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A CONCEPTUAL ECOLOGICAL MODEL OF FLORIDA BAY

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Abstract: Florida Bay is a large and shallow estuary that is linked to the Everglades watershed and is a target of the Greater Everglades ecosystem restoration effort. The conceptual ecological model presented here is a qualitative and minimal depiction of those ecosystem components and linkages that are considered essential for understanding historic changes in the bay ecosystem, the role of human activities as drivers of these changes, and how restoration efforts are likely to affect the ecosystem in the future. The conceptual model serves as a guide for monitoring and research within an adaptive management framework. Historic changes in Florida Bay that are of primary concern are the occurrence of seagrass mass mortality and subsequent phytoplankton blooms in the 1980s and 1990s. These changes are hypothesized to have been caused by long-term changes in the salinity regime of the bay that were driven by water management. However, historic ecological changes also may have been influenced by other human activities, including occlusion of passes between the Florida Keys and increased nutrient loading. The key to Florida Bay restoration is hypothesized to be seagrass community restoration. This community is the central ecosystem element, providing habitat for upper trophic level species and strongly influencing productivity patterns, sediment resuspension, light penetration, nutrient availability, and phytoplankton dynamics. An expectation of Everglades restoration is that changing patterns of freshwater flow toward more natural patterns will drive Florida Bay's structure and function toward its pre-drainage condition. However, considerable uncertainty exists regarding the indirect effects of changing freshwater flow, particularly with regard to the potential for changing the export of dissolved organic matter from the Everglades and the fate and effects of this nutrient source. Adaptive management of Florida Bay, as an integral part of Everglades restoration, requires an integrated program of monitoring, research to decrease uncertainties, and development of quantitative models (especially hydrodynamic and water quality) to synthesize data, develop and test hypotheses, and improve predictive capabilities. Understanding and quantitatively predicting changes in the nature of watershed-estuarine linkages is the highest priority scientific need for Florida Bay restoration.

Key Words: ecosystem restoration, estuaries, Florida Bay, Everglades, adaptive management, seagrass, freshwater flow, salinity effects

BACKGROUND

Florida Bay is a triangularly shaped estuary, with an area of about 2200 km^2 that lies between the southern tip of the Florida mainland and the Florida Keys (Figure 1). About 80% of this estuary is within the boundaries of Everglades National Park and much of the remainder is within the Florida Keys National Marine Sanctuary. A defining feature of the bay is its shallow depth, which averages about 1 m (Schomer and Drew 1982). Light sufficient to support photosynthesis can reach the sediment surface in almost all areas of the bay, resulting in dominance of seagrass beds as both a habitat and a source of primary production. The shallowness of Florida Bay also affects its circulation and salinity regime. Except for basins near the northern coast (near freshwater sources), the bay's water column is vertically well-mixed and usually isohaline. In contrast, its complex network of shallow mud banks restricts horizontal water exchange among the bay's basins and between these basins and the Gulf of Mexico (Smith 1994, Wang et al. 1994). In areas with long residence times, the salinity of Florida Bay water can rise rapidly during drought periods due to excess of evaporation over precipitation and freshwater inflow (Nuttle et al. 2000). Salinity levels as high as twice that of seawater have been measured (McIvor et al. 1994). Another defining feature of the bay is that its sediments are primarily composed of carbonate mud, which can scavenge inorganic phosphorus from bay waters (DeKanel and Morse 1978).

Until the 1980s, Florida Bay was perceived by the public and environmental managers as being a healthy and stable system, with clear water, lush seagrass beds, and highly productive fish and shrimp populations. In the mid-1980s, however, catches of pink shrimp decreased dramatically (Browder et al. 1999), and in 1987, a mass mortality of turtle grass (*Thalassia testudinum* Banks & Soland ex. Koenig) beds began (Robblee et al. 1991). By 1992, the ecosystem appeared to change from a clear water system, dominated by benthic primary production, to a turbid water system, with algae blooms and resuspended sediments in the water column. The conceptual ecological model presented here focuses on these changes in seagrass communities and water quality as central issues to be considered by environmental managers.

The Florida Bay Conceptual Ecological Model is one of eleven regional models that are being used as tools for synthesis, planning, assessment, and communication within the adaptive management framework of the Everglades Restoration Plan. This framework and a summary of all of the conceptual ecological models are described in Ogden et al. (2005). Overviews of the history and challenges of Everglades restoration are presented in Ogden et al. (2005) and Sklar et al. (2005). The format and symbols of the Florida Bay model follows that of Ogden et al. (2005) and the other conceptual models published in this issue of *Wetlands*. Furthermore, the organization of this paper follows the conceptual model diagram, with major sections on drivers and stressors, and ecological attributes (generally structural components of the ecosystem) and their links to stressors. A final section considers expectations and uncertainties regarding future responses to restoration efforts.

This simple model does not address spatial complexity in Florida Bay. Florida Bay is, indeed, not so much a singular estuary, but a complex array of more than forty basins, with distinct characteristics, that are partitioned by a network of mud banks and islands (Schomer and Drew 1982, Fourqurean and Robblee 1999). The structure of vegetative habitats, as well as water quality and ecosystem processes, vary distinctly with this spatial variation. Nevertheless, only a single, generic model is described and intended to summarize the main characteristics and trends of the bay. While the structure of this model is appropriate for most areas of the bay, the relative importance of model components differ considerably among subregions. Any application of this model (e.g., recommendations for a specific set of monitoring parameters and guidelines) must accommodate the degree of spatial variability of the bay.

