

ST. LUCIE ESTUARY AND INDIAN RIVER LAGOON CONCEPTUAL ECOLOGICAL MODEL

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Abstract: The St. Lucie Estuary is one of the largest brackish water bodies on the east coast of Florida, USA and a major tributary to southern Indian River Lagoon. The Indian River Lagoon is a biogeographic transition zone, rich in habitats and species, with the greatest species diversity of any estuary in North America. Habitats and species diversity in the lagoon system are believed to be affected by the decline in water and sediment quality. The health of the system is being affected by water management and land-use development in this rapidly growing area of South Florida. These affects are expressed through the six major stressors identified in this conceptual ecological model. The model diagram and its associated text describe the effects of these stressors on the key ecological attributes of the system and are a way to describe both the well-known linkages and pathways between these stressors and the detrimental impacts they have on the ecology of the system. This model also provides a means to describe some of the uncertainties and associated research that will be needed to fine tune our understanding of some of the more complicated ecological interactions and interdependencies in order to carry out effectively the goals and objectives of Everglades restoration in this system and adaptively manage the restoration into the future.

Key Words: St. Lucie Estuary, submerged aquatic vegetation, oyster, Indian River Lagoon, restoration, marine muck sediments, Comprehensive Everglades Restoration Plan, hydrologic restoration, fish abnormality

BACKGROUND

The St. Lucie Estuary and Southern Indian River Lagoon Conceptual Ecological Model boundary extends from the northern St. Lucie County line, located north of Fort Pierce Inlet, south to Jupiter Inlet, and east to the five kilometer limit in the Atlantic Ocean to include nearshore reefs. The western boundary extends to open-channel headwaters of the North and South Forks of the St. Lucie Estuary and Taylor Creek near the Fort Pierce Inlet and up to coastal canal structures (C-23, C-24, C-25, and C-44) (Figure 1). The St. Lucie Estuary is one of the largest brackish water systems on the southeast coast of Florida, USA. The estuary intersects the Southern Indian River Lagoon near the St. Lucie Inlet, which is also its outlet to the Atlantic Ocean. Fort Pierce Inlet provides an additional connection between the Southern Indian River Lagoon and the Atlantic Ocean. The Indian River Lagoon receives discharges from Taylor Creek, C-25 Canal, Moores Creek, and Virginia Avenue Canal to the north of St. Lucie Estuary and from minor drainage areas located north of Fort Pierce (Woodward-Clyde 1994). No major tributaries drain to Indian River Lagoon from St. Lucie Inlet south to the Jupiter Inlet.

Urban and agricultural development and its accompanying drainage canal network has resulted in a greatly expanded St. Lucie Estuary watershed. The pre-drainage watershed estimated at 415 square kilometers now covers an area approximately three times that size (Haunert et al. 1994). Major canals in the watershed include the C-23 and C-24, which were constructed as part of the Central and South Florida Flood Control Project. In addition, the St. Lucie Canal (C-44), a U.S. Army Corp of Engineers navigation and flood control canal, links the St. Lucie Estuary to Lake Okeechobee. The C-25 Canal watershed, located north of the St. Lucie Estuary, has increased drainage into the Ft. Pierce Inlet section of the Indian River Lagoon.

The major anthropogenic changes in both the St. Lucie Estuary and C-25 watersheds are significant alterations in the timing (excess wet season flows, insufficient dry season flows), distribution, quality, and volume of fresh water entering the estuary, lagoon and ocean (Haunert et al. 1994). Despite these impacts, the St. Lucie Estuary and the Indian River Lagoon represent important aquatic habitats, with significant environmental and economic values. Understanding how these systems respond to stressors will provide a basis

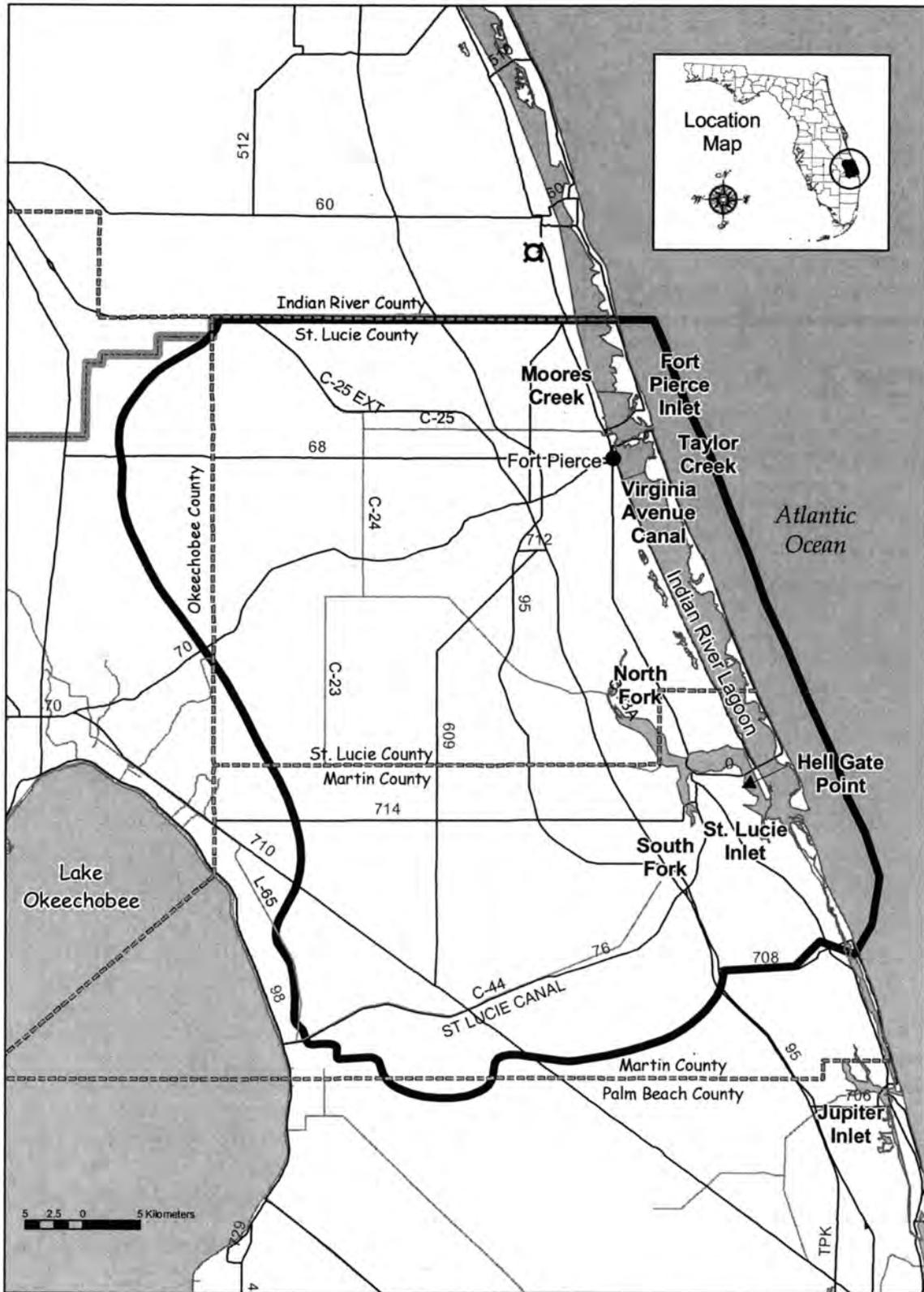


Figure 1. Boundary of the St. Lucie Estuary and Indian River Lagoon Conceptual Ecological Model.

St. Lucie Estuary and Indian River Lagoon Conceptual Ecological Model

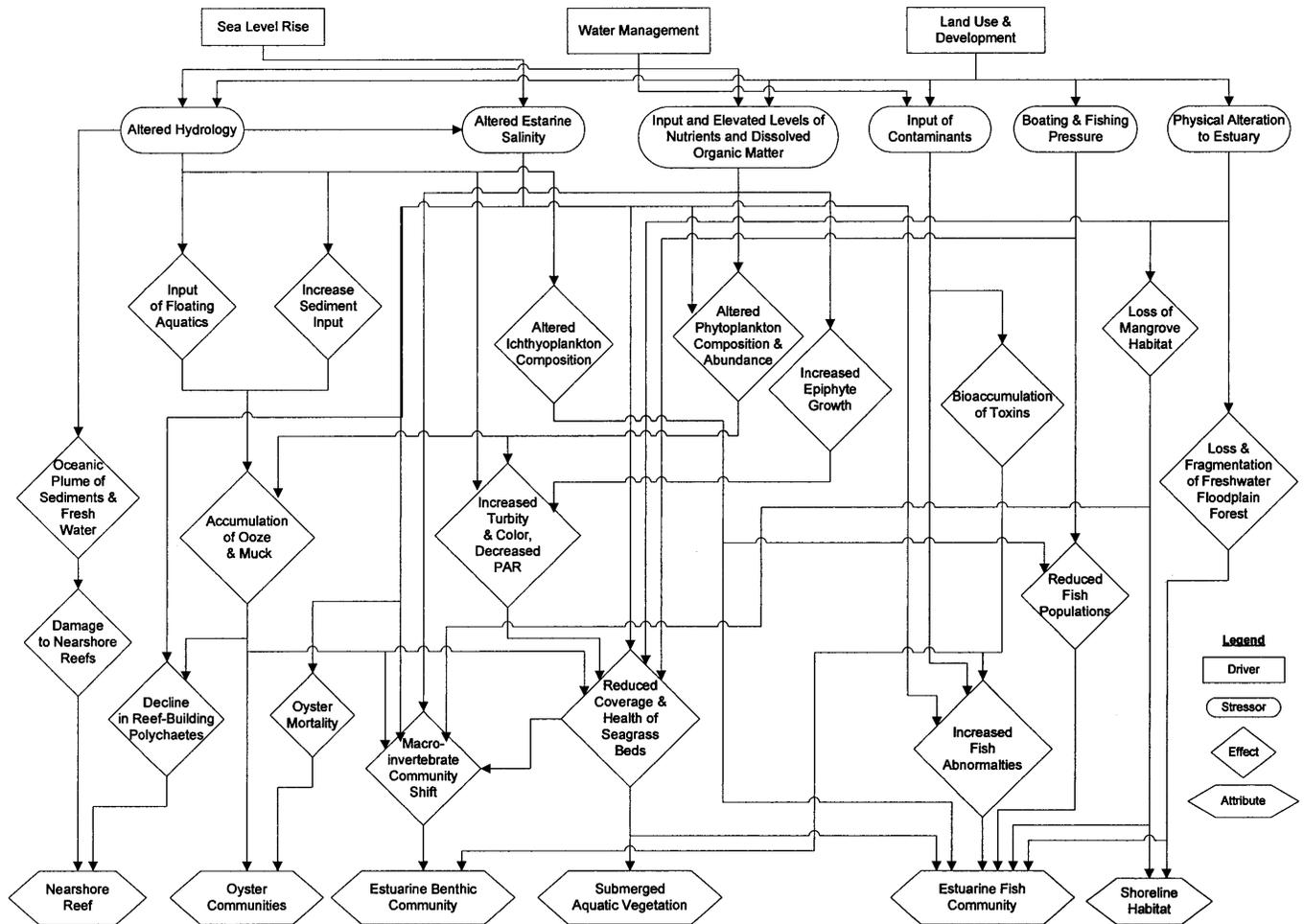


Figure 2. St. Lucie Estuary and Indian River Lagoon Conceptual Ecological Model Diagram.

for well-informed management decisions relative to restoration activities.

EXTERNAL DRIVERS AND ECOLOGICAL STRESSORS

External drivers that result in ecological stressors in the St. Lucie Estuary and Indian River Lagoon include agricultural and urban land use and development and ensuing construction and operation of water management systems, both in local watersheds of the estuary and lagoon and in the larger drainage basin of Lake Okeechobee (Figure 2). Sea-level rise is also a factor that affects the ecology of these systems that should be considered during restoration efforts.

These drivers result in six major stressors. Lake Okeechobee regulatory releases, basin flood releases, and basin water withdrawals alter freshwater flow volume and timing, which in turn, alters estuary salinity and increases turbidity and color, which in turn de-

crease photosynthetically-active radiation (PAR). Agricultural and urban land-use practices compounded by regulatory and flood releases alter hydrology and result in increased loads of nutrients and dissolved organic matter and contaminants. Physical alterations to the estuaries and adjacent tributaries have resulted from construction and maintenance of inlets and development of shoreline and adjacent wetlands. Boating and fishing pressure is also a stressor to the system.

Altered and unstable estuarine salinity has had the most significant effect on the estuary. In 1975, the South Florida Water Management District began baseline investigations to determine seasonal presence of biota. Their goal was to document short-term reactions of estuarine organisms under various salinity conditions during controlled regulatory releases and watershed runoff events (Haunert and Startzman 1980, 1985, D.E. Haunert, South Florida Water Management District, pers. comm.). In 1987, researchers at the South Florida Water Management District began to ap-

ply a resource-based management strategy similar to the "valued ecosystem component" approach developed by the U.S. Environmental Protection Agency's National Estuary Program (USEPA 1987). The aim of this strategy is to define management objectives that can provide a suitable salinity and water quality environment for key species. Using this approach, a favorable range of inflow and related salinity was identified for oysters and submerged aquatic vegetation (SAV). This favorable range of flows and their resultant salinities are referred to as the "salinity envelope." A series of curves for salinity regimes in the St. Lucie Estuary was developed by providing a salinity model with constant inflows until a steady salinity gradient was obtained. Using these salinity curves, preferred salinity envelopes for oysters and SAV have been illustrated. This provides a method to predict where healthy populations of valued ecosystem components would exist if the favorable range of flows and salinity is not violated beyond the tolerance limits of the target biota (i.e., the frequency and duration of events attributable to natural variation of flows from a pre-development watershed). A geographic information system (GIS) was used to define specific locations within designated valued ecosystem component distributions. Factors in addition to salinity that were considered for oysters and SAV included appropriate depth and type of sediment. A salinity envelope was established for the St. Lucie Estuary based on a flow range of 10 to 57 cubic meters per second, previous research on oysters and SAV, as well as predicted monthly mean salinity from various inflows at designated areas.

ECOLOGICAL ATTRIBUTES

Submerged Aquatic Vegetation

In a field study conducted by Woodward-Clyde in 1997, the only significant SAV beds in the St. Lucie Estuary were found in the lower estuary near Hell Gate Point. Shoal grass (*Halodule wrightii* Aschers.) was the dominant species throughout most of this area, with the federally-listed Johnson's seagrass (*Halophila johnsonii* Eiseman) as the secondary species. The only other SAV found during that study was individual scattered blades of widgeon grass (*Ruppia maritima* Linnaeus), wild celery (*Vallisneria Americana* Michx.), and common water nymph (*Najas guadalupensis* (Spreng.) Magnus) in the South Fork of the estuary. A small area of widgeon grass was also documented in the North Fork. Although not found in the estuary, additional seagrasses that are important to and normally documented in the Indian River Lagoon include three *Halophila* species (including *Halophila*

johnsonii), *Syringodium filiforme* Kuetz., and *Thalassia testudinum* Banks & Soland. ex Koenig.

A target of Florida State's Surface Water Improvement and Management (SWIM) seagrass program is to restore and maintain seagrasses to a depth of 1.7 m lagoonwide (Virnstein and Morris 1996). Between 1992 and 1999, the maximum southern Indian River Lagoon seagrass area (3,995 hectares) occurred in 1996, representing approximately 50 percent of the target area (i.e., area of lagoon bottom with a depth of 1.7 m or less). The lowest area mapped during this period occurred in 1999 when seagrass covered approximately 39 percent (3,162 hectares) of the target area. The St. Lucie Estuary GIS Application Model developed by Woodward-Clyde for the South Florida Water Management District in 1998 identified major areas of the estuary suitable for seagrass establishment.

Oyster Communities

Eastern oysters (*Crassostrea virginica* Gmelin 1791) are highly valued as food, but their ecological significance remains under-appreciated and understudied (Coen et al. 1999a). Individual oysters filter 4–34 liters of water per hour, removing phytoplankton, particulate organic carbon, sediments, pollutants, and microorganisms from the water column. This process results in greater light penetration immediately downstream, thus promoting the growth of submerged aquatic vegetation. Although oysters assimilate the bulk of the organic matter that they filter, the remainder is deposited on the bottom where it provides food for benthic organisms. Furthermore, the oyster's ability to form large biogenic reefs (Coen et al. 1999b) qualifies it as a keystone species. Oysters and the complex, three-dimensional, reef structure they form, attract numerous species of invertebrates and fishes.

Oysters and other bivalves, such as mussels and clams, found in the St. Lucie Estuary and Indian River Lagoon are sensitive to salinity, loss of suitable hard bottom substrate, and high levels of total suspended solids in the water column. Oysters have been documented in the past as abundant in the estuary and lagoon. In a survey completed in 1998, their distribution was limited to approximately 81 hectares from the estimated historic coverage of 567 hectares. A restoration target of 365 hectares of healthy oyster beds has been established based on reestablishing an appropriate salinity regime in the areas where a potentially suitable bottom habitat was indicated by the St. Lucie Estuary GIS Application Model (Woodward-Clyde 1998).

Estuarine Fish Communities/Sport and Commercial Fisheries

The St. Lucie Estuary and Indian River Lagoon provide habitats and nursery grounds for a variety of estuarine fish communities. Species richness in many of the fish communities of the estuary and lagoon has decreased since the 1970s when baseline data were collected. In addition to the general decrease in species richness, specific fish communities seem to be affected by salinity and habitat changes (Gilmore 1977, Gilmore et al. 1983).

