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LAKE OKEECHOBEE CONCEPTUAL ECOLOGICAL MODEL

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Abstract: With a surface area of nearly 1,800 square kilometers, Lake Okeechobee is a prominent central feature of the South Florida aquatic ecosystem. The lake provides regional flood protection, supports a prized recreational fishery, provides habitat for migratory waterfowl and regional wading bird populations, and is a source of fresh water for irrigation, drinking, and restoration of downstream ecosystems. The main stressors on Lake Okeechobee are (1) large inputs of phosphorus from agricultural and other anthropogenic land uses in the watershed, (2) unnatural variation in water levels due to channelization of inflows and dike containment, and (3) rapid expansion of non-native plants. Ecological effects are complicated due to three distinct in-lake zones with different water chemistry, physical properties, and biota. A central pelagic zone has turbid, nutrient-rich water and phytoplankton dominance; a shallow south and western near-shore zone has submerged plant or phytoplankton dominance (at low vs. high water levels, respectively); and a western littoral zone is dominated by emergent wetland plants. Changes in water level influence the flow of nutrients between zones, thereby creating a synergistic effect between stressors. Under high water conditions, there is considerable advective transport of nutrients from the pelagic zone into the littoral zone. Under low water conditions, the littoral zone is cut off hydrologically and is a rainfall-driven oligotrophic wetland. Low water also facilitates drying and wildfires in the littoral zone, which in turn has an influence on expansion of non-native plants and recovery of native plants from buried seed banks. All of these factors influence fish, wading birds, and other animals, which depend on littoral and near-shore plant communities for nesting and foraging habitat. This paper describes our current knowledge of these complex processes, the lake's expected responses to ongoing and planned restoration programs, and key areas of uncertainty requiring future research.

Key Words: shallow lake, littoral zone, wetland, water level, nutrient loading, conceptual model

BACKGROUND

Lake Okeechobee is a large freshwater lake located at the center of South Florida's interconnected aquatic ecosystem. The lake is shallow (average depth less than 3 meters), originated about 6,000 years ago during oceanic recession, and under natural conditions probably was 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 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) (Steinman et al. 2002a). Construction of a dike around the lake in the early to mid-1900s reduced the size of the pelagic 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 the size of the natural one. The lake also has been impacted in recent decades by inputs of nutrients from agricultural activities in the northern part of its watershed (Flaig and Havens 1995, Havens et al. 1996a, Engstrom et al. 2005). The littoral zone has been invaded by 15 species of non-native plants, most notably *Melaleuca quinquenervia* ((Cav.) Blake) and torpedograss (*Panicum repens* Linnaeus), which have expanded over large areas, displacing native plants.

Despite these human impacts, and resulting ecosystem degradation, Lake Okeechobee continues to be a critical aquatic resource of South Florida, providing a wide array of ecosystem services. It is anticipated that hydrologic restoration projects carried out under a US

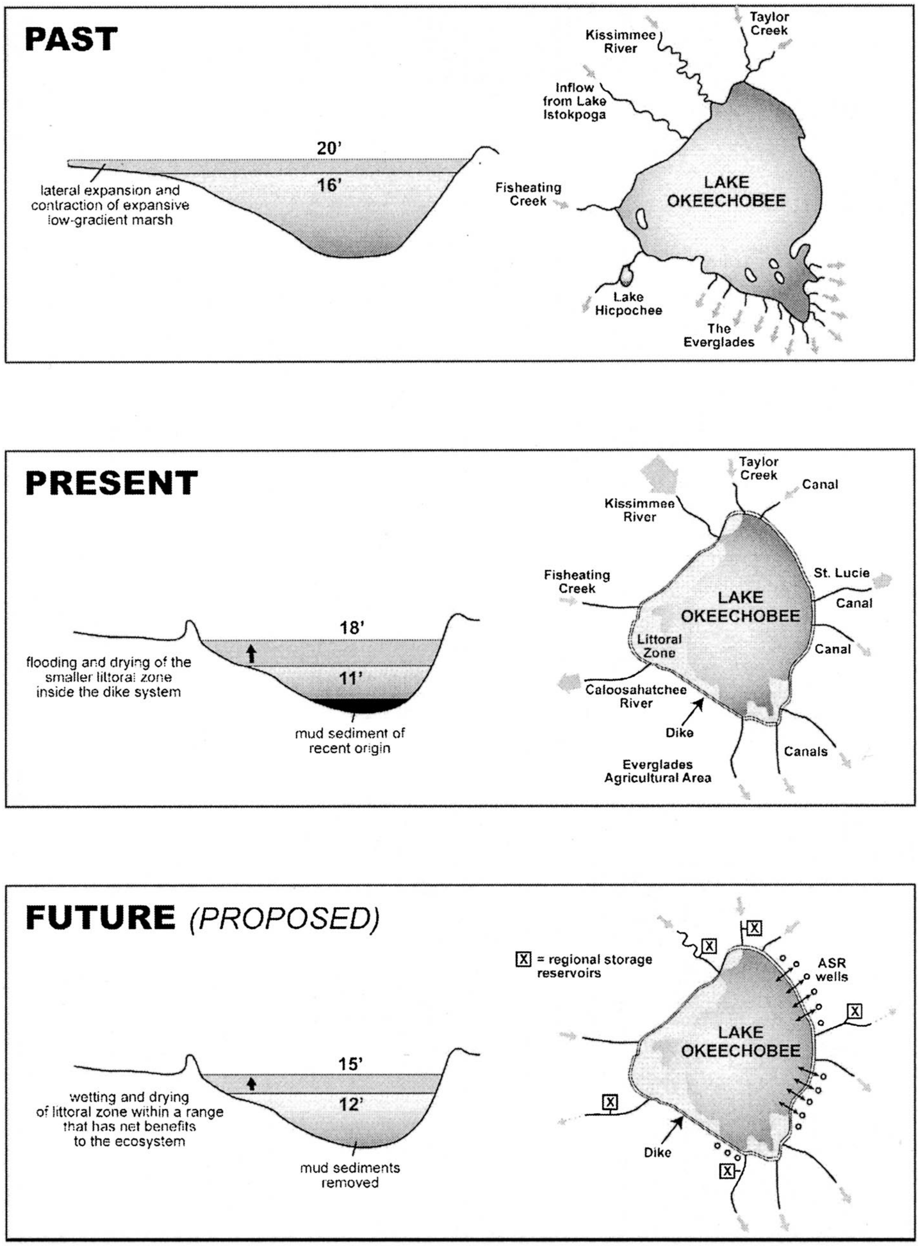

Figure 1. Map of Lake Okeechobee and part of its surrounding watershed, showing conditions prior to construction of the Central and Southern Florida (C&SF) Project (PAST), today's conditions (PRESENT), and conditions anticipated after completion of the CERP (FUTURE). The figures show the spatial extent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

$8 billion (1999 dollars) regional program called the Comprehensive Everglades Restoration Plan (CERP), along with other local and regional restoration efforts, will improve hydrologic conditions in the lake and substantially reduce nutrient loads (Figure 1). The conceptual ecological model for Lake Okeechobee described in this paper indicates how these changes in stressors are expected to affect attributes of the ecosystem that are of value to nature and society. Subsequent sections of this paper focus on external drivers (forcing variables), in-lake ecological stressors, attributes (ecological and societal values), and ecological processes that link stressor and attributes in this ecosystem.

EXTERNAL DRIVERS AND ECOLOGICAL STRESSORS

Seven in-lake stressors (Figure 2, ovals) that have strong impacts on the lake's natural and societal values

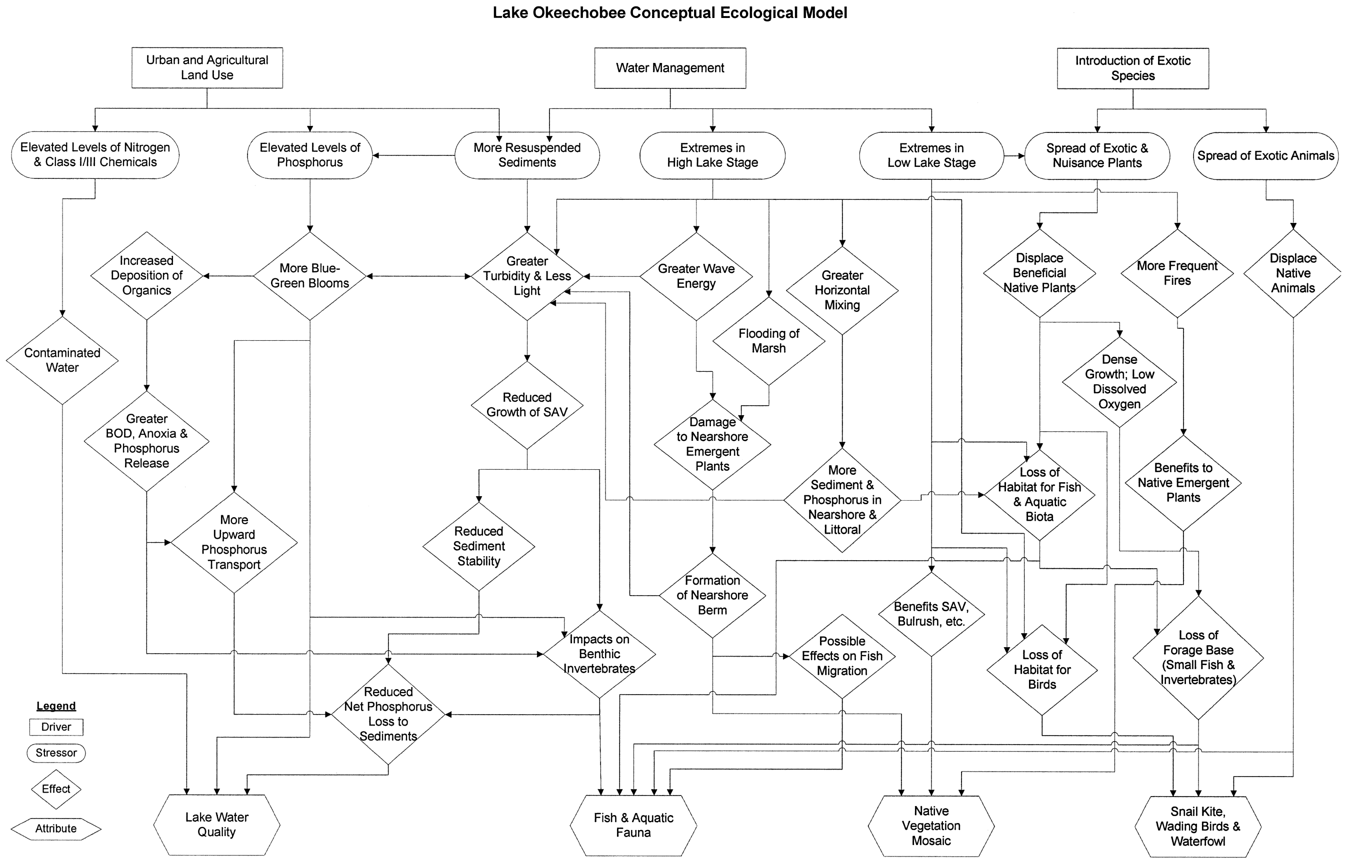

Figure 2. Lake Okeechobee Conceptual Ecological Model Diagram.

