

Florida Bay: A History of Recent Ecological Changes

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ABSTRACT: Florida Bay is a unique subtropical estuary at the southern tip of the Florida peninsula. Recent ecological changes (seagrass die-off, algal blooms, increased turbidity) to the Florida Bay ecosystem have focused the attention of the public, commercial interests, scientists, and resource managers on the factors influencing the structure and function of Florida Bay. Restoring Florida Bay to some historic condition is the goal of resource managers, but what is not clear is what an anthropogenically-unaltered Florida Bay would look like. While there is general consensus that human activities have contributed to the changes occurring in the Florida Bay ecosystem, a high degree of natural system variability has made elucidation of the links between human activity and Florida Bay dynamics difficult. Paleocological analyses, examination of long-term datasets, and directed measurements of aspects of the ecology of Florida Bay all contribute to our understanding of the behavior of the bay, and allow quantification of the magnitude of the recent ecological changes with respect to historical variability of the system.

Introduction

Rapid changes occurred in Florida Bay (Fig. 1) between 1987 and 1991. A multiyear drought was influencing southern Florida, and salinity in central Florida Bay approached 70. In the autumn of 1987, large expanses of seagrasses began to die-off across much of Florida Bay. Concurrent with the beginning of seagrass die-off, the shrimp harvest on the Tortugas Grounds declined to record lows. In 1991, turbidity and phytoplankton abundance in Florida Bay increased dramatically, reducing penetration of light in the water column. In hard-bottom regions of southwestern Florida Bay, a mass mortality of sponges followed the onset of increased turbidity. By 1991, concern for the health and integrity of the Florida Bay ecosystem was widespread among the public, management agencies, commercial fishermen, and scientists. From the concern over recent changes in Florida Bay emerged a joint program of the federal government and the State of Florida directed at restoring the greater Everglades ecosystem, including Florida Bay. As is often the case, the public's perceptions of the condition of Florida Bay, and of the possible causes of the changes, were only weakly supported by available scientific evidence. In this

paper, we outline the perceived problems of Florida Bay, review the published scientific research addressing these perceived problems, describe the unique ecosystem of the bay, and summarize the results of recent long-term research in the Florida Bay ecosystem.

The seagrass die-off that began in 1987 was characterized initially by the rapid death of dense stands of turtle grass, *Thalassia testudinum* (Zieman et al. 1988; Robblee et al. 1991). The appearance of seagrass die-off varied, most strikingly it was patchy in character often with abrupt boundaries. Unlike seagrass losses documented from many other places in the world (e.g., Cambridge et al. 1986; Giesen et al. 1990), this early die-off of seagrass was not accompanied or preceded by noticeable decreases in water clarity or increases in colonization by epiphytes (Robblee et al. 1991; Fourqurean et al. 1993). Evidence is mounting that hypoxia and sulfide toxicity may have been the proximate cause of this early die-off (Carlson et al. 1994), but the ultimate mechanisms leading to seagrass die-off are still poorly known. Factors hypothesized to have led to the early seagrass die-off include loss of the estuarine nature of the system over many decades; overdevelopment of seagrass beds; chronic hypersalinity; in-filling of the bay due to lack of severe storms; abnormally warm late summer and fall temperatures (Zieman et al. 1988); eutrophi-

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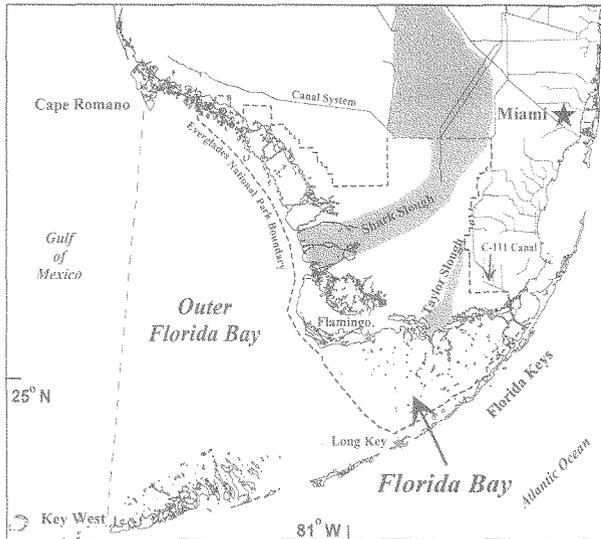


Fig. 1. Map of Florida Bay and the locations of freshwater flows and coastal water bodies that influence the bay.

cation (Lapointe and Clark 1992); and pathogens (Durako and Kuss 1994). Few of these hypothesized causal factors have been adequately investigated.

In the spring of 1991, Florida Bay exhibited a shift from a system characterized by clear water to one of extensive and persistent turbidity and phytoplankton blooms. While declines in water clarity were obvious to even casual observers, the magnitude of that change in clarity is difficult to assess because few historical data exist on phytoplankton abundance or turbidity in Florida Bay. The clarity of the water column for a few years immediately prior to and after 1991, however, can be compared. During the summer of 1988, Florida Bay was relatively clear, with light attenuation (k_d) from 13 sites across Florida Bay averaging $0.51 \text{ m}^{-1} \pm 0.19 \text{ m}^{-1}$ (Fourqurean and Zieman 1991). During 1989–1990, chlorophyll concentrations were very low throughout Florida Bay, generally around $1 \mu\text{g l}^{-1}$ (Fourqurean et al. 1993). Over the period August 1993 to September 1994, chlorophyll concentrations as high as $40 \mu\text{g l}^{-1}$ and k_d values as high as 2.82 m^{-1} were observed in central Florida Bay (Phlips et al. 1995; Phlips and Badylak 1996). Although such turbid water events are known as algal blooms, it is important to note that the majority of the light attenuation in the water column is attributable to suspended solids and color, not phytoplankton (Phlips et al. 1995).

