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Primary Research Paper

Aquatic vegetation and largemouth bass population responses to water-level variations in Lake Okeechobee, Florida (USA)

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Abstract

A five-year study examined the responses of submerged aquatic vegetation (SAV), emergent vegetation, and largemouth bass (*Micropterus salmoides*) to variations in water level in a large lake in Florida, USA. SAV was assessed using a combined transect survey/spatial mapping approach, emergent vegetation was quantified with aerial photography and GIS, and bass were surveyed by electro-shocking. During the period leading up to this study (1995–1999), water levels were high in the lake, and the SAV was reduced in spatial extent and biomass, compared to its condition in the early 1990s. Spatial extent of emergent vegetation also was low, and largemouth bass surveys indicated low densities and failure to recruit young fish into the population. This was attributed to the lack of critical vegetative habitat. In spring 2000, the lake was lowered by discharging water from major outlets, and this was followed by a regional drought. Water levels dropped by 1 m, and there was widespread development of *Chara* lawns in shoreline areas, with coincident increases in water clarity. There was some germination of vascular SAV, but *Chara* was the extreme dominant, such that structural complexity remained low. There was no substantive improvement in bass recruitment. During 2001, water levels declined further, and emergent plants germinated in exposed areas of the lake bottom. SAV was restricted to sites farther offshore, and continued to be dominated by *Chara*. There again was no bass response. In 2002, conditions changed when water levels increased to a moderate depth, flooding shoreline habitat to ~0.5 m. Vascular SAV increased in biomass and spatial extent, such that the community developed a high structural complexity. At the same time, emergent aquatic plants developed dense stands along the western shoreline. Largemouth bass had a strong recruitment of young fish for the first time in 5 years. Recruitment continued to be successful in 2003, when spatial extent of SAV was somewhat reduced by higher water but total biomass and diversity remained high. These results demonstrate an important effect of inter-annual variation in water depth on the population dynamics of aquatic plants and fish in a subtropical lake.

Introduction

Lakes occurring in subtropical regions, where there is large seasonal and inter-annual variation in rainfall and net evapotranspiration (Abtew, 2001) can display considerable variation in water level, particularly when those lakes have relatively short residence times and/or are regulated for water supply or flood control (Steinman et al., 2002). Large variations in water level can influence ecosystem dynamics if there is deep inundation of the littoral zone, causing flooding stress to aquatic vegetation, or at the other extreme, drying of a substantive portion of the littoral habitat. Prolonged deep flooding can result in losses of both emergent and submerged aquatic vegetation

(SAV) due to light limitation (Schwarz et al., 2002; Havens, 2003) and/or increased shoreline wave energy (Havens et al., 2001). When the vegetation is lost, changes in water quality can occur, including increased turbidity and algal blooms (Scheffer et al., 1994; Jeppesen et al., 1998; Blindow et al., 2002). Depending on the circumstances, periods of extreme low water may be the only means of attaining the critical irradiance necessary for net growth of SAV if the lake has switched to a turbid state (Scheffer, 1998). Extreme low water also may be required for the germination of shoreline emergent vegetation (Cronk & Fennessy, 2001).

Changes in aquatic vegetation caused by variation in water level can have secondary impacts on fish populations, both by food web effects (Crowder & Cooper 1982) and through loss of structural habitat (Valley & Bremigan, 2002; Pratt & Smokorowski, 2003). Plant communities and their associated epiphytic algae support macro-invertebrates, which in turn provide a food resource for forage fish that are consumed by piscivores. The vegetation also provides refuge for young fish, so that they have some chance to avoid predation (Savino & Stein, 1982; Rozas & Odum, 1988). Thus a loss of aquatic vegetation might be expected to result in a deteriorated condition of adult fish, and potentially the absence of entire year classes in the population.

We observed a large-scale loss of aquatic vegetation and impacts to fisheries in Lake Okeechobee, Florida, USA, when high water conditions persisted from 1995 to 1999. The spatial extent of SAV, which had been documented at 12,000 ha encompassing the North, West, and South shoreline areas in 1992 (Richardson & Harris, 1995), was reduced to two less than 1000 ha by 1999, and the plants were restricted to two beds in sheltered bays (Havens et al., 2001). The spatial extent of emergent vegetation, including bulrush (*Scirpus*) and cattail (*Typha*), also was reduced, with evidence that much of this loss was due to physical uprooting by wave energy (Havens et al., 2001). The Florida Fish and Wildlife Conservation Commission (FWC) reported at public meetings that the lake's most economically important sport fish, the largemouth bass, failed to recruit significant numbers of young fish into its population.