originate from five distinct external drivers or sources (Figure 2, rectangles). Elevated concentrations of nitrogen and various chemical contaminants are by-products of agriculture or other human activities in the watershed. For readers not familiar with US water quality standards, the terms Class I and III in Figure 2 refer to a long list of chemicals considered important for determining the suitability of a water body for drinking or fish/wildlife habitat, respectively. These contaminants may periodically affect certain regions of the lake near points of water entry from contaminated tributaries. For example, elevated levels of fecal coliform bacteria sometimes are found in water from tributaries draining land with intense animal agriculture. A more wide-spread ecosystem stress is the presently elevated loading of phosphorus, largely responsible for the rapid eutrophication of the lake in the last two decades (Brezonik and Engstrom 1999, Engstrom et al. 2005). Primary sources of phosphorus pollution are agriculture, followed by urban and other sources (Flaig and Havens 1995). As a result of decades of large agricultural inputs, soils in the watershed, sediments of tributaries, and the lake's bottom sediments contain large quantities of phosphorus (Olila and Reddy 1993, Flaig and Reddy 1995, Fisher et al. 2001). These external soils and internal sediments represent large secondary sources of phosphorus loading to the lake. Deep straight canals without any substantial vegetated zones facilitate rapid delivery of phosphorus in runoff water to the lake.

Lake Okeechobee's pelagic zone has elevated concentrations of resuspended sediments from soft organic mud covering about 50% of the central lake bottom. Wind mixes the shallow water column, resuspending the upper few centimeters of mud. 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, Engstrom et al. 2005).

Variations in rainfall, evapotranspiration, water supply deliveries from the lake, and operation of the C&SF Project affect water levels in the lake. At times, water levels are extremely high or low, and these events have various impacts on the lake's biota. Impacts of high and low water now are more severe because the lake is encircled by a dike. Under natural conditions, water was able to expand and recede over a large low-gradient marsh to the west and south. Today, when lake's stage (surface elevation) exceeds 4.6

m National Geodetic Vertical Datum (NGVD), water stacks up over the smaller (yet still over 400 square kilometer) littoral zone, flooding it to a greater depth. When lake stage falls below 3.4 m, the entire littoral zone is dry, and lateral expansion cannot occur to the east due to a relatively steep drop off in the lake's bottom contours. Hence, extreme high or low lake levels of any duration, or moderate high or low lake levels of prolonged (greater than 6 months) duration, can cause significant harm to the ecosystem, as described below in greater detail. A certain degree of natural variation in lake stage, between 3.7 and 4.6 m, has been shown to benefit the ecosystem (Smith et al. 1995, Smith 1997) and is a desired result of regional hydrologic restoration.

In recent decades, Lake Okeechobee has experienced a rapid expansion of non-native and nuisance plants and the introduction and expansion of certain non-native animals. The only known impacts to date are associated with certain plants in the littoral zone. *Melaleuca* and torpedograss, which were introduced to the lake for dike stabilization and cattle forage, have substantially displaced native plants. Other non-native plants include *Hydrilla verticillata* (L.F. Royle), water hyacinth (*Eichhornia crassipes* (Mart.) Solms), and water lettuce (*Pistia stratiotes* L*innaeus*). Non-native animals in the lake now include fish (*Tilapia aurea* Steindachner), mollusks (*Corbicula fluminea* O.F. Muller), and microinvertebrates (*Daphnia lumholtzi* Sars). Their effects, if any, have not been documented.

ECOLOGICAL ATTRIBUTES

Attributes of Lake Okeechobee's ecosystem encompass the overall ecological state of the lake and reflect several societal uses, including fishing, drinking water quality, hunting, wildlife observation, and recreational boating. Two non-ecological factors that are also influential, water supply and flood control, are not included as attributes in this particular model but represent sources of high and low lake stage.

Water Quality

The term water quality is subjective and is used in a variety of ways in the literature. Here, good water quality is defined as high transparency and low levels of nutrients and phytoplankton, which in turn, favors development of submerged aquatic plants, diverse habitat for fish, and a resource base that supports wading birds and other wildlife. Water quality also affects the taste, odor, and cost of treating drinking water, and it can affect downstream ecosystems that receive water from the lake. The occurrence of good water quality in Lake Okeechobee has been reduced since the 1970s by large external nutrient loads and unnaturally high water levels (Canfield and Hoyer 1988, Havens et al. 1996, Havens 1997).

The lake has experienced high rates of phosphorus loading in recent decades due to altered land use in the watershed. At present, loading is in excess of 500 metric tons per year, far greater than the 140 metric tons per year mandated by the Florida Department of Environmental Protection (FDEP 2000) Total Maximum Daily Load (TMDL) Rule for total phosphorus. The TMDL represents a loading rate that is considered necessary to protect the ecosystem from imbalance and corresponds to an in-lake total phosphorus concentration goal of 40 ppb (Havens and Walker 2002). Total phosphorus concentrations measured in the lake today (greater than 110 ppb) are more than double those measured in the early 1970s, when the South Florida Water Management District first began to collect water quality data on a regular basis (James et al. 1995b, Havens et al. 2003a).

Transparency of water in the pelagic zone is low (typically <20 cm Secchi depth), due to resuspension of a thin layer of fluid mud sediments by wind and waves (Maceina and Soballe 1991, Hanlon et al. 1998). When water levels in the lake are high, following periods of heavy rainfall, the turbid water is transported from the pelagic to the near-shore zone (Maceina 1993, Havens 1997) where reduced transparency can lead to a reduced biomass of submerged plants (Havens et al. 2004b). High levels of phosphorus in the pelagic water can result in blooms of noxious cyanobacteria (Havens et al. 1998). When present at high densities, these algae can cause taste and odor problems for the five municipalities that obtain drinking water from the lake. When blooms peak and then collapse, reduced dissolved oxygen concentrations and bloom decay products impact certain aquatic biota (Jones 1987, Paerl 1988).

Fish and Aquatic Fauna

Lake Okeechobee supports an economically important sport fishery for largemouth bass (*Micropterus salmoides* Lacepede) and black crappie (*Pomoxis nigromaculatus* Lesueur in Cuvier & Valenciennes), 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 local economies and have an asset value in excess of $100 million (Bell 1987). Another estimate (Furse and Fox 1994) values the fishery at more than $300 million, considering only recreational fish species.

In total, the fish community of Lake Okeechobee includes >40 native species (Bull et al. 1995, Havens et al. 1996b). These fish provide a food resource for wading birds, alligators (*Alligator mississippiensis* Daudin), and other animals that forage in the lake. Fish use both littoral and pelagic zones, and some top predators (including largemouth bass, and Florida gar, *Lepisosteus platyrhincus* DeKay) migrate between the two zones (Fry et al. 1999). Gut analyses and stable isotope data indicate that fish depend on a wide range of food resources, including benthic macro-invertebrates and zooplankton (Havens et al. 1996b, Fry et al. 1999). Those resources, in turn, are dependent on a continual input of energy from plant, periphyton and phytoplankton primary productivity, and allochthonous inputs of carbon that can fuel bacterial growth. Fish also depend on aquatic plant communities for spawning habitat and as refuge from predators (Fox et al. 1993).

Human impacts have altered the resource base and aquatic plant habitat that support the lake's fishery. Changes include eutrophication-related shifts in macro-invertebrate and plant community structure (Warren et al. 1995) and the periodic loss of certain plant community components due to high-water stresses (Havens et al. 2004b).

Native Vegetation Mosaic

The littoral zone of Lake Okeechobee was formed after construction of a dike around the lake in the mid-1900s. The lake's natural littoral zone was much larger and occurred west and south of its present location (Havens et al. 1996a, Steinman et al. 2002a). The littoral zone supported a diverse array of native plants when it was first surveyed (Pesnell and Brown 1976), including large areas of spikerush (*Eleocharis* sp.), sawgrass (*Cladium jamaicense Crantz*), willow (*Salix caroliniana* Michx.), and beakrush (*Rhynchospora tracyi* Britt.). At the south end of the lake, there were remnant stands of pond apple (*Annona glabra* Linneaus), and the western shoreline had a nearly continuous band of dense bulrush (*Scirpus* sp.) immediately lakeward of a zone dominated by spikerush and submerged plants. Today, the littoral vegetation is substantially different (Richardson and Harris 1995). Upland areas previously dominated by beakrush (*Rhynchospora* spp.) and mixed grasses now are dominated by torpedograss. For many years, *Melaleuca* also was widespread, but now it has largely been eradicated in a state and federal program using contact herbicides (SFWMD 2002). The spatial extent of willow has declined, and cattail (*Typha* spp.) has expanded to surround once pristine spikerush sloughs in the interior littoral zone. Shoreline bulrush and spikerush are sparse (<50%) relative to historic spatial extent. Submerged plants were largely eliminated from the near-shore pelagic region in the late 1990s; however, a marked recovery occurred during a period of low water from 2000 to 2002 (Havens et al. 2004b).

Submerged plants reduce water-column nutrient concentrations and associated algal blooms by (1) stabilizing lake sediments with their roots; (2) reducing water flow velocity and shearing stress on sediments due to wave attenuation; (3) trapping sediment material; and (4) direct uptake of phosphorus from the water by epiphytic algae, or through precipitation with calcium when pH is elevated due to plant photosynthesis (Carignan and Kalff 1982, Murphy et al. 1983, Burkholder et al. 1990, Vermaat et al. 2000). In Florida lakes, up to 96% of the combined water-column and plant phosphorus can occur in tissues of plants, epiphyton, and in precipitated calcium phosphate (Canfield et al. 1983).

