LAKE OKEECHOBEE CONCEPTUAL ECOSYSTEM MODEL

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INTRODUCTION

Lake Okeechobee is a large (1,730 km^2) freshwater lake located at the center of the interconnected south Florida aquatic ecosystem. The lake is shallow (average depth <3 m), originated about 6,000 years ago during oceanic recession, and under natural conditions probably was a slightly eutrophic and had vast marshes to the west and south. The southern marsh was contiguous with the Florida Everglades, which received water as a broad sheet flow from the lake during periods of high rainfall (Gleason 1984).

Modern-day Lake Okeechobee differs in size, range of water depths, and connections with other parts of the regional ecosystem (Figure 1) (Havens et al. 1996). Construction of the Herbert Hoover Dike in the early to mid-1900s reduced the size of the lake's open-water zone by nearly 30%, resulted in a considerable reduction in average water levels, and produced a new littoral zone within the dike that is only a fraction of size of the natural one. The lake also has been impacted in recent decades by excessive inputs of nutrients from agricultural activities in the watershed (Flaig and Havens 1995). These nutrients have exerted the most dramatic impacts on the open-water region, where large algal blooms have occurred, along with accumulation of soft organic mud bottom sediments, which cause the lake water to become highly turbid when they are resuspended during windy periods (Maceina and Soballe 1990). The littoral zone has been invaded by 15 species of exotic plants, most notably *Melaleuca quinquenervia* and *Panicum repens* (torpedo grass), which have expanded over large areas, displacing native plants. Despite these human impacts, and a consensus that the lake's overall health has been greatly degraded by human actions, Lake Okeechobee continues to be a vital aquatic resource of south Florida, with irreplaceable natural and societal values. It is anticipated that the CERP, along with other local and regional restoration efforts, will improve hydrologic conditions in the lake (Figure 1), and that this will lead to improvements in the ecological attributes of the system.

An ecosystem conceptual model was developed for Lake Okeechobee restoration planning purposes. This model indicates, *via* a simple box-and-arrow diagram (Figure 2) how various cultural stressors affect attributes of the ecosystem that are of value to nature and society. The model is comprised of a top-to-bottom hierarchy of sources, stressors, ecosystem effects, attributes, and performance measures. For each performance measure there is a quantitative target (a desired endpoint of CERP and other local/regional restoration efforts) and a suite of monitoring parameters. The model for Lake Okeechobee is complex because the lake is comprised of three distinct components that have dramatically different structure and function: a littoral marsh, a near-shore region, and an open water (pelagic) region. Stressors in one zone may have indirect effects that cross the boundary into another. The lake conceptual model was developed in the context of this heterogeneity. The model also reflects the lake's present spatial extent, rather than the larger historical boundaries.

EXTERNAL DRIVERS AND ECOLOGICAL STRESSORS

Seven in-lake stressors that have strong impacts on the lake's natural and societal values originate from five distinct external sources (Figure 2). Elevated concentrations of **nitrogen and class I/III chemical contaminants**, including chloride (Cl^-) certain pesticides, and total dissolved solids (TDS), are by-products of agriculture or other human activities in the watershed. These contaminants may have detrimental effects in the ecosystem, but in general, are focused in particular locations (e.g., near input sources). A much greater concern, from the standpoint of ecosystem effects is the elevated level of **phosphorus**. High concentrations of this nutrient, which are largely responsible for the rapid eutrophication of the lake in the last two decades, are a result of excessive inputs from the watershed. The primary source of phosphorus pollution is agriculture, with lesser contributions from urban and other sources (Flaig and Havens 1995). As a result of decades of high inputs, the soils in the watershed, the sediments of tributaries, and the lake's bottom sediments now contain large quantities of phosphorus (Olila and Reddy 1993, Flaig and Reddy 1995). These soils and sediments represent large secondary sources of phosphorus loading to the lake. The deep canals of the C&SF Project facilitate delivery of phosphorus and other chemical stressors to the lake.

The pelagic region of Lake Okeechobee experiences elevated concentrations of **resuspended sediments**, whose source is a region of soft organic mud that covers about 50% of the central lake bottom. When wind mixes the shallow water column, the upper few cm of mud are resuspended. The spatial extent, depth, and phosphorus content of this mud have increased rapidly in the last 100 years, coincident with agricultural development and increased nutrient inputs from the watershed (Brezonik and Engstrom 1999). The Herbert Hoover Dike may facilitate sediment accumulation by preventing natural flushing that once may have occurred during high water events.

Variations in rainfall, evapotranspiration, water supply deliveries from the lake, and operation of the C&SF Project (including the regulation schedule, supply side management, and compliance with any Minimum Water Level criteria) have the potential to affect water levels (stage) in the lake. This becomes stressful to the ecosystem when there is **prolonged or extreme high or low lake stage**. The impacts of high and low stage are more severe than they would have been when the dike did not encircle the lake. Under natural conditions, water was able to expand and recede over a large low-gradient marsh to the west and south. Today, when lake stage exceeds 15 ft NGVD, water simply stacks up over the small littoral zone, flooding it to a greater depth. When lake stage falls below 11 ft, the entire littoral zone is dry, and lateral expansion is constrained to the east due to a relatively steep drop off in the lakes bottom contours. Hence, extreme high or low lake levels of any duration, or moderate high or low lake levels of prolonged (>12 months) duration, can cause significant harm to the ecosystem, as described below in greater detail. In contrast to the harmful effects of extremes, a certain degree of natural variation in lake stage, between 12 and 15 ft NGVD, has been shown to be benefit the ecosystem (Smith et al. 1995; Smith 1997) and is a desired hydrologic result of the CERP.

In recent decades, Lake Okeechobee has experienced a rapid expansion of **exotic and nuisance plants** and the introduction and expansion of certain **exotic animals**. The plants have been the greatest concern to date. There now are 15 species of exotic plants in the lake's littoral zone. Species that have caused the most substantial harm are *Melaleuca* and torpedo grass (*Panicum repens*), which were purposely introduced to the region, for dike stabilization and cattle forage, respectively. Other exotic plants that have stressed the lake's values include *Hydrilla* sp., water hyacinth (*Eichhornia crassipes*), and water lettuce (*Pistia stratiotes*). Exotic animals in the lake now include fish (*Tilapia aurea)*, mollusks (*Corbicula fluminea*), and microinvertebrates (*Daphnia lumholtzii*). Each of these species exerts different impacts on the ecosystem, as discussed below. Many of these species have been accidentally introduced to the lake, and this situation is likely to continue, as new species are introduced to the United States and subsequently spread by boats and other mechanisms into Florida waters. Certain species known to have dramatic ecological and the ability to tolerate conditions in the lake impacts (e.g., the zebra mussel) should be monitored for presence / absence on a regular basis.

ECOLOGICAL ATTRIBUTES

The Conceptual Model working group identified four major attributes associated with the Lake Okeechobee ecosystem (Figure 2). The attributes encompass the overall ecological health of the lake, and they also reflect the quality of several societal uses of the resource, including fishing, drinking water quality, hunting, wildlife observation, and recreational boating. Two non-ecological attributes that are strongly linked with the lake, water supply and flood control, are not included as attributes in the conceptual ecosystem conceptual model. Those cultural attributes are reflected in models of the Lake Okeechobee Service Area and the Lower East Coast; both have their own set of performance measures, some of which reflect water supply from the lake and flood protection. In the Lake Okeechobee ecosystem conceptual model, they represent sources of high and low lake stage (ecological stressors) and are indicated as such.

The first attribute is **lake water quality**, which directly affects the quality of the habitat for vegetation, fish, and other wildlife. Poor water quality in the last two decades can be linked with reduced overall health of the biotic components of the ecosystem (Havens et al. 1996). Water quality in the lake also affects drinking water quality, and it can affect the health of downstream ecosystems (the St. Lucie and Caloosahatchee Estuaries and the Florida Everglades) that receive water from the lake. The second attribute is the lake's **fish and aquatic fauna.** Lake Okeechobee supports a commercial and recreational fishery that has an estimated economic value in excess of $480 million US dollars (Furse and Fox 1994). The fishery also supports a diverse community of birds and other animals. The third attribute of the lake is a diverse **native vegetation mosaic**. It provides nesting and foraging habitat for fish and other animals, areas of beauty for recreation, and the ability to mitigate poor water quality. This vegetation mosaic has been seriously degraded due to expansion of exotic plants in the littoral region and nearly a complete loss of submerged plant beds in the near-shore region due to high water levels and turbidity. The fourth attribute is the lake's diverse community of birds and animals that includes **snail kites, wading birds, and water fowl**. The littoral zone of Lake Okeechobee provides one of the largest habitats in south Florida for the federally-endangered snail kite (Bennetts and Kitchens 1997), and it supports large resident and migratory populations of wading birds (Smith et al. 1995). A variety of migratory water fowl reside in the lake during winter, and the alligator population is one of the largest in the state of Florida.

ECOSYSTEM EFFECTS

The pathways linking cultural stressors to ecological attributes are complex (Figure 2), and have a solid foundation in research and modeling conducted by scientists at the SFWMD, Florida Fish and Wildlife Conservation Commission (FFWCC), and Florida public universities. As we learn more about how the ecosystem functions, it is possible that additional pathways could be added to the model, or adjustments made to existing pathways. The model is a flexible planning tool that, at any given time, reflects the current state of scientific knowledge about Lake Okeechobee. Ecosystem effects are described here in the context of sets of working hypotheses regarding how each identified attribute in the model is thought to be affected by the major ecosystem stressors.

LAKE WATER QUALITY

Water quality in Lake Okeechobee has been dramatically affected by nutrients associated with human activities in its watershed. Total phosphorus concentrations measured in the lake today (>100 ppb) are more than double those measured in the early 1970s, when the SFWMD first began to collect water quality data on a regular basis (James et al. 1995a). The high concentrations reflect a long history of excessive phosphorus inputs to the system (James et al. 1995b) and today, an internal load of phosphorus from the lake sediments approximately equals that of the external load in magnitude (Olila and Reddy 1993). Turbidity of the lake water also is high, especially in the central pelagic region, due to resuspension of sediment material from the lake bottom (Maceina and Soballe 1991, Hanlon et al. 1998). During times when lake stage is high (>15 ft) there appears to be substantial transport of turbid, phosphorus-laden water from mid-lake to the south and west shoreline areas (Maceina 1993, Havens 1997), where another water quality problem occurs -- the development of dense blooms of noxious cyanobacteria (blue-green algae). When these algae occur in high densities they can cause taste, odor, and trihalomethane problems for the five municipalities that draw water from the lake for drinking. When the blooms peak and then collapse, aquatic animal life is threatened because of reduced dissolved oxygen concentrations and decay products from the algae (Jones 1987, Paerl 1988).