Algal blooms in Florida Bay have had a negative impact on benthic flora and fauna. Attenuation of light in the water column reduced the amount of light reaching the bottom to levels below that required for the maintenance of seagrass beds over

much of the bay (Phlips et al. 1995). The algal blooms were not a constant phenomenon at any one location within the bay, rather they waxed and waned, becoming more widespread and intense during winter (e.g., Butler et al. 1995). Because seagrasses can withstand suboptimal light levels for some time by relying on stored energy reserves (Pirc 1985; Czerny and Dunton 1995), the response of Florida Bay seagrass to decreased light was tempered, as was the response of *Halodule wrightii* beds to reduced water quality associated with a brown tide in the Laguna Madre, Texas (Onuf 1996b). Other benthic organisms were more directly affected by the algal blooms. In southwestern Florida Bay, algal blooms caused near 100% mortality of sponges (of the genera *Speciospongia*, *Ircinia*, *Hippiospongia*, *Spinosella*, and *Vergangia*) between November 1991 and June 1993 (Butler et al. 1995). The mechanisms causing death in these sponges is not well understood, but may be due to direct toxicity of cyanobacteria, or to interference of filtering caused by the size or concentration of particles (Butler et al. 1995). Early life stages of the spiny lobster, *Panulirus argus*, the most valuable fisheries species in the Florida Keys (Hunt 1994), depend on sponges for shelter (Herrnkind et al. 1994); the loss of sponges was hypothesized to lead to a decrease in the nursery role of Florida Bay for spiny lobsters.

Florida Bay has been assumed to be the principal inshore nursery habitat supporting the Tortugas pink shrimp fishery, until recently the largest commercial fishery in Florida (Costello and Allen 1966). Shrimp harvests declined to historic lows during the latter half of the 1980s, roughly coincident with seagrass die-off in Florida Bay (National Marine Fisheries Service 1989; Robblee et al. 1991; Robblee and DiDomenico 1991; Nance 1994). Loss of seagrass habitat and declining environmental conditions in Florida Bay were hypothesized as the cause of the declines in the shrimp fishery.

Florida Bay is an area of variable salinity. Historically, hypersalinity in the bay has occurred as a result of cyclic drought conditions in south Florida (Fig. 2). Droughts in the 1950s, 1960s, and 1970s led to salinity exceeding 50 psu in the central parts of Florida Bay by the end of the drought period. The regional drought of 1987–1991 caused salinity in Florida Bay to rise steadily through 1990, for the years 1989–1990 large areas of central Florida Bay averaged over 50 psu (Fourqurean et al. 1992). The coincidence of seagrass die-off, declines in the harvest of shrimp, and hypersalinity focused attention initially on the possible role of hypersalinity, and the role of upstream diversion of freshwater, in precipitating the events in Florida Bay.

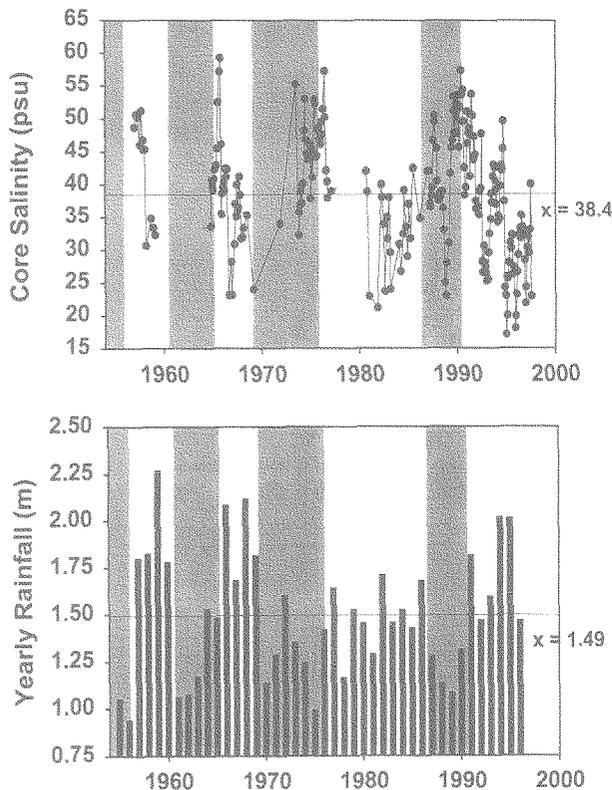


Fig. 2. Salinity data from the central region of Florida Bay indicate that salinity has been variable since the 1950s, with at least one major period of hypersalinity during each decade. Mean salinity of this region over the period has been 38.4‰. Yearly total rainfall at Miami International Airport since 1955 indicates the temporal pattern in rainfall; yearly mean at this station is 1.49 m. Shaded periods indicate periods of below-normal rainfall, note how salinity in Florida Bay is high following drought periods.

The watershed of Florida Bay, the Everglades, has been highly managed and engineered for agriculture, flood control, and water supply for a growing population in south Florida (Light and Dineen 1994). Since 1881, human activities have increasingly disrupted the natural flow of freshwater from the Everglades into Florida Bay. Water that might have flowed into Florida Bay has been diverted to tide in either the Atlantic Ocean or the Gulf of Mexico and stored upstream in conservation areas. It is not clear what effect these diversions have had on the environment of Florida Bay, but Smith et al. (1989) estimated that as much as 59% of the fresh water that flowed into the marine system from Shark Slough may have been lost to upstream water management.

Although the changes observed in Florida Bay over the last decade have focused attention on the linkages between the ecology of the bay and upstream water management practices, it is important to keep in mind that events in Florida Bay occurred contemporaneously with other ecological

events in the Caribbean-Gulf of Mexico region. Estuaries in the region experienced notable ecological events as well: the algal blooms in Florida Bay occurred at the same time as the brown tide, a bloom of a new species of phytoplankton in the class Pelagophyceae, was affecting seagrass beds in the Laguna Madre, Texas, on the western edge of the Gulf of Mexico (Onuf 1996a,b). A high incidence of bleaching was observed among many of the reef-building corals of the Florida Keys fringing reef (Jaap 1985; Williams et al. 1987). Bleaching was not restricted to the Florida Keys; corals from all over the world were affected (Williams and Bunkley-Williams 1990). An epidemic wiped out one of the major herbivores on Caribbean reefs, the long spined sea urchin *Diadema antillarum* (Lessios et al. 1983; Lessios et al. 1984).

To provide perspective on recent changes in Florida Bay, it is necessary to evaluate these phenomena relative to the historical variability of the ecosystem. This special issue of *Estuaries* brings together much of the long-term research on Florida Bay, with the goals being to understand the behavior of the ecosystem and to place the recent changes in historical perspective.