Due to relatively large fluctuations in water depth (from <0.5 to >2 m), the near-shore region switches between clear (shallow depth) and turbid (deeper depth) states (Havens et al. 2004a). This response is typical of shallow eutrophic lakes and is largely due to the influences of submerged plants noted above (Scheffer 1989, Moss et al. 1996). In Lake Okeechobee, submerged plants are affected during deep water periods by light limitation and erosion from wave energy. In the late 1990s, when water was deep in the near-shore zone, successive frontal systems and associated wave energy eroded large areas of submerged vegetation and emergent wetland plants, producing a 2–3 m high berm of pulverized plant material along the western lake shore. The result of this was both a loss of important habitat for fish and wildlife and also a substantive barrier to materials transport and animal movement between the littoral and near-shore zones. These berms were colonized with shrubs and small trees and became lasting features of the landscape. Under a hydrologic regime that reduces the occurrence of extreme high water levels, berm formation may decline. Existing berms may require physical removal during low water periods, as was done along a 30 km section of shoreline in 2001.

Snail Kite, Wading Birds, and Waterfowl

Historically, Lake Okeechobee's littoral zone has provided one of South Florida's largest habitats for the federally-endangered snail kite (*Rostrhamus sociabilis* Vieillot) (Bennetts and Kitchens 1997), and it has supported large resident and migratory populations of wading birds (Smith et al. 1995) and water-fowl. Snail kites nest and forage in the littoral zone; other habitats include Everglades National Park, the Water Conservation Areas, Big Cypress basin, and lakes and wetlands located north and east of Lake Okeechobee. Kites migrate across the South Florida landscape (Bennetts and Kitchens 1997) and, therefore, cannot be managed effectively in a site-specific context. Nevertheless, managing the lake so that conditions do not preclude use by kites during times when other habitats are dry is considered important to their survival in the regional system. In extreme droughts, Lake Okeechobee is sometimes the only major wetland habitat with adequate water levels to support kite foraging—but not if the littoral zone is taken over by cattail and other invasive plants.

The lake 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 1957–1978 showed typically 4,700 nests per year, with peaks in 1972 and 1974. During those years, approximately 10,000 pairs of wading birds nested on the lake, mostly white ibis (*Eudocimus albus* Linnaeus) at the King's Bar colony, near the mouth of the Kissimmee River. It was considered one of the largest and most important wading bird colonies in central Florida. After an increase in average water levels in the lake in 1978 (when the flood control schedule was changed), the number of wading bird nests declined, then stabilized at about 2,000 nests (David 1994) through 1992, the last year for which there were systematic nest surveys (Smith and Collopy 1995).

Wading birds respond to water levels through changes in nest numbers, as illustrated above, but they also adjust their foraging habitat (Smith 1995) and choice of prey (Smith 1997a). When water levels are low, wading birds forage in submerged vegetation, whereas at moderate lake levels, they select habitat with emergent vegetation such as *Eleocharis*, *Rhynchospora*, *Panicum*, *Nymphaea*, and sparse *Typha* (Smith et al. 1995). When lake levels are very high, some species of wading birds forage more often in habitats outside of the perimeter levee. Collectively, these wading bird responses to hydrologic fluctuations illustrate the linkage between the lake and surrounding wetlands and the importance of a diverse macrophyte community within the lake.

Lake Okeechobee hosts more than 100,000 migratory waterfowl, although numbers vary greatly between years (Chamberlain 1960, Bellrose 1976) and are reduced substantially by multiple years of deep flooding, such as the late 1990s. Migratory behavior may allow birds to exploit seasonally rich and variable habitats in the regional landscape.

Most prevalent in mid-winter surveys of the lake are lesser scaup (*Aythya affinis* Eyton), with 50,000–300,000 inhabiting the near-shore zone. Scaup dive for food in water up to several meters deep (Bellrose 1976), but their diet on Lake Okeechobee is unknown. The second most abundant species has been the ring-necked duck (*Aythya collaris* Donovan). 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, 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 to 1995, to an average of 489 from 1996 to 2000. This 92% decline was apparently due to loss of submerged plants, combined with availability of alternate habitat locations. Qualitative observations indicate that duck densities increased markedly in 2001–2003 when water levels were lower and aquatic vegetation became abundant in the near-shore zone—quantitative surveys have not been conducted.

Dabbling ducks prefer marshy areas and are more difficult to survey than diving ducks. An average of 338 dabbling ducks was detected between 1991 and 2000 (mid-winter inventory by Florida Fish and Wildlife Conservation Commission). Considering the potential 36,000 ha of habitat, this number is extremely low and may reflect sub-optimal habitat conditions. For comparison, Johnson and Montalbano (1984) detected an average of 11,886 dabbling ducks just in Fisheating Bay in 1981 and 1982. High water levels impede dabbling ducks because they rarely dive to feed and prefer water less than 30 cm 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 growth of moist soil vegetation, important to producing seeds that ducks prefer (Goodwin 1979, Fredrickson and Taylor 1982).

HYPOTHESIZED LINKAGES BETWEEN STRESSORS AND ATTRIBUTES

Pathways linking stressors to ecological attributes (Figure 2, arrows and diamonds) are based on research and modeling at South Florida Water Management District, the Florida Fish and Wildlife Conservation Commission, and the University of Florida. Ecosystem effects are described in the context of working hypotheses regarding how each attribute is affected by major ecosystem stressors.

Lake Water Quality

Internal Phosphorus Loading Maintains High Water Column Phosphorus. A large fraction of phosphorus entering the lake is stored in bottom sediments (James et al. 1995a), and with a long history of large inputs, sediments now contain over 30,000 metric tons of phosphorus in the upper 10 centimeters alone (Olila and Reddy 1993, Fisher et al. 2001). It has been estimated that the gross internal load of phosphorus from lake sediments approximately equals the external load in magnitude (Olila and Reddy 1993). Phosphorus can be mobilized into the overlying water column by diffusion (Moore et al. 1998), wind resuspension (Hanlon 1999), and bioturbation (Van Rees et al. 1996). This internal loading makes the ecosystem resilient to changes in phosphorus concentration when external inputs vary, a common feature of shallow eutrophic lakes (Sas 1989, Moss et al. 1996). However, if external loads decline substantially, the phosphorus-rich surface sediments are expected to be covered by new sediment material with reduced phosphorus content. Rates of internal loading should then decline, perhaps over several decades. It is important to note that, while there is a high rate of gross loading from sediments to overlying water, the net flux on a yearly basis is into the sediments—albeit at a lower rate in recent years compared to the 1970s and 1980s (Havens and James 1997, Havens and Schelske 2001).

Fisher et al. (2001) compared sediment pore-water phosphorus collected from the lake in 1988 versus 1998 and found that the concentraiton had more than doubled. Pore-water phosphorus is unbound phosphorus, essentially a surplus or non-assimilated fraction. The increase in pore-water phosphorus may reflect a reduction in binding sites and, hence, a reduction in assimilative capacity of the lake. If external phosphorus loading remain high, a further loss of sediment assimilative capacity might occur, or alternatively, the trend might reverse with reduced loads.

A number of biological changes in the lake also could affect the system's capacity to assimilate phosphorus (Havens and Schelske 2001). Diatoms have been replaced by cyanobacteria in the water column as the dominant phytoplankton (Cichra et al. 1995, Havens et al. 2003a), and this change could decrease phosphorus loss rates to sediments because cyanobacteria settle more slowly than diatoms (Reynolds 1984). Among benthic macro-invertebrates, oligochaetes have replaced chironomids and other insect larvae as the dominant taxa, largely because they tolerate anoxic conditions 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 lake water because oligochaetes pump large quantities of soluble phosphorus from sediments into 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 on the benthos, providing another pathway for upward phosphorus transport. There is a potential for reversal of these biological changes if phosphorus loads are substantially reduced.

High Lake Stages Exacerbate Nutrient Effects. A probable link between high lake stage and elevated concentrations of total phosphorus (Canfield and Hoyer 1988, Havens 1997) indicates a complex underlying mechanism, ranging from large-scale changes in water-circulation physics to alterations in biological community interactions. An early hypothesis (Maceina 1993) was that high stage allows greater horizontal transport of phosphorus from the pelagic to near-shore zone. Evidence for this hypothesis is largely observational but has been supported by South Florida Water Management District's Lake Okeechobee Hydrodynamic Model. The underlying mechanism is related to water currents and morphology of the lake basin. Wind moving across the lake surface creates basin-wide circulation gyres (Jin et al. 2000) whose spatial extent is affected by water depth. When lake stage is low (less than 4.0 m), an elevated ridge of limestone along the south and west perimeter of the lake hinders mixing of water between pelagic and near-shore zones. This reduces phosphorus and sediment transport to the near-shore zone and is responsible, in part, for low phosphorus concentrations and high transparency that occurs in that zone when stage is low (Maceina 1993, Havens 1997).

Another factor at low lake stage is uptake of phosphorus by submerged plants. When stage is low, the lake can support a large spatial extent of submerged plants (Hopson and Zimba 1993, Havens et al. 2002, Havens et al. 2004a). In 1989, after stage declined to below 3.4 m, remote sensing indicated that submerged plants covered 12,400 hectares of the lake bottom (Richardson and Harris 1995), and in summer 2000 when stage declined to below 3.7 m during a drought, total extent of submerged plants was 17,700 hectares. Large spatial extent persisted through summers 2001 and 2002 (Havens et al. 2004) but declined in 2003 with increased lake stages.

Benthic micro-algae and *Chara*, a macro-alga, also increase in biomass and spatial extent under low stage conditions in Lake Okeechobee (Steinman et al. 1997a, b, 2002b), and they can compete directly for water-column phosphorus with phytoplankton (Havens et al. 1996c, Hwang et al. 1998). High lake stage suppresses growth of plants and attached algae due to light limitation from mechanisms previously described. Hence, lake stage can affect water-column phosphorus concentrations by determining the relative mass of that nutrient that occurs in rooted plants and periphyton versus phytoplankton (Havens et al. 2001b).

High Phosphorus Concentrations Affect Blooming of Cyanobacteria. A 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 surplus concentrations relative to algal demands. When that occurs, some other nutrient element (most often nitrogen) becomes secondarily limiting to algal growth (Schelske 1984). Havens (1995) described a trend in water quality of Lake Okeechobee indicative of a transition towards secondary nitrogen limitation after the early 1980s, and Aldridge et al. (1995) and Phlips et al. (1997) found that nitrogen was secondarily limiting to phytoplankton growth in the 1990s. Havens et al. (2003a) confirmed that nutrient availability favors dominance by cyanobacteria, which almost always dominates the phytoplankton. 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 nitrogen fixation (Horne 1977). Taxa with this capacity include *Anabaena*, and *Aphanizomenon*; these taxa (and others, including *Microcystis*) predominate in Lake Okeechobee when there are surface blooms of algae.