In addition to phosphorus and its related water quality problems, Lake Okeechobee is considered impaired by the US Environmental Protection Agency based on its standards for dissolved oxygen, un-ionized ammonia, chlorides, coliform bacteria, and iron. From an ecosystem perspective, however, the major concerns are related to the excessive phosphorus levels and their direct and indirect effects. The following hypotheses describe the major factors considered to affect phosphorus dynamics in the lake.

Hypotheses and Predictions:

Hypothesis 1 - High rates of external phosphorus loading from tributaries and internal phosphorus loading from contaminated lake sediments are responsible for the high concentrations of phosphorus that occur in the water column of Lake Okeechobee.

The lake has experienced high rates of phosphorus loading from its watershed for many decades (SFWMD 1997). At present the loading is in excess of 600 metric tons/y, far greater than the amount considered appropriate by the USEPA (2000) or Florida Department of Environmental Protection (2000) to protect the ecosystem. When phosphorus enters the lake, a large fraction is stored in the lake sediments (James et al. 1995b). Due to the long history of high inputs, those sediments now contain over 30,000 metric tons of phosphorus in their upper 10 cm alone (Olila and Reddy 1993). This phosphorus can be mobilized into the overlying water column by various processes, including diffusion (Moore et al. 1998), wind re-suspension (Hanlon 1999), and bioturbation (Van Rees et al. 1996). This internal loading makes the lake ecosystem very resilient to changes in its phosphorus concentration when external inputs vary, a situation that is common in shallow eutrophic lakes (Sas 1989, Moss et al. 1996). From a management standpoint, this means that lake responses to load reductions based on the implementation of elements in CERP and the Lake Okeechobee Protection Plan are likely to occur with a long time lag. Eventually, however, phosphorus-rich surface sediments are expected to be covered by new sediment material with reduced phosphorus content. When this occurs, rates of internal loading should begin to decline.

Prediction - Watershed-scale treatment facilities (including large reservoirs and stormwater treatment areas) constructed under CERP and the Lake Okeechobee Protection Plan, along with enhanced phosphorus source control, will result in reduced rates of phosphorus loading to the lake. Given a sufficient period of time (perhaps decades or more), internal loading rates also will decline. The net result should be a decline in lake water phosphorus concentrations, but the timing of this response is uncertain.

Hypothesis 2 - H*igh lake stage results in conditions that exacerbate the problem of phosphorus pollution in the lake's water column.*

While it is clear that there is a link between stage and total phosphorus (Canfield and Hoyer 1988, Havens 1997), the underlying mechanisms may be complex, ranging from large-scale changes in the physics of water circulation to alterations in the interaction between biological communities. One of the first effects to be suggested (Maceina 1993) was that at high stage there is greater horizontal transport of phosphorus from the mid-lake region, where concentrations are highest due to the re-suspension of underlying mud sediment, into more phosphorus-deficient near-shore areas. The evidence for this hypothesis was largely observational, but it has been supported with results from the SFWMD Lake Okeechobee Hydrodynamic Model. The underlying mechanism is related to underwater currents and the morphology of the lake basin. When wind moves across the lake surface it creates large circulation gyres (Jin et al. 2000) whose spatial extent is affected by water depth. When lake stage is low (<13 ft), an elevated ridge of limestone along the south and west perimeter of the lake hinders mixing of water between the mid-lake and shoreline regions. This is thought to reduce phosphorus and sediment transport to the shoreline region and be responsible, in part, for the low phosphorus concentrations and high transparency that occur there when stage is low (Maceina 1993, Havens 1997).

Another factor that may become important at low lake stage is uptake of phosphorus by submerged macrophytes. During years when stage is low, the lake can support a large spatial extent of submerged macrophytes (Hopson and Zimba 1993). For example, in 1989, after stage declined to below 11 ft, remote sensing indicated that submerged plants covered 12,400 ha of the lake bottom (Richardson and Harris 1995). In summer 2000, after a managed lake recession operation and a decline in stage to below 12 ft, the total extent of submerged plants determined from an intensive field survey was 17,700 ha.

Submerged macrophytes have the capability to reduce water column phosphorus concentrations by a number of processes. These include: (1) stabilization of lake sediments by their roots; (2) a reduction of water flow velocity and shearing stress on sediments due to wave attenuation (Vermaat et al. 2000); (3) trapping of sediment material; (4) direct uptake of phosphorus by roots in the sediments or from the water by epiphytic algae (Carrigan and Kalff 1982, Burkholder et al. 1990). In Florida lakes up to 96% of the combined water column and macrophyte phosphorus can occur in the tissues of macrophytes (Canfield et al. 1983).

Benthic micro-algae and *Chara*, a macro-alga, also can become abundant under low stage conditions in Lake Okeechobee (Steinman et al. 1997a,b), and these algae can directly compete for water column phosphorus with phytoplankton (Havens et al. 1996, Hwang et al. 1998). When lake stage is high, the growth of macrophytes and attached algae is suppressed due to light limitation caused by the deeper water and the high turbidity that accompanies greater materials transport from the mid-lake region. Hence lake stage can affect water column phosphorus concentrations by determining the relative mass of that nutrient that occurs in attached macrophytes and algae (high when lake stage is low) or phytoplankton (high when lake stage is high).

Prediction - When alternative water storage locations (ASR wells and regional storage reservoirs) are brought on line under CERP, it is predicted that there will be a reduced number of high lake stage events in Lake Okeechobee. This should directly benefit water quality in the lake, by providing conditions where there is both reduced horizontal transport of phosphorus into the shoreline area and increased growth of macrophytes and attached algae that can remove phosphorus from the water.

Hypothesis 3 - Biological and chemical changes that occurred in the lake due to cultural eutrophication have contributed to a "positive feedback" that helps maintain high phosphorus concentrations due to a lack of ecosystem assimilative capacity.

A phosphorus mass-balance for the lake indicates that every year, approximately 400 metric tons of that element is stored in lake sediments (James et al. 1995b). Hence the lake is described as a "net sink" for phosphorus. However, since the early 1970s, this internal storage of phosphorus has been declining (Havens and James 1997), suggesting that the lake's assimilative capacity is being used up. That might occur for example, if the binding sites (calcium and iron minerals) on sediment particles became saturated with phosphorus. There is some evidence that this is occurring. Fisher et al. (2000) compared the concentrations of sediment pore-water phosphorus in samples collected from the lake in 1988 vs. 1998, and found that they had more than doubled. Pore-water phosphorus is unbound phosphorus that essentially is a surplus or non-assimilated fraction. At this point we assume that this increase in pore-water phosphorus reflects a reduction in binding sites, and hence a reduction in assimilative capacity. However, more research is needed to verify that the increase in pore-water phosphorus is not attributable to other factors, such as increased rates of phosphorus diagenesis.

If external phosphorus loading rates remain high, a further loss of sediment assimilative capacity might occur. On the other hand, this trend might be reversed after a period of substantially reduced loads.

Along with these chemical processes, there have been a number of biological changes in the lake that could reduce the system's capacity to assimilate phosphorus (Havens and Schelske 2000). In the lake's water column, diatoms have been replaced by cyanobacteria as the dominant phytoplankton (Cichra et al. 1995), and this could decrease the rate of phosphorus transport to sediments because cyanobacteria settle much slower than diatoms in the lake's water column (Reynolds 1984). Among the benthic macro-invertebrates, oligochaetes have replaced chironomids and other insect larvae as the dominant taxa (Warren et al. 1995), largely because they are able to tolerate the anoxic conditions that occur in the lake's enriched sediments (Warren et al. 1995). This macro-invertebrate trend may have resulted in a reduced net loss of phosphorus from the lake water because oligochaetes pump large quantities of soluble phosphorus from the sediments into the overlying water when they feed (Van Rees et al. 1996). Likewise, the lake's fish community contains a relatively large proportion of taxa that feed in the benthos, providing another pathway for upward phosphorus transport. There is a potential for reversal of these biological changes if phosphorus loads to the lake are substantially reduced.

Prediction - If projects implemented under CERP and the Lake Okeechobee Protection Act result in substantially reduced loads of phosphorus to the lake and lower water column phosphorus concentrations, there might be a reversal of physio-chemical and biological trends that have recently led to a low phosphorus assimilative capacity. If this occurs, lake assimilative capacity could increase, and might proceed more rapidly than presently anticipated.

Hypothesis 4 - Blooms of noxious cyanobacteria and their associated effects on water quality are a direct consequence of high phosphorus concentrations.

The relationship between cyanobacteria blooms and phosphorus enrichment has been well established in the literature (Horne 1979, Paerl 1988). In lakes with prolonged high rates of external loading, phosphorus often reaches concentrations where it is in surplus relative to algal demands. When this occurs, some other nutrient element (most often nitrogen) becomes "secondarily limiting" (Schelske 1984) to algal growth. Havens (1995) documented a trend in lake water quality indicative of a transition towards secondary nitrogen limitation after the early 1980s, and Aldridge et al. (1995) and Phlips et al. (1997) documented that nitrogen now is the primary limiting factor for phytoplankton growth in the lake. In contrast, Brezonik et al. (1979) documented that there once was considerable phosphorus limitation. Nitrogen limitation favors dominance by bloom-forming cyanobacteria that can (1) remain buoyant in the water column, and (2) obtain nitrogen from the atmosphere by the process of nitrogen fixation (Horne 1977). Taxa that have this capacity include *Anabaena*, *Microcystis*, and *Aphanizomenon*; these taxa predominate in Lake Okeechobee when it experiences severe algal blooms.

Prediction - If projects carried out under CERP and the Lake Okeechobee Protection Plan result in reduced in-lake phosphorus concentrations, levels of surplus phosphorus may be reduced to the extent that phosphorus again becomes the nutrient most often limiting to phytoplankton growth. That condition would favor dominance of diatoms and other algae over cyanobacteria, resulting in a reduction in the frequency of algal blooms.

FISH AND AQUATIC FAUNA

Lake Okeechobee supports a nationally recognized sport fishery for largemouth bass (*Micropterus salmoides*) and black crappie (*Pomoxis nigromacultus*), as well as a commercial fishery for various catfish and bream (*Lepomis* spp.). According to Fox et al. (1993) these fisheries generate nearly $30 million per year for the local economies and they have an asset value that is in excess of $100 million (Bell 1987). Another estimate (Furse and Fox 1994) places the value of the fishery at more than $300 million, and considers only the recreational fish species.

In addition to the sport and commercial species, Lake Okeechobee supports a diverse community of fish, including (in total) 41 species (Bull et al. 1995, Havens et al. 1996b). These fish provide a food resource for wading birds, alligators, and other animals that use the lake as a foraging habitat. Fish use both the littoral and pelagic regions of the lake and some of the top predators (including largemouth bass and Florida gar, *Lepisosteus platyrhincus*) display a migration between the two habitats (Fry et al. 1999). Gut analysis and stable isotope data indicate that the fish depend on a wide range of food resources, including benthic macro-invertebrates and zooplankton (Havens et al. 1996b, Fry et al. 1999). These in turn are dependent on a continual input of energy in the form of plant, periphyton and phytoplankton primary productivity, and allochthonous inputs of carbon that can fuel bacterial growth. Fish also depend on the lake's aquatic plant communities to provide them with spawning habitat, to serve as a refuge from the environment and predators, and to support the complex food web described above (Fox et al. 1993).