Description of the Florida Bay Ecosystem

PHYSICAL SETTING

Florida Bay (ca. 25°05'N, 81°45'W) is the body of water bounded on the north by the mainland of the Florida peninsula, on the east and south by the chain of islands known as the Florida Keys, and on the west by the Gulf of Mexico (Fig. 1). The exact geographical boundaries of Florida Bay are difficult to define, given the open nature of the connection between the Gulf of Mexico and the bay. To many, the geographical extent of Florida Bay is restricted to the shallow (< 3 m), mud-bank dominated region east of the boundary of Everglades National Park. To others, Florida Bay encompasses all of the area north of the Florida Keys and east of a line drawn from Cape Romano to Key West. To avoid confusion over the boundary of the bay, we will refer to the shallow area east of the Everglades National Park boundary as Florida Bay, and the more open area west of Florida Bay as outer Florida Bay. Long-term research has been concentrated within Florida Bay because of the recent ecological changes in this area and because Florida Bay lies almost entirely within Everglades National Park.

GEOLOGICAL SETTING

Florida Bay is separated from the Atlantic Ocean and the Straits of Florida by a nearly unbroken ridge of Pleistocene coralline limestone (the Key Largo Formation) that makes up the nearly con-

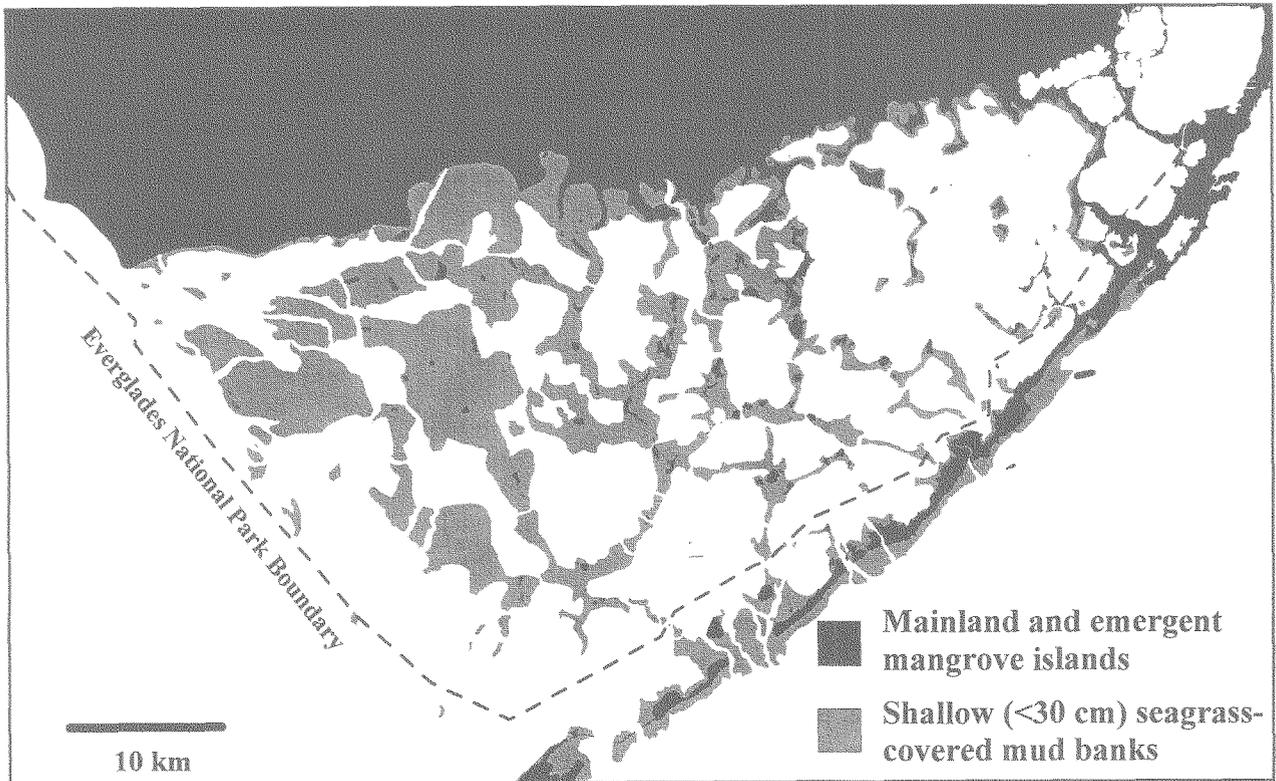


Fig. 3. Shallow carbonate mudbanks subdivide Florida Bay into a series of semi-isolated basins, which locally are called lakes.

tinuous barrier of the Florida Keys. Florida Bay is compartmentalized into basins (locally, called lakes) by a series of carbonate mud banks (Fig. 3). These mud banks lay on top of an almost planar surface of Pleistocene pelletoidal lime packstone and grainstone (the Miami Limestone, Perkins 1977). This microkarst has solution holes several centimeters deep. From the Florida mainland the surface slopes downward to the southwest, such that the bedrock is ca. 1.5 m below mean low water (MLW) in northeast Florida Bay and ca. 3 m below MLW along the southwestern margin of Florida Bay (Perkins 1977; Wanless and Tagett 1989). The mud that comprises the mud banks is of biogenic origin. The most important organisms contributing to the skeletal remains include calcareous green algae, seagrass epiphytes (spirorbid polychaetes, soritid foraminiferans, encrusting coralline algae), molluscs, and stony corals (Stockman et al. 1967; Nelsen and Ginsburg 1986; Bosence 1989; Frankovich and Zieman 1994). The slope of the limestone basement of Florida Bay and the rise in sea level in the Holocene led to a gradual flooding of Florida Bay. The southwestern portion of the bay flooded with seawater about 4,500 ybp, while the eastern parts of Florida Bay flooded as recently as 1,500 ybp (Enos and Perkins 1979). The spatial

variation in the relative rates of sediment accumulation and wave energy, coupled with sea-level rise, leads to four zones of mudbank dynamics in Florida Bay: an outer destructional zone, in which banks are being eroded faster than they are accumulating; a western constructional zone where mud supply outpaces sea level rise and therefore an area of bank accretion; a central migrational zone, in which erosion and deposition are quasi-equal so that the mud banks move about but are maintained in an equilibrium; and an inner destructional zone where banks are eroding due to scant sediment supply (Wanless and Tagett 1989; Fig. 4).