Fish and Aquatic Fauna

Macro-invertebrates in Pelagic Sediments are affected by Nutrient Loading. Sustained high rates of nutrient loading and phytoplankton production have resulted in a high rate of organic loading to the lake sediments, high rates of bacterial metabolism, and hypoxic or anoxic conditions in near-surface sediments. These conditions collectively favor the dominance of pollution-tolerant macro-invertebrates such as certain oligochaetes. Warren et al. (1995) found that, between the early 1970s and early 1990s, the relative abundance of oligochaetes increased in pelagic sediments from 30 to 80% of the total community. This large relative abundance persisted during the last decade (G. Warren, Florida Fish and Wildlife Conservation Commision, personal communication), and species known to be pollution-tolerant (e.g., *Limnodrilus hoffmeisteri* Claparede) 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. These trends are nearly identical to those observed in Lake Erie when it underwent rapid eutrophication between 1930 and 1960 (Carr and Hiltunen 1965).

Predominance of oligochaetes is a concern because they can contribute substantially to internal loading of phosphorus. They also 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.

Pelagic Zooplankton is Controlled by Resources and Fish Predation. Zooplankton of Lake Okeechobee is comprised of 61 native and one non-native species (Havens et al. 1996b, Havens and East 1997) and includes rotifers (Rotifera), copepods (Copepoda), and sparse amounts of cladocerans (Cladocera). Total biomass correlates significantly with nutrient and chlorophyll *a* concentrations, both in field surveys and controlled experiments (Crisman et al. 1995, Beaver and Havens 1996, Havens et al. 1996c).

Dominance of large cyanobacteria in the lake's phytoplankton may sometimes limit the biomass of zooplankton because the algae cannot be directly grazed by the dominant zooplankton (Havens and East 1997). As a result, a 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).

Large cladocerans that can graze filamentous and colonial cyanobacteria are absent in Florida lakes (Crisman and Beaver 1990). At least two factors might explain their absence: 1) high rates of grazing by fish over many decades has caused local extinction of the largest and most visible zooplankton taxa (large *Daphnia*); and/or 2) high water temperatures preclude occurrence of large cladocerans during all but the coolest months of the year.

The predation hypothesis has the strongest support but requires further study. Crisman and Beaver (1990) documented that, in fish-free enclosures in the near-shore zone, the biomass of small cladocerans increased substantially compared to the open lake. Lake Okeechobee and other regional lakes support high densities of threadfin shad (*Dorosoma petenense* Gunther) and other zooplanktivores, and reports from the Florida Fish and Wildlife Conservation Commission indicate that densities of young-of-year fish of many species are most abundant in late spring to early summer, the time when zooplankton biomass typically decreases to a low level and cladocerans disappear from the plankton (Havens et al 2000, Tugend and Allen 2000). East et al. (1999) found that abundance of native *Daphnia ambigua* (Scourfield) is reduced dramatically during summer, whereas *Daphnia lumholtzi* (Sars), a tropical non-native, increases during that period. The non-native species has large spines that may provide a greater defense against fish predation during summer months. However, it also is reported to be more tolerant of high water temperatures.

Pelagic and Near-shore Macro-invertebrates are Regulated by the Status of Submerged and Emergent

Plants. When low-to-moderate water levels occur in the lake, resulting in dense *Hydrilla*, peppergrass, bulrush, and eelgrass, the biomass and taxonomic diversity of macro-invertebrates is maximal (Warren and Vogel 1991). Many of these animals, including grass shrimp (*Palaemonetes paludosus* Gibbes), amphipods such as *Hyalella azteca* (Saussure), and larvae of the midge genera *Dicrotendipes*, *Glyptotendipes*, and *Rheotanytarsus*, are integral to the diets of largemouth bass, black crappie, redear sunfish (*Lepomis microlophus* Guenther), and bluegill sunfish (*Lepomis macrochirus* Rafinesque).

Coincident with a decline in submerged plants in the late 1990s, most macro-invertebrate habitat was lost. In a June 2000 survey, Warren and Hohlt (Florida Fish and Wildlife Conservation Commission unpublished data) recorded extremely low densities of invertebrates in habitats (bulrush and mud sediments) that formerly (1987–1991) supported large numbers. Scientists and resource managers also noticed a near absence of winged adult midges emerging 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. Without ongoing monitoring, we cannot determine the extent to which macro-invertebrates recovered as a result of lower water levels and increased plant biomass in 2000–2003.

Macro-invertebrates in the Littoral Zone are Controlled by Variations in Hydroperiod, Structure of Plant Habitat, and Dissolved Oxygen. The littoral zone fauna includes at least 174 macro-invertebrate taxa (Havens et al. 1996b), representing several functional and taxonomic groups. Analyses 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. 2003b). Macro-invertebrates were found to account for greater than 40% of volumetric gut contents of redear sunfish (*Lepomis microlophus* Guenther), bluegill sunfish, largemouth bass, and bowfin (*Amia calva* Linnaeus) in Moonshine Bay, in the west-central littoral zone.

Warren and Hohlt (1994) examined littoral macro-invertebrate community structure on spikerush, torpedograss, bulrush, and cattail. Because of their growth habits, torpedograss, *Pontederia* (pickerelweed) and cattail habitats had low dissolved oxygen concentrations and sparse macro-invertebrates. Spikerush habitat, with a more open vertical plant growth form, had a lower production of recalcitrant detrital material, higher dissolved oxygen concentrations, and a more diverse macro-invertebrate assemblage.

One prominent component of the littoral community is the Florida apple snail (*Pomacea paludosa* Say). This species is a principal food item for snail kites (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 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, repopulation of large areas following prolonged dry downs requires multiple years of favorable conditions. For example, a prolonged period of extreme low stage in 2000–2001 appears to have nearly eliminated the apple snail population from the littoral zone. Animals did not recover until after winter 2003–2004 (author's personal observations).

Another factor that can significantly impact apple snails is reversal of lake stage during the egg-laying period. Snails lay their eggs several centimeters above the water surface on emergent stems of spikerush, 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 loss of stem adhesion (Turner 1994). Likewise, if water levels drop markedly, high mortality may occur due to lack of lack of water and food resources for the young snails the emerge from eggs.

Research dealing with apple snail growth responses to varying food types indicates that nutrient content of grazed material also could affect snail populations. Sharfstein and Steinman (2001) maintained young apple snails in laboratory cultures and provided animals with either epiphyton associated with spikerush stems, epiphyton of bladderwort (*Utricularia* spp.), or metaphyton collected from near sediment surface. These are three distinct and typical components of 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 other food types, perhaps because bladderwort epiphyton had a higher nitrogen and chlorophyll content. Changes in plant community structure that shift periphyton towards dominance by less nutritious forms could potentially result in reduced apple snail growth. Substantial changes in periphyton taxonomic structure have been demonstrated in controlled experiments (Havens et al. 1997) and generally match results from the Everglades.

Pelagic Fish are Affected by Nutrient Inputs, which Determine Phytoplankton and Macro-invertebrate Biomass. Bull et al. (1995) studied distribution of fish in open-water habitats of the lake during late 1980s and early 1990s, sampling fish at 25 sites with a large trawl net. They found that deeper central and north regions of the lake supported distinct fish assemblages, which differed from those found in near-shore and littoral habitats. The central assemblage was dominated by threadfin shad and black crappie in summer and by black crappie and white catfish (*Ameiurus catus* Linnaeus) in winter. Abundance of shad significantly correlated with phytoplankton chlorophyll *a* concentrations, reflecting a feeding preference by shad for phytoplankton and zooplankton (Baker and Schmitz 1971). White catfish abundance was strongly correlated with water depth, indicating that they tend to forage in cooler deep water areas of the lake, to prey on benthic macro-invertebrates, detritus, and smaller fish (Havens unpublished gut content data). Bull et al. (1995) documented that the north pelagic region supports the highest densities of fish in both summer and winter, probably due to high food availability. Phlips et al. (1995) found that this region, which is in closest proximity to large nutrient inputs from agricultural lands, has high phytoplankton biomass. 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* (Malloch), a chironomid that occurs at high densities (up to 21,000 per square meter) in nutrient-rich mud sediments in the northern region (Warren et al. 1995).

Near-shore Fish Depend Heavily on Structurally-Diverse Submersed and Emergent Plant Assemblages. Fisheries research on other lakes shows that vascular aquatic plants provide multiple benefits to fish communities including 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, bulrush, eelgrass, peppergrass, and *Hydrilla* provide habitat for a variety of sport and forage fish (40 species total) in the near-shore area (Furse and Fox 1994).

Furse and Fox (1994) noted that eelgrass, peppergrass, and spikerush provide habitat in the lake for juvenile sport fish and small forage fish, and that bulrush, *Hydrilla* and peppergrass account for most recreational fishery value. Bulrush recreational value was four times greater than that estimated for any other component of the vegetation community in the near-shore area. A widespread decline of bulrush and other aquatic vegetation in the late 1990s, coincident with high water levels, led to significant declines in population density and recruitment of bass and other fish in the lake. After water levels were low in 2000–2002 and vegetation strongly rebounded, fish recovered, with age distributions indicating healthy populations in 2002–2004 (Havens et al. 2005).

Habitat Structure, Resource Base, and Hydrology Affect Littoral Fish. In general, a lake's vegetated littoral zone provides important habitat for fish, particularly small taxa and juvenile stages of larger species, which use the littoral zone as a refuge from predators and a foraging area (Werner et al. 1983, Rozas and Odum 1988). In Lake Okeechobee, surveys by Chick and McIvor (1994) found a large biomass and diversity of fish in the littoral zone, with distinct assemblages occurring in different plant habitats (eelgrass, peppergrass, and *Hydrilla*). This is similar to the findings of Furse and Fox (1994), except that the study's focal point was interior and northern littoral regions, rather than near-shore areas. Fry et al. (1999) also documented, using stable isotope data, that some 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 fisheries. This finding is important, indicating the complexity 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-leaved plants with different densities and growth forms. However, certain rapidly expanding non-native and nuisance plants create conditions that generally are not favorable for fish, with particular concern for torpedograss and cattail.