As a result of human impacts on the lake, there have been dramatic changes in both the resource base that supports the fishery and the aquatic plant communities that provide fish habitat. These changes include eutrophication-related shifts in macro-invertebrate and plant community structure, and large-scale loss of certain plant community components due to stresses associated with high water. In fall 1999, scientists at the Florida Fish and Wildlife Conservation Commission (FFWCC) reported declines both in the population size and early age classes of important sport fish, a result that likely is related to some of the ecosystem changes that recently have occurred. Other components of the lake's wildlife community (e.g., wading birds and migratory water fowl) also may have been affected by eutrophication and high-water related changes in the food web and habitat structure.

Hypotheses and Predictions:

The hypotheses presented here are closely linked with those provided under the sections of this document dealing with "native vegetation mosaic" and "snail kites, wading birds, and alligators." This reflects the tight linkage between these components of the lake's food web. The focus of this section is on fish and invertebrate animals. Hypotheses generally are related to particular regions of the lake (i.e., littoral, near-shore, and pelagic), although it is recognized that certain species migrate between these habitats.

Hypothesis 1 - The species composition, abundance, and biomass of benthic macro-invertebrate communities in the lake's pelagic region are primarily affected by the high rates of loading of nutrients and organic carbon to that region.

As a result of sustained high rates of nutrient loading and high rates of phytoplankton production, there has been a high rate of organic loading to the lake sediments, high rates of bacterial metabolism, and hypoxic or anoxic conditions in the near-surface sediments. These conditions collectively favor the dominance of "pollution tolerant" macro-invertebrates such as certain oligochaetes. Warren et al. (1995) documented that between the early 1970s and early 1990s, the relative abundance of oligochaetes increased in the pelagic sediments from 30 to 80% of the total community. This high relative abundance persisted during the last decade (Warren, personal communication), and species known to be pollution-tolerant (e.g., *Limnodrilus hoffmeisteri*) continued to be abundant. At the same time, species that previously occurred in the lake and still occur in nearby unpolluted lakes (various ephemeropterans and trichopterans), have become rare or absent in Lake Okeechobee. These trends are nearly identical to those observed in Lake Erie when it underwent rapid eutrophication between 1930 and 1960 (Carr and Hiltunen 1965).

The predominance of oligochaetes is a concern for two reasons. First, as mentioned above, they can contribute substantially to the internal loading of phosphorus. Second, they do not have an adult stage that emerges from the water (as occurs for ephemeropterans, trichopterans, and other aquatic insects), and therefore do not provide a food resource for animals that feed on such emergent forms. This includes migratory waterfowl and a variety of fish.

Prediction - If projects implemented under CERP and the Lake Okeechobee Protection Plan result in a substantial reduction in phosphorus loading to the lake, at some time in the future the surface lake sediments may be less enriched with nutrients and organic matter. If this occurs the sediments will be a more favorable habitat for a diverse benthic macro-invertebrate community, and the dominance of oligochaetes should decline. The timing and extent of this recovery are uncertain.

Hypothesis 2 - The biomass of zooplankton in the lake's open water region is controlled by *resource supply, while taxonomic composition is determined primarily by predation and temperature tolerance.*

The zooplankton of Lake Okeechobee is comprised of 61 native and one exotic species (Havens et al. 1996b, Havens and East 1997), and includes rotifers, copepods, and sparse amounts of cladocerans. The total biomass correlates significantly with nutrient and chlorophyll concentrations (Crisman et al. 1995, Beaver and Havens 1996), suggesting resource limitation. This conclusion is supported by results of experimental nutrient-addition studies (Havens et al. 1996c). Havens and East (1996) also documented that the dominance of large cyanobacteria in the lake's phytoplankton community may contribute to resource limitation because the algae cannot be directly grazed by many of the lake's zooplankton. As a result, the major pathway for energy transfer to zooplankton involves multiple steps (phytoplankton → excreted organic carbon → bacteria → protozoa → zooplankton) and low ecological transfer efficiency (Havens et al. 2000). One reason this may occur is that the abundance of large cladoceran zooplankton, which can directly graze large algae at high rates, is very low in Florida lakes (Crisman and Beaver 1990).

Two factors may explain the absence of large cladocerans: (1) high rates of grazing by fish eliminates the largest most visible zooplankton taxa (large cladocerans); and (2) high water temperatures preclude the occurrence of cladocerans during all but the coolest months of the year. Both hypotheses are supported by experimental research on other lakes, as well as by work on Lake Okeechobee. Crisman and Beaver (1990) documented that in fish-free enclosures in the near-shore region of the lake, cladoceran biomass increased dramatically, and Beaver and Havens (1996) noted that the very high biomass of threadfin shad (*Dorosoma petenense*), a voracious zooplanktivore, should preclude occurrence of any large cladocerans. East et al. (1999) found that abundance of the native *Daphnia ambigua* is reduced dramatically during summer, when water temperatures are high, but *D. lumholtzi*, a tropical exotic, increases during that period. The exotic species also has large spines that may provide a greater defense against fish predation during summer months. Total zooplankton biomass generally is lower during mid-summer then in spring and fall in Lake Okeechobee and other Florida lakes.

Predictions - If projects implemented in CERP and the Lake Okeechobee Protection Plan result in reduced nutrient inputs to the lake and declines in phytoplankton and bacterial biomass, the total biomass of zooplankton might be expected to decline. However, this decline might be ameliorated by improvements in food quality (a shift from inedible cyanobacteria to edible diatoms). Effects of CERP on the taxonomic structure of zooplankton are uncertain because factors controlling this attribute may not be influenced by the project.

Hypothesis 3 - Macro-invertebrates in the near-shore region of the lake are strongly dependent on the habitat values provided by submersed and emergent macrophytes.

Under favorable conditions, near-shore macrophyte habitat, including *Hydrilla verticillata, Potamogeton illinoinsis* (peppergrass), *Scirpus* sp. (bulrush) and *Vallisneria americana* (eelgrass) support a high biomass of macroinvertebrates (Warren and Vogel 1991). Many of these mnacroinvertebrates, including the grass shrimp *Palaemonetes paludosus*, the amphipod *Hyalella azteca*, and larvae of the midge genera *Dicrotendipes, Glyptotendipes*, and Rheotanytarsus, are integral to the diets of largemouth bass, black crappie, redear sunfish (*Lepomis microlophus)*, and bluegill sunfish (*L. macrochirus*).

With the recent (1990s) declines in near-shore macrophytes, much of the habitat for invertebrates important in the diets of sport fish has been eliminated. In a June 2000 survey, Warren and Hohlt (FFWCC, unpublished data) recorded extremely low densities of invertebrates in habitats (bulrush and mud sediments) that formerly (1987-1991) supported high numbers. Scientists and members of the public who frequent the lake also noticed a near absence of winged adult midges emerging from the lake during summer 2000. As noted above, these kinds of changes have potential negative consequences for birds and fish that depend on immature and adult invertebrates as a food resource. The extent to which these communities recover as a result of low water levels (<12 ft) and increased macrophyte biomass in 2000 remains to be seen.

Prediction - If projects implemented in CERP result in a reduced frequency of prolonged and/or extreme high lake stage events, the near-shore bulrush community is likely to recover some of its previously greater spatial extent and density. When this occurs there should be a concomitant increase in the abundance of macroinvertebrates dependent upon submersed and emergent macrophyte habitats.

Hypothesis 4 - Macroinvertebrate community structure in the littoral zone is affected by variation in hydroperiod, distribution of plant communities, and dissolved oxygen concentrations.

Warren and Hohlt (1994) and Warren and Vogel (unpublished data) examined littoral macroinvertebrate community sturcture on *Eleocharis* sp. (spikerush), *Panicum repens* (torpedograss), *Pontaderia sp.,* bulrush, and *Typha* sp. (cattail). Because of their growth habits, the torpedograss, *Pontaderia* and cattail habitats were characterized by low dissolved oxygen concentrations and poor quality macroinvertebrate communities. Spikerush habitat had a more vertical growth form and lower production of thatch material, and was characterized by higher dissolved oxygen concentrations and a higher quality macroinvertebrate community.

Based on surveys conducted by the FFWCC, we also know that the littoral zone includes at least 174 macro-invertebrate taxa (Havens et al. 1996b), representing a wide range of functional and taxonomic groups. Analysis of fish gut contents and stable isotope studies reveal that macro-invertebrates represent important diet components for small forage fish and sport fish in the interior littoral zone (Havens et al., manuscript in prep.). Macro-invertebrates were found to account for >40% of the volumetric gut contents of redear sunfish, bluegill sunfish, largemouth bass, and bowfin (*Amia calva*) at a sampling site in Moonshine Bay, located in the west-central littoral zone.

One of the most visible members of littoral macro-invertebrate community, from a resource management perspective, is the Florida apple snail (*Pomacea paludosa*). This species is a principal food item for the federally endangered Everglades snail kite (*Rostramus sociabilis)* (Bennetts and Kitchens 1997), and it also is consumed by certain wading birds, migratory water fowl, turtles, and small alligators. As such, it is an important component of the littoral food web. Research dealing with apple snails in south Florida (Turner 1996, Darby et al. 1997) indicates that: (1) the most favorable habitat for these animals includes a mosaic of sparsely and densely vegetated habitats; (2) animals survive only for 12 to 18 months, and lay their eggs on emergent vegetation during a 4 to 12 week period between March and July; and (3) juvenile snails can survive drying for 2 to 3 months. Dry-downs are not necessarily harmful to the snail populations, as long as they do not coincide with the peak period of egg production or last for many months, so that a large percentage of the existing population is killed. Since snails are slow-moving animals, re-population of large areas following prolonged dry downs may require multiple years of favorable conditions.

Another factor that can significantly impact apple snails is reversal of lake stage during the egg laying period. Snails lay their eggs several cm above the water surface on the emergent stems of spike rush, bulrush, cattail and other plants (Darby et al. 1997). If lake stage rises during this period and eggs become flooded, they experience high mortality due to physiological effects on developing snail embryos and from loss of adhesion to stems (Turner 1994).