The mud banks in Florida Bay restrict circulation in the bay. Tides along the western margin of Florida Bay range from a Gulf of Mexico-influenced mixed semidiurnal tide with a mean tidal range of 61 cm in the Flamingo area, to an Atlantic Ocean-influenced semidiurnal tide with a mean tidal range of 17 cm in the Long Key area. Tidal energy is quickly attenuated by the mud banks, such that there is essentially no lunar tide over most of central and northeastern Florida Bay (Turney and Perkins 1972; Holmquist et al. 1989c). The passing of storm fronts and the associated change in wind direction can override lunar tides through-

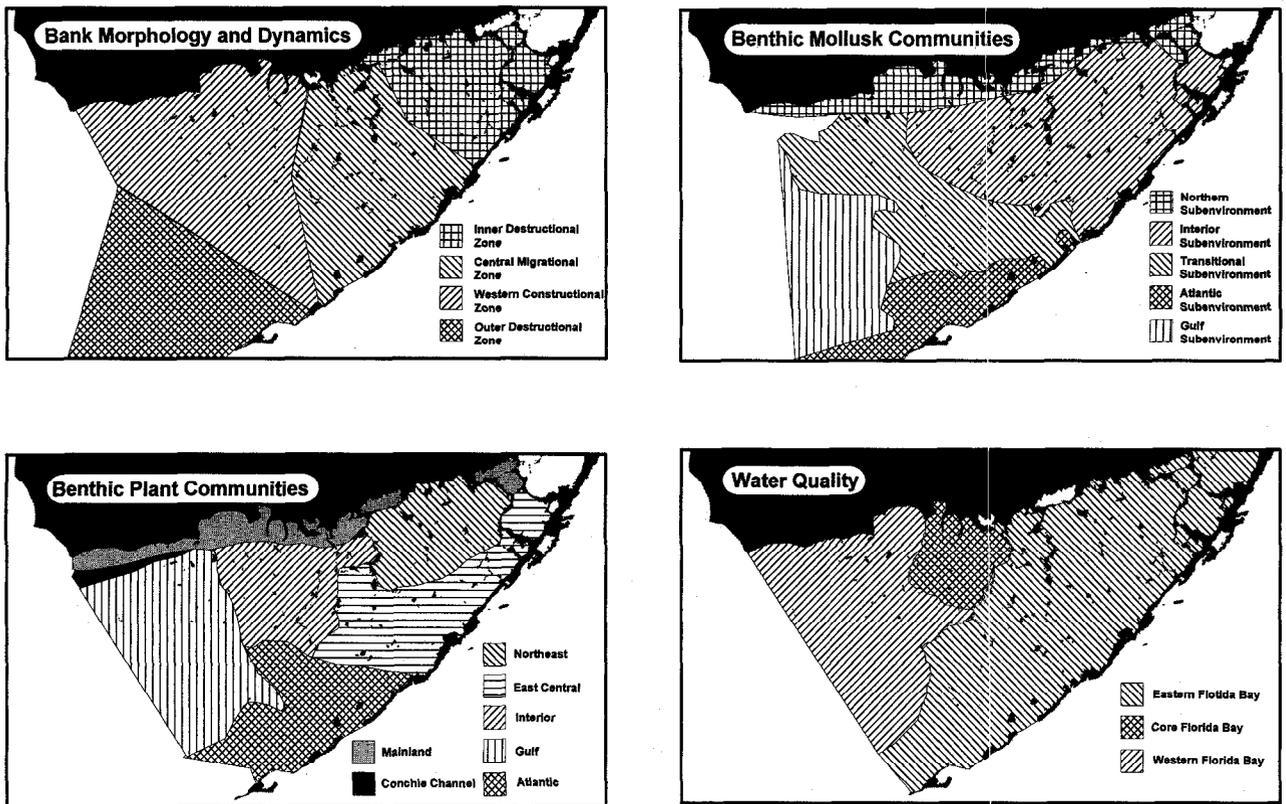


Fig. 4. Many schemes have been used to divide Florida Bay into discrete zones. A. Bank morphology and dynamics divide the bay into four zones (Wanless and Tagett 1989). B. Benthic mollusk communities indicate four zones (Turney and Perkins 1972). C. Benthic plant communities have been used as the basis for delineating six zones (Zieman et al. 1989). D. Water quality assessment supports the definition of three zones (Boyer et al. 1997).

out Florida Bay. Annual cycles in mean water depth lead to as much as a 30 cm difference in mean water level over the course of the year; water depths are greatest during August–November, and shallowest during February–May (Holmquist et al. 1989c).

HYDROLOGICAL SETTING

Florida Bay is subtropical, and experiences tropical savanna climate characterized by a relatively warm wet season from May to October and a cooler dry season from November to April. The bay receives about 1.2 m of rain a year, with roughly 75% of the precipitation falling in the wet season (Schomer and Drew 1982). Annual evaporation is of the same magnitude as precipitation. Mean annual temperature is 24.5°C, with a mean monthly low temperature of 20°C in January and a mean monthly high temperature of 28°C in August. Direct freshwater runoff into Florida Bay is primarily through Taylor Slough and indirectly as sheet flow overland from the C-111 Canal downstream into northeastern Florida Bay (Fig. 1). The importance

of groundwater flow of freshwater into Florida Bay is poorly known.

ECOLOGICAL SETTING

The water column in Florida Bay is generally oligotrophic, and historically phytoplankton biomass has been quite low throughout the system. Although phytoplankton in Florida Bay are generally phosphorus limited (Fourqurean et al. 1993; Philips 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 phosphorus (DIP) concentrations are near detection limits (20 nM), while concentrations of dissolved inorganic nitrogen (DIN) can be relatively high (median value 3.3 μM , but concentrations > 10 μM are not uncommon) and dominated by ammonium (Fourqurean et al. 1993; Boyer et al. 1997). Water quality characteristics have been used to subdivide Florida Bay into three major zones: a western zone of relatively stable marine conditions and near-Redfield N:P ratios for

seston; a central zone with a tendency to hypersalinity, high N:P ratios for seston, and high concentrations of dissolved organic matter; and an eastern zone with highly variable salinity and generally high concentrations of DIN and very high N:P ratios for seston (Boyer et al. 1997; Fig. 4).