Submerged aquatic vegetation communities provide habitat and nursery grounds for juvenile stages of reef and recreationally important fishes in the St. Lucie Estuary and Indian River Lagoon (Virnstein et al. 1983, Lewis 1984). This community includes mutton snapper (*Lutjanus analis* Cuvier), yellowtail snapper (*Ocyurus chrysurus* Bloch), lane snapper (*Lutjanus synagris* Linnaeus), yellowtail parrot fish (*Sparisoma rubripinne* Valenciennes in Cuvier and Valenciennes), gag grouper (*Mycteroperca microlepis* Goode and Bean), pinfish (*Lagodon rhomboides* Linnaeus), tarpon (*Megalops atlanticus* Valenciennes in Cuvier and Valenciennes), common snook (*Centropomus undecimalis* Bloch), crevalle jack (*Caranx hippos* Linnaeus), spotted sea trout (*Cynoscion nebulosus* Cuvier and Valenciennes), and redfish (*Sciaenops ocellatus* Linnaeus). The distribution of these juvenile fishes requires a stenohaline and stenothermic condition in seagrass beds.

Ichthyoplankton recruitment into the St. Lucie Estuary and Indian River Lagoon is diminished due to freshwater flushing resulting from regulatory discharges during key times of the year (Gaines and Bertness 1992). Estuarine fish species that are negatively affected include spotted seatrout, common snook, opossum pipefish (*Micropis brachyurus* Bleeker), and lower trophic level fishes. The spotted seatrout is an estuarine-dependant species that is specifically associated with seagrass beds in the estuary and lagoon. Post-larval and juvenile densities in seagrass beds, particularly shoalgrass, reflect seasonal changes in salinity and the subsequent extent and health of those beds (R. G. Gilmore, Coastal and Ocean Science, Inc., pers. comm. 2000).

The opossum pipefish seems to represent a good indicator of both estuarine and freshwater conditions in the St. Lucie Estuary. Specific ambient water temperatures, salinities, and ocean current access limit effective breeding of opossum pipefish populations to the Loxahatchee River and the St. Lucie and St. Sebastian Rivers of the Indian River Lagoon (Gilmore 1999). The pipefish is presently a federal candidate for threatened species status. Adult opossum pipefish live

in *Polygonum* and *Panicum* beds of freshwater bank vegetation. Populations at representative sites appear to be indicators of appropriate wet and dry season salinity. Recruitment of pipefish into the St. Lucie River occurs during a period of low water flow in the normal dry season. Release of large volumes of fresh water during this time is likely to have a deleterious impact on juvenile pipefish movement upstream (Gilmore 1999).

Large freshwater releases from the St. Lucie Canal in the winter of 1998 produced significant incidences of fish disease and mortality, promoted toxic dinoflagellate blooms, and reduced the overall biodiversity of estuarine and freshwater fish communities within the Indian River Lagoon, a condition that persisted for several months after cessation of the discharges (Gilmore personal data and observations May 1998). In 1979, 1980, and March 1998, within several weeks of sudden releases of large volumes of water (greater than 226 cubic meters per second) into the St. Lucie Estuary, an increased prevalence (greater than 6 percent) of fish with ulcerative mycosis, which is caused primarily by a fungus, was recorded (Florida Fish and Wildlife Conservation Commission/Florida Marine Research Institute unpublished data). Since March 1998, monthly surveys conducted by Florida Marine Research Institute documented a low level of persistence of ulcerative mycosis in fish, particularly in silver mullet (*Mugil curema* Valenciennes in Cuvier and Valenciennes), striped mullet (*Mugil cephalus* Linnaeus), and sheepshead (*Archosargus probatocephalus* Walbaum in Artdi). The incidence of ulcerative mycosis is consistently correlated with discharges related low salinity conditions (Kane et al. 2000, (J. Landsberg, Florida Marine Research Institute, pers. comm. 2000)) and is known elsewhere in the United States to be attributed to the fungus *Aphanomyces invadens* (Blazer et al. 1999). The range of fish health problems in the St. Lucie and Indian River systems has been attributed to low salinity due to excessive freshwater inputs and associated pathogens, contaminants, and potentially harmful algal bloom species. The frequency of abnormalities seems to have increased in recent years (Gassman et al. 1994 Fournie et al. 1996, Browder et al. 1997, Gabriel 1999). A study is currently underway to determine if there are links between fish abnormalities and toxins transported into the estuary with the freshwater discharges.

Although harvesting of fish and shellfish by the human population of the region has been shown to extend at least 8,000 years ago to the Ais and Timucuan Indians, the first commercial fisheries did not develop until the 1890s. Woodward-Clyde (1994) documented a shift in commercial finfish species composition to a higher proportion of lower priced species taken more

recently. The increased harvest of species such as menhaden and mullet may also have an effect on the overall ecology and productivity of the lagoon. One species, the spotted seatrout, has shown a steady and significant decrease in landing (over 50 percent) from 1962 to 1988. Because this species is almost entirely dependent upon the lagoon throughout its life cycle, this decline is likely a consequence of conditions within the lagoon. Recreational fishing pressure continues to increase within the St. Lucie Estuary and Indian River Lagoon as a result of the increased numbers of both full-time residents and tourists. The number of fishing trips by residents alone increased from 806,067 in 1970 to 1,811,815 in 1990 and is estimated to be 2,890,448 by 2010 (Woodward-Clyde 1994).

Estuarine Benthic Communities

Benthic macroinvertebrate communities in the St. Lucie Estuary and Indian River Lagoon are sensitive to bottom type, water quality, and salinity fluctuations. A decrease in diversity of benthic organisms and increase in the numbers of pollution-tolerant macroinvertebrates, such as the polychaete worm, *Glycinde solitaria*, can indicate deteriorating water quality in the estuary and lagoon. Haunert and Startzman (1985) showed that fluctuation in salinity between periods of high and low discharge caused alternating shifts between estuarine and freshwater species. Their results indicated an overall reduction of 44 percent of the benthic macroinvertebrates. The greatest change in benthic species composition occurred in the newly created oligohaline zone (0.5 to 5 ppt). Some species of macroinvertebrates (i.e., freshwater midges) showed significant increases, and there was an introduction of six freshwater species under these conditions. At least four estuarine species were recorded as lost from the oligohaline zone. Changes in biodiversity and speciation in the benthic communities as a result of restoration actions have been studied in the Indian River Lagoon by Virnstein (1990).

Shoreline Habitat

Mangrove wetlands and the emergent bank vegetation of tributaries of the St. Lucie Estuary and Indian River Lagoon support fish and macroinvertebrate communities and help prevent siltation due to bank erosion. These once ubiquitous shoreline habitats have decreased in spatial extent and function through habitat loss and the loss of connectivity. A significant portion of the floodplain in the North Fork of the St. Lucie River is completely or partially cut off from river's main branch because of dredging conducted during the 1920s to 1940s. As a result of these dredging activi-

ties, certain natural communities, including floodplain swamp, floodplain forest, hydric hammock, and oxbows (blackwater river and stream), are no longer fully connected to the existing main branch, resulting in a loss of natural filtration of water-borne nutrients originating in the watershed. Pilot projects are underway to reconnect mangrove and freshwater wetlands to the main channels of the North and South Forks.

Nearshore Reef

Three to five kilometers offshore from the Atlantic Coast between the St. Lucie and Ft. Pierce Inlets, a nearshore reef forms bands of unique marine habitat. This nearshore reef, built by Sabellarid polychaetes, represents the northern extent of Sabellarid reef worms. The reef provides foraging habitat for federally-endangered green sea turtles (*Chelonia mydas* Linnaeus). The nearshore reef has been adversely affected by high level freshwater discharges and the resulting silt and salinity plumes that are found primarily to the south of the St. Lucie and Ft. Pierce Inlets (Gilmore pers. comm. 2000). Approximately 66 percent of the seagrass fishes in the lagoon are catadromous species that spawn on the continental shelf where fish biodiversity is influenced by various reef structures and is also susceptible to sedimentation (Gilmore 1988). Major live coral reefs, *Oculina varicosa* (Lesueur), are only abundant on the shelf edges between 60 and 100 m. These complex rock, *Sabellarid*, and coral structures provide important habitat that supports a diverse benthic fish community on the continental shelf whose associated faunas increase the lagoon fish biodiversity adjacent to ocean inlets such as the St. Lucie Inlet (Gilmore 1995).

ECOLOGICAL EFFECTS: CRITICAL LINKAGES BETWEEN STRESSORS AND ATTRIBUTES/ WORKING HYPOTHESES

Several major causal pathways appear to account for the decline in the ecological attributes of the St. Lucie Estuary and Indian River Lagoon. These casual pathways are based on key hypotheses developed during the conceptual ecological model workshops. These hypotheses determine the content and organization of the St. Lucie Estuary and Indian River Lagoon Conceptual Ecological Model. A discussion of the causal pathways is provided below, followed by the key hypotheses, which are organized, for the most part, by attribute; estuarine geomorphology is also a subheading, but it is not an attribute. It may arguably be a stressor, but more information is needed before including it in this conceptual ecological model.

The overarching ecological impact to the St. Lucie

Estuary and Indian River Lagoon is the alteration of estuarine salinity zones. Changes in the distribution, timing, and rapidity of change of salinity include low saline events, due to basin and Lake Okeechobee regulatory water releases, and hypersaline events, due to excessive basin water withdrawals and drought conditions.

Accompanying the regulatory water releases is the transport of massive volumes of organic and inorganic sediments, which contribute to deposits of muck in the estuaries (Gunter and Hall 1963, Pitt 1972, Shrader 1984). The large accumulations of muck covering the bottom of the estuary dramatically decrease the quality and quantity of suitable habitat for benthic macroinvertebrates, oysters, and finfish. High volume releases create an oceanic plume of colored water and suspended solids extending to the nearshore reef in the Atlantic Ocean, reducing light penetration and exacerbating siltation. Together, altered salinity and siltation can have negative impacts to important components of the estuarine and nearshore reef ecosystems, including SAV, phytoplankton, fish and macroinvertebrate communities, fish-eating birds, and reef-building polychaetes (Haunert 1988). The recurring high-flow conditions in the St. Lucie Estuary have significantly reduced the numbers of oysters, and the frequency at which these high flows occur has impeded recovery (Cake 1983). Damage to the nearshore reef habitat, especially to chicken-liver sponge communities, can result in secondary effects on juvenile green sea turtles via reduced food supply (J.A. Browder, National Oceanic and Atmospheric Administration, pers. comm. 2000). Changes in temporal and spatial patterns of salinity envelopes can be significant stressors to fish and shellfish populations. Lowered salinities can result in atypical freshwater conditions that are conducive to the persistence of fish pathogens, such as fungi, that have been implicated as a causal factor for lesioned fish within the St. Lucie Estuary (J. Landsberg, Florida Marine Research Institute, pers. comm. 2000).

The loss and fragmentation of habitat due to human development results in the direct loss of mangrove wetlands and emergent bank vegetation upon which fish and macroinvertebrate communities depend. Increased inputs of nutrients and dissolved organics degrade water quality, which in turn alters phytoplankton composition and abundance. Increased levels of toxicants from agricultural run-off, urban development, and the boating industry (i.e., metals and pesticides) can cause adverse impacts to aquatic food webs including fish-eating birds. A decrease in the numbers, diversity, and health of fisheries may also have secondary effects on the health and mortality of the resident dolphin population in the Indian River Lagoon (Browder pers. comm. 2000).

Submerged Aquatic Vegetation

Relationship of Submerged Aquatic Vegetation to Altered Estuarine Salinity Envelope. Changes in normal salinity ranges can adversely affect SAV. Different species of SAV have different desirable salinity ranges. When the salinity falls outside these optimal ranges, adverse impacts to the size, density, and species compositions of seagrass beds can occur.

Relationship of Submerged Aquatic Vegetation to Input of Nutrients and Dissolved Organic Matter. The input of increased levels of nutrients and dissolved organic matter effect SAV abundance and health by increasing the phytoplankton levels, epiphyte growth, and water color, which can affect the amount of light penetration in the water column and its availability to SAV communities.

Relationship of Submerged Aquatic Vegetation to Increased Epiphyte Growth. Increased epiphyte growth can be caused by both increases in available nutrients that accelerate their growth and/or a decrease in grazers that regulate the abundance of epiphytes. This increase in epiphytes can shade the blade of the SAV, thus decreasing the amount of light that can be absorbed by the plant and used for photosynthesis.

Relationship of Submerged Aquatic Vegetation to Accumulation of Muck and Ooze. SAV communities require suitable substrate for successful recruitment and establishment. Large deposits of muck that have replaced normal substrate in the estuary and portions of the Indian River Lagoon have contributed to the decrease in extent of SAV beds.

Relationship of Submerged Aquatic Vegetation to Boating Pressure. The increase in the numbers of boats in the lagoon has contributed to the decrease in extent of SAV beds. Shallow areas, which normally contain the healthiest and most abundant beds, are most likely to be impacted when boats run aground or their props come in close proximity to the grass beds. Boat props and wave action from boat wakes also re-suspend flocculant muck sediments, which decreases light penetration to seagrass beds.

Relationship of Physical Alterations in the Estuary to Submerged Aquatic Vegetation Distribution, Abundance, and Health. The physical alterations in the estuary that have an adverse impact on SAV include the destruction of natural shoreline and replacement with hardened shoreline such as bulkhead and seawalls. As the shallow sloping shorelines, which absorb rather than reflect wave energy, are eliminated, the area available with the appropriate depth for SAV recruitment and growth decreases.

Oyster Communities

Relationship of Oysters to Extreme Alterations of the Estuarine Salinity Envelope. Extremely large rainfall events in the local watershed or large volume releases from Lake Okeechobee lead to massive amounts of fresh water entering the primary canal systems, which convey the water quickly into the estuary, causing a sudden drop in salinity. This sudden drop in salinity, if maintained over an extended period of time usually greater than two weeks, can lead to significant mortality in the oyster population.

Relationship of Oysters to Lower Level Releases of Fresh Water that Result in Sub-Optimal Salinity Conditions in the Estuary. Less extreme but still undesirable fluctuations in salinity stress the oyster population and may (depending on the timing and severity of the salinity change) affect the reproductive success during that given time frame. Oyster reproduction is triggered when the water reaches the correct temperature; therefore, the time of year when these low salinity events occur are crucial to success of the spawn in a given year. The overall health of the oysters is also compromised during these episodes, making the oyster more susceptible to predators and disease.

Relationship of Oysters to Muck Accumulation. Oyster recruitment is negatively effected by the accumulation of muck in the estuary, which makes an unsuitable substrate for spat settlement. Areas that once contained sand and/or shell have been covered by these very soft, unconsolidated sediments. Freshwater flows carry excessive levels of silt, clay, and organic material into the estuary and lagoon. Alteration of freshwater flow can also result in an increase in the transport of floating aquatic vegetation from the canal system into the estuary, which then degrade and contribute to the rate of muck accumulation. Increased volume of fresh water from the watershed also increases nutrient loads, which have contributed to algal blooms. As the algae dies off and settles, it may exacerbate the muck formation.

Estuarine Fish Communities

Relationship of Estuarine Fish Communities to Reduced Coverage and Health of Submerged Aquatic Vegetation. SAV provides nursery grounds for many fish and invertebrate communities. A reduction in size and health of SAV beds effects the location, abundance, and speciation of fisheries in the estuary.

Relationship of Estuarine Fish Communities to Increased Levels of Toxins. Toxins introduced to the estuary with the freshwater inputs can bioaccumulate in fish, which may be one causative factor in the ob-

served increased frequency of fish abnormalities. Certain species of fish, such as the silver mullet and sheepshead seem to be more susceptible than others to the effects of toxins.

Relationship of Estuarine Fish Communities to Loss of Mangrove Habitat. Mangroves supply both structural refuge for juvenile fish and an important component in the detrital food web. Destruction of the mangrove shorelines, which once lined large areas of the lagoon and estuary, has negatively impacted the fisheries in the estuary and lagoon. In large areas of the estuary, all natural shoreline has been lost to development.

Relationship of Estuarine Fish Communities to Loss and Fragmentation Floodplain Forest. The loss and fragmentation of freshwater floodplain forest, which historically dominated the shoreline in the oligohaline zones of the North and South Forks of the estuary has decreased the quality of that habitat. Areas of shoreline where natural forest, shrub, or emergent vegetation has been lost due to development no longer provide necessary habitat and nursery areas for juvenile fisheries. These oligohaline zones provide refuge to juvenile fish from larger predatory fish that prefer higher salinities.

Estuarine Benthic Communities

Relationship of Macroinvertebrate Community Shift to Altered Salinity Envelope. The macroinvertebrate community consists of largely sessile organisms that cannot escape adverse conditions but rather are extirpated by sudden and dramatic shifts in salinity that change diversity and species composition of benthic invertebrates in the estuary and lagoon. Increase in nutrients and toxins carried into the estuary with the fresh water can also cause a shift to more pollutant tolerant species or provide conditions conducive to colonization by opportunistic species. Toxins can also bioaccumulate causing a decline in the health of the communities and adversely impact aquatic food webs.

Shoreline Habitat

Relationship of Loss of Mangroves and Loss of Freshwater Floodplain Forest to Physical Alterations to the Estuary. Physical alterations to the estuary caused by increased population in the coastal zone has led to the conversion of natural shoreline, both mangrove and freshwater floodplain, to seawalls, bulkheads, and other types of hardened shoreline. This loss of habitat impacts many other important components of the estuary including fisheries, crabs, macroinvertebrates, and birds.

Nearshore Reef

Relationship of Nearshore Reef to Altered Freshwater Flows. Oceanic plumes of fresh water and their associated sediment and pollutant loads can damage nearshore reefs. During periods of extreme discharge events, large volumes of fresh water exit the St. Lucie Estuary through the St. Lucie Inlet and impact the nearshore reefs. This highly colored fresh water carries with it sediments that affect the health and abundance of the nearshore reef community.