Research dealing with apple snail growth responses to varying food types indicates that the nutrient content of grazed material also could affect the populations. Sharfstein and Steinman (2000) maintained young apple snails in laboratory cultures, and provided the animals with either the epiphyton associated with spike rush stems, epiphyton of bladderwort, or metaphyton collected from near the sediment surface. These are three distinct and typical components of the periphyton community in the lake's central littoral zone (Havens et al. 1997). Snails feeding on bladderwort epiphyton grew significantly more than snails feeding on the other food types, perhaps because the bladderwort epiphyton had a higher nitrogen and chlorophyll content. Changes in plant community structure that shift the periphyton towards a dominance by less nutritious forms could potentially result in reduced apple snail growth. The extent to which human factors might be expected to bring about such a change is unclear.

Prediction - Three major predictions emerge from what is presently known about the littoral macroinvertebrate community. First, it is predicted that apple snails and other beneficial invertebrates will benefit from lake stage operations that minimize the frequency of prolonged spring draw-downs that dry out their habitat (i.e., prolonged lake stages below 12 ft). Second, it is predicted that snails and other invertebrates will benefit from operations that minimize the occurrence of stage reversals during the March-July period of maximal egg laying. Third, it is predicted that snails and other invertebrates will benefit from lake stage operations and other management actions (e.g., exotics control) that maintain a diverse mosaic of native littoral vegetation types, including spike rush, bladderwort, bulrush, sawgrass, and other emergent species.

Hypothesis 5 - The abundance and taxonomic composition of fish in the lake's pelagic zone is affected by nutrient inputs to the system, which determine the biomass of phytoplankton in the water column and macro-invertebrates in the benthos.

Bull et al. (1995) studied the distribution of fish in open-water habitats of the lake during the late 1980s and early 1990s, sampling fish at 25 sites with a large trawl net. They found that the deeper central and north regions of the lake supported distinct fish assemblages, which differed from those found in the near-shore and littoral habitats. The central assemblage was dominated by threadfin shad (*Dorosoma petenense*) and black crappie (*Pomoxis nigromaculatus*) in summer, and by black crappie and white catfish (*Ameirus catus*) in winter. The abundance of shad was significantly correlated with phytoplankton chlorophyll *a* concentrations. This reflects a feeding preference for phytoplankton and zooplankton (Baker and Schmitz 1971). White catfish abundance was strongly correlated with water depth, indicating the fact that these species tend to forage in the cooler deep water areas of the lake, where they prey on benthic macro-invertebrates, detritus, and smaller fish (Havens et al., manuscript in prep). Bull et al. (1995) documented that the north pelagic region is strongly dominated by threadfin shad and black crappie. It supports the highest densities of these species both in summer and winter, probably due to high food availability. Phlips et al. (1995) documented that the north region, in closest proximity to high nutrient inputs from agricultural tributaries, displays high phytoplankton biomass. The phytoplankton provides a direct source of food for shad, and also a source of organic matter loading to support a high biomass of benthic macro-invertebrates. Black crappie prey heavily on *Chironomus crassicaudatus*, a chironomid that occurs at extremely high densities (up to 21,000 per m^2) in the nutrient-rich mud sediments that occur in the northern region (Warren et al. 1995).

Prediction - Substantial reductions in nutrient loading to the lake, brought about by projects in CERP or the Lake Okeechobee Protection Plan, might lead to declines in the abundance of certain fish taxa (e.g., threadfin shad, black crappie). These fish presently occur at high densities due to an abundance of food resources (phytoplankton and certain chironomids) linked to high rates of nutrient inputs. On the other hand, other changes in the lake that benefit certain fish might counteract these declines. Crappie recruitment has been low in recent years (Michael Allen, University of Florida, personal communication) and this has been linked to high lake stage. Hence a rehabilitated lake, with lower stages and reduced nutrient loads, might actually support a healthier population of that sport fish than is the case for the existing lake system.

Hypothesis 6 - Fish in the near-shore region depend heavily on the occurrence of a healthy community of submersed and emergent plants.

Fisheries research conducted on other lakes has shown that vascular aquatic plants provide multiple benefits to fish communities. These include: (1) substrate and cover for spawning (Loftus and Kushlan 1987); (2) habitat for foraging (Janacek 1988); and (3) protective habitat for larval and young adult stages of fish (Barnett and Schneider 1974, Conrow et al. 1990). In Lake Okeechobee, Furse and Fox (1994) documented that bulrush, eelgrass, peppergrass, and *Hydrilla* provide important habitat for a variety of sport and forage fish (40 species total) in the near-shore area.

Furse and Fox (1994) noted that eelgrass, peppergrass, and spikerush provide important habitat in the lake for juvenile sport fish and small forage fish, and that bulrush, hydrilla, and pondweed account for most of the lake's recreational fishery value. Bulrush recreational value was four times higher than that estimated for any other component of the vegetation community in the near-shore area. Given these multiple functions, and the large-scale loss of both submerged aquatic vegetation, spikerush, and bulrush that has occurred in the last decade (details below), it is not surprising that in the most recent fisheries survey (October 1999), scientists noted significant declines in population densities and young age classes of economically important sport fish (FFWCC, unpublished data). It remains to be seen whether these populations will substantially recover in 2000, when a period of low lake stages has allowed for a limited recovery of the submerged plants and bulrush.

Prediction - If the modified hydrologic regime under CERP results in conditions that are more favorable for growth of submerged aquatic vegetation and bulrush in the near-shore zone of the lake, there will be substantial benefits to the lake's fish community.

Hypothesis 7 - Fish that spend all or part of their life cycle in the littoral zone of Lake Okeechobee are affected by factors that significantly alter the structure of the habitat, its resource base, and its water quantity and quality.

In general, a lake's vegetated littoral zone provides important habitat for fish, in particular for small forage fish taxa and the juvenile stages of larger species, which use the littoral zone as a refuge from predators and as a foraging area (Werner et al. 1983, Rozas and Odum 1988). In the case of Lake Okeechobee, surveys by Chick and McIvor (1994) documented a high biomass and diversity of fish in the littoral zone, with distinct fish assemblages occurring in different plant communities (eelgrass, peppergrass, and hydrilla). This is similar to the findings of Furse and Fox (1993) except that in this case, the focal point of the study was the interior and northern littoral regions, rather than the near-shore area. Fry et al. (1999) also documented, using stable isotope data, that a variety of fish may begin life in the lake's littoral zone and then migrate out into deeper water as they grow in size and "move up" in the food chain.

Chick and McIvor (1994) concluded that the littoral zone should be viewed as a complex landscape, comprised of distinct habitats that provide varying resource, refuge, and other features for the fisheries. This finding is important, but it seriously complicates our ability to understand the full suite of factors affecting fish while they are in the littoral zone. The landscape contains more than 30 distinct vegetation types, including emergent, submerged, and floating-leaf plants with dramatically different densities and growth forms. One thing that seems clear, however, is that certain rapidly expanding exotic and nuisance plants create conditions that generally are not favorable for fish. Species of particular concern are torpedograss and cattail. Greater detail regarding the expansion of these plants and conditions favoring their dominance is provided below under "native vegetation mosaic." In brief, both species have spread over tens of thousands of acres in the lake's littoral zone, displacing native plant communities that provide good habitat for fish and wildlife.

One of the displaced plants, spikerush, provides particularly good habitat for fish (Chick and McIvor 1994). It includes enough open water to allow large fish to effectively forage, but also provides cover associated with the emergent plant stems and associated whorls of bladderwort (*Utricularia* spp.) that are common in this habitat. The spikerush community also supports a high diversity of macro-invertebrates and attached periphyton that provide a food resource for the fish. In contrast, both torpedograss and cattail display a very dense growth form, with little open water for animals to move through and, as a result of the poor light conditions, little or no periphyton. Water quality inside dense stands of torpedograss also is not suitable for aquatic animals. Nighttime dissolved oxygen concentrations typically are near zero and mid-day values are as low as 0.5 mg/L (SFWMD, unpublished data).

The spread of torpedograss, as discussed below, may largely be a function of the occurrence of low lake stage, since expansion is favored when there is little or no standing water over the sediment surface. Expansion of cattail may be a function of phosphorus inputs from the pelagic zone and periods of long hydroperiod (Newman et al. 1996). The conditions that promote cattail expansion also may be responsible for the increased density of water lily (*Nymphaea* spp.) that has been observed in the interior littoral zone in the last several years. In areas where the density of this plant is high, there has been a deep accumulation of dead leaf material and coarse organic detritus, sometimes leaving only 5 to 10 cm of open water column. This habitat is not considered to be suitable for fish foraging or reproduction (FFWCC staff, personal communications). Recent years of long hydro-period also have allowed a deep accumulation of periphyton and detritus in spikerush areas, such that sandy substrate (good fish nesting habitat) is less available.

Predictions - If projects implemented in CERP result in a reduced occurrence of prolonged high or low stage, the conditions that have favored expansion of cattail, water lily, and torpedograss should be reduced in their occurrence. This situation, along with active measures (controlled fires and/or herbicide application) to kill torpedograss and cattail, should provide benefits to the lake's fish and wading bird communities.

Other aquatic fauna

There is insufficient information at this time to formulate hypotheses or predictions regarding other aquatic animals in the lake. The lake's littoral zone is used by society as a resource for hunting frogs and collecting snakes and turtles for commercial sales, but the distribution and abundance of these animals is unknown. The only study to consider herptofauna in the lake (USACE 1999) included sampling only at a few selected locations, but indicated that there are at least 15 common species. These included a variety of snakes, frogs, and turtles. The number of animals collected was reduced to near zero during a period when lake stage became very high, but it was impossible to determine if this was a real environmental impact or an artifact of low sampling efficiency (the traps were designed for sampling in shallower water).

NATIVE VEGETATION MOSAIC

The littoral zone of Lake Okeechobee, in its current form, is a relatively recent system. Much of it was formed after construction of the Herbert Hoover Dike in the mid-1900s and control of the lake at a lower average surface elevation than under pre-settlement conditions. The lake's natural littoral zone probably was much larger and occurred to the west and south of its present location (Havens et al. 1996, Steinman et al. 2000a). Despite its young age, the existing littoral zone supported a diverse array of native plants when it first was mapped in the early 1970s (Pesnell and Brown 1973). The community included large areas of spikerush, sawgrass (*Cladium jamaicensis*), willow (*Salix caroliniana*) and beakrush (*Rhynchospora tracyi*). At the south end of the lake there were remnant stands of pond apple (*Annona glabra*) and along the western shore there was a nearly continuous band of dense bulrush immediately lake-ward of a zone dominated by spike rush and submerged plants. Although there is no quantitative record, various anecdotal reports from the early 1970s indicate that the submerged plant beds were both widespread and dense, including species such as eelgrass and peppergrass, which are favorable habitats for fish (Furse and Fox 1993).