Seagrass communities dominate the bottom of Florida Bay. Of the 2,000 km² of Florida Bay, 95% of the bottom is covered by seagrass (Zieman et al. 1989). This is only a fraction of the 5,500 km² of seagrass beds in the Florida Keys area (Iverson and Bittaker 1986). *Thalassia testudinum* is by far the most abundant species of seagrass in Florida Bay. Seagrass standing crop increases from ca. 30 g (dry wt.) m⁻² in northeastern Florida Bay to ca. 125 g (dry wt.) m⁻² along the western margin (Zieman et al. 1989). This east-west gradient is driven by gradients in sediment accumulation (Zieman et al. 1989) and availability of phosphorus, the limiting nutrient for seagrass growth in Florida Bay (Fourqurean et al. 1992).

Characteristics of the benthic plant communities were used to delineate six ecological zones within Florida Bay in 1984, before the seagrass die-off (Zieman et al. 1989; Fig. 4). Northeast Florida Bay was characterized by sparse, patchy beds of *T. testudinum*, interspersed with locally abundant *Halodule wrightii*. In east-central Florida Bay, greater sediment accumulation allowed greater biomass of *T. testudinum* than in the northeast, and *H. wrightii* was rare. The interior of Florida Bay was a dense monoculture of *T. testudinum*. The mainland region was very heterogeneous, with dense *T. testudinum* beds interspersed with dense beds of *H. wrightii*; *Ruppia maritima* was also locally abundant. The Gulf region was a dense mixture of *T. testudinum*, *H. wrightii*, and *Syringodium filiforme*. In the Atlantic zone, dense stands of *T. testudinum* were restricted to mudbanks; in deeper waters, there was generally a hard-bottom community of sponges and soft corals.

Variation in the physical environment of Florida Bay is reflected in the abundance and distribution of faunal species and has led to distinct mollusc communities in Florida Bay (Turney and Perkins 1972; Fig. 4). Fish and invertebrate communities in Florida Bay are a mixture of Antillean, Caribbean, and Gulf of Mexico species. Over 250 species of fish have been recorded from Florida Bay (Lofthus 1994). Fluctuating environmental conditions and lack of suitable habitat are thought to restrict much of the very diverse tropical fish (over 500 species) and invertebrate fauna found on the Atlantic Ocean side of the Florida Keys (Starck 1968; Holmquist et al. 1989b) from penetrating and establishing within Florida Bay. Generally animal density and diversity decreases from west to east in

Florida Bay (Holmquist et al. 1989b). This pattern is driven by the gradients in seagrass density, seagrass species composition, net tidal flow, temperature and salinity (Sogard et al. 1989; Thayer and Chester 1989). Most species with Antillean affinities are present only along the southwestern boundary of the bay (Holmquist et al. 1989a, b). Sponges, hard corals and soft corals are generally limited to hardbottom habitats found in southwestern Florida Bay. These habitats provide critical habitat for tropical species enhancing the diversity gradient present in the bay.

Florida Bay stands out in South Florida for its nursery and sport fishery function. Lobster (*Panulirus argus*) and the pink shrimp (*Penaeus duorarum*) support large fisheries, and both are critical to the economy of South Florida. These crustaceans are dependent on Florida Bay during their early life stages. Many of the commercially and recreationally important fish species (e.g., gray snapper, *Lutjanus griseus*; snook, *Centropomus undecimalis*; red drum, *Sciaenops ocellata*) live in Florida Bay as adults, but spawn outside of Florida Bay. On the other hand, spotted seatrout (*Cynoscion nebulosus*) spend their entire life in the bay. Florida Bay supports a sport fishery from which 700,000–800,000 fish are removed annually by hook-and-line (Tilmant 1989). Most commercial harvesting of fish from Florida Bay was stopped when the bay was added to Everglades National Park in 1950. Until the early 1980s commercial fishermen removed large quantities of striped mullet (*Mugil cephalus*), spotted seatrout, and gray snapper from Florida Bay (Tilmant 1989).

Florida Bay supports one of the most species-rich piscivorous avifaunas in North America. Fourteen species of long-legged wading birds (Ciconiiformes), in addition to large populations of brown pelicans, double-crested cormorants, shore birds and birds of prey, occur in Florida Bay. Some species of birds have had stable or growing populations over the last century, for example great white herons, roseate spoonbills, and reddish egrets (Powell et al. 1989b) and bald eagles (W. B. Robblee unpublished data). Other species are declining, however. Osprey populations have declined about 50% in Florida Bay, presumably because of poor habitat quality and low food supply (Bowman et al. 1989). In addition to the diverse bird fauna, other threatened and endangered vertebrates occur in the bay, including American alligators (*Alligator mississippiensis*), American crocodiles (*Crocodylus acutus*), green sea turtles (*Chelonia mydas*), and West Indian manatees (*Trichechus manatus*).

Summary of Contributed Papers

The 14 research papers in this volume contribute a great deal to our knowledge of the Florida Bay ecosystem. Paleoecological studies help to put recent changes in the bay ecosystem into an historical perspective. Long-term monitoring projects describe in detail the magnitude of the recent changes in the bay's ecosystem within the necessary context of spatial and temporal variability and address hypothesized relationships between biological characteristics of the bay and driving variables. Both types of research can be used to evaluate the potential effects of management of the south Florida ecosystem on the status of Florida Bay.

PALEOECOLOGICAL HISTORY

Quantitative data on the state of the Florida Bay ecosystem date back to the 1950s, when systematic surveys of Florida Bay were conducted (Finucane and Dragovich 1959; Tabb et al. 1962). These data provide an incomplete and biased representation of the bay because many of the anthropogenic changes to the watershed of Florida Bay had already occurred by the 1950s (Light and Dineen 1994) and because climatic cycles may operate over decadal time scales or longer. However, the history of the bay has been recorded in the skeletons of organisms inhabiting the bay: analysis of coral and sediment cores allows us to infer past environmental conditions. Paleoecological studies suggest Florida Bay is more isolated from upland and oceanic influences now than in the 1800s, that the mean salinity of all of Florida Bay is higher, and that the magnitude of salinity variation may have increased in central and eastern Florida Bay.