EXTERNAL DRIVERS AND ECOLOGICAL STRESSORS

Following observations of Florida Bay's dramatic ecological changes in the 1980s, it was commonly assumed that a direct cause of these changes was a long-term increase in salinity, which in turn was caused by the diversion of freshwater away from Florida Bay via South Florida Water Management District canals. However, subsequent research has indicated that these ecological changes may not be attributable to a single cause. While decreased freshwater inflow and resultant increased salinity have been part of the problem, it appears that other human activities, as well as natural forces, may have also played a role (Boesch et al. 1993, Armentano et al. 1997, Fourqurean and Robblee 1999). The conceptual ecological model presented here includes both natural and anthropogenic sources of stress (Figure 2). The discussion of external drivers and ecological stressors below is organized by stressor (ovals in Figure 2), with consideration of the main drivers (rectangles in Figure 2) that influence each stressor.

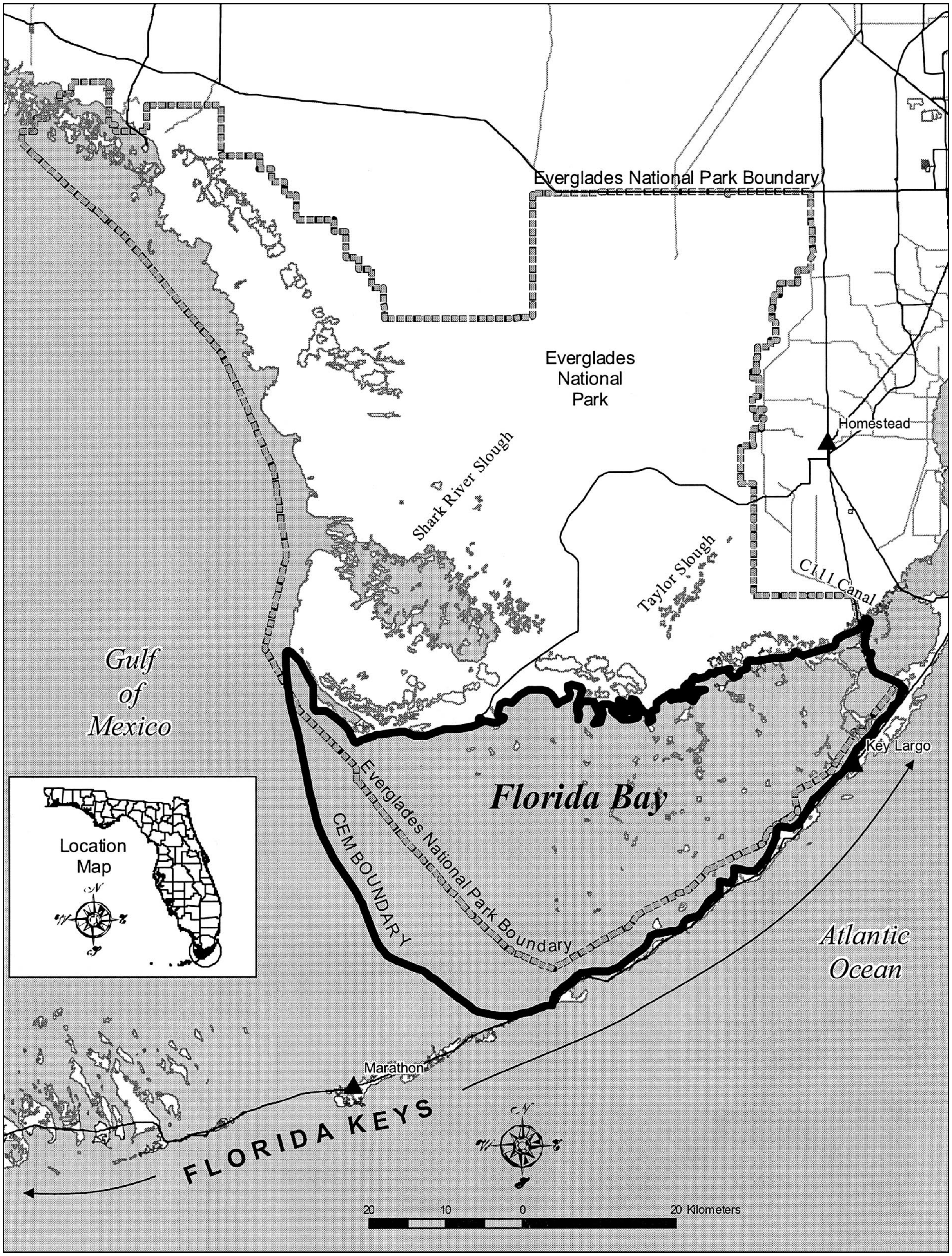

Figure 1. Geographic setting and boundary of the Florida Bay Conceptual Ecological Model (CEM).

