of these processes within the algal and SAV community structures are needed.

Given the shallow depth and restricted circulation of Florida Bay, internal cycling and transformations of nutrients probably have a strong influence on the structure and productivity of bay communities. These nutrient pathways and transformations have not been well studied. Essential measurements include nutrient uptake by primary producers (especially seagrass and phytoplankton), the exchange of nutrients between the sediments and the water column, the diagenesis of nutrients within the sediments (especially phosphorus–carbonate reactions and nitrogen transformations), and microbial and inorganic reactions within the water column (such as nitrification and phosphorus sorption to and removal from suspended sediment).

- How do we deal with the spatial heterogeneity of internal nutrient cycling in the bay?

There is no unified field theory for ecology—process rates from one area may not be applicable to another. What other factors are important in driving these processes?

- What is the quantitative role of microphytobenthos in nutrient cycling and how is this likely to change with Everglades restoration?

  The microphytobenthos has been shown to be influential in regulating benthic flux rates. Fluxes in the form of drift seagrasses and algae have not been determined.

- To what extent is atmospheric deposition of nutrients contributing to ecological changes in Florida Bay? What is temporal variability (including long-term trend) of this nutrient source?

  Atmospheric inputs have been shown to be a significant component of external nutrient loading, especially of nitrogen. There are no estimates of long-term trends in atmospheric nutrient-loading at present.

- Is ground water an important nutrient source in Florida Bay? If so, what is the spatial and temporal pattern of this input?

  Given the high nutrient content of the groundwater beneath most of the bay, any groundwater flux approaching recently published rates (about 1 cm d^{-1}) would result in a very high nutrient flux. The accuracy of these estimates should be checked—sites with significant upward groundwater advection should be identified; if found, nutrient concentrations at these sites should be measured.

Summary of Ongoing Research

- Continued monitoring of ambient water quality in Florida Bay.
- Continued monitoring of freshwater inflows and loads with expansion of network along Florida Bay and southwest Florida gulf coast beginning.
- Continued monitoring of coastal circulation and biological and chemical parameters, with interpretation of transport and exchange of south Florida coastal waters.
- Expanded research into nutrient cycling in wetland/mangrove areas and seagrasses/epiphytes.
- Study of carbonate system–phosphorus–iron relations.
- Characterization of chemical structure of organic carbon and nitrogen from wetland/mangrove areas.
- Assessment of microbial bioavailability of organic carbon and nitrogen from wetland/mangrove areas.
- Expanded measurements of benthic nitrogen fixation, nitrification, and denitrification rates.
- Measurements of phytoplankton nitrogen uptake rates.
- Quantification of microbial loop parameters: heterotrophic bacterial numbers, bacterial production, nanoflagellate/protist grazing rates, and phytoplankton primary production.
- Effects of variability in regional climate, freshwater inputs, disturbance, and perturbations on the coastal Everglades ecosystem.
- Development of nitrogen and phosphorus mass-balance models and measurements of nutrient cycling rates in Florida Bay.
- Assessment and monitoring of dissolved nitrogen in Florida Bay.
- Measurement of nutrient fluxes through Florida Keys passes.
- Monitoring of salinity and estimates of fluxes of water and total nitrogen and phosphorus across the southern Everglades mangrove zone.
- Development of an integrated hydrodynamic and water-quality model to evaluate relationships with freshwater flow and oceanic/gulf hydrodynamics and exchange is in a planning phase.
- Seagrass uptake kinetics of phosphorus.
- Influence of dissolved organic matter on seagrass, epiphyte, and phytoplankton productivity.
- Seagrass survival and productivity under single and multiple stresses.
- Dynamic simulation model analysis of spatial patterns of seagrass productivity, community structure, and nutrient demand.

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Chapter 6

Plankton Blooms

Team Leaders Gary Hitchcock (University of Miami), Ed Phlips (University of Florida),
Larry Brand (University of Miami), Douglas Morrison (ENP, PMC)

Introduction

Question 3*—What regulates the onset, persistence, and fate of planktonic algal blooms in Florida Bay?*

From the 1950s to the mid 1980s, Florida Bay was characterized by expansive seagrass beds, mangrove islands, and crystal-clear water. In the past 16 years, there have been some dramatic changes in the ecology of Florida Bay; examples are the die-off of large areas of seagrass and the appearance of intense blooms of planktonic algae. There is a general consensus in the scientific community that these phenomena are indicative of changes in key environmental conditions within the bay. The shift in primary producers and the alteration of the photic environment in Florida Bay have been hypothesized to have major effects on the flora and fauna of the bay (*e.g.,* Boesch *et al.,* 1993). Fourqurean and Robblee (1999) have recently reviewed many of the changes. In this paper, we examine the current state of knowledge about the character and causes of planktonic algal blooms in the bay.

In reviewing the scope of our knowledge on algal blooms in Florida Bay, it is important to keep in mind that detailed monitoring of water quality in the bay has been underway for just over a decade. This is a somewhat surprising fact considering the importance of this aquatic resource to Florida and the surrounding waters of the Atlantic Ocean and Gulf of Mexico. One of the factors that triggered the initiation of extensive multidisciplinary research in the bay was the on set of massive cyanobacterial blooms over large areas of the bay in the early 1990s.

The first quantitative indications of major increases in phytoplankton densities in the interior regions of Florida Bay came from chlorophyll *a* data collected by Florida International University (FIU) (Boyer *et al.,* 1997, 1999). Boyer *et al.*'s (1999) research, which began in 1988, indicated a significant step increase in chlorophyll levels in 1991–1992. The increase in algal biomass within the bay was corroborated by incidental observations by individuals frequenting the bay for other research and recreation activities. In 1993, a separate research group from the University of Florida joined FIU in monitoring efforts that revealed high concentrations of cyanobacteria in the central portion of Florida Bay (Figure 6.1; Phlips and Badylak, 1996; Phlips *et al.,* 1999). In 1994, the phytoplankton research efforts were expanded further to include the Florida Marine Research Institute [now the Fish and Wildlife Research Institute]. All three research teams observed large cyanobacterial blooms in the central regions of the bay, particularly during the summer and fall (Phlips *et al.,* 1999; Steidinger *et al.,* 2001).

During the same period, algal blooms were also recorded in the western region of the bay (Figure 6.1). However, these blooms were typically dominated by diatoms, not by cyanobacteria. (Phlips and Badylak, 1996; Phlips *et al.,* 1999; Steidinger *et al.,* 2001) Recent efforts by researchers from the University of Miami focusing on the western bay have provided further support for the importance of diatom blooms in the western region. Analysis of sediment cores from the western side of Florida Bay indicate that diatom blooms along the western margin were a well-established feature by 1970, significantly prior to the increases in cyanobacteria blooms within the bay's interior (Jurado, 2003). Most recently, chemotaxonomic studies of phytoplankton in the bay have been initiated using full-spectrum photodiode array detectors and high-performance liquid chromatography analysis (Louda, 2001).

Regional Differences

The observed disparity in the quantity and quality (*i.e.,* composition) of phytoplankton biomass in different parts of the bay manifests the need to view phytoplankton dynamics by ecological zones. In contrast to the numerous phytoplankton blooms encountered in the western and central regions of Florida Bay, almost no blooms are located in the eastern portion of the bay (Figure 6.1). There have been several efforts to divide Florida Bay into ecologically distinct zones. These zonal breakdowns have been based on a variety of parameters, including geology (Prager *et al.,* 1996), distributions of benthic plants (Zieman *et al.,*

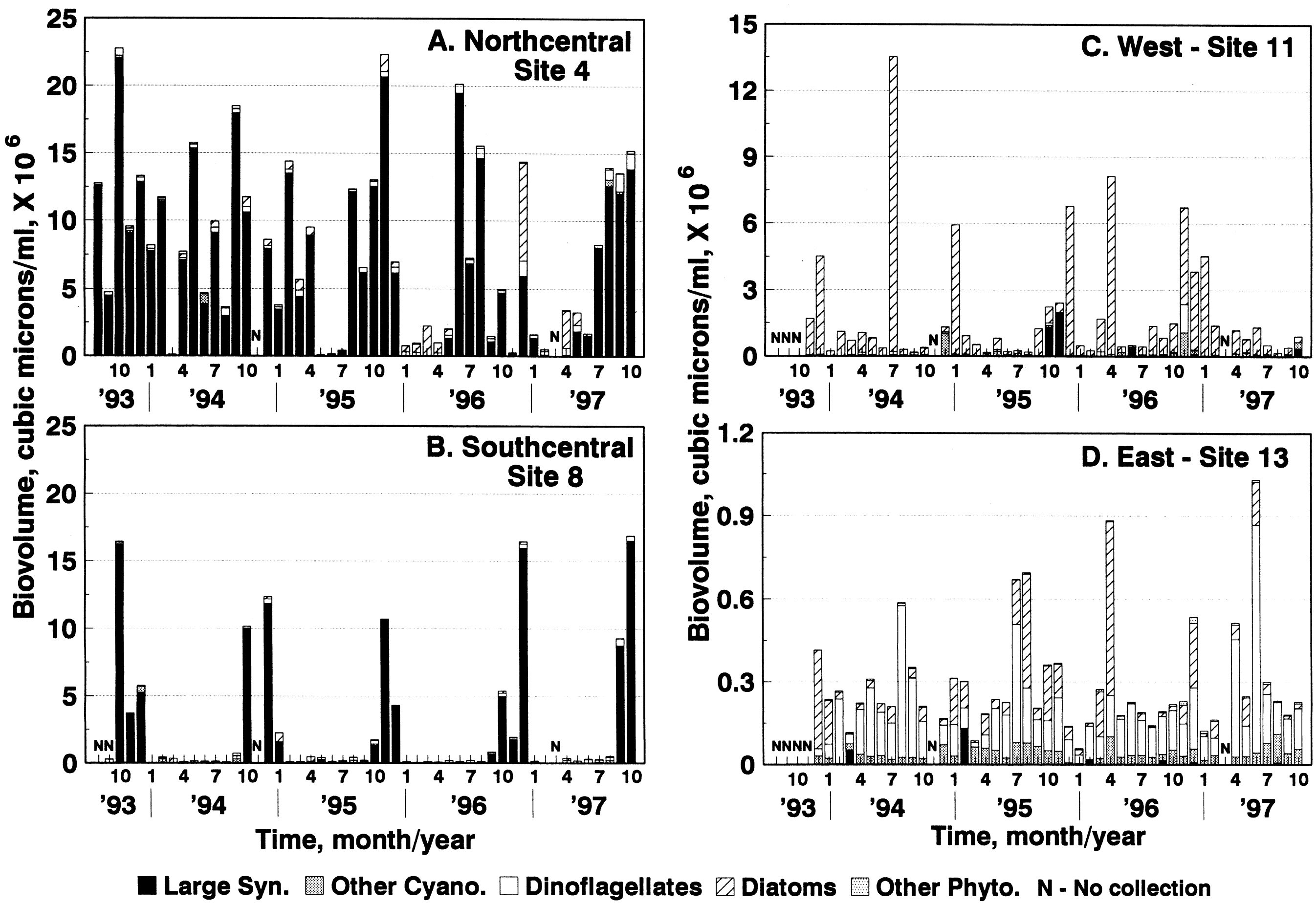

Figure 6.1 *Biovolume of* Synechococcus elongatus *(Large Syn.), other cyanobacteria, dinoflagellates, diatoms and other phytoplankton at four sampling sites representative of different regions of Florida Bay (Phlips* et al.*, 1999).*

1989), faunal distributions (Thayer and Chester, 1989; Holmquist *et al.*, 1989), and water-quality characteristics (Phlips *et al.*, 1995, Boyer *et al.*, 1997, 1999; Burd and Jackson, 2001). These efforts have yielded from 3 to 20 zones with different boundary designations. The lack of consensus on the specific boundaries and number of zones is largely attributable to differences in the choice of parameters used in the discrimination of the regions.

If the focus is limited to the frequency of phytoplankton blooms and the general composition of the blooms, it is possible to define three general regions that roughly follow longitudinal lines of demarcation (Figure 6.2): (1) The eastern region of the bay, east of 80°39′W and west of the Florida Keys, where major phytoplankton blooms are seldom observed; (2) the central region of the bay, between 80°39′W and 80°49′W, where bloom concentrations of cyanobacteria (*i.e.*, greater than 1 million cells per ml) are regularly encountered; and (3) the western region of the bay, west of 80°49′W, which experiences periodic blooms of diatoms. These regions provide a useful context for discussing both the character of blooms in the bay and the factors that control them.

In the most general terms, phytoplankton standing crops are dictated by factors that control gains and losses of algal biomass (Figure 6.3). From a gain perspective, the most obvious contributor to the increase in phytoplankton biomass is cell growth. Net growth rates are under the control of resource availability, such as nutrient and light, and of factors that affect the rates of photosynthetic and respiratory activity, such as temperature, salinity, and oxygen level. Algal biomass can also increase as a consequence of inputs to the water column from the benthos through resuspension or inflows of water from adjacent environments.

In terms of loss functions, one of the most important overriding considerations is water residence time. In many coastal ecosystems, phytoplankton biomass is limited by the flushing-rate of water that has lower phytoplankton content. Flushing rates are generally related to a combination of rainfall inputs, tidal mixing, and

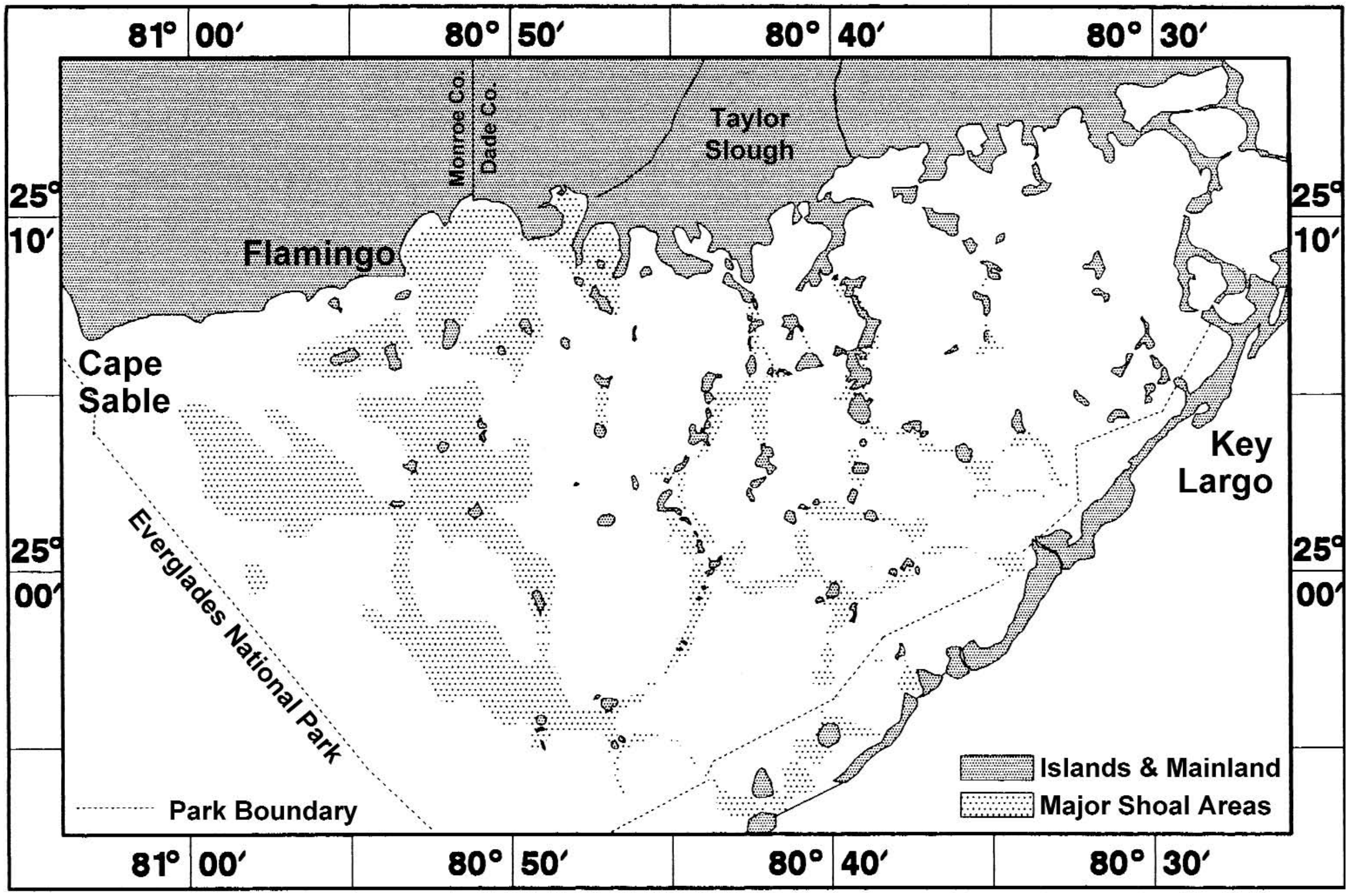

Figure 6.2 *Florida Bay basin configurations.*

wind-driven circulation. Many environments with long residence times tend to have higher phytoplankton crops than do environments with short residence times, assuming that nutrient and light availability are similar (Monbet, 1992). There are also biological processes that contribute to the loss of biomass in many aquatic ecosystems, such as grazing by benthic and planktonic filter-feeding organisms. The rates of loss are closely tied to the structure and abundance of the grazer community and to environmental factors that affect the rate of activity, such as salinity, temperature, and phytoplankton composition (*e.g.*, presence of toxic species).

Summary of Research

Research to date indicates that there are three ecologically distinct regions within the bay from the standpoint of algal blooms: the northeastern, central, and western regions. The nature and causes of blooms can be most appropriately summarized within the context of these three regions (Table 6.1).

NORTHEASTERN REGION

- Algal blooms are largely absent from the northeastern region of Florida Bay. The phytoplankton community of the northeastern region is a diverse mixture of cyanobacteria, dinoflagellates, diatoms, and microflagellates, none of which form blooms.
- The lack of algal blooms in the northeastern region of Florida Bay is largely attributable to the severe phosphorus limitation characteristic of the region. Despite significant water inflows to the region from the Everglades, the very low phosphorus levels in these inputs combined with the calcium-carbonate rich waters of the region, result in nutrient-limited conditions.

CENTRAL REGION

- Large algal blooms have been a common feature of the central region since 1992. The focal point for blooms in the central region is in the north-central region from Rankin Basin extending into Whipray Basin. The greatest bloom activity is generally in the summer and early fall, although blooms have been

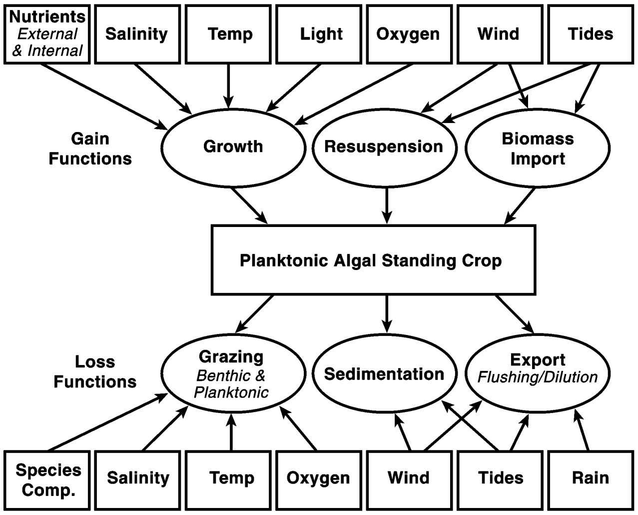

Figure 6.3 *Gain versus loss-functions for phytoplankton standing crops.*

observed in other seasons. In the fall and early summer, blooms originating in the northern central region are pushed southward by prevailing wind-driven circulation into the southern central region, where they can spread out into the Atlantic reef tract through cuts in the Florida Keys. The dominant bloom-forming alga in the central region is the picoplanktonic cyanobacterium *Synechococcus* cf. *elongatus,* though several species of diatoms and dinoflagellates occasionally occur in bloom proportions.

- Nutrient limitation of phytoplankton growth in the central region appears to switch back and forth from phosphorus to nitrogen. The nature of the sources of nutrients for blooms in the central region has been a subject of considerable debate, yielding several hypotheses: (1) a significant supply of nutrients for algal production is available from the flocculent muddy sediments within the region; (2) a groundwater source of phosphorus is present within the region that, in combination with nitrogen from the northeastern region, feeds algal blooms; (3) nutrients from the shelf region west of the bay are available to blooms in the central region via tidal exchange; and (4) atmospheric deposition is a significant source of nutrients (particularly N) for algal primary production. These hypotheses are not mutually exclusive, and several mechanisms may be operational at the same time.
- The domination of blooms in the central region by *Synechococcus* cf. *elongatus* is attributable to the unique ecophysiological characteristics of this species of cyanobacterium. These characteristics include (1) wide tolerance to salinity, (2) superior ability to compete for phosphorus at low concentrations, (3) ability to regulate buoyancy and thereby take advantage of nutrients available in the sediments, and (4) lower susceptibility to grazing losses.

WESTERN REGION

- Algal blooms are also a common feature of the western region of Florida Bay. In contrast to the cyanobac-

Table 6.1 *Summary of research on plankton blooms by region.*

	West	Central	East
General Characteristics	Phlips and Badylak, 1996 Boyer *et al.,* 1997, 1999 Phlips *et al.,* 1999 Steidinger *et al.,* 2001 Jurado, 2003	Phlips and Badylak, 1996 Boyer *et al.,* 1997, 1999 Phlips *et al.,* 1999, 2002 Steidinger *et al.,* 2001	Phlips and Badylak, 1996 Boyer *et al.,* 1997, 1999 Phlips *et al.,* 1999 Steidinger *et al.,* 2001
Nutrients		Lapointe *et al.,* 1990, 1994 Robblee *et al.,* 1991 Carlson *et al.,* 1994 Durako, 1994 Zieman *et al.,* 1994 Paul *et al.,* 1995a,b Tomas *et al.,* 1999 Lapointe *et al.,* 2002	
Composition and Growth Rates	Tomas *et al.,* 1999 Jurado, 2003	Richardson *et al.,* 2001	
Grazing and Flushing		Lynch and Phlips, 2000 Brenner *et al.,* 2001	

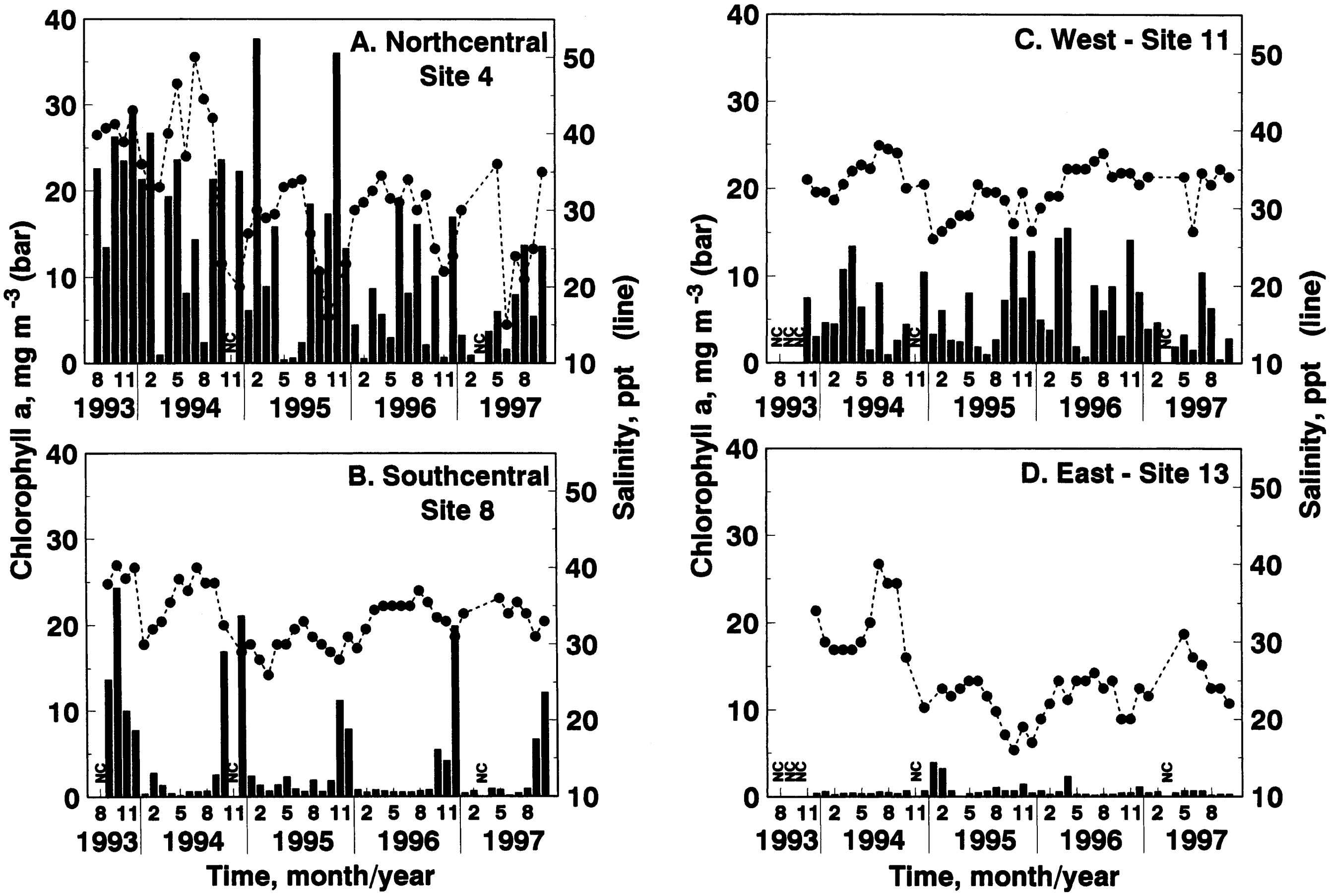

Figure 6.4 *Chlorophyll* a *concentrations and salinities at sampling sites representative of different regions in Florida Bay (Phlips* et al.*, 1999).*

terial blooms in the north-central region, these blooms are dominated by diatoms. The diatom-dominated blooms in the western region are mainly composed of *Rhizosolenia* spp., although *Chaetoceros* spp. and pennates are major genera in terms of cellular biomass. Diatom blooms in the western region begin in late summer and are advected into the bay from shallow coastal waters off Cape Sable.

- The diatom-dominated blooms in western Florida Bay are mainly limited in their growth by nitrogen, either singly or in combination with phosphorus and/or silicon supply. Temperature, salinity, and light do not appear to be important factors in the initiation or maintenance of diatom blooms. Maximum growth rates of the diatom community during bloom initiation in the western region range from 1 to 2 day^{-1} (first-order rate constant) based on increases in netplankton (greater than 5 μm size fraction), chlorophyll *a*, or biogenic silica. The onset of diatom blooms on the western Florida Shelf appears to be associated with enhanced riverine outflow, predominantly from the Shark River. The onset of increased diatom biomass occurs within the riverine, low-salinity plume near Cape Sable.

Eastern Florida Bay

Phytoplankton abundance is lower in the eastern part of the bay than it is in the other two zones within the bay (Figure 6.1). Chlorophyll *a* concentrations in the eastern bay are typically less than 2 mg m^{-3} throughout the year. Phlips *et al.* (1999) reported that the maximum chlorophyll *a* concentrations in this region were less than 5 mg m^{-3} between August 1993 and October 1997, with most values less than 1 mg m^{-3} (Figure 6.4). Similarly, Boyer *et al.* (1997, 1999) observed low chlorophyll *a* concentrations in eastern Florida Bay for the period between 1989 and 1997 (mean = 0.85 mg m^{-3}).

The phytoplankton communities in the eastern bay are principally composed of centric diatoms (*e.g., Thalassiosira* sp.), dinoflagellates (*e.g., Protoperidium* spp., *Ceratium* sp., *Prorocentrum micans*), and small cyanobacteria that constitute the major fraction of cellular biovolume (Phlips and Badylak, 1996). Steidinger *et al.* (2001) reported that the dominant phytoplankton taxa in the region from fall 1994 to early summer 1995 were dinoflagellates, whereas cyanobacteria were the most abundant taxa from late 1996 to spring 1997. Cellular biovolume serves as a useful index to phytoplankton biomass that is independent of physiologically induced changes in pigment concentrations such as those that occur in chlorophyll *a*. In eastern Florida Bay, total phytoplankton biovolume is less than 1 μm^3 ml^{-1}, a value much less than that in the western and central bay (Figure 6.1) (Phlips *et al.,* 1999).

Two factors result in strong phosphorus limitation of primary production in the region, helping to explain the low phytoplankton concentrations that typify this region of the bay. The eastern region of Florida Bay receives significant freshwater inputs from Taylor Slough and the C-111 canal system. Salinity values in the eastern basins are on average lower than in the central and western bay, with typical values from 20 practical salinity units (psu) to 30 psu (Figure 6.4) (Phlips *et al.,* 1999). The external surface-water inputs to eastern Florida Bay are very low in phosphorus (Boyer *et al.,* 1999). In addition, the high concentrations of calcium in the region tend to bind free phosphate.

Central Florida Bay

Over the past twelve years, the central region of Florida Bay has been the site of intense and prolonged algal blooms. In the eastern region of the bay, biovolumes of phytoplankton seldom exceeded 1 million μm^{-1}/ml; however, in the central bay phytoplankton biovolumes have regularly exceeded 10 million μm^{-1}/ml (Phlips *et al.,* 1999). The intensity of blooms in the central bay is somewhat masked by the fact that the chlorophyll content of phytoplankton in the central region is relatively low when compared to the chlorophyll content in the western bay and some other coastal ecosystems in Florida (Phlips *et al.,* 1999, 2002). It has been hypothesized that this is partially attributable to the very shallow depth of the central region of the bay (generally less than 2 m), resulting in high light availability and sun-adaptation by algal cells (Phlips *et al.,* 1999). It is also possible that the domination of the plankton community by the cyanobacterium *Synechococcus* cf. *elongatus* and the nutrient limitation contribute to the low ratio. Irrespective of the causes for the low ratios, it is important to consider the ratio when evaluating the intensity of blooms in the bay. For example, peak chlorophyll concentrations in the St. Johns River in northeast Florida are three to four times those in central Florida Bay, but the peak biovolumes of phytoplankton are very similar (Phlips *et al.,* 2000). These considerations manifest the fact that the 20–40 mg m^{-3} chlorophyll levels commonly encountered in central Florida Bay are representative of serious bloom conditions, whereas similar chlorophyll levels in other ecosystems might be viewed as moderate bloom levels.