Estuarine Geomorphology

Relationship of the Exchange of Atlantic Ocean Water with the Indian River Lagoon and St. Lucie Estuary to Sea-Level Rise. Predicted rates of sea-level rise during the next century (up to 0.6 m) will increase the exchange and circulation of Atlantic Ocean water with that in the Indian River Lagoon and the St. Lucie Estuary. The effect of this would be a more saline condition overall and a shift in the location and salinity ranges in the estuary. This shift could effect the location and health of most of the flora and fauna in the estuary, including SAV, oysters, benthic communities, and shoreline vegetation.

RESEARCH QUESTIONS

Ecological changes resulting from restoration of freshwater flows to the St. Lucie Estuary and Indian River Lagoon will be influenced by interrelated causal relationships, some of which possess low levels of certainty. All of these restoration uncertainties involve freshwater flow into the estuary and lagoon. Several of these relationships are based purely on volume, timing, and distribution of fresh water itself, while others include elevated levels of nutrients and toxins that are associated with flows originating from the developed watershed.

Submerged Aquatic Vegetation

Relationship of Submerged Aquatic Vegetation to Input of Nutrients and Dissolved Organic Matter. What effect does increased levels of nutrients and dissolved organics have on light attenuation and its subsequent effect on distribution, health and abundance of SAV in the St. Lucie Estuary and Indian River Lagoon?

Relationship of Submerged Aquatic Vegetation to Increased Epiphyte Growth. What is the relationship of the amount of epiphyte coverage found on SAV with location, abundance, and diversity of different species of SAV in the St. Lucie Estuary and Indian River Lagoon?

Estuarine Benthic Community

Relationship of Macroinvertebrate Community Shift to Altered Salinity Envelope. What effect do undesirable salinity shifts have on diversity and community species composition of macroinvertebrates in the St. Lucie Estuary and Indian River Lagoon?

Oysters

Relationship of Oysters to Lower Level Releases of Fresh Water That Result in Less Than Ideal Salinity Conditions in the St. Lucie Estuary. What is the functional relationship between lower volume and longer time frame releases on health and long-term survivability and reproduction of the oyster community in the St. Lucie Estuary?

Estuarine Fish Community

Relationship of Estuarine Fish Communities to Salinity Fluctuations. How do changes in salinity affect the reproductive success and juvenile growth of fish in the estuary? How do sudden and dramatic salinity changes influence the prevalence of fish with lesions? What is the functional relationship between salinity regimes, fish reproduction and growth, fish lesions, and the proliferation of certain fish pathogens and potentially harmful algal bloom species?

Relationship of Estuarine Fish Communities to Increased Levels of Toxins. What is the functional relationship between toxins and abnormalities and/or lesions found on fish in the St. Lucie Estuary and Indian River Lagoon?

Nearshore Reef

Relationship of Nearshore Reef to Altered Freshwater Flows. What effect do large volume releases from either Lake Okeechobee or the St. Lucie Estuary watershed have on nearshore reefs and their associated faunal communities?

Sea-Level Rise

Relationship of the Exchange of Atlantic Ocean Water with the Indian River Lagoon and St. Lucie Estuary to Sea Level Rise. What is the relationship of sea level rise to the estuary "salinity envelope"?

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LOXAHATCHEE WATERSHED CONCEPTUAL ECOLOGICAL MODEL

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Abstract: Historically, the Loxahatchee River watershed included an area of more than 560 km². The drainage basin was comprised primarily of pine flatwoods interspersed with cypress sloughs, hardwood swamps, marshes, and wet prairies. Rain falling on the basin was directed through natural topography into wetlands, treated by natural biological and chemical action, and slowly released to the receiving water bodies, the Loxahatchee River and Estuary and the Indian River Lagoon. Today, approximately 434 km² of the original watershed drain to the Atlantic Ocean through Jupiter Inlet. The watershed still includes substantial amounts of upland, freshwater wetland, riverine, and estuarine habitats, but large areas have been developed for urban and agricultural land uses. Development in the watershed, stabilization of the inlet, and dredging of the estuary and river have resulted in saltwater intrusion in the river, destruction of riverine cypress forest along the river, and upstream migration of seagrasses and mangroves. A conceptual ecological model, in the risk assessment framework, was developed for the Loxahatchee system to characterize the wetland, riverine, and estuarine components of this complex and diverse system. This model was developed as a means to build understanding and consensus among scientists and managers regarding the linkages between ecological stressors and attributes in the Loxahatchee river system. These relationships lead to development of a set of working hypotheses that explain how observed shifts in the distribution of riverine floodplain plant communities, oysters, seagrasses and other key species are related to increases in salinity in the river and estuary that have occurred during the past century in response to changing land use, climate change and water management practices. Basic and applied research is needed to address questions related to ecosystem structure and mechanisms that control the abundance and distribution of plants and animals in this system.

Key Words: Loxahatchee River, riverine cypress swamp, conceptual ecological model, altered hydrology, saltwater intrusion, elevated nutrients, mangroves, submerged aquatic vegetation, fish communities, oysters, nearshore reef

BACKGROUND

Historically, the Loxahatchee River watershed included and drained more than 565 km² of inland sloughs and wetlands. The drainage basin was comprised primarily of pine flatwoods interspersed with cypress sloughs, hardwood swamps, marshes, and wet prairies. Rain falling on the basin was directed through natural topography into the wetlands, treated by natural biological and chemical action, and slowly released to receiving water bodies, the Loxahatchee Estuary and Indian River Lagoon. Today, approximately 435 km² of the original watershed drains to the Atlantic Ocean through Jupiter Inlet (Figure 1). The watershed includes upland, freshwater wetland, riverine and estuarine habitats. Outflow from the watershed also affects Indian River Lagoon and nearshore reefs.

Major freshwater wetland systems within the watershed include Loxahatchee Slough, Hungryland Slough, Grassy Waters Preserve, J. W. Corbett Wildlife Management Area, Pal Mar, and Jonathan Dickinson State Park. Some areas such as the J. W. Corbett Wildlife Management Area, Grassy Waters, and Jonathan Dickinson State Park are owned by the state or local government entities and have management plans in place to protect these areas from further harm or to restore damaged wetland systems. Other areas such as Pal Mar and the Atlantic Coastal Ridge property are in the process of acquisition (SFWMD 2000). The southern half of Loxahatchee Slough, considered historically to be the headwaters of the federally-designated Wild and Scenic Northwest Fork of the Loxahatchee River, has been impounded to form the Grassy Waters Preserve, which is owned by the City of West Palm Beach.

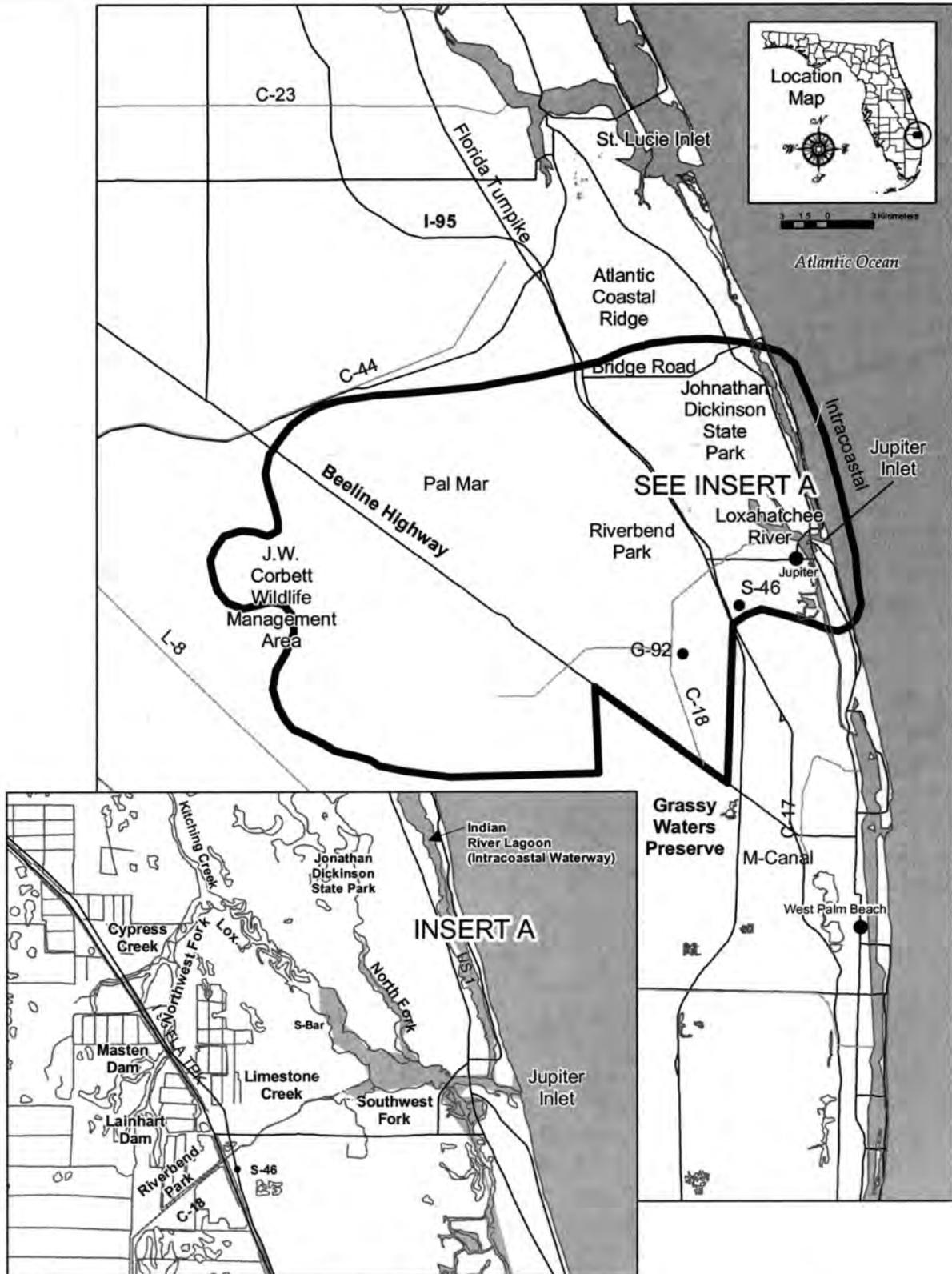


Figure 1. Boundary of the Loxahatchee Watershed Conceptual Ecological Model.

Grassy Waters Preserve is a managed wetland ecosystem that also provides drinking water to the City of West Palm Beach, the Town of Palm Beach, and other communities.

The riverine portion includes the area of the Northwest Fork located upstream from where the eastern boundary of Jonathan Dickinson State Park intersects the river, as well as that portion of the North Fork that lies upstream from the estuary within the park boundaries. Some major tributary streams, such as the North Fork, Northwest Fork, and Kitching Creek, exist today much within historic configurations. Furthermore, watersheds of these tributaries lie largely within Jonathan Dickinson State Park or other state-owned lands and are protected from development. Other tributaries, such as the Southwest Fork, Limestone Creek, Lake Worth Creek, and Cypress Creek, have been greatly altered due to dredging, channelization, and adjacent land development.

The Loxahatchee River historically received flow into the Northwest Fork from the Loxahatchee Marsh (Slough) and the Hungryland Slough. Both of these wetland areas drained to the north and east from a low divide or ridge that was located along the grade that was used to construct the Beeline Highway (State Road 710) (Parker et al. 1955). Historically, these areas were characterized by swampy flatlands interspersed with small, often interconnected ponds and streams that produced sheet flow. Flow from the ridge along State Road 710 could be directed north or south, depending on local conditions. Drainage patterns were determined by rainfall distribution and the poorly defined natural land forms of the area.

The predrainage wetland and slough mosaic of the Loxahatchee watershed was a shallow, clear-water, low nutrient system. Aside from fire and infrequent frosts, unique vegetation of the freshwater area of the watershed evolved in response to both low-nutrient water quality conditions and seasonal fluctuations of water levels driven by rainfall, percolation to ground water, and discharge through naturally meandering sloughs, creeks, and rivers.

A conceptual ecological model, in the risk assessment framework (Ogden et al. 2005), was developed for the Loxahatchee watershed to describe wetland, riverine, estuarine, and nearshore components of this complex and diverse system (Figure 2). Each component of the system (i.e., wetland, river, estuary, and nearshore), could be viewed as an ecological subsystem and expanded into a detailed model. Conceptual ecological models can serve as communication, planning, and assessment tools that are useful to both scientists and policymakers. The Loxahatchee Watershed Conceptual Ecological Model is one of 11 such regional models that have been developed to describe

key features of the South Florida ecosystem at a scale that is appropriate for both local and regional planning and management applications.

Within the conceptual model, *drivers* are the major external forces that have large-scale influences on natural systems. In the Loxahatchee watershed, these were identified as sea-level rise and climate change, regional and local water management, and land-use and development activities. *Stressors*, which are the resulting physical or chemical changes that occur in natural systems in response to drivers, include altered hydrology, elevated loadings of dissolved and suspended materials in the water column, physical alterations, and increased boating and fishing activity. These drivers and stressors have a wide range of *ecological effects* throughout the system, many of which are linked to and dependent on other effects. *Attributes* are the biological elements or components that represent overall ecological conditions in the natural system. Attributes are selected to represent known or hypothesized effects of stressors and elements of systems that have important human values. Arrows represent pathways by which the effects of drivers are passed through the system ultimately to influence the attributes.

EXTERNAL DRIVERS

Sea-Level Rise and Climate Change

Hydrologic conditions throughout the watershed are dominated by high average annual rainfall, wet and dry seasonal rainfall variations, periodic events of extreme flooding (e.g., hurricanes), severe droughts, and freezes. Extreme droughts, associated fires, and floods may have dramatic effects on ecological conditions in the watershed and river, resulting in destruction or degradation of large areas of native vegetation. Severe freezing conditions occur infrequently but can result in changes to vegetation communities that may persist for years. Such stresses can provide opportunities for invasion or replacement of tropical species, such as red mangroves (*Rhizophora mangle* Linnaeus) by more cold-tolerant species such as cypress (*Taxodium distichum* (Linnaeus) L.C. Rich) or maples (*Acer rubrum* Linnaeus) or by invasive exotic species such as Brazilian pepper (*Schinus terebinthifolius* Raddi).

Sea-level rise has had a significant effect on the river and estuary during the past century (McPherson et al. 1982) and is expected to have even greater effects during the next 50 years. Rising sea level will alter upstream hydrology and salinity conditions in the river as salt water moves further upstream (Hu 2002) and will result in changes to water management actions due to increasing water levels downstream from major

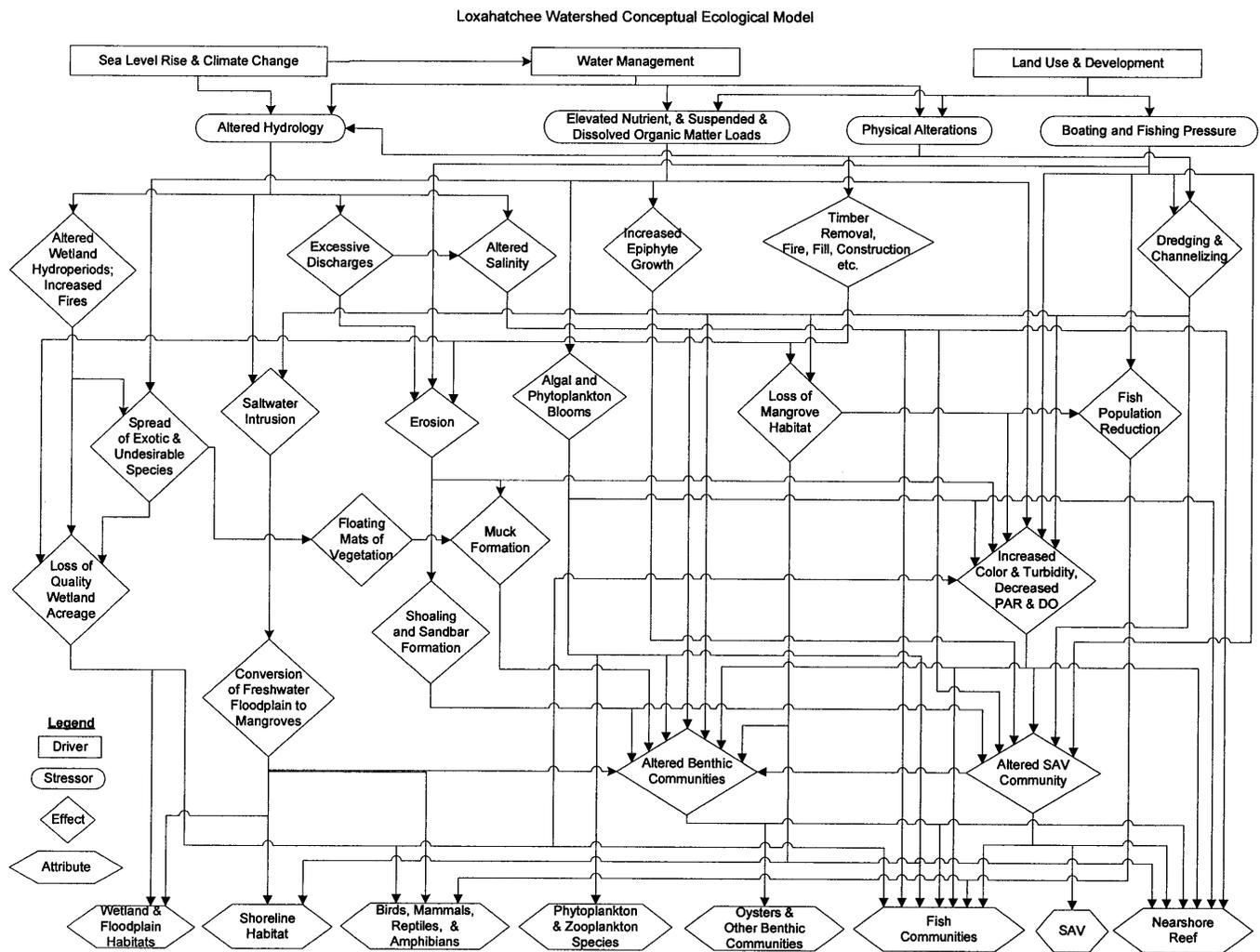


Figure 2. Loxahatchee Watershed Conceptual Ecological Model Diagram.

coastal control structures. Future sea-level rise (Douglas 1991, 1992) may also affect exchange of sediment through the inlet and deposition of sediment in the river channel.