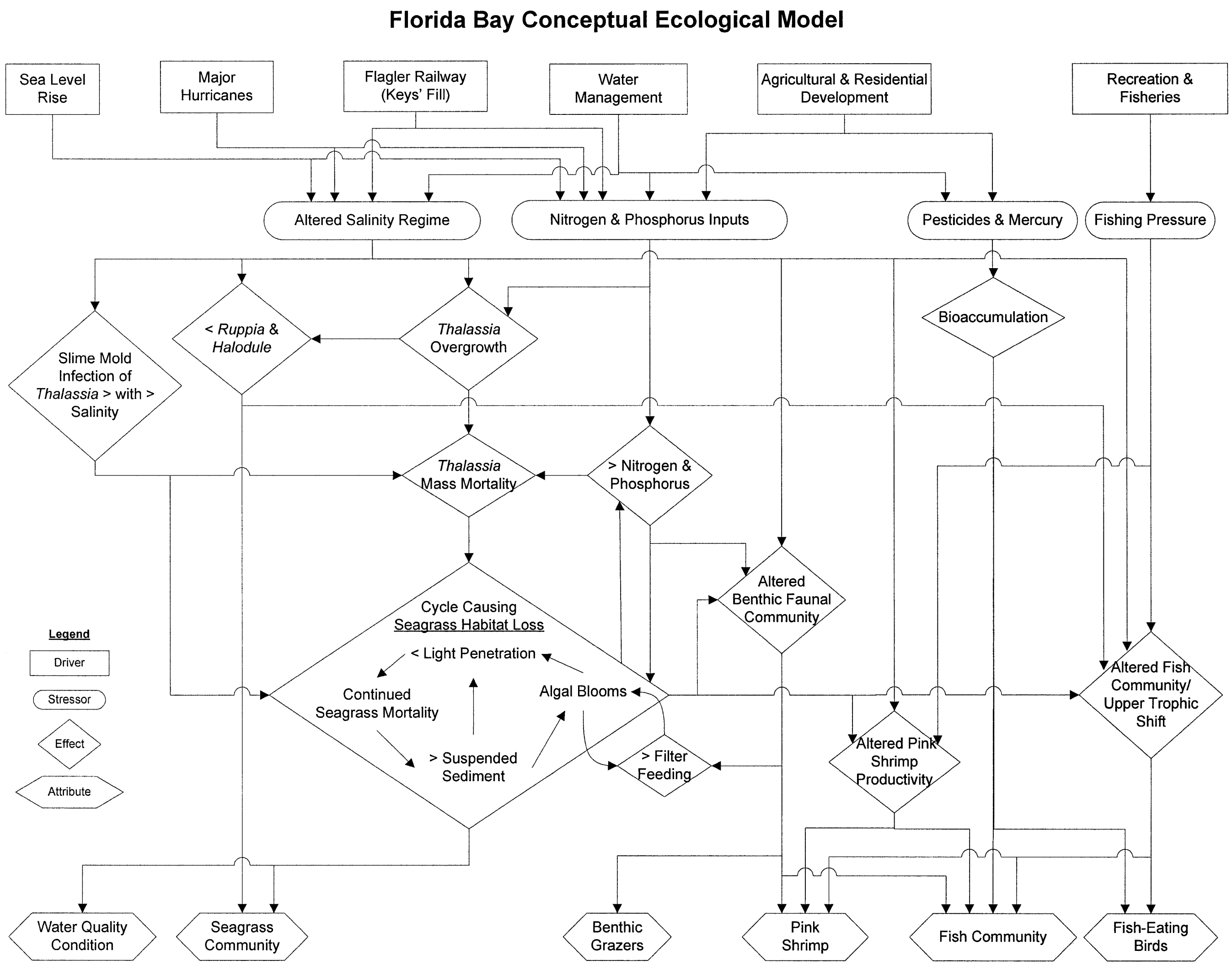

Figure 2. Florida Bay Conceptual Ecological Model Diagram. The format of this figure follows Ogden et al. (2005). Rectangles represent major external drivers of ecological change, ovals represent ecological stressors, diamonds represent ecological linkages and functions that mediate the effect of stressors on attributes, and hexagons represent ecosystem attributes to be monitored as part of the adaptive assessment process. Increases or decreases noted in diamonds with ''< *Ruppia* and *Halodule*'' and ''> Nitrogen and Phosphorus'' refer to pre-restoration changes.

Altered Salinity Regime

Florida Bay's salinity regime varies greatly over time and space. This variation ranges from coastal areas that can be nearly fresh during the wet season, to large areas of the central bay that can have salinity levels near 70 psu during prolonged droughts, to nearly stable marine conditions (about 35 psu) on the western boundary of the bay or near Florida Keys' passes. The main factors that determine the salinity regime in the bay are the inflow of freshwater from the Everglades, the difference between rainfall and evaporation over the bay, and exchange with marine waters of the Gulf of Mexico and Atlantic Ocean. Both freshwater inflow and exchange with the Atlantic have changed drastically in the past hundred years, resulting in an alteration of the bay's salinity regime (Swart et al. 1999, Brewster-Wingard et al. 2001, Dwyer and Cronin 2001).

Freshwater inflow to Florida Bay decreased in volume and changed in timing and distribution during the twentieth century because of water management. Hydrologic alteration began in the late 1800s but accelerated with construction of drainage canals by 1920, the Tamiami Trail by 1930, and the Central and South Florida (C&SF) Project and the South Dade Conveyance System from the early 1950s through 1980 (Light and Dineen 1994). With diversion of freshwater to the Atlantic and Gulf of Mexico coasts to the north, the bay's mean salinity inevitably increased. Isotopic studies of carbonate preserved in coral skeletons and buried ostracod shells confirmed this trend (Swart et al. 1999, Dwyer and Cronin 2001). Paleoecological studies also indicated that salinity variability within the bay also changed during the twentieth century, with an increase in variability in the northeastern bay, where freshwater inflows are channelized (Brewster-Wingard et al. 2001), and a decrease in variability in the southern bay (Swart et al. 1999).

Paleoecological studies indicated that a cause of salinity changes in the southern bay was construction of the Flagler Railway across the Florida Keys from 1905 to 1912 (Swart et al. 1996, 1999). In the nineteenth century, prior to railway construction and water management, southern Florida Bay had a lower mean salinity and more frequent periods of low (10 psu−20 psu) salinity than during the twentieth century. The extent and frequency of high salinity events in the southern bay does not appear to have changed between centuries. The bay's salinity regime changed abruptly around 1910 because passes between the Keys were filled to support the railway. Thus, water exchange between Florida Bay and the Atlantic Ocean was decreased, and this probably caused an increase in water residence time and a change in water circulation patterns within the bay.

Two important natural controls of salinity, sea-level rise and the frequency of major hurricanes, must also be considered. Florida Bay is a very young estuary, the product of sea level rising over the shallow slope of the Everglades during the past 4,000 years (Wanless et al. 1994). With rising sea level, the bay not only became larger but also became deeper. With greater depth, exchange of water between the ocean and the bay increased. All else being equal, this would result in a more stable salinity regime with salinity levels increasingly similar to the ocean. However, a factor that has counteracted rising sea level is accumulation of sediment, which makes the bay shallower. Most sediment that accumulates in Florida Bay is carbonate precipitated from water by organisms living in the bay (Bosence 1989). The extent to which these sediments accumulate is a function of the biology of these organisms (including skeletal carbonate production), chemical dynamics in the water column and sediments, and the physical energy available to transport some of these sediments from the bay. Major hurricanes are thought to be important high-energy events that can flush the bay of accumulated sediments. However, since 1965, no major hurricane has directly affected Florida Bay. Resultant sediment accumulation, with associated alteration of depth, circulation patterns, residence time, salinity, and nutrient storage may have influenced ecological changes in recent decades.