Previously published analyses of chronologies from corals collected in extreme southwestern Florida Bay indicated that conditions in the bay seem to have changed abruptly in the early part of the twentieth century. Coral fluorescence patterns suggest a major (up to 59%) decrease in freshwater runoff to Florida Bay during the period 1912–1931 and a decoupling of runoff and rainfall after 1931 (Smith et al. 1989). Construction of the causeways of the Overseas Railway in the Florida Keys during 1906–1914, which effectively reduced the exchange of water between the Atlantic Ocean and Florida Bay, coincides with periods of below-average growth rates of coral in the bay (Hudson et al. 1989). The isotopic composition of coral skeletons also indicates there was a major change in the environment of southwestern Florida Bay during the period 1907–1912; $\delta^{18}\text{O}$ records suggest that the bay became slightly more saline after this period, and $\delta^{13}\text{C}$ data indicates that organic matter oxidation increased after this period (Swart et al. 1996).

These results imply that mixing between Florida Bay and the surrounding ocean changed.

A major limitation of the published coral chronology work for Florida Bay is that all of the data come from two coral heads that are very close together in southwestern Florida Bay; hence our ability to infer past conditions in other parts of the bay has been limited. Swart et al. (1999) examined how the variation in the stable isotopes of C and O in smaller corals from other regions of Florida Bay, and found that these smaller corals showed variations similar to the larger, well-studied corals, suggesting the long-term records from southwestern Florida Bay can be applied bay-wide. They reexamined the record from the well-studied corals and concluded that, while there have been periods of hypersalinity throughout the record (1824–1993), the 1989–1990 period had the highest salinity signal (as recorded by oxygen isotopes) in the record.

Corals are not the only organisms that record chemical proxies of water quality. Small mollusc shells also record the degree of oceanic and terrestrial influence at sites across the bay; $\delta^{13}\text{C}$ of the shells of *Brachiodontes exustus* and *Transennella* spp. is heavier at more marine sites, and $\delta^{18}\text{O}$ of the shells is lighter at more marine sites (Halley and Roulier 1999). Moving down the core, the analyses of these mollusc shells indicate water chemistry of the bay changed during the period 1910–1940; the $\delta^{13}\text{C}$ of these shells indicate circulation in the bay decreased during this period, leading to increased oxidation of organic matter within the bay. These data corroborate the finding of a major shift in Florida Bay water quality early in this century as indicated by coral chronology.

The community composition of small, shell-forming invertebrates is also influenced by environmental conditions. Brewster-Wingard and Ishman (1999) found that modern foraminiferal and mollusc assemblages were correlated with salinity and substrate type. They used these correlations to interpret changes in the environment of Florida Bay as recorded in two cores from the central bay. The composition of the faunal assemblages at these sites suggest average salinity has been increasing in Florida Bay from 1880 to the present, and that salinity fluctuations have had greater frequency and amplitude since about 1940.

LONG-TERM DATASETS

In light of the paleoecological data that indicate that Florida Bay has been changing over time scales of 100+ years, it may be a misnomer to refer to any of the datasets documented in this special issue as "long-term," because the longest period covered by any of the physical and biological data

sets is 30 yr (Ehrhardt and Legault 1999). Systematic monitoring of salinity, water level, and rainfall began in Florida Bay in the early 1980s, only after it was recognized that upstream water management practices were affecting Florida Bay. This physical monitoring network was expanded, and water quality monitoring implemented, only after the seagrass die-off of the late 1980s.

Because most of Florida Bay is within Everglades National Park, many of the components (e.g., seagrass communities and grassbed resident fishes, decapod crustaceans, larval fishes) of the Florida Bay ecosystem had been inventoried by the Park before the events of the late 1980s. Using these data sets, comparisons of the state of the ecosystem before and after the seagrass die-off and algal blooms can be made. Surveys of the distribution and abundance of seagrasses and macroalgae were conducted in 1983–1984 (Zieman et al. 1989), providing a baseline for comparison of the baywide effects of the seagrass die-off. Hall et al. (1999) found that the distribution of the dominant seagrass species (*Thalassia testudinum*) was no different in 1994 than in 1984; but the biomass of *T. testudinum* was 28% less in 1994 than in 1984. The abundance of the subordinate seagrass species (*Halodule wrightii* and *Syringodium filiforme*) decreased by over 90% between surveys. This comparison illuminates an important point: even though the original seagrass die-off event affected only dense seagrass beds dominated by *T. testudinum*, the ecosystem-level effects followed caused an almost complete loss of other seagrass species.

Quantitative surveys of the seagrass-resident fish and crustacean communities on representative shallow banks in Florida Bay were conducted by G. V. N. Powell and his colleagues prior to the seagrass die-off in the mid 1980s (Sogard et al. 1987; Holmquist et al. 1989a; Sogard et al. 1989). A comparison of the fish community at that time with the fish community present 10 yr later revealed that differences were confined to sites affected by seagrass die-off (Matheson et al. 1999). The 1987–1989 seagrass die-off was density dependent, with only the dense *Thalassia testudinum*-dominated meadows experiencing die-off (Robblee et al. 1991; Hall et al. 1999). Following the seagrass die-off, the faunal communities associated with these dense seagrass beds in the mid-1980s changed much more than communities from less well-developed seagrass beds following the seagrass die-off. At sites that experienced a loss of seagrass cover, seagrass canopy-dwelling fish and crustaceans (e.g., the rainwater killifish, *Lucania parva*; and the caridean shrimp, *Thor floridanus*) declined markedly (80–90%), while seagrass-independent ben-

thic forms (e.g., the code goby, *Gobiosoma robustum*) generally increased (Matheson et al. 1999).

Seagrass die-off and subsequent algal blooms were significant enough to affect not only seagrass-bed resident species but other components of the ichthyofauna as well. Composition and abundance of the fish fauna susceptible to trawls was different in 1994–1996 than before the 1987–1989 seagrass die-off (Thayer et al. 1999). Prior to the seagrass die-off, fish abundance and diversity was highly correlated with seagrass abundance and species composition in Florida Bay (Thayer and Chester 1989). Following the seagrass die-off and algae blooms, total density of juvenile and small adult fishes did not change, despite significant reductions in seagrass density (Thayer et al. 1999). However, the species composition and trophic position of the fish fauna did change. There was an increase in the importance of pelagic, planktivorous fish species (e.g., *Anchoa mitchilli*, the bay anchovy) after the seagrass die-off and the advent of persistent algal blooms. The density of larval forms of these planktivorous fishes also increased compared to the mid 1980s, but the densities of demersal fish larvae were not different in 1994–1996 compared with 1984–1985 (Powell et al. 1989a).