Today the vegetation mosaic of the littoral zone is dramatically different (Richardson and Harris 1995). Upland areas that previously were dominated by beakrush and mixed grass assemblages now have been infested by the invasive exotic torpedograss. Certain areas have become dominated by the exotic tree melaleuca (*Melaleuca quinquenervia*), although much of that species has been killed by herbicide (SFWMD 1997). The spatial extent of willow has declined and there has been a large expansion of cattail. Pristine spikerush sloughs in the interior littoral zone now are surrounded by cattail (an invasive nuisance species) and torpedograss and contain a higher density of water lily (*Nymphaea* spp.) than in the 1970s. The long-shore bulrush stands now are sparse (just 50% of the former coverage) relative to their historic amounts, and the shoreline spike rush community no longer exists. Submerged vegetation was largely eliminated from the near-shore pelagic region in the late 1990s, although a marked recovery has occurred during a period of low water levels in spring-autumn 2000.

Hypotheses and Predictions:

Three main factors have interactively affected the native vegetation mosaic in Lake Okeechobee. These factors are *altered hydroperiod*, *excessive phosphorus loading*, and the *introduction and expansion of exotic plants*. The following general hypotheses describe how these factors are thought to affect the vegetation mosaic attribute, and are organized by geographic region (littoral zone, near-shore bulrush zone, and near-shore submerged vegetation zone).

Hypothesis 1 - In the littoral zone, the distribution of native and exotic plants primarily is determined by hydroperiod.

Short hydroperiod regions support native species including spikerush, beakrush, willow, and cordgrass (*Spartina bakeri*), and exotic species including torpedograss, melaleuca, and brazillian pepper (*Schinus terebinthifolius*). Long hydroperiod regions support spikerush, cattail, sawgrass, bladderwort, and water lily. Periods of extremely short or long hydroperiod (low and high lake stage events) that have occurred since the early 1970s are considered largely responsible for changes in the relative distribution of these plants.

Two periods of very low lake stage, in 1980-81 and 1989-90, may be responsible for much of the expansion that has occurred in exotic plant populations. Controlled experiments with melaleuca (Lockhart 1995) and torpedograss (Smith et al. 2000) have shown that these species cannot successfully invade native plant habitat that is inundated with water. Melaleuca seeds cannot effectively germinate under water, and fragments of torpedograss (this plants main mode of colonization) cannot establish roots when water depths exceed 50 cm. However, once these plants are established (e.g., during a period when water depth is low), they can tolerate relatively deep and prolonged flooding. Field observations indicate that much of the expansion of Melaleuca and torpedograss in the littoral zone occurred following droughts in 1981 and 1980, when lake stage fell below 11 ft, creating favorable habitat for colonization by seeds and fragments over nearly the entire littoral landscape.

When lake stage is low there also is an increased probability of fire occurring in the littoral zone, either due to natural causes (e.g., lightening strikes) or in controlled burn programs. Fires have documented benefits to the littoral vegetation mosaic. Fires burn away accumulated thatch in dense stands of emergent macrophytes, opening up the habitat to wildlife, and they also burn away much of the above-ground biomass of torpedograss monocultures, which allows for more effective control of this exotic with herbicide (Hanlon and Langeland 2000). Fires also allow buried seeds to germinate from the exposed sediments, providing the potential for species to re-colonize the habitat (Williges and Harris 1995).

Several years of high lake stage in the late 1990s are considered responsible for changes that have occurred in the dominance of native plant species in the interior littoral zone. From 1994 to 2000, lake stage exceeded 17 ft on four occasions and never fell substantially below 13 ft. These conditions may have favored development of dense stands of water lily in a west-central littoral region called "Moonshine Bay" where there previously was only spike rush and bladderwort. The dense lily communities may have degraded this habitat for fish and wildlife use due to a thick accumulation of dead leaf material and coarse organic detritus, which occupies up to 80% of the water column depth at some sites (SFWMD staff, personal observation).

Prediction - Because the lake stage regime expected under CERP more closely mimics that which occurred in the early 1970s, it is expected to favor the type of littoral vegetation mosaic that occurred at that time. However, the new stage regime is likely to include periods of low lake stage, which will have both positive effects (drying and oxidation of accumulated organic debris) and negative impacts (increased spread of exotics). An aggressive program to control the spread of torpedograss is under development, and along with the ongoing Melaleuca eradication program, may be a critical long-term measure to complement the modified hydroperiod that is established by CERP.

Hypothesis 2 - Excessive inputs of phosphorus from the lake's pelagic zone have promoted the spread of cattail in certain littoral areas and may have contributed to the expansion of water lily.

The pelagic zone of Lake Okeechobee has total phosphorus concentrations that average over 100 ppb (James et al. 1995), while concentrations in the interior littoral zone are typically between 10 and 15 ppb (Havens et al. 1997, Hwang et al. 1998). At high lake stage, currents transport phosphorus-rich water from mid-lake towards the pelagic-littoral interface (Maceina 1993, Havens 1997) and into the littoral zone proper. This phenomenon recently has been documented by the District's lake hydrodynamic model and by evaluation of water quality data during recent years when lake stage has been high. Studies of periphyton communities in the littoral zone indicate that there have been nutrient impacts similar to those observed in the Everglades (McCormick et al. 1996).

Aerial photographs and early maps (Pesnell and Brown 1973) of the littoral zone indicate that in the 1970s there was little or no cattail in the area of Moonshine Bay. In general, the area was characterized by a near-monocluture of spikerush. Today there is dense cattail along the edges of all boat trails leading from open water into Moonshine Bay from the north and west. There also is a dense "wall" of cattail along nearly the entire eastern edge of the littoral zone, where the plant community is in direct contact with pelagic water (Richardson and Harris 1995). Stimulation of cattail growth by phosphorus enrichment and high water levels in Lake Okeechobee is consistent with results from experimental research carried out in the Everglades (Newman et al. 1996).

Prediction - Under CERP, it is anticipated that the duration and return frequency of high water events will be reduced, and phosphorus inputs to the lake also should decline as a result of components of CERP and the Lake Okeechobee Protection Program. Taken together these actions are expected to result in less phosphorus transport into the littoral zone, and a reduced rate of cattail expansion.

Hypothesis 3 - Prolonged periods of deep water, combined with damage from wind-driven waves, have dramatically reduced the spatial extent and biomass of near-shore bulrush stands and submerged aquatic vegetation.

Recent estimates indicate that the spatial extent of bulrush has been reduced by 50% from its recorded maximum in the early 1970s (Florida DEP, unpublished data). Two factors may interactively have contributed to this decline. First, long periods of deep standing water may have resulted in conditions where only a small percentage of the plant's photosynthetic tissues were above water (Hanlon 2000). Under those circumstances, bulrush has been documented to draw on its underground rhizomes as an energy reserve, until eventually the plants have insufficient energy for net growth and survival (van der Valk 1994).

In a similar manner, high water had resulted in a dramatic decline in the spatial extent of submerged aquatic vegetation by 1999, following several years of high lake stage. High water levels have two related effects on underwater irradiance, and in turn, on the rate of growth and survival of submerged plants. First, when lake stage is high, light reaches the bottom only in a limited area close to the lake shore, where depths are shallow. This limits the lake-ward extent of submerged plant habitat. Second, under high stage conditions, there is increased transport of sediment-laden water from the mid-lake area (where these sediments are resuspended by wind) to the near-shore area that supports submerged plants (Maceina 1993, Havens 1997). When combined with a deeper water column, the increased turbidity results in little or no light reaching the lake bottom. Research has shown that submerged plant biomass in Lake Okeechobee is negatively correlated with water depth (Hopson and Zimba 1993) and that the highest submerged plant biomass occurs when stage is very low (Phlips et al. 1993).

Once submerged plants are lost, a positive feedback maintains the turbid condition. Without plants to stabilize sediments, there is increased sediment resuspension and no competition with phytoplankton for nutrients. Resuspended sediments and algal blooms result in higher turbidity, which prevents plant recovery. This cycle is very difficult to break once it is established (Scheffer 1989). Only dramatic actions, such as a considerable lowering of stage, allow plants to re-colonize the site. Once this occurs, however, the plants can establish a different feedback loop that maintains clear water (the plants support sediments and they also remove nutrients from the water so that algal blooms do not occur).

During summer 2000, there was a switch from turbid conditions to clear water conditions in much of the lake's near-shore area. This coincided with a submerged plant recovery following a SFWMD "managed recession" operation that removed ~1 ft of water from the lake, after which an additional 2 ft of water left the system by evapotranspiration and water supply deliveries. The lake reached a stage of below 12 ft and remained below 13 ft for >5 months (to date).

Prediction - The goals of CERP include both a lowering of average water levels in the lake and a reduced frequency of extreme high water levels (when damaging wave effects occur). Under those conditions, the distribution and abundance of bulrush and submerged plants are expected to increase.

Hypothesis 4 - High water levels have eroded the eastern lakeward edge of the littoral zone and resulted in the accumulation of a dense organic "berm" of dead plant material and lake sediment at the pelagic-littoral interface.

According to biologists who have worked on the lake since the 1960s, these organic berms are a common feature of the impounded system. The recent berm, however, is considered to be the most large-scale and permanent one ever to have occurred.

In some areas the berm is over 1 m tall, greater than 10 m wide, and it has established a community of woody vegetation including small willow trees. Scientists at the Florida Fish and Wildlife Conservation Commission have expressed concern that this organic berm is ecologically harmful because: (1) it may prevent normal water exchange between the littoral zone and marsh, in particular, it may block the egress of water from the marsh after periods of heavy rainfall over that area; (2) it may block normal migration routes for fish; and (3) it may act as a "break-wall" that does not gradually attenuate waves in the manner that an edge of vegetation would, and this causes erosion of sediments and any submerged plants that might develop at its lake-ward edge.

District staff have documented that the lake-ward edge of the littoral zone and the berm are highly dynamic, forming and eroding in much the same manner that a sandy beach is eroded and re-deposited elsewhere by strong surf. In the case of the lake, however, the erosion is of the littoral plant community itself. Hanlon (2000) documented by comparison of historic GIS vegetation maps that the lake-ward edge of the northwest littoral zone was eroded by up to 300 m between 1996 and 1999. During a period of particularly high lake levels (near 18 ft) in fall-winter 1998, staff documented recession of the littoral edge of up to 10 m in just 90 days. Output from the District's lake hydrodynamic model indicates that under high stage conditions, and in the absence of dense bulrush stands to attenuate wave energy, there are strong long-shore currents that could scour sediments and submerged plants, and erode the lakeshore along much of the western edge.

Prediction - Under the lower lake stage schedule of CERP, it is predicted that littoral shoreline erosion and berm formation should be substantially reduced. It may be necessary, however, to carry out a project to remove the organic material that has accumulated during high water periods pre-CERP implementation.

SNAIL KITES, WADING BIRDS, AND WATERFOWL

Snail Kites

The littoral zone of Lake Okeechobee is designated as one of the critical habitats (Federal Register 42 [155]:40685-40688) for the Everglades Snail Kite, a federally-endangered species. Snail Kites use the littoral zone as a habitat for nesting and foraging; other habitats for this bird include Everglades National Park and the Everglades Water Conservation Areas, the Big Cypress basin and lakes & wetlands located to the north and east of Lake Okeechobee. Kites are known to migrate extensively across the south Florida landscape (Bennetts and Kitchens 1997), and as such, cannot be effectively managed in a site-specific context.