Over the twelve years since the initiation of major phytoplankton blooms in central Florida Bay, the most intense blooms have occurred during the summer and early fall, except during 1993 and 1994, when high phytoplankton standing crops persisted throughout the year. Three of the past ten years (1993, 1994, and 1998) had particularly intense blooms. In central Florida Bay, phytoplankton blooms originate in the northern part of the region. For most of the peak bloom season (May–September), phytoplankton populations in the south-central region are relatively low. However, in the fall and early winter, passing cold fronts, along with the concomitant shift in wind direction to the north, displace phytoplankton-rich water southward. This recurring pattern is apparent in the appearance of bloom concentrations of phytoplankton as far south as the Florida Keys reefs.

Cause of Blooms in the Central Region

The apparent rise of planktonic algae blooms in the central region of Florida Bay in the early 1990s raises two fundamental questions: (1) What changes occurred in the region that facilitated the onset of the blooms, and (2) What are the nutrient sources that have sustained blooms since that time? In relation to the first question, the onset of blooms indicates one of two possibilities: (1) more nutrients were made available for phytoplankton production either through redirection of internal reserves and/or increases in external loading, and/or (2) biomass loss terms were dramatically reduced. The presence of a thick, organic sediment layer in the north-central region of Florida Bay indicates that this region of the bay has historically been productive. Prior to the 1990s, seagrasses were most likely the dominant primary producers in the central bay. Even after 1990, seagrasses were still present in the region, although were not as prominently as in previous years.

One of the principal hypotheses about the cause of phytoplankton blooms in the central bay focuses on the role of seagrass die-off in making internal nutrient reserves available for planktonic production (Robblee *et al.,* 1991; Carlson *et al.,* 1994; Durako, 1994; Zieman *et al.,* 1994). There are a number of ways that the reduction of seagrass populations could enhance nutrient availability for planktonic production, including (1) through the addition of recyclable nutrients from dead seagrass, (2) by increasing access to sediment-bound nutrients via increased resuspension and diffusion, and (3) by reducing competition for nutrients between phytoplankton and epiphytic or benthic algae living in seagrass communities. In addition to increasing nutrient availability, the reduction in seagrass communities can affect phytoplankton loss processes. The populations of filter-feeding organisms associated with seagrasses can influence phytoplankton densities, particularly in very shallow environments like Florida Bay. The physical presence of dense seagrass beds also increases the sedimentation of algae by reducing the potential for resuspension of algae and sediments.

The importance of seagrass die-off in the stimulation of phytoplankton blooms is not a universally accepted concept. Some researchers have suggested that this line of reasoning is backwards and that increases in planktonic production have actually led to the demise of seagrasses (Lapointe *et al.,* 2002). The authors of this hypothesis cited observations by local users of the bay of increases in turbidity prior to the seagrass die-off in the late 1980s as evidence (DeMaria, 1996). However, these observations were principally restricted to the western region of the bay and therefore do not provide substantial insight into what occurred in the central bay during the 1980s. The north-central region of the bay is very shallow (generally less than 2 m deep), and it remains to be demonstrated if blooms could cause the demise of seagrass populations as a result of decreased light availability. It is possible that such an argument might be more tenable in the western bay and shelf environments, where average depths are greater.

Irrespective of which came first, the seagrass die-off or the algae bloom, the central questions remain the same: what are the sources of nutrients for phytoplankton blooms and has the trophic state of the central bay increased over the past few decades. It is important to consider the possibility that the overall pool of nutrients may have remained stable but that the distribution has changed, along with changes in loss terms. This argument falls within the concept of "alternative stable states." Under this scenario a major environmental disruption that resulted in seagrass die-off could have ushered in environmental conditions conducive to the persistence of phytoplankton blooms. Such disruptive events could include major storms, prolonged drought or flood periods, or a major shift in nutrient loading.

The first step in addressing these questions is to identify what nutrients actually limit the production potential of phytoplankton in the central bay. There is little doubt that primary production in the eastern region of the bay is strongly phosphorus-limited (Lavrentyev *et al.,* 1998; Tomas *et al.,* 1999). There is also significant evidence indicating that the western region of the bay and adjacent shelf environment are commonly limited by nitrogen or nitrogen-phosphorus co-limitation. This information suggests that there is an excess supply of phosphorus to this region. The nutrient limitation status of the central bay is more ambiguous. A number of biogeochemical indicators, such as the ratios of total nitrogen (TN): total phosphorus (TP) and inorganic N:inorganic P, indicate that phosphorus should be the most limiting nutrient (Fourqurean *et al.,* 1993; Boyer *et al.* 1997, 1999). However, it is well known that many organic N molecules are not readily available to phytoplankton, whereas many organic P molecules are bioavailable due to the activity of phosphatase enzymes (Vitousek and Howarth, 1991). The results of nutrient-enrichment bioassays in the central region of the bay suggest that the limiting status can alternate between phosphorus and nitrogen (Tomas *et al.,* 1999). This observation implies that at different times, changes in the loading rate of either nutrient could stimulate increases in phytoplankton production. A number of hypotheses have been forwarded regarding potential sources of phosphorus and nitrogen for phytoplankton blooms in the central region of Florida Bay. Many of these hypotheses deal specifically with the north-central region of the bay, where blooms appear to originate. It is important to recognize that these hypotheses are not mutually exclusive. It is likely that various pathways of nutrient supply operate simultaneously, even though the relative importance of each varies over time and space.

HYPOTHESIS 1—INTERNAL SUPPLY OF NUTRIENTS

There are a number of potential internal sources of nitrogen and phosphorus for phytoplankton production (Rudnick *et al.,* 1999). The thick layer of flocculent organic sediments found in the north-central region of the bay represents a potential pool of bioavailable nitrogen and phosphorus. The recent die-off of seagrasses in the region has made this pool more accessible via enhanced diffusion and resuspension processes. There has been considerable debate within the scientific community about whether the size of this pool and the rate of supply from the sediments are sufficient to sustain the blooms observed over the past decade. The size and availability of the sediment nutrient pool is certainly an issue that warrants further attention. The current information available is insufficient to either accept or reject this hypothesis.

There are a number of biological processes that affect the internal supply rate of bioavailable nutrients. For example, nitrogen fixation by autotrophic and heterotrophic bacteria and cyanobacteria is a potential source of nitrogen. In some aquatic ecosystems, nitrogen fixation can represent a major source of nitrogen (Phlips *et al.,* 1986). Conversely, denitrification processes can result in a loss of bioavailable nitrogen. The relative roles of nitrogen fixation and denitrification are the subject of ongoing research (Cornwell, 2001).

Other key elements of internal supply of nutrients for phytoplankton production are the rates of recycling of nutrients within the north-central region and of export of nutrients from the region. Due to the severe restriction of tidal exchange of water between the north-central region and the waters of the Gulf of Mexico and the Atlantic Ocean, water residence times are long. The restriction should provide more time for recycling and less opportunity for nutrient washout. Initial modeling efforts indicate that residence times in the north-central region are on the order of months (Jackson and Burd, 1999; Top *et al.* 2001) and could be extended during drought periods. Very little is known about the actual rate constants for recycling, sedimentation, or export of nutrients.

HYPOTHESIS 2—GROUNDWATER SOURCES OF PHOSPHOROUS

Phosphorite deposits were created during the Miocene in northeastern Florida and subsequently transported into south Florida by Appalachian erosion, resulting in high phosphorus levels observed in geological formations in certain areas of south Florida (Brand, 1996). Groundwater outflows from these formations can contain high phosphorus levels (Brand, 2002). The distribution of water-column phosphorus correlates well with the phosphorite deposits (Brand, 2002). There has been an effort, though unsuccessful to date, to discover direct phosphorus-rich groundwater inputs within the north-central region of Florida Bay. In a less direct manner, phosphate mining in central Florida may have increased the input of phosphorus into the southwestern coast of Florida. It has been hypothesized that the phosphorite deposits are a persistent source of phosphorus that has not changed significantly over the past few thousand years (Brand, 2002). Although phosphate mining over the past century may have increased the input of phosphorus into coastal waters, the extent to which P from this source was transported to Florida Bay and how this has changed over the past century is unknown. The timing of phytoplankton blooms (in the 1990s) does not seem to support a hypothesis that this P source has been an important factor driving changes in Florida Bay phytoplankton. There is little evidence that phosphorus input to Florida Bay has increased substantially in the past two decades. Overall, many questions remain about the importance of groundwater inputs of nutrients to algal blooms in Florida Bay, but there is an active research effort underway (Corbett *et al.,* 2000).

HYPOTHESIS 3—EXTERNAL LOADING OF NUTRIENTS

Current information on geographical gradients of critical nutrient elements in and around Florida Bay suggests that two of the major external surface-water sources of bioavailable nitrogen for the north-central region are the eastern half of the bay and the Everglades boundary. Conversely, phosphorus gradients in the region indicate that the most likely source of bioavailable phosphorus is from the western portion of the bay. These nutrient gradients suggest that the blooms in the north-central part of the bay could be fed by nitrogen inputs from the east and by phosphorus inputs from the west.

It has been hypothesized that phytoplankton blooms in north-central Florida Bay are a result of increases in nitrogen loading related to recent changes (since 1980) in water-management practices in southeast Florida (Brand, 2002). The following scenario is envisioned for explaining the increase in N load to Florida Bay. In the early 1980s, agricultural runoff from the Everglades Agricultural Area (EAA) was diverted south via the South Dade Conveyance System (Light and Dineen, 1994; South Florida Water Management District, 1992). Walker (1991) observed significant increases in nitrate in water flowing south through the C-111 canal toward Florida Bay and through the S12A station where water flows into the Shark River system. Unfortunately, there is little nitrogen concentration data for Florida Bay before the beginning of the large regional monitoring program in 1989. Therefore, it is difficult to determine the degree to which nitrogen levels in the north-central region of Florida Bay were affected by the later alterations in flow. This scenario also depends on several assumptions for which the evidence is currently lacking or insufficient. The primary assumption is that there is sufficient water exchange between the western shelf, the putative source of phosphorus, and the north-central bay to sustain blooms. Current hydrodynamic data are insufficient to establish this rate of exchange. There is also a need to more carefully examine the nutrient-limitation status of phytoplankton in the central bay. As mentioned above, chemical data indicate that the north-central region should be phosphorus-limited, but bioassay data indicate a mixed limitation status.

HYPOTHESIS 4—SEWAGE AS A SOURCE OF NUTRIENTS

Another potential source of nutrients is sewage and other nutrient-rich freshwater runoff from land in nearby areas of high human activity. In the case of Florida Bay, this would primarily be the heavily populated Florida Keys. Human activities in the Florida Keys generate considerable amounts of N and P (U.S. EPA, 1992), and a fraction of this is clearly entering the local waters (Lapointe *et al.*, 1990, 1994; Shinn *et al.*, 1994; Paul *et al.*, 1995a,b). The problem with this hypothesis is that the source of nutrients is downstream of the algal blooms, not upstream. Sewage may be causing local eutrophication and leading to algal overgrowth of the coral reefs downstream but cannot be the source of the nutrients generating the algal blooms upstream to the northwest. Concentrations of nitrogen, phosphorus, and chlorophyll all decrease, not increase, along transects from northern Florida Bay to the Florida Keys. The algal blooms in Florida Bay are, in fact, the farthest from the Florida Keys and the human population.

HYPOTHESIS 5—ATMOSPHERIC INPUTS

Until recently, the potential role of atmospheric deposition of bioavailable nutrients in supporting algal blooms in Florida Bay was largely discounted. However, recent information indicates that such inputs may indeed be an important element to the broader nutrient budget of the bay (Rudnick *et al.*, 1999).

Domination by Cyanobacteria

One outstanding feature of algal blooms in the central region of Florida Bay is the domination of the cyanobacterium *Synechococcus* cf. *elongatus.* A study of algal blooms in the region from 1993–1997 showed that *S.* cf. *elongatus* represented over 90% of total phytoplankton biovolume in most instances when total phytoplankton biovolume exceeded 5 million µm^3/ml (Phlips *et al.*, 1999). Although cyanobacteria are the most abundant phytoplankton in central Florida Bay, other taxonomic groups can play important roles (Phlips *et al.*, 1999; Steidinger *et al.*, 2001). For example, between May 1994 and April 1995, the diatoms *Cyclotella choctawatcheeana* and *Chaetoceros* cf. *salsugineus* were frequently important elements of phytoplankton biomass (Steidinger *et al.*, 2001). Again, in July 1995, March 1996, and January 1997, diatoms were numerous.

Based on empirical observations and experimental studies, a number of hypotheses have been forwarded to explain the domination of *Synechococcus* cf. *elongatus* in the central region of Florida Bay. Several of these hypotheses are based on some of the unique ecophysiological characteristics of this cyanobacterium. Several research groups have demonstrated the broad range of salinities over which *S.* cf. *elongatus* can sustain high growth rates (5–50 psu; Phlips and Badylak, 1996; Richardson, 2001). Because of the isolation of central Florida Bay from tidal mixing and the proximity of the north-central bay to the adjoining Everglades, this region is subject to wide swings in salinity. For example, salinities exceeded 40 psu during the drought period of 1992–1994 but dropped to as low as 11 psu during subsequent flood periods, such as 1995 and 1997 (Figure 6.4) (Phlips *et al.*, 1999; Boyer *et al.*, 1999). The euryhaline tolerances of *S.* cf. *elongatus* probably provide the cyanobacterium with an advantage in terms of long-term prominence. However, it does not fully explain the fact that intense blooms of *S.* cf. *elongatus* have been observed during times when salinities have remained in a moderate range (25–35 psu.)

Another factor that may contribute to the success of *S.* cf. *elongatus* is its ability to compete for nutrients at low concentrations (Richardson, 2001). As a picoplanktonic species, one might expect *S.* cf. *elongatus* to have low half-saturation constants for nutrient uptake, strictly because of surface area to biovolume considerations. Experimental studies have provided support for this hypothesis. A study of the kinetics of phosphorus (PO_4-P)-dependent growth compared four important phytoplankton species found in the bay: the cyanobacterium *Synechococcus* cf. *elongatus,* an unidentified spherical picoplanktonic cyanobacterium, and the diatoms *Chaetoceros* cf. *salsugineus* and *Cyclotella choctawhatcheeana* (Richardson *et al.*, 2001). The results of growth tests revealed maximal growth rates for *S.* cf. *elongatus,* the spherical cyanobacterium, *C.* cf. *salsugineus,* and *C. choctawhatcheeana* of 1.38, 1.37, 2.48, and 3.37 divisions day^{-1}, respectively. The half-saturation constant for growth, K_u, was determined to be 0.005–0.05 µmol liter^{-1} for the latter three species. The K_u for *S. elongatus* could not be determined because the growth rate was still maximal at the lowest test concentration of phosphate. A test of phytoplankton resource-based competition using Equilibrium Resource Competition theory predicts that *S.* cf. *elongatus* is the superior competitor under phosphorus-limitation over the range of salinities examined (15–50 psu). The superior competitive ranking of *S.* cf. *elongatus* can be attributed to the exceptionally low K_u values. The model ranked the spherical cyanobacterium second in terms of phosphate competition, with the diatoms last. In competition experiments under steady and varying P-limitation, *S.* cf. *elongatus* also dominated in terms of biovolume at the end of all experiments at all salinities. Thus, with sufficient time, *S. elongatus* should competitively displace all the other species under phosphorus-limited conditions. Competition experiments further revealed that under nitrogen-limiting conditions, the two species of cyanobacteria usually co-dominated in terms of biovolume under steady- and non-steady-state conditions. In summary, under both steady-state and non-steady-state conditions, the cyanobacterium *S.* cf. *elongatus* is the superior competitor for orthophosphate and can frequently outcompete diatoms under N-limiting conditions.

Related to the question of nutrient competition is the ability of *S.* cf. *elongatus* to regulate its buoyancy by altering the presence of gas vesicles (Phlips and Bledsoe, unpublished data). Under phosphorus-limited conditions, the presence of gas vesicles diminishes and *S.* cf. *elongatus* cells lose buoyancy. It has been suggested that with the loss in buoyancy, nutrient-depleted cells sink to the sediment–water interface, where they can take advantage of higher nutrient availability (Phlips *et al.,* 1999).

Besides the characteristics that may enhance the competitive advantage of *S.* cf. *elongatus* in acquiring resources for growth, there may also be ways this species is favored by lower magnitudes of certain loss terms. Butler *et al.* (1995) proposed that *S.* cf. *elongatus* was responsible for the observed demise of sponges in Florida Bay because of its adverse effect on the filtration apparatus of sponges. Although there is evidence that sponges can effectively filter out *S.* cf. *elongatus* from the water column (Lynch and Phlips, 2000), the long-term effects of filtering the mucilage-producing cyanobacterium are not known. Irrespective of the direct effects of *S.* cf. *elongatus* on sponge health, it is clear that the diminishing sponge populations in the bay result in reduced grazing pressure on phytoplankton and thereby increase the potential for blooms (Lynch and Phlips, 2000).

As in the case of sponges, the relationship between *S.* cf. *elongatus* and other grazers, both benthic (*e.g.,* bivalves) and planktonic (*e.g.,* zooplankton), are not well defined. There is evidence that zooplankton grazing rates are periodically high enough to affect phytoplankton population dynamics (Brenner *et al.,* 2001). In grazing experiments, daily metabolic carbon demand of the net zooplankton community ranged from less than 2% to greater than 100% of the phytoplankton carbon stock. Microphytoplankton growth rates ranged from 0.08 to 2.33 divisions d^{-1} at 50% available light. Diatoms, dinoflagellates, and the cyanobacterium *Synechococcus* typically dominated the microphytoplankton community, although chlorophytes and prasinophytes were occasionally major constituents. Microzooplankton grazing rates ranged from 0.00 to 5.28 d^{-1}, and their average ingestion rates ranged from 0.67 to 3.42 mg C m^{-3} d^{-1}. These ingestion rates correspond to a daily ingestion demand ranging from less than 1% to greater than 300% of the initially available carbon, indicating that microzooplankton are capable of exerting a controlling influence on the phytoplankton community. Despite the observed grazing rates, the frequency of cyanobacterial blooms in the north-central region of the bay demonstrates that grazing activity is frequently not sufficient to prevent blooms, although it may play a role in their ultimate demise. There is no information on whether the domination of *S.* cf. *elongatus* in the north-central region is in any way related to selective avoidance by grazers, either benthic or planktonic.

Western Florida Bay

The highest phytoplankton biovolume in western Florida Bay generally occurs in the late summer to winter, when the annual diatom bloom reaches its seasonal peak. Phytoplankton composition in the western bay is distinct from composition in the central bay because a higher proportion of total biovolume occurs in diatoms. Phlips and Badylak (1996) were the first to identify the species composition of bloom components in western Florida Bay. They found that centric (predominantly *Rhizosolenia*) and pennate (*Cocconeis, Navicula, Surirella*) diatoms were dominant species in terms of cell abundance in December 1993. Steidinger *et al.* (2001) subsequently reported that other taxa, especially cyanobacteria, may also account for a large fraction of total biovolume in western Florida Bay and could equal the biovolume attributed to diatoms. In 2000 and 2001, Jurado (2003) conducted a study of netphytoplankton (diatom) silica demand at Carl Ross Key in western Florida Bay. She found that centric diatoms (predominantly *Rhizosolenia* spp., *Chaetoceros* spp., and *Thalassiosira nitzschiodes*) and pennate diatoms (*Nistchia, Navicula, Gyrosigma* spp.) dominated the netphytoplankton fractions (greater than 5 µm). These observations are in general agreement with Phlips and Badylak's (1996) results. Peak concentrations of chlorophyll *a* (2–9 mg m^{-3}) were higher than values observed in the eastern bay but less than concentrations in the north-central basins. Netplankton chlorophyll *a* accounted for more than 50% of total pigment biomass.

Although relatively few, if any, observations of phytoplankton-community species composition in western Florida Bay exist prior to 1990, biogenic silica in the sedimentary record from Carl Ross Key suggest that an increase in the abundance of diatoms has occurred since 1960 (Figure 6.5). Biogenic silica is a distinct marker for the presence of diatoms. Although only two values exist from the sedimentary record before 1960, the vertical profile suggests that biogenic silica concentrations increased from less than 1 mg silicon (Si) to greater than 1 mg Si (g sediment)$^{-1}$ sometime

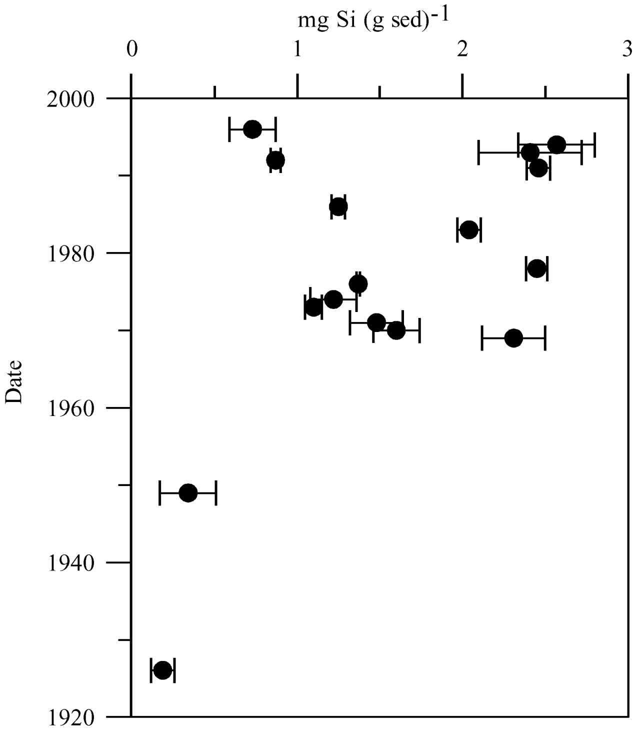

Figure 6.5 *Vertical profile of biogenic silica in a sediment core from Carl Ross Key. The sediment samples with corresponding dates were kindly provided by Dr. J. Trefrey, Florida Institute of Technology (Jurado, 2003).*

after 1950, although values in the last decade have been highly variable. This trend suggests that enhanced diatom biomass in western Florida Bay has developed within the past four or five decades.

Cellular division rates determine the success of a species in the natural environment. Net growth rates equal the difference between the cellular division rate and the sum of all processes that represent losses, including grazing, sinking, advection, and death. Net increases in phytoplankton communities of as little as 0.1 day^{-1} result in an increase of less than 1 to greater than 20 mg m^{-3} chlorophyll *a* in less than a month. Although we have no direct measures of netphytoplankton growth rates in western Florida Bay, community growth rates for netplankton have been estimated from increases in chlorophyll *a* and biogenic silica in dilution gradient experiments. This method, principally developed by Landry and Hassett (1982) and their colleagues, provides a measure of maximum growth. In March 2001, when phytoplankton abundance was low, netplankton chlorophyll *a* exhibited growth rates of 1.5 day^{-1}, increasing to 2.9 day^{-1} in May, July, and September, as netplankton biomass increased. By November 2001, netplankton biomass had reached a stationary phase, and maximum growth rates were again ca. 1 day^{-1}. Grazing losses ranged from 0.6 to 1.75 day^{-1} in these experiments, yielding net growth rates of 0.5 (November) to greater than 1.3 day^{-1} in May and September. Although these experiments represent only the potential for diatom growth *in situ,* they suggest that conditions in summer-fall provide diatoms with a setting for growth rates that exceed the sum of losses.

Exchange of surface waters in western Florida Bay with the West Florida Shelf is evident in the nature of the phytoplankton community and property distributions. Salinity values in western Florida Bay show less temporal variability than in the central or eastern basins. On average, basins in the western bay have a higher average salinity (mean = 35.2 psu) and lower average TN (30.5 µmol kg^{-1}) and dissolved inorganic nitrogen (DIN) (<2 µmol kg^{-1}) than do those in the eastern or central bay (Boyer *et al.,* 1999). Chlorophyll *a* concentrations from the long-term FIU monitoring program averaged 1.9 mg m^{-3}, which, as suggested by Phlips *et al.* (2000), is less than the average values in the central bay but higher than in the eastern bay.

Ratios of TN:TP (x = 55.6) and DIN:SRP (soluble reactive phosphorus) (x = 51.8) in the western bay are higher than Redfield values but lower than those in either the eastern or central basins. These characteristics suggest that the western bay is strongly influenced by the surface waters of the West Florida Shelf that exchange along the boundary of Everglades National Park. The influence of coastal processes is evident in tidal exchange, which is much greater in the western bay than in the interior or eastern basins because the amplitude of the tides is damped from west-to-east across the bay (Wang *et al.,* 1994).

Bioassays at two locations along the western margin of Florida Bay (Sprigger Bank and Sandy Key) indicate that nitrogen is a primary nutrient that limits phytoplankton growth (Tomas *et al.,* 1999). In more than 70% of the bioassays between March 1994 and May 1997, Tomas found that nitrogen in combination with silica stimulated growth more than did individual additions of phosphorus or silica. When individual nutrients were excluded from otherwise complete enrichments (all nutrients – N, or all nutrients – P), the lack of nitrogen yielded a final biomass that was similar to controls. Phosphorus limitation of phytoplankton growth rates was detected in about 20% of all experiments, and iron was even less frequently identified as a nutrient potentially limiting growth.

The responses to N and Si enrichments are consistent with the marine waters that flow into the western margin of Florida Bay and the fact that diatoms frequently dominate these waters. The observations of

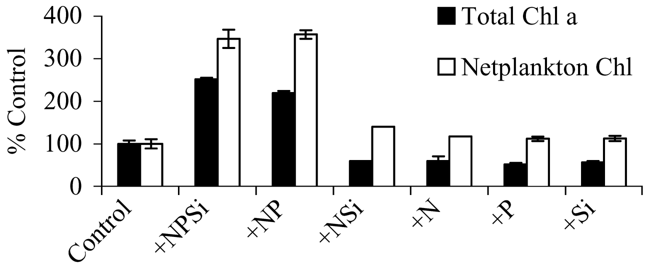

Figure 6.6 *Bioassay results from September 2000 at Carl Ross Key (Jurado, 2003). Values correspond to increases in chlorophyll* a *biomass relative to a control in an incubation of 24 hours. The total phytoplankton community was filtered on Whatman GF/F filter, and the netplankton fraction on a 5-µm Nuclepore filter. The combination of nitrogen plus phosphorus or silicon typically results in the greatest stimulation of phytoplankton growth.*

Tomas *et al.* (1999) were confirmed by Jurado (2003), who found that nitrogen was the principal nutrient limiting both total phytoplankton and netplankton (diatom) growth in western Florida Bay during the 2000–2001 diatom bloom (Figure 6.6). Bioassays were made in September and November 2000, as diatom abundance increased, and in January and March 2001, when diatom biomass declined. The results consistently showed that enrichments with nitrogen, and secondarily silica or phosphorus, stimulated growth of natural populations incubated under simulated in situ conditions. An assessment of temperature and irradiance during the course of the year suggests that these two parameters did not effectively limit the growth of diatoms in western Florida Bay. Thus nutrient supply may be the main factor that accounts for the enhanced growth of diatoms in summer and fall in western Florida Bay.

Seasonal distributions of salinity, nutrients, chlorophyll *a*, and biogenic silica on the West Florida inner shelf, south from the Ten Thousand Islands to the western boundary of Everglades National Park, indicate that diatom blooms observed in western Florida Bay originate in coastal waters off the southwestern Florida Shelf. These features develop in the shallow coastal waters west of Cape Sable and are associated with the low-salinity plume emanating from the Shark River and other riverine sources along the southwestern Florida coast. A chlorophyll *a* "plume" spreads south from Cape Sable to the western margin of Florida Bay during the fall (Figure 6.7). Bimonthly cruises of the NOAA SFERPM Program between 1998 and 2003 have mapped surface-water properties (salinity, nutrients, chlorophyll *a*, and particulate matter) in this region. Spatial distributions of these properties indicate that the Shark River is a major source of nutrients, especially silicate, supporting the diatom bloom. Concentrations of dissolved inorganic nutrients in the Shark River plume at bimonthly intervals indicate that the average concentrations of silicon, inorganic nitrogen, and phosphorus in the plume of the Shark River indicate excess silicate relative to inorganic nitrogen and phosphorus. Little seasonal variation exists in nutrient concentrations, so the volume of freshwater flow appears to be the primary determinant of nutrient flux to the inner shelf.