In response to this documented ecosystem stress, and concern among the public, resource management agencies, and elected officials, the South Florida Water Management District (SFWMD) carried out an emergency operation to lower water levels in the lake (Steinman et al., 2002). In spring 2000, water was discharged from the lake through major outlets to the East, West, and South, dropping water levels by approximately 30 cm. A drought then occurred in south Florida, and water level fell another 70 cm. It declined further and remained low until the fall of 2001. Here we describe some of the ecosystem-level responses to this natural experiment, considering data from 1999 to 2003, and focusing on: (1) responses of the SAV and emergent shoreline plant communities; and (2) changes in largemouth bass recruitment success.

Our expectation regarding bass was that successful recruitment of young fish into the population would not resume until a diverse assemblage of aquatic vegetation was re-established in the lake. If the recovering community of plants became dominated by a low growing monoculture (e.g., *Chara* or *Lyngbya*), successful bass recruitment was not expected to occur. The rationale was that a structurally diverse vegetation community provides both the refuge and food resources necessary for survival of young fish.

Study site

Lake Okeechobee (Latitude 26 °58′ N, Longitude 80 °50′ W) is a large (Area ~1730 km^2), shallow (mean depth 2.7 m, maximum depth 5 m) lake that has experienced accelerated eutrophication in recent decades. It occurs in a region with a subtropical climate, a distinct summer wet season (higher rainfall, water temperatures 30–35 °C, ~14 h photoperiod), and a winter dry season (lower rainfall, water temperatures 15–25 °C, ~12 h photoperiod). The lake has a pelagic zone of approximately 1180 km^2, where primary producers are exclusively phytoplankton. Along the western shoreline, there is a large (430 km^2) littoral wetland with a mosaic of aquatic vegetation, and on a shoreline shelf between these two zones, there is a 120 km^2 shoal that can support a diverse community of SAV, bulrush (*Scirpus californicus*), spikerush (*Eleocharis* spp.), and knot grass (*Paspalidium germinatum*). Dominant submerged species are shrimpgrass (*Chara zeylanica*), *Hydrilla verticillata*, tapegrass (*Vallisneria americana*), Illinois pondweed (*Potamogeton illinoinensis*), and southern naiad (*Najas guadalupensis*). The fish community includes over 25 taxa that vary in relative biomass between the pelagic, littoral wetland, and shoal areas (Furse & Fox, 1994; Bull et al., 1995). Dominant species (based on their numeric density) include threadfin shad (*Dorosoma petenense*), black crappie (*Pomoxis nigromaculatus*), bluegill (*Lepomis macrochirus*), white catfish (*Ameiurus catus*), gizzard shad (*Dorosoma cepedianum*), redear (*Lepomis microlophus*), and Florida gar (*Lepisosteus platyrhincus*).

Sampling methods

Submerged aquatic vegetation – transect sampling

SAV was sampled along fixed transects (Fig. 1) established perpendicular to the shoreline in the South, West, and North near-shore zone of Lake Okeechobee. No transects occurred on the eastern side of the lake, which is deeper and has a shoreline of large rocks with little or no vegetation. Sampling began in May 1999 and is ongoing. Frequency has varied over the life of the program, with bi-monthly sampling in 1999, monthly or