Water Management

Water management activities in the watershed during the past century, including construction of major canals and secondary drainage systems and discharges for flood protection, have changed the system's hydrology, resulting in rapid decline of water levels in the basin, saltwater intrusion in the river and adjacent aquifer during dry periods, and high rates of discharge during wet periods (Birnhak 1974, McPherson *et al.* 1982, SFWMD 2002a, b). Construction and operation of canals and ditches have increased transport of sediment, organic materials, and agricultural chemicals, resulting in periodic low levels of dissolved oxygen (DO), bacterial contamination, and high concentrations

of nutrients in the river and estuary (FDEP 1998, 2000a).

Land Use and Development

During the past sixty years, significant portions of the watershed have been converted from upland forests and wetlands to urban, residential, and agricultural development (TCRPC 1999, Martin County Planning Department 2000). Construction of transportation corridors and drainage facilities, as well as dredging and filling of shorelines and wetlands to accommodate growth, have resulted in altered hydrology, loss or degradation of natural ecosystems, increased severity of fires, and adverse water quality conditions (Alexander and Crook 1975, McPherson and Sabanskas 1980, Wanless *et al.* 1984, Law Environmental 1991a, FDEP 1998, TCRPC 1999).

ECOLOGICAL STRESSORS

Altered Hydrology

Hydroperiods in floodplain wetlands, flow patterns, and salinity have been altered by water management practices and land-use changes (Land et al. 1972, Birnhak 1974, Mote Marine Laboratory 1990a, b). Freshwater runoff to the estuary occurs more rapidly and abruptly during wet periods to prevent flooding; the estuary thus receives higher maximum flows. During dry periods, insufficient fresh water is released, resulting in upstream encroachment of saline waters (Rodis 1973a, b, Alexander and Crook 1975).

When excessive discharges of fresh water are made to the estuary during wet periods, much of the flood water from the upper (southern) end of the Loxahatchee River watershed is collected by the C-18 canal and shunted into the Southwest Fork through the S-46 structure. Under these conditions, rapid changes in salinity occur in the estuary and adjacent marine waters, resulting in destruction of benthic and seagrass communities in the estuary, displacement of fishes, and stress or damage to offshore reef communities. Significant erosion can also occur in the watershed and along the river channel during these excessive discharges, which may cause trees to fall and block the river channel, damage floodplain vegetation, and cause shoaling in the estuary. Flood management discharges also erode stream channels, alter channel morphology, and deposit sand and mud further downstream (USA-CE 1966, Law Environmental 1991b). Periodically, the system is impacted by massive releases of fresh water that destroy estuarine and marine communities throughout the river, estuary, and adjacent coastal waters (Rodis 1973b, Allen et al. 1997, Dent and Ridler 1997).

Such extreme flood-control discharges may create a plume of fresh water that prevents tidal marine waters from entering the inner estuary. The low salinity plume may act as a "plug" or barrier to successful colonization of habitats in the Loxahatchee by many organisms. In a typical natural scenario, offshore areas provide larvae and juveniles to the estuary, and in turn, the estuary provides adult fish that spawn offshore. A persistence of low salinity conditions could interfere with both processes. Early larval and juvenile stages are particularly vulnerable to poor water quality conditions (including lowered salinity). Some organisms may avoid low salinity areas, delay settling in nursery habitats, and thus be at greater risk of predation. Organisms may also die or become stressed by exposure to adverse salinity levels. Low salinity exposure may cause eggs or larvae to settle prematurely in inappropriate habitats, leading to reduced survival (Reagan 1985, Forward 1989). Haloclines produced by low sa-

linity fronts may cause larval organisms to concentrate along the edge of the plume, exacerbating these risks (Kingsford and Gray 1996).

Adverse impacts have occurred in the watershed due to reduced wet season water levels and dry season flow. In many areas of the watershed, distribution, extent, species composition, and health of freshwater wetlands have changed in response to altered hydrology. Drained wetlands are subject to more severe fires, resulting in a conversion from sloughs to prairies and from wet prairies to pineland communities. These hydrologic changes also provided conditions that were favorable for the invasion of exotic species (Alexander and Crook 1975, Zahina et al. 2001, M. J. Duever, SFWMD, pers. comm.). Vegetation patterns have shifted from natural wet prairie and cypress communities to uplands or to cattail (*Typha* spp.) and willow (*Salix caroliniana* Michx.)-dominated wetland systems. Large areas of existing and former wetlands have been invaded by exotic vegetation, especially Brazilian pepper (*Schinus terebinthifolia*, Raddi), melaleuca (*Melaleuca quinquenervia* (Cav.) Blake), and Old World climbing fern (*Lygodium microphylla* (Cav.) R. Br). Reduction of flow to the Northwest Fork and consequent upstream intrusion of salt water in the river have also resulted in loss of cypress trees in the floodplain and replacement by mangroves (Rodis 1973b, Alexander and Crook 1975).

Elevated Loads of Nutrients, Pollutants, and Suspended and Dissolved Organic Matter

Nutrient enrichment has been identified as a water quality problem throughout the Loxahatchee watershed. Nutrients are carried by stormwater runoff and ground-water flow to wetlands and canals, and they eventually reach the river and estuary. Drainage of the watershed has also resulted in oxidation and release of nutrients from organic wetlands soils. Water quality impacts many features in this system, including wetland soils and plant communities, sediment accumulation, trophic status of lakes, rivers, and estuaries, and water color, turbidity, and oxygen levels (Sonntag and McPherson 1984, Law Environmental, Inc. 1991b, FDEP 1998). Pollutants in the form of coliform contamination and high levels of pesticides also occur periodically in certain parts of the river, tributaries, and adjacent coastal waters (FDEP 1998).

Historically, major wetlands of the Loxahatchee watershed were physically connected to the Everglades through sheet flow and have experienced similar ecological responses due to disturbance and increased nutrient loads (Davis 1994, David 1996, Lodge 1998). Such changes include replacement of sawgrass (*Cladium jamaicense* Crantz) marsh by cattails (*Typha dom-*

ingensis Pers.) and invasion of wetland forests and tree islands by melaleuca and climbing fern. Grassy Waters Preserve has experienced ecological modifications adjacent to the M Canal, where an encroaching cattail front is replacing sawgrass marsh due to disturbance of the substrate and influx of nutrients (Graves unpubl. data). Loxahatchee Slough and adjacent wetlands have been extensively invaded by melaleuca, and the Loxahatchee Slough, Loxahatchee River floodplain, and adjacent wetlands in Jonathan Dickinson State Park have been extensively invaded by climbing fern.

Periodic large releases of fresh water, construction activities in the watershed, and formation and movement of large rafts of floating aquatic plants (i.e., water lettuce [*Pistia stratiotes* Linnaeus]) have created undesirable sediment deposits in the Northwest Fork. Muck deposits are aggregations of clay and fine silt-sized particles that tend to have a high content of organic materials and form a soft, unstable ooze that covers underlying sand or mud substrates. They occur in the North Fork of the estuary due, in part, to migration of these riverine deposits. Sand deposits also occur due to transport through the inlet, which primarily affect seagrass communities, benthic invertebrates, and shoaling in the lower estuary (Sonntag and McPherson 1984, Antonini *et al.* 1998, FDEP 1998).

Introduction of nutrients into an oligotrophic freshwater system adversely influences DO concentrations due to accelerated vegetative litterfall and decomposition (Graves *et al.* 1998). In such areas, DO levels often fail to meet criteria for freshwater Class III waters. Periodic sampling data indicate that DO concentrations show a decreasing trend within the Northwest Fork. Low oxygen levels primarily affect fish and invertebrate populations (FDEP 1996, 1998, 2000a; Loxahatchee River District 1996).

The Loxahatchee River and its tributaries drain extensive areas with organic soils. Runoff from such areas generally possesses high color content. Periodic discharges of agricultural and urban stormwater runoff also contribute high levels of turbidity. Both of these factors influence oxygen levels and water clarity, with resultant impacts on plankton, macroinvertebrate, and submerged plant communities (Strom and Rudolph 1990, FDEP 1998, R.C. Dent, Loxahatchee River District, pers. comm.).

Physical Alterations

Physical structure of the watershed has been significantly altered to provide flood protection and drainage for agricultural and urban development. Major features that presently influence drainage in the river basin are the C-18 canal, Florida Turnpike, Interstate 95 (I-95), Beeline Highway, and Bridge Road (State Road 708).

These features now act as important unnatural drainage corridors and sub-basin divides. Special drainage districts and landowners operate and maintain an extensive system of secondary canals within the basin. Many areas that once were part of an interconnected network of wetlands, ponds, and sloughs are now traversed by drainage canals, ditches, roads, super highways, well-drained farms, citrus groves, golf courses, and residential developments. The drainage system has lowered groundwater levels and significantly altered surface-water flows to the river and estuary (McPherson and Sabanskas 1980).

In the 1930s and 1940s, cypress trees were harvested from large areas of the floodplain for timber. During this period, major roads and drainage canals were constructed in the basin. Low dams (Masten Dam and Lainhart Dam) were constructed in the Northwest Fork to maintain higher water tables in the upstream basin and prevent overdrainage of the floodplain and adjacent lands (Cary Publications 1978).

Major forks of the Loxahatchee Estuary were channeled to remove natural sandbars and oyster reefs that restricted boat access. However, these features also provided a barrier to inland migration of salt water. In the late 1950s, the C-18 canal was completed, which drained wetlands in Loxahatchee Slough and diverted fresh water from Northwest Fork to Southwest Fork of the Loxahatchee River. This project redirected almost all freshwater flows away from Northwest Fork from the early 1960s up to 1974. In 1974, the G-92 structure was constructed to reconnect the C-18 canal and Loxahatchee Slough with the Northwest Fork (SFWMD 2002a).

Historically, the natural mouth of the estuary, Jupiter Inlet, was a small and shallow passage that opened and closed periodically as the result of natural conditions, except when it was periodically dredged. In 1947, it became permanently opened by the United States Army Corps of Engineers (McPherson and Sabanskas 1980). Since that time, the inlet has provided a twice-daily influx of saline waters into Loxahatchee River (Jupiter Inlet District 1999).

Coastal development has resulted in loss or conversion of significant portions of mangrove and saltmarsh habitats that historically existed in the Southwest, North, and Northwest Forks of the estuary. Saline and brackish marshes and mangrove swamps are indispensable components of the estuarine system and processes of South Florida. They are primary producers of the estuarine food web and cleanse and filter terrestrial runoff waters. Effects of fill on coastal wetlands are severe (DOI 1974). By removing the filtering action of coastal wetlands, development has resulted in increased turbidity and a decline in water quality (Vines 1970, Law Environmental 1991b).

Boating and Fishing Pressure

Loxahatchee River and Estuary are extensively used for navigation and recreation. Boating pressure is a stressor to the estuary through direct impacts such as seagrass scarring and sediment resuspension. Indirect effects occur due to dredging and construction activities to improve boat access, mooring and servicing, widening of Jupiter Inlet, and channelization of the river and estuary. These changes have destroyed and degraded natural shoreline and benthic communities, increased saltwater penetration upstream in the river, increased turbidity, and decreased oxygen levels (USACE 1966, Vines 1970, DOI 1974, Hill 1977, Cary Publications 1978, Law Environmental 1991b, Antonini et al. 1998). Sandbars, oyster bars, other benthic organisms and submerged aquatic vegetation (SAV) are eliminated by dredging. Borrow areas are rarely recolonized by SAV due to excessive depths. Suspended solids created by dredging may cover and suffocate productive adjacent bottom communities. Water circulation within these borrow areas is typically poor, causing these depressional areas to act as sinks for silt and other suspended materials.

Fishing pressure from sport and commercial fisheries has impacted standing stocks of many species (Post et al. 1999), with resultant impacts throughout the food web. Local fisheries seem to show some improvements in response to changes in the management process (FDNR 1985, Muller et al. 1996, FDEP 2000a, b).

ECOLOGICAL ATTRIBUTES

Wetland Habitats in the Watershed and the Floodplain

Species composition and distribution of plant communities in a given locale are primarily functions of climate, soil type, and suitable water conditions, including depth of water table, length and frequency of inundation, and water quality. These plant communities, in turn, provide food and/or habitat for various birds, fish, and other wildlife. Changes in distribution, abundance, and species composition of plant communities therefore have a direct effect upon type and quality of associated animal communities (Alexander and Crook 1975, McPherson et al. 1982, Sharitz and Gibbons 1989, Kraus et al. 1999, Martin County Planning Department 2000).

Freshwater wetlands within the watershed include swamps, sloughs, marshes, and wet prairies. These wetlands occur primarily as strands and traces that follow major overland drainage routes or as irregular, isolated depressions surrounded by pine-forested uplands. The hydrology of these areas is mostly influenced by local rainfall and runoff. Floodplain habitats are areas

immediately adjacent to the River channel that are influenced by inflow from the tributaries and the rise and fall of tidally-driven water-level fluctuations.

Within the Loxahatchee River Floodplain, delineation can be made between areas that support healthy cypress trees and associated freshwater hardwood trees and understory vegetation and areas that are dominated by mangroves. This separation of community types occurs primarily because of the salinity regime, which in turn is determined by freshwater flow (FDNR 1985, FDEP and SFWMD 2000). Because freshwater flow was insufficient for a long period of time, mangrove communities have displaced cypress/wetland plant communities on much of the floodplain (McPherson et al. 1982, Pezeshki et al. 1987, FDEP and SFWMD 2000, 2002a).

In areas that are dominated by cypress, the forest canopy may extend to heights of 18–24 m and consists of three or more distinct layers. Each layer has different light levels and provides habitat for epiphytic plants and various mammals, reptiles, and birds. In areas where the cypress forest has been replaced by mangroves, the canopy is greatly diminished and is generally less than 9 m, providing much less habitat diversity and a correspondingly less rich flora and fauna (SFWMD 2002a). This has affected the types of fish and wildlife that use these areas (FDNR 1985, FDEP and SFWMD 2000).

Shoreline Habitat

Shoreline habitat refers to plant communities, primarily mangroves and an associated understory of salt-tolerant species that border the estuary. Overall distribution and abundance of mangroves reflects the extent of saltwater penetration into the river system. Four species of mangroves occur in the Loxahatchee River system: red mangroves, white mangrove (*Laguncularia racemosa* (Linnaeus) Gaertn. f.), black mangrove (*Avicennia germinans* Linnaeus), and buttonwood (*Conocarpus erectus* Linnaeus). All contribute to system productivity, but red mangroves tend to provide better habitat for estuarine species (Heald and Odum 1970).

Birds, Mammals, Reptiles, and Amphibians

The combination of climate, vegetation, and water bodies in the Loxahatchee River area has resulted in a large diversity of animal species. Numerous vertebrate species inhabit the area surrounding Northwest Fork. Many of these are identified as endangered, threatened, or of special concern by Florida Fish and Wildlife Conservation Commission, or they are listed

as threatened or endangered by United States Fish and Wildlife Service (USFWS).

Aquatic vertebrates are numerous in marshes, lakes, and streams in the river area. The West Indian manatee (*Trichechus manatus latirostris* Linnaeus) frequents the Loxahatchee River Estuary (Packard 1981). The entire Loxahatchee River has been designated by USFWS as a critical habitat for the West Indian manatee (USFWS 1996). Numerous turtles also live in and around the river. Wading birds observed in freshwater marshes and wetlands include wood storks (*Mycteria americana*, Linnaeus), herons (*Egretta* spp.) and white ibis (*Eudocimus albus*, Linnaeus). Amphibians are also abundant, including frogs and sirens in freshwater reaches of the system. Many freshwater fish species also inhabit the marshes, and saltwater fish species inhabit the estuary. These are discussed under Fish Communities.

Mammals and birds are frequently encountered along the riverbank. The more commonly seen species include raccoon (*Procyon lotor* Linnaeus), opossum (*Didelphis virginiana* Kerr), white-tailed deer (*Odocoileus virginianus* Zimmermann), osprey (*Pandion haliaetus* Linnaeus), barred owl (*Strix varia* Barton), egrets, herons, and ibis (SFWMD 2002a).

The Loxahatchee National Wild and Scenic River and Jonathan Dickinson State Park contain 52 federal and state species that are endangered, threatened, or of special concern (23 animals and 29 plants). Those species having a federal designation include the American alligator (*Alligator mississippiensis* Daudin), eastern indigo snake (*Drymarchon corais couperi* Holbrook), Florida scrub jay (*Aphelocoma coerulescens* Bosc), bald eagle (*Haliaeetus leucocephalus* Linnaeus), wood stork (*Mycteria americana*, Linnaeus), Everglades snail kite (*Rostrhamus sociabilis plumbeus* Vieillot), and West Indian manatee (FDEP 1998). Additional species have been identified as being either endangered, threatened, or of special concern by the Florida Committee on Rare and Endangered Plants and Animals. The threatened osprey often nests in dead cypress trees in the lower Northwest Fork. Great egret (*Ardea alba* Linnaeus), black-crowned night heron (*Nycticorax nycticorax* Linnaeus), and yellow-crowned night heron (*Nyctanassa violacea* Linnaeus), classified as "species of special concern," are also found in the Loxahatchee River area.