On the southwestern Florida Shelf, exogenous nutrients that support diatom growth are derived from the Shark River plume and along-shore flow. Increased freshwater flow from rivers often occurs in June at the onset of the rainy season and provides silicates to the inner shelf that contribute to development of the diatom bloom. Between 1998 and 2000, the diatom-dominated bloom on the inner shelf began between August and October. Estimates of the fluxes of nitrate, phosphate, and silicate from along-shore advection (based on bimonthly nutrient measurements and alongshore currents from ADCP currents made by T. Lee and colleagues) and that from the Shark River (derived from river discharge and bimonthly nutrient measurements) were for the period of bloom inception in 1999 (Jurado,

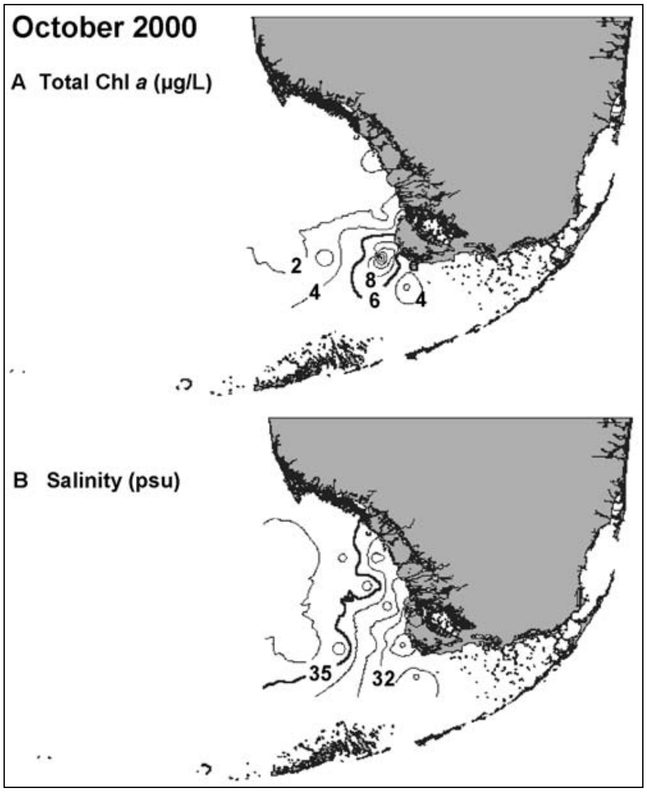

Figure 6.7 *Contours of total chlorophyll* a *concentrations (top) and surface salinity (bottom) in October 2000 during the peak of the annual diatom bloom. Maximum chlorophyll* a *concentration was 17 mg* l^{-1} *off middle Cape Sable (Jurado, 2003).*

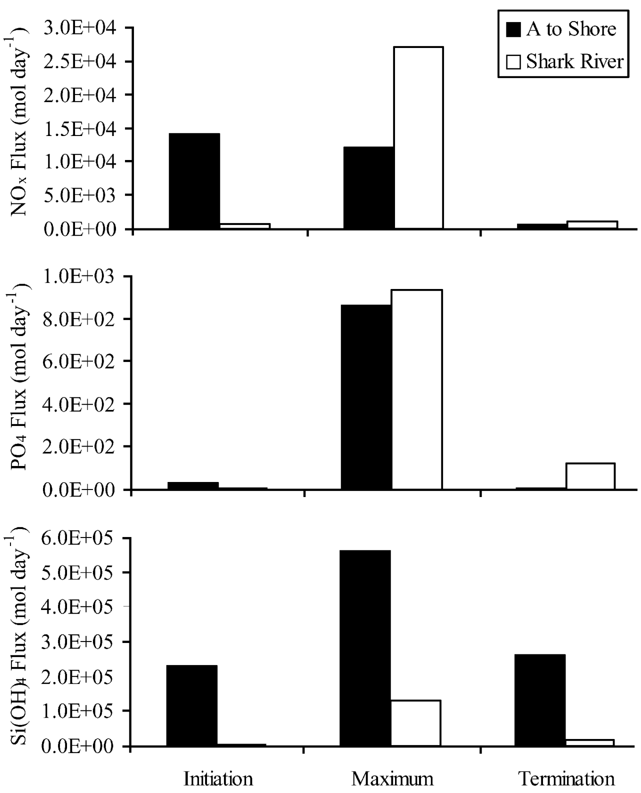

Figure 6.8 *Comparison of inorganic nutrient fluxes from alongshore advection and Shark River during three phases of the 1999 diatom bloom on the southwestern Florida Shelf near Cape Sable. Alongshore flow is based on currents from ADCP A, which is located nearshore, just north of Shark River (Jurado, 2003).*

2003). This is the latest year in which Shark River flow data were available at the time the estimates were made. The resulting flux estimates suggest that during bloom inception, exogenous nutrient sources that support diatom bloom development are largely met by the southerly flow along the southwestern Florida Shelf (Figure 6.8). When the bloom is at its maximum, after the onset of the rainy season, Shark River is a major source of nitrate, nitrite, and phosphate. Alongshore advection of silicate appears to be the primary source of this essential nutrient for diatoms, at least in that year.

In summary, diatom blooms in the western basins of Florida Bay are a seasonal extension of blooms that initiate on the southwestern Florida Shelf. Various species of *Rhizosolenia* and *Chaetoceros* are the dominant members of this assemblage, in combination with pennates that are likely resuspended from the bottom. Diatoms begin net growth (*i.e.,* growth rates exceed losses) with the onset of the rainy season. Bioassays suggest that nitrogen, often in combination with phosphorus and/or silica, potentially "limit" growth. Nutrients that support diatom growth are derived from riverine sources, principally Shark River, and along-shelf (southerly) advection. The relative contribution of inorganic nitrogen, phosphorus, and silicon varies with the stage of the bloom, and likely varies yearly with variations of river discharge and alongshore flow.

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Chapter 7

Seagrass Ecology

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

Introduction

Question 4*—What are the causes and mechanisms for the observed changes in the seagrass community of Florida Bay? What is the effect of changing salinity, light, and nutrient regimes on these communities?*

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 they are in south Florida (Fourqurean *et al.,* 2002). Seagrasses are the dominant biological community in Florida Bay, historically covering more than 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 less than 2 m; Schomer and Drew, 1982), seagrasses are also the dominant physical feature of the bay, and their presence greatly affects physical, chemical, geological, and 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 which are commercially important to 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 and 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 and reducing nutrient and particulate loads in the waters reaching the reef tract (Kenworthy *et al.,* 1998). Continued loss of seagrasses along this margin and proposed increases in water flow from the Everglades could result in greater exports of nutrients and particulates 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 in 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 show 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 a rapid growth of human populations. This coastal distribution also places seagrass communities at the end of the watershed pipe, so the health of these communities reflects not only direct coastal influences but larger-scale, landscape-to-regional influences as well. Because most seagrasses are benthic-perennial plants, they are continuously subjected to stresses and disturbances that are associated with changes in water quality along the land–sea interface. To a large extent, seagrass abundance determines public perception regarding the "health" of the coastal waters of Florida (Goerte, 1994; Boesch *et al.,* 1993, 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 originated 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.,* 2002). The spatial patterns of changes in abundance from 1995 to 2000 suggest that the most perturbed environment in Florida Bay with respect to seagrasses is currently along the western and southern margins of the bay. Much of the focus of management and restoration efforts in south Florida have been directed toward landscape-scale modifications and an extensive flood-control system to increase the quantity of freshwater delivered to northeastern Florida Bay and, more recently, to 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 (each 0.25 m^2) taken in the bay from 1995 to 2000 by the Fisheries Habitat Assessment Program (FHAP; Durako *et al.,* 2002), 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.,* 2001). The entire south Florida coastal zone, including the areas west of Florida Bay and within the Florida Keys National Marine Sanctuary (FKNMS), is dominated by seagrass habitats. Fourqurean *et al.,* (2002) assessed seagrass species composition and density at 1,207 sites distributed across 19,402 km^2 of nearshore marine and estuarine environments in south Florida. At these sites, a total of 8,434 quadrats (each 0.25 m^2 total area = 2,108.5 m^2) were sampled from 1996 to 1998. At least one species of seagrass was observed at 1,056 of the 1,207 sites, or 87.5% of all sampling sites. *Thalassia testudinum* (turtlegrass) was the most commonly encountered species, being found at 898 sites. *Halodule wrightii* (shoalgrass) was the second most commonly encountered species, occurring at 459 sites, followed by *Syringodium filiforme* (manateegrass, 239 sites), *Halophila decipiens* (paddlegrass, 96 sites), *Ruppia maritima* (widgeongrass, 41 sites) and *Halophila engelmannii* (stargrass, 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; http://people.uncw.edu/durakom/seagrass/seagrass.htm). This event was first observed by backcountry fishing guides who reported the occurrence of "potholes" in the seagrass beds in 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 die-off 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 die-off has been found outside of the densest seagrass beds within Florida Bay, and no primary seagrass die-off has occurred in sparse- or medium-density beds within the bay.

PRIMARY SEAGRASS DIE–OFF

The first phase of primary seagrass die-off occurred during the relatively dry and clear period of 1987 to early 1991. During this period, density, standing crop, and productivity of *Thalassia* were high but then declined as the 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 die-off (Zieman *et al.,* 1999). In addition, *Batophora oerstedi* and *Halodule* spread rapidly into die-off patches (Thayer *et al.,* 1994). At this time, Florida Bay waters as a whole remained as clear as they had been in the years just prior to the die-off, with limited turbidity from suspended sediments in the immediate vicinity of the denuded die-off 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, which were associated with the loss of seagrasses on the western banks and was most severe in the western and central bay (Phlips and Badylak, 1996). These blooms may have been initiated by the nutrients liberated by the die-off of seagrasses (Butler *et al.,* 1995). Loss of seagrass cover was the major factor of 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 losses 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; Kenworthy *et al.,* 1998; Rose *et al.,* 1999) were also observed. From 1992 to 1995, salinities showed a progressive decline throughout the bay (Boyer *et al.,* 1999).

During this time, there was speculation regarding how much seagrass had been lost, with as much as 100,000 acres (40,000 ha) estimated with no supporting data. With the decline in water clarity, aerial photography became useless in determining seagrass distribution over much of Florida Bay. Because of the

Table 7.1 *Florida Bay seagrass die-off milestones.*

Event or Observation	Date	Significant Publication/Research Initiated
SPOT image shows no die-off patch in Rabbit Key Basin, Johnson Key Basin, or Rankin Lake.	Feb 2, 1987	
"Potholes" seen in *Thalassia* beds in Rankin Lake and Cross Bank by back-country fishing guides.	Summer 1987	FIU/SERP water-quality monitoring initiated.
Heat stress kills tagged conch in Hawk Channel (Berg); coral bleaching at Looe Key (Causey); fish dying on Cross Bank (Holmquist, Robblee).	Jul 1987	
Robblee observes die-off patches along north shore of Johnson Key.	Late Fall 1987	
Guides contact Susan Bell about dying seagrasses.	Mar 1988	
Guides meet Mike Robblee and Jim Tilmant at Little Rabbit Key and observe extensive die-off. ENP consults Jay Zieman.	Apr 1988	Robblee and Zieman visit Rankin Lake and Johnson Key Basin.
	May 1988	Zieman provides ENP a trip report on die-off, indicating its uniqueness and stressing need to monitor and conduct research. Carlson-Durako survey Johnson Key Basin.
Zieman observes lesions were not apparent. Robblee and Holmquist observe phytoplankton bloom NE of Long Key.	Spring–Summer 1988	
SPOT imagery shows large die-off patch in Rabbit Key Basin.	Jun 1988	
	Sep 1988	Robblee provides memo on seagrass die-off to Superintendent Finley. Finley provides funds for researchers to evaluate die-off.
	Nov 1988	ENP-sponsored field trip: Robblee, Carlson, Durako,Fourqurean, Muehlstein, Porter, and Zieman visit die-off areas. *Labyrinthula* detected.
	Apr 1989	Durako initiates studies on morphometric changes, Braun-Blanquet abundance, and demography. Carlson begins studies on hypoxia/sulfide-ADH, ethylene, H_2S, conducts bucket experiments.
	May 1989	Robblee initiates studies of seagrass associated animal responses to die-off in Rankin Lake, Johnson and Rabbit Key basins. Monitoring of plant community response to *Thalassia* die-off initiated.
	Jun 1989	Zieman completes version 1 of his conceptual model of seagrass die-off. Zieman initiates long-term *Thalassia* productivity measurements near four core die-off areas.
	Jul 1990	Thayer *et al.* investigate plant community response to die-off in Johnson and Rabbit Key basins.
Halodule begins to colonize die-off patches.	1990–1991	

Table 7.1 *Florida Bay seagrass die-off milestones. (continued)*

Event or Observation	**Date**	**Significant Publication/Research Initiated**
Earliest observation of persistent turbidity caused by tidally resuspended sediments observed in Johnson Key Basin. Kuss, DiDomenico, Robblee observers.	Apr 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.
Cyanobacteria bloom begins in Rabbit Key basin.	Nov 1991	
Hurricane Andrew passes over south Florida; has little direct impact on Florida Bay.	Aug 24, 1992	
High rainfall occurring the week after Andrew washes mangrove "rot" into Florida Bay. Zieman observes that this event began the severe turbidity events in the bay.	Approx. Sep 1, 1992	
Major turbidity plume from western Florida Bay reaches Big Pine Key.	Dec 22, 1992	
	Apr 1993	Zieman *et al.* look at light-reduction effect on *Thalassia* in Rabbit Key basin and Sunset Cove.
	Oct 1993	Hefty *et al.:* DERM initiates seagrass monitoring of northeastern basins.
	Jun 1994	Hall-Durako: 107 stations previously sampled in 1983–84 are resampled for decadal comparison of seagrass abundance.
	Oct 1994	Series of faunal studies conducted in mid-1980s are repeated as a part of the decadal comparison program: Thayer, Matheson and Camp, Robblee.
	Nov 1994	Durako-Hall: Preliminary test of EMAP-based Braun-Blanquet sampling.
Very wet spring and summer; true estuarine conditions exist throughout Florida Bay.	Spring 1995	Durako-Hall: Fish Habitat Assessment Program (FHAP) initiated. Landsberg-Blakesley: *Labyrinthula* spatial and temporal dynamics.
	Oct 1995	Montague initiates field studies in northern Florida Bay; starts construction of a mesocosm system to look at effects of salinity fluctuations.
Halophila engelmannii first observed in Johnson Key basin, suggests a shade-adapted community.	Oct 1996	
	Aug 1997	Stumpf examines satellite imagery to detect changes in seagrass abundance from 1986–1997.
Rudnick: Florida Bay ecosystem conceptual model.	1997	
	Oct 1997	Carlson-Blakesley initiate banktop die-off studies.
	Nov 1997	Fourqurean *et al.* sample two areas in Rabbit Key Basin to examine scale-based variability in potential *Thalassia* ecoindicators.
Flowering of *Thalassia* and *Halodule* widespread.	May 1998	

Table 7.1 *Florida Bay seagrass die-off milestones. (continued)*

Event or Observation	Date	Significant Publication/Research Initiated
Hurricane Georges passes west of Florida Bay.	Sep 1998	
"Classic" die-off patches present on bank edge east of Big Rabbit Key. Barnes Key eastern bank and basin dense *Thalassia,* crystal-clear water.	Oct 1998	
	Fall 1998	Koch: Sulfide phytotoxicity studies on *Thalassia*.
New "classic" die-off observed in Barnes Key area and in Sunset Cove.	Jan 1999	Hall-Blakesley 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.	Apr 1999	
Flowering of *Thalassia* and *Halodule* again observed in core samples from several stations.	May 1999	
Hurricane Irene passes west of Florida Bay.	Oct 1999	
Flowering of *Thalassia* observed in field, recruiting seedlings observed in cores.	May 2000	

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 FHAP was initiated during spring 1995. The turbid conditions in western Florida Bay from 1995 to 1997 made measuring and interpreting seagrass losses and changes in species distributions more complicated because of the 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 degraded water quality because mortality was signified by a general thinning of shoots, 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.*, 1999a) and between 1995 and 1998 (Durako *et al.*, 2002) 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.*, 1989, 1999): at stations associated with primary seagrass die-off, standing crop declined from 1989 to 1995; standing crop remained stable from 1995 through 1997; and standing crop 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 to 2001 (Figure 7.1), 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 eastern 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 five years, relative *Thalassia* abundance has dropped from being more than five 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 (Durako *et al.*, 2002). During fall 1996, the small-bodied, low-light-adapted seagrass *Halophila engelmannii* was observed at one station in Johnson Key Basin. 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 the fall of 1998 uprooted much of the *Halophila* in Johnson Key Basin (it was observed only at five stations nine days after the storm); reduced the cover of *Thalassia* (especially in areas where it had been sparse); and removed much of the litter layer on the bottom. However, by spring 1999, *Halophila* cover increased in Johnson Key Basin, and this species was observed in Rankin Lake, Whipray Basin, and Twin Key Basin. This rapid increase in spatial distribution suggests the hurricane may have played a role in distributing *Halophila* propagules (Durako *et al.*, 2002). Longer internodes and deep apical meristems on short shoots of *Thalassia* at Barnes Key were observed shortly after Hurricane

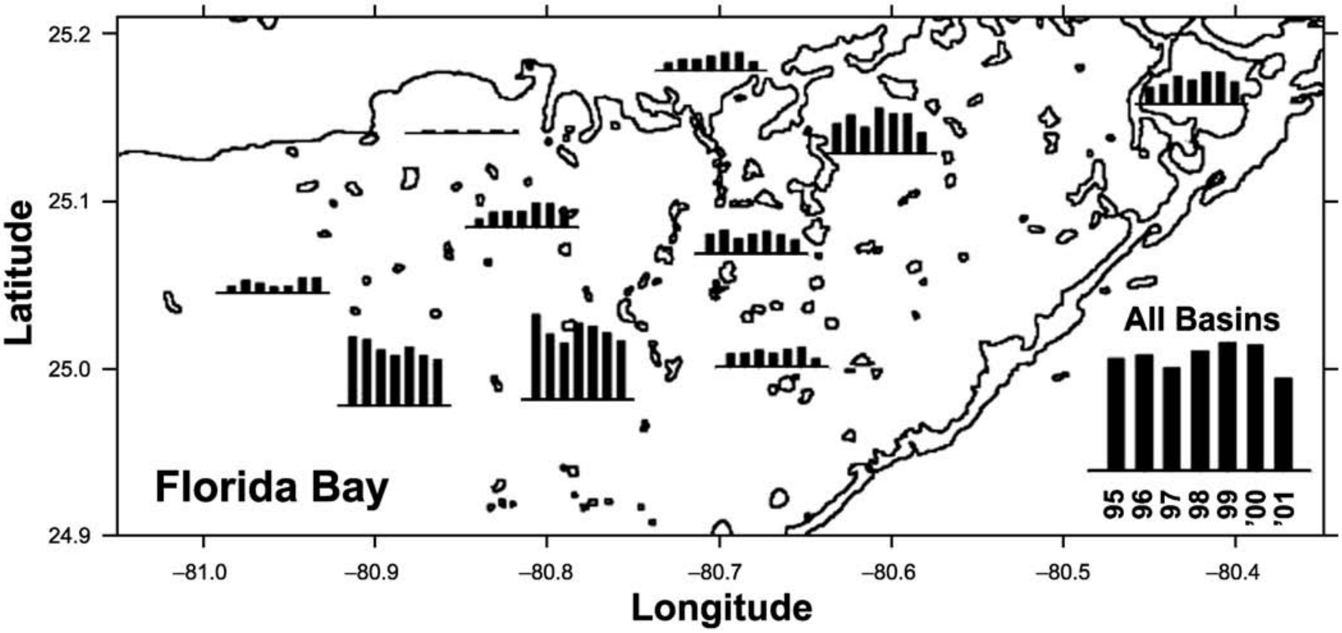

Figure 7.1 *Changes in relative abundance, as determined by Braun-Blanquet sampling, of* Thalassia *from spring 1995 to spring 2001.*

Georges, suggesting the hurricane resuspended sediments in Florida Bay. Hurricane Irene also reduced seagrass 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.,* 2002). 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 and the appearance and spread of *Halophila engelmannii* are often associated with declining light availability.

Since 1998, there has been an upturn in abundance,

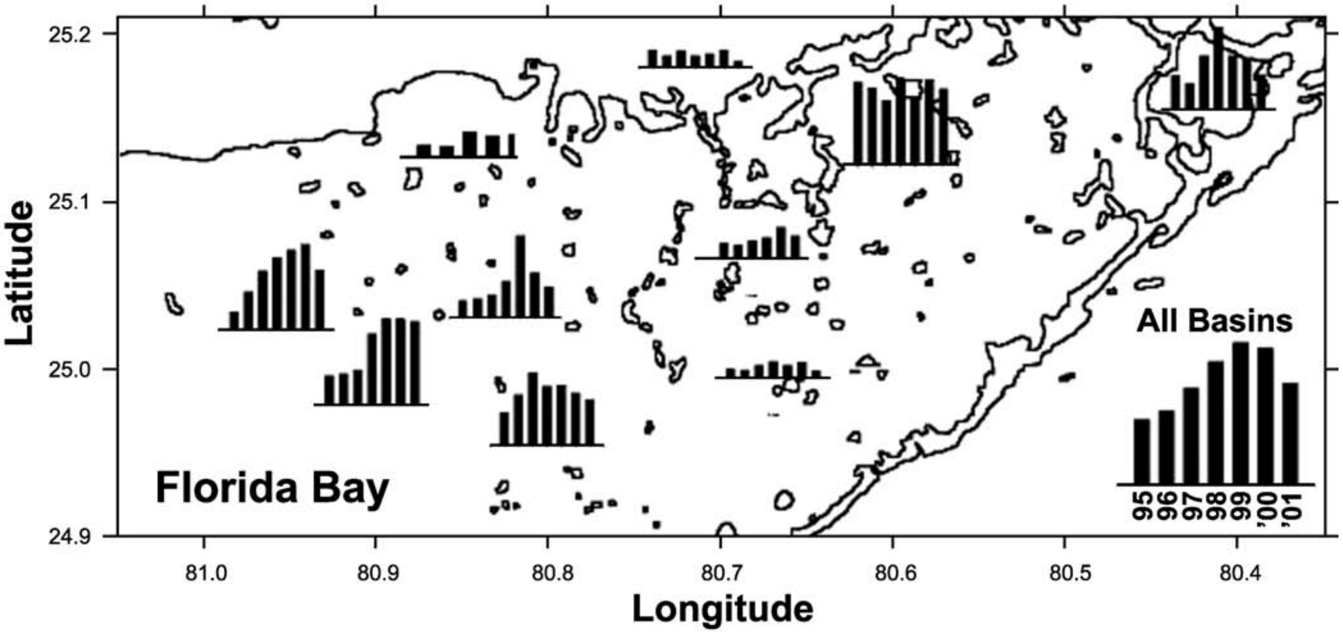

Figure 7.2 *Changes in relative abundance, as determined by Braun-Blanquet sampling, of* Halodule *from spring 1995 to spring 2001.*

productivity, standing crop, and flowering of *Thalassia* and *Halodule* that seems to be associated with improving water clarity (Zieman *et al.,* 1999; Durako *et al.,* 2002). Some of this improvement in water clarity may be due to a decrease in unvegetated bottom (Durako *et al.,* 2002). However, as recovery begins to occur at the original die-off sites, a new instance of primary seagrass die-off that began in January 1999 has been observed north of Barnes Key. 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.,* 1999). Seagrasses affected by the new die-off have 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," whereas the rest of the blade looked green and healthy (Carlson *et al.,* 1990).

PALEOECOLOGICAL INVESTIGATIONS

Although not part of the seagrass research program, paleoecological investigations add relevant information for understanding 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 are apparently 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 Die-Off

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

The Zieman *et al.* (1999) model (Figure 7.3), has three major phases: A *Developmental Phase* (A–C), in which a combination of natural and anthropogenic processes contributed to an extensively developed (overdeveloped, actually) *Thalassia* ecosystem; an *Initiation Phase* (D–G), in which the heavily developed system interacted with a suite of environmental stresses to produce the initial die-off episodes; and a *Maintenance Phase* (G–L–G and repeat), in which the process became self-sustaining. In this model, the interactions of the dense *Thalassia* and the environmental stresses formed the primary trigger to the initial die-off episodes.

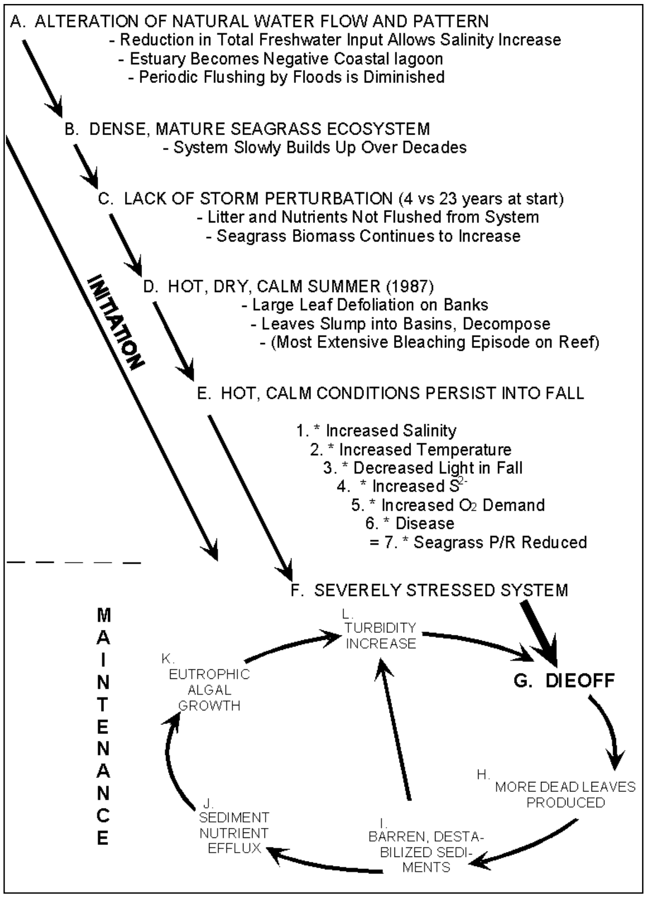

Figure 7.3 *Zieman* et al. *model for seagrass die-off.*

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 a 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, and both have changed little in the past decade.

As research progressed and the conceptual models matured, seagrass researchers found much common

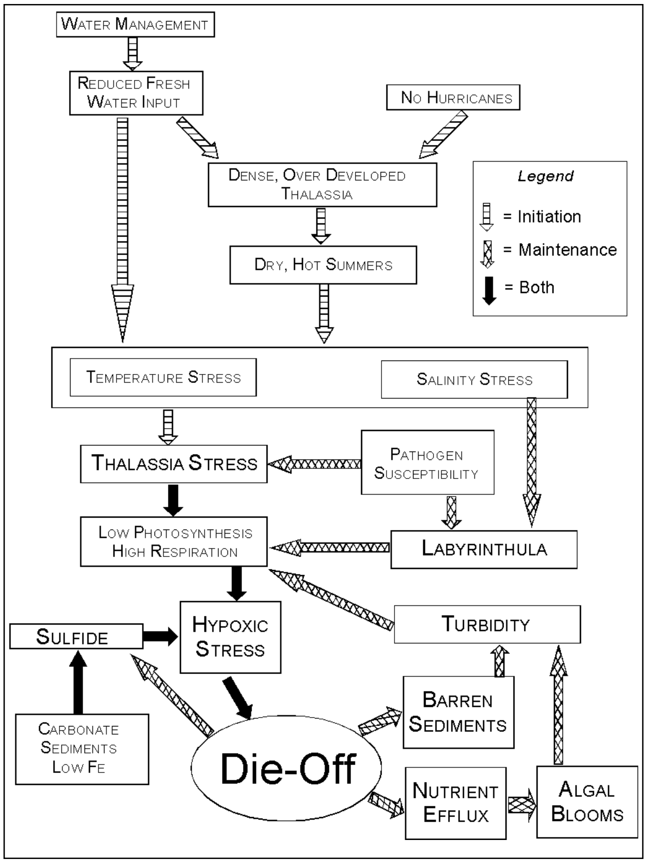

Figure 7.4 *Carlson and Durako model for seagrass die-off.*

ground on which to agree. Among these points of agreement are the following:

- Primary seagrass die-off is species-specific, restricted to *Thalassia testudinum.*
- Primary die-off occurs only in very dense beds; sparse and medium-density beds have never been shown to have primary die-off.
- Primary die-off has occurred in Florida Bay only. It has occurred in continentally influenced regions of the bay with reduced circulation and reduced flushing.
- Primary die-off occurs principally during 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, primary die-off does not occur in the hottest months of summer.
- Researchers with experience in Florida Bay prior to the initial primary die-off found the waters to be clear and the seagrasses mostly free from epiphytes during 1987–1989. Reduced water clarity and epiphytic growth followed seagrass die-off by several years.

Factors such as high water temperature, prolonged hypersalinity, and excessive seagrass biomass (due to lack of recent disturbances, including hurricanes and reduced salinities), which lead 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 that 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 die-off or for the first several years (Boyer *et al.,* 1999).

Lesions were frequently observed on blades of *Thalassia* in areas affected by die-off, but 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 short-shoots affected by die-off (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 *et al.* 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) die-off versus mortality induced by light stress to the recent losses of *Thalassia* in western Florida Bay is problematic. There is a high spatial coincidence between the distribution patterns of seagrass loss, *Labyrinthula* abundance (Landsberg *et al.,* 1996; 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 sub-climax (See fig. 13 in Zieman, 1982) as well as offering a low-salinity refugium from disease—*Labyrinthula* has never been found in Florida Bay at salinities below 15 practical salinity units (psu) (Blakesley *et al.,* 1998).

Summary of Research

Research on seagrass dynamics has focused on the

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

Research Topic	Plant Growth and Metabolism	Seagrass Die-off and Recovery
General Characteristics		Robblee *et al.*, 1991; Fourqurean *et al.*, 1992; Thayer *et al.*, 1994; Hall *et al.*, 1999a,b; Stumpf *et al.*, 1999; Zieman *et al.*, 1999; Durako and Hall, 2000; Bacon *et al.*, 2001; Durako *et al.*, 2002
Temperature and Salinity	Chesnes *et al.*, 1999	Blakesley *et al.*, 1998; Boyer *et al.*, 1999; Fourqurean *et al.*, 2003
Light Attenuation	Williams and McRoy, 1982; Dunton and Tomasko, 1994; Thayer *et al.*,1994; Frankovich and Zieman, 2001; Holmquist *et al.*, 1989	Prager, 1998; Stumpf *et al.*, 1999; Fourqurean *et al.*, 2003
Nutrients	Fourqurean *et al.*, 1992, 2003	Butler *et al.*, 1995; Fourqurean *et al.*, 2003
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	Porter and Muehlstein, 1989; Muehlstein, 1992; Blakesley *et al.*, 1998, 1999a,b
Dense Grass Beds	Durako, 1995; Hall *et al.*, 1999a	Durako, 1994, 1995; Durako *et al.*, 2001
Sediment Characteristics		Carlson *et al.*, 1994
Climate		
Freshwater Inflow		Fourqurean *et al.*, 2003

influence of internal conditions in the ecosystem and external driving factors on plant growth and metabolism. It has also emphasized documentation of the sequence and pattern of seagrass die-off and recovery in Florida Bay (Table 7.2). The principal findings of this work are as follows:

- 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 (greater than 2–4 mmol); self-shading of shoots; nighttime/early morning anoxia/hypoxia in meristems; and increased susceptibility to 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 between 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 difficult.
- 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 colonization by *Halodule* and *Ruppia.* The cause of this loss is unknown. Primary acute die-off (rapidly developing dead patches within dense beds) is known to be currently occurring (initiated in 1999) only 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 robust species communities to develop; low salinity may also provide refugia from disease because *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, discriminant-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.

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* die-off. However, the causative mechanisms responsible for initiating the die-off remain incompletely understood (Robblee *et al.,* 1991; Carlson *et al.,* 1994; Durako, 1994; Durako and Kuss, 1994; Durako *et al.,* 2002)."
>
> —Durako *et al.,* 2002

Changes in plant morphology and metabolism measured in the field provide indicators of response of seagrasses to environmental stressors in advance of die-off. Zieman *et al.* (1999) reported 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 (15-cm diameter) obtained during the springs of 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, 2001). This is very similar to the branch frequency of 0.28 observed during the early die-off from 1989 to 1990 (Durako, 1994). The relationship between rhizome branching in 1998 and shoot density changes from 1998 to 1999 was significant ($P < 0.0001$); however, the r^2 value of 0.12 was low.