The availability of multiple wetland habitats is considered to be critical for kites and is the foundation of the "meta-habitat hypothesis" proposed by Bennetts and Kitchens (1997). In this hypothesis, the risk to the regional population is minimized by the ability of kites to move to different habitats within the regional network as the quality of localized habitats fluctuates. For this to be effective, it is important that conditions in the habitats not be degraded to the extent that they are no longer usable during a time when Snail Kites require their use. For example, when a regional drought occurs, the littoral zone of Lake Okeechobee may represent the only large wetland system with suitable foraging and nesting conditions. Hence the lake should not be degraded to the extent that it loses its apple snail populations or suitable foraging (e.g., spike rush slough areas) and nesting (e.g., willow) habitat.

Hypotheses and Predictions:

Hypothesis 1 - Snail kite foraging habitat in the littoral zone is degraded when dense cattail or torpedograss replaces relatively open spikerush habitat.

Bennetts and Kitchens (1997) noted that the quality of habitat for kites is adversely influenced both by certain changes in water quality and the expansion of exotic plants. In each case, the key factor is replacement of relatively open foraging habitat with habitat dominated by dense vegetation. They note that in the Everglades, nutrient enrichment favors dominance of cattail, and that this could impact kites, which require relatively open water areas for foraging because they must detect their prey visually (Sykes 1987, Bennetts et al. 1988). Likewise, dense stands of torpedograss cannot support animal prey due to low dissolved oxygen, and do not permit effective foraging by visual predators since the vegetation typically hides the water column. The same probably holds true where spikerush develops dense growth of floating-leaf plants such as water lily.

Hypothesis 2 - Snail kite foraging habitat in the littoral zone is degraded when the abundance of apple snails is substantially reduced.

Apple snails are the major food item of the Snail Kite. Therefore, if environmental conditions (e.g., a prolonged dry down coincident with the season of egg laying or a lake stage reversal after eggs are laid) result in a major "crash" of apple snails, the habitat will be unfavorable for kites until the food resource recovers.

Hypothesis 3 - Snail kite nesting habitat in the littoral zone is degraded when the spatial extent of sawgrass and willow is reduced.

According to Bennetts and Kitchens (1987), Snail Kites nest primarily in willow and other woody vegetation types. Hence the spatial extent of these plant types will directly affect whether or not the littoral zone represents viable habitat for kite nesting. Two factors contributing to loss of this habitat in Lake Okeechobee include prolonged periods of deep water and the expansion of torpedograss.

Hypothesis 4 - The Lake Okeechobee littoral zone is essential habitat for the Florida population of Snail kites during periods of extensive drought.

This hypothesis follows directly from the meta-habitat hypothesis of Bennetts and Kitchens (1987) and their findings regarding use of the lake by kites during years when other regional habitats are dry due to drought conditions.

Wading Birds

Lake Okeechobee has long been recognized as an important nesting location for wading birds. Anecdotal records from National Audubon Society game wardens during the 1940s documented large concentrations of nesting birds at the Lake (David 1994). More quantitative surveys during the period 1957-1978, showed that there were typically about 4700 nests per year, with peaks in nesting effort in 1972 and 1974. During those years, there were approximately 10,000 wading bird nests on the Lake, mostly of White Ibis at the

King's Bar colony, near the mouth of the Kissimmee River. It was considered to be one of the largest and most important wading bird colonies in central Florida. After an increase in the Lake regulation schedule in 1978, wading bird nesting effort declined and stabilized at about 2000 nests (David 1994), at least up until 1992, when it was last surveyed (Smith and Collopy 1995).

Hypotheses and Predictions:

The primary hypotheses to explain the general decline in nesting effort after 1978 as well as individual years of low nesting effort, is that increased Lake water levels water decreased the quality or quantity of habitat. The following hypotheses describe in more detail how water levels affect wading bird nesting on the Lake.

Hypothesis 1 – Seasonal lake stage recessions benefit wading bird populations.

In the Everglades, fish populations are 2-4 times higher in marshes that are inundated than in areas that dry out regularly (Loftus and Eklund 1994). However, as water levels fall during the dry season, small depressions in the marsh surface act as places where fish become concentrated. Fish concentrations increase by a factor of from 20 to 150 in the Everglades and Big Cypress National Preserve (Carter et al. 1973, Loftus and Eklund 1994, Howard et al. 1995). These patches of concentrated prey are typically shallow with no vegetation. Thus, individual fish become more vulnerable to capture and wading bird feeding success is increased (Kushlan 1976). Although these high-density food patches may be scattered in the landscape, wading birds have adaptations such as white plumage and social foraging that allow them to minimize their search time (Kushlan 1981, Erwin 1983). Thus, at the landscape scale, wading birds are able to exploit small patches of highly available prey and large foraging aggregations indicate good feeding conditions. Species such as Wood Storks, White Ibises, and Snowy Egrets appear to be more dependent, than are other wading bird species, on good feeding conditions to have years of high reproductive output (Gawlik in review). Hydrologic patterns that produce the maximum number of these patches with high prey availability (i.e., high lake stages at the end of the wet season and low lake stages at the end of the dry season) tend to produce good wading bird nesting effort (Smith and Collopy 1995).

Prediction – Because the lake stage regime expected under CERP more closely mimics that which occurred in the early 1970s, the frequency at which the marsh dries should increase and favor increased reproduction for Snowy Egrets and White Ibises.

Hypothesis 2 – Large stands of willow are beneficial to wading bird nesting.

In Everglades and Lake Okeechobee, most wading bird colonies occur in willow trees (Zaffke 1984, Frederick and Spalding 1994). Willow is thought to be the preferred nesting substrate because it can tolerate longer hydroperiods than most tree species and therefore is usually in deeper water than other species. Wading birds seem to prefer to nest in deep water because it increases the likelihood that their nests will remain surrounded by water throughout the nesting season. Such conditions reduce the probability of their nests being predated by raccoons (Frederick and Spalding 1994). Despite the tolerance for long hydroperiods, even willow can not withstand prolonged periods of deep water. It Lake Okeechobee, high water has had negative impacts on willow stands in certain lower elevation regions of the littoral zone. Therefore it is possible that the preferred nesting sites for wading birds could be a factor limiting population sizes.

Prediction - The goals of CERP include both a lowering of average water levels in the lake and a reduced frequency of extreme high water levels. If this water management regime stops the loss of willow or increases the amount of willow, then nesting habitat quality for wading birds will be remain stable or increase.

Waterfowl

Lake Okeechobee hosts more than 100,000 migratory waterfowl in many years (ongoing mid-winter surveys of FFWCC), although the numbers vary greatly between years (Chamberlain 1960, Bellrose 1976). Migratory behavior allows these birds to exploit seasonally rich and variable habitats in the regional landscape (Weller 1969).

Most numerous in the mid-winter surveys are lesser scaup (*Aythya affinis*), which inhabit the pelagic zone of the Lake and whose numbers range from 50,000 to 300,000. Scaup dive for their food in water up to several meters deep (Bellrose 1976) and their diet on Lake Okeechobee is unknown. The second most abundant species has been the ring-necked duck (*Aythya collaris*), Florida's most harvested duck. Close to half of all Ring-necked Ducks wintering in the Atlantic Flyway formerly used Lake Okeechobee (Bellrose 1976), but the spread of *Hydrilla*, a highly preferred food, apparently has spread ringnecks around Florida (Johnson and Montalbano 1984, Jeske 1985, Esler 1990). Ring-necked duck numbers on Lake Okeechobee fell from an average of 5,807 from 1991-1995, to an average of 489 from 1996-2000. This 92% decline was apparently due to the loss of submerged plants on the lake during this period of high water, combined with the availability of alternate habitat locations.

Fisheating Bay is surveyed independently of the rest of the lake for waterfowl, and Ring-necked Duck numbers in that location declined from a 5-year average of 5,190 in 1991-1995 to 2,798 in 1996-2000 (data were missing in 1999), a 46% change. During the same period, American coots (*Fulica americana*) declined by 77% on the larger part of the lake, from a 5-year average of 15,303 between 1991-1995, to an average of 3,508 from 1996-2000. In Fisheating Bay, coots increased from 13,805 in 1991-1995 to 19,546 in 1996-2000, although lake-wide, there still is an overall downward trend (21%). Like ring-necked ducks, coots feed on submerged vegetation (Bellrose1976, Montalbano et al. 1979, Esler 1990) and their declining numbers are likely correlated with declining acres of those plants in the lake. The higher numbers of birds in Fisheating Bay may be due to the few surviving areas of H*ydrilla* and other submerged plants (e.g., *Vallisineria*) that remained.

Dabbling ducks prefer marshy areas and are more difficult to accurately survey than the diving ducks discussed above. An average of 338 dabbling ducks was detected on the lake between 1991-2000 (mid-winter inventory, FFWCC). Considering that there are a potential 90,000 acres of habitat for these birds, this number is extremely low and reflects impaired habitat conditions. For comparison, Johnson and Montalbano (1984) detected an average of 11,886 dabbling ducks just in Fisheating Bay during a study in 1981-82. High water levels impede dabbling ducks from using the lake because they rarely dive to feed and prefer water less than 1 ft deep (White and James 1978, Johnson and Montalbano 1984, Gray 1993). Chronic high water levels, or more specifically, lack of a spring dry down, prevent the growth of moist soil vegetation that is important in producing seeds that many ducks prefer (Goodwin 1979, Fredrickson and Taylor 1982).

Hypotheses and Predictions

Hypothesis 1 - Numbers of ring-necked Ducks and Coots decline when submerged vegetation is lost due to high water levels.

Waterfowl numbers in any location in a given year are related to size of the fall flight, weather and habitat conditions north of Florida, and habitat conditions in the Florida peninsula. Lake Okeechobee is large enough that waterfowl will find it and if suitable habitat is available, they will use it in some numbers, related to quality of the habitat. Quality habitat in this case is submerged vegetation.

Hypothesis 2 - Numbers of dabbling ducks (genus Anas and Aix) are strongly correlated with areas of water less than 6 inches deep, and presence of a spring recession.

Dabbling ducks are expected to respond positively to quality habitat (Goodwin 1979). A spring recession produces somewhat predictable vegetation responses (Richardson et al. 1995) and shallow water for foraging.