Phytoplankton and Zooplankton

Phytoplankton play an important role in aquatic ecosystems as a source of primary productivity. They obtain dissolved nutrients such as phosphorus, nitrogen, and trace elements from the water column and convert them to proteins and carbohydrates and cellular struc-

tures. The Loxahatchee system contains freshwater, brackish, and marine species, but the residence time in the freshwater areas is generally very short. There have been no specific studies of plankton in this system, but the phytoplankton communities typically consist of microscopic green and blue-green algae, diatoms, dinoflagellates, and more complex forms such as *Volvox* spp. When nutrients from runoff or rainfall enter the system, phytoplankton typically respond and produce high concentrations of organisms within a few days.

Zooplankton generally range in size from protozoans to the juveniles and larvae of larger fishes. The major components, besides larvae and juvenile of larger organisms, consist of copepods, amphipods, chaetognaths, rotifers, and jellyfishes. These animals feed on the phytoplankton and serve as intermediaries in the food web, transferring energy to higher predators. Zooplankton populations tend to increase rapidly once phytoplankton become abundant and eventually reach high enough concentrations to suppress or dramatically reduce the concentration of phytoplankton. Seasonal variations in plankton abundance therefore occur, based on the reproductive cycles of larger organisms, but also on cycles of nutrient influx from the watershed, increased phytoplankton productivity, and subsequent zooplankton blooms (Havens *et al.* 1996).

Oysters and Other Benthic Communities

Benthic macroinvertebrate communities in the Loxahatchee Estuary are sensitive to bottom type, water quality, and salinity fluctuations. Dent *et al.* (1998) profiled the macroinvertebrate community present in the Loxahatchee Estuary. Analysis of macroinvertebrate data has shown a decrease in number and diversity of animals that live in the water of the Northwest Fork downstream from Riverbend Park (Loxahatchee River District 1996).

Benthic communities need suitable substrate for successful recruitment and establishment. Hard substrates such as shell and rock provide excellent surfaces for colonization by oysters, barnacles, sponges and attached algae. Coarser sands, dense silt, and mud provide a relatively stable environment for burrowing worms, mollusks, and fishes. Very fine sediments, clay-size particles or less that are referred to in this particular context as "muck," especially in areas that have high wave action or low DO levels, provide unsuitable habitat.

Oysters are a particularly important component of the benthic invertebrate community in the Loxahatchee Estuary. In the Northwest Fork, the largest living oysters (80–90 mm) were found between river kilometers 6.4 and 9.7, where average high tide surface salinities were between 7 and 22 parts per thousand (ppt) and

ranged from about 2 to 28 ppt. The river delta (also known as "S-Bar") located at approximately river kilometer 7.2 played a controlling role in upriver salinities and was the most active oyster ground (Law Environmental, Inc. 1991a).

Fish Communities

In 1965, 267 species of fishes, consisting of 169 genera and 78 families occurred in and along the river and its estuary (Christensen 1965). Freshwater fish include largemouth bass (*Micropterus salmoides* Lacepede), speckled perch (*Pomoxis nigromaculatus* Lesueur in Cuvier & Valenciennes), bluegill (*Lepomis macrochirus* Rafinesque), shellcracker (*Lepomis microlophus*, Guenther), redbreast (*Lepomis auritus* Linnaeus), warmouth (*Chaenobryttus gulosus* Cuvier in Cuvier and Valenciennes), bowfin (*Amia calva* Linnaeus), gar (*Lepisosteus platyrhincus* DeKay), channel catfish (*Ictalurus punctatus* Rafinesque), and many species of minnows. Many saltwater fish inhabit the estuary. These include common snook (*Centropomus undecimalis* Bloch), tarpon (*Megalops atlanticus* Valenciennes in Cuvier and Valenciennes), black mullet (*Mugil cephalus*), silver mullet (*Mugil curema*), bluefish (*Pomatomus saltatrix* Linnaeus), jack (*Caranx* sp.), sheepshead (*Archosargus probatocephalus* Walbaum in Artdedi), drum (*Sciaenops ocellatus*, Linnaeus), silver perch (*Bairdiella chrysoura* Lacepede), grouper (*Mycteroperca* spp.), snapper (*Lutjanus* spp.), flounder (*Paralichthys* spp.), and seatrout (*Cynoscion nebulosus* Cuvier in Cuvier and Valenciennes).

Within the estuary, seagrass communities, mangroves, oyster reefs, and stable benthic communities provide critical refugia and food sources for juvenile fish such as redfish, grouper, snook, and spotted seatrout. Decline in juvenile abundance and distribution of these and other species, along with an overall decrease in species richness may be related to fishing pressure and a decline in suitable habitat and/or a result of alterations in salinity regime and timing of freshwater discharges (Christensen 1965, Browder and Moore 1981, M. Hedgpeth, SFWMD, pers. comm.).

Submerged Aquatic Vegetation

Five species of seagrasses are commonly observed in the Loxahatchee Estuary. Shoal grass (*Halodule wrightii* Aschers.) tends to be the most abundant species. Stargrass (*Halophila* spp.) sometimes occurs with shoal grass, but its biomass tends to be insignificant except in localized areas. Presence of Johnson's seagrass (*Halophila johnsonii* Eiseman), an endangered species (NMFS 2000), in the Loxahatchee Estuary was noted by Kenworthy (1992). Manatee grass (*Syringodiu-*

ium filiforme Kuetz.) and turtlegrass (*Thalassia testudinum* Banks & Soland. ex Koenig) occur rarely in the estuary. Various species of macroalgae occur in the estuary on an occasional basis, either attached to rocks or shell or forming discrete patches within the seagrass communities (Ridler et al. 1999). Shoal grass has the broadest salinity tolerance, followed by turtle grass and manatee grass. Stargrass is the most stenohaline species of those in the study area (Zieman 1982). Turtlegrass has an optimum range of 24–35 ppt.

Distribution and composition of seagrass communities changes considerably from year to year. A comparison of grass bed distributions performed between 1994, 1996, and 1998 showed that over half of the 0.34 km² of seagrass present in 1994 had been lost by 1996, and that a slight recovery had occurred by 1998 when 0.18 km² were present (Ridler et al. 1999). This change in seagrass cover was attributed to scouring, which deepened the Northwest and Southwest Forks during the fall of 1995, whereupon sediments thus removed were transported and deposited in the central embayment area of the estuary (Jupiter Inlet District 1999). Salinity, temperature, and water clarity are quite variable in the estuary. By contrast, in the north arm of the Intracoastal Waterway, inflow of ocean water maintains relatively high salinity, moderate temperature, and relative high water clarity. Manatee grass and turtlegrass are dominant and form dense stands under these conditions.

Nearshore Reef

Significant, well-developed coral reef systems occur near Jupiter Inlet and are the northern extreme of zoogeographic distribution (Japp and Hallock 1990). Quantity and quality of water discharged from Loxahatchee Watershed has effects on nearshore habitats near Jupiter Inlet, and changes to water management strategies may alter current conditions. River discharges may transport sediments to nearshore reef areas and decrease light penetration through alteration of water color, clarity, and nutrients. These factors may directly or indirectly affect the health of corals through increased sedimentation directly on corals, stimulation of phytoplankton or macroalgal species that may shade or overgrow coral colonies, and through decreased light availability or alteration of color frequencies needed by symbiotic zooxanthellae in hard coral tissues.

ECOLOGICAL EFFECTS: CRITICAL LINKAGES BETWEEN STRESSORS AND ATTRIBUTES/WORKING HYPOTHESES

Ecological effects and critical linkages are based on key working hypotheses. Hypotheses are presented below, organized by attribute or groups of attributes.

Wetland and Floodplain Habitats

Wetlands Degraded by Altered Hydrology due to Land Development, Construction and Water Management. Land development, construction, operation of drainage and flood-control facilities, and consumptive use withdrawals in the watershed, especially during the past fifty years, have resulted in localized and region-wide changes in major wetland systems in the Loxahatchee River watershed and floodplain (TCRPC 1999, Martin County Planning Department 2000). Lowering of the water table throughout the watershed due to canal construction and the need to protect land development has resulted in a net loss of an estimated 10,000,000 cubic meters of storage in the C-18 basin alone (SFWMD 2002a). Major wetland systems have been drained for agricultural and urban development. Other, mostly adjacent, wetlands have been altered to become upland dry prairies or pine forests, primarily dominated by Florida Pine (*Pinus elliottii* Engelm.) and saw palmetto (*Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.)

Saltwater Intrusion Caused Conversion of Freshwater Floodplain Forests to Mangroves. Increased saltwater intrusion due to construction of Jupiter Inlet, navigational improvements to the estuary and river, drainage of the watershed, and declining ground-water levels has been associated with a loss or degradation of freshwater plant communities and expansion of saltwater-tolerant plants upstream, especially in the Northwest Fork (McPherson and Halley 1996). Recent studies have shown that one of the first signs of stress in the freshwater swamp community is reduction in the number of seedlings and saplings of canopy species as the saltwater interface approaches (SFWMD 2002a). Another early change is dramatic reduction in diversity and abundance of understory plant species (SFWMD 2002a). The most dramatic effect is the loss (death) of mature cypress trees and replacement by mangroves (Alexander and Crook 1975, Duever and McCollom 1982). A proposed mechanism for replacement of cypress trees in the floodplain by salt tolerant mangroves is the toxic effect of saltwater penetration into floodplain soils. Salt penetration into soils occurs due to upstream movement of saltwater in the river channel and reduced seepage of fresh ground water from adjacent uplands.

Mangrove- to Cypress-Dominated Shoreline Shift Will Have Significant Unpredictable Effects on Productivity and Diversity of Coastal Ecosystems. A major ecological process that drives trophic structure and productivity in estuarine and coastal systems is quality and quantity of biological material that is transported from the adjacent watershed and river into the estuary

and converted to biomass of estuarine and marine organisms. This process is initiated by ingestion of leaf litter by secondary consumers and microbial decomposition of leaf litter. Mangroves are an excellent source of high quality leaf litter (Odum *et al.* 1982). Less is known about quantity and quality of leaf litter produced by cypress and other freshwater swamp trees. A shift from mangrove-dominated river shoreline to cypress-dominated shoreline is thus likely to have significant, although largely unpredictable, effects on productivity and diversity of coastal ecosystems.

Habitat Disturbance Provides Opportunities for Invasion by Exotic Species. Exotic species are thought to invade most successfully in areas where dominant native vegetation has been damaged or stressed. Such damage often opens up soil to light, allowing seeds of exotic species to germinate. Also, stress caused by lowered water tables damages or slows growth of native wetland species and allows more aggressive exotic plants such as melaleuca, Brazilian pepper, and Old World climbing fern to become established. In freshwater areas, introduction of nutrients allows cattails to proliferate and displace other littoral zone emergent species, such as sawgrass, and causes water hyacinth (*Eichhornia crassipes* (Mart.) Solms), water lettuce, or hydrilla (*Hydrilla verticillata* (L.f.) Royle) to expand in open waters. These changes result in degradation of aquatic habitat and formation of dense mats of vegetation, which may be transported downstream to create deposits of rotting vegetation in the estuary.

Shoreline Habitat

Mangrove Distribution Has Changed Due to Development and Reduced River Flows. Mangroves serve important ecological functions, which include primary productivity, filtering of particles and nutrients, and stabilization of shorelines and habitat. Fragmentation of mangrove communities has occurred due to shoreline development and dredge and fill activities. In the Loxahatchee River and Estuary, approximately 40% of the shoreline is bordered by mangroves. Extensive areas of mangrove and salt marsh have been lost due to construction and resultant turbidity from runoff and pollution (Law Environmental Inc. 1991b). Losses of mangrove throughout the region have been linked to declines in sport and commercial fisheries (Christenson 1965, Gilmore 1995). Coastal saltmarsh and mangrove communities have been almost completely eliminated from the estuarine portions of the North Fork and Southwest Fork due to shoreline development. Remaining mangroves are located primarily in areas

where they did not occur historically, through colonization of freshwater marshes and swamps.

Restoration Activities Will Result in Overall Loss of Regional Mangrove-Associated Estuarine Communities. River restoration efforts that increase the amount of freshwater flow down the River will result in downstream movement of the saltwater interface. Areas of the floodplain that are dominated by mangroves will experience a shift in vegetation as these areas become increasingly invaded by freshwater species. The established mangroves will not necessarily disappear completely but, over time, will be displaced by faster growing freshwater floodplain species. Mangroves living in fresh water do not serve the same ecological function as mangroves that live in salt or brackish areas. Mangroves in marine systems support a diverse community of associated barnacles, oysters, crabs etc. These communities also provide food and shelter for marine and estuarine fishes. Restoration efforts that result in an increase in freshwater flow during dry periods would result in overall loss of these associated mangrove communities. No suitable downstream locations are available for mangrove colonization because such areas have already been altered by development and bulkheading of shorelines.

Influx of Dissolved Nutrients Results in Increased Plankton Productivity. Plankton populations typically increase during dry periods when runoff water has higher levels of nutrients, water clarity is greater, and retention time is increased. Excessive concentrations of nutrients result in phytoplankton blooms that may be toxic or have adverse effects on oxygen concentrations, benthic communities, and seagrasses. Changes in the watershed that affect the quantity and quality of runoff and/or the retention time in the system may lead to increased occurrences of undesirable phytoplankton blooms.

Oysters and Other Benthic Communities

Water Quality Degradation and Rapid Salinity Changes have Adverse Effects on Benthic Communities. Sudden and severe shifts in salinity lead to changes in species composition, decreased diversity, and decreased species richness of benthic invertebrates in the estuary (USEPA 1999). Excess nutrients can create enhanced feeding opportunities for organisms, causing an imbalance among competing types. Less desirable, stress-tolerant species may become dominant under nutrient-enriched, low oxygen conditions.

Influx of Sediments and Suspended Solids Changes the Structure and Composition of Benthic Communities. Benthic communities need suitable substrate for

successful recruitment and establishment. High velocity discharges from the Northwest Fork carry larger sand and gravel particles that result in shoaling at the point where the river discharges to estuary (S-shoals). Sandbars form in the central embayment apparently primarily due to sand carried into the river through the inlet. Sandbar formation may cover existing benthic communities and oysters but may also create new habitat for floodplain species and seagrasses (Hill 1977, Law Environmental 1991a, Antonini et al. 1998).

Discharges from the river and runoff from adjacent development also carry very fine suspended materials and clay-size particles. These materials settle to the bottom to form "muck," especially when they form deep deposits in areas that have low wave action. These substrates generally provide unsuitable habitat for benthic organisms and have displaced or modified normal substrates in the North and Northwest forks of the estuary. These fine sediments also become resuspended during discharge events or due to wave action, resulting in increased turbidity and decreased light penetration that may reduce dissolved oxygen levels and smother benthic communities.

A Decline in Oysters during the Past 100 Years Has Resulted in Loss of Other Estuarine Species. Oysters, clams, and scallops are natural components of estuaries and were historically abundant in the system (Estevez 1998, Leverone 2000). Although currently less abundant and less commercially and recreationally important (Sackett 1888, Chamberlain and Doering 1998a), oysters continue to be an important resource due to their ability to filter suspended materials from the water column and form stable substrate for colonization by other organisms. Reduction in oyster coverage occurred due to shell mining, dredging of channels, bar removal, altered freshwater inflow, increasing loads of suspended solids, and changes in hydrodynamics. This decrease has resulted in an overall decline in health, abundance, and distribution of the oyster reef community within the estuary (Law Environmental 1991b).

Upstream Movement of Salt Water in the Loxahatchee Estuary Has Impacted the Health of Oyster Communities. Salinity is an important factor that determines distribution of coastal and estuarine bivalves. Although oysters can tolerate exposure to a wide range of salinities for short periods, they require a smaller range of salinity variation to remain healthy and reproduce. Adult oysters typically tolerate a salinity range of 2 to 40 ppt but normally occur at salinities between 10 and 30 ppt (Gunter and Geyer 1955). Short pulses of freshwater inflow can greatly benefit oyster populations by killing predators (Owen 1953), but excessive freshwater inflows may kill an entire popula-

tion (Gunter 1953, Schlesselman 1955, MacKenzie 1977). Changes in salinity can also affect the physiological condition of oysters (Kinne 1964), which in turn affects functional processes in oyster-dependent ecosystems (Dame 1996).

Reduced flows of fresh water from the river and increased influx of saltwater through the inlet have caused dry season increases in salinity in the Loxahatchee Estuary that induce stress, reduce oyster health, and promote the spread of parasites and predators. Protozoans, such as those that cause the disease, Dermo (*Perkinsus marinus* (Mackin, Owen & Collier) Levine), are a common source of oyster mortality. Intensity of Dermo outbreaks is controlled by salinity and temperature (Dame 1996) and is more severe in areas of high salinity (Burreson and Calvo 1996).

Fish and Benthic Communities

Loss of Submerged Aquatic Vegetation Results in a Loss of Fish and Benthic Communities. Dense seagrass blades and rhizomes associated with the grasses provide food for invertebrates and small fishes and protection from potential predators (Zieman 1982). SAV also provide a substrate for colonization by epiphytic algae, as well as food and habitat for numerous epibenthic and infaunal invertebrates. Changes in SAV community health, abundance, distribution, structure, and species composition, along with changes in the natural salinity regime, have been associated with losses of mollusk, shrimp, and crab populations and decreases in larval and adult fish recruitment in Florida estuaries. Fish densities are typically greater in grass bed habitat than in adjacent habitats (Reid 1954, Tabb *et al.* 1962, Roessler 1965, Weinstein *et al.* 1977).

Increased Plankton Productivity Affects Fish and Benthic Communities. Phytoplankton are an essential component of the diet of many animals that live in the estuary, including nektonic (free swimming) fishes, crabs, and shrimp that graze on or within the plankton, and benthic organisms such as worms, clams, and coral that filter plankton from the water column. Excessive growth of phytoplankton (blooms), on the other hand, may be toxic or have adverse effects on oxygen concentrations, benthic and fish communities, and seagrasses. Species of gamefish (e.g., common snook and tarpon), as well as commercially important species such as pink shrimp (*Farfantepenaeus duorarum* Burkenroad) blue crabs (*Callinectes sapidus* Rathbun), and American oysters (*Crassostrea virginica* Gmelin) depend on a healthy distribution, abundance, and balance between phytoplankton and zooplankton communities for sustenance, growth, and reproduction.