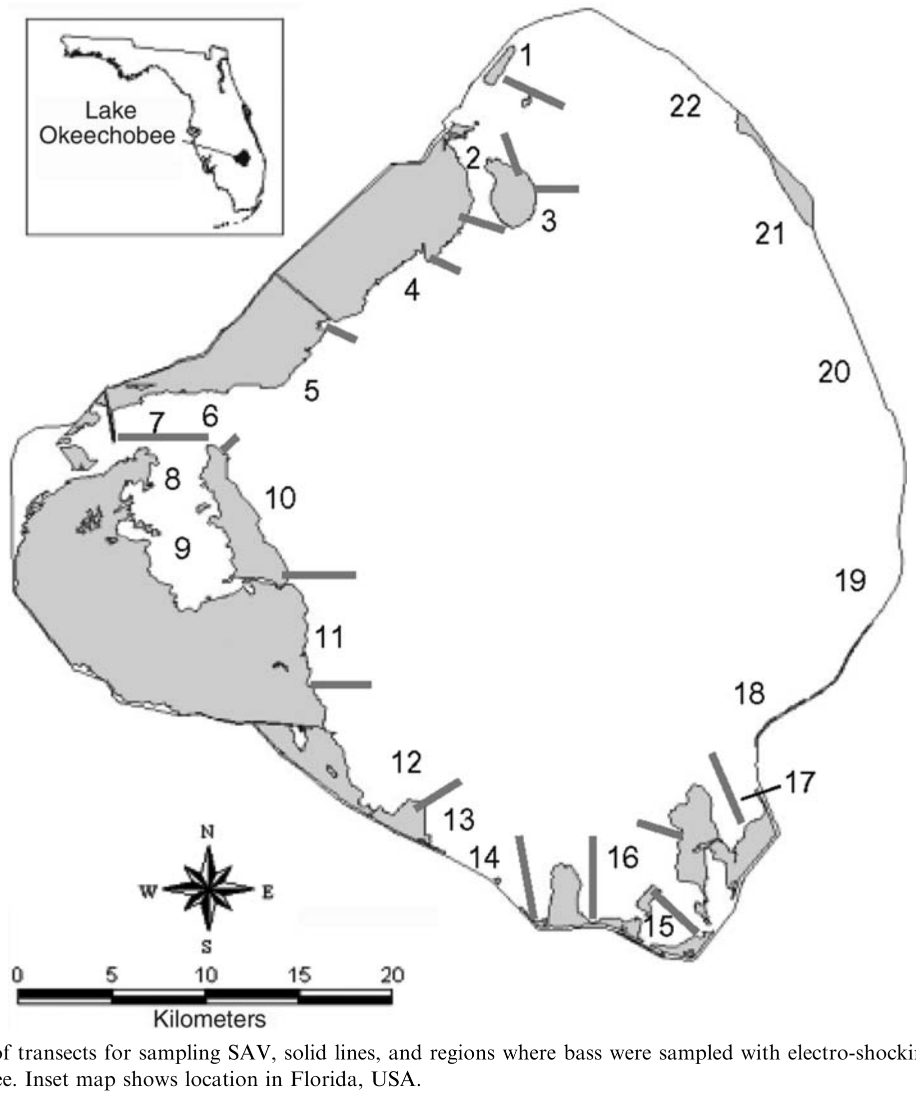

Figure 1. Map of transects for sampling SAV, solid lines, and regions where bass were sampled with electro-shocking (numbers) in Lake Okeechobee. Inset map shows location in Florida, USA.

bi-monthly sampling in spring–summer 2000–2002, and quarterly sampling from 2002 to present. Here we examine averaged data from May to September in each sampling year (in 2003, there only were data from July), which is considered relevant for comparison with bass population data collected each fall. From 1999 to January 2001, and after June 2001, SAV sampling was done at three fixed stations along each transect. The most distant point offshore on each transect corresponded to the maximal lakeward extent of submerged plants during a period of low water in the late 1980s, when transects were established (Zimba et al., 1995). The other two stations were located at approximately 50 m from the shoreline, and at the mid-point between the terminal stations. From April to June 2001, when water levels were low and certain shoal stations were dry, additional stations were added at the lakeward end of transects because plants expanded farther offshore. In some transects, as many as six stations were sampled, while in others, just one station was used.

From 1999 to mid-summer 2000, submerged plants were sampled by harvesting all material enclosed by three 0.5 m^2 weighted plastic frames, which were randomly tossed from the boat at each station. Sampling of *Chara*, which was < 30 cm tall during this study, was done with three samples of a small Ponar dredge (total area sampled 0.08 m^2). During winter, or when water depth was greater than 2 m, we first surveyed the station by randomly swimming over the bottom. If no plants were observed, additional sampling was not performed. Starting in August 2000, the sampling method was modified to increase efficiency and ensure greater consistency in sampling at different times of the year and at stations of varying depth. The vascular plants and *Chara* were collected by triplicate samples of a tool constructed from two standard garden rakes, bolted together to create a tongs-like device that sampled 0.3 m^2 of plants. A comparison of quadrat vs. tong sampling indicates a good agreement between methods, over the range of plant taxa and sediment types sampled (Havens et al., 2004). In the laboratory, the plant samples were sorted by species, stripped of epiphyton, and dried in ovens at 60 °C until successive measurements of biomass confirmed that weight loss no longer was occurring. Dry weight biomass was expressed on a per area basis (g dw m^{-2}).