Carlson *et al.* (1994) have reported that alcohol dehydrogenase (ADH) increases in *Thalassia* exposed to hypoxic conditions, exacerbating the carbon drain on below-ground tissues. Apical meristem density and branch frequency (rhizome apical density normalized to short-shoot density) may act as "ecoindicators" of the potential for increase or decrease 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 effects of discharges from electrical power plants can result in mortality during the warm summer months, although the productivity of these species may have been enhanced during the winter (Barber and Behrens, 1985). *Thalassia* may show 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 below or above 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); *Syringodium* has maximal growth between 23°C and 29°C, whereas for *Thalassia* maximal growth occurs between 23°C and 31°C (Zimmerman and Livingstone, 1976). In shallow bays with widely fluctuating temperatures, *Thalassia, Syringodium,* and *Halodule* have narrower leaf widths, suggesting increased stress (McMillan, 1978). *Ruppia* has a wide tolerance to temperatures (7°–35°C) and has 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 a low biomass of submerged plants (Montague and Ley, 1993). Mesocosm studies (Chesnes *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 die-off still remains unclear. Salinities during the initial die-off episodes in 1987–1989 were accompanied by hypersalinities ranging from 45 psu to 70 psu. The Barnes Key die-off clearly did not correlate with this level of salinity but showed many of the other stresses that accompanied the primary die-off. Although the role of hypersalinity may vary relative to other stresses, low salinity provides refugia from *Labyrinthula,* because infection by that organism does not occur at <15 psu (Blakesley *et al.,* 1999b).

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.* (2001) have continuously measured subsurface and bottom photosynthetically active radiation (PAR) at seven stations in Florida Bay since the fall of 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 measurements have been collected monthly. Diffuse attenuation coefficients vary seasonally and between basins within Florida Bay: attenuation is higher in winter than in summer and is generally higher in the basins that 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 (greater than 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 red algae being more dominant in western high-flow areas of the bay (Frankovich and Fourqurean, 1997). Fleshy epiphytes have restricted distributions, occurring only near bird islands and near the Keys. The cyanobacterium *Lyngbya* is very common in the *Syringodium filiforme* beds in the west (Frankovich and Zieman, 2001). 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 (greater than 40%) than in the western region (ca. 20%). Calcium carbonate derived from calcareous algae and resuspended sediment composes 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, 2001). 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 than 5% of bay-wide averages (Frankovich and Zieman, 2001). Highest epiphyte loads are in areas of highest seagrass productivity, so epiphytes are not reducing production (Frankovich and Zieman, 2001).

Grazers may have an important role in controlling epiphyte abundance. Snails (50/m^2) and hermit crabs are

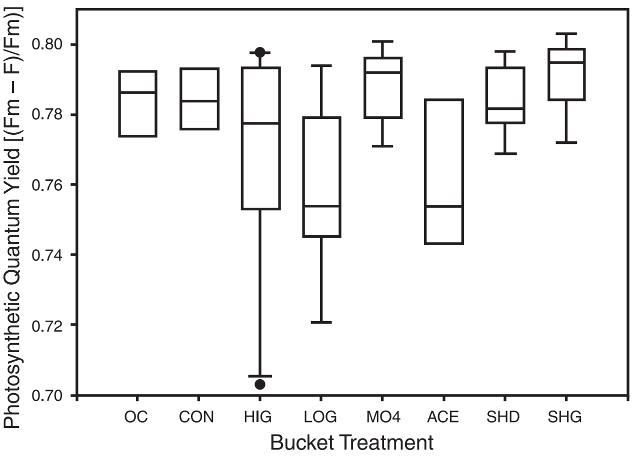

Figure 7.5 *Photosynthetic quantum yields of* Thalassia *in Carlson buckets exposed to high glucose (HIG), low glucose (LOG), molybdate (MO4), acetate (ACE), shaded (SHD), and shaded with glucose (SHG) relative to controls inside (CON) and outside (OC) plots.*

conspicuous at Rabbit Key Basin (Frankovich and Fourqurean, 1997). In Florida Bay, *Bittium* occurs at densities of about 3/m^2, whereas in the Indian River Lagoon, *Bittium* occurs at densities of 20/*Halodule* short-shoot or at 1000s/m^2 .

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 data are in the FHAP dataset). Jeff Holmquist found that *Laurencia* accumulation did not kill underlying *Thalassia.*

Nutrients

Worldwide, many estuaries have undergone loss of seagrasses as a result of eutrophication. 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 usually follow rather than cause seagrass die-offs. As stated above, epiphyte loads on seagrasses are relatively low in Florida Bay and do not seem to be reducing production.

Sulfide

Carlson *et al.* (1994) and Erskine and Koch (2000) have explored the potential links between elevated sediment-sulfide concentrations and seagrass mortality (a hypothesis long proposed to account for seagrass die-off). 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 greater than 2–4 mmol 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 less than 2 mmol, no die-off has been observed. However, photosynthetic rates in *Thalassia* increase as a function of increasing sulfide up to 6 mmol, and sulfide levels up to 10 mmol 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 us understand how sulfide concentrations may influence seagrass growth and abundance and to 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), although both treatments should have increased sediment sulfide levels.

Labyrinthula *Infection*

A theoretical model for die-off as a disease (Blakesley *et al.*, 1999a) has suggested three different roles that *Labyrinthula* might play in Florida Bay under different environmental conditions. These roles include (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 less than 15 psu). 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 (Muehlstein *et al.*, 1988). Environmental stressors (abiotic factors), such as low light or high temperatures, may weaken *Thalassia* and, in combination with the infection by pathogenic *Labyrinthula,* may 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.

Blakesley *et al.*'s (1999a) 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 by acting as an opportunistic secondary pathogen.

Under the same conditions but without environmental stress, Blakesley *et al.* (1999b) suggested that *Labyrinthula,* acting as a primary pathogen, could still cause"thinning"or patchy die-off. *Labyrinthula* occurrence was found to have significant adverse influences on branching frequency (*P* = 0.03), shoot density (*P* = 0.004), and apical density (*P* = 0.033) (Paxson and Durako, 2001), suggesting that this microorganism may have an adverse influence on seagrass growth and carbon balance (*sensu* Durako and Kuss, 1994).

The occurrence of *Labyrinthula* has also been shown to affect photosynthetic characteristics of *Thalassia* (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 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 by using a Diving-PAM were significantly lower in regions of *Thalassia* leaves that had visible lesions. These patterns agree with those previously reported by Durako and Kuss (1994). However, close-interval Diving-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 only 1 m inside the bed. This indicates that photosynthesis may be reduced even in the absence of visible lesions. The Diving-PAM data also revealed 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 the lethal threshold is for lesion coverage.

Sediment Characteristics

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

Seagrass die-off has been observed only in biogenic carbonate sediments, which are usually low in iron. However, Florida Bay carbonate sediments have relatively high iron levels (Carlson *et al.,* 1994). Spatially, iron levels are high near the mainland and toward the west. The role of atmospheric deposition of iron to Florida Bay remains poorly understood. Addition of iron to sediments decreases the flux of sulfide to *Thalassia* (Carlson bucket experiments) and results in a small but significant 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.,* 2001 [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."
>
> —Fourqurean *et al.,* 2002

Correlation with Patterns of Water Quality

Fourqurean *et al.* (2003) developed a discriminant function model that uses seagrass species occurrence and abundance data from 677 locations and water-quality data from 28 monitoring stations in Florida Bay. This model predicted that the distribution of benthic habitat types in Florida Bay would likely change if water quality was affected by changes in water delivery to the bay. Specifically, an increase in seasonal delivery of fresh water 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 Die-Off

The production of distribution and abundance maps of the seagrasses has proven valuable, and these maps provide a quantitative record of distribution and abundance at both basin and bay scales. The changes between maps provide clear visualization of where and how much the distribution and abundance changes and

Table 7.3 *Characteristics of seagrass die-off 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 µmol). Levels vary in different zones, but highest values are 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 (= 1,600 µmol) in bare, sparse, and dense seagrass zones.

can thus point to "hot spots" that may be related to specific forcing events or conditions. The use of seagrass cover has become an assessment standard in the region (FKNMS, DERM, FHAP). Cover may be a more sensitive performance measure to short-term changes than density because density changes require mortality and recruitment of short-shoots, whereas cover can also vary in response to changes in the leafiness of short-shoots. Short-shoot density may be a better longer-term performance measure and 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 (greater than 15 psu) and dense *Thalassia* beds—necessary elements for *Labyrinthula* infection and transmission. However, the data from the two sites revealed important differences that are summarized in Table 7.3.

These differences strongly suggest that the mechanisms for the die-offs in Barnes Key and Sunset Cove are not the same. Blakesley *et al.* (1999b) proposed that the acute die-off in Barnes Key resulted from a series of events beginning with heat stress and an initial infection or disease (not *Labyrinthula*-induced) that rapidly kills the infected seagrass. The resultant large amount of decaying belowground 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 appears to be directly caused by *Labyrinthula* acting as a primary pathogen. Sediment-sulfide levels may remain relatively low in all the vegetative zones tested simply because the slow death of *Thalassia* roots and rhizomes results in a smaller decaying belowground biomass. As a result, the sediment-sulfide levels may remain lower in the vegetative zones than in contrast to the Barnes Key. 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 that the short-shoot meristems of *Thalassia* at the Barnes Key die-off site became anoxic during the night in November and remained anoxic for up to five hours (Borum *et al.,* 2001). In contrast, leaf meristems at Rabbit Key Basin did not become 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 did samples from Rabbit Key Basin. *Thalassia* at Barnes Key is very dense, with over 1,200–1,500 short-shoots/m^2, a very high biomass (SC 300 g/m^2), low turnover rate of grass blades (1.2%/day), and very thick litter layer. In Rabbit Key Basin, densities are also high (1,200–1,300 short-shoots/m^2), but biomass (SC 109 g/m^2) and turnover rates (1.7%/day) are more moderate (Zieman *et al.,* 1999). 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 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.,* 2001), and this area has been recolonized by *Halodule* and *Ruppia.* This new seagrass die-off led to a plan for a series of observations and experiments to test several of the hypotheses that might explain seagrass die-off.

Modeling Change in Benthic Communities

Statistical modeling was commissioned by the Central and Southern Florida Comprehensive Review Study (Restudy) of the U.S. Corps of Engineers consistent with recommendations from the 1998 Seagrass Modeling Workshop (Fourqurean *et al.,* 2003). 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. This statistical model will not address mechanisms or degree of change in water quality that result from Restudy scenarios; other models (such as 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.,* 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. However, because the statistical relationships will be based on data from a larger number of marine areas and 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 and colleagues are developing a hierarchical approach to modeling the interaction between plant and physical processes in Florida Bay that involves two distinct spatial scales—the demographic unit (ca. 10 m^2) and the landscape unit (ca. km^2). 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 the landscape unit. This approach provides a hierarchical framework in which 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 and inputs of dead organic matter) are described statistically for the demographic units and used to define the biological environment for each landscape unit. In this manner, the heirarchical framework functions as a dynamic, interactive GIS in which each parameter and process is described and simulated at the appropriate temporal and spatial scales.

Current Research

Field Assessment

- FHAP is continuing spring and fall sampling and has incorporated (since spring 2001) measurements of photosynthetic characteristics of *Thalassia* using Diving-PAM-fluorometry at each station in addition to the Braun-Blanquet and standing-crop measurements.
- FWRI (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" being conducted by Koch and Durako. The results of this study are intended to help determine the parameters for the unit model with data from Florida Bay seagrasses.
- FWRI (Carlson) bucket experiments have been conducted to examine effects of multiple stressors (sulfide, nitrogen, and light) on seagrasses *in situ*.

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Chapter 8

Higher-Trophic-Level Species

Lead Author Joan A. Browder
Contributors Cynthia Yeung, Thomas Schmidt, Mark J. Butler, IV, Maria Criales, Allyn Powell,
Don DeAngelis, David Evans, Larry Settle, Bill Sharp, Craig Faunce, Jerald Ault, Anne Marie Eklund,
G. Lynn Wingard, Gordon Thayer, Darlene Johnson, David Rumbold, Jeffrey Chanton, C. Chasar,
Jerome Lorenz, Ed Matheson, James Colvocoresses, Michael Robblee, Laura Engleby,
Chris Koenig, Samantha Whitcraft

Introduction

Question 5*—What is the relationship between environmental and habitat change and the recruitment, growth, and survivorship of animals in Florida Bay?*

In the context of the Florida Bay Science Program, higher-trophic-level species (HTLS) include zooplankton; benthic invertebrates such as sponges, mollusks, crustaceans (particularly decapods); fishes; marine mammals; marine reptiles; and water birds. Scientific input about HTLS in the bay is critical to the successful restoration of Florida Bay and associated coastal ecosystems because HTLS are both ecologically and economically important and are viewed as important by the public. Performance measures based on HTLS are essential to protecting and restoring Florida Bay in the Comprehensive Everglades Restoration Plan (CERP) implementation process.

HTLS integrate the condition of the ecosystem and reflect it in their responses to environmental change. Question 5 investigates how HTLS respond to changes in the characteristics of the ecosystem, such as benthic communities, water quality, and circulation, and exchange with adjacent ecosystems and the effect of human activities on these characteristics. Question 5 also investigates how HTLS are affected by fishing. Some HTLS play a critical role in regulating ecosystem functions, so changes due to fishing or other causes, anthropogenic or natural, can have repercussions on the entire Florida Bay ecosystem.

The higher-trophic-levels component of the Florida Bay Science Program has approached Question 5 by addressing the following questions:

- How do human activities (*e.g.,* water management, fishing) and major natural factors influence biological processes affecting growth, survival, and recruitment of fishery species, protected species, and keystone species in Florida Bay?
- How do HTLS community composition and trophic structure vary in time and space, what factors are responsible, and what processes are affected by the variation?
- What major processes influence transport of presettlement stages of fish and invertebrates to and into Florida Bay, what is their schedule, what parts of the bay are most affected, and what is their importance to recruitment to fisheries inside and outside of the bay?
- What animals affect major ecological processes in the bay, such as primary productivity and nutrient cycling, and what is the magnitude of this role?

Substantial progress has been made on these topics but much remains to be done. This chapter synthesizes recent results, examines historical information relevant to the central question, and identifies needed future work.

Description of Higher-Trophic-Level Species in Florida Bay

The HTLS component of the Florida Bay Science Program encompasses all the animals of the system. Recent work on higher trophic levels in Florida Bay builds on prior research in coastal waters of Everglades National Park (ENP) before or in the 1950s and 1960s, summarized by Tilmant (1989) and Tabb and Roessler (1989); in the 1970s by Schmidt (1979); and in the 1980s by Thayer and Chester (1989), Powell *et al.* (1989), Sogard *et al.* (1989), Holmquist *et al.* (1989), Robblee *et al.* (1991), and Ley *et al.* (1994). More than 250 fish species are known to occur in Everglades National Park coastal waters (Loftus, 2000), although Schmidt (1979) found only 128 fish species in Florida Bay. Tabb (1966) concluded that individuals of most species left ENP waters for unknown seaward spawning areas when they reached sexual maturity.

A synthesis of past research for the March 1998

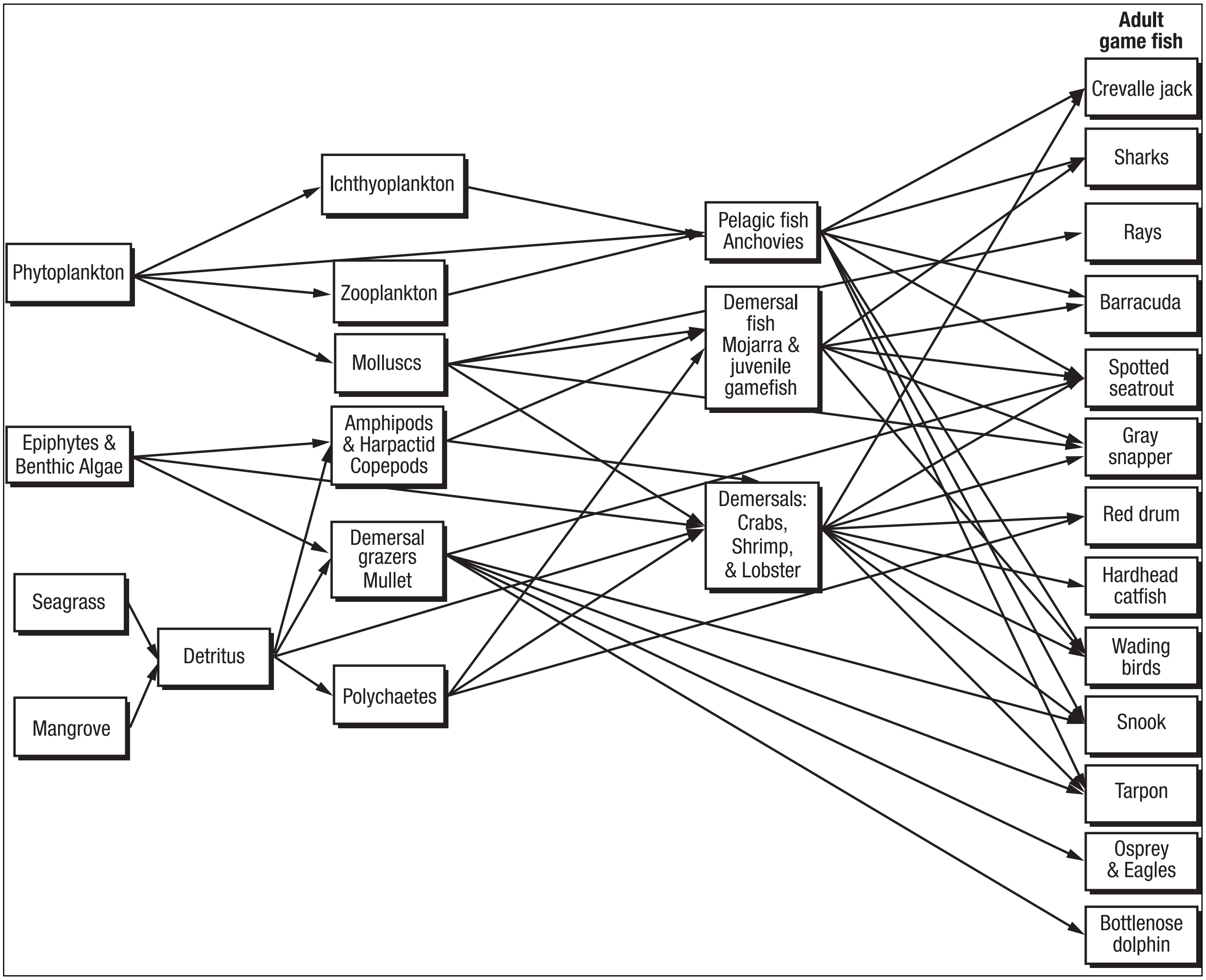

Figure 8.1 *Trophic levels in Florida Bay.*

HTLS Group Report (Browder *et al.,* 1998) organized the animals of the bay into a generalized food web (Figure 8.1). The primary producers at the food-web base include phytoplankton, epiphytes, benthic algae, seagrass, and mangroves. The Florida Bay fauna is made up of herbivores, detritivores, planktivores, and piscivores at three or four trophic levels. Within the bay, the food web has two major branches: pelagic (water-column) and benthic (on or near the bottom), which may converge at the highest trophic levels. Most of the following information is summarized from Browder *et al.* (1998), but new information has been added as cited.

In the pelagic branch of the food web, filter-feeding planktonic stages of fishes, crustaceans, mollusks, and other taxa feed on phytoplankton (*e.g.,* diatoms, dinoflagellates) in the water column and are preyed upon by small, schooling pelagic fish such as bay anchovies and hardhead silversides. The benthic branch includes filter feeders (*e.g.,* sponges, bivalve mollusks, ascidians, polychaetes) and demersal grazers or detritivores, such as amphipods, harpacticoid copepods, polychaetes, striped mullet, and post-settlement stages of mollusks and other invertebrates. The next level of benthic consumers includes a host of small demersal fish and macroinvertebrates that feed on small invertebrates. Dominant members of this group include gulf toadfish, goldspotted killifish, rainwater killifish, dwarf seahorse, dusky pipefish, gulf pipefish, spotfin mojarra, silver jenny, white grunt, pigfish, pinfish, and silver perch (Thayer *et al.,* 1999). Pink shrimp and many taxa of small caridean and penaeoidean shrimp also are numerically abundant in the bay (Holmquist *et al.,* 1989; Robblee, personal communication). Juvenile spiny lobsters are abundant in the southwestern portion of the bay south of major mud bank barriers (Field and Butler, 1994; Herrnkind *et al.,* 1997). The limited research in the bay and nearby areas suggests that the demersal fish in the bay are generalists that eat a variety of benthic invertebrates (Zieman, 1981; Schmidt, 1993a; Ley *et al.,* 1994).

Florida Bay supports several highly sought-after game fish, including red drum, spotted seatrout, gray snapper, snook, tarpon, and bonefish (Schmidt *et al.,* 2001, 2002). Sharks are commonly seen during aerial surveys (S. Bass, personal communication) and include nurse sharks, bonnethead sharks, and lemon sharks. Rays (*e.g.,* sting rays and manta rays) are commonly seen on aerial surveys. Small fish and macroinvertebrates are the prey of these larger fish. Within the Florida Bay area, gray snapper and red drum principally eat shrimp and crabs, whereas barracuda, seatrout, and snook eat more fish than crustaceans (Marshall, 1954; Croker, 1960; Yokel, 1966; Fore and Schmidt, 1973; Rutherford *et al.,* 1983; Schmidt, 1986, 1989; Harrigan *et al.,* 1989; Hettler, 1989). Of the abundant forage fish, those that appear to be important in the diet of some piscivorous fishes are gulf toad fish (lemon sharks, red drum, and bonefish), pinfish (lemon sharks and snook), hardhead silversides (snook), goldspotted killifish (barracuda), and rainwater killifish (barracuda and spotted seatrout) (Schmidt, 1986, 1989; Crabtree *et al.,* 1998; Koenig *et al.,* 2001). In southern Florida Bay, juvenile lobsters constitute a large fraction of the diets of a variety of fish: nurse sharks, bonnethead sharks, southern stingrays, bonefish, permit, and gulf toadfish (Smith and Herrnkind, 1992). Small mollusks are abundant in Florida Bay and are probably fed on by rays and fish such as sheepshead. The pink shrimp, *Farfantepenaeus duorarum,* is a key component of trophic webs. This species is an important prey of game fish (Croker, 1960; Stewart, 1961, Yokel, 1966; Rutherford *et al.,* 1983; Schmidt, 1986, 1989; Hettler, 1989) and wading birds (Palmer, 1962), linking them to small grazers and detritivores supported by algae and seagrass and mangrove detritus (Fry *et al.,* 1999). The abundant small caridean shrimps in Florida Bay are the principal prey of juvenile pink shrimp (Schwamborn and Criales, 2000).

The many piscivorous water birds that live in the bay seasonally or year-round eat small fish and macroinvertebrates such as crabs and shrimps, although this is poorly documented. Piscivorous birds in the bay include double-crested cormorants, brown pelicans, red-breasted mergansers, laughing gulls, ring-billed gulls, royal terns, many wading bird species, and bald eagles and ospreys. The most abundant wading bird species in the bay seasonally are white ibis and great egrets (Browder and Bass, unpublished data). The bay is a major habitat for the great white heron, roseate spoonbill, and reddish egret. All of these species feed in Florida Bay proper or in shallow ponds on the bay's islands.

The bottlenose dolphin is another high-level predator in Florida Bay and, based on studies elsewhere in south Florida, probably feeds on fish at several trophic levels. The American crocodiles that occur in the northern bay and the American alligators that penetrate the northern bay during wet years are also predators on the bay's small-fish populations.

Two large grazing animals, the West Indian manatee and the adult green sea turtle, may have once been more abundant in Florida Bay than they are today. They also may have influenced the structure and productivity of seagrasses as a result of their grazing. A review by Thayer *et al.* (1984) described the dietary importance of seagrass to various herbivores and the influence of herbivory on seagrass systems. Green turtles once were the primary consumers of seagrasses in the Caribbean, but they are now few in number everywhere. In a major feeding area in Nicaragua, *Thalassia testudinum* made up 87% of the diet of green sea turtles, and other seagrasses (*Syringodium filiforme* and *Halodule wrightii*) made up another 5%. Grazing by green sea turtles may have profound influences on the seagrass community that are different from the effects of grazing by other herbivores. Green sea turtles may feed on *Thalassia* preferentially. They are known to maintain discrete grazing plots in a *Thalassia* bed and feed repeatedly on the new growth in these plots until food quality deteriorates. It is possible that the presence of grazing sea turtles might prevent the type of high-biomass *Thalassia* monoculture that preceded the seagrass die-off in Florida Bay of the late 1980s. The possible impact of loss of sea turtles on Florida Bay was discussed by Jackson *et al.* (2001). Grazing by manatees may have a more disruptive effect than that by turtles because the rhizophore is disturbed and might jeopardize recovery (Thayer *et al.,* 1984). The density of large herbivores in Florida Bay today may be too low for them to have much influence on the present ecosystem.

Seagrass is the main diet of the caridean seagrass shrimp (Schwamborn and Criales, 2000). Seagrass is also important in the diet of sea urchins and has been reported to be in the diets of some fishes (Thayer *et al.,* 1984). Even where grazing animals are more abundant, it is likely that more energy travels from seagrass to consumers through the detrital than the grazing food web. In Florida Bay today, only the detrital food web is significant.

A conceptual model developed to help guide Florida Bay HTLS research is shown in Figure 8.2. The

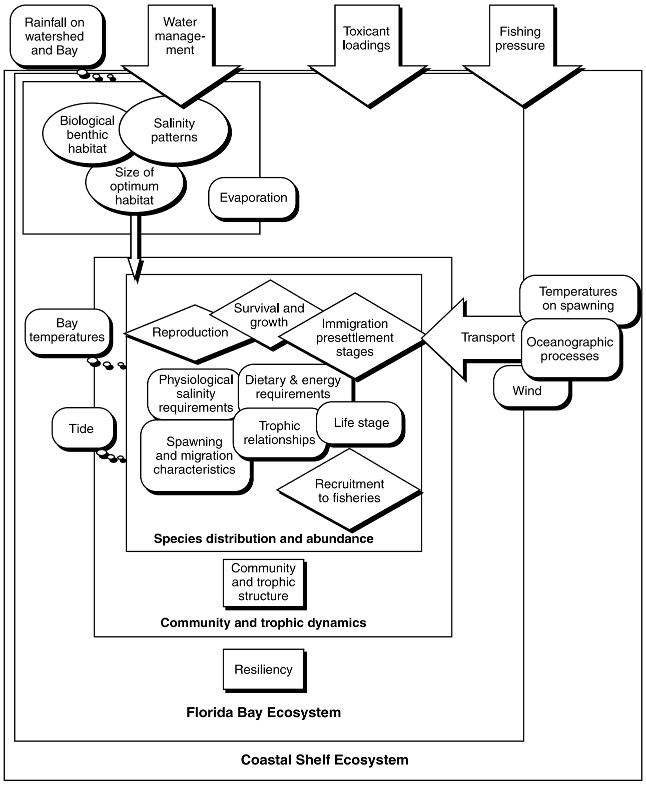

Figure 8.2 *Conceptual model of factors affecting higher-trophic-level species in Florida Bay.*

model incorporates the following major concepts:

- Critical ecosystem characteristics (*i.e.*, salinity, water quality, and biological benthic habitat) directly influence HTLS at the individual species level. Species- and community-level response represents the aggregate influence of these characteristics integrated over HTLS populations;
- Changes in HTLS at the species and community level occur as the result of driving processes acting on Florida Bay as a whole. These processes influence HTLS by their effect on critical ecosystem characteristics and by controlling the movement of HTLS into and out of Florida Bay;
- At the shelf scale, potentially influencing factors include temperatures on spawning grounds, larval transport processes, and fishing;
- The scope of research on HTLS of Florida Bay must include within-bay, cross-boundary, and greater coastal ecosystem processes, and these processes should be examined at time scales from seasons to decades;
- Higher-trophic-level processes and patterns potentially affected by water management occur at the population, community/trophic, and ecosystem level;
- HTLS responses to water management are expected to occur through water management effects on salinity, the area of co-occurrence of biologically favorable salinity and habitat, the condition of biological habitat (*e.g.*, seagrass, sponge, coral), animal movements, and loading of nutrients or toxicants;
- Intrinsic factors potentially influencing responses to water management include physiological salinity requirements, dietary and energy requirements, and trophic relationships, all of which may differ by species, life stage, and spawning and migration characteristics;
- At the bay scale, other factors with the potential to influence HTLS include salinity-temperature interactions, toxicant concentrations in freshwater inflow, and fishing.

Processes Driving Change in the Ecosystem

Preceding chapters describe some major ecosystem characteristics that influence higher-trophic-level-species in Florida Bay: salinity, water quality, and benthic habitat. All are subject to change, and an understanding of how they might change is being developed in other parts of the Florida Bay program. Determining how their change might affect these species is being determined by HTLS research. Relationships between processes driving change, ecosystem characteristics, and characteristic species and communities of Florida Bay are highly relevant to the CERP, which will influence the change-driving processes. Defining and quantifying these relationships is crucial to preparing performance measures to restore or protect Florida Bay. Augmenting the descriptions of ecosystem characteristics in the preceding chapters are studies on mercury. These studies are defining previously unknown spatial patterns of mercury and methylmercury concentrations in Florida Bay waters, sediments, and biota.

The quest for answers to Question 5 must extend beyond Florida Bay to include the greater ecosystem that supports the movements of species into and out of the bay and the processes that affect these movements. Animal movements, as well as the flow of water, connect Florida Bay not only to the upstream Everglades and coastal mangrove areas but also to the Florida Keys, the reef tract, the southwestern Florida shelf, and the Dry Tortugas. Many higher-trophic-level species range between the bay and the coastal reefs during their life cycle. The processes driving change in the Florida Bay ecosystem extend beyond the bay both upstream and downstream.