Nitrogen and Phosphorus Inputs

Productivity and food-web structure in all ecosystems are strongly influenced by internal nutrient cycling and import and export of these nutrients. Throughout the world, estuarine ecosystems have undergone dramatic ecological changes because they have been markedly enriched by nutrients derived from human activity (National Research Council 2000). These changes have often been catastrophic, with loss of seagrasses, increased algal blooms, and increased incidence of hypoxic and anoxic events. Augmentation of nitrogen and phosphorus inputs to an estuary is a potentially important stressor.

The degree to which nitrogen and phosphorus inputs have stressed Florida Bay is unclear. In general, the bay is relatively rich in nitrogen and poor in phosphorus, especially towards the eastern region of the bay (Boyer et al. 1997). This spatial pattern is at least partly a function of natural biogeochemical processes (e.g., P retention by the bay's carbonate sediments and relatively low N in adjacent marine waters) and thus may have existed prior to recent human influences. Little direct evidence confirms that nutrient inputs to the bay or concentrations within the bay have increased during the past century, but with expanding agricultural and residential development in South Florida, and particularly development of the Florida Keys, some nutrient enrichment almost certainly has occurred (Lapointe and Clark 1992, Orem et al. 1999). Anthropogenic nutrients that enter Florida Bay are derived not only from local sources (fertilizers and other wastes from agricultural and residential areas), but also from remote sources. Contributions of nutrients from atmospheric deposition and from the Gulf of Mexico, which may include nutrients from the phosphate fertilizer industry of the Tampa-Port Charlotte area and residential development from Tampa to Naples, are significant external nutrient sources (Rudnick et al. 1999).

Different sub-regions of the bay are differentially influenced by these local or remote sources, depending on the magnitude of inputs, relative abundance of different nutrients, internal cycling pathways and rates, and water residence time (Boyer et al. 1997, Rudnick et al. 1999, Childers et al. 2005). Algal bloom occurrence in the central and western bay is influenced by a combination of these factors (Tomas et al. 1999, Brand 2002). Despite the lack of definitive data, it is, nevertheless, a reasonable hypothesis that a chronic increase in nutrient inputs occurred in Florida Bay in the twentieth century and that this increase contributed to the bay's recent ecological changes. Development of a water quality model driven by appropriately scaled hydrodynamic and hydrologic models is essential to understand and evaluate quantitatively the potential effects of past nutrient inputs and predict the effects of future management scenarios.

Water management is a driver of nutrient stress in that the canal system can transport materials through wetlands toward the bay, decreasing nutrient retention by wetlands and thereby increasing inputs to the bay. Altered nutrient transport via canals may also alter the chemical composition of nutrients entering the bay. These inputs from the Everglades and the Gulf of Mexico are affected not only by changes of freshwater flowing from Taylor Slough and Shark River Slough, but also by changes in the bay's circulation. Nutrient cycling and retention within the bay are sensitive in particular to changes in residence time (a function of circulation) that were caused by Flagler Railway construction, as well as the balance of sea-level rise and sedimentation or sediment removal by major hurricanes. Hurricanes may be particularly important, as nutrients (organic and inorganic) can accumulate in sediments, and the absence of major hurricanes during the past few decades may have resulted in an accumulation of nutrients.

Pesticides and Mercury

With the widespread agricultural and residential development of South Florida, application and release of pesticides and other toxic materials has increased. Deposition of mercury from local and global sources has also increased in the past century and is of particular concern because of high concentrations of methylmercury in upper trophic level species (Cleckner et al. 1998). Altered biogeochemistry resulting from changes in water quality (e.g., sulfate availability), which in turn affects methylation rates, has also played a role in increased mercury bioaccumulation (Cleckner et al. 1999). Pesticides and mercury are of concern because they can affect human health through consumption of fish or other biota with high concentrations of these toxins and because other species also may be adversely affected by these compounds. To date, no evidence links observed ecological changes in Florida Bay to inputs of toxic compounds. Nevertheless, endocrine-disrupting endosulfans, with concentrations that could have biological effects, have been found in upstream canals and the biota of associated lakes (Scott et al. 2002, G. Graves, personal communication). Additionally, mercury levels remain elevated in fish in eastern Florida Bay despite decreases observed elsewhere (Strom and Graves 2001, Evans et al. 2003). Water management affects the distribution of these toxic materials and potentially their transport to Florida Bay (Scott et al. 2002, Rumbold et al. 2003). Controlling water levels in wetlands may also influence the decomposition of pesticides and mercury methylation rates because these processes are sensitive to the presence of oxygen and sulfate in soils, which are affected by water levels.

Fishing Pressure

For any species that is the target of recreational or commercial fishing, fishing pressure directly affects population dynamics and community structure. Commercial fishing has been prohibited within Everglades National Park since 1985, but populations that live outside of the Park boundaries for at least part of their life cycle, including most of Florida Bay's sportfish species, are affected by fisheries (Tilmant 1989). Recreational fishing pressure within the Park also affects these populations (e.g., the size structure of the gray snapper assemblages [Faunce et al. 2002]).

ECOLOGICAL ATTRIBUTES

The set of Florida Bay's attributes presented here (hexagons in Figure 2) includes both indicators of ecosystem condition and attributes deemed to be intrinsically important to society. Attributes, in most cases, are biological components of the ecosystem, including seagrass, mollusks, shrimp, fish, and birds, but also an aggregated attribute (water-quality condition) that includes phytoplankton blooms, turbidity, and nutrient concentrations. While the list of biological components is broad, it is clear from their links to stressors (see diamonds and associated arrows, linking to stressors in ovals, in Figure 2) that these attributes are not equally weighted; the most significant and causally interconnected attribute of this conceptual ecological model is the seagrass community. Details of each attribute and its linkages to the conceptual model's set of stressors are given below.