UNCERTAINTIES / RESEARCH QUESTIONS

WATER QUALITY

Internal vs. external loads - Despite a considerable amount of research dealing with sediment-water phosphorus dynamics and internal loading in Lake Okeechobee, there is uncertainty regarding the timing of lake response to external load reductions. Particularly important factors that could influence the response include: (1) the rate of phosphorus deposition by particle sedimentation; (2) the depth of the "active sediment layer" that interacts with the overlying water column; (3) the rate of burial of sediment material into deep storage where it no longer plays a role in the lake's phosphorus cycle; and (4) removal by mineral formation. In the recent Lake Okeechobee TMDL (total maximum daily load) process, there were differing viewpoints among experts regarding these factors, indicating an area of research need.

Lake stage vs. phosphorus - Although there is good evidence that lake stage affects water column total phosphorus concentrations in both the pelagic and littoral regions of Lake Okeechobee, some of the key mechanisms still have not been quantified to the extent that they can be incorporated into predictive models. Effects of stage on water currents and horizontal materials transport now can be effectively modeled using the lake hydrodynamic model, as can transport of nutrients into the littoral zone. Effects of plants and attached algae on water column phosphorus concentrations, however, presently cannot be predicted, despite the fact that they may be of considerable importance under moderate and low stage conditions. Efforts are underway to quantify how submerged plant communities respond to changes in underwater irradiance. This information, along with results of studies to quantify effects of plants on nutrients and turbidity, is needed for development of a landscape-type model of near-shore water quality and plant distribution. Similar information needs to be collected and incorporated into the models for periphyton and benthic algae, since these components of the community have the potential to attain a high biomass.

Phosphorus assimilative capacity - Although results from other shallow lakes indicate that biological recovery from cultural eutrophication in Lake Okeechobee might result in a greater lake assimilative capacity, the magnitude of these effects is uncertain. In order to periodically re-evaluate (and perhaps modify) the lake phosphorus loading target, there is a need to quantify some of the key relationships and incorporate them into predictive models. This will require an evaluation of phosphorus sources and sinks associated with algal settling, cyanobacteria vertical migration, oligochaete feeding and bioturbation, and aquatic insect emergence. Long-term assessment of the magnitude of these processes needs to accompany model development and validation. There also is a need to determine whether recent increases in sediment dissolved phosphorus reflects a loss of assimilative capacity or increased diagenesis.

Phosphorus and algal blooms - The relationship between excess phosphorus concentrations and algal bloom development is well established in the general limnological literature and in the literature dealing with Lake Okeechobee. That blooms will decline if in-lake phosphorus concentrations are substantially reduced is quite certain. One area of uncertainty that does exist, however, is the extent to which algal blooms in themselves might make the lake resilient to recovery. The taxa of cyanobacteria that occur in Lake Okeechobee are known to occur in a "dormant" state at the sediment surface, and during formation of blooms they may be responsible for a large transport of phosphorus upward from the sediments to the water column (Barbiero and Welch 1992, Havens et al. 1998). Quantifying the magnitude of this process would increase the certainty of predictions of lake recovery from excessive phosphorus loading.

In regard to the effects of blooms, we also lack information regarding quantitative linkages between bloom occurrence / magnitude and important societal values, such as drinking water quality (taste, odor, trihalomethanes), recreational use of the water resource, and fishing.

Since the lake is highly visible as a public natural resource and is the headwaters for the Everglades, we believe that it is important to quantify these relationships so that performance measures can be developed for these potential benefits of the project.

FISH AND AQUATIC FAUNA

Macro-invertebrates and zooplankton

Based on responses of other eutrophic lakes, it can be predicted with a relatively high degree of certainty that if the pelagic sediments develop a less enriched character due to reduced phosphorus inputs, the abundance of pollution-tolerant oligochaetes will decline and other less tolerant species will return. The timing and magnitude of recovery is uncertain, but can be determined with long-term monitoring.

Likewise there is a relatively high certainty that restoration of near-shore bulrush and submerged vegetation communities will result in an increased abundance of the macro-invertebrate taxa that use that habitat.

The uncertainty regarding responses of littoral macro-invertebrates to CERP is greater, reflecting a general lack of information about how invertebrate communities are distributed across that landscape. There has been a considerable amount of research in south Florida dealing with apple snails, and therefore there is a greater certainty regarding the responses of those particular animals.

Factors affecting zooplankton biomass and composition are relatively well studied, and long-term monitoring should suffice to document that timing and magnitude of any major changes in that community. It will be particularly important to keep track of abundances of cladocerans (including the exotic *Daphnia lumholtzii*) since these animals are the most effective grazers of phytoplankton and the optimal food resources of zooplanktivorous fish.

Open-water and littoral fish communities

The diet habits of fish in the pelagic region have been well documented, and the factors related to their distribution and abundance were quantified in a comprehensive study. Therefore there is relatively little uncertainty regarding responses of these fish to CERP. The timing and magnitude can be determined from the long-term monitoring program.

There also is relatively little uncertainty that near-shore fish habitat will be enhanced if CERP results in a reduced frequency of damaging high water levels. Benefits to the fish community are relatively predictable, and can be evaluated with long-term monitoring.

There is greater uncertainty regarding littoral fish because only a few of the region's major plant community types have been sampled for these animals. To accurately predict how CERP will affect the lake's fishery, which depends heavily on the littoral zone, better information is needed regarding use of particular native and exotic plant assemblages.

Furthermore, only preliminary diet studies have been conducted in the littoral zone (only in Moonshine Bay), and a more in depth study of feeding habits is needed to predict how littoral fish will respond to changes that CERP might cause at lower trophic levels.

Other animals

One area of great uncertainty regarding the lake ecosystem is in regard to reptiles, amphibians, and other aquatic animals that utilize the littoral zone as foraging and/or nesting habitat. Only limited survey studies have been performed. These need to be supplemented with more detailed studies of the relationship between vegetation, hydroperiod and aquatic animal occurrence, as well as studies to determine the role of the animals in the littoral food web. Preliminary data indicate that some of these animals (e.g., certain frogs) may be food resources for economically important species such as the largemouth bass.

NATIVE VEGEGATION MOSAIC

Littoral zone and hydroperiod - The uncertainty associated with this general relationship is quite low, because the linkage has been established experimentally in Lake Okeechobee (Steinman et al. 1997, 2000b) and on other systems as well as by multivariate models and GIS in Lake Okeechobee. One key area of uncertainty that now is under investigation is identification of a hydroperiod range that is least favorable for expansion of torpedograss into native plant-dominated habitat. In addition, the link between water lily expansion and long hydroperiod is circumstantial, since this species is known to respond both to hydroperiod and increased phosphorus inputs (McCormick et al. 1999). Because dense water lily degrades spikerush habitat, this is an area of uncertainty that merits further consideration.

Littoral zone and phosphorus - The uncertainty associated with this relationship also is low, again because we can draw inferences from research conducted in the nearby Florida Everglades. However, while nutrient effects on primary producers (plants and periphyton) are well established, little is known about how nutrients affect higher trophic levels in the littoral food web. It may be particularly important to quantify experimentally how increased or decreased nutrient-induced changes in plants and periphyton affect the productivity of certain key animal species such as apple snails (prey for snail kites) or small forage fish (prey for sport fish taxa and wading birds).

Bulrush & submerged vegetation and high water - It is clear that prolonged or extreme high water has damaging effects on these components of the lake's plant community. However, the causal mechanisms are only generally understood. Given the critical role that these plants play in terms of water quality and fish/wildlife habitat, research is needed to identify the "lake stage window" (yearly range of water levels) that is required to support a healthy community. There also is a need to determine conditions necessary to allow recovery of the community when unfavorable conditions do occur (e.g., two successive years of high rainfall and high stage). District staff also intends to modify the existing lake water quality model so that it can predict, with a fine spatial scale, the extent of submerged vegetation that might occur under different lake stage management scenarios. That tool will be useful to the RECOVER process, because it will allow plan evaluations by the RET to include not only hydrologic and water chemistry predictions, but also predictions regarding responses of one of the lake's key biological communities.

Shoreline erosion and berm formation - Erosion of the western shoreline has been linked with high lake stage and wind-driven waves, and long-term monitoring will continue in order to keep track of any further shoreline degradation. The ecological impacts of the organic berm have not been documented, but this may not be a particularly high research priority if plans call for its removal.

SNAIL KITES, WADING BIRDSS, AND WATER FOWL

Prey Availability and water level recession - The uncertainty associated with this general relationship is fairly low. One of the first studies of wading birds in south Florida (Kahl 1964) reported this general relationship and subsequent studies, both observational (Kushlan 1976) and experimental (Gawlik in review), have substantiated it. The main area of uncertainty is in how different species will respond and why the level of response is still quite variable among years.

Nesting substrate as a population constraint - The uncertainty associated with this relationship is high. It is not clear whether the lack of willow as a nesting substrate is limiting the population size of any species of wading birds on the Lake. More importantly, there is no information on the consequences of birds using less preferred nesting substrate. It is assumed that the use of less preferred nest sites will reduce nesting success, but if that assumption is invalid then there will be little effect on the overall population size.

HYDROLOGIC PERFORMANCE MEASURES

A key feature of the Lake Okeechobee conceptual model is the high degree of interconnectedness; any given stressor may impact ecological attributes directly, or impact those same attributes indirectly, by exacerbating the effects of other stressors. Two stressors that display particularly strong effects (direct and indirect) on the attributes are high and low water levels. Taken together, they have the potential to affect the rate of lake eutrophication, the spatial extent and overall health of submerged and emergent plant communities, fisheries, birds, other wildlife, and the quality of water taken from the lake from human uses.

Water inputs and lake levels also are the variables most directly impacted by proposed components of the CERP. Therefore a suite of hydrologic performance measures was developed based on our understanding of the ecosystem and used by the Restudy Alternative Evaluation Team (AET) to evaluate potential impacts of various planning alternatives on lake ecosystem health. The Regional Evaluation Team (RET) of CERP will use these same performance measures during implementation of the program. Five priority performance measures were calculated, weighted and summed using the River of Grass Evaluation Model (ROGEM) for Lake Okeechobee. The Lake Okeechobee ROGEM is comprised of metrics (Suitability Index Variables, or SIVs) that describe the fluctuation and timing of lake stages. The model assumes that restoration of a more natural (within the constraints of the dike system) hydroperiod would result in positive biotic responses of the lake community.

SIVs in the ROGEM range from 0 (worst score) to 1.0 (best score). Relationships between hydrologic attributes and SIVs in this model are not linear. Instead, they reflect expert opinion that the degree of ecosystem stress is exacerbated by an increasing occurrence of undesirable events. This gives rise to a curvilinear relationship between hydrologic attributes and their SIVs. I.e., once the ecosystem has been stressed, further stresses bring about more dramatic responses than were evidenced following the single event. At a certain point (considered here to be 4 events or more per decade), the degree of stress is so severe that the system cannot recover its ecological and societal functions. The five SIVs used in the model are as follows.