Fish Communities

Salinity Conditions Affect Fish Habitat. Changes in flow from the Northwest Fork have resulted in increased penetration of estuarine and marine species upstream in the river during dry periods, a decreased extent of freshwater habitat, and a decline in diversity and abundance of native freshwater fish species in the lower reaches of the river (Christensen 1965, Mote Marine 1990a, b, M. Hedgepeth, SFWMD, pers. comm.). At the same time, incursion of mangroves into the Northwest Fork and increased growth of seagrasses in the Central Embayment have provided additional habitat and food for estuarine and brackish species

Salinity Conditions Affect Juvenile Fish. Rapid or extreme alterations in the salinity regime can have adverse effects on the sensitive life history stages of many estuarine species (Emery and Stevenson 1957, Odum 1970, Lindall 1973, Perry and McIlwain 1986, Chamberlain and Doering 1998b, Trexler and Loftus 2001). For example, eggs of spotted seatrout are neutrally buoyant at about 20–22 ppt (Pattillo *et al.* 1997). Trout spawn during warmer months of the year (Lassay 1983) and thus depend on the presence of high salinity levels during summer months. Occurrence of lower than normal salinity conditions during this period could thus lead to reduction or elimination of an entire year-class of spotted seatrout.

Reduced Levels of Dissolved Oxygen have Adverse Effects on Fish Communities. Increased loadings of nutrients, suspended solids, and dissolved organic material from the watershed result in greater biological oxygen demand (BOD) in the river and lower ambient DO levels. Water quality in the river is periodically below state standards for Class III Waters. Rapid or extreme reduction in oxygen concentrations may result in fish mortality, but often the effects of chronic exposure to reduced oxygen levels are more subtle, including changes to species composition, health and distribution of fish communities in the river, a decline in species diversity, and an increase in abundance of pollution-tolerant and low oxygen-tolerant species.

Fish and Higher Vertebrates

Loss of Mangrove Shoreline Habitat Leads to a Decline in Fishes and Higher Vertebrates. Oligohaline and mesohaline wetlands of the mangrove estuary support resident communities of small fishes and invertebrates that are an important intermediate trophic level for support of wading birds, raccoons, and other higher consumers (Lorenz 2000). Many taxa of fish including important fisheries species occupy mangrove

habitats during significant portions of their life histories (Porter and Porter 2002). Three species, gray snapper (*Lutjanus griseus* Linnaeus), blue striped grunts (*Haemulon sciurus* Shaw), and great barracuda (*Sphyraena barracuda* Walbaum in Artedi) seem especially dependent upon mangrove habitat and are permanent residents within its root structure (Porter and Porter 2002). Mangrove roots also serve as staging habitat for certain estuarine transients that are resident on coral reefs as adults.

Submerged Aquatic Vegetation

Changes in Salinity Affect Submerged Aquatic Vegetation Communities. Changes in salinity of the Loxahatchee estuary during the past century have likely had significant effects on SAV species composition and distribution, although no data are available prior to the 1960s. Different species of SAV have different salinity preferences and tolerances. When salinities are outside of these ranges, SAV may experience a reduction in densities and distribution (Chamberlain and Doering 1998b). Increases or decreases in salinity may give one species a competitive advantage (Livingston 1987). Tabb et al. (1962) stated, "Most of the effects of man-made changes on plant and animal populations in Florida estuaries are a result of alterations in salinity and turbidity" (see also Zieman 1982, Mote Marine Laboratory 1990a, b, Ridler et al. 1999).

Changes in Water Quality Affect Submerged Aquatic Vegetation. Even relatively minor changes in nutrient concentrations can greatly reduce productivity of seagrasses and lead to broad habitat changes (Livingston 1984). Increased influx of nutrients into the Loxahatchee Estuary, from urban and agricultural lands, may have negative impacts on SAV through increased growth of epiphytes (Murray et al. 1999) and phytoplankton (Livingston 1987, Durako 1988), which decreases light availability. Increased epiphyte growth can also be caused by changes in benthic communities that result in a decrease in grazers. Reduced light penetration can diminish or eliminate previously healthy seagrass meadows (Zieman 1982) by impairing photosynthesis, growth, and reproduction.

Boating Pressure Impacts Shorelines and Submerged Aquatic Vegetation. The increase in numbers of boats and boat traffic in the estuary has decreased stability of shorelines and extent of SAV beds. Shallow areas, which normally contain the healthiest and most abundant beds, are most likely to be impacted by channel dredging, grounding of boats, or damage by boat propellers. Construction of docks, piers, and access channels also impacts SAV beds and shoreline vegetation. Increased wave action due to boat wakes also impacts

substrate stability and light penetration, especially in areas where natural shorelines have been replaced by bulkheads and seawalls (SFWMD 1995).

Nearshore Reef

Altered Freshwater Flow Regimes Affect Species Composition of Nearshore Reef Communities. The Loxahatchee River Estuary, seagrass beds, and benthic communities, as well as the low salinity mangrove habitat that exists within the Northwest Fork of the river, provide habitat and food sources for juveniles of a number of species that spend their adult lives on offshore reefs (Haunert and Starzman 1985). Changes in salinity in the estuary that affect the utilization of these areas as a nursery for species that later inhabit the reefs will thus have an effect on species composition of reef communities.

Major Discharge Events Impact Nearshore Reef Communities. Increased freshwater flows during major discharge events from the C-18 canal and S-46 structure result in increased loads of turbidity, sediment, and nutrients and dramatic decreases in salinity. Highly turbid water and fallout of suspended solids directly impact the survival of coral animals.

Algal Blooms Affect Nearshore Reef Communities. Competition is an important process that determines structure and composition of reef communities. Macroalgae compete with zooxanthellae of corals for light and nutrients. Thus, over-colonization of reefs by macroalgae, often associated with or stimulated by excessive concentrations of dissolved nutrients in the water column, is an important step during reef degradation (McCook et al. 2001). Even slight increases in nutrients can have catastrophic consequences and result in blooms of macroalgae and filamentous algae (Lapointe 2000).

RESEARCH QUESTIONS

Ecological changes are expected to occur as a result of redirection and increased freshwater flow, resulting in reestablishment of freshwater habitat in the river and changes to estuarine ecosystems. Research is needed to gain a better understanding of these relationships.

Relationship of Salinity Conditions to Inlet Configuration and Sea-Level Rise. The relationship of sea-level rise to the Loxahatchee Estuary's salinity envelope needs to be determined. Also, the effect sea-level rise will have on the ability of increased flows to maintain freshwater conditions within designated Wild and Scenic sections of the Loxahatchee River needs to be

determined. The effect that construction and maintenance of the inlet has on the ability to maintain freshwater conditions upstream in the river also needs to be evaluated.

Relationship of Mangrove Communities to Freshwater Inflows. Research is needed in the Loxahatchee system to determine 1) effects of changing the volume of freshwater flow from the river on the long-term distribution and health of mangroves in the river floodplain and the estuary, 2) the relative habitat value of mangroves and the habitat and food value of associated communities of attached plants and animals that live on mangroves in fresh water vs. the value of these communities in brackish and saline waters (i.e., what overall ecological values are provided by a mangrove living in fresh water relative to those provided by a mangrove living in brackish or salt water?).

Relationship of Submerged Aquatic Vegetation to Salinity, Turbidity, Input of Nutrients, and Dissolved Organic Matter. Research is needed to determine 1) the effects that increased loads of nutrients and dissolved organic materials from increased flows will have on light attenuation and 2) its subsequent effect on distribution, health, and abundance of SAV in the estuarine part of Loxahatchee watershed. Also, the relationship of epiphyte coverage found on SAV to location, abundance, and diversity of species in the estuarine part of the Loxahatchee watershed needs to be determined.

How Construction and Water Management Activities Affect Shoaling and Benthic Communities. Implementation of the Comprehensive Everglades Restoration Plan and other water management changes are expected to affect shoaling in the river and estuary. Research is needed on two fronts. 1) How will the final design of CERP projects in the watershed will affect shoaling and turbidity during normal operations and episodic high flow events? Increased turbidity, reduced light penetration, and downstream deposition of sediments will likely have adverse impacts on seagrasses, oysters, and benthic invertebrate communities. 2) How can water management practices be modified to enhance recolonization of areas depauperated by past discharges and to better protect established communities, especially oysters and seagrasses?

Relationship of Estuarine Fish Communities to Habitat Distribution and Loss. Research is needed to determine the appropriate salinity gradient that should be maintained, from interior coastal wetlands through the nearshore zone, to optimize diversity and abundance of estuarine fish species and salt-tolerant freshwater fish in the estuarine part of the Loxahatchee watershed. Also, dominant communities of fishes that use the

freshwater and mangrove floodplain forests need to be determined.

Relationship between Habitat Disturbance and Exotic Invasive Species. The principle that habitat disturbance or stress provides an opportunity for invasion by exotics is generally agreed upon. Throughout South Florida, this has proven to be especially true for exotic plant species. Many exotic animal species have also gained a foothold in South Florida, but in general, their spread has not been as closely tied to habitat disturbance. Little is known about the distribution, abundance, relative threats, or potential control methods for exotic animal species in the Loxahatchee watershed. These subjects need further investigation, especially given the large, relatively remote tracts of undeveloped and publicly-owned lands that exist in this watershed.

By contrast, several exotic plant species have made their presence well known in the Loxahatchee watershed. Old World climbing fern and Brazilian pepper, for example, are not only spreading across disturbed landscapes but are also are also successfully invading healthy plant communities. Additional research, as well as active management, is needed immediately to manage this nuisance vegetation effectively.

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CALOOSAHATCHEE ESTUARY CONCEPTUAL ECOLOGICAL MODEL

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Abstract: The Caloosahatchee Estuary is a large estuarine ecosystem, located on Florida's lower west coast, that supports a productive and diverse floral and faunal community. Major modifications to the hydrology of the Caloosahatchee watershed through water management, including water releases from Lake Okeechobee into the Caloosahatchee River, along with land-use transformations, increased development, and dredging for navigation, have resulted in alterations within the estuary. Changes in estuarine salinity, flows, and nutrient inputs, along with physical alterations to the estuary as a result of these stressors, can affect estuarine fishes and manatees, as well as benthic communities including several species of bivalves, such as oysters, scallops, and clams. Additionally, the submerged aquatic vegetation and mangrove shoreline habitat are affected through a variety of processes associated with these changes. As a result, these estuarine attributes can be used as indicators of restoration success.

Key Words: Caloosahatchee, estuary, conceptual model, southwest Florida, altered salinity, altered hydrology, nutrients, toxins, boating and fishing pressure, physical alterations, oysters, benthic community, submerged aquatic vegetation, estuarine fish community, manatee, shoreline mangrove habitat

BACKGROUND

The Caloosahatchee River and its estuary are located on the lower west coast of Florida, USA. The Caloosahatchee River was originally a shallow, meandering river with headwaters in the proximity of Lake Hicpochee and tidal influence almost to the town of La Belle. To accommodate navigation, flood-control and land-reclamation needs, the freshwater portion of the river was reconfigured into a canal known as C-43. Many secondary canals were constructed to irrigate and drain the agricultural holdings associated with the river. In addition, three lock-and-dam structures (S-77, S-78, and S-79) were added to control river flow and stage height. The final downstream structure, S-79, also acts as an impediment to saltwater intrusion to the river.

Today, the Caloosahatchee River extends 105 km from Lake Okeechobee to San Carlos Bay, entering the Gulf of Mexico near the city of Fort Myers, Florida. The freshwater portion ranges from 50 to 130 m in width and 6 to 9 m in depth. Many of the original bends remain as oxbows along both sides of the canal. The width of the estuarine portion is irregular, from 160 m in the upper portion to 2,500 m downstream at San Carlos Bay (Scarlatos 1988). The narrow section extends from Franklin Lock and Dam (S-79) to Beautiful Island. This area has an average depth of 6 m, and the area downstream of Beautiful Island has an

average depth of 1.5 m (Scarlatos 1988). The pattern and period of flow of the Caloosahatchee River are highly variable (Drew and Schomer 1984).

The tidal Caloosahatchee basin includes portions of Lee and Charlotte counties. The estuary between Franklin Lock and Shell Point is 42 km long and is bordered by the city of Fort Myers on the southern shore and the city of Cape Coral on the northern shore. Water discharges from the Caloosahatchee River, passes Shell Point, and enters the Gulf of Mexico from San Carlos Bay. Because of the estuary's long and narrow configuration, changes in wind, tide, runoff, or precipitation can have effects on estuarine features such as flow, water depth, salinity, and turbidity. Due to the dynamic nature of the estuary, characterization of the system is difficult and has not previously been attempted. This model is an attempt to develop such a characterization.

Major changes in hydrology of the Caloosahatchee watershed are results of significant modifications in land and canal development, as well as water-management policy. Adverse ecological impacts in the estuary have occurred as a result of these hydrologic changes (SFWMD 2000B). Despite these impacts, the Caloosahatchee Estuary continues to be an important environmental and economic resource. Understanding how this system responds to stressors will provide a basis for well-informed management decisions.

The model boundary for the Caloosahatchee Estuary

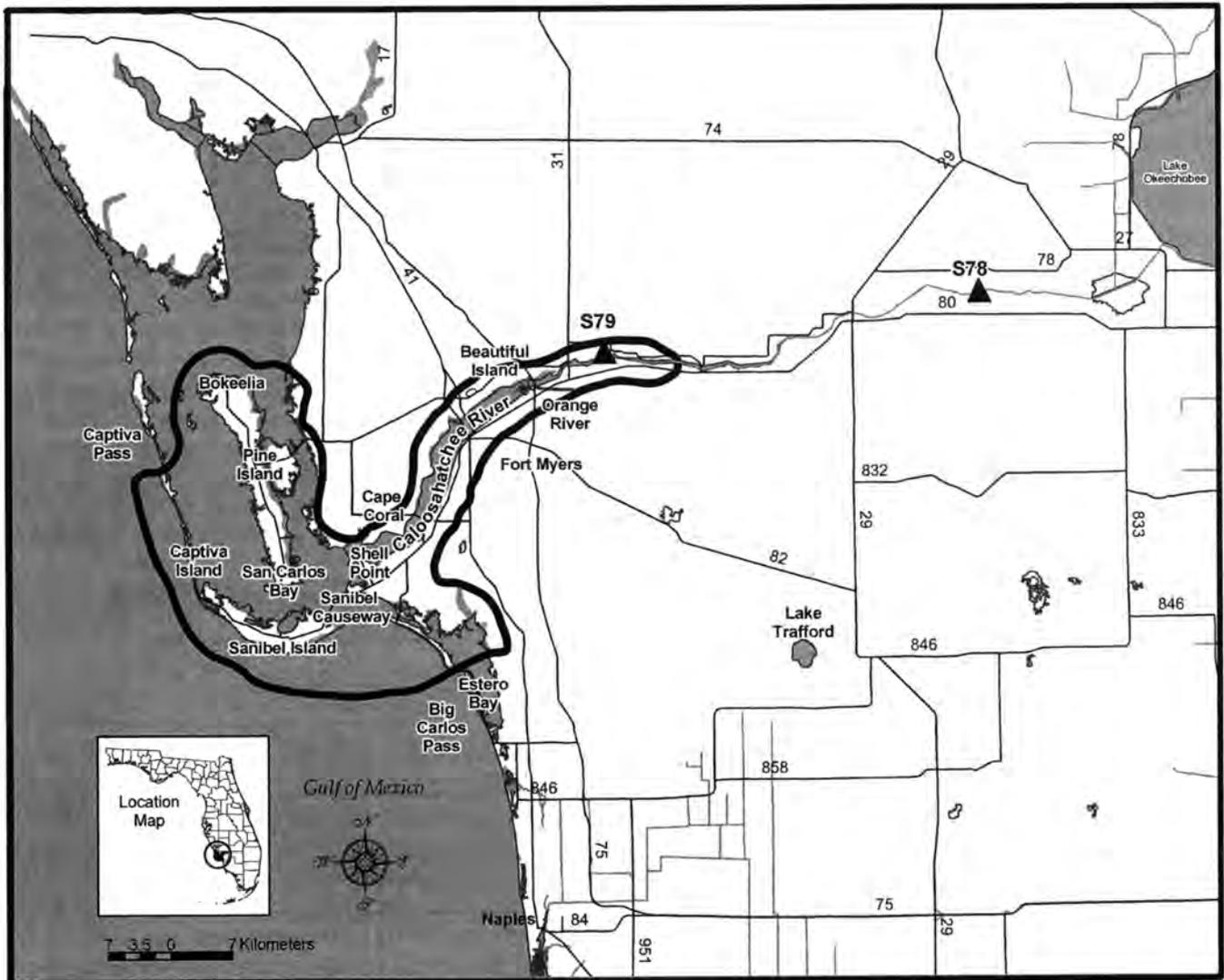


Figure 1. Boundary of the Caloosahatchee Estuary Conceptual Ecological Model.

Conceptual Ecological Model extends east to the S-79 structure, also known as the W.P. Franklin Lock and Dam (Figure 1). This is the most downstream structure and marks the beginning of the Caloosahatchee Estuary. From there, the model extends southwest through Estero Bay and into the Gulf of Mexico through Big Carlos Pass and includes a freshwater plume that extends approximately 5 km offshore. The town of Bokerelia, at the northern end of Pine Island, serves as the northern boundary. The model's western boundary extends 5 km offshore of Sanibel and Captiva Islands, making a turn through Captiva Pass.