These decadal scale comparisons of components of the Florida Bay ecosystem present compelling evidence for changes in the structure and function of the Florida Bay ecosystem. Seagrass die-off was followed by a decrease in the abundance and diversity of animals that are dependent on seagrass habitat. The relative importance of a planktonic food web increased in comparison to a seagrass-based detrital food web.

Decadal comparisons have an inherent weakness: while they may provide excellent data on the differences between two time periods, it is difficult to determine whether differences are the result of a trend or merely within the range of the natural variation within the system. The three decadal comparisons presented in this issue are relatively robust because they generally compare measures made over multiple years for each time period; but they still represent only two points in time. Continuous monitoring programs are needed to determine if significant differences, such as the differences between pre- and post-die-off periods documented in these three papers, are the result of long-term trends.

Florida Bay is an important nursery supporting the Tortugas shrimping grounds (Costello and Allen 1966). Because of this fishery's economic importance, landings and catch per unit effort have been monitored since 1960 (Bohnsack et al. 1994). Ecological changes in Florida Bay provide the opportunity to evaluate the relationship of Florida

Bay and the Tortugas fishery. Ehrhardt and Legault (1999) have capitalized on this long-term record of fisheries statistics, and from it have generated estimates of pink shrimp recruitment to the Tortugas fishery. A model that considers regional rainfall, temperature, sea level, and wind speed was successful in predicting variations in recruitment in the fishery. Because Florida Bay is hypothesized to be the nursery area for this fishery (Nance 1994), Ehrhardt and Legault have used variations in recruitment to the fishery over the past 30 yr to infer the status of the Florida Bay ecosystem. Similarly, Browder et al. (1999) observed relationships between juvenile shrimp density in western Florida Bay and these variables as well as with water level upstream in the Everglades; sea-surface temperature was strongly correlated with the density of juvenile shrimp. Hence these authors conclude that variations in the 30-yr fisheries data can be used to infer habitat quality of the nursery area, Florida Bay, supporting the Tortugas fishery. There was a very significant reduction in pink shrimp recruitment during the period 1982–1993; roughly coincident with the major ecological events in Florida Bay (hypersalinity, seagrass die-off, and algal blooms). Rebounds in recruitment in 1994–1995 suggest that Florida Bay has regained some of its quality as a shrimp nursery following these ecological events. Using a growth and survival model, Browder et al. (1999) demonstrate that large year-to-year variation in recruitment conditions for the Tortugas fishery may occur on some nursery grounds, and that production may differ considerably among nursery grounds within the same year simply as a function of differing temperature and salinity in the different nursery areas.

Since the 1930s there has been a recognized need to monitor the status of the American crocodile in Florida Bay, when it was realized that this population was isolated, declining, and threatened by human activities in South Florida. Mazzotti (1999) has analyzed data on nesting of crocodiles in Florida Bay over the period 1970–1995, and found that nesting attempts increased over the time period while nesting success decreased slightly. Most of the increase in nest attempts occurred in northwestern Florida Bay, representing a significant westward expansion of the crocodile's range in Florida Bay since the 1970s. While the increases in nest attempts, and therefore population size, augers well for the survival of the crocodile population in Florida Bay, Mazzotti points out that human-induced changes in groundwater levels and surface water salinities have the potential to affect nest success and crocodile growth rates. There is the potential for humans to manage freshwater

flow in South Florida to augment the population of the endangered American crocodile.

The salinity of surface water in the mangrove forests along the northeastern margin of the bay is controlled by freshwater runoff to northeast Florida Bay from Taylor Slough and the C-111 Canal. These mangrove swamps support not only crocodiles, but are also the primary foraging ground for many of Florida Bay's nesting wading birds during the dry season. Many sportfish species also forage in these mangrove habitats. The community of small demersal euryhaline fishes are a critical component of the mangrove food web; they are the prey base for larger organisms, and they are consumers of smaller prey. Water levels and salinity strongly influence the biomass of small fish found in the mangroves (Lorenz 1999). Composition of the fish community is also dependent on salinity; so changes in amount and timing of freshwater flows have the potential to change the small euryhaline fish community of the mangrove zone and thereby alter the mangrove food web.

Freshwater flows in south Florida have been extensively engineered to provide flood control and drainage of wetlands for agricultural and urban uses (Light and Dineen 1994); these engineering projects have changed the flow of freshwater (Smith et al. 1989) and undoubtedly the loading of nutrients into Florida Bay. Cultural eutrophication of Florida Bay, the result of human-induced changes in nutrient flows to the bay, has been suggested as a cause of the recent changes in the Florida Bay ecosystem (Lapointe and Clark 1992). There is good evidence that domestic wastewater is a significant source of nutrients for the groundwater and confined embayments and canals of the Florida Keys (Lapointe et al. 1990; Lapointe and Clark 1992; Lapointe and Matzie 1996); however, the contention that nutrient loading from the Everglades watershed to Florida Bay may be responsible for eutrophication of the bay has not been confirmed. Indeed, Fourqurean et al. (1993) cite distribution patterns of nutrients in Florida Bay as evidence that freshwater runoff is a minor contributor to the nutrient budget of Florida Bay.

Rudnick et al. (1999) found that the annual loading of nitrogen and phosphorous to Florida Bay from the Everglades watershed was variable and largely controlled by the volume of water flowing into Florida Bay. These nutrient loadings are nitrogen-enriched with respect to phosphorous; and the Everglades marshes and sloughs are presently removing a major fraction of the nitrogen and phosphorous in the water that flows through the watershed before discharging into Florida Bay. Rudnick et al.'s budgetary analysis concluded that loading of N and P from the Everglades is a small

part of the total mass balance of these elements in Florida Bay; less than 3% of the P inputs and less than 12% of the N inputs to Florida Bay come from freshwater runoff. The long-term data records of freshwater flow in the Everglades contain no indications of anomalously high freshwater discharge in the years leading up to the seagrass die-off in 1987, but there was a very high input of P into the headwaters of Shark Slough in 1985 (Rudnick et al. 1999). As these authors point out, P that flows into the headwaters of Shark Slough is rapidly taken up by the oligotrophic Everglades marsh and it is very unlikely that this pulse of P ever reached Florida Bay. If human alteration of nutrient loading were responsible for the seagrass die-off, then the die-off could only be the cumulative response to decades of nutrient loading. In contrast to most other estuaries, because human alteration of the Everglades watershed has surely decreased the flow of water to Florida Bay (Smith et al. 1989; Light and Dineen 1994), it is likely that humans have actually decreased the watershed's contribution to the nutrient budget of Florida Bay. Another interesting component of the behavior of Florida Bay is that increased freshwater loading may actually lead to a decrease in the phosphorus content of the water column. Freshwater entering the mangrove forest on the northern fringe of the bay from Taylor Slough has a lower P content than normal bay water; hence freshwater dilutes the P content of the water column (Boyer et al. 1999; Rudnick et al. 1999).