The principal anthropogenic processes potentially driving change in the Florida Bay ecosystem are water management, contaminant and nutrient inputs, causeway and bridge construction in the Florida Keys, and fishing. Climatic variation and oceanographic processes are other instruments of change in the Florida Bay ecosystem and may cause year-to-year and long-term variation.

WATER MANAGEMENT

By affecting freshwater inflow to Florida Bay, water management can affect Florida Bay's HTLS through the effects of freshwater inflow on salinity patterns, nutrients, organic detritus, and contaminant loads. Salinity directly affects physiological processes that determine growth, survival, and reproductive rates of many higher-trophic-level-species. The area in which a favorable salinity range overlaps with other favorable conditions (*i.e.,* shoreline, depth, or bottom habitat) in areas accessible to appropriate life stages determines the productive capacity of the bay for a given species. Salinity gradients may provide orientation cues that promote the successful immigration into the bay of postlarvae spawned offshore that use the bay as a nursery ground. Nutrients and organic detritus may have positive or negative effects depending on concentration. In excess, they degrade habitat (via reduced water clarity, low dissolved oxygen, etc.).

Effects of water management on salinity patterns, nutrients, and contaminant loads are being studied in other parts of the Florida Bay science program. A major emphasis of the HTLS science plan is determining the possible effect of changes in salinity on animal species and communities. Water management may affect higher-trophic-level organisms through effects on important living benthic habitat such as seagrass and sponges (*e.g.,* through salinity, nutrient, turbidity, or other effects on the organisms that form living benthic habitat), and these potential effects are also being evaluated through studies of relationships of HTLS to living benthic habitat.

FISHING

Many coastal fisheries in south Florida have ecological connections to Florida Bay. Especially notable of these are the commercial fishery for pink shrimp and the commercial and recreational fisheries for gray snapper and spiny lobster. These species and others (sparids, grunts, other snapper, and even groupers) found on the Florida Keys reef tract and in the waters near the Dry Tortugas spend part of their life cycle in Florida Bay. Reef waters near Marathon in the middle Keys are an important spawning ground for gray snapper (Rutherford, 1989). Shelf waters near the Dry Tortugas islands are the most important commercial fishing grounds for pink shrimp in Florida, and Florida Bay is the major pink shrimp nursery ground. Florida Bay also contains important spiny lobster nursery habitat, and Everglades National Park is a fishing-free sanctuary for spiny lobster. Nearby areas and parts of Florida Bay outside of ENP support recreational and commercial fishing for Spanish mackerel, spiny lobster, and other species.

Recreational fishing is an expanding sport in the Florida Keys, the Tortugas waters, and Florida Bay, both within and outside ENP boundaries. The number of fishing trips in ENP in 2001 was the highest ever reported (Schmidt *et al.,* 2002). ENP began phasing out commercial fishing in the bay in the early 1980s, when analyses of recreational and commercial fishery data suggested that overfishing might be occurring. Since then, recreational fishing regulations have been strengthened. Later analyses have suggested that environmental factors affect abundance (Tilmant *et al.,* 1989; Schmidt *et al.,* 2002). The ratio of kept fish to total fish caught changed dramatically from the 1980s to the 1990s. This may be an artifact of regulatory changes (legal size limits, bag limits, seasonal closures); however, it may be indicative of an increased catch of sizes that were too small to keep (*i.e.,* below legal size limits). This issue will be addressed in current and future analyses of size-frequency distributions in the creel census data by ENP and the Fish and Wildlife Research Institute.

The growing demand for fish and the popularity of fishing have increased the pressure on fishery populations in south Florida. Fishing pressure is especially reflected in declining size and density of snappers and groupers and changes in the trophic structure of fish assemblages on reefs (Ault *et al.,* 1998). These changes are apparent even in the Tortugas area and are consistent with similar changes previously detected in the Florida Keys (Ault *et al.,* 1998; Bohnsack *et al.,* 1999; Schmidt *et al.,* 1999). The observed decline in fish abundance may be due to loss of coral habitat. For example, the total area of Caribbean reef-building corals *Acropora palmata* and *Acropora cervicornis* has declined by 93% and 98% respectively since 1983 (Miller *et al.,* 2002).

OCEANOGRAPHIC PROCESSES

The Loop Current and Florida Current and their countercurrents, the Tortugas Gyre, and coastal eddies are oceanographic features that may influence the migration of postlarvae to Florida Bay and to the Florida Keys reef tract from offshore spawning areas. These processes may affect the timing of abundance peaks and year-class strength in fish and macroinvertebrate populations in the bay and on the reef tract.

The Florida Keys reef tract extends almost without interruption along the entirety of the Florida Keys and is the core component of the Florida Keys National Marine Sanctuary. Florida Bay is connected to the reef tract through interisland channels. Regional-scale and local-scale oceanic processes that affect the reef tract likely also affect Florida Bay. Reef tract populations are replenished not only by their spawning locally but also by their spawning upstream of the reef tract. The upstream distance of sites contributing larvae is principally determined by current velocity and larval development rate, which ranges from 2 weeks in some invertebrates and fish to up to 12 months in spiny lobster. Recruitment of some species to the Florida Keys reef tract from as far away as the western Caribbean has been postulated. The argument for multiple upstream larval sources for the Florida spiny lobster population is especially strong, given the wide geographic range of the species and its extraordinarily long planktonic larval life (Lyons, 1980; Yeung *et al.,* 2000; Yeung and Lee, 2002), and is supported by mtDNA analysis (Silberman *et al.,* 1994).

Having more local sources of larvae may be important to most populations. The lower southwest Florida shelf in the vicinity of the Dry Tortugas is one potential source of recruitment to the Florida Keys reef tract and Florida Bay. The islands of the Dry Tortugas and their surrounding shallow waters lie roughly 150 km (70 miles) west of Key West and are known for remoteness and relatively unspoiled marine richness (Ault *et al.,* 2002b; Franklin *et al.,* 2003). The coastal shelf in the vicinity of the Dry Tortugas is the major spawning ground for pink shrimp in Florida. Recent research is discovering luxuriant, previously unknown and unmapped coral reefs near the Dry Tortugas and near the Marquesas, which lie between the Dry Tortugas and Key West (Miller *et al.,* 2001).

CAUSEWAY/BRIDGE CONSTRUCTION

The flow connecting Florida Bay to the Atlantic Ocean through Lignum Vitae, Indian Key, and Teatable Key channels was reduced by the construction of the Flagler railroad, which became the Overseas Highway. This construction, which occurred in the early 1900s, partially blocked tidal passages and affected bay circulation and associated water quality (Healy, 1996). By affecting transport between the bay and the Gulf of Mexico and Atlantic Ocean, the construction areas may also have affected the immigration of postlarvae and early juveniles into Florida Bay. The U.S. Corps of Engineers is leading a study to determine whether Keys passes should be enlarged to restore the health of Florida Bay. The Corps is planning a pilot study of the effect of enlarging passes that have been restricted by the highway. The pilot study will be performed in passes located between Fat Deer (Marathon) and Grassy keys.

Research Approaches

A major focus of Florida Bay HTLS research has been to characterize the responses of species and species groups to environmental and habitat conditions that vary in space and time. The topic has been approached via modeling, statistical analyses, experiments, and field measurements. Modeling, supported by laboratory experiments, was used to characterize the response of individual organisms and was applied to pink shrimp, spiny lobster, sponges, and spotted seatrout to examine functional responses to salinity and temperature and their consequences for populations. Separately, statistical analyses of historical resource survey data were used to characterize the response of 11 forage species and 9 fishery species to environmental variables at the population and community level. Field studies were conducted to characterize the spatial and temporal patterns of immigration of early life stages into Florida Bay from offshore spawning grounds and the density of juveniles on Florida Bay nursery grounds. Most work has included an examination of the possible effects of salinity because salinity is likely to be affected by inland water management.

A more recent focus of Florida Bay HTLS research has been to examine the effect of HTLS on critical ecosystem characteristics, such as water quality and benthic habitat, that determine habitat quality and define distinct communities. In this regard, sponges are a major interest because of the recent decline in sponge biomass in the bay. Sponges are capable of regulating water clarity through their filter feeding, and the volume of water filtered is largely determined by sponge biomass density, which has declined substantially in recent years.

Field sampling and comparative analysis of data from fished and unfished areas provided information on the effect of fishing on individual species and species composition.

Comparative studies provided evidence that fishing in ENP affects size distribution within species (gray snapper) and the species composition of communities. Underwater visual resource surveys on the reef tract and near the Dry Tortugas have found signs of overfishing of fish species that occur both on the reef tract and in Florida Bay.

One approach to examining the effect of water management on HTLS has been through statistical analyses relating fishery catch or catch per unit effort to indices of freshwater inflow to Florida Bay and nearby southwestern Florida coastal waters. Another approach, already mentioned above, has been to examine the effect of salinity on processes that affect the abundance of these species.

Table 8.1 *Research topics defined by Question 5 (cells in the matrix) and key references to the associated research.*

Research Topic	Population Level—Species Abundance and Community	Individual Level—Growth and Survival
General Characteristics	Read *et al.,* 2001; Limouzy-Paris *et al.,* 1997; Costello *et al.,* 1986; Robblee *et al.,* 1991; Thayer and Chester, 1989; Powell *et al.,* 1989; Chester and Thayer, 1990; Thayer *et al.,* 1999; Powell, 2002, 2003; Powell *et al.,* 2004; Schwamborn and Criales, 2000; Stevely and Sweat, 2001	Settle *et al.,* 2001; Powell *et al.,* 2004
Salinity Pattern	Schmidt *et al.,* 2001; Browder *et al.,* 1999, 2002; Brewster-Wingard *et al.,* 2001; Camp *et al.,* 2001; Matheson *et al.,* 2001; Field and Butler, 1994; Lorenz, 2001a	Browder *et al.,* 1999, 2001b, 2002; Butler *et al.,* 2001a; Butler, 1999, 2003; Field and Butler, 1994; Wuenschel, 2001; Richards and DeAngelis, 2001
Water Quality	*Water quality effect on HTLS:* (No results reported) *HTLS effect on water quality:* Stevely and Sweat, 2001; Peterson and Fourqurean, 2001	*Water quality effects on contaminants and humans, piscivorous birds, mammals, and reptiles:* Evans and Crumley, 2000; Sepulveda *et al.,* 1998; *Effects on invertebrates:* Scott *et al.,* 2002
Biological Benthic Habitat	*Habitat effect on HTLS:* Dennis and Sulak, 2001; Robblee *et al.,* 2001; Matheson *et al.,* 2001; Powell *et al.,* 2001a,b; Ortner *et al.,* 2001; Robblee *et al.,* 2001; Chanton *et al.,* 2001; Herrnkind and Butler, 1994; Field and Butler, 1994; Butler *et al.,* 1995; Butler, 2003; Koenig *et al.,* 2001 *HTLS effect on habitat:* Rose *et al.,* 1999; Peterson and Fourqurean, 2001	*Habitat effect on HTLS:* Butler *et al.,* 1995; Butler, 2003
Coastal Transport (Larval) Process	Field and Butler, 1994; Yeung *et al.,* 2001; Yeung and Lee, 2002; Jones *et al.,* 2001; Browder *et al.,* 2001a, 2002; Butler *et al.,* 2001b; Criales *et al.,* 2003	Settle *et al.,* 2001; Yeung and Lee, 2002; Acosta and Butler, 1997; Criales and Lee, 1995; Criales and McGowan, 1993, 1994; Jones *et al.,* 2001; Jones *et al.,* 1970; Tabb *et al.,* 1962; Roessler *et al.,* 1969; Smith, 2000; Butler *et al.,* 2001
Water Management and Hydrology	Browder, 1985; Sheridan, 1996 Browder, 2000; Johnson *et al.,* 2002a	Lorenz, 2001a, 2001b
Fishing	Faunce *et al.,* 2002; Bohnsack *et al.,* 2001; Schmidt *et al.,* 2001	

Summary of Recent Results

The following summary of recent results, presented as bullets, is organized under specific research questions (subsets of the four topic questions identified above) to provide an overview of progress. Table 8.1 organizes research activities into specific topics, and these topics provide a general framework for a series of sections synthesizing recent results and conclusions, by specific research topic.

Does salinity affect survival and growth, do salinity patterns affect faunal abundance and distributions, and will changes in salinity patterns affect the bay's nursery function?

- Five species of sponges found in Florida Bay expe-

rience high mortality rates at low salinity. None survived at 15 practical salinity units (psu) (laboratory experiments).
- Pink shrimp from Florida Bay are more sensitive to low salinity than to high salinity. The salinity of maximum physiological survival varies with temperature. Pink shrimp are more tolerant of high salinity at high temperature and low salinity at low temperature. Acclimation improves survival at high salinity (55 psu) but not at low salinity (5–10 psu). Growth of pink shrimp is optimal at a salinity of 30 psu (laboratory).
- A salinity optimum of 35 psu has been reported for postlarval Caribbean spiny lobster. The extreme salinities that sometimes occur in portions of Florida Bay are lethal to lobster postlarvae (laboratory).
- Larval and juvenile spottedseatrout survival and growth are low at salinities over 45 psu (laboratory).
- Temperature and salinity have an interactive effect on the metabolic rate of young spotted seatrout. Their metabolic rate in relation to size is biphasic and changes isometrically with body mass in early stages, approximating an exponential relationship near unity, but changes isometrically thereafter (laboratory).
- Spotted seatrout catch rates in the recreational fishery are negatively related to indices of freshwater inputs to Florida Bay (analyses of creel census data).
- Western Florida Bay is a major nursery ground for spotted seatrout (field study). The high density of planktonic postlarvae suggests that central Florida Bay may also be a major nursery ground when conditions allow. Salinities greater than 45 psu have frequently occurred in central Florida Bay in the past, which may limit this area's nursery value.
- Pink shrimp recruitment from Florida Bay could differ between years, seasons, and regions of the bay due solely to observed salinity and temperature variation (simulation model).
- Observed salinities during a wet and a dry year caused a predicted decline in lobster recruitment of approximately 25% in the area of Florida Bay directly affected by salinity variation (individual-based model).
- Habitat, tidal amplitude, freshwater inflow to Florida Bay, and salinity were the most widely influential variables explaining density in 11 forage species in a meta-analysis of data from historical surveys. Seagrass density and tidal amplitude each were significant for 10 species, seagrass type and freshwater inflow each were significant for 9 species, and salinity was significant for 7 species (statistical analyses of combined data sets).

Does water management affect the productive capacity of Florida Bay?
- When used in alternative testing to select the preferred plan for CERP, a statistical model relating an abundance index of pink shrimp in the Tortugas fishery to freshwater inflow to ENP at the Tamiami Trail during certain months predicted that "natural system" flows (as compared to the 1995-base case or any alternative) consistently produced highest shrimp abundance over a 31-yr period. The selected alternative was predicted to lead to abundances intermediate between predictions for the natural system and 1995-base case.
- Remnants of molluscan faunas obtained in cores suggest that molluscan faunal diversity and absolute abundance in eastern and central Florida Bay began a decline in the 1960s or earlier and reached a low in the 1970s. The low species diversity and the increased abundance of *Brachidontes exustus* are evidence of a system under stress.
- Fish density in the wet season is positively related to water depth in coastal marshes and the length of time during which water depths are greater than 12.5 cm. Maximum concentration (to roughly twice dry-down density) in low spots (*e.g.*, creeks and shallow pans) occurs when water depths decline below 12.5 cm in adjacent marshes. Successful roseate spoonbill nesting occurred in past years during dry season when mean water depths in the coastal marshes were less than 12.5 cm. Nesting failures in recent years can be explained by out-of-season water releases from the C-111 Canal.

What affects the balance between benthic and pelagic trophic networks in Florida Bay?
- The seagrass die-off was a suspected cause of a shift from benthic to pelagic dominance in the fish community, because bay anchovy abundance was much greater in 1995 than in 1984–1985. Recent findings discount this possible cause. The abundance of bay anchovy in the western bay has fluctuated since it reached a maximum in 1995. The diversity and overall abundance of canopy-dwelling fauna have increased since 1995 without a return to the original *Thalassia*-dominated seagrass canopy.
- Bay anchovy abundance may be related to the presence of salinity fronts. Bay anchovy abundance was negatively correlated with salinity and positively correlated with salinity standard deviation, chlorophyll, and an index of freshwater inflow in an analysis of historic data. A study in the Manatee River associated low mean salinity and high salinity standard deviation with the presence of fronts and found a relationship between anchovy egg abundance and these indicators of fronts.

- Seagrass diversity may determine faunal density. A principal components analysis suggested that faunal species have affinities to certain seagrass types—*Thalassia, Halodule,* or *Syringodium*—or with macroalgae. Seagrass type was a significant explaining variable in a meta-analysis of faunal density in Florida Bay, and faunal density in relation to seagrass type varied differently depending on faunal species. No faunal species was identified that had pure *Thalassia* as its sole affinity.

Do bottom and shoreline habitats affect abundance and community composition?

- Mangrove prop-root habitat in northeastern Florida Bay had significantly more fish larvae than did nearby open-water sites or nearshore areas without mangroves, but it had a lower density and diversity of both forage fish and juvenile predator fishes than found in similar habitat in the Bahamas and Puerto Rico, leading to the hypothesis that the low densities were caused by isolation from offshore sources of larvae or juveniles.
- Seagrass density was a significant explaining variable for density for 10 of 11 key forage species examined, and seagrass type was a significant explaining variable for density of 9 of the 11 species.

Does fishing affect fish populations?

- According to a comparison of the length-frequency distributions inside and outside of an area in the park protected from fishing, recreational fishing in Everglades National Park affects the size structure of gray snapper.
- Evidence of overfishing is seen in gray snapper and other species on the reef tract.

Is spatial variation in influencing factors (e.g., freshwater inflow, tidal mixing) reflected in distinct regional patterns in species distributions and community and trophic composition in Florida Bay?

- Peak concentrations of postlarval pink shrimp are roughly an order of magnitude greater in passes leading into western Florida Bay than in channels to Florida Bay through the Florida Keys. Movement into the bay occurs on the flood tide. The timing of high immigration rates is more predictable when shrimp immigrate from the west than from the east.
- Based on stable isotope analyses, the central bay has a strongly seagrass-based trophic structure, whereas the western bay has a more plankton-dominated trophic structure. The eastern bay offers a non-seagrass-based diet (likely more water-column based). The trophic structure of the southwestern bay is based on macroalgae.
- Northern Florida Bay is probably not a significant nursery area for red drum.

Is temporal variation in recruitment strength of spiny lobster, snapper, and pink shrimp related to oceanographic processes, especially to the Tortugas gyres?

- Spiny lobster postlarvae that recruit throughout the year had peaks of influx into the bay at the Middle Keys coinciding with the presence of eddy and countercurrent conditions.
- Larval duration of gray snapper varied from one year to the next and, within the first year, ranged from 35.50 to 41.45 days.
- Peak abundance of gray snapper larvae in Florida Keys channels occurred in summer 1997 and was coincident with a well-developed Loop Current (high latitudinal extent) favoring gyre formation off the Dry Tortugas, where gray snapper spawning aggregations occur.
- Temporal variability was observed in the influx of pink shrimp postlarvae through two channels in the Middle Keys and may be related to the position of the leading edge of the cyclonic eddies relative to the channels. Pink shrimp larvae at the spawning grounds seem to be retained by the circulation of the Tortugas gyre.

Are urban and agricultural sources, carried by the C-111 canal, responsible for high methylmercury in Florida Bay and its biota?

- Sources of elevated mercury concentrations in fish from northeastern Florida Bay include (1) methylmercury in runoff from the Everglades and (2) *in situ* mercury methylation in sediments from both the mangrove transition zone and the open bay itself.
- Mercury concentrations were higher along a Taylor River–Little Madeira Bay sampling transect than along a C-111 canal–Joe Bay transect, suggesting that the urban and agricultural runoff that more strongly influences the C-111 canal–Joe Bay transect is not the most important source of mercury to the bay and its biota.

Did the former density of sponges in Florida Bay influence water quality to the extent that the sponge die-off that followed seagrass die-off led to water-quality conditions that impeded the recovery of seagrass?

- At pre-die-off (before 1992) densities, sponges in Florida Bay may have been capable of filtering the entire water column in 24 hours. Recovery of the largest and most abundant species has been extremely slow. At present densities, filtering takes an estimated four days. Sponges are efficient filters of small (<5 µm) planktonic particles. Loss of sponges may have reduced water clarity and affected seagrass recovery.

Do predators seek areas of higher prey abundance?

- Bottlenose dolphin were found in areas of highest density of potential prey, supporting the working hypothesis that they search out feeding areas with higher prey concentrations. Dolphin and prey densities are higher in the east-central and south-central bay than they are in the northeastern bay. However, densities of both dolphin and prey are lower in the east-central and south-central bay than they are in other coastal areas.

Distribution of Species and Patterns of Abundance

Spatial variation in the influence of environmental and physical factors shaping Florida Bay, especially substrate, freshwater inflow, and degree of mixing with waters of the Atlantic and the Gulf of Mexico, have led to substantial regional differences in animal distributions within the bay. For example, the southern bay is prime habitat for juvenile spiny lobster, which are found in few other parts of the bay. On the other hand, juvenile pink shrimp occur most densely in the western bay. Animal distributions have been used to define distinct subregions of the bay, beginning with Turney and Perkins' (1972) delineations based on mollusks. Subregional delineations based on animals roughly correspond to those based on seagrasses (Zieman *et al.*, 1989) and water quality (Boyer, 1997). Short-term and long-term temporal variations in environmental variables accentuate regional differences in bay habitat (for example, the northeastern bay has the most seasonally variable salinities). Temporal variation also undermines efforts to better describe and understand regional differences (for example, the northcentral bay can be hypersaline one summer and mesohaline another, creating an entirely different environment for animals during the same time of year). Recent research has expanded our understanding of how animal distributions vary spatially and temporally and the most likely reasons for the variation. Results of studies that address the spatial and temporal variations of a number of parameters follow.

Field studies have expanded the knowledge of spawning areas and spawning periods. Powell (2003) and Powell *et al.* (2002, 2004) determined that spotted seatrout spawning occurs primarily in western Florida Bay. Spawning at Bradley Key and Palm Key had been observed historically, but spawning at Whipray Basin and Little Madeira Bay was determined for the first time in 1994–1995 sampling. Based on collections and hatch-date estimates from 1995 collections, they determined that spawning occurred principally during the summer, with spawning peaks in May and June. Larvae were collected over a wide range of bottom types with and without seagrass, in waters with temperatures between 20°C and 35°C (majority 26°–34°C) and salinities between 12 psu and 41 psu (majority 25–40 psu). Consistently high densities of larvae were collected at Whipray Basin, which is located in the central portion of the bay and is a valuable juvenile nursery area despite low seagrass above-ground standing crop and occasional (two occasions during sampling—40 psu and 41 psu) hypersaline conditions in 1998 and 1999.

Nursery grounds of several other gamefish species that occur in Florida Bay as adults are not yet documented in Florida Bay. Recently Powell *et al.* (2002) attempted to locate Florida Bay nursery grounds of red drum, which occur in Florida Bay and spawn in the nearby Gulf of Mexico. Based on the work of Peters and McMichael (1987) in Tampa Bay, Powell *et al.* (2002) concluded that northern Florida Bay was the only suitable nursery habitat for red drum in the bay. Powell *et al.* (2002) sampled intensively there, and concluded that limitations on larval transport from offshore waters was preventing red drum from using this part of the bay as nursery habitat. Colvocoresses (unpublished data) found young juvenile red drum in the East River of Little Madeira Bay and near the mouth of McCormick Creek, but the Powell *et al.* (2002) work suggests that the occurrence of red drum juveniles in northern Florida Bay is not a seasonally regular event.

Read *et al.* (2001) studied bottlenose dolphin in the eastern half of Florida Bay and found that densities of prey organisms in trawl samples were higher in areas where bottlenose dolphin had been feeding than in samples taken elsewhere. This supported their hypothesis that dolphin seek out feeding areas with higher prey concentrations. These investigators found a greater abundance of dolphins in the east-central and south-central parts of the bay than they found in the northeastern bay. (Their study did not include the western bay.) They suggested that the low abundance of dolphins in the northeastern bay might be related to the lower fish densities that have been reported there by other investigators. In 20 surveys conducted in all four seasons, they encountered 23 groups of bottlenose dolphins, consisting of 133 individuals. They concluded that the entire bay area they surveyed contained relatively few dolphins, corresponding to the low density and diversity of potential prey items overall. In all seasons and areas, Read *et al.*'s (2001) trawl catches were dominated by mojarras (family Gerreidae).

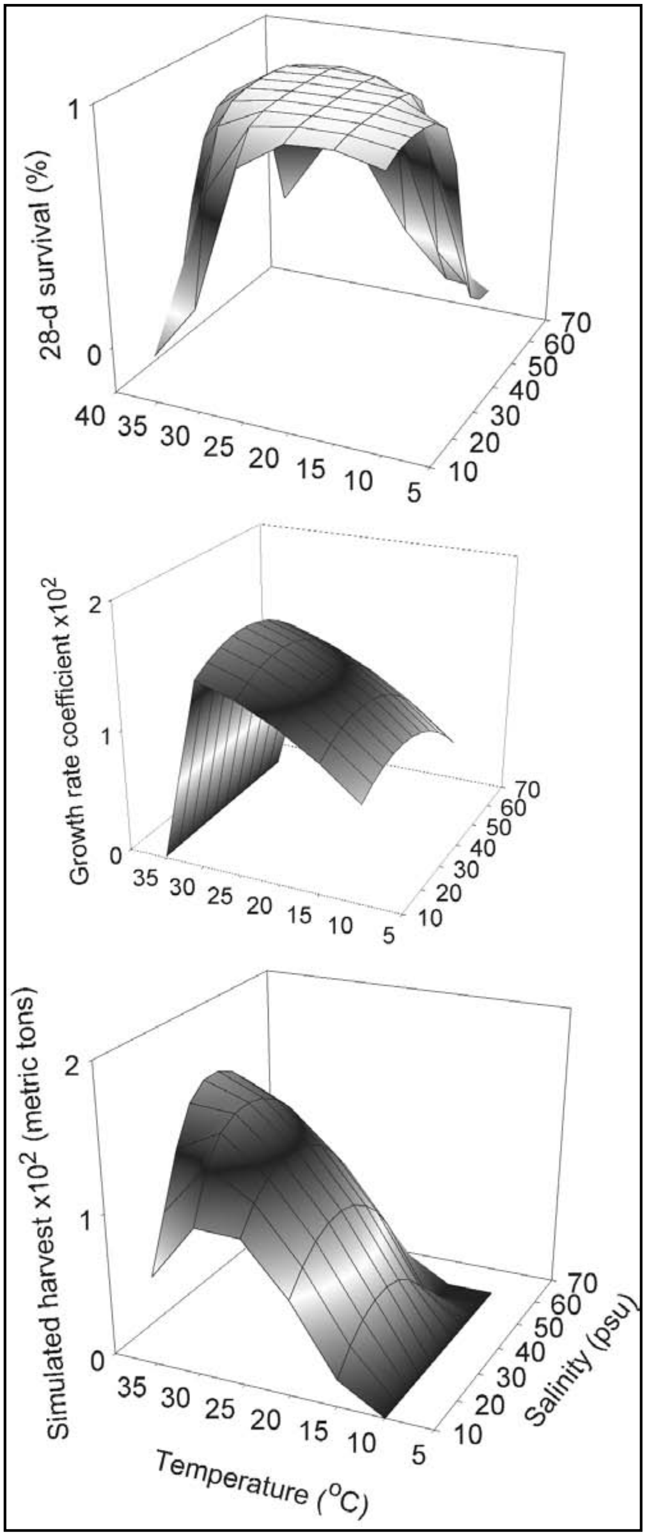

Figure 8.3 *Response curves of survival, growth, and potential offshore harvest of pink shrimp in relation to salinity and temperature (Browder* et al., *2002).*

Effect of Ecosystem Characteristics on Growth and Survival

Work on this topic addresses the principal question: How do growth and survival of individuals in each HTLS vary through the range of environmental conditions defined by salinity, water quality, and benthic habitat found in Florida Bay? Major working hypotheses are as follows:

- Salinity directly affects the growth and survival of HTLS;
- The carrying capacity of Florida Bay nursery areas is related to the overlap of favorable salinity and favorable bottom or shoreline habitat.

Effect of Salinity on Growth and Survival

Simulation models and associated experimental trials suggest that several Florida Bay species, each with optimal habitat in a different part of the bay, can be affected by changes in freshwater inflow and the resultant changes in salinity patterns. Both pink shrimp and spiny lobster could be adversely affected by the extreme high salinity that often occurs in the north-central part of the bay and sometimes spreads westward into optimal shrimp nursery habitat and southward into optimal lobster habitat. Lobster and shrimp could both be adversely affected by low salinities in otherwise suitable habitat and locations.

The effects of salinity and temperature on the growth, survival, and subsequent recruitment and harvest of pink shrimp (*Farfantepenaeus duorarum*) were examined via laboratory experiments and a simulation model (Browder *et al.,* 2002). The pink shrimp is an ecologically and economically important species that has major nursery grounds in Florida Bay. Experiments were conducted to determine the response of juvenile growth and survival to temperature (15°–33°C) and salinity (2–55 psu), and the results were used to refine an existing model (Browder *et al.,* 1999). Results of these experiments (Figure 8.3a,b) (Browder *et al.,* 2002) indicated that juvenile pink shrimp can tolerate a wide range of salinities in their optimal temperature range (20°–25°C), but the salinity tolerance range narrows with distance from that range. Acclimation improved survival at extremely high salinity (55 psu) but not at extremely low salinities (*i.e.,* 5–10 psu). Analyses of the laboratory data suggested that growth rate increases with temperature until tolerance is exceeded beyond approximately 35°C. Growth is optimal in the midrange of salinity (30 psu) and decreases as salinity increases or decreases. Potential recruitment and harvests from regions of Florida Bay were simulated

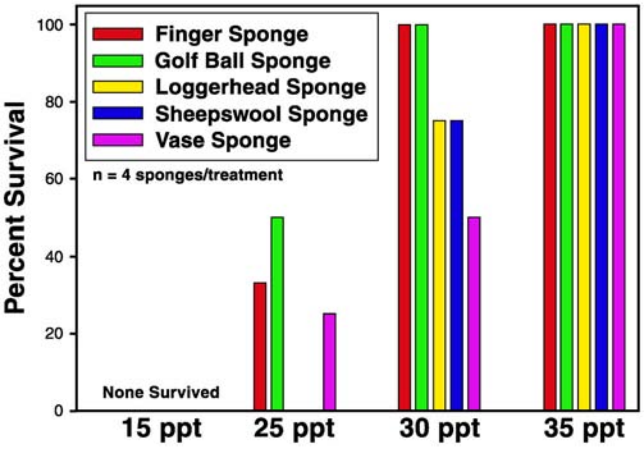

Figure 8.4 *Survival of five sponge species at four salinities at winter water temperatures for four weeks (Butler, 2005).*

based on locally observed daily temperatures and salinities. The simulations predicted that potential harvests might differ between years, seasons, and regions of the bay solely on the basis of temperature and salinity. Results indicated that harvests on the Tortugas shrimp grounds could be affected by spatial extent, location relative to suitable bottom habitat, and duration of unfavorable temperatures within a favorable salinity range.