Seagrass Community

The structural and functional foundation of the Florida Bay ecosystem is its seagrass community (Zieman et al. 1989, Fourqurean and Robblee 1999). These plants are not only a highly productive base of the food web, but are also a principal habitat for higher trophic levels and strongly influence the physical and chemical nature of the bay. Understanding how seagrasses affect water quality is essential to understanding the bay's current status and predicting its response to restoration and other human activities.

Seagrasses affect water quality by three mechanisms: nutrient uptake and storage, binding of sediments by their roots, and trapping of particles within their leaf canopy. With growth of dense seagrass beds, these mechanisms drive the bay towards a condition of clear water, with low nutrient availability for algae growth within the water column and low concentrations of suspended sediment in the water. Paleoecological studies and historic observations suggest that *T. testudinum* in Florida Bay proliferated and increased in density during the mid-twentieth century (Brewster-Wingard and Ishman 1999, Zieman et al. 1999, Cronin et al. 2001), while other common species (*Halodule wrightii* Aschers and *Ruppia maritima* Linnaeus) likely decreased in distribution and density. From the 1960s through the mid-1980s, dense *T. testudinum* beds expanded throughout central and western Florida Bay, and the water column was reported to be crystal clear (Zieman et al. 1999). Largely following the conceptual model of Zieman et al. (1999), we hypothesize that with the onset of a *T. testudinum* mass-mortality event in 1987 (Robblee et al. 1991), the three mechanisms given above reversed, initiating a cycle (large diamond in Figure 2) that contributed to additional seagrass habitat loss (or at least inhibited recolonization) and favored the persistence of more turbid water with episodic algal blooms (Stumpf et al. 1999).

Causes of the 1987 mass-mortality event can be considered at two time scales—a multi-decadal period that poised *T. testudinum* beds for collapse and a short-term period (of days–months) in 1987 when proximate factors triggered mortality (Zieman et al. 1999). We hypothesize that changes in two stressors, salinity and a chronic and low-level increase in nutrient availability, occurred over several decades and caused *T. testudinum* beds to grow to an unsustainable density (designated ''overgrowth'' in Figure 2) by the mid-1980s. It is also likely that a decrease in shoal grass (*Halodule wrightii*) and widgeon grass (*Ruppia maritima*) occurred with the *T. testudinum* increase. *Thalassia testudinum* overgrowth may have occurred because the species had a competitive advantage over other seagrass species when the bay's salinity regime was stabilized, with few periods of low salinity (Zieman et al. 1999). Nutrient enrichment also may have played a role, with a chronic accumulation of nutrients caused by increased inputs over decades or decreased outputs because of the absence of major hurricanes or closure of Florida Keys' passes. Once *T. testudinum* beds were poised for collapse, multiple factors that acted over a short time scale are hypothesized to have been a proximate cause of mortality in 1987. These factors are thought to be related to high respiratory demands of dense grass beds and accumulated organic matter. During the summer of 1987, with high temperatures and hypersaline water, respiratory demand may have exceeded photosynthetic production of dissolved oxygen, causing sulfide concentrations to increase to lethal concentrations (diagram from Durako et al. in McIvor et al. 1994, Carlson et al. 1994). This hypothesis regarding the proximate cause of seagrass mass mortality is supported by a recent *in situ* study in Florida Bay (Borum et al. 2005) that showed the importance of anoxia and sulfide in surficial sediments as a potential cause of *T. testudinum* mortality.

Regardless of the cause of the mass-mortality event, once this event was initiated, the ecology of Florida Bay changed. A cycle resulting in continuing seagrass habitat loss is depicted in the conceptual ecological model. Continued seagrass mortality results in increased sediment resuspension (Prager and Halley 1999, Stumpf et al. 1999) and increased nutrient (nitrogen and phosphorus) release from sediments, stimulating phytoplankton growth in the water column. The presence of both phytoplankton and suspended sediment result in decreased light penetration to seagrass beds. This decreased light can limit seagrass growth and sustain the feedback loop.

Dynamics of this feedback loop are probably not independent of the salinity regime. Seagrass wasting disease, caused by a slime mold (*Labyrinthula* sp.) infection, is more common at salinities near or greater than seawater ($\geq$ 35 psu) than at low (15 to 20 psu) salinities (Blakesley et al. 2003). High salinity may have played a role in the initial seagrass mass mortality event but more likely has served to promote seagrass re-infection since that event. Incidence of this disease may therefore be directly affected by water management actions.

If the state of the seagrass community is to be used as a criterion to decide success of environmental restoration efforts, scientists and managers must specify the desirability of alternative states. Based on studies of historic changes of seagrass communities in Florida Bay and anecdotal information (Brewster-Wingard and Ishman 1999, Zieman et al. 1999, Cronin et al. 2001), it is likely that the Florida Bay of the 1970s and early 1980s, with lush *T. testudinum* and clear water, was probably a temporary and atypical condition. From an ecological perspective, restoration should generally strive for a more diverse seagrass community with lower *T. testudinum* density and biomass than during that anomalous period. A diversity of seagrass habitat is expected to be beneficial to many upper trophic level species (Thayer et al. 1999).

Water Quality Condition

Water quality condition reflects the light field, nutrient availability in the ecosystem, and algal blooms in the water column. All of these characteristics are closely related to the condition of seagrasses and food web structure and dynamics of the bay. While these characteristics have been monitored and researched since the early 1990s, earlier information is scarce for salinity and almost non-existent for the above water quality characteristics. Thus, at the present time, we do not know whether nutrient inputs to the bay have actually increased in recent decades or whether periods with sustained algal blooms and high turbidity occurred in the past.