Water quality, as indicated by nutrient concentration and phytoplankton abundance, of Florida Bay was not a concern of managers before the seagrass die-offs during 1987–1989 and the subsequent algal blooms. Because there were no perceived problems, data on these aspects of water quality are very scarce for the period preceding the ecological changes in the bay. Regular assessment of water quality in the bay began in 1989 (Fourqurean et al. 1993; Boyer et al. 1997). Water quality is spatially variable within the bay, and it varies on intra- and interannual time scales (Boyer et al. 1999). In all of Florida Bay, salinity decreased from 1991 to 1997. The decrease was the result of lessening of the regional drought since 1990 (Fig. 2). Water clarity in Florida Bay declined markedly in 1991; this decline has been attributed to plankton blooms but it is important to note that a large component of the change in water clarity is an increase in suspended non-phytoplankton particles (Phlips et al. 1995). Phytoplankton abundance exhibited different patterns in each zone of the bay: chlorophyll concentrations decreased markedly over the period in the eastern bay; increased from 1989 to 1994 then decreased in the central bay; and

have not changed in the western bay (Boyer et al. 1999). In contrast to the patterns of phytoplankton, turbidity has increased in all areas of the bay since 1991. In a seagrass-dominated ecosystem like Florida Bay, any increases in turbidity are likely to have an impact on the seagrasses, the dominant primary producers in the ecosystem. It is likely that the loss of seagrasses from Florida Bay between 1984 and 1994 is partially because of the increased turbidity of the water column (Hall et al. 1999).

Unfortunately, so few in situ measurements of water clarity and bottom cover exist for the period preceding the seagrass die-off and algal blooms of the late 1980s and early 1990s. This lack of data can be partly ameliorated by using archived satellite images. Stumpf et al. (1999) have collected 12 yr of images from National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer (AVHRR) satellite. Using field-collected data on water clarity, chlorophyll concentration, and bottom cover, reflectance data in the satellite images can be interpreted as indicators of water clarity and bottom cover. These analyses confirm the anecdotal observations made about water clarity preceding the seagrass die-off. In areas affected by the die-off, the water column was very clear ($k_d \approx 0.1 \text{ m}^{-1}$) from 1985 to 1988; after this time, the water column became much more turbid. The satellite data also record decreases in seagrass density over 200 km², or about 10%, of Florida Bay. Stumpf et al. (1999) suggest that there may also have been a decrease in seagrass cover in the shallow region of the Gulf of Mexico immediately to the west of Florida Bay just prior to the first recorded incidents of seagrass die-off within Florida Bay, but this interesting contention remains untested with field data.

Seagrass beds within Florida Bay decreased in biomass by 28% between 1984 and 1994; these decreases occurred in only the dense seagrass areas of the bay (Hall et al. 1999). The losses were severe enough over 10% of the area of the bay as to show up on satellite images (Stumpf et al. 1999). Zieman et al. (1999) have been measuring seagrass standing crop and growth rate at permanent stations within Florida Bay since 1989. While seagrass biomass decreased at these sites between 1989 and 1995, the mass-specific growth rate of *Thalassia testudinum* increased over the time period. Some of this increase can be explained by the gradually decreasing salinity of Florida Bay over this time, because productivity of *T. testudinum* was negatively correlated with summer salinity. It is also possible that some of the growth rate increase is a consequence of decreasing biomass and the resulting decrease in self-shading. Whatever the reason, by 1995 seagrass growth rate returned to the relatively

high rates measured historically in south Florida and declines in seagrass biomass had stopped at the permanent sites; these are positive signs for the health of the Florida Bay ecosystem.

Summary

The research represented in this volume strengthens our understanding that Florida Bay is a heterogeneous ecosystem in both space and time. While early suspicions centered on upstream water management practices as the causal agents in the rapid changes occurring in Florida Bay since 1987, no clear evidence supporting this has been developed yet. Florida Bay has changed over the past decade from a clear-water, seagrass-dominated ecosystem to one in which phytoplankton plays a more important role. The distribution of *Thalassia testudinum*, the dominant seagrass across the bay, has changed little since 1987, but biomass of *T. testudinum* and the distribution of other seagrass species have. Locally the dominance of *T. testudinum* has declined, with a concomitant increase in the importance of other seagrass species and habitat complexity. Much of the fauna that is typical of Florida Bay is inextricably tied to seagrass habitat. Dramatic declines in the abundance of dominant seagrass-associated fishes and invertebrates occurred following seagrass die-off. Similarly planktivorous fishes, previously a minor component of the Florida Bay fish community, have expanded greatly, presumably in response to persistent algal blooms in the bay. The ecological implications of these changes and their influence on the trophic structure of Florida Bay is not understood.

There are positive signs that the shift from a clear-water, seagrass-dominated system to a system characterized by turbid water and persistent algal blooms may reverse itself and that Florida Bay may not have been permanently altered. Seagrass growth rate is up and seagrass loss has slowed, and algal blooms are abating in the central part of the bay. Fishing on the Tortugas shrimp grounds has also rebounded from the low harvest of the late 1980s. Salinity in Florida Bay has been decreasing since 1991, mostly as a consequence of increased rainfall.

Taken in total, the work described in this volume demonstrates that the natural state of the Florida Bay ecosystem is one of variability and change. For this reason, a clear causal link between recent changes in the ecosystem and human activities in the ecosystem eludes detection. To their credit, governments and resource managers have adopted a precautionary approach and are proceeding in recognition of the possible ecological consequences of their actions. Indeed, long-term plans for the renovation of the water management infrastruc-

ture have ecosystem restoration as a principal goal. But, restoration to what state? The insight to be drawn from this volume is that the objectives for a restored Florida Bay must take account of its inherently variable nature. To manage the bay as a static system would alter the nature of Florida Bay far more than may have already occurred.

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