One plant that has been displaced by non-natives is spikerush. It provides particularly good habitat for fish (Chick and McIvor 1994), including enough open water to allow effective foraging, but also providing cover associated with emergent plant stems and associated whorls of bladderwort. The spikerush community also supports a large diversity of macro-invertebrates and attached periphyton that provide a food resource for fish. In contrast, both torpedograss and cattail (invasives) have a dense growth form, with little open water for animals to move through, poor light, and 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 milligrams per liter (South Florida Water Management District unpublished data).

Native Vegetation Mosaic

Hydroperiod Determines the Spatial Distribution of Native and Non-native Plants. Richardson et al. (1995) showed that hydroperiod alone explained most of the spatial variation in littoral plant taxonomic structure in Lake Okeechobee. Short hydroperiod regions support native species, including spikerush, beakrush, willow, and cordgrass (*Spartina bakeri* Merr.), and non-native species including torpedograss, *Melaleuca*, and Brazilian pepper (*Schinus terebinthifolius* Raddi.). Long hydroperiod regions support spikerush, cattail, sawgrass, bladderwort, and waterlily. Periods of extremely short or long hydroperiod (low and high lake stage events) since the early 1970s are considered largely responsible for changes in relative distribution of these plants.

Two periods of very low lake stage, in 1980–1981 and 1989–1990, may be responsible for expansion that has occurred in non-native plant populations. Controlled experiments with *Melaleuca* (Lockhart 1995) and torpedograss (Smith et al. 2004) have shown that these species cannot successfully invade native plant habitat inundated with water. *Melaleuca* seeds cannot germinate under water, and torpedograss fragments (the plant's main mode of colonization) cannot establish roots when water depths exceed 50 centimeters. However, once 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 expansion of *Melaleuca* and torpedograss in the littoral zone occurred following droughts in 1981 and 1980, when there were favorable habitat for colonization by seeds and fragments. Further expansion of torpeodgrass occurred during the 2000–2001 drought (SFWMD 2002).

Low lake stage increases fire probability in the littoral zone due to lightning strikes, arson, and controlled burn programs. Fires have documented benefits to the littoral vegetation since they burn away accumulated detritus in dense stands of emergent plants, opening up the habitat to wildlife, and burn aboveground biomass of torpedograss monocultures, which allows for effective control with herbicides (Hanlon and Langeland 2000). Fires also allow buried seeds to germinate from exposed sediments, providing colonization windows for native plants (Williges and Harris 1995).

Phosphorus Inputs Have Promoted Spread of Cattail and Waterlily. The pelagic zone of Lake Okeechobee has total phosphorus concentrations that average over 110 ppb (James et al. 1995b), 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 pelagic-littoral interface (Maceina 1993, Havens 1997) and into the littoral zone proper.

Aerial photographs and early maps (Pesnell and Brown 1976) of the littoral zone indicate that the 1970s had little or no cattail in Moonshine Bay area, but rather a near-monoculture of spikerush. Today, dense cattail grows along edges of all boat trails leading from open water into a central littoral area called Moonshine Bay from the north and west. There is a dense community of cattail along 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 the Everglades (Newman et al. 1996).

Deep Water and Damage from Wind-Driven Waves Reduce Near-Shore Bulrush Stands and Submerged Aquatic Vegetation. Recent estimates indicate that, by late 1990s, spatial extent of bulrush was reduced by more than 50% from its recorded maximum in early 1970s (Florida Fish and Wildlife Conservation Commission unpublished data). This reduction may be due to long periods of deep standing water, resulting in conditions where only a small percentage of plant photosynthetic tissues were above water (Hanlon 2005). 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 resulted in a dramatic decline in spatial extent of submerged plants by 1999, following several years of high lake stage. High water levels affect underwater irradiance and, in turn, the rate of growth and survival of submerged plants. 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 lakeward extent of submerged plant habitat (Havens et al. 2003a). Under high stage conditions there is increased transport of sediment-laden water from the pelagic zone to near-shore areas that support submerged plants (Maceina 1993, Havens 1997). Research has shown that submerged plant biomass in Lake Okeechobee is negatively correlated with water depth (Hopson and Zimba 1993, Havens 2003), and the greatest submerged plant biomass occurs when stage is very low (Phlips et al. 1993). Controlled experiments also have confirmed a cause-effect relationship between underwater irradiance and growth rates of submerged plants from the lake (Grimshaw et al. 2002).

Once submerged plants are lost, a positive feedback maintains the turbid condition. Without plants to stabilize sediments, sediment resuspension increases, and this results in increased turbidity of the water column. Light levels reaching the lake bottom are then insufficient to support growth of periphyton and rooted plants, and phytoplankton in the water column dominates primary productivity (Havens et al. 2001b). Algal blooms contribute to further reductions in light availability, which prevents plant recovery. This cycle is difficult to break once it is established (Scheffer 1989). Only a major change in conditions, such as the rapid lowering of stage that occurred in 2000–2001 (Havens et al. 2001), allows plants to recolonize. Once this occurs, however, plants can establish a different feedback loop to maintain clear water.

High Water Levels Have Resulted in Erosion of the Littoral Fringe Area. The lakeward edge of the littoral zone is exposed to high wave energy when water levels in the lake are above 5.2 m. As a result, the edge is dynamic, forming and eroding similar to a sandy beach being eroded and redeposited by strong surf. This process has led to loss of vegetation in some regions and deposition of debris berms along others. Hanlon (2005) used geographic information system (GIS) vegetation maps to quantify up to 300 meters erosion of the littoral edge between 1996 and 1999. During a period of particularly high lake levels (near 5.5 m) in fall-winter 1998, they documented recession of the littoral edge up to 10 meters in just 90 days. Output from South Florida Water Management District's lake hydrodynamic model (Jin et al. 2000) indicates under high stage conditions, and in the absence of dense bulrush stands to attenuate wave energy, there are strong longshore currents that could scour sediments and submerged plants and erode the lakeshore along much of the western edge.

Snail Kites

Kites Have Been Impacted by Cattail and Torpedograss Expansion, Declines in Apple Snails and Loss of Willow in the Littoral Zone. Bennetts and Kitchens (1997) noted that quality of habitat for kites is adversely influenced by changes in water quality and expansion of non-native plants. The key factor is replacement of relatively open foraging habitat with habitat dominated by dense vegetation. In the Everglades, nutrient enrichment favors dominance of cattail, which could impact kites because they require relatively open areas for foraging to detect 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 vegetation typically hides the water surface.

Apple snails are the major food item of 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, habitat will be unfavorable for kites until the food resource recovers.

According to Bennetts and Kitchens (1997), snail kites nest primarily in willow and other woody vegetation types. Hence, spatial extent of these plant types will directly affect whether or not the littoral zone represents viable habitat for kite nesting. Factors contributing to habitat loss in Lake Okeechobee include prolonged periods of deep water and expansion of torpedograss.

Availability of multiple wetland habitats is considered to be critical for kites and is the foundation of ''meta-habitat hypothesis'' proposed by Bennetts and Kitchens (1997). In this hypothesis, risk to a regional population is minimized by the ability of kites to move to different habitats within regional networks as quality of localized habitats fluctuates. For kites to survive, conditions in their habitats should not be degraded so that they are no longer functional during times when there use is required by the population. 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 an extent that it loses its apple snail populations or suitable foraging (e.g., spikerush slough areas) and nesting (e.g., willow) habitat.

Wading Birds

Seasonal Lake Stage Recessions Benefit Wading Bird Populations. The water level in Lake Okeechobee determines which habitats wading birds use (Smith 1995), but within those habitats, the abundance and distribution of birds is a function of the dry season recession in water levels (Smith et al. 1995, Smith 1997b). When water levels stop receding or start to rise, birds become dispersed and less abundant. The best explanation for why receding water affects the distribution of birds is that receding water both increases the density of prey in small patches and it increases the vulnerability of prey to being captured; collectively termed prey availability (Gawlik 2002). 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 20 to 150 in the Everglades and Big Cypress National Preserve (Carter et al. 1973, Loftus and Eklund 1994, Howard et al. 1995) during typical recession events. Patches with concentrated prey are typically shallow with no vegetation; therefore, individual fish become more vulnerable to capture and wading bird feeding success is increased (Kushlan 1976).

Although high-density food patches may be scattered in the landscape, wading birds have adaptations such as white plumage and social foraging to minimize search time (Kushlan 1981, Erwin 1983, Gawlik 2002). At the landscape scale, wading birds exploit small patches of highly available prey, and large foraging aggregations indicate good feeding conditions. Species such as wood storks (*Mycteria americana* Linnaeus), white ibises, and snowy egrets (*Egretta thula* Molina) appear to be more dependent than are other wading bird species on good feeding conditions to allow years of high reproductive output (Gawlik 2002). Hydrologic patterns that produce maximum numbers of patches with high prey availability (i.e., high lake stages at the end of wet season and low lake stages at the end of dry season) produce good wading bird nesting effort (Smith and Collopy 1995).

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, Smith 1995). Willow is thought to be the preferred nesting substrate because it can tolerate longer hydroperiods than most tree species and 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 probability of their nests being preyed upon by raccoons (Frederick and Spalding 1994). Despite tolerance for long hydroperiods, even willow cannot withstand prolonged periods of deep water. In 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 preferred nesting sites for wading birds could be a factor limiting population sizes.

RESEARCH QUESTIONS

The conceptual model provides an organizing tool for the extant information about the Lake Okeechobee ecosystem. It also helps us to identify areas of uncertainty where additional research is required to support management of the resource.

Nutrient Dynamics and Algal Blooms

Most research dealing with phosphorus in Lake Okeechobee has focused on the pelagic zone, yet the major areas used by fish, wildlife, and humans are the near-shore and littoral zones, where many biological, physical, and chemical processes may be important. In particular, the processes associated with dense beds of aquatic plants may have major effects on water-column nutrients. Transport of phosphorus between the lake's major zones also is not effectively quantified at this time.

Likewise, there has been little research to quantify the nitrogen dynamics in any region of this lake, except for some measurements of denitrification in the 1980s and nitrogen fixation in the mid-1990s. Given the sub-tropical locale and large external sources of nitrogen to this system, biologically-mediated processes are likely to control nitrogen dynamics and play a role in how the lake responds to nutrient load reductions. This is a critical area for future research.

In regard to algal blooms, we lack information regarding quantitative linkages between bloom occurrence, toxin production, and important societal values, such as drinking water quality, recreational use of water, and fishing. Since the lake is highly visible as a public natural resource and is the headwaters for the Everglades, it is important to quantify these relationships so that performance measures can be developed for these potential benefits.