Butler *et al.* (2001a) explored the effect of changing salinity on lobster and hard-bottom habitat, especially as it might relate to lobster microhabitat (*i.e.,* various species of sponges and octocorals). Salinity experiments at winter temperatures have recently been completed for several sponge species (Figure 8.4). The results indicate that there is reduced survival for an increasing number of species as salinity decreases (Butler *et al.,* 2001a). None of the five species tested survived at 15 psu. Field and Butler's (1994) results concerning salinity and temperature effects on postlarval lobsters suggested a salinity optimum of 35 psu. Survival rates at salinities other than 35 psu were low below 18°C and above 33°C.

Powell *et al.* (2004) examined temperature-related spatial and temporal variation in growth and survival of spotted seatrout between areas and months. They found a strong parabolic relationship between temperature and the growth of juveniles (22–60 d) but no significant relationship between temperature and the growth of larvae. They did not have an appropriate distribution of samples to look at spatial and temporal variation in relation to salinity.

In a laboratory experiment, Wuenschel *et al.*(2001, 2002) found a significant interactive effect of temperature and salinity on routine metabolic rates of spotted seatrout. They found a biphasic metabolic rate that changed isometrically with body mass in early stages of larval growth, approximating the exponential relationship near unity proposed in previous studies, and changed allometrically thereafter. Response surfaces describing the effects of temperature and salinity on maximum consumption and growth rates were also developed from laboratory experiments.

The optimal salinity for spotted seatrout may differ for each life stage. Schmidt *et al.,* 2001, 2002) found a negative correlation between annual average spotted seatrout catch rates and indices of freshwater inputs to the bay. Johnson *et al.* (2002a) found a low but significant negative correlation between spotted seatrout catch rates and bay salinity but thought it could be the spurious result of fish concentrating during hypersaline events in more limited favorable habitat with increased vulnerability to fishing. There is indirect evidence that hypersaline conditions reduce survival of spotted seatrout in the early-settlement stage. Although larval concentrations suggest that central Florida Bay is a major spawning ground for spotted seatrout (Powell, 2003), juvenile spotted seatrout appeared to extend their range into the central portion of the bay when hypersaline conditions were absent (Thayer *et al.,* 1999; Powell, personal communication), but this has to be tested more rigorously. Citing Alshuth and Gilmore (1994), Powell (2003) noted that spotted seatrout eggs do not float at salinities less than 15 psu, so egg survival might be virtually zero percent at 0–15 psu. On the other hand, laboratory experiments of spotted seatrout in Texas suggest that the species does not spawn at salinities greater than 30 psu (Wakeman and Wolschlag, 1977; Taniguchi, 1980).

Effect of Water Quality on Growth and Survival

The staff of Everglades National Park maintain a record of fish kills in Florida Bay (Schmidt, 1993b; Schmidt and Robblee, 1994). These deaths are believed to occur because of low dissolved oxygen in the water column. The mass mortalities are usually reported in the Snake Bight area, where episodic low dissolved oxygen may be caused by a combination of extremely shallow water, high summer temperatures, poor tidal and wind mixing, and high respiration rates. High ammonia levels recently reported by Boyer (personal communication) are another possible source of mortality.

Contaminants in Florida Bay biota have been investigated previously. Tissues of fish, macroinvertebrates, and birds were analyzed for concentrations of heavy metals, pesticides, and polychlorinated biphenyls (PCBs) in fish and macroinvertebrates (Ogden *et al.,* 1974). Concentrations of DDT, arsenic, and methylmercury in marine animals were high enough to warrant further investigation and led to later air-quality studies in ENP. As part of a larger study of the possible effects of mosquito control in Monroe County, the Environmental Protection Agency (Anonymous, 1980) examined fish and shellfish tissues and water for concentrations of certain pesticides, including Naled and Batex. They found negligible amounts of Naled in fish and shellfish, although oysters accumulated an average of 0.007 ppb of Naled. Batex was not found in detectable amounts in either fish or shellfish. Results may have been biased on the low side by the dry-season conditions that prevailed.

A multiyear study in the C-111 canal and associated sites in Florida Bay was undertaken in order to determine other contaminant risks that may exist in south Florida (Scott *et al.,* 2002). According to extensive surface-water data and results from analyses of sediment, tissue, and semipermeable membrane devices, canal contamination seems to be derived from the extensive agricultural production that drains into the C-111 canal. The results of this study indicate that runoff from agricultural fields led to quantifiable pesticide residues found in both canal and bay surface water, at levels that occasionally exceeded current water-quality criteria. The major pesticide of concern was endosulfan, which was detected at 100% of the sites sampled. The decision to alter the C-111 canal flow and allow increased freshwater flow into the adjacent Everglades may result in discharges of pesticides through Everglades National Park and into Florida Bay. Endosulfan concentrations are highest in the northeastern part of Florida Bay, where the special sensitivity of pink shrimp could cause mortalities. Low pink shrimp densities in northeastern Florida Bay have been documented since at least the 1960s (Costello *et al.,* 1986). Other factors (*e.g.,* extreme and variable salinities, absence of broad banks, sparse seagrass coverage) may limit the presence of pink shrimp in the northeastern bay, but no investigation of the possible effect of endosulfan on pink shrimp in the bay has been made.

Health advisories are now posted in eastern Florida Bay warning of elevated levels of mercury in some higher-trophic-level fish. Thirty percent of spotted seatrout sampled from eastern Florida Bay exceed Florida's no-consumption advisory level of 1.5 $\mu g/g^{-1}$ (Evans *et al.,* 2001). Jack crevalles also contain comparably high mercury concentrations (Evans, personal communication). Other species of gamefish and forage fish, although not as high in mercury as these two species, have concentrations several times those found in the western bay or elsewhere in Florida. These high concentrations may put humans, other mammals, birds, and reptiles at risk. Reduction in body burdens of mercury in top carnivores is one of the success criteria listed by the South Florida Ecosystem Restoration Task Force. Work is underway by Marnie Billie at FIU to assess the ecological risk of consumption of Florida Bay fish by piscivorous ospreys in the bay. Planned restoration activities in the Everglades will change freshwater deliveries to Florida Bay. These deliveries could alter the existing high levels of mercury in some Florida Bay gamefish through enhanced mercury fluxes as well as altered productivity and food web structure, which influence mercury bioaccumulation.

Effect of Benthic Habitat on Growth and Survival

This issue has generally been approached by relating benthic habitat to animal densities, which implies survival and growth, rather than by measuring habitat effects on growth and survival directly. The fact that faunal densities are correlated with certain benthic habitats suggests that growth and survival are highest in the appropriate habitat. See section on effect of benthic habitat on abundance.

Immigration, Growth, and Survival of Offshore-Spawning Fishes that Use Florida Bay as a Nursery

In an effort to understand spatial and temporal patterns of variability in immigration, growth, and survivorship of upper-trophic-level fishes, Settle (unpublished data) examined these life history attributes in several important species in the bay. Juvenile great barracuda using the bay as nursery habitat are the product of protracted spawning, which is centered during the summer but with nearly 15% occurring from late fall and winter. Spawning during these later periods has not been previously reported in south Florida and may suggest that either some spawning does occur in the region during those times or that some barracuda in the bay originate from elsewhere in the species' distribution. The youngest individuals are found in the Atlantic transition, gulf transition, and western subregions of the bay, suggesting ingress from both the Atlantic channels and the open Gulf of Mexico. Cohort-specific growth rates of young fish (age 30–150 d) ranged from 1.44 to 2.65 mm d^{-1} during the 1990s. Over the same period, growth was significantly slower in two faunally depauperate subregions, the eastern and the turbid western bay. Relative condition (weight/length) of this species over the period 1973 to 2000 declined during the early to mid-1990s and appears to be returning to values observed during the 1970s and mid-1980s. The overall instantaneous natural mortality rate was 0.02656. Average survival was 97.38% d^{-1}. Cohort-specific growth rates of juvenile lane snapper (age 30–242 d), which primarily inhabit the gulf transition and western subregions, showed significant intra- and interannual variation and ranged from 0.59 to 0.93 mm d^{-1}. Snappers spawned during the spring and summer grew faster than those spawned during fall and winter, and fish spawned during 1998 grew faster than those spawned in 1997. Instantaneous natural mortality both years was 0.03636, and average survival was 96.43% d^{-1}.

Effect of Ecosystem Characteristics on Species Distribution and Community and Trophic Structure

Work on this topic addresses the major questions: Do HTLS' community composition or trophic structure in Florida Bay vary in time and space, what factors are responsible for this variation, and what processes are affected? Major working hypotheses are as follows:

- The abundance of HTLS is low in the northeastern portion of Florida Bay because of high-amplitude variation in salinity, low density of seagrass, lack of extensive banks, restrictions on the immigration of postlarvae, or a combination of all of these factors;
- Changes in community composition are related to changes in salinity, which can be influenced by water management, although the effect of benthic habitat, tidal exposure, rainfall, and oceanographic events may need to be filtered out to see these effects;
- Changes have occurred in the species composition of mollusks, foraminifera, and other sessile species in Florida Bay, and these changes reflect changes in salinity, water quality, and the cover and composition of benthic vegetation;
- Spatial and temporal patterns in trophic pathways vary depending on salinity, water quality, and abundance and type of benthic vegetation;
- Widespread sponge mortalities may affect both hard-bottom and seagrass communities;
- Fishing reduces the number and size of some apex predators, causing shifts in community structure; and
- Changes in community composition are related directly to changes in benthic habitat.

Effect of Salinity on Species Abundance and Community Structure

Several studies suggest that hypersalinity affects the benthic fauna of Florida Bay. Schmidt (1977) reported lower forage fish diversity, biomass, and numbers in northcentral Florida Bay in salinities greater than 45 psu. Johnson *et al.* (2002a,b) noted that "evenness" (an index of community structure) among 11 dominant species, as estimated from statistical model predictions, was lower in 1990, a year of extreme high salinity in the bay, than in 1995, a wet year. Lyons (1999) observed fewer species in the molluscan community in the hypersaline part of Florida Bay. A simulation model based on experimental data (Browder *et al.*, 2002) predicted lower juvenile pink shrimp densities and fewer potential recruits to the Tortugas fisheries from the hypersaline central part of Florida Bay. Based on relative concentrations of smallest-stage seatrout postlarvae, Powell (2003) determined that central Florida Bay is a major spawning ground for spotted seatrout; however, there is evidence that at salinities greater than 45 psu, survival and growth of larval and juvenile spotted seatrout could be diminished (Wuenschel, 2002). The frequency and duration of hypersaline events in the central bay might, therefore, affect survival and growth of young seatrout and, consequently, the abundance of this species. Powell (2002) noted that densities of the postlarvae of many species collected with an epibenthic sled were higher in the central bay, indicating that many species may be disproportionately exposed to hypersaline conditions in an otherwise favorable nursery area. Sogard *et al.* (1989) found lower species richness of both epibenthic and water-column fishes. Holmquist *et al.* (1989) found a lower species richness of macroinvertebrates in the central bay, which was characterized by low tidal range and hypersaline conditions during their studies. They concluded that water circulation and salinity patterns were influential in structuring Florida Bay's epibenthic faunal communities.

HISTORICAL DISTRIBUTIONS OF MOLLUSKS AS INDICATORS OF PAST SALINITY PATTERNS

Historical records of salinity and bottom vegetation were reconstructed based on molluscan assemblages in shallow sediment cores. An analysis by Brewster-Wingard *et al.* (2001) suggested that molluscan assemblages in Florida Bay have undergone distinct changes over the past 100–200 years. *Brachidontes exustus,* a euryhaline species tolerant of diminished water quality and a wide range of salinities, accounts for more than 80% of the molluscan fauna in the upper portions of six cores. Four cores from central and eastern Florida Bay and one from Featherbed Bank in Biscayne Bay suggest decreases in molluscan faunal diversity and absolute abundance that began perhaps in the 1960s or earlier and reached a low in the early 1970s (Figure 8.5).

The dominance of *Brachidontes* and the decreases in faunal richness and abundance are indicative of a

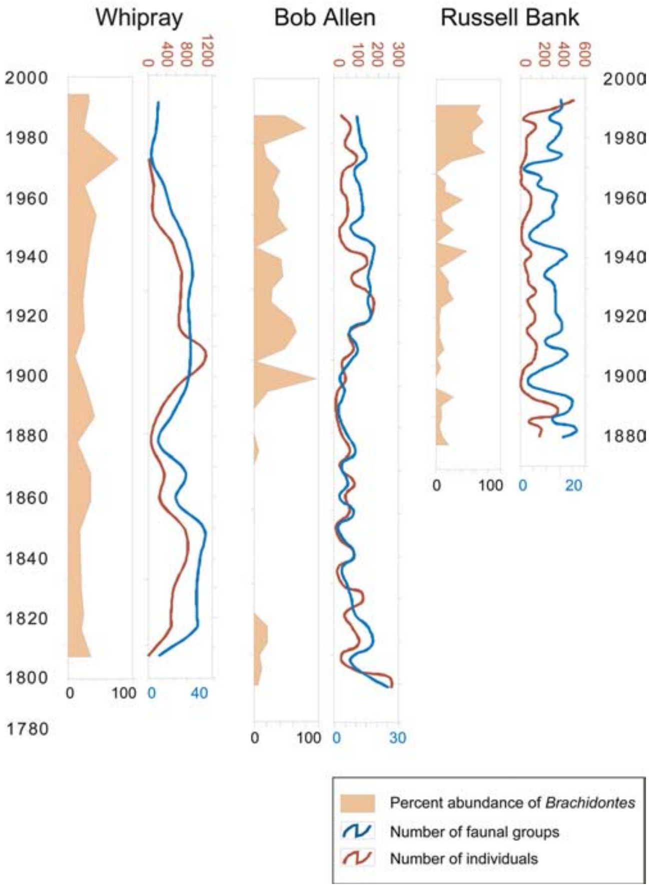

Figure 8.5 *Historical view of the dominance of a molluscan water-quality indicator in the molluscan fauna (Brewster-Wingard* et al., *2001) at three Florida Bay locations.* Brachidontes *tolerates conditions that other mollusks cannot. Experiments are underway to better define the conditions tolerated by* Brachidontes.

system under stress. Interestingly, the transition-zone cores from the mouth of Taylor Creek and in Manatee Bay do not show the decline in faunal diversity and absolute abundance exhibited in the other cores. Based on their analysis of molluscan epiphytic species within the cores, Brewster-Wingard *et al.* (2001) concluded that common factors are affecting the faunas and their associated bottom vegetation across eastern and central Florida Bay, despite the isolation of some of the basins.

Effect of Water Quality on Species Abundance and Community Structure

Ortner *et al.* (2001), who examined possible relationships between chlorophyll, zooplankton, and anchovy from January 1994 through January 1999, found no evidence that phytoplankton blooms were causing a fundamental shift in community structure and trophic dynamics in Florida Bay. Copepod concentrations were not related to chlorophyll concentrations, and anchovy density was not related to copepod concentrations. On the other hand, Johnson *et al.* (2002a) found a significant relationship between bay anchovy density and chlorophyll *a* concentrations. Intermittent high anchovy densities might be due to the attraction of anchovies to unvegetated bottoms and high turbidity (Patillo *et al.,* 1997). Peebles' (2002) study of bay anchovy egg densities in the Manatee River suggests that structured, spatially and temporally intensive sampling of bay anchovy eggs may reveal relationships with prey abundance, salinity fronts, and freshwater inflow not obvious from previous sampling in Florida Bay.

Effect of Benthic Habitat on Species Abundance and Community Structure

FISH DISTRIBUTIONS IN MANGROVE PROP–ROOT HABITAT

Dennis and Sulak (2001) found that prop-root sites in northeastern Florida Bay had significantly more fish larvae than did nearby open-water sites or nearshore areas without mangroves. However, the densities of both forage fish and juvenile predator fishes were lower among mangrove prop-root habitats in Little Madeira Bay, Trout Cove, and Manatee Bay than in prop-root habitats in the Bahamas and Puerto Rico. They proposed that isolation from offshore sources of larvae or juveniles was the reason for the low densities. In support of this conclusion, they found that the concentration of larval fish was much greater on the leeward side of Key Largo than at their northeastern Florida Bay mangrove prop-root sites. Fish density and biomass were greater in mangrove prop-root habitats than in adjacent fringing seagrass areas. In a previous study by Thayer *et al.* (1987), they determined that the mangrove prop-root habitat in Florida Bay and nearby areas was occupied by a distinct faunal assemblage.

CANOPY–DWELLING FISH AND MACROINVERTEBRATE ASSEMBLAGES IN RELATION TO SEAGRASS

Densities of many macroinvertebrate and fish species in Florida Bay are higher inside seagrass beds than outside them (Holmquist *et al.,* 1989; Sogard *et al.,* 1989; Thayer and Chester, 1989; Thayer *et al.,* 1999; Matheson *et al.,* 2001). Johnson *et al.* (2002a) analyzed the combined data of 6 field studies (including those cited above) and quantified the relationship between animal density and seagrass density for 11 key forage species. They found that of the 10 species whose densities were significantly related to seagrass, 5 were densest in dense seagrass, 4 were densest in moderately dense seagrass, and 1 was densest in sparse seagrass. Bottom or seagrass type was a significant variable explaining the densities of 10 forage species. Three species were densest in *Syringodium,* three were densest in *Halodule,* two were densest in mixed grasses with *Syringodium,* and one was densest in mixed grasses with *Thalassia.* One, bay anchovy, was densest in areas without seagrass.

SHIFTS BETWEEN BENTHIC AND PELAGIC ZOOPLANKTIVORES

A prevailing hypothesis has been that the seagrass die-offs and phytoplankton blooms experienced beginning in the late 1980s provoked a trophic shift in western Florida Bay from a system based principally on benthic production to one based principally on water-column production. This hypothesis grew out of comparisons of the fish and macroinvertebrate community compositions in 1984–1985 to those in 1994–1995. Thayer *et al.* (1999) compared the fish assemblages of 1984–1985 to those of 1994–1995 in three regions of the bay and found that canopy-dwelling species had declined and that pelagic zooplanktivores dominated the fauna. Robblee *et al.* (2001) compared benthic vegetation, fish, and macroinvertebrate assemblages found in Johnson Key Basin in 1985 to those found there in 1995. They observed a decrease in *Thalassia* and *Syringodium* and an increase in *Halodule* and bare bottom. They found a decrease in *Farfantepenaeus duorarum* (pink shrimp), seagrass-associated caridean shrimps (–65%), and seagrass-associated fishes (–81%) and concluded that the decline in seagrass-associated species was a result of seagrass die-off.

The hypothesis that loss of seagrass would result in a trophic shift of fish was discounted by sampling data beyond 1995. The juvenile and small-resident fish assemblage in collections of Powell *et al.* (2001b) made during 1996–2000 (especially 1998) differed markedly from that in 1994–1995 and resembled the assemblage observed in 1984–1985. The change from canopy-dwelling to pelagic zooplanktivores from 1984–1985 to 1994–1995 was followed by a change back to canopy dwellers in 1998–1999. The investigators concluded that the recovery of an assemblage of fish species dominated by seagrass canopy dwellers cannot be wholly explained by recovery of seagrasses because there is no evidence of seagrass recovery on a subdivision-wide basis in 1999–2000 relative to 1994–1995. In fact, seagrass densities in 1999–2000 were much lower than in 1984–1985 (Powell *et al.,* 2001b).

Ortner *et al.* (2001) also refuted the hypothesis of a trophic shift related to loss of seagrass coverage and an increase in phytoplankton blooms. They concluded that the recent history (1994–2000) of phytoplankton, zooplankton, and planktivorous fish abundances provides little or no support for the concept of a fundamental, persistent shift from a demersal benthic-based food web to a pelagic water-column-based food web. Furthermore, there seems to be no clear relationship between plankton bloom incidence or intensity and the abundance of zooplanktonic herbivores, nor is there a relationship between the abundance of the bay anchovy and its preferred copepod prey.

An alternative hypothesis for the observed fluctuation in dominance between demersal and water-column species is that the density of the small-juvenile and small-resident canopy-dwelling fish assemblage is influenced by the sporadic dominance of pelagic zooplanktivorous clupeiforms that might be related to water column chlorophyll *a* concentrations (Powell *et al.,* 2001b).

Another alternative hypothesis is that the establishment of a more heterogeneous bottom habitat, occupied by *Halodule* and *Syringodium* as well as some *Thalassia,* might be responsible for the recovery of canopy-associated species after 1995 (Robblee, personal communication) An exploratory principal component analysis revealed four PCs, each of which could be interpreted to relate to a vegetation component: *Thalassia* (PC1), *Halodule* (PC2), *Syringodium* (PC3), and macroalgae (PC4) (Robblee *et al.,* 2001). Pink shrimp correlated with PC2 and PC3. The rainwater killifish was correlated with PC1. Affinities of various species to certain types of seagrass habitat might lead to greater overall abundance if seagrass habitat diversity increases. This is supported by the work of Johnson *et al.* (2002a), who found that densities of various species varied, depending upon the type of seagrass they were found in and that no species was found at highest density in pure *Thalassia* beds. This result is especially valuable because Somerfield *et al.* (2002) concluded that even large faunal effects of seagrass habitat heterogeneity might be difficult to detect. This hypothesis might explain the recovery of canopy-dwelling species after 1995 but not the fluctuations in bay anchovy density.

Peebles' (2002) study of bay anchovy egg abundance in the Manatee River provides insight on the bay anchovy fluctuations in Florida Bay. Using a spatially and temporally intense sampling strategy, Peebles (2002) found that nighttime bay anchovy egg abundance in Manatee Bay was positively related to *Acartia tonsa* abundance the previous day. Bay anchovy appeared to spawn immediately upstream from salinity fronts (which he defined as a change of 1 psu/km) that concentrated their prey. The effect of freshwater inflow on bay anchovy egg abundance was non-linear. Peak abundance occurred when salinity fronts formed near the river mouth. Egg abundance declined when these fronts advanced seaward of the river mouth but was lowest when fronts were weak or absent during low-flow periods. The presence of a salinity front was associated with relatively low mean salinity and high standard deviation in salinity. In their analysis of a data set compiled from several studies, Johnson *et al.* (2002a) found a significant relationship between bay anchovy density and salinity (negative relationship), standard deviation in salinity (positive relationship), and freshwater inflow index (positive relationship) in Florida Bay. Peebles' (2002) study might explain the mechanisms behind these relationships.

EFFECTS OF MACROALGAE ON ANIMAL ABUNDANCE

The pattern of settlement of spiny lobster postlarvae in southwestern Florida Bay may be highly dependent on the location of red macroalgae (*Laurencia*), crevice shelters and planktonic postlarval abundance (Herrnkind and Butler, 1994). Mud banks that restrict transport, unfavorable salinity, and scarcity of hard-bottom settlement habitat may severely restrict the presence of spiny lobster in the interior bay (Field and Butler, 1994).

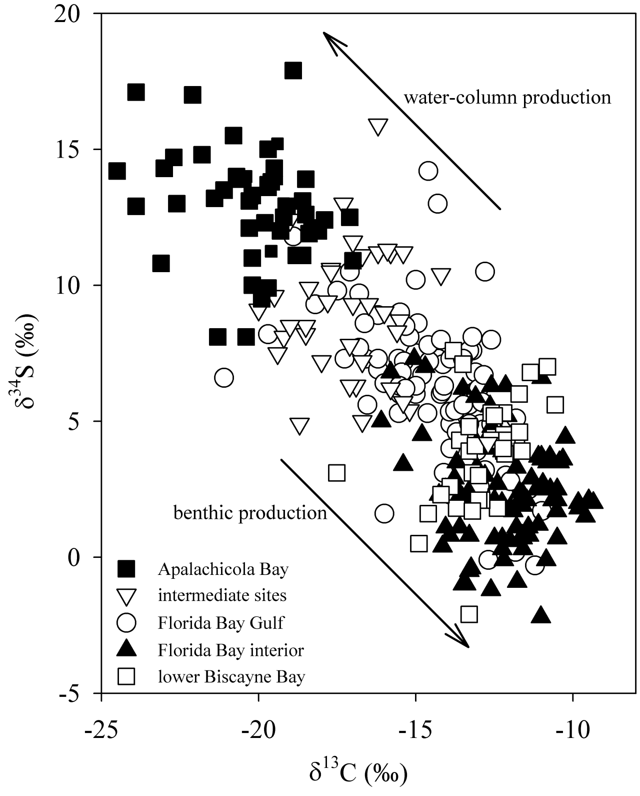

Figure 8.6 *Summary comparison of consumer tissue $\delta^{13}C$ vs $\delta^{34}S$ from several Florida coastal ecosystems. Data illustrate the gradient in stable isotope values as trophic dependence shifts from seagrass beds "benthic", $\delta^{13}C$-enriched, $\delta^{34}S$-depleted) to the water-column ("planktonic") ($\delta^{13}C$-depleted, $\delta^{34}S$-enriched) (Chanton and Lewis, 2002).*

EFFECT OF SPONGES ON JUVENILE SPINY LOBSTER

Butler *et al.* (1995) documented widespread sponge mortality coinciding with months-long, extensive cyanobacterial blooms in the south-central part of Florida Bay in the early 1990s (1991, 1992, 1994). They showed with field experiments that the loss of sponges affected the distribution of spiny lobster juveniles, which use crevices beneath sponges as nursery habitat. Use of artificial shelters increased following the sponge decline. Juvenile spiny lobster abundance declined 23% at sites without artificial substrates and increased 76% at sites with artificial substrates. The long-term effect of sponge mortality on lobster abundance is not known, but shelter such as that provided by sponges reduces the risk of predation (Herrnkind and Butler, 1994). Based on their results, the authors suggested that loss of shelter might lead to increased predation on animals that remain in areas without shelter or are in search of shelter. Loss of area with shelter may cause crowding and resource limitation in areas of remaining shelter (Butler *et al.*, 1995). Other animals that use sponges as habitat include stone crabs (*Menippe mercenaria*), spider crabs (*Mithrax* spp.), toadfish (*Opsanus beta*), and octopus (*Octopus* spp.).

SPATIAL VARIABILITY IN TROPHIC RELATIONSHIPS

The relative importance of seagrass and phytoplankton in food webs differs across the bay, and neither is important in certain parts of the bay. Chanton *et al.*'s (2001) evaluation of stable carbon (C), nitrogen (N), and sulfur (S) ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) data for producers and consumers in Florida Bay indicated that the interior of the bay has a strongly seagrass-based trophic structure, whereas the gulf (outer or western) sites in the bay shift toward a more plankton-dominated trophic system (Figure 8.6). It is not yet certain whether the shift in Figure 8.6 reflects natural spatial variation or a temporal trend forced by changing environmental conditions in the bay. Stable carbon, nitrogen, and sulfur data in Figure 8.7 from Evans *et al.* (2001) confirm Chanton *et al.*'s (2001) description of the trophic structure of the interior and western bay. In addition, the data suggest a nonseagrass-based diet (likely a more pelagic-, or water-column-, based food web) in the eastern bay.

Predominant food webs in the hard-bottom communities of Florida Bay (mainly the southwestern bay) and bayside hard-bottom communities in the Florida

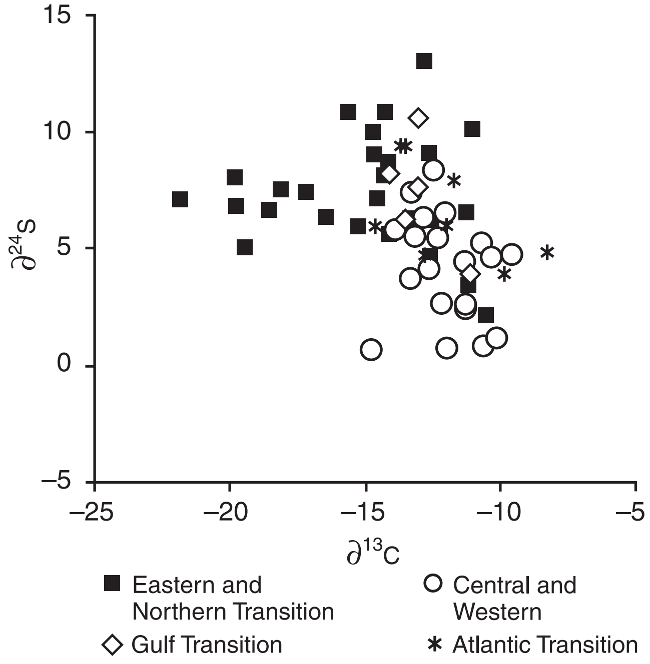

Figure 8.7 *Stable isotope analysis of Florida Bay gamefish to support methylmercury studies in Florida Bay (Evans* et al., *2001). The analysis complements the view of the bay in the previous figure by adding information on the bay's eastern and northern transition zones.*

Keys are based on macroalgae rather than seagrass, according to stable-isotope analyses (C, N, and S) conducted by Behringer and Butler (1999). They sampled macroalgae, seagrass, suspended particulate organic matter (POM), sediment POM, sponges, gastropods, holothurians, bivalves, and spiny lobsters. With the exception of suspension feeders, the hard-bottom animals were trophically independent of seagrass.

Koenig *et al.* (2001) found spatial, temporal, and ontogenetic dietary shifts in the major prey of red drum. They speculated that the differences were due to differences in prey availability. This is consistent with observations about the abundance of various prey, which differs by region. They were not able to detect spatial or seasonal differences in the diet of snook, possibly because of the lower resolution of the snook diet data.

Variation in Ecosystem Characteristics

Effects of Animals on the Ecosystem

Specific questions being addressed by this research are as follows: (1) how do animals affect their ecosystem, and what are the consequences of change in animal abundance or distribution for the rest of the system? (2) What is the ecological role of sponges in the ecosystem, and what does the loss of sponges in southwestern Florida Bay and an increasing fishery for some sponge species portend?