EXTERNAL DRIVERS AND ECOLOGICAL STRESSORS

External Drivers

Sea level rise is an important non-societal driver (Figure 2) (Wanless et al. 1994) and will act indepen-

dently of other societal-driven stressors. Sea-level rise is likely to cause the landward movement of marine conditions into mangrove estuaries and coastal wetlands (Day and Templet 1989, Reid and Trexler 1992, Tampa Bay Regional Planning Council 1993, Cone et al. 2004). Societal-driven external drivers in the Caloosahatchee Estuary include water management, land use and development, and navigation (Figure 2). Water management practices, including modification of river discharge, have resulted in drastic modifications to estuarine systems (Chamberlain and Doering 1998b). These changes have caused large fluctuations in volume, timing, and frequency of freshwater inflow to the estuary (Chamberlain and Doering 1998a) and, in turn, have had a negative impact on the ecology of the estuarine system through alteration of salinity zonation (Harris et al. 1983, Sklar and Browder 1998, Chamberlain and Doering 1998a, Doering et al. 1999, Doer-

Caloosahatchee Estuary Conceptual Ecological Model

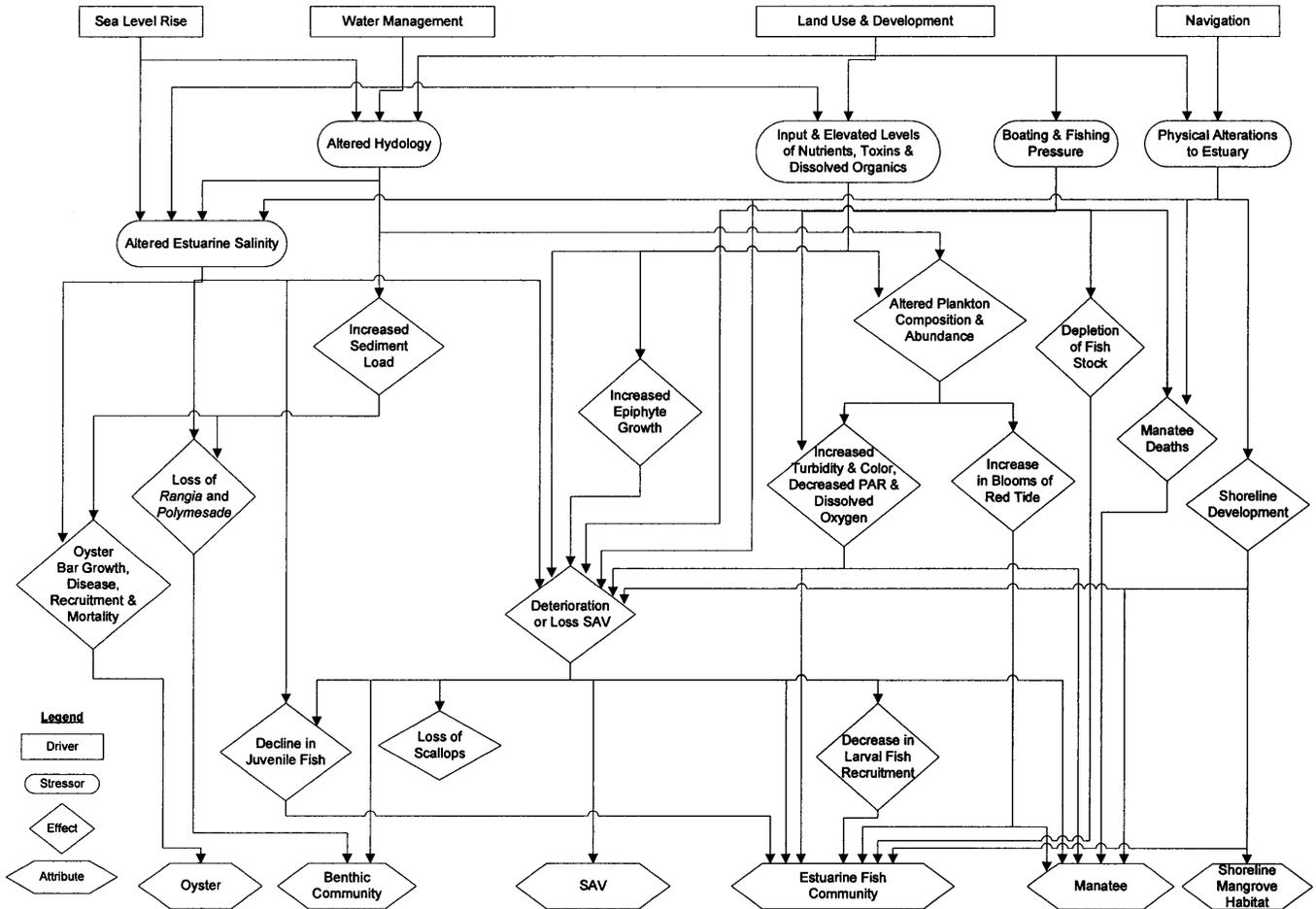


Figure 2. Caloosahatchee Estuary Conceptual Ecological Model Diagram.

ing and Chamberlain 2000, Doering et al. 2001, Doering 2002, Volety and Tolley 2002, Hunt and Doering 2005). Land use in the watershed is predominately agriculture in the east and urban in the west. Runoff from these areas contributes to degrading water quality conditions in the river and estuary (FDEP 2005), and withdrawals during dry season due to urban and agriculture demand leave little fresh water for the estuary. In addition, the need for navigation from the east coast through Lake Okeechobee to the west has resulted in dredging and channelization of the original Caloosahatchee River to the current C-43 canal.

Ecological Stressors

Altered Hydrology. Altered hydrology is one predominant stressor on the system, taking the form of cumulative water-use withdrawals (demand) and over drainage, along with regulatory releases from Lake Okeechobee. This causes changes in quantity, timing, and quality of flows to the estuary, in addition to harm

to wetlands and ground-water resources (SFWMD 2000a). Altered hydrology is exacerbated by physical changes made in the watershed, which include development of a complex network of secondary canals, enlargement of C-43 to convey more water, and the addition of three water-control structures on C-43, which regulates the flow from Lake Okeechobee to the estuary.

Altered Estuarine Salinity. Altered estuarine salinity has resulted from man-made hydrologic modifications that have dramatically altered natural quantity, quality, timing, and distribution of flows to the estuary, often without proper regard to the biological integrity of the estuary (Haunert et al. 2000). During the wet season (summer and fall), rainfall runoff that was historically retained within the undeveloped watershed now reaches the river in greater volume and in less time (USACE 1957). Additionally, construction of S-79 has geographically truncated the estuary by restricting the movement of low salinity water to the upper reaches

of the estuary during the dry season. Alterations in delivery of fresh water at S-79 cause salinity to vary widely in time and space (USACE 1957). Such rapid and unnatural fluctuations in salinity can cause damage to estuarine organisms and communities, including impacts on submerged plant abundance and distribution (Doering and Chamberlain 1999), and may contribute to the loss of the natural gradient of grass species between downtown Fort Myers and the mouth of the river. Low flow deliveries have been addressed in the development of a Minimum Flow and Level (MFL) for the Caloosahatchee Estuary (Doering, pers. comm.). A MFL is the limit at which further withdrawals would be significantly harmful to the water resources or ecology of the area.

Physical Alterations to the Estuary. Physical alterations, including conversion of wetlands, dredging of channels, spoil disposal, changes in shoreline, snagging of navigation hazards, and decrease in spatial extent of the estuary through construction of barriers (such as S-79) (Harris et al. 1983) have impacted presence and abundance of species. Addition of the Intra-coastal Waterway and the Sanibel Causeway altered water flow and habitat (Harris et al. 1983). Changes in the physical dimension of the estuary that resulted from the addition of S-79, reduced (or eliminated) the upstream oligohaline portion of the estuary, especially during dry season (Chamberlain and Doering 1998a). This salinity zone is an important nursery and feeding area for juvenile stages of desirable sport and commercial fishes. Construction and operation of water-control structures may interfere with migration patterns of many estuarine species. By acting as a barrier between freshwater and saline water habitats, the structures have historically resulted in deaths of Florida manatees (*Trichechus manatus latirostris* Linnaeus) attempting to pass through these structures (Odell and Reynolds 1979, O'Shea et al. 1985, FWC 2005a).

Input and Elevated Levels of Nutrients, Toxins, and Dissolved Organics. Inputs and elevated levels of nutrients, toxins and dissolved organics affect phytoplankton and SAV populations. Studies in the Caloosahatchee River and Estuary have been unable to detect serious contamination of sediments with toxins (La Rose and McPherson 1983, Fernandez et al. 1999). It is recommended that monitoring be continued.

Boating and Fishing Pressure. Boating pressure is a stressor to the estuary through direct impacts, such as seagrass scarring and water quality degradation. Fishing pressure from sport and commercial fisheries has impacted standing stocks of many species (Post et al. 1999) and, in turn, impacted those species depending on fish as their primary food source. Recent resource

trends for local fisheries show some increase as a result of changes in management process (Muller et al. 1996, McMichael 1997).

ECOLOGICAL ATTRIBUTES

Submerged Aquatic Vegetation

Submerged aquatic vegetation (SAV), for the purpose of this conceptual ecological model, includes only vascular underwater plants that live throughout the estuary and in near-coast waters. SAV provides habitat and nursery grounds for many fish and invertebrate communities and are especially important in benthic-based primary productivity. Manatees, waterfowl, and wading birds rely heavily on seagrass systems as forage areas. SAV help maintain water clarity by trapping fine sediments and improve water quality by taking up large quantities of nutrients that would otherwise accelerate eutrophication of the estuarine system.

Tapegrass (*Vallisneria americana* Michx.) is the dominant SAV in the upper Caloosahatchee Estuary, where salinities average less than 10 ppt (Hunt and Doering 2005). *Vallisneria americana* is thought to be an important habitat for a variety of freshwater and estuarine invertebrate and vertebrate species, including some commercially and recreationally important fishes (Bortone and Turpin 1999). Additionally, it can serve as a food source for the Florida manatee. Shoal grass (*Halodule wrightii* Aschers.), turtle grass (*Thalassia testudinum* Banks & Soland. ex Koenig), and manatee grass (*Syringodium filiforme* Kuetz.) are the most common higher salinity grasses in the Caloosahatchee Estuary.

Degraded water quality and physical alterations, such as the Sanibel Causeway, the Franklin Lock and Dam (S79), and the Intra-coastal Waterway have shown negative impacts to seagrasses. The result has been a regional decrease of seagrass coverage (McNulty 1972, Harris et al. 1983, Chamberlain and Doering 1998a). This decline negatively impacts fish and invertebrate communities. It also causes destabilization of sediments and shifts primary productivity from benthic macrophytes to phytoplankton, providing negative biofeedback to further affect seagrass beds.

Oysters

Oyster bars provide several important functions, including habitat and food for a wide range of other species (Coen et al. 1999, Tolley et al. 2005) and water filtration (Newell 1988). They are sensitive to salinity and siltation. High salinity levels increase negative effects from saltwater predators such as oyster drills

(Hofstetter 1977, White and Wilson 1996) and the protozoan parasite *Perkinsus marinus* (Dermo) (Volety 1995), the primary oyster pathogen in the Gulf of Mexico (Soniati 1996). Historical records indicate that oyster reefs were once significant features of the Caloosahatchee River, at times presenting significant hazards to navigation, especially in the lower river between Redfish Point and Punta Rassa (Sackett 1888). The loss of oysters in this area is thought to be the result of shell mining, altered freshwater inflows, and changes in the hydrodynamics of the system (Chamberlain and Doering 1998a).

Benthic Community

Open bottoms in the Caloosahatchee Estuary are composed of mixtures of sand, mud, shell, and bedrock. Macroinvertebrates, including mollusks, inhabit the sand/muck open bottom of the estuary and are dominant elements of both the estuarine and tidal river Caloosahatchee ecosystems. *Rangia cuneata* (G.B. Sowerby, I), a member of the clam family Mactridae, and *Polymesoda caroliniana* (Bosc.), in the family Corbiculidae, are commonly found associated with mud and sandy bottoms in the Caloosahatchee Estuary. Both of these mollusks require lower salinities and can be used as indicators of estuarine condition. Furthermore, because mollusks leave behind their shells upon death, it is possible to look at death assemblage to construct historical salinity regimes. Shell characteristics such as size, shape, and ornamentation vary according to salinity and can be used to construct historical salinity regimes.

Although once plentiful in parts of San Carlos Bay and, at lower densities, in the mouth of the Caloosahatchee (Leverone 2000), bay scallops (*Argopectin irradians* Lamarck) are now essentially absent from southwest Florida estuaries (Leverone 1993). Bay scallops are sensitive to water temperature and salinity alterations and are highly susceptible to changes in water quality, making them very good indicators of ecosystem health (FWC 2000). Increasing scallop populations to resemble historic distributions within the model boundary is currently a goal of the Charlotte Harbor Estuarine Program (CHNEP 1999).

Estuarine Fish Community

Within the estuary, seagrass communities provide critical refugia for juvenile fish such as redfish (*Sciaenops ocellatus* L.), gag grouper (*Mycteroperca microlepis* Goode & Bean), Goliath grouper (*Epinephelus itajara* Lichtenstein), common snook (*Centropomus undecimalis* Bloch), and spotted seatrout (*Cynoscion nebulosus* Cuvier in Cuvier and Valenci-

ennes). With a decline in seagrass habitat (McNulty 1972, Harris et al. 1983, Chamberlain and Doering 1998a) and the alterations in the salinity regime and timing of freshwater discharges, it can be expected that there has also been a decline in juvenile abundance and distribution of these and other species, shifts in the center of abundance for some species, and/or an overall decline in species richness, although there is no historic data available to support or discredit this claim.

Commercial and recreational fishing pressure has also increased along the west coast of Florida. With this increase, there has been a decline in reported landings (Post et al. 1999). In Lee County, clear evidence for this decrease can be seen with the spotted seatrout, where there has been a decline in catch per unit effort from 1986 to 1995 (Bortone and Wilzbach 1997).

The blue crab (*Callinectes sapidus* Rathbun) fishery is the largest, year-round fishery in the upper and middle portion of the Caloosahatchee River. The fishing effort is intense, and several hundred crab traps are deployed daily. Fishery landings data may be a good indicator of overall productivity of the system. In addition, because blue crabs move freely about the system, they may be good monitors of localized changes in conditions relative to temperature, salinity, and other water quality parameters.

Manatees

Manatees are a very visible and publicly appreciated feature of the Caloosahatchee Estuary. Also called sea cows, manatees are large aquatic mammals that are commonly found in coastal, estuarine, and some riverine habitats. They prefer waters with salinities less than 25 parts per thousand (ppt) but can move freely between fresh and salt water (USFWS 1999). In the Caloosahatchee Estuary, the largest concentration of manatees is found in the upper tidal reaches of the estuary near the Orange River and the warm water outflow of the Florida Power and Light power generating plant (USFWS 1995).

Lee County leads the west coast of Florida in the total number of manatee deaths (FWC 2005a). Some of these deaths can be attributed to cold stress, watercraft collisions, and entanglement with crab lines, gill nets, and monofilament fishing line. Lee County also leads all other west coast counties in the number of deaths in the categories of dependent calves, natural causes, and undetermined (FWC 2005a).

Shoreline Mangrove Habitat

Mangrove shoreline habitats in the Caloosahatchee Estuary have decreased in spatial extent and in func-

tion. Large areas of mangroves have been lost or fragmented through dredge-and-fill activities (Estevez 1998, National Safety Council 1998). These mangrove shorelines are sensitive to alterations in upland drainage, and in some areas, drainage for agricultural and urban development has reduced overland flows of fresh water to mangroves. This drainage increases concentrated runoff, changing the salinity balance, reducing flushing of detritus, and washing nutrients directly into the estuary without the benefit of filtration by the mangrove system (Estevez 1998).

ECOLOGICAL EFFECTS: CRITICAL LINKAGES BETWEEN STRESSORS AND ATTRIBUTES/WORKING HYPOTHESES

Submerged Aquatic Vegetation and Plankton

Relationship of Altered Salinity and Submerged Aquatic Vegetation. Working hypothesis: Altered estuarine salinity resulting from hydrologic alterations caused by water-management practices has resulted in a decrease in the spatial extent of SAV in the Caloosahatchee and a change in the distribution, densities, and the relative species abundance. Different species of SAV have different desirable salinity ranges. When salinity falls outside of these ranges, the SAV is negatively impacted, and reductions in densities and aerial extent may occur (Chamberlain and Doering 1998b). Increases or decreases in salinity may give one species a competitive advantage over another (Livingston 1987). Tabb et al. (1962) stated, "Most of the effects of man-made changes on plant and animal populations in Florida estuaries are a result of alterations in salinity and turbidity."

Relationship of Submerged Aquatic Vegetation and Salinity to Mollusk Populations and Fish Recruitment. Working hypothesis: Negative changes in SAV community structure and function along with changes in natural salinity regime have resulted in substantial losses of mollusk populations and a decrease in larval and adult fish recruitment into the estuary. Fish densities are typically greater in grass bed habitat within South Florida's estuaries and coastal lagoons than in adjacent habitats (Reid 1954, Tabb et al. 1962, Roesler 1965, Yokel 1975, Weinstein et al. 1977). Grass beds provide cover and protection from predation for animals living in them (Zieman 1982, Heck et al. 1997). Reduction in size and health of SAV beds affects location, abundance, and species composition of fisheries in the estuary (S. Bortone, Sanibel Captiva Conservation Foundation Marine Lab, pers. comm.).

Relationship of Submerged Aquatic Vegetation to Nutrients. Working hypothesis: Increased loading of nu-

trients to the estuary resulting from land-use changes has had negative impacts on SAV through increased epiphytic growth and decreased light. Reduction in penetration of light in the water column is often blamed for the reduction or loss of previously healthy seagrass meadows. Because seagrasses are rooted plants attached to the bottom, reduced light reduces photosynthesis, growth, and reproduction. Increased nutrients, such as nitrogen and phosphorous, can lead to light deprivation by stimulating the growth of phytoplankton. These blooms cloud the water and severely diminish sunlight penetration (Livingston 1987). This turbidity can increase to such a level that seagrasses persist only in patches (Zieman 1982). Nutrients can also trigger a thick growth of epiphytes, which can also block the sunlight before it can reach the surface of the seagrass (Murray et al. 1999). In fact, nutrient input has such an effect that relatively minor changes in water quality can lead to sharp reductions in the productivity of seagrasses, which can lead to broad habitat changes (Livingston 1984). Light deprivation is cited as a major source of seagrass decline in Florida estuarine systems (Durako 1988).