Invertebrates, Fish, and other Aquatic Fauna

Based on responses of other eutrophic lakes, it can be predicted with a relatively high degree of certainty that if pelagic sediments display reduced organic loading and anoxia, as a result of reduced phosphorus inputs, abundance of pollution-tolerant oligochaetes will decrease and other less tolerant species will return. Likewise, there is a relatively high certainty that restoration of near-shore bulrush and submerged vegetation communities will result in increased abundance of macro-invertebrate taxa. There is less certainty regarding the response of littoral macro-invertebrates to nutrient reductions and hydrologic restoration, reflecting a general lack of information about how invertebrate communities are distributed across the littoral landscape.

Factors potentially controlling distribution and abundance of pelagic and near-shore fish have been examined in short-term survey studies, and there is some preliminary information on diets of major fish in the pelagic, near-shore, and littoral zones. Beyond that, we know very little about how the lake's fishery responds to changes in vegetation community structure, nutrient loads, and changes in resource composition (e.g., zooplankton and macro-invertebrates). Given the importance of fish as a recreational resource and as food for wading birds and other animals in the lake, this is a critical information gap.

Even less is known about reptiles, amphibians, and other animals that use the lake for foraging and/or nesting. Only limited survey studies have been performed and need to be supplemented with detailed studies of relationships between vegetation, hydroperiod, and aquatic animal occurrence, as well as studies to determine the role of animals in the littoral food web. Given the absence of information in this area, a logical starting point for a research program is a synthesis of available information from other sub-tropical sytems from the literature.

Littoral Vegetation Mosaic

The relationship between certain taxa of emergent littoral vegetation and hydroperiod is relatively well-known because the link has been established from intensive GIS mapping and multivariate modeling (Richardson et al. 1995) and because controlled experiments have shown how variations in water level affect establishment and growth of key plant taxa (Smith et al. 2004). The focus of experiments has been on torpedograss, *Melaleuca*, and spikerush. Studies are needed for other dominant littoral plant taxa. For example, a link between waterlily expansion and long hydroperiod is circumstantial, since this species is known to respond both to hydroperiod and increased phosphorus inputs (SFWMD 1999). Because dense waterlily degrades spikerush habitat, this merits further consideration.

There is some understanding of how littoral periphyton responds to nutrients, as a result of a series of controlled experiments (Havens et al. 1997, 2004), and we can draw inferences about how phosphorus inputs may have led to increased cattail spatial extent in certain littoral locations based on research in the Everglades. Less is known about how changes in phosphorus input affect other littoral plants or the higher trophic levels that they support.

Snail Kites, Wading Birds, and Waterfowl

There is considerable uncertainty about how structure of littoral zone vegetation affects nesting success of wadinig birds in Lake Okeechobee. For example, we do not know whether large-scale losses of willow documented in recent decades are limiting the population size of any species of wading birds that use the lake. Likewise, there is no information on the consequences of birds using less preferred nesting substrate. These questions, and similar issues regarding snail kites and migratory waterfowl, need to be considered in a regional context.

SUMMARY

A conceptual model was developed to illustrate major linkages between stressors (e.g., excessive phosphorus inputs, water-level regulation, invasion by non-native species), ecological processes, and values (e.g., fishing, wildlife habitat, ecotourism) in Lake Okeechobee, the largest lake in the southeastern USA. The model was used to synthesize current research results, to develop hypotheses and predictions about how conditions in the lake will change in response to regional restoration projects, and to identify gaps in knowledge about the system. For this ecosystem, results indicate a predominance of information regarding processes related to phosphorus dynamics in the pelagic zone and plant-hydroperiod interactions in the littoral zone. Considerably less is known about nitrogen dynamics, near-shore and littoral nutrient dynamics, plant-animal habitat interactions, and food-web processes. There is considerable uncertainty regarding how fish, amphibians, reptiles, and birds will respond to reduced nutrient loading and changes in seasonal fluctuation of water levels in this lake. Additonal research in these areas may lead to substantive changes in the structure of the model presented here and perhaps to changes in science-based recommendations of how to manage this large lake ecosystem.

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LITERATURE CITED

Aldridge, F. J., E. J. Phlips, and C. L. Schelske. 1995. The use of nutrient enrichment bioassays to test for spatial and temporal distribution of limiting factors affecting phytoplankton dynamics in Lake Okeechobee, Florida. Archiv fur Hydrobiologie, Advances in Limnology 45:177–190.

Baker, C. D. and E. H. Schmitz. 1971. Food habits of adult gizzard and threadfin shad in two ozark reservoirs. p. 385–395. *In* G. E. Hall (ed.) Reservoir Fisheries and Limnology. American Fishery Society, Washington, DC, USA.

Barbiero, R. P. and E. B. Welch. 1992. Contribution of benthic blue-green algal recruitment of lake populations and phosphorus translocation. Freshwater Biology 27:249–260.

Barnett, B. S. and R. W. Schneider. 1974. Fish populations in dense submersed plant communities. Hyacinth Control Journal 12:12–14.

Beaver, J. R. and K. E. Havens. 1996. Seasonal and spatial variation in zooplankton community structure and their relation to possible controlling variables in Lake Okeechobee. Freshwater Biology 36: 45–56.

Bell, F. W. 1987. The Economic Impact and Valuation of the Recreational and Commercial Fishing Industries of Lake Okeechobee, Florida. Florida Game and Fresh Water Fish Commission, Tallahassee, FL, USA.

Bellrose, F. C. 1976. Ducks, Geese and Swans of North America. Stackpole Books, Harrisburg, PA, USA.

Bennetts, R. E., M. W. Callopy, and S. R. Beissinger. 1988. Nesting Ecology of Snail Kites in Water Conservation Area 3A. United States Geological Survey, Biological Resources Division, Cooperative Fish and Wildlife Research Unit, Gainesville, FL, USA.

Bennetts, R. E. and W. M. Kitchens. 1997. The Demography and Movements of Snail Kites in Florida. United States Geological Survey, Biological Resources Division, Cooperative Fish and Wildlife Research Unit, Gainesville, FL, USA. Technical Report 56.

Brezonik, P. L., E. C. Blancher, V. B. Myers, C. L. Hilty, M. K. Leslie, C. R. Kratzer, G. D. Marbury, N. R. Snyder, T. L. Crisman, and J. J. Messer. 1979. Factors Affecting Primary Production in Lake Okeechobee, Florida. Clewiston, FL, USA. Report 07-79-01 to the Florida Sugar Cane League.

Brezonik, P. L. and D. R. Engstrom. 1999. Modern and historic accumulation rates of phosphorus in Lake Okeechobee, Florida. Journal of Paleolimnology 20:31–46.

Bull, L. A., D. D. Fox, D. W. Brown, L. J. Davis, S. J. Miller, and J. G. Wullschleger. 1995. Fish distribution in limnetic areas of Lake Okeechobee, Florida. Archiv fur Hydrobiologie, Advances in Limnology 45:333–342.

Burkholder, J. M., R. G. Wetzel, and K. L. Klomparens. 1990. Direct comparison of phosphate uptake by adnate and loosely attached microalgae within an intact biofilm matrix. Applied and Environmental Microbiology 56:2882–2890.

Canfield, D. E., Jr., K. A. Langeland, M. J. Maceina, W. T. Haller, J. V. Shireman, and J. R. Jones. 1983. Trophic classification of lakes with aquatic plants. Canadian Journal of Fisheries and Aquatic Sciences 40:1713–1718.

Canfield, D. E. and M. V. Hoyer. 1988. The eutrophication of Lake Okeechobee. Lake and Reservoir Management 4:91–99.

Carr, J. F. and J. K. Hiltunen. 1965. Changes in the bottom fauna of western Lake Erie from 1930 to 1961. Limnology and Oceanography 10:551–569.

Carignan, R. and J. Kalff. 1982. Phosphorus release by submerged plants: significance to epiphyton and phytoplankton. Limnology and Oceanography 27:419–427.

Carter, M. R., L. A. Burns, T. R. Cavinder, K. R. Dugger, P. L. Fore, D. B. Hicks, H. L. Revells, and T. W. Schmidt. 1973. Ecosystems Analysis of the Big Cypress Swamp and Estuaries. Region IV, United States Environmental Protection Agency, Atlanta, GA, USA.

Chamberlain, E. B., Jr. 1960. Florida Water Populations, Habitats and Management. Federal Aid Project W-19-R, Florida Game and Fresh Water Fish Commission, Tallahassee, FL, USA. Technical Bulletin No. 7. Ecological Report Number DI-SFEP-74-51.

Chick, J. H. and C. C. McIvor. 1994. Patterns in the abundance and composition of fishes among beds of different plants: viewing the littoral zone as a landscape. Canadian Journal of Fisheries and Aquatic Sciences 51:2873–2882.

Cichra, M. F., S. Badylak, N. Henderson, B. H. Rueter, and E. J. Phlips. 1995. Phytoplankton community structure in the open water zone of a shallow subtropical lake (Lake Okeechobee, FL, USA). Archiv fur Hydrobiologie, Advances in Limnology 45: 157–175.

Conrow, R. A., A. V. Zale, and R. W. Gregory. 1990. Distribution and abundance of early life stages of fishes in a Florida lake dominated by aquatic plants. Transactions of the American Fisheries Society 119:521–528.

Crisman, T. L. and J. R. Beaver. 1990. Applicability of biomanipulation for managing eutrophication in the subtropics. Hydrobiologia 200:177–185.

Crisman, T. L., E. J. Phlips, and J. R. Beaver. 1995. Zooplankton seasonality and trophic state relationships in Lake Okeechobee, Florida. Archiv fur Hydrobiologie, Advances in Limnology 45: 213–232.

Darby, P. C., P. L. Valentine-Darby, R. E. Bennetts, J. D. Croop, H. F. Percival, and W. M. Kitchens. 1997. Ecological Studies of Apple Snails (*Pomacea paludosa*). Florida Cooperative Fish and Wildlife Research Unit, Gainesville, FL, USA.

David, P. 1994. Wading bird nesting at Lake Okeechobee, Florida: an historic perspective. Colonial Waterbirds 17:69–77.

East, T. L., K. E. Havens, A. J. Rodusky, and M. A. Brady. 1999. *Daphnia lumholtzi* and *Daphnia ambigua*: population comparisons of an non-native and a native cladoceran in Lake Okeechobee, FL, USA. Journal of Plankton Research 21:1537–1551.

Engstrom, D. E., S. P. Schottler, P. R. Leavitt, and K. E. Havens. 2005. A re-evaluation of cultural eutrophication of Lake Okeechobee, Florida, using mult-proxy sediment records. Ecological Applications, in press.