Studies of nutrient export from southern Everglades canals and creeks flowing into Florida Bay have provided insights regarding the relationship between patterns of freshwater discharge, nutrient dynamics, and output to Florida Bay (Rudnick et al. 1999, Davis et al. 2003, Sutula et al. 2003). Results show that phosphorus loads to the bay do not greatly increase with increased freshwater inputs to the bay, but given the phosphorus limitation of the eastern bay, any increase in phosphorus availability is likely to affect productivity patterns. Unlike phosphorus, total nitrogen loads probably do increase with more freshwater flow (Rudnick et al. 1999), and algal growth in western and sometimes central Florida Bay can be nitrogen limited (Tomas et al. 1999). The potential thus exists for hydrologic restoration to increase nitrogen loading and stimulate phytoplankton blooms (Brand 2002). Because most of the nitrogen that is exported from the Everglades to the bay is in the form of organic compounds (Rudnick et al. 1999), the fate of these compounds within the bay is a critical unknown; if these compounds are easily decomposed and their nitrogen becomes available to algae, then increased freshwater flow could stimulate algal growth. In addition to organic nitrogen decomposition rates, other critical unknowns regarding the availability of nitrogen for algal productivity include rates of nitrogen fixation and denitrification within the bay and the residence time of water in bay's sub-basins.

Finally, as emphasized earlier, light penetration through Florida Bay waters is a key to the health of seagrasses. Light penetration is largely a function of turbidity from algae and suspended sediment. Although light levels were potentially limiting to seagrass growth during the early and mid-1990s, in more recent years, only the northwest corner of the bay is potentially light-limiting (Kelble et al. 2005). For successful restoration of Florida Bay, light penetration must be sufficient to ensure viable seagrass habitat. Such a light-penetration criterion has been used in other estuaries (Dennison et al. 1993) and is an important success criterion for Florida Bay.

Benthic Grazers

Consumption of phytoplankton by bivalves and other benthic filter feeders and suspension feeders (especially sponges and tunicates) may have significant impacts on the distribution, magnitude, and duration of algal blooms. Increases or decreases in algal blooms may be related to significant increases or decreases in grazer abundance and biomass. Decreased grazing may have occurred in the 1990s because of seagrass habitat loss, which could have decreased grazer abundance. Additionally, grazers may have been negatively affected by cyanobacterial blooms (*Synechococcus* sp., the dominant phytoplankter in central Florida Bay's blooms [Phlips and Badylak 1996]). These blooms may have played a role in the large-scale mortality of sponges in southern Florida Bay in the early 1990s (Butler et al. 1995). Such a loss of grazers would have enabled larger blooms to occur, decreasing light penetration, and thereby reinforcing the feedback loop of seagrass mortality and algal blooms.

Benthic grazers abundance, biomass, species composition, and distribution are valuable in a monitoring program not only because of their functional link with phytoplankton blooms, but also because these grazers are ecological indicators. Paleoecological and recent studies of the bay have inferred that long-term changes in molluscan species composition are largely a function of salinity and seagrass habitat availability (Brewster-Wingard and Ishman 1999).

Pink Shrimp

Pink shrimp (*Farfantepenaeus duorarum* Burkenroad) are economically important to society as a highly valued fishery species and are also ecologically important as a major dietary component of game fish and wading birds. Furthermore, pink shrimp are an indicator of Florida Bay's productivity because the bay and nearby coastal areas are primary shrimp nursery grounds. This nursery supports the shrimp fishery of the Tortugas grounds (Ehrhardt and Legault 1999). Hydrologic and ecological changes in the Everglades and Florida Bay may have impacted this fishery, which experienced a decrease in annual harvest from about 4.5 million kg per year in the 1960s and 1970s to only about 0.9 million kg per year in the late 1980s (Ehrhardt and Legault 1999). This decrease may have been associated with seagrass habitat loss or high salinity (50 to 70 psu) during the 1989–1990 drought; experiments have shown that pink shrimp mortality rates increase with salinities above about 35 psu, and growth rates are optimal at 30 psu (Browder et al. 2002). Shrimp harvest statistics indicate that shrimp productivity increases with increasing freshwater flow from the Everglades (Browder 1985). This may be because greater freshwater inflows reduce the frequency, duration, and spatial coverage of hypersaline events in Florida Bay (Browder et al. 1999, 2002). The statistical relationship between indices of freshwater flow and shrimp productivity is sufficiently robust to be used by the National Marine Fisheries Service in management of the offshore fishery (Sheridan 1996).

Fish Community

The health of Florida Bay's fish populations is of great importance to the public; sport fishing is a major economic contributor to the region (Tilmant 1989). Recruitment, growth, and survivorship of these fish populations are affected by many factors, including salinity, habitat quality and availability, food-web dynamics, and fishing pressure. Changes in mangrove and seagrass habitats are likely to influence the structure and function of the fish community. However, seagrass mass mortality appears to have had a greater influence on fish community structure than on the absolute abundance of fish; no dramatic bay-wide decreases in fish abundance were observed along with seagrass mass mortality (Thayer et al. 1999). Rather, a shift in fish species composition occurred as a result of seagrass habitat loss and sustained algal blooms. When demersal fish markedly declined, pelagic fish such as the bay anchovy, which feed on phytoplankton, increased (Thayer et al. 1999). More recently, changes in the opposite direction have been observed (Powell et al. 2001). While causes of these changes are not well-established, there is no question that stressors, such as altered salinity regimes, not only affect upper trophic level populations directly but also affect them indirectly through habitat and food-web changes.

Another important stressor that needs to be considered with regard to fish populations is the impact of pesticides and mercury. As concentrations of mercury and some pesticides greatly increase in upper trophic level species, such as sport fish (via the process of bioaccumulation) that people eat, a human health issue potentially exists. Pesticides and mercury can also have ecological impacts by physiologically stressing organisms (particularly reproductive functions). While toxic contaminant inputs to Florida Bay do not appear to be associated with recent large-scale changes in the bay ecosystem, biotic exposure to toxicants could change in association with restoration-related changes in upstream water management.