A. An <u>extreme low lake stage</u> (<11 ft) performance measure (**SIV_{MINX}**) indicates the frequency of events that: (1) result in a loss of over 95% of the littoral zone as habitat for aquatic biota; and (2) promote expansion of exotic plants. The goal is to have a minimal number of these events. A score is calculated as follows:
- Stage never falls below 11 ft = 1.0
- Stage falls below 11 ft on 1 occasion per 10 yrs = 0.9
- Stage falls below 11 ft on 2 occasions per 10 yrs = 0.7
- Stage falls below 11 ft on 3 occasions per 10 yrs = 0.4
- Stage falls below 11 ft on 4 or more occasions per 10 yrs = 0

B. A <u>moderate low lake stage</u> (<12 ft) performance measure (**SIV_{MINM}**) indicates the frequency of prolonged (>12 continuous month) events that substantially reduce the littoral area available as wildlife habitat, and promote exotic plant expansion. The goal is to have a minimal number of these events. A score is calculated as follows:
- Stage never falls below the 12 ft / 12 month criterion = 1.0
- Stage falls below the 12 ft / 12 month criterion on 1 occasion per 10 yrs = 0.9
- Stage falls below the 12 ft / 12 month criterion on 2 occasions per 10 yrs = 0.7
- Stage falls below the 12 ft / 12 month criterion on 3 occasions per 10 yrs = 0.4
- Stage falls below the 12 ft / 12 month criterion on $\geq$ occasions per 10 yrs= 0

C. An <u>extreme high lake stage</u> (>17 ft) performance measure (**SIV_{MAXX}**) indicates the frequency of events that: result in wind and wave damage to the shoreline plant communities that provide critical habitat for recreational fish and other wildlife; and transport phosphorus-laden pelagic water into pristine interior regions of the littoral zone. The goal is to have a minimal number of these events. A score is calculated as follows:
- Stage never exceeds 17 ft = 1.0
- Stage exceeds 17 ft on 1 occasion per 10 yrs = 0.9
- Stage exceeds 17 ft on 2 occasions per 10 yrs = 0.7
- Stage exceeds 17 ft on 3 occasions per 10 yrs = 0.4
- Stage exceeds 17 ft on $\geq$ 4 occasions per 10 yrs = 0

D. A moderate high lake stage (>15 ft) performance measure (**SIV_{MAXM}**) indicates the frequency of prolonged (>12 continuous months) events. These events limit light penetration to the lake bottom, resulting in a loss of the benthic plants and algae that stabilize sediments and provide habitat for invertebrates and fish; and promote greater circulation of phosphorus-rich turbid waters from mid-lake to less eutrophic near-littoral regions, where phosphorus inputs stimulate algal blooms. The goal is to have a minimal number of these events. A score is calculated as follows:

- Stage never exceeds the 15 ft / 12 month criterion = 1.0
- Stage exceeds the 15 ft / 12 month criterion on 1 occasion per 10 yrs = 0.9
- Stage exceeds the 15 ft / 12 month criterion on 2 occasions per 10 yrs = 0.7
- Stage exceeds the 15 ft / 12 month criterion on 3 occasions per 10 yrs = 0.4
- Stage exceeds the 15 ft / 12 month criterion on $\geq$ 4 occasions per 10 yrs = 0

E. A spring recession performance measure (**SIV_{VAR}**) indicates the number of years during which January to May lake levels decline from near 15 ft to 12 ft, without any reversals greater than 0.5 ft. These conditions are favorable to nesting birds and other wildlife in the marsh. They also allow for re-invigoration of willow stands, and permit fires to burn away cattail thatch. The goal is to have a substantial number of events. A score is calculated as follows:

- Stage recession between January and March from >14 ft to <13 ft NGVD, with no reversal greater than 0.5 ft NGVD, occurring every yr = 1.0
- Stage recession occurring only in 9 out of 10 yrs = 0.9
- Stage recession occurring only in 8 out of 10 yrs = 0.7
- Stage recession occurring only in 7 out of 10 yrs = 0.4
- Stage recession occurring only in 6 or fewer out of 10 yrs = 0

SIV Priority Weights

The five SIVs address important aspects of how water level and its seasonal variation affects the ecological attributes of Lake Okeechobee. However, the SIVs are not considered of equal importance in regard to indicating an absolute level of stress (or benefit). A weighting scheme was developed, on the basis of best professional judgement, to reflect the relative importance of each SIV as an index of lake ecosystem health. For simplicity, a weighting scale of 1 to 5 (1 being least important, and 5 being most important) was used.

The SIVs associated with the >17 ft and >15 ft / 12 month criteria were given priority weights of 5. Extreme or prolonged high water levels have been documented to affect numerous ecosystem attributes, including littoral plant and periphyton communities, benthic plants and periphyton, fisheries habitat, and water quality (including turbidity, phosphorus, and algal blooming). These effects are well documented by scientific research (Sheng and Lee 1991, Havens 1997, Steinman et al. 1997).

The SIVs associated with the <11 ft and <12 ft / 12 month criteria were given priority weights of 4. Extreme or prolonged low lake stages also may cause harm to the ecosystem, but the impacts are less documented, and are not considered as serious on a lake-wide basis. I.e., the effects primarily are restricted to the littoral zone proper, and negative impacts (e.g., loss of fisheries habitat) may in part be compensated for by enhanced growth of submerged plants in the southern near-shore pelagic region.

The SIV for spring lake level recession describes a seasonally-variable hydro-pattern that is considered by experts to benefit a variety of littoral zone values, including wading birds and certain native plant communities (Smith et al. 1995). It is the only SIV that relates to seasonal variation in lake levels. Therefore it is given a weight of 5.

A Community Suitability Index (CSI) integrates the scores of five hydrologic SIVs and their respective weighting factors, and has an overall range of 0 to 1.0:

$$CSI = (4*SIV_{MINX} + 4*SIV_{MINM} + 5*SIV_{MAXX} + 5*SIV_{MAXM} + 5*SIV_{VAR}) / 23$$

ECOLOGICAL PERFORMANCE MEASURES

To quantify the current status of Lake Okeechobee and its responses to implementation of CERP components, it will be necessary to develop and implement a comprehensive ecological monitoring program. This program should focus on a set of ecological performance measures, which are measures of ecosystem attributes that have quantifiable targets (restoration goals or expectations). A set of specific monitoring parameters will be associated with each performance measure that is included in the program. By adopting this approach, it should be possible to quantify the status of the ecosystem at various scales of resolution, at any point before, during, or after completion of the CERP. Assuming that the hydrologic performance measures used in the planning process reflect conditions that are beneficial to the ecosystem, the overall “scores” of ecological performance measures should increase as the project is completed. If ecological scores do not display expected trajectories during the project, this may serve as an indicator that some adaptive management needs to occur (i.e., changes in structural or operational aspects of the project).

The Lake Okeechobee Conceptual Model working group developed a set of performance measures, targets, and monitoring parameters associated with the four ecosystem attributes (lake water quality, fish & aquatic fauna, native vegetation mosaic, and snail kite, wading birds & waterfowl) in the conceptual model. The information is summarized in Table 1, and details regarding each performance measure are provided in the standard Performance Measure Documentation Sheets developed by the Adaptive Assessment Team (AAT) of CERP. The following text highlights important points that are not explicitly indicated in the tables. The information should be considered a starting point for development of the ecological monitoring program. Detailed planning will need to consider the spatial and temporal aspects of sampling that are required for each parameter, the degree to which recommended parameters already are being monitored by certain state and federal agencies, methods to evaluate uncertainty (both for measured values and targets), and standard procedures for data collection, evaluation, reporting, and archiving.

WATER QUALITY

A number of the water quality parameters relate to the degree of cultural eutrophication of the lake. Given the high degree of uncertainty about the lake's natural trophic state, the targets do not correspond with "restoration," but rather, the attainment of water quality conditions as good as observed in a period of record (1973-1999) when quantitative data were collected. During the early 1970s, when total phosphorus concentrations were near 40 ug/L and total nitrogen to phosphorus ratios were above 30:1, blooms of blue-green algae were rare, and transparency was higher, especially in the near-shore region. Other parameters relate to toxic materials (Class I and III parameters) that can affect both the lake ecosystem and drinking water quality.

It is important to note that all water quality targets listed in Table 1 represent lake-wide average conditions. Given that the lake is heterogeneous in regard to water quality, the final monitoring program should establish region-specific (littoral, near-shore, pelagic) performance measures and targets. For example, the lake-wide total phosphorus target is 40 ug/L, while appropriate regional targets are likely to be approximately 5 ug/L (interior littoral), 20 ug/L (near-shore), and 70 ug/L (central pelagic). Likewise, targets related to bloom-forming cyanobacteria might be zero for the interior littoral region, somewhat higher than the lake-wide average for the near-shore region, and close to zero for the central pelagic (light limited) region.

FISH AND AQUATIC FAUNA

In addition to performance measures related to fish *per se*, it is noteworthy that some of the measures related to aquatic fauna and native vegetation mosaic determine the quality of the littoral and near-shore habitat for fish foraging and spawning, and quality of the lake food web from the standpoint of supporting a productive fishery. Without this information it would be impossible to determine the cause of any unexpected fisheries declines during the CERP implementation, and this would seriously compromise adaptive management. As is the case for water quality, the fisheries performance measures should be expanded to specify targets for distinct lake regions.

NATIVE VEGETATION MOSAIC

Performance measures focus on the littoral and near-shore regions, where vascular plants occur in the lake. In the littoral region, the performance measures reflect a primary objective of reducing the spatial extent of exotic and nuisance plant species, and restoring lost native plant communities. In the near-shore region, the performance measures focus primarily on restoring submerged vegetation communities and bulrush stands, which were lost during recent years of high lake stage. Elimination of the near-shore berm also is included as a target.

SNAIL KITE, WADING BIRDS, AND WATER FOWL

Performance measures related to birds are problematic, because for some key species (including the Everglades Snail Kite), population dynamics are better evaluated on a system-wide basis, rather than for particular system components such as Lake Okeechobee. Snail kites migrate over much of the Florida peninsula (Bennett and Kitchens 1997), nesting in different areas as a function of habitat availability under different drought / flooding regimes. During some years the lake may provide habitat for a large number of kites and other birds, while in other years, numbers may be substantially reduced. Hence the overall performance of these attributes may best be determined by a system-wide program.

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Figure 1. Map of Lake Okeechobee and part of its surrounding watershed, showing conditions prior to construction of the C&SF Project (PAST), todays conditions (PRESENT), and conditions anticipated after completion of the CERP (FUTURE). The figures show the spatial extent of the lake's open water region, the magnitude of various inflows and outflows, and ranges of water levels under each condition.

Figure 2. The Lake Okeechobee Conceptual Model, as described in the text. Rectangles at the top of the model are **external drivers**, ovals are **ecological sressors**, diamonds are **ecosystem effects**, hexagons are ecological **attributes**, and parallelograms are **performance measures**, all as defined in the text. Arrows indicated links, with arrowheads pointing towards the item being affected.