Esler, D. 1990. Waterfowl habitat use on a Texas reservoir with *Hydrilla*. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 44:390–400.

Erwin, R. M. 1983. Feeding habitats of nesting wading birds: spatial use and social influences. The Auk 100:960–970.

FDEP. 2000. Draft Phosphorus Total Maximum Daily Load (TMDL) for Lake Okeechobee. Florida Department of Environmental Protection, Tallahassee, FL, USA.

Fisher, M. M, K. R. Reddy, and R. T. James. 2001. Long-term changes in the sediment chemistry of a large shallow subtropical lake. Lake and Reservoir Management 17:217–232.

Flaig, E. G. and K. E. Havens. 1995. Historical trends in the Lake Okeechobee ecosystem I. Land use and nutrient loading. Archiv fur Hydrobiologie Monographische Beitrage 107:1–24.

Flaig, E. G. and K. R. Reddy. 1995. Fate of phosphorus in the Lake Okeechobee watershed, Florida, USA: overview and recommendations. Ecological Engineering 5:127–142.

Fox, D. D., S. Gornak, T. D. McCall, D. W. Brown, and C. J. Morris. 1993. Lake Okeechobee Fisheries Investigations Completion Report. Florida Game and Fresh Water Fish Commission, Tallahassee, FL, USA.

Frederick, P. C. and M. G. Spalding. 1994. Factors affecting reproductive success of wading birds (Ciconiiformes) in the Everglades ecosystem. p. 659–692. *In* S.M. Davis and J.C. Ogden (eds.) Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Fredrickson, L. H. and T. S. Taylor. 1982. Management of seasonally flooded impoundments for wildlife. United States Fish and Wildlife Service, Washington, DC, USA. Research Publication # 148.

Fry, B., P. L. Mumford, F. Tam, D. D. Fox, G. L. Warren, K. E. Havens, and A. D. Steinman. 1999. Trophic position and individual feeding histories of fish from Lake Okeechobee, Florida. Canadian Journal of Fisheries and Aquatic Sciences 56:590–600.

Furse, J. B. and D. D. Fox. 1994. Economic fishery valuation of five vegetation communities in Lake Okeechobee, Florida. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 48:575–591.

Gawlik, D. E. 2002. The effects of prey availability on the numerical response of wading birds. Ecological Monographs 72:329–346.

Goodwin, T. M. 1979. Waterfowl management practices employed in Florida and their effectiveness on native and migratory waterfowl populations. Florida Scientist 3:123–129.

Gray, P. N. 1993. The Ecology of a Southern Mallard: Florida's Mottled Duck. Ph. D. Dissertation. University of Florida, Gainesville, FL, USA.

Grimshaw, H. J., K. E. Havens, B. Sharfstein, A. Steinman, D. Anson, T. East, R. Maki, A. Rodusky, and K. R. Jin. 2002. The effects of shading on morphometric and meristic characteristics of Wild Celery (*Vallisneria americana*) transplants from Lake Okeechobee, FL, USA. Archiv fur Hydrobiologie 155:65–81.

Hanlon, C. G., R. L. Miller, and B. F. McPherson. 1998. Relationships between wind velocity and underwater irradiance in a shallow lake (Lake Okeechobee, FL, USA). Journal of the American Water Resources Association 34:951–961.

Hanlon, C. G. 1999. Relationships between total phosphorus concentrations, sampling frequency, and wind velocity in a shallow polymictic lake. Lake and Reservoir Management 15:39–46.

Hanlon, C. G. and K. Langeland. 2000. Comparison of experimental strategies for control of torpedograss. Journal of Aquatic Plant Management 38:40–47.

Hanlon, C. G. 2005. The distribution of bulrush (*Scirpus californicus*) and influence of environmental conditions on plant growth during a 26 year period in a shallow subtropical lake. Aquatic Botany, in press.

Havens, K. E. 1995. Secondary nitrogen limitation in a subtropical lake impacted by non-point source agricultural pollution. Environmental Pollution 89:241–246.

Havens, K. E., N. G. Aumen, R. T. James, and V. H. Smith. 1996a. Rapid ecological changes in a large subtropical lake undergoing cultural eutrophication. Ambio 25:150–155.

Havens, K. E., L. A. Bull, G. L. Warren, T. L. Crisman, E. J. Phlips, and J. P. Smith. 1996b. Food web structure in a subtropical lake ecosystem. Oikos 75:20–32.

Havens, K. E., T. L. East, and J. R. Beaver. 1996c. Experimental studies of zooplankton-phytoplankton-nutrient interactions in a large subtropical lake (Lake Okeechobee, FL, USA). Freshwater Biology 36:579–597.

Havens, K. E. 1997. Water levels and total phosphorus in Lake Okeechobee. Lake and Reservoir Management 13:16–25.

Havens, K. E. and T. L. East. 1997. Carbon dynamics in the grazing food chain of a subtropical lake. Journal of Plankton Research 19: 1687–1711.

Havens, K. E., T. L. East, A. J. Rodusky, and B. Sharfstein. 1997. Littoral periphyton responses to nitrogen and phosphorus: and experimental study in a subtropical lake. Aquatic Botany 63:267–290.

Havens, K. E. and R. T. James. 1997. A critical evaluation of phosphorus management goals for Lake Okeechobee. Lake and Reservoir Management 13:292–301.

Havens, K. E., E. J. Phlips, M. F. Cichra, and B. L. Li. 1998. Light availability as a possible regulator of cyanobacteria species composition in a shallow subtropical lake. Freshwater Biology 39: 547–556.

Havens, K. E., K. A. Work, and T. L. East. 2000. Relative efficiencies of carbon transfer from bacteria and algae to zooplankton in a subtropical lake. Journal of Plankton Research 22:1801–1809.

Havens, K. E. 2003. Submerged aquatic vegetation correlations with depth and light attenuating materials in a shallow subtropical lake. Hydrobiologia 493:173–186.

Havens, K. E., D. Fox, S. Gornak, and C. Hanlon. 2005. Aquatic vegetation and largemouth bass population responses to water level variations in Lake Okeechobee, Florida (USA). Hydrobiologia 539:225–237.

Havens, K. E., J. Hauxwell, A. C. Tyler, S. Thomas, K. J. McGlathery, J. Cebrain, I. Valiela, A. D. Steinman, and S. J. Hwang. 2001b. Complex interactions between autotrophs in shallow marine and freshwater ecosystems: implications for community responses to nutrient stress. Environmental Pollution 113:95–107.

Havens, K. E., K. R. Jin, A. J. Rodusky, B. Sharfstein, M. A. Brady, T. L. East, N. Iricanin, R. T. James, M. C. Harwell, and A. D. Steinman. 2001a. Hurricane effects on a shallow lake ecosystem and its response to a controlled manipulation of water level. The Scientific World Journal 1:44–70.

Havens, K. E. and C. L. Schelske. 2001. The importance of considering biological processes when setting total maximum daily loads (TMDL) for phosphorus in shallow lakes and reservoirs. Environmental Pollution 113:1–9.

Havens, K. E., M. C. Harwell, M. A. Brady, B. Sharfstein, T. L. East, A. J. Rodusky, D. Anson, and R. P. Maki. 2002. Large-scale mapping and predictive modeling of submerged aquatic vegetation in a shallow eutrophic lake. The Scientific World Journal 2:949–965.

Havens, K. E. and W. W. Walker, Jr. 2002. Development of a total phosphorus concentration goal in the TMDL process for Lake Okeechobee, FL, USA. Lake and Reservoir Management 18:227–238.

Havens, K. E., B. Gu, and C. Kendall. 2003b. Stable isotope food web analysis of a large subtropical lake: alternative explanations for 15-N enrichment of pelagic vs. littoral fisheries. The Scientific World Journal 3:613–622.

Havens, K. E., R. T. James, T. L. East, and V. H. Smith. 2003a. N: P ratios, light limitation, and cyanobacterial dominance in a subtropical lake impacted by non-point source nutrient pollution. Environmental Pollution 122:379–390.

Havens, K. E., B. Sharfstein, M. A. Brady, T. L. East, M. C. Harwell, R. P. Maki, and A. J. Rodusky. 2004a. Recovery of submerged plants from high water stress in a large subtropical lake in Florida, USA. Aquatic Botany 78:67–82.

Hopson, M. S. and P. V. Zimba. 1993. Temporal variation in the biomass of submersed plants in Lake Okeechobee, FL, USA. Journal of Aquatic Plant Management 31:76–81.

Horne, A. J. 1977. Nitrogen fixation—a review of this phenomenon as a polluting process. Progress in Water Technology 8:359–372.

Horne, A. J. 1979. Nitrogen fixation in Clear Lake, California. Diel studies on Aphanizomenon and Anabaena blooms. Limnology and Oceanography 24:329–241.

Howard, K. S., W. F. Loftus, and J. C. Trexler. 1995. Seasonal dynamics of fishes in artificial culvert pools in the C-111 basin, Dade County, Florida. Florida International University and National Biological Service, Miami, FL, USA.

Hwang, S. J., K. E. Havens, and A. D. Steinman. 1998. Phosphorus kinetics of planktonic and benthic assemblages in a shallow subtropical lake. Freshwater Biology 40:729–745.

James, R. T., B. L. Jones, and V. H. Smith. 1995a. Historical trends in the Lake Okeechobee ecosystem II. Nutrient budgets. Archiv fur Hydrobiologie, Monographische Beitrag 107:25–47.

James, R. T., V. H. Smith, and B. L. Jones. 1995b. Historical trends in the Lake Okeechobee ecosystem III. water quality. Archiv fur Hydrobiologie, Monographische Beitrag 107:49–69.

Janacek, J. A. 1988. Literature Review on Fish Interactions with Aquatic Plants with Special Reference to the Upper Mississippi River. Upper Mississippi River Conservation Commission, Rock Island, IL, USA.

Jeske, C. W. 1985. Time and Energy Budgets of Wintering Ring-Necked Ducks (Aythya collaris) (L.) in North-Central Florida. M.S. thesis, University of Florida, Gainesville, FL, USA.

Jin, K. R., J. H. Hamrick, and T. Tisdale. 2000. Application of three-dimensional hydrodynamic model for Lake Okeechobee. Journal of Hydraulic Engineering 126:758–771.

Johnson, F. A. and F. Montalbano. 1984. Selection of plant communities by wintering waterfowl on Lake Okeechobee, Florida. Journal of Wildlife Management 48:174–178.

Jones, B. 1987. Lake Okeechobee eutrophication research and management. Aquatics 9:21–26.