EFFECTS OF ANIMALS ON BENTHIC HABITAT

Benthic grazing animals in exceptionally high densities can adversely affect benthic vegetation in Florida Bay. A dense aggregation of the variegated sea urchin (*Lytechinus variegatus*) caused severe, localized defoliation of a seagrass bed in outer Florida Bay during 1997–1998 (Rose *et al.*, 1999). Macia and Lirman (1999) described the population dynamics of this aggregation and Rose *et al.* (1999) described the short-term effect of this aggregation on the benthic community. Subsequent monitoring of the aggregation during 1998–1999 revealed that urchin densities progressively declined, as did their effect on seagrass biomass. However, as of 2002, seagrass biomass in the area of the meadow that underwent the most severe defoliation remained drastically reduced compared to areas that had not been damaged by urchins (W. Sharp, personal communication).

ROLE OF SPONGES IN REGULATING WATER QUALITY

The working hypothesis is that the large-scale loss of suspension-feeding sponges may have rendered the Florida Bay ecosystem susceptible to recurring phytoplankton blooms (Peterson and Fourqurean, 2001). Sponges are capable of filtering large volumes of water when feeding. Widespread sponge mortalities occurred in Florida Bay from 1992 to 1994. By 1995, total sponge biomass was a fraction of its former level: there had been a 70% decline in the Long Key area and an 84.6% decline in the Marathon area (Stevely and Sweat, 2001). Loss of sponge biomass in Florida Bay may be having major ecological effects on water quality (Stevely and Sweat, 2001; Peterson and Fourqurean, 2001)

Sponges are a particularly dominant structural feature of Florida Bay seagrass and hard-bottom habitats, functioning as efficient filters of small (less than 5 µm) planktonic particles. Previous studies have illustrated that the grazing pressure of filter-feeding bivalves may control phytoplankton abundance. If the presence of sponges increases light availability to the benthic plant communities, then sponges may reduce the shading effects of phytoplankton blooms, and the loss of sponges in Florida Bay may have cascading effects on the associated seagrass community (Peterson and Fourqurean, 2001).

Since the initial seagrass die-off in the late 1980s, blooms have swept over extensive portions of the bay north of the middle Keys and have persisted for months. The proliferation of the cyanobacterium (*Synechococcus*) and diatom (*Rhizosolenia*) blooms has caused widespread concern among scientists and water managers. These blooms have the potential for disrupting the ecology of the bay and harming benthic plant communities by depleting oxygen, producing toxins, and reducing the light levels in the bay. Some regions of Florida Bay exhibit high levels of algal and/or nonalgal suspended solids, resulting in low light penetration. Although phytoplankton blooms were not likely the cause of the initial seagrass die-off, the reduction in light caused by high phytoplankton standing crops may have contributed to poor seagrass recovery and more recent seagrass die-offs.

Prior to the widespread sponge mortalities that occurred from 1992 to 1994, Stevely and Sweat (2001) collected data on the abundance of commercial sponges (*Spongia* and *Hippospongia*) and the entire sponge community at 15 locations in the Middle and Upper Keys (4 locations were within Everglades National Park). They have been evaluating the recovery of the sponge community annually since 1994 and have identified to family, genus, or species level approximately 95% of the sponges counted. In general, recovery of the largest and most abundant sponge species (in the genera *Spheciospongia* and *Ircinia*) has been extremely slow. The first significant indication of recovery of these species was found at Marathon in 1999 and 2000, but recovery was still not apparent at Long Key by April of 2001. These large species represented 70% of the sponge community biomass prior to the mortalities.

Based on their data prior to the 1992–1994 mortalities, Stevely and Sweat (2001) estimated that the mean sponge abundance was 0.725 sponges/m^2 and mean sponge biomass volume was 364 ml/m^2. Based on a sponge pumping rate of 10,000 times the sponge volume per day (Reiswig, 1974; Reiswig, personal communication), the sponge biomass could therefore pump 3,640 liters of seawater per square meter per day. Since the water column in the study area was approximately three meters deep, sponge biomass could be expected to pump the equivalent of the entire water column in 24 hours (Stevely and Sweat, 2001). The loss of 75% of sponge biomass might be expected to lengthen the time required to pump the water column from one day to four days.

Peterson and Fourqurean (2001) speculate that system-wide trophic dysfunction caused by the sponge die-off has potentially contributed to the magnitude of the nuisance phytoplankton blooms, and that the loss of these organisms can explain why this system remains susceptible to recurrent blooms of phytoplankton and cyanobacteria.

Oceanographic Effects on Larval Transport and Recruitment

Major questions related to this topic are (1) What processes are involved in the transport of presettlement stages of fish and invertebrates to the boundaries of Florida Bay, and what are their schedules? and (2) What pathways do early life stages of offshore-spawned HTLS use to enter Florida Bay, what is the relative importance and extent of penetration into the bay's interior by these pathways, and what factors influence transport and settlement?

Many species associated with the reef tract and the southwestern Florida shelf spend some part of their life cycle in Florida Bay. For example, Florida Bay is a major nursery ground for pink shrimp that are harvested in waters off the Dry Tortugas, the most economically important pink shrimp fishing ground in the state. Florida Bay also contains important spiny lobster nursery habitat, and Everglades National Park is a fishing-free sanctuary for spiny lobster. Water flows and animal movements connect Florida Bay not only to the upstream Everglades and coastal mangrove areas but also to the Florida Keys, the reef tract, the southwest Florida shelf, and the Dry Tortugas. Many HTLS range between the bay and coastal reefs within their life cycle. The development of scientific knowledge about HTLS of the bay, therefore, must extend beyond Florida Bay to address the greater ecosystem that supports these species and the processes that affect their movements. For example, research should include the Loop and Florida currents and countercurrents, the Tortugas Gyre, and coastal eddies. The effect of these processes on larval transport and the distribution and abundance of HTLS in the bay must be addressed to improve the ability to distinguish effects of changes in freshwater inflow.

Florida Bay lies between the Atlantic Ocean and the Gulf of Mexico and is connected to both of these bodies through regional-scale circulation and exchange processes and the oceanic boundary currents that influence these processes. The southwest Florida Shelf to the west and the Keys coastal zone to the east and south of Florida Bay interact with each other and the bay through the tidal channels between the Keys and also by means of their boundary currents (Herrnkind and Butler, 1994; Lee *et al.,* 2001). A dominant process potentially affecting water transport and the transport of eggs and larvae to Florida Bay is the strong, coherent response to alongshore wind-forcing coupled with seasonal stratification in response to variations in wind-mixing, air-sea exchange, and river runoff along the nearshore western shelf. Boundary current dynamics and eddy processes are also critical larval transport mechanisms that operate both on the regional and local scales. Transport response to prevailing easterly winds may vary along the Florida Keys as a result of the curvature of the coastline (Lee and Williams, 1999), but they are expected to favor onshore larval transport between the Lower Keys and the Dry Tortugas, where the coastline is east-west oriented. Onshore convergence of the Florida Current can also facilitate transport into the coastal zone of the Keys, and this occurs mainly in the upper Keys where the shelf narrows and curves northwards (Yeung and Lee, 2002).

The area of the Dry Tortugas is an important spawning site for penaeid shrimps, spiny lobsters, and some species of snappers and groupers (Limouzy-Paris *et al.,* 1997). Pink shrimp larvae were retained by the Tortugas gyre circulation for a period of two weeks (Criales and Lee, 1995). Coastal eddies originating from the Dry Tortugas and propagating downstream may be a mechanism to deliver presettlement stages from spawning site to nursery sites on the reef tract and in Florida Bay (Yeung *et al.,* 2001; Criales *et al.,* 2003). The lower southwestern shelf in the vicinity of the Dry Tortugas is a potential source of recruitment to the Florida Keys reef tract and Florida Bay for both reef fish and pink shrimp.

Frontal eddies of the Loop Current in the Gulf of Mexico that propagate southward along the outer edge of the western shelf may be trapped and develop into persistent gyres off the Dry Tortugas (Fratantoni *et al.,* 1998; Yeung and Lee, 2002). The subsequent arrival of another frontal eddy or the abrupt retreat of the Loop Current may dislodge the gyre, which then moves eastward along the southeastern shelf off the Florida Keys in the form of a transient coastal eddy. The Tortugas gyre provides a mechanism for retaining larvae for periods of weeks to up to three months (Lee *et al.,* 1994).

EDDIES AND GYRES

Working hypotheses about the transport of larvae to the boundaries of the bay are as follows: (1) Presettlement stages are transported and detrained into the coastal zone of the Florida Keys by coastal eddies. (2) Spawning and nursery sites for pink shrimp, spiny lobsters, and some snappers are linked through the evolution of the coastal eddies from the Tortugas gyre. (3) The formation of the Tortugas gyre is enhanced by a well-developed Loop Current (high latitudinal intrusion) whose dynamics may be modulated by climatic shift. (4) Snapper larvae entering Florida Bay originate from spawning stocks that form seasonal aggregations off the Dry Tortugas. (5) Year-class strength of six snapper species is enhanced by increased larval retention and nutrient-enrichment of the pelagic larval habitat via gyre-induced upwelling during spawning season off the Dry Tortugas (Criales and McGowan, 1994; Criales and Lee, 1995; Jones *et al.,* 2001; Yeung *et al.,* 2001; Yeung and Lee, 2002).

Supply of early-life-stage recruits is a major limiting factor of the year-class strength of aquatic species. Presettlement stages of the spiny lobster, snapper, and pink shrimp that inhabit Florida Bay as juveniles and/or adults enter the bay from the ocean through interisland channels.

The eddy hypothesis of regional recruitment has important implications over larger temporal and spatial scales. Because coastal eddies originate from the Dry Tortugas, they may constitute the essential transport link between the spawning and nursery grounds. Moreover, eddy formation at the Dry Tortugas is associated with Loop Current frontal dynamics, which are in turn modulated by long-term climatic variability (Yeung *et al.,* 2001; Yeung and Lee, 2002).

Observed larval distribution patterns of some crustaceans in the Florida Keys coastal zone corroborate many of the predictions based on key coastal transport processes. Early-stage phyllosomata (less than 2 months old) were concentrated within or at the boundaries of a gyre in the pattern hypothesized for passive drifters (Yeung and Lee, 2002). The abundance of strong-swimming spiny lobster postlarvae was not highly correlated with wind-driven currents that can affect the coastal transport of more passive drifters (Acosta and Butler, 1997). High concentrations of pink shrimp larvae were found in the Tortugas Gyre in late spring–early summer (Criales and Lee, 1995). High densities of larvae and postlarvae of 10 different shrimp families were found

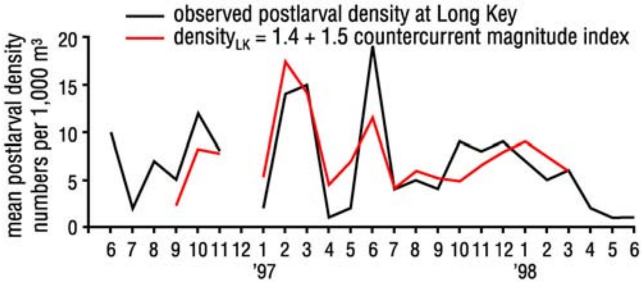

Figure 8.8 *Monthly mean influx density of spiny lobster postlarvae observed at Long Key and the predicted density (density_{LK}) using an index of countercurrent magnitude in a simple regression model ($r^2 = 0.50$, $F_{1,16} = 17.90$, $P < 0.0006$) (Yeung* et al., *2001). The index is the average magnitude of the countercurrent component for the periods two weeks prior to and three days during sampling taken at a current meter moored at Tennessee Reef in the middle Keys. Satellite imagery confirmed that in most cases, enhanced coastal countercurrents coincided with the presence of a cyclonic mesoscale eddy in the vicinity.*

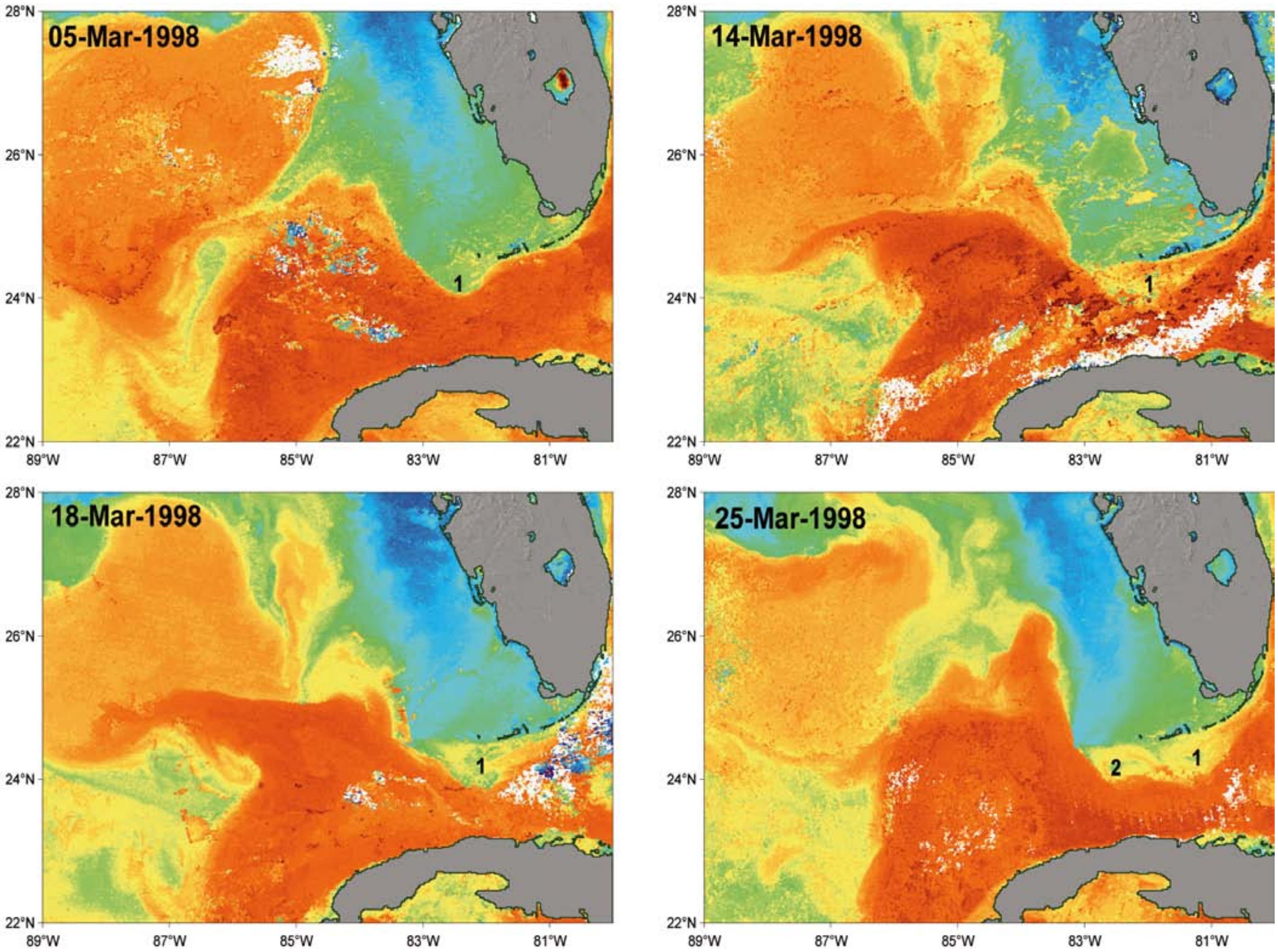

Figure 8.9 *Example of a sequence of satellite SST images used to infer gyre displacement and progression down the Straits of Florida (Yeung* et al., *2001). Warmer waters are red, cooler waters are blue. The centers of each of two gyres (***1** *and* **2***) present during this period are indicated. On March 5, a gyre (***1***) was centered off the Dry Tortugas; by March 14, it had begun moving downstream; and by March 25, the upstream frontal eddy (***2***) responsible for its displacement is clearly evident.*

off Looe Key during the presence of a gyre (Criales and McGowan, 1993, 1994).

Variability in the supply of larvae may be related to the development of mesoscale eddies and their associated countercurrents on the oceanside of the channels. Peak influx of spiny lobster postlarvae into the bay through the middle Keys coincided with the presence of eddy and countercurrent conditions (Figures 8.8, 8.9) (Yeung *et al.,* 2001; Yeung and Lee, 2002).

Temporal and spatial variability in the supply of spiny lobster postlarvae to Florida Bay nursery grounds may interact with local nursery-habitat structure to influence recruitment and year-class strength. Butler *et al.* (2001b) used an individual-based model to address this question. They tested eight scenarios of variability describing postlarval supply (Uniform, Volumetric, Gradient, Broken Stick–Static, Broken Stick–Variable, Pulsed, Aggregated, and Random). Their results indicated that random variation in the arrival of postlarvae among regions of the Florida Keys leads to the highest recruitment, whereas persistently patchy settlement (*i.e.,* pulsed and aggregated scenarios) yields the lowest. Analyses of field data suggested that the random supply was the most realistic scenario. Field data were based on artificial collectors positioned at eight sites in the Florida Keys.

Eddy transport processes may also affect supply and nutritional condition of pink shrimp and snapper presettlement stages entering Florida Bay through the Florida Keys. Influx of early-life-stage recruits was monitored monthly on the new moon for two years at two tidal channels on opposite ends of the middle Keys: Whale Harbor (east end) and Long Key Channel (west end). Back-counted birth dates based on counts of otolith daily increments suggested that snapper larval duration during the first year varied across species and ranged from 35.50 to 41.45 days (Jones *et al.*, 2001). Preliminary analyses of Year-2 samples suggested that larval durations differed from those of Year 1. Peak abundance of snapper larvae in the channels occurred in the summer of 1997 and was coincident with a well-developed Loop Current (high latitudinal extent) favoring gyre formation off the Dry Tortugas, where snapper spawning aggregations occur. Criales *et al.* (2003) showed that the temporal pattern of immigration of postlarval pink shrimp differed substantially between Long Key Channel and Whale Harbor Channel (Figure 8.10). The influx of postlarvae at Long Key channel was lower in magnitude but steadier than the influx at Whale Harbor. Long Key channel showed the highest postlarval influx in late spring–summer, whereas the postlarval influx through Whale Harbor (downstream from Long Key in terms of the Gulf Stream and associated shelf gyre processes) showed both spring–summer and winter peaks. The winter peak may be associated with the countercurrent generated by eddies (Figure 8.10). This high variability over small spatial scales suggests the influence of mesoscale processes.

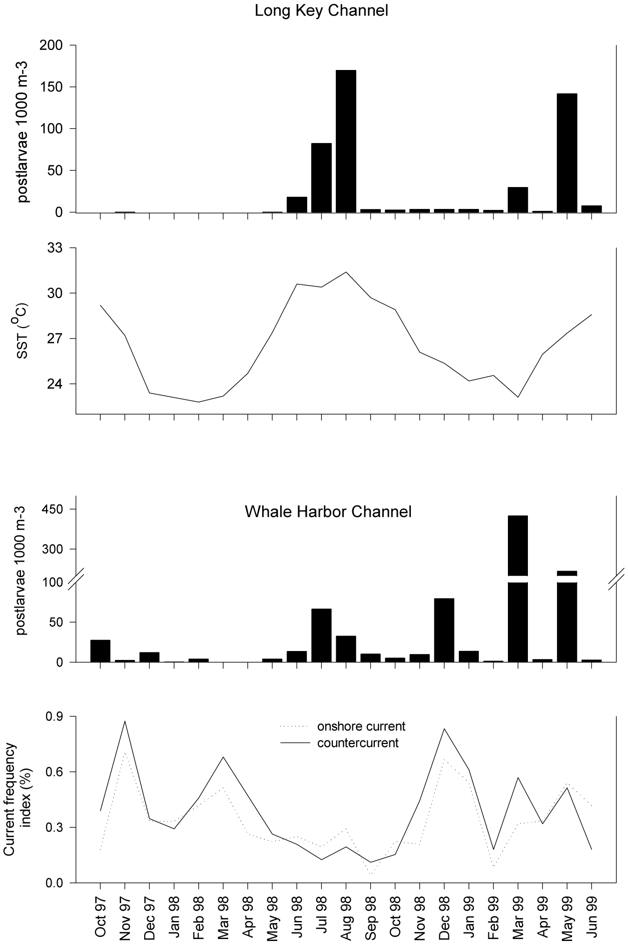

Figure 8.10 *Mean monthly postlarval influx of pink shrimp has different temporal patterns in channels of the middle Florida Keys (Criales* et al., *2003). At Long Key Channel (the two upper graphs), larval concentrations are associated with surface temperature. At Whale Harbor Channel, larval concentrations were associated with the coastal countercurrent flow.*

MOVEMENT INTO AND WITHIN FLORIDA BAY

Other working hypotheses that relate principally to movement of postlarvae into the bay are as follows: (1) Pink shrimp postlarvae enter Florida Bay from two directions: west (across the southwestern shelf) and southeast (through the Lower Keys). The western and southeastern pathways vary in importance and are affected differently by physical oceanographic factors and tides. (2) Sufficient numbers of pink shrimp larvae enter the bay's interior for the interior bay to be a significant nursery ground and source of recruits to the fishery during years of favorable conditions. (3) Snappers settle outside Florida Bay but near the boundary and enter Florida Bay as juveniles. (4) The abundance of bay-dependent species that are spawned offshore is lower in northeastern Florida Bay because of weak transport across the bay.

Transport across the lower and middle Keys has previously been the most recognized pathway of larval transport to Florida Bay because past studies (Criales and McGowan, 1994; Yeung, 2001) have shown that local winds, Florida Current flow, and coastal eddies interact to influence the onshore transport and recirculation of larvae in the Florida Keys. New work, based on synchronized sampling of postlarvae on both sides of Florida Bay, indicates that the dominant pathway of influx of postlarval pink shrimp into Florida Bay is from the west (Browder *et al.*, 2002). Peak concentrations of pink shrimp postlarvae in water moving into the bay from the west (through Sandy Key and Middle Ground channels) were substantially larger than in water moving into the bay from the southeast (Whale Harbor Channel). The temporal pattern from the west consisted of one large, sustained summer peak (Figure 8.11). In contrast, peak concentrations at Whale Harbor were observed in February, May, and July and were smaller (Figure 8.11). Prior studies examined the influx of pink shrimp postlarvae from the southeast (Allen *et al.*, 1980) and west (Tabb *et al.*, 1962; Roessler *et al.*, 1969; Robblee *et al.*, 1991), but these studies were not designed in a way that would allow us to make comparisons now.

Pink shrimp nursery grounds are on the western

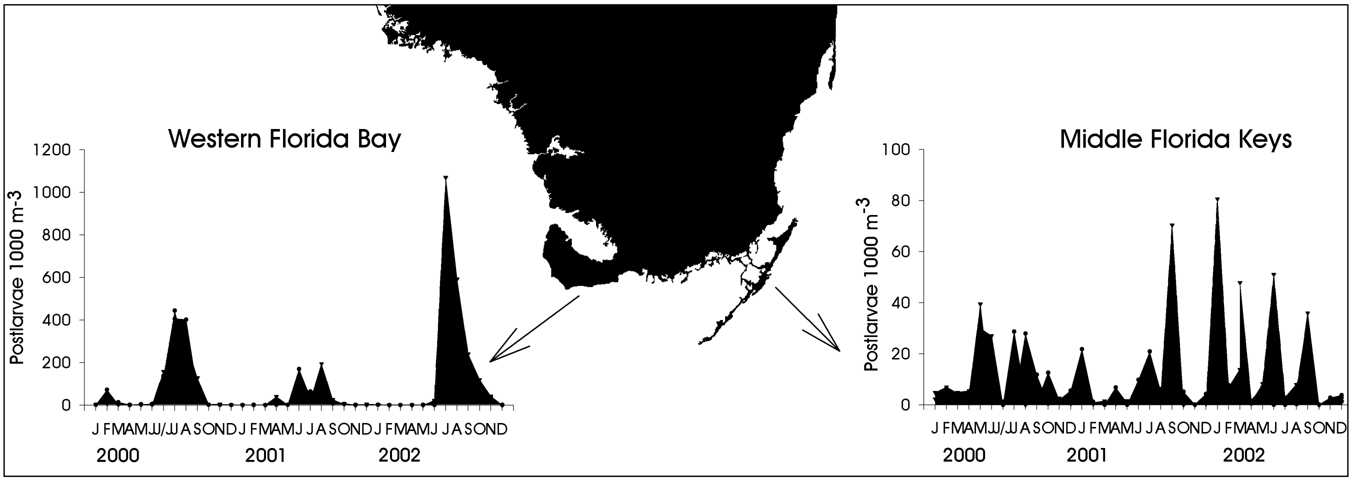

Figure 8.11 *The temporal pattern of monthly pink shrimp postlarval influx on the western side of the bay (upper-graph) differs from the Middle Florida Keys stations (lower-graph) but is similar to that at Long Key Channel the two previous years (Figure 10, upper graphs, (Criales* et al.*, 2003).*

side of the bay (Robblee *et al.,* 1991), not in the east (Costello *et al.,* 1986). The larvae spawned north of the Dry Tortugas on the relatively shallow shelf may escape from the strong flow of the Florida Current and move northeast toward the bay with the winds and tidal currents.

Effect of Human Activities

This topic was approached by addressing three major questions:

- What are the potential effects of water management and other human activities on recruitment, growth, and survivorship of HTLS?
- What is the potential effect of water management on bioaccumulation of mercury?
- How does fishing, both within the bay and outside the bay, affect fishery populations and our ability to detect effects of water management on recruitment, growth, and survival?

Some critical working hypotheses relative to these questions were as follows:

- The timing and amount of freshwater releases to coastal wetlands adjacent to Florida Bay affect the nesting success of wading birds in northeastern Florida Bay.
- Changes in water management that affect the spatial coverage, intensity, and duration of hypersalinity affect shrimp, lobster, and other species.
- Abrupt and out-of-season releases of large volumes of fresh water into Florida Bay and coastal waters adversley affect benthic fauna and fish, shrimp, and lobster recruitment.
- Increased freshwater inflow to northeastern Florida Bay will increase the load of mercury entering the bay and the body burden of mercury in bay HTLS.
- Fishing on the reef tract, in the Tortugas, and throughout the bay affects the population structure and abundance of predator fish species in Florida Bay.

WATER MANAGEMENT AND WADING–BIRD NESTING SUCCESS

Linkages of water management, fish production, and roseate spoonbill nesting success in wetlands adjacent to northern Florida Bay have been quantified in studies by Lorenz (2001a,b). Other investigators have proposed that fish availability to wading birds during their nesting season in south Florida is influenced by two main factors: the extent to which water covers wetlands during the wet season and the consistency of the decrease in water depth and water coverage during the following dry season. Lorenz (2001b) demonstrated the effectiveness of the process of expansion and contraction of water area in enhancing prey availability to wading birds in the coastal marshes immediately north of eastern Florida Bay. He determined that fish density during the wet season is positively related to water depth in the marsh and the length of time in which depths in the marsh are greater than 12.5 cm. He found that concentrations of fish in topographic lows occur—and reach roughly twice dry-down density—when water depths in the adjacent marsh decline below 12.5 cm. Roseate spoonbills that nest on islands in northeastern Florida Bay feed in these coastal marshes during the nesting season, which coincides with the usual dry season. Lorenz (2001b) examined their nesting record in relation to water-level data and determined that, in general, mean water levels at his fish-sampling sites in the coastal marshes were lower than 12.5 cm during successful roseate spoonbill nesting periods and higher than 12.5 cm during failed nesting periods. Furthermore, prey availability at the sites during successful nesting periods was twice that during failed nesting periods. On the other hand, nesting failed to occur during several recent years that might have been expected to support successful nesting. This failure may be explained by out-of-season water releases from the nearby C-111 canal. These releases have been shown to raise water levels in the coastal wetlands. Such releases during spoonbill nesting periods could cause prey to become dispersed and result in nesting failure.

The coastal marshes north of Florida Bay were principally oligohaline prior to the extensive drainage and water diversion that occurred with water management (Egler, 1952). Since the time that hydrologic modification was begun, mangroves have encroached inland, and there are other indications that the coastal marshes have become more saline (Ross *et al.,* 2000). Lorenz's (2001a) study of coastal fish populations demonstrated that fish densities were substantially greater and that community composition in the coastal wetlands immediately north of northeastern Florida Bay resembled that of an oligohaline marsh in recent years of exceptionally high rainfall, when conditions approximated predrainage conditions. Fish densities were substantially greater in the years of oligohaline conditions. This study demonstrated that it is possible to regain wetland productivity with restoration of more natural hydrologic responses to rainfall.

Several time series are being developed for birds in Florida Bay. The database on nesting activity in bald eagles extends back to the late 1950s and continues. The osprey database is also lengthy, albeit interrupted, and continues. Monthly data on the abundance and activity of water birds in Florida Bay is five years in length and still growing. These databases provide the opportunity to analyze bird activity in the bay in relation to freshwater inflow and other conditions that might affect these birds' food supply. This information also is available for use in trophic network models. Information on the diet of water birds in Florida Bay is very limited and largely anecdotal.

EFFECTS OF WATER RELEASES ON RECRUITMENT AND BENTHIC FAUNA

Some statistical studies have directly connected abundance indices from fishery data to indices of freshwater flow to Florida Bay and the southwestern coast. These freshwater flows are affected by water releases to ENP at the Tamiami Trail and by the management of water levels and releases in the South Dade Conveyance system on the eastern border of ENP. Changes in catch rates in fisheries can provide a rough index of change in relative abundance. In an analysis of ENP catch and effort data, Schmidt *et al.* (2001) found that an index of freshwater runoff to Florida Bay and adjacent coastal waters was positively related to snook catch rates but negatively related to spotted seatrout catch rates. Change in harvests can provide a rough index of abundance when change in effort is taken into account. Browder (1985) found a positive relationship between pink shrimp harvests in the Tortugas fishery and a freshwater inflow index (water levels at P35 in ENP). Analyses by Browder (2000) and Sheridan (1996) suggested that freshwater inputs as either rainfall or runoff influence pink shrimp catch rates. Browder's (1985, 2000) work suggested that the timing of freshwater inputs affects harvests and catch rates. Johnson *et al.* (2002a) found that water releases at the Tamiami Trail were a significant variable explaining the density of 9 of 11 dominant species in Florida Bay's forage fish assemblage (Table 8.2).