Submerged aquatic vegetation–mapping

In late summer each year (August–September), the SFWMD also developed maps of the lake's SAV in order to estimate spatial extent. This qualitative sampling did not examine plant biomass. Detailed methods and results are provided in Havens et al. (2002), and therefore only summary methods and results are provided here. Basically, the shoreline shoal area was overlaid by a 1×1 km grid (0.5×0.5 km grid in 2000) in ArcInfo®, the center points of each grid cell were loaded into GPS units, and SAV was sampled at those points by navigating to them by boat and sampling plants with the tongs device described above. Several hundred sites were sampled each year. Field data were downloaded from the GPS logger into ArcInfo®, where maps were developed for each of the measured attributes and spatial extents were calculated in hectares. It was assumed that data collected at the center-point of a grid cell represented what occurred in that entire cell. While this may introduce error into the results, it was a necessary assumption given the large spatial scale of sampling. No mapping was done in 1999, however, a rough estimate of the spatial extent of SAV was developed by the SFWMD and FWC based on aerial photographs of surviving plant beds and qualitative field surveys.

Emergent aquatic vegetation

Temporal changes in the distribution and areal coverage of bulrush and the other emergent plants located along the lakeward edge of the littoral zone were evaluated by the SFWMD using color infra red (IR) photographs collected each spring from 1999 to 2003. Stereo pairs of photographs were viewed using a Bausch and Lomb zoom 95 transfer stereoscope. The boundary lines of each plant community were traced onto transparent sheets of acetate according to the unique spectral signatures emitted on the color IR photographs. Each traced polygon defined the location and areal coverage of a monotypic plant community, a mixed plant community, or open water. The polygons were scanned, converted into a GIS coverage using ArcInfo®, and labeled according to the type of plant community they represented. The final geo-referenced vegetation maps were used to evaluate the distribution of emergent plants and to quantify their spatial extent.

Bass population structure

In October 1999–2003, the FWC conducted annual sampling events at 22 sites around Lake Okeechobee via electrofishing (Fig. 1). Electrofishing gear consisted of a 5.5 m aluminum boat equipped with a 90 horsepower engine, 5000 W generator and a VVP-15 coffelt electroshocker unit. Within each of the 22 sites, three repetitions of 15 min duration were conducted totaling 990 min of effort. All stunned largemouth bass were collected, measured to the nearest millimeter of total length (TL), weighed to the nearest gram (g) and live released. Length structure was analyzed by apportioning length frequency distributions into 2 cm length groups (i.e. 2–3.99 cm equaled the 2 cm length group). Length frequency plots and catch rates (CPUE; fish per minute) were then generated for each of the 4 years. Annual length frequency plots were examined for changes in distribution patterns while observed catch rates were used to evaluate changes in density. Length frequency plots and catch rates were then compared to corresponding annual vegetation density data to evaluate possible linkages between recruitment success and vegetation expansion.

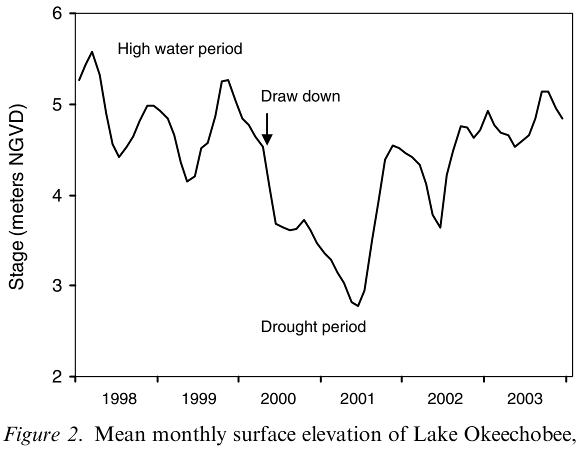

Figure 2. Mean monthly surface elevation of Lake Okeechobee, Florida, January 1998 to December 2003.