Among the many fish species that could be used as indicators of the health of the ecosystem's upper trophic level, the spotted sea trout (*Cynoscion nebulosus* Cuvier in Cuvier and Valenciennes) is unique because it is the only major sport fish species that spends its entire life in the bay (Rutherford et al. 1989). Changes in the bay's sea trout population and toxic residues in this species thus reflect changes in the bay itself, as well as upstream restoration actions that affect the quantity and quality of water entering the bay. Sea trout are a particularly good restoration indicator for central Florida Bay, where they are commonly found and where prolonged periods of hypersalinity are common. This species is known to be sensitive to hypersalinity; density of post-larvae has been found to be greatest at an intermediate salinity range of 20–40 psu (Alsuth and Gilmore 1994). For northeastern Florida Bay, the abundance of common snook (*Centropomus undecimalis* Bloch), red drum (*Sciaenops ocellatus* Linnaeus, 1766), crevalle jack (*Caranx hippos* Linnaeus), and mullet are also being considered as potential restoration indicators.

Fish-Eating Birds

Florida Bay and its mangrove coastline are important feeding and breeding grounds for waterfowl and wading birds. Conceptual ecological models for other regions of the Everglades, particularly the Everglades Mangrove Estuaries Conceptual Ecological Model (Davis et al. 2005), present more detailed descriptions of the use of bird populations as ecological indicators and consider a wide variety of birds. For the Florida Bay Conceptual Ecological Model, we consider only fish-eating birds that are characteristic of the marine environment, such as great white herons, reddish egrets, osprey, brown pelicans, and cormorants. These birds are important predators within the bay and are potentially impacted by any stressors that affect their prey base, including salinity changes, nutrient inputs, toxic compounds, and fishing pressure. As with other top predators, these bird species may also be especially vulnerable to toxic contaminants.

RESTORATION RESPONSES: EXPECTATIONS AND UNCERTAINTIES

In this section, we present a prospective view of Everglades restoration. The Conceptual Ecological Model, while largely based on past ecological dynamics, still serves as a guide. The foremost purpose of this section is to identify those components and linkages (with associated ecological processes) that are most sensitive to changing watershed management, have a strong effect on the entire estuarine ecosystem, and yet are poorly understood relative to the information needs of the adaptive management process. This includes consideration of salinity and hydrodynamics, nutrient inputs and phytoplankton blooms, and benthic habitat and higher trophic level responses to restoration. Working hypotheses regarding each of these high priority aspects of the Florida Bay conceptual model are also presented here. We use the term ''working hypothesis'' in the sense that the described predictions and relationships, while generally not testable with strict experimental control, can be assessed as part of a long-term adaptive management program.

Salinity Responses

The conceptual model explicitly illustrates the central importance of water management on the Florida Bay ecosystem, largely mediated through changing salinity. An expectation of the Everglades restoration plan is that salinity in the bay will decrease, expanding the spatial extent and duration of oligohaline to polyhaline conditions, while decreasing the extent and duration of hypersaline conditions. However, a quantitative understanding of the relationship between wetland hydrologic conditions, freshwater flow, and resultant salinity throughout the bay is still lacking. An important step toward gaining this understanding and a predictive capability for environmental management is the synthesis of a broad array of available hydrologic, hydrodynamic, and salinity information within a hydrodynamic model. Development of such a model is challenging, given the shallow and complex morphology of Florida Bay. To date, restoration planning has only used simple statistical estimates of salinity, largely as a function of wetland water stages, and these estimates have been limited to near-shore embayments. Predicting salinity change within the entire bay requires understanding of changing water inputs, exchanges, and circulation. The effects of restoration efforts thus will be strongly influenced not only by changing freshwater flow, but also by sea-level rise and changing bay morphology.

Working Hypotheses: Relationships of Mud Bank Dynamics, Sea-Level Rise, and Circulation. Circulation and salinity patterns, and thus ecological patterns, are strongly influenced by Florida Bay's mud banks, which are dynamic features. The response of these banks to sea-level rise and the changing frequency and intensity of tropical storms cannot confidently be predicted. Based on the persistence of mud-bank spatial distributions over centuries and past patterns of accretion (Wanless and Tagett 1989), we hypothesize that sediments will accrete on banks at rates comparable to rates of sea-level rise and that the spatial pattern of banks and basins will remain largely unchanged in future decades, despite the likelihood that tropical storm activity will increase during the coming decade (Goldenberg et al. 2001). If these hypotheses are true, then water circulation within the bay will continue to be restricted by mud banks, even with sea-level rise, and exchange of bay water with seawater of the Atlantic Ocean and Gulf of Mexico will not markedly increase. However, as the depth of basins increases (historic sediment accretion of banks has greatly exceeded sediment accretion in basins; Wanless and Tagett (1989)), the residence time of water in basins and the potential for stratification and oxygen stress would also increase. Moreover, with increased depth, light penetration to seagrass communities would decrease. Alternatively, if mud bank accretion does not keep up with sea-level rise, the exchange and circulation of Gulf of Mexico and Atlantic water in Florida Bay will increase, shifting the bay from an estuarine to a more marine system and minimizing the influence of any watershed restoration actions. Such increased circulation could also ameliorate the historic effect of the Flagler Railway and Keys Highway, which decreased water exchange between the bay and Atlantic, increased water residence time in the bay, and probably changed circulation and salinity patterns. Finally, with rising sea level, the mangrove shoreline along the northern bay will likely move inland.