SPATIAL PATTERNS OF MERCURY AND METHYLMERCURY

Widespread patterns of elevated mercury (Hg) concentrations in game fish and forage fish have been observed in eastern Florida Bay (Evans *et al.,* 2001). Within this region, highest concentrations of both methylmercury and total mercury have been observed in water and sediments in the mangrove transition zone near the inflows of Everglades freshwater through Joe Bay and Little Madeira Bay (Rumbold *et al.,* 2003). Incubation studies with stable mercury isotopes revealed substantial *in situ* methylation in open-water bay sediments as well. Inputs of bioavailable Hg(II) may be a critical-determining factor driving this methylation. Concurrent seasonal variations in both methylmercury and total mercury concentrations were observed in sediment, water, and forage fish, with peak concentrations occurring during the warm rainy season near the coast, where Everglades runoff enters the bay. No significant long-term temporal trends in mercury levels in gamefish can be observed as yet for the period 1996–2001. From these results, it has been concluded that the sources of elevated mercury concentrations in fish from northeastern Florida Bay include (1) methylmercury in runoff from the Everglades and (2) *in situ* mercury methylation in sediments from both the mangrove transition zone and the open bay itself (Rumbold *et al.,* 2003). Mercury concentrations seem to be higher along a Taylor River–Little Madeira Bay sampling transect than along a C-111 canal–Joe Bay transect, suggesting that the urban and agricultural runoff that most strongly influences the C-111 canal–Joe Bay

Table 8.2 *Summary of forage fish models and significant factors. S = the factor was significant for that species. NS = factor was not significant. A number following an S means the significant effect was lagged by that many months. The bottom row represents the number of species where that factor is statistically significant.*

Species	Gear	Month	Temp.	Depth	Salinity	Habitat	Seagrass Type	Seagrass Density	Tidal Amplitude	Sea Level	Wind	Rain	Flow
Transitory species													
F. duoraram	S	NS	S	NS	NS	S	S*	S	S	S-3	NS	NS	NS
L. rhomboides	NS	S	S	S	NS	NS	S	S	S	NS	NS	S-1	S-1
Mojarras	S	NS	S	NS	NS	S	S*	S	S	S-2	S-2	S-2	S-2
Pelagic species													
A. mitchilli	S	S	S	S	S	S	S	S	S	NS	S-2	NS	S
Resident species													
O. beta	NS	S	S	NS	S	S	NS	S	S	NS	S-3	NS	S-3
G. robustum	S	S	NS	S	NS	S	S	S	S	NS	NS	S-2	S-1
F. carpio	S	NS	NS	NS	S	S	NS	NS	NS	NS	S	NS	S-2
S. scovelli	S	S	S	S	S	S	S	S	S	NS	NS	NS	S-2
M. gulosus	S	NS	NS	NS	S	S	S	S	S	NS	NS	NS	S-2
L. parva	S	NS	NS	NS	S	S	S	S	S	NS	NS	S-3	NS
H. zosterae	NS	S	NS	NS	S	S	S	S	S	NS	NS	NS	S-2
Significance	8	6	6	4	7	10	9	10	10	2	4	4	9

* The significant effect occurred only between presence vs. absence of seagrass.

transect is not the most important source of mercury to the bay and its biota. All of these processes could change with restored Everglades freshwater flows and might be further altered by changes in nutrient inputs and trophic processing.

EFFECT OF FISHING ON AGE STRUCTURE AND ABUNDANCE OF PREDATORS

Faunce *et al.* (2002) provided evidence that fishing in areas of northern Florida Bay open to recreational fishing affects target fish populations there. The modal length of gray snapper (*Lutjanus griseus*) along mangrove shorelines is substantially larger in the Crocodile Sanctuary of Everglades National Park, where fishing has been excluded since 1980, than in other parts of Florida Bay in Everglades National Park and the nearby Biscayne National Park, where fishing is allowed. Modal lengths were 25–30 cm TL in the Crocodile Sanctuary vs. 15–20 cm TL elsewhere. Future work may be needed to clearly separate effects of fishing from effects of differences in habitat. Ley *et al.* (1999) found a similar pattern. Other studies (Bohnsack *et al.*, 2001; Ault *et al.*, 2002a,b) suggest that fishing affects reef fish populations, some of which spend part of their life cycle in Florida Bay. On the other hand, Schmidt *et al.*'s (2001, 2002) recent analyses of Everglades National Park creel census data shows that catch rates were positively correlated with fishing rates for four target species—spotted seatrout, red drum, snook, and gray snapper—suggesting that fishing pressure was not affecting overall abundance.

Modeling Change in Higher-Trophic-Level Species

Two types of models have thus far been applied to HTLS research in Florida Bay. Empirical, statistical models have been used to explore data for patterns that suggest the major processes driving variation in species abundance and community structure. Complementing these models are simulation models, often incorporating population dynamics, to examine the sensitivity of individual organisms to varying characteristics of their habitat, such as bottom cover and salinity.

Statistical Models

EXPLORATORY GENERAL ADDITIVE MODELS

Johnson *et al.* (2001, 2002a,b) assembled a database for Florida Bay that integrated six independent forage fish/macroinvertebrate studies conducted between 1974 and 1997. The database was used to examine the dynamics of 11 key forage species. General additive models were used to determine which major forcing functions and habitat factors control the abundance and distribution of these key forage species. The most widely influential variables explaining abundance and distribution were seagrass density, habitat, and tidal amplitude, which were significant variables for 10 species, followed by seagrass type and freshwater inflow to the bay (9 species), salinity (7 species), and temperature and month (6 species). Depth, wind, and rainfall (4 species each) and sea level (2 species) were less important variables in predicting the abundances of forage species (Table 8.2). The U-shaped relationships of three species (*Gobiosoma robustum, Floridichthys carpio,* and *Lucania parva*) to salinity suggested they might be adapted to extreme conditions (high and low salinities). The majority of species were positively correlated with seagrass density, with the exception of the pelagic bay anchovy (*Anchoa mitchilli*), *F. carpio,* the toadfish (*Opsanus beta*), and the gobies *Microgobius gulosus* and *G. robustum,* which were more abundant in sparse seagrass. The specific types of bottom cover were important for seven animal species, as follows: *Syringodium* (*M. gulosus, Lagodon rhomboides, Hippocampus zosterae,* and *L. parva*), *Halodule* (*Farfantepenaeus duorarum, Syngnathus scovelli*), *Thalassia* (*G. robustum*), and no seagrass (*A. mitchilli*). Three taxa (*F. duorarum, L. rhomboides,* and *Eucinostomus* spp.) that spawned outside of the bay showed relationships with tidal amplitude, sea level, and/or wind, which suggests that transport mechanisms may affect abundance.

FORECASTS OF THE TORTUGAS SHRIMP FISHERY

Several empirical statistical models have been used to relate Tortugas catches or catch rates to indices of freshwater inputs to Florida Bay. Browder (1985) found a statistical relationship between quarterly Tortugas catches and the average water level in ENP monitoring well P35. Later, Sheridan (1996) developed a statistical model that related annual Tortugas catches to Everglades well data, rainfall data, and air temperature and sea level measured at Key West the previous spring and summer. The Sheridan model, which was updated every year with new data, successfully predicted Tortugas catches for the upcoming year for a number of years.

More recently, Browder (2000) developed a statistical model relating annual average Tortugas catch rates to the rainfall of several prior months. Two models were developed, one for recruits to the fishery (assumed to be shrimp in the 68-count per pound category) and another for larger shrimp. These models were designed to make rainfall-based predictions of catch rates that could be compared with observed catch rates to separate effects of south Florida's highly variable rainfall from effects of change in water management. Modeling results suggested that timing as well as quantity of rainfall influence catch rates. The two rainfall-based models, which were based on data for biological years (July–June) 1964–1965 through 1994–1995, had high r^2 (0.89 and 0.76, respectively), but their predictions differed greatly from observations in five subsequent years, when few if any water management changes had occurred (Browder, 2001, unpublished report).

A second empirical model was prepared (Browder, 2000) to test alternative configurations of the water management system proposed in the "Restudy" that developed the CERP. This model related Tortugas catch rates of recently recruited shrimp to releases of fresh water into Everglades National Park at its northern boundary immediately downstream from the leveed Everglades Water Conservation Areas. The model, based on data for the period 1964–1965 through 1994–1995, explained 92% of the variation in average annual catch rate. Total monthly water releases for several months of the year explained more than 57% of the variation in catch rate. The rest of the explained variance was due to other variables. These included large-shrimp catch rates the previous year and monthly average Key West air temperature (as a proxy for water temperature) for several months. The relationship between catch rate and water flow was positive for some months and negative for others, suggesting that timing as well as volume is important. When used in alternative testing, the model predicted consistently higher annual catch rates for the "Natural System" than for the "1995 base case" or any alternative, suggesting that south Florida's predrainage hydrologic system provided the best conditions for pink shrimp production. To make these predictions, the output of hydrologic models served as input to the shrimp model.

Another analysis examined pink shrimp recruitment to the Tortugas grounds in relation to observed salinity in the western and central bay (Browder, 2000). Because of limitations in available salinity data, the time series analyzed was very short compared to that available for relating recruitment to rainfall and water releases to Everglades National Park. A weak, but significant, relationship was found between monthly recruitment and time-lagged monthly average salinity in both areas.

Simulation Models

A simulation model was developed to predict survival, growth of juvenile pink shrimp cohorts, and potential harvests from these cohorts as a function of temperature and salinity in Florida Bay (Browder *et al.,* 1999). The model was recently refined with data from new laboratory experiments (Browder *et al.,* 2002). The model structure consists of three algorithms, which govern (1) physiological survival as a function of temperature and salinity; (2) growth as a function of temperature, salinity, and total length; and (3) survival from predation as a function of total length. The model is driven by observed daily temperatures and salinities from specific locations in Florida Bay. The model simulates juvenile densities in that part of the bay and potential recruitment (and related harvests) to the Tortugas fishery from that part of the bay.

A spatially explicit individual-based model for Caribbean spiny lobster (*Panulirus argus*) was developed in 1993 (Butler, 1994). Reformulations of the same model have been used to investigate a variety of issues, including (1) the potential effect on lobster recruitment of a massive loss of nursery habitat structure that was due to a sponge die-off (Butler, 2003), (2) the consequences of temporal and spatial variation in postlarval supply on recruitment (Butler *et al.,* 2001b), (3) the effect of nursery habitat structure and geographic specificity on recruitment (Butler *et al.,* 2001b), and (4) the direct and indirect consequences of altered salinity on recruitment (M. Butler, personal communication). The ecological aspects of recruitment included in this model start with the arrival of spiny lobster postlarvae in the nearshore nursery and terminate when larger juveniles begin to enter fishermen's traps. The recruitment process is explicitly incorporated into this model by superimposing on the model's spatial landscape the daily ecological processes faced by juvenile spiny lobsters: settlement, growth, shelter, selection, mortality, and movement. The model tracks each hypothetical lobster from settlement until recruitment to 50-mm carapace length. Settlement occurs once every 28 days, corresponding to the lunar cycle. Growth is a discontinuous process involving molts. Daily mortality is a function of various aspects of habitat and lobster-habitat interactions. Simulations with the model were run for observed extreme conditions: a wet year (1995) and a dry year (1993). The direct effects of salinity were limited to approximately 20% of the lobster nursery area, where salinity varies naturally. Simulation results suggested that lobster recruitment during a very wet or dry year would be similar. In both cases, recruitment declined by approximately 25% in the area directly affected by salinity changes, which resulted in an approximately 5% decline in recruitment over the entire Florida Keys region, as compared to control simulations where salinity was stable at 35 psu. Other simulations predicted that the lobster population would be surprisingly resilient to sponge die-off. Although nearly the entire sponge community was decimated over approximately 20% of the nursery area, this loss of habitat was predicted to result in only a 16% decline in lobster recruitment in the perturbed region and a 2% decline over the entire Florida Keys region. The model allowed a follow-up analysis of "why this is so." Apparently the effect was not just because the supply of postlarvae was three times higher in the post-die-off year simulated, but mainly because juvenile lobster movement to nearby unaffected areas and shifts in shelter use on sites affected by sponge die-off, a response supported by field evidence (Butler *et al.,* 1995; Herrnkind *et al.,* 1997).

Richards (2003) examined the relationships of temperature and salinity to growth rates in crocodiles (*Crocodylus acutus*) by tracking 30 radio-tagged hatchlings in the vicinity of the Turkey Point Power Plant for up to several weeks. Water temperatures in habitats in which the hatchlings were tracked were within the range 29°–35°C, a range in which temperature is not expected to have a detrimental effect on growth (Mazzotti *et al.,* 1986). Richards found that temperature had no effect on most measures of growth. Although laboratory work has shown that salinity has a strong negative effect on mass in hatchling American crocodiles (Dunson, 1982), field observations suggest that they can survive and grow in highly saline areas (Lang, 1975; Mazzotti, 1983). Richards also found that salinity did not significantly affect growth rates, supporting these field observations. Two of the individuals in very high salinities (approximately 60 psu) grew at the same rate as most individuals in low-salinity water. In the laboratory, Mazzotti and Dunson (1984) showed that hatchling *C. acutus* maintained in seawater (35 psu) grew well if given periodic access to brackish water (4 psu). Richards observed that hatchlings used hollows in the banks of canals and ponds and also that four individuals on five occasions (sometimes accompanied by other hatchlings) moved out of their low-salinity pond and into the hypersaline canal areas at night and returned to their pond the following day. These observations support the hypothesis that crocodiles may have behavioral adaptations for escaping adverse effects of salinity.

Substantial progress has been made in the development of a bioenergetically based individual larval spotted seatrout model to simulate metabolic rate, consumption, and growth as a function of temperature and salinity (Wuenschel *et al.,* 2004). The model follows the basic energy budget equation in which consumption equals the sum of metabolism, excretion, and growth, and each component is a function of fish size, temperature, and salinity, where appropriate. The final model will incorporate variability for each component, which will enable researchers to model a population of individuals, rather than just the average individual. Laboratory experiments (*n* = 779, SL 4.5–39.5 mm) provided the basic information for the model.

A spatially explicit prey-predator model for spotted seatrout and pink shrimp coupled to physical processes was developed for Biscayne Bay (Ault *et al.*, 1999, 2003; Wang *et al.*, 2003). The spotted seatrout component of the model was individual-based.

Ongoing Research

Projects

At the time of the 2001 Florida Bay Conference, five new (or continuing) HTLS projects funded for two years by the NOAA Coastal Oceans Program had barely started. Although these studies have made substantial progress to now, their results were not presented at the Florida Bay Conference, and only a portion of these results were available for this synthesis. These projects are briefly described below.

MODELING PINK SHRIMP RECRUITMENT FROM FLORIDA BAY

In this project, we are continuing to develop a simulation model and the associated performance measures to evaluate the potential effect that upstream water-management changes resulting from efforts to restore the Greater Everglades ecosystem have had upon Florida Bay. This work seeks to (1) clarify the effects of freshwater inflow and seagrass habitat on Florida Bay's pink shrimp nursery function, (2) determine the major influences of meteorological and oceanographic processes on postlarval pink shrimp and their recruitment to the fishery, and (3) improve the ability to predict recruitment to the Tortugas fishery in response to changes in water management. As part of this work, a spatially explicit recruitment model will be developed from the existing unit model; postlarval immigration pathways, transport rates, and influencing factors will be described and quantified; and historical data on pink shrimp density will be analyzed and used to further refine and verify the model.

REGIONAL ASSESSMENT OF SPONGE DYNAMICS AND SPONGE FISHERY IMPACTS

This project is part of a multiyear investigation of the hard-bottom communities of Florida Bay and the Florida Keys. It combines modeling, laboratory experiments, and fieldwork to explore the relationship of spiny lobster population dynamics to spatiotemporal patterns in the structure of bottom habitat and environmental variables. The current project focuses on sponges, but some elements also pertain to spiny lobsters and octocorals. The four principal objectives of the project are (1) to describe size-specific population dynamics information (*e.g.*, growth and reproductive status) needed to model and manage commercial sponge species, (2) to determine the effects of commercial fishing on sponges and the bycatch of the sponge fishery, (3) to experimentally test the tolerance (*e.g.*, survival, susceptibility to disease, changes in behavior) of selected hard-bottom-dwelling species (*e.g.*, five sponge species, two octocoral species, and three size-classes of spiny lobster) to different salinities and periods of exposure at winter (18°C) and summer (28°C) water temperatures, and (4) to incorporate new and existing information into a spatially explicit simulation model to quantitatively compare the effects of potential management strategies on the sustainability of the sponge fishery and its effects on hard-bottom community structure in the Florida Keys National Marine Sanctuary.

POPULATION STUDIES, ABUNDANCE, HABITAT USE, TROPHIC DESCRIPTIONS, AND REPRODUCTIVE STATUS OF MARINE TURTLES INHABITING FLORIDA BAY

The purposes of this study are (1) to capture and tag sea turtles in Florida Bay to continue long-term monitoring of individual growth rates, foraging-site fidelity, residency rates, health status, and trends in abundance, (2) to elucidate the trophic role of loggerheads as apex predators in Florida Bay, (3) to provide detailed descriptions of loggerhead habitat use and behavior, and (4) to examine the sexual maturity and reproductive frequency of adult-sized loggerheads inhabiting Florida Bay. The principal study area is the central-western region.

REEF–FISH COMMUNITY DYNAMICS AND LINKAGES WITH FLORIDA BAY

This continuing project will apply a visual sampling strategy to quantify coral-reef fish community changes. The project has the following goals: (1) to provide intensive and precise spatial and habitat-specific fishery-independent assessment of reef fish communities; (2) to document trends in reef fish size and abundance within and outside no-take zones in the Florida Keys reef tract; (3) to test specific hypotheses predicting continuing changes in reef fish communities as the result of no-take protection; (4) to provide a precise and spatially explicit database for assessing any future reef fish population changes resulting from Everglades restoration actions; (5) to provide managers with options for optimizing long-term survey design strategies to identify reef-fish population changes; and (6) to correlate the linkages between reef fish communities and fishing, habitat, oceanographic, and other physical processes to guide appropriate experimental studies on dynamic mechanisms and to develop predictive models.

DEVELOPMENT OF SPATIALLY EXPLICIT MODELS TO PREDICT GROWTH–POTENTIAL OF AGE–0 GRAY SNAPPER, *LUTJANUS GRISEUS*, IN FLORIDA BAY DURING RESTORATION OF FRESHWATER FLOWS

The general goal is to examine patterns of growth in juvenile gray snapper and develop a bioenergetic model of growth that is a function of temperature, salinity, and fish size. This model will be extended into a spatially explicit calculation of potential fish growth using historical environmental data as well as predicted changes in the environment of Florida Bay under different water-management strategies. Specific objectives are (1) to quantify patterns in juvenile gray snapper growth through a retrospective analysis of previously collected samples, (2) to examine the relationships between juvenile gray snapper growth and temperature and salinity using previously collected samples and historical monitoring data, (3) to develop an individual-based bioenergetic model for juvenile gray snapper under a range of temperature and salinity conditions, (4) to recalibrate and validate the bioenergetic model by comparing predicted growth with observed growth, and (5) to develop a spatially explicit model that predicts growth-potential of young snapper throughout Florida Bay under various freshwater flow regimes.

UPSTREAM LARVAL SUPPLY TO FLORIDA BAY—THE DRY TORTUGAS CONNECTION

This project explores the pathways and transport processes for migration of larval fish, shrimp, and lobster from the Dry Tortugas to Florida Bay. Emphasis is on the role of episodic, mesoscale events, such as those involving eddies and the Tortugas gyre. The hypothesis to be tested is that the presence of a coastal eddy enhances the influx of presettlement recruits into Florida Bay. Densities of incoming recruits in the middle and lower Keys during the presence and absence of an eddy are being compared. This is a continuation of a previous south Florida program project for which substantial progress has been made in relating spiny lobster larval transport to eddies and gyres (Yeung *et al.,* 2001). Planned work seeks to determine what happens closer to the origin of eddies at the Dry Tortugas and lower Keys and the importance of the western recruitment pathway in connecting the Dry Tortugas with Florida Bay over the southwestern Florida shelf. Coordinated sampling at Southwest Channel in the Dry Tortugas and bayside at Northwest Channel will attempt to link the newly spawned snapper larvae to subsequent early-settlement stages.

ATLAS OF LIFE HISTORIES OF JUVENILE AND SMALL RESIDENT SPECIES IN FLORIDA BAY

The atlas will include information on the range, reproduction, diet, spatial and temporal abundance and distribution, and length-frequency distributions in the bay. This work is being conducted with NMFS base funding.

ATLSS MODEL OF COASTAL WETLAND FISHES

A spatially explicit model of the resident fishes of the coastal wetlands is being developed by Cline *et al.* (2001) to further explore the relationships determined by Lorenz (2001a,b). The model uses the object-oriented modeling framework provided by the Across Trophic Level System Simulation (ATLSS), which is now being applied to the Everglades. Development of the coastal fish model will extend ATLSS into the coastal marshes and provide a basis for expanding the wading bird elements of ATLSS into the coastal zone.

Unresolved Issues and Questions: Research Needs

Criteria used to propose future research topics were as follows: (1) follow-up of promising recent research expected to sharpen or broaden answers to Question 5; (2) addressing promising new hypotheses that replace failed hypotheses; (3) development of performance measures based on species and communities most likely to be affected by CERP changes; and (4) addressing gaps in the current program when new information suggests higher priority should be assigned. The following series of topic areas fit one or more of these criteria.

LOCATION OF NURSERY AREAS OF MAJOR GAME FISH SPECIES

Many sought-after game fish species are found in Florida Bay as preadults and adults, but the current nursery grounds of most their populations are not delineated. This includes red drum, snook, tarpon, bonefish, and gray snapper. Recently, Powell (2003) delineated nursery grounds for spotted seatrout in central and western Florida Bay. Colvocoresses (unpublished data) found red drum juveniles in the East River of Little Madeira Bay at a salinity of 6 psu; however, efforts by Powell (2002) to find red drum nursery grounds in northern Florida Bay were unsuccessful, possibly because the appropriate salinity was not present during sampling. Efforts need to be directed at the southwestern mangrove estuaries of Everglades National Park, the most likely place to find the type of red drum habitat described by Peters and McMichael (1987) (*i.e.,* low-energy, low-salinity [range = 0–25 psu, mean = 7 psu], turbid, backwater environments"…of a river at the head of the bay"). Odum and Heald (1972) collected many red drum juveniles in the Whitewater Bay system (North River), and this system could be a nursery area for red drum found as adults and subadults in Florida Bay. Tabb *et al.* (1962) found early-settlement-stage bonefish and tarpon in the Buttonwood Canal–Flamingo area. There has been no follow-up to better define the nursery areas of these species. Early-settlement-stage snook have not been found south of Chokoloskee (T. Schmidt, personal communication), although similar habitat appears to occur between Chokoloskee and Cape Sable. The settlement grounds for gray snapper that enter the bay are not well defined, although Rutherford *et al.* (1989) identified mixed seagrass beds of *Syringodium-Thalassia-Halodule* in western Florida Bay as best settling-out habitats for juvenile gray snapper. The nursery areas of some of these species are likely to be in the front lines of changes caused by new water-management structure and operations. These nursery areas need to be delineated so that the potential effect of water-management changes on salinity patterns, nutrient inputs, and other conditions in these areas can be predicted.

INFLUENCE OF HABITAT AND ENVIRONMENTAL VARIABLES ON SPECIES COMPOSITION AND TROPHIC DYNAMICS

The following nonmutually exclusive hypotheses about factors influencing the abundance and relative abundance of water column and seagrass canopy species should be explored:

Hypothesis 1—Density and abundance of bay anchovy is related to salinity fronts.

Hypothesis 2—Density and abundance of canopy species is related to seagrass diversity.

Regional trophic-web models should be developed to integrate existing and future information on food webs and trophic structure in Florida Bay. Information on water birds and large marine vertebrates (sharks, rays, bottlenose dolphins, and sea turtles) should be incorporated into the models. The trophic-web models should be viewed as precursors to an ecosystem model to be developed in a subsequent funding phase. The work should include the use of stable isotope analyses, including use of museum specimens (assuming the work to develop methods for processing museum material has been completed).

Statistical analyses of historical resource survey data should be expanded and the results used to design and quantify trophic-web and ecosystem models. The database assembled by Johnson *et al.* (2001) provides the opportunity to develop trophic network models for Florida Bay. As a result of major differences in the food-web base, separate network models should be prepared for each of the bay's subregions (Butler *et al.,* 2001b; Chanton *et al.,* 2001; Evans *et al.,* 2001;). Network models previously prepared for the bay by R. Ulanowicz (University of Maryland) and A. Acosta (Florida's Fish and Wildlife Research Institute) would provide a starting point for a new effort. Acosta (personal communication) observed that network modeling suffered from a lack of biomass information on benthic organisms. This is still a serious deficiency, although some data on sponge biomass have been gathered. Molluscan samples collected by W. Lyons and archived at the Fish and Wildlife Research Institute could be used to develop data on molluscan biomass. Analyses and comparisons of trophic structure in the various regions of the bay could be used to organize information about HTLS and assess effects of salinity changes resulting from changes in water management.

FACTORS AFFECTING POSTLARVAL IMMIGRATION

IMMIGRATION INTO THE BAY'S INTERIOR

HTLS researchers, building on the work of physical oceanographers, have gained some knowledge about the pathways, mechanisms, and oceanographic factors influencing immigration of offshore-spawned larvae and postlarvae to the eastern edge of Florida Bay. However, little information exists on physical processes that influence the immigration of postlarvae onto potential nursery grounds in the bay's interior. This information is highly relevant because it would better elucidate the ecological importance and potential economic importance of reducing the frequency, duration, and intensity of hypersaline conditions in the interior of the bay. To what extent is and how much of the interior of the bay is accessible to offshore-spawned species? What factors cause the accessibility of the inner bay to vary? This information would allow researchers to determine what benefits of improved conditions might bring to these species. Greater coordination of biological and physical research on the movement of water and early-life stages into the bay's interior is needed. Physical research in the interior of the bay was initiated last year, opening new opportunities for collaboration.

IMMIGRATION TO FLORIDA BAY

Recent research suggests that the major pathway for transport of pink shrimp postlarvae from the Tortugas to Florida Bay may be across the southwestern Florida shelf. Research on larval immigration to Florida Bay nursery grounds from the west is hampered by a lack of physical oceanographic work that addresses questions biological researchers need to answer. For example, what dynamic, physical structures might enable early-life stages spawned near the Dry Tortugas to reach the bay from the west? Net flows across a hypothetical boundary of the bay stretching from Cape Sable to Marathon have been described (Smith, 2000), but the flow characteristics along the bay boundary (boundary of the bay proper) that stretches from Cape Sable to Long Key are less known. Water movement across this boundary from both the west and the south needs to be studied by oceanographers in integrated studies with biologists studying immigration of early-life stages onto Florida Bay nursery grounds.

EFFECT OF LARVAL BEHAVIOR AND FRESHWATER INFLOW ON LARVAL IMMIGRATION RATES

Freshwater inflow may provide directional cues or otherwise influence the rate of larval immigration from offshore spawning grounds to nearshore nursery grounds. This topic has not been explored with respect to Florida Bay species since Hughes (1969a,b) conducted experiments suggesting that presettlement pink shrimp postlarvae move vertically in the water column in response to salinity gradients. He proposed that this behavioral response resulted in net shoreward transport of postlarvae on flood tides. Hughes' results raise questions that have never been addressed regarding the possible role of freshwater inflow in postlarval immigration of pink shrimp and other species: Do the volume and timing of freshwater inflow influence the magnitude of influx of postlarvae to Florida Bay?

EFFECT OF SALINITY ON SURVIVAL AND GROWTH

Integrated studies that might include models, supporting field studies, laboratory experiments, and statistical analyses should be conducted to determine the relationships between salinity, survival, growth, and other biological processes. For example, the shrimp model should be applied to assessing potential nursery grounds in the mangrove estuaries of ENP and examining the possible effects of alternative management strategies on the larger Florida Bay system that includes these areas. Another needed application is in interpreting juvenile density data in relation to postlarval immigration and fisheries data. A spotted seatrout individual-based model should be developed to integrate all the recently acquired new information about this species in the bay. Questions about the impact of hypersaline conditions in the central bay on year-class strength of spotted seatrout need to be addressed. The lobster model should be expanded to integrate new information on salinity tolerance of lobster and living components of lobster habitat. Following up on modeling results, field experiments should attempt to quantify the effect on growth and survival of movements away from undesirable conditions (*i.e.*, hypersalinity or hyposalinity).

QUANTIFICATION OF SIZE–RELATED PREDATION MORTALITY

Better quantification of size-related predation mortality is needed to adequately address the effects of salinity on survival through the effect of salinity on growth. This issue is especially pertinent to pink shrimp, spotted seatrout, gray snapper, and lobster. Results are needed to refine and quantify simulation models.

EFFECTS OF WATER QUALITY ON SURVIVAL AND GROWTH

This question has not been specifically addressed in current research in Florida Bay. Effects of both nutrient enrichment and common chemical contaminants on Florida Bay fish and macroinvertebrates may be relevant to determining the effects of changes in water management.

EFFECTS OF BENTHIC HABITAT ON SETTLEMENT, SURVIVAL, AND GROWTH

What characteristics of habitat lead to initial settlement? How do characteristics of settlement habitat affect survival and growth? How faithful are animals to the location of first settlement? What causes movement and where do animals go? Information on these questions is needed to further refine simulation models.

IDENTIFICATION OF OTHER SOUTH FLORIDA COASTAL AREAS WITH ENHANCED MERCURY BIOACCUMULATION IN FISH

Previous work (Rumbold *et al.*, 2003) identified the transitional mangrove ecotone in northeastern Florida Bay as a region of enhanced mercury and methylmercury concentrations in water, sediments, and fish. In unpublished data, Evans found concentrations of mercury in red drum and crevalle jack from Whitewater Bay that were comparable to those found in the same species in northeastern Florida Bay. Whitewater Bay is a mangrove-dominated embayment just north of western Florida Bay that receives some runoff from the Shark River, an area of known mercury contamination in fish. It seems likely that other estuarine recipients of Shark River drainage could support fish with high mercury concentrations. The sensitivity of fish from the mangrove ecotone of the entire Ten Thousand Islands complex of southwestern Florida suggests the need for a monitoring program to establish mercury concentrations in susceptible fish species. A research effort to determine the mercury sources and responses to future CERP changes in the volume and timing of freshwater flows should be made.

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