Results

Variation in water levels and related conditions

Mean surface elevation of the lake was high in the late 1990s, leading up to the time period encompassed by this 5-year study. In 1999, the minimal stage was >4 m national geodetic vertical datum (NGVD, formerly mean sea level), and maximal stage was over 5.2 m (Fig. 2). Under those circumstances, the shelf area that supports SAV was submersed in up to 2 m of turbid (Secchi depths <0.2 m) water (Havens et al., 2001). Stage rapidly dropped in spring 2000, when the managed recession occurred, and then remained relatively constant during that summer at near 3.7 m, such that the shoal areas had <0.5 m deep water and displayed significant increases in transparency by late summer, coincident with rapid expansion of *Chara* (Havens et al., 2004). There was a further decline in stage from fall 2000 to summer 2001, when the lake had a record low stage of 2.8 m, at which time much of the shoal area became dry. The habitat was re-inundated in fall 2001, when normal rainfall patterns returned to south Florida and high watershed runoff resulted in a rapid increase of stage to near 4.5 m. Stage then declined again in 2002, to near 4 m during the summer months. During 2003 stage varied between 4.5 and 5.0 m.

Aquatic vegetation recovery

The mean summer biomass of SAV along the transects was near 5 g dw m^{-2} in 1999 (Fig. 3(a)), with nearly all of the biomass concentrated in two beds located in the south and west shoal regions (Havens et al., 2004). In 2000, when stage declined after the managed recession, SAV biomass increased, on average, to 12 g dw m^{-2}. The spatial extent of SAV (Fig. 3(b)) increased from an estimated 1500 ha in summer 1999 to nearly 18,000 ha in summer 2000. Total SAV biomass continued to increase from 2001 to 2003, although not as dramatically as between the first 2 years of sampling. Total spatial extent of SAV was 14,500 ha in 2001, 17,500 ha in 2002, and 12,600 ha in 2003. The decline in spatial extent in 2003 was attributed to prolonged high water from fall 2002 to summer 2003, and a period during winter 2002 when high stage coincided with strong

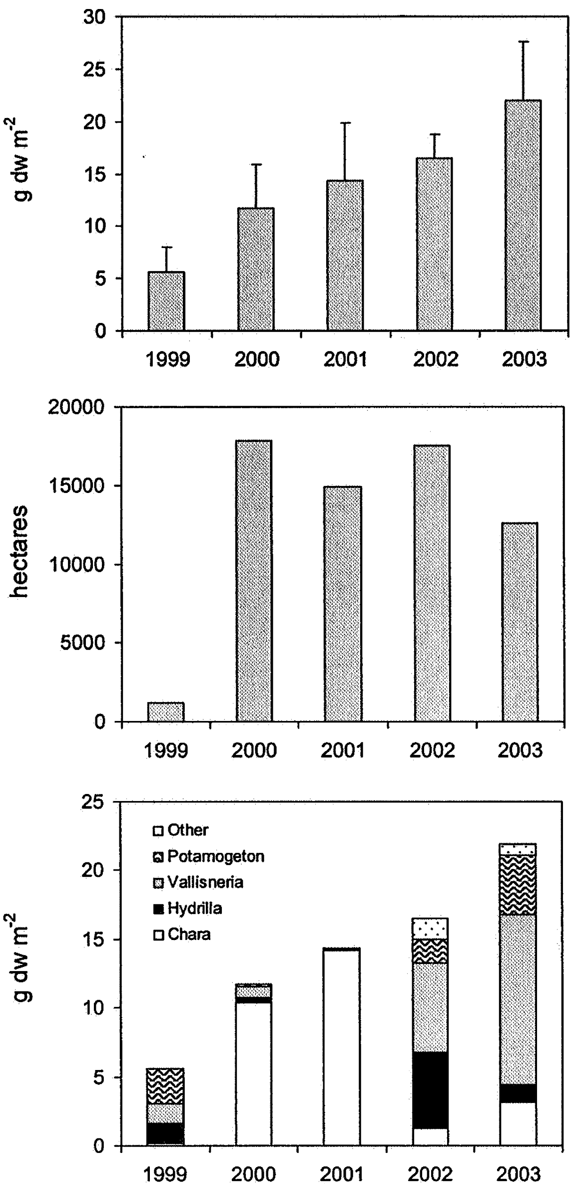

Figure 3. Submerged aquatic vegetation (SAV) data from Lake Okeechobee for the period from 1999 to 2003, showing (a) summer mean biomass of plants surveyed along transects; (b) spatial extent of plants determined by late summer mapping; and (c) mean summer taxonomic composition of the plants surveyed along the transects.

southeast winds that produced large waves. These waves uprooted plants in exposed shoal areas. However, lake-wide SAV biomass was not reduced