Kahl, M. P., Jr. 1964. Food ecology of the wood stork (*Mycteria americana*) in Florida. Ecological Monographs 34:97–117.

Kushlan, J. A. 1976. Wading bird predation in a seasonally fluctuating pond. The Auk 93:464–476.

Kushlan, J. A. 1981. Resource use strategies of wading birds. Wilson Bulletin 93:145–163.

Lockhart, C. S. 1995. The effect of water level variation on the growth of *Melaleuca* seedlings from the Lake Okeechobee littoral zone. MS Thesis. Florida Atlantic University, Boca Raton, FL, USA.

Loftus, W. F. and J. A. Kushlan. 1987. Freshwater fishes of southern Florida. Bulletin of the Florida State Museum, Biological Sciences 31:147–344.

Loftus, W. F. and A. Eklund. 1994. Long-term dynamics of an Everglades small-fish assemblage. p. 461–484. *In* S. M. Davis and J. C. Ogden (eds.) Everglades: the Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL, USA.

Maceina, M. J. and D. M. Soballe. 1991. Wind-related limnological variation in Lake Okeechobee, Florida. Lake and Reservoir Management 6:93–100.

Maceina, M. J. 1993. Summer fluctuations in planktonic chlorophyll *a* concentrations in Lake Okeechobee, Florida: the influence of lake levels. Lake and Reservoir Management 8:1–11.

McCormick, P. V., P. S. Rawlik, K. Lurding, E. P. Smith, and F. H. Sklar. 1996. Periphyton-water quality relationships along a nutrient gradient in the northern Florida Everglades. Journal of the North American Benthological Society 15:433–449.

Montalbano, F., S. Hardin, and W. M. Hetrick. 1979. Utilization of *Hydrilla* by ducks and coots in central Florida. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 33:36–42.

Moore, P. A., K. R. Reddy, and M. M. Fisher. 1998. Phosphorus flux between sediment and overlying water in Lake Okeechobee, Florida: spatial and temporal variations. Journal of Environmental Quality 27:1428–1439.

Moss, B., J. Madgwick, and G. Phillips. 1996. A Guide to the Restoration of Nutrient-Enriched Shallow Lakes. Environment Agency, Broads Authority, United Kingdon.

Murphy, T., K. Hall, and I. Yesaki. 1983. Co-precipitation of phosphate and calcite in a naturally eutrophic lake. Limnology and Oceanography 28:58–67.

Newman, S., J. B. Grace, and J. W. Koebel. 1996. Effects of nutrients and hydroperiod on Typha, Cladium and Eleocharis: Implications for Everglades restoration. Ecological Applications 6:774–783.

Olila, O. G. and K. R. Reddy. 1993. Phosphorus sorption characteristics of sediments in shallow eutrophic lakes of Florida. Archiv fur Hydrobiologie 129:45–65.

Paerl, H. W. 1988. Nuisance phytoplankton blooms in coastal, estuarine, and inland waters. Limnology and Oceanography 33:823–847.

Pesnell, G. L. and R. T. Brown. 1976. Map of the vegetation of Lake Okeechobee, Florida. South Florida Water Management District, West Palm Beach, FL, USA.

Phlips, E. J., P. V. Zimba, M. S. Hopson, and T. L. Crisman. 1993. Dynamics of the plankton community in submerged plant dominated regions of Lake Okeechobee, FL, USA. Proceedings International Association of Theoretical and Applied Limnology 25: 423–426.

Phlips, E. J., F. J. Aldridge, and P. Hansen. 1995. Patterns of water chemistry, physical and biological parameters in a shallow subtropical lake (Lake Okeechobee, FL, USA). Archiv fur Hydrobiologie, Advances in Limnology 45:117–135.

Phlips, E. J., M. Cichra, K. E. Havens, C. Hanlon, S. Badylak, B. Rueter, M. Randall, and P. Hansen. 1997. Relationships between phytoplankton dynamics and the availability of light and nutrients in a shallow subtropical lake. Journal of Plankton Research 19: 319–342.

Reynolds, C. S. 1984. The Ecology of Freshwater Phytoplankton. Cambridge University Press, Cambridge, United Kingdom.

Richardson, J. R. and T. T. Harris. 1995. Vegetation mapping and change detection in the Lake Okeechobee marsh ecosystem. Archiv fur Hydrobiologie, Advances in Limnology 45:17–39.

Richardson, J. R., T. T. Harris, and K. A. Williges. 1995. Vegetation correlations with various environmental parameters in the Lake Okeechobee marsh ecosystem. Archiv fur Hydrobiologie, Advances in Limnology 45:41–61.

Rozas, L. P. and W. E. Odum. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. Oecologia 77:101–106.

Sas, H. 1989. Lake Restoration by Reduction of Nutrient Loading: Expectation, Experiences, Extrapolations. Academia Verlag Richarz, Berlin, Germany.

Scheffer, M. 1989. Alternative stable states in eutrophic shallow freshwater systems: a minimal model. Hydrobiological Bulletin 23:73–85.

Schelske, C. L. 1984. In situ and natural phytoplankton assemblage bioassays. p. 15–47. *In* L. E. Shubert (ed.) Algae as Ecological Indicators. Academic Press, New York, NY, USA.

SFWMD. 1999. Everglades Interim Report. South Florida Water Management District, West Palm Beach, FL, USA.

SFWMD. 2002. Surface Water Improvement and Management (SWIM) Plan—Update for Lake Okeechobee. South Florida Water Management District, West Palm Beach, FL, USA.

Sharfstein, B. and A. D. Steinman. 2001. Growth and survival of the Florida apple snail (Pomacea paludosa) fed three naturally occurring plant assemblages. Journal of the North American Benthological Society 20:84–95.

Smith, J. P. 1995. Foraging flights and habitat use of nesting wading birds (Ciconiiformes) at Lake Okeechobee, Florida. Colonial Waterbirds 18:139–158.

Smith, J. P. and M. W. Collopy. 1995. Colony turnover, nest success and productivity, and causes of nest failure among wading birds (Ciconiiformes) at Lake Okeechobee, Florida (1989–1992). Archiv fur Hydrobiologie, Advances in Limnology 45:287–316.

Smith, J. P., J. R. Richardson, and M. W. Collopy. 1995. Foraging habitat selection among wading birds (Ciconiiformes) at Lake Okeechobee, Florida, in relation to hydrology and vegetative cover. Archiv fur Hydrobiologie, Advances in Limnology 45:247–285.

Smith, J. P. 1997*a*. Nesting season food habits of four species of Herons and Egrets and Lake Okeechobee, Florida. Colonial Waterbirds 20:198–220.

Smith, J. P. 1997*b*. An energy-circuit population model for Great Egrets (*Ardea alba*) at Lake Okeechobee, Florida, USA. Ecological Modelling 97:1–21.

Smith, D. H., R. M. Smart, and C. G. Hanlon. 2004. Influence of water level on torpedograss establishment in Lake Okeechobee, Florida. Lake and Reservoir Management 20:1–13.

Steinman, A. D., R. H. Meeker, A. J. Rodusky, W. P. Davis, and S. J. Hwang. 1997a. Ecological properties of charophytes in a large subtropical lake. Journal of the North American Benthological Society 16:781–793.

Steinman, A. D., R. H. Meeker, A. J. Rodusky, W. P. Davis, and C. D. McIntire. 1997b. Spatial and temporal distribution of algal biomass in a large subtropical lake. Archiv fur Hydrobiologie 139: 29–50.

Steinman, A. D., K. E. Havens, H. J. Carrick, and R. VanZee. 2002a. The past, present, and future hydrology and ecology of Lake Okeechobee and its watershed. p. 19–37. *In* J. Porter and K. Porter (eds.) The Everglades, Florida Bay, and Coral Reefs of the Florida Keys: An Ecosystem Sourcebook. CRC Press, Boca Raton, FL, USA.

Steinman, A. D., K. E. Havens, A. J. Rodusky, B. Sharfstein, R. T. James, and M. C. Harwell. 2002b. The influence of environmental variables and a managed water recession on the growth of charophytes in a large subtropical lake. Aquatic Botany 72:297–313.

Sykes, P. W., Jr. 1987. The feeding habits of snail kite in Florida, USA. Colonial Waterbirds 10:84–92.

Turner, R. L. 1994. The effects of hydrology on the population dynamics of the Florida apple snail (*Pomacea paludosa*). Special publication SJ94-SP3, St. Johns River Water Management District, Pilatka, FL, USA.

Turner, R. L. 1996. Use of stems of emergent plants for oviposition by the Florida apple snail (*Pomacea paludosa*) and implications for marsh management. Florida Scientist 59:34–49.

van der Valk, A. G. 1994. Effects of prolonged flooding on the distribution and biomass of emergent species along a freshwater wetland coenocline. Vegetatio 110:186–196.

Van Rees, K. C. J., K. R. Reddy, and P. S. C. Rao. 1996. Influence of benthic organisms on solute transport in lake sediments. Hydrobiologia 317:31–40.

Vermaat, J. E., L. Santamaria, and P. J. Roos. 2000. Water flow across and sediment trapping in submerged plant beds of contrasting growth form. Archiv fur Hydrobiologie 148:549–562.

Warren, G. L. and M. J. Vogel. 1991. Lake Okeechobee invertebrate studies. Study II in the Lake Okeechobee-Kissimmee River-Everglades Resource Evaluation Report. Wallop-Breaux Project F-52 Completion Report to the United States Department of Interior, Washington, DC, USA.

Warren, G. L. and D. A. Hohlt. 1994. Lake Okeechobee invertebrate community investigations. Study IV in the Lake Okeechobee-Kissimmee River-Everglades Resource Evaluation Report. Wallop-Breaux Project F-52 Completion Report to the United States Department of Interior, Washington, DC, USA.

Warren, G. L., M. J. Vogel, and D. D. Fox. 1995. Trophic and distributional dynamics of Lake Okeechobee sublittoral benthic invertebrate communities. Archiv fur Hydrobiologie, Advances in Limnology 45:317–332.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

White, D. H. and D. James. 1978. Differential use of fresh water environments by wintering waterfowl of coastal Texas. Wilson Bulletin 90:99–111.

Williges, K. A. and T. T. Harris. 1995. Seed bank dynamics in the Lake Okeechobee marsh ecosystem. Archiv fur Hydrobiologie, Advances in Limnology 45:79–94.

Zaffke, M. 1984. Wading bird utilization of Lake Okeechobee marshes 1977–1981. South Florida Water Management District, West Palm Beach, FL, USA. Technical Publication 84–9.

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