Relationship of Plankton to Nutrients. Working hypothesis: Changes in plankton composition occur when there is an increase in nutrients or an alteration in the natural hydrology of the system. Water quality is also a major determinant of the health and condition of estuarine systems. Changes in water quality are often the linkage between the stressor and the ecosystem value. The amount of nutrients entering the Caloosahatchee River and Estuary has important effects on the water quality of the system. Organisms use these nutrients, but excessive amounts may have negative impacts (Neilson and Cronin 1981). Algal blooms and epiphyte growth can cause decreased water clarity and block sunlight for aquatic plants (Day et al. 1989). As algae die, organic decomposition depletes the oxygen in the water (eutrophication) (LaRose and McPherson 1983, Drew and Schomer 1984, Day et al. 1989). Low levels of dissolved oxygen have negative effects on fish and other aquatic organisms (Heyl 1998). The Florida Department of Environmental Protection has set water quality standards for the state (Florida Statutes. 62-40.430). Although these are often moving targets, they should be met for the Caloosahatchee to ensure a healthy system. In addition, the Charlotte Harbor National Estuary Program has defined a specific list of water quality parameters that should be measured to determine the status of the system (CHNEP 1999).

Relationship of Current and Historical Submerged Aquatic Vegetation Coverage to Potential Distribution. Working hypothesis: SAV in the Caloosahatch-

ee Estuary should increase as estuarine conditions improve. Extent of this increase depends on available area with suitable salinity, substrate, water clarity, and temperature. A number of factors, like color and suspended solids, can influence water clarity and light penetration. Different species of SAV have distinct requirements for light. Research indicates that *Thalassia testudium*, *Halodule wrightii*, and *Syringodium filiforme* require levels of at least 10–15% of surface irradiance, while *Halophila decipiens* (Ostenf.), *Halophila engelmannii* (Aschers.), *Halophila johnsonii* (Eiseman), and *Ruppia maritime* (Linnaeus) appear to have somewhat lower requirements, perhaps as low as 2–3% of surface irradiance (URS Greiner Woodward Clyde 1999).

Most seagrasses appear to tolerate a wide range of substrate conditions. Virtually all seagrasses seem to grow on sandy or silty muds and on sands with some mud content (Reid 1954, Voss and Voss 1955, Phillips 1960) and require a sufficient depth of sediment for proper development. Substrates also contain nutrients, especially nitrogen and phosphorous, available for SAV growth (Duarte 1991). Microbially-mediated chemical processes in marine sediments provide a major source of these nutrients (Capone and Taylor 1980).

Each species of SAV has its own temperature and salinity tolerance ranges and their tolerance to salinity variation is similar to their temperature tolerances. *Halodule wrightii* is the most broadly euryhaline, *Thalassia testudium* is intermediate, and *Syringodium filiforme* and *Halophila* have the narrowest tolerance ranges (McMillian 1979, Zieman 1982). *Vallisneria americana* is generally a freshwater grass but can tolerate salinities of near 10 ppt. Therefore, *Vallisneria* is also an important component of the oligohaline estuarine SAV community (Twilley and Barko 1990, Adair et al. 1994, Kraemer et al. 1999).

Oysters

Relationship of Oysters to Other Estuarine Species. Working hypothesis: The decrease in oyster reef habitat in the Caloosahatchee Estuary has resulted in a decrease in other estuarine species that utilize the oyster reef habitat. Oysters, clams, and scallops are natural components of southern estuaries in the U.S. and were documented to be abundant in the Caloosahatchee system (Sackett 1888, Estevez 1998, Leverone 2000). Oyster reefs provide a complex, three-dimensional reef structure serving as essential habitat for numerous species of invertebrates and fishes (e.g., blue crab, stone crabs, mud crabs, grass shrimps, blennies, gobies, killifishes, skillettfish) (Tolley et al. 2005). Furthermore, many of these organisms serve as forage for

important fisheries species (e.g., sheepshead (Murphy and MacDonald 2000, Tolley et al. 2005), bluefish (Harding and Mann 2001), spotted seatrout (McMichael and Peters 1989), red drum (Peters and McMichael), birds (e.g., yellow-crowned night heron (Watts 1988)), and mammals (e.g., raccoons).

Relationship of Oysters to Sediment Loads. Working Hypothesis: Oyster population in the Caloosahatchee and surrounding estuary has decreased due to an increase in sediment loads resulting from man induced alterations to the natural hydrology. Although adult oysters have effective morphological adaptations for feeding in much higher levels of suspended solids than are usually encountered under normal conditions (Nelson 1922, Kennedy 1996), their pumping rates become significantly reduced (Nelson 1922, Loosanoff and Tommers 1948). Suspended solids may clog gills and interfere with filtering and respiration of oysters (Coke 1983). Discharges from Lake Okeechobee may increase sediment loads to the estuary, and these can have detrimental effects on oysters and other filter feeding bivalves.

Relationship of Salinity to Oysters. Working hypothesis: Alterations of flows have lead to dry season increases in salinity in the estuarine portion of the river. This increase in salinity increases negative physiological effects on oysters and from saltwater predators in the area. Salinity is important in determining the distribution of coastal and estuarine bivalves. Adult oysters in the Gulf of Mexico normally occur at salinities between 10 and 30 ppt but tolerate a salinity range of 2 to 40 ppt (Gunter and Geyer 1955). Short pulses of freshwater inflow can greatly benefit oyster populations by killing predators, such as oyster drills and welks that cannot tolerate low salinity water (Owen 1953, Marshall 1954). Excessive freshwater inflows may kill entire populations of oysters (Gunter 1953, Schlesselman 1955, MacKenzie 1977). Changes in salinity can also affect structural and functional properties of these bivalves through changes in 1) total osmotic concentration, 2) relative proportions of solutes, 3) coefficients of absorption and saturation of dissolved gases, and 4) density and viscosity (Kinne 1964).

Protozoa are probably the most common cause of epizootic outbreaks that result in mass mortalities on oysters. One of the most important is Dermo, caused by a member of the phylum Apicomplexa, *Perkinsus marinus* (Mackin, Owen, and Collier). It is characterized by emaciation of the digestive gland of the oyster. Dermo has limits imposed by salinity and temperature (Dame 1996) and is more intense in areas of higher salinities (Burreson and Ragone Calvo 1996, Calvo et al. 1996, Chu and Volety 1997, La Peyre et al. 2003).

Fisheries

Relationship of Submerged Aquatic Vegetation to Juvenile Fish Abundance. Working Hypothesis: A decline in the amount of seagrass habitat/coverage has occurred in the Caloosahatchee drainage. A consequence of this decline is a reduction in potential habitat for a number of seagrass dependent species and, especially, juvenile life stages of most estuarine dependent species. Gag (*Mycteroperca microlepis* Goode and Bean) and spotted seatrout are two estuarine-dependent species. Larval gag use sea grass beds as a settlement substrate after having hatched offshore on natural hard bottom structures. Larvae settle in the higher salinity areas of San Carlos Bay and Pine Island Sound in the spring of each year. After attaining a size of about 60 to 80 mm total length, they migrate offshore to take up residence on offshore reefs (Jory and Iverson 1989). Juvenile spotted seatrout use grass beds for protection from predation, while adults feed on many of the seagrass associated species such as shrimps and smaller fishes (Pearson 1929, Miles 1950, Perret et al. 1980). Concomitant with reduction in habitat for specific life-history stages of selected species, reduction in grass beds also has led to an overall reduction in species diversity within the system (S. Bortone, Sanibel Captiva Conservation Foundation Marine Lab, pers. comm.).

Relationship of Salinity and Freshwater Discharge to Juvenile Fish. Working Hypothesis: Alterations in natural salinity regime and timing of freshwater discharges have resulted in a decline in juvenile fish abundance, distribution, and species richness. Alterations in salinity regime place undue stress on sensitive life-history stages of many estuarine species (Odum 1970, Lindall 1973, Perry and McIlwain 1986, Chamberlain and Doering 1998b). While estuarine species generally adapt to cope with varying salinity conditions and cycles, they are not so robust as to accommodate large shifts in the timing cycle of salinity regimes. A simple case in point is the egg stage of spotted seatrout. Trout eggs are neutrally buoyant at about 20–22 ppt (Pattillo et al. 1997). They spawn during the warmer months of the year (Lassuy 1983). Large and protracted reductions in salinity during summer months could lead to reduction or elimination of an entire year-class of spotted seatrout.

Relationship of Fish to Red Tide. Working Hypothesis: An increase in occurrence of red tide in southwest Florida has contributed to increased mortality in estuarine fishes. Red tide was first identified during a catastrophic mortality event of marine fishes and other animals that took place between November 1946 and August 1947 (Gunter et al. 1948). Since then, inves-

tigations of literature have shown over 50 years documented with what was presumably red tide off of Florida's west coast (FWC 2004). Regardless, due to scarcity of these data, it is undetermined if there has been an actual increase in occurrence or severity of red tide in Florida waters. Red tides typically occur in late summer and early fall months but have occurred in every month of the year. They begin about 15–65 km off shore and are transported inshore by currents and winds. These red tide blooms have been associated with invertebrate, fish, bird, and marine mammal mortalities (Gunter et al. 1948, Bossart et al. 1998, Landsberg and Steidinger 1998).

Relationship of Blue Crab Fishery to Temperature, Salinity, and Other Water Quality Parameter. Working Hypothesis: Changes in temperature, salinity and other water quality parameters can have had a negative impact on local blue crab fishery. Complete fishery information on this species can be used to measure production status of the estuary. Due to its environmental requirements, the ubiquitous blue crab and its fishery can serve as important monitors for the health and condition of the estuarine system. Factors affecting distribution and survival include substratum, food availability, available shelter, water temperature, and salinity (Perry and McIlwain 1986, Chamberlain and Doering 1998b).

The blue crab fishery data base has a long history in the area and can be easily monitored for catch and effort. Concomitantly, the availability of environmental data from the system allows determination of the association of the fishery status relative to environmental conditions. Thus, continued but more intense long-term monitoring of the blue crab fishery, when coupled with currently recorded environmental parameters such as temperature, salinity, nutrient conditions, and geographic information system (GIS) mapped land-water features will permit direct determination of the association that blue crab production (as measured by catch per unit effort statistic) has with environmental water quality in the system (Bortone pers. comm.).

Relationship of Fishing Pressure to Local Fisheries. Working Hypothesis: An increase in local fishing pressure has resulted in a decrease in the populations of several important game fish. Historical data on landings and fishing effort are not comprehensive enough to establish a clear relationship between these two variables. Fishing pressure on some species seems to have increased (e.g., Bortone and Wilzbach 1997). Potential effects on the population structure, life history, and species composition of fish communities in the study area have not been documented. The recently introduced fisheries-independent monitoring program in the

study area will provide critical data on fish populations that have been previously lacking.

Florida Manatee

Relationship of Manatee Populations and Submerged Aquatic Vegetation. Working Hypothesis: Preferred manatee habitat is characterized by availability of SAV. A change in the spatial extent and density of SAV in the Caloosahatchee will result in a loss of essential manatee habitat and subsequently a decrease in the local manatee population. Manatees depend on SAV for food and habitat in the Caloosahatchee Estuary. Seagrass beds and mangroves provide important areas for manatee foraging, calving, resting, and mating.

Manatees are euryphagic herbivores and feed on a variety of submergent, emergent, and floating vegetation, with seagrasses comprising the largest component of their diet in South Florida (Hartman 1979, Zieman 1982, Smith 1993). Manatees usually forage in shallow grass beds that are adjacent to deeper channels (Hartman 1979, Powell and Rathbun 1984). Some manatees have been observed to return to the same seagrass beds year after year and may show preference for certain areas (USFWS 1999).

Relationship of Manatee Populations to Habitat Loss and Boating Pressure. Working Hypothesis: Manatee use of the Caloosahatchee River is affected by increase in boating pressure and a decrease in water quality. Manatees and their habitats are continually threatened by human activity, such as habitat loss for residential and commercial purposes, increased turbidity levels from upland urbanization activities, pollution from discharge and storm water runoff, aquatic recreational and commercial activities, and alterations of natural hydrology. Presently, one of the greatest threats to manatees in southwest Florida is the high rate of mortality caused by collisions with watercrafts (FWC 2005a). Boat channels are often used by manatees to travel from one region to another (Curran 1989, Sirenia Report 1993). Manatees are not always able to avoid boats using these channels, making them vulnerable to collisions. The increase in watercraft in shallow coastal areas for fishing and sightseeing also increases the likelihood of a manatee injury or death as boats pass over them.

The State of Florida has seen a substantial increase in the number of registered boaters, with over ninety percent registered for recreational use (Marine Mammal Commission 1992, Wright et al. 1995). Ackerman et al. (1995) found that the number of manatees killed in collisions with watercrafts each year correlated with

the total number of pleasure and commercial watercrafts registered in Florida.

Another significant threat to manatees is loss and degradation of habitat, resulting from direct damage by aquatic recreational and commercial boating activities, coastal construction, and pollution from sewage discharge and storm-water runoff (Marine Mammal Commission 1992, Smith 1993). Seagrass beds that manatees rely on for foraging incur direct damage from boat propellers (Zieman 1982, Dawes et al. 1997). Propeller dredging of bottom habitat by boats, propeller wash, and wave wake disturbance cause boat-induced turbidity. Sediments around seagrasses become unconsolidated and suspended. This delays recolonization of grasses for two to five years or longer, depending on species type.

Relationship of Manatees to Red Tide. Working Hypothesis: Red tide is responsible for an increase in manatee mortality in Southwest Florida. The association between red tide and mortality of marine mammals is not well-established. Some instances of bottlenose dolphin mortalities have been blamed on the toxin because of their coincidence with red tide blooms (Gunter et al. 1948, Geraci 1989). Also, a link has been suggested for the death of seven manatees in 1963 from a red tide event near Fort Myers (Layne 1965, Bossart et al. 1998).

An unusual number of manatee deaths were documented in 1996 (U.S. Marine Mammal Commission 1996). The beginning and ending of this event coincided with an inshore bloom of *Karenia brevis* Davis, known as red tide, in southwest Florida (Baden 1996). Research found that critical circumstances contributing to high manatee mortality appeared to be related to concentration and geographic distribution of red tide outbreaks, in relation to salinity, as well as persistence of the bloom in relation to distribution of manatees and their length of exposure to the red tide (Landsberg and Steidinger 1998). Eighty-one of 149 manatee deaths associated with this bloom of red tide occurred in Lee County, primarily in the Caloosahatchee Estuary (K. Dryden, United States Fish and Wildlife Service [USFWS], pers. comm.). In 2003, 98 manatee deaths were attributed to a red tide event. Between March 5, 2005 and April 10, 2005, red tide is suspected to be the cause of 52 manatee deaths (FWC 2005b).

Shoreline Mangroves

Relationship of Mangrove System Function and Shoreline Fragmentation. Working Hypothesis: The fragmentation of shoreline along the Caloosahatchee Estuary and adjacent Charlotte Harbor has resulted in

negative impacts to the ecosystem function of the remaining mangrove ecosystem. Mangroves provide a number of ecological services, including stabilization of sediments and shoreline, habitat for terrestrial and aquatic organisms, and water quality improvement. Destruction of mangroves through shoreline development and dredge-and-fill activities results in a chain of reactions that affect estuarine and off-shore production. In Tampa Bay, 44% of the mangrove and salt marsh land has been lost due to construction and turbidity from runoff and pollution (Lewis and Estevez 1988). This loss has been linked to declines in fin fish and commercial shrimping in the region (Dawes 1998).

Relationship of Mangrove System Productivity and Upland Flows. Working Hypothesis: Productivity in shoreline mangrove systems is depressed as a result of diminished upland flows of fresh water to mangroves. Low salinity mangrove forests have been recognized as critical nursery habitat for species such as blue crab, snook, tarpon (*Megalops atlanticus* Valenciennes in Cuvier and Valenciennes), and ladyfish (*Elops saurus* Linnaeus) (Odum et al. 1982, Gilmore et al. 1983, Lewis et al. 1985). Much of this habitat has been lost or highly modified. In many areas, freshwater upland flows to these mangrove systems have been decreased or depleted due to a rerouting of water through canals. Changes in freshwater discharge have also altered the structure of mangrove forests. Reduction and modification of this habitat type may represent a limiting factor in total population sizes of some estuarine-dependent species (Lewis 1990).

RESEARCH QUESTIONS

Key uncertainties concerning ecological responses to hydrologic restoration in the Caloosahatchee Estuary have led to the creation of a set of research questions. What are the historical distribution, present coverage, and potential coverage of SAV and oyster bars in the Caloosahatchee Estuary? What areas in the estuary potentially provide optimal conditions for SAV and oyster re-establishment? Will alteration in the coverage of SAV and oyster bars in the Caloosahatchee Estuary, due to changing salinity regime, provide a more suitable environment for estuarine invertebrates and fishes? Will this lead to an increase in population density and community diversity?

How does catch per unit effort of the blue crab fishery respond to the combined effects of temperature, salinity, and other water quality parameters in the Caloosahatchee estuary? Can blue crab catch per unit effort be used as an indicator of estuarine health in the estuary? Will changes in salinity, nutrient load, and

water residence time due to restoration of the recommended estuarine salinity envelope reduce occurrence of red tide in inland waters at times coincident to manatee movement between inland and estuarine waters? As CERP projects are built, answers to these questions will provide a sound basis for the adaptive assessment process.

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