Water Quality Responses

Restoration of the Everglades will have effects on the watershed's estuaries beyond changing freshwater input and salinity. Restoration will also affect material (particularly dissolved nutrient) inputs as stormwater treatment areas decrease nutrient inputs to the Everglades (Chimney and Goforth 2001) and changing hydrologic conditions modify biogeochemical cycles and transport within the wetlands. Changing flow and salinity will affect biogeochemical cycling within the estuaries via direct effects of salinity on abiotic processes (e.g., phosphorus sorption-desorption) and indirect effects of changing community structure and associated physical and biogeochemical characteristics (e.g., sediment stabilization and resuspension with changing seagrass cover). The ecological consequences of these changes are uncertain, but one concern is that phytoplankton blooms could be stimulated by Everglades restoration because of potential increases in nitrogen inputs (Brand 2002). Nevertheless, an expectation of Everglades restoration is that such a change in Florida Bay water quality will not occur. Development of a coupled hydrodynamic-water quality model of the bay, combined with monitoring and research of biogeochemical processes will improve understanding and adaptive management responses to this and other aspects of the restoration.

Working Hypotheses: Relationships of Water Quality and External Nutrient Sources. Changing the flow of water through the Everglades and resultant changes in the structure and function of these wetlands will alter the delivery of materials to downstream coastal ecosystems, including Florida Bay. Quantitative predictions of these changes are not possible at this time, but it is reasonable to expect that phosphorus outputs from the Everglades, which are very low, will not change, and nitrogen outputs from the Everglades, which are much greater (Rudnick et al. 1999), could change. Given that most nitrogen output is in the form of dissolved organic matter (DOM), a major uncertainty is the extent to which this DOM can be decomposed by heterotrophic bacteria and phytoplankton and provide nutrients (particularly nitrogen) for phytoplankton. Depending upon the proportion of this bioavailable DOM and the relationship of DOM quality and quantity to freshwater flow, restoration of natural water inflows from the Everglades could affect the composition, magnitude, duration, and distribution of phytoplankton blooms.

Hydrologic restoration of the Everglades could also affect Florida Bay water quality by changing water circulation and water residence time in the bay. Increased freshwater inputs from the Everglades, with lower phosphorus concentrations than in Gulf of Mexico waters, could decrease phosphorus inputs from the Gulf (moving the zone of influence of P-limiting Everglades water westward in the bay) and thus decrease the density and prevalence of *Synechococcus* blooms in central Florida Bay (Boyer and Jones 1999). Furthermore, the magnitude of phytoplankton blooms varies as a function of the residence time of waters within the bay's basins and exchange of these waters with adjacent marine waters. Increased freshwater flow, along with the potential restoration of passes through the Florida Keys, could decrease bay water residence time and phytoplankton blooms.

Working Hypotheses: Relationships of Water Quality and Changing Internal Bay Structure and Function. Everglades restoration will affect Florida Bay water quality via changes in the bay's internal biogeochemical cycles. These internal changes will likely be mediated through changing seagrass community structure and function. An expectation of the restoration is that changing salinity will increase seagrass species diversity and spatial heterogeneity such that large scale *T. testudinum* die-off events will be prevented. In turn, water-quality degradation associated with such events will be prevented. Die-off events can increase phytoplankton growth because of increased sedimentary nutrient mobilization, decreased benthic uptake of nutrients and resultant reduction in competition for water-column nutrients, and decreased grazing pressure from benthic filter feeders (due to loss of their habitat). Sediment resuspension due to seagrass die-off can supply additional water-column nutrients via both porewater advection and desorption of surface-bound nutrients from resuspended particles. The latter process is salinity dependent and will be affected by hydrologic restoration, which may thus influence phosphorus availability for phytoplankton (with lower phosphorus availability as a function of lower salinity).

Nitrogen cycling and availability within the bay are likely to change with restoration, and these internal changes are likely to have greater effects on phytoplankton production than those derived from changing nitrogen inputs from the Everglades. Recent studies found that rapid and variable rates of nitrogen fixation and denitrification occur within bay sediments (particularly benthic microbial mats) and seagrass beds (Nagel 2004, Evans 2005). There is high uncertainty regarding the magnitude of large-scale (space and time), integrated rates of nitrogen cycling, and changes that may occur with restoration.

Seagrass Community and Trophic Web Response

An expectation of Everglades restoration is that changing patterns of freshwater flow toward more natural patterns will drive Florida Bay's seagrass community and trophic web toward its pre-drainage condition.

Working Hypotheses: Multiple Factors Affect the Florida Bay Seagrass Community. Spatial coverage, biomass, production, and taxonomic composition of seagrass beds in Florida Bay are controlled by the combined and inter-related effects of light penetration, epiphyte biomass, nutrient availability, sediment depth, salinity, temperature, sulfide toxicity, and disease. Decreased salinity caused by increasing freshwater flow will have a direct effect on seagrass communities through physiological mechanisms, resulting in greater spatial heterogeneity of seagrass beds, a decrease in the dominance of *T. testudinum*, and an increase in coverage by other seagrass species (*H. wrightii* through much of the bay and *R. maritima* near the northern coast of the bay). Decreased salinity will also decrease the infection of *T. testudinum* by the slime mold, *Labyrinthula*. Light availability will depend upon phytoplankton growth and sediment resuspension, which depend both on nutrient availability, grazing, and stabilization of sediments by seagrass beds.

Working Hypotheses: Changing Salinity and Seagrass Habitat Will Alter Fish Community Structure. Fish and invertebrate species in Florida Bay are expected to be affected by Everglades restoration efforts via responses to changing salinity and habitat. Decreasing salinity, and especially reducing the frequency and duration of hypersaline events, will increase the growth and survival of estuarine species (especially juvenile pink shrimp and juvenile spotted seatrout) and enhance the use of Florida Bay as a nursery. Increased seagrass habitat diversity and heterogeneity (with less area covered by high density *T. testudinum*) and minimizing large-scale *T. testudinum* die-off events will increase the survivorship and population size of these and other higher trophic level species. Both recreational and commercial fisheries are thus expected to benefit from Everglades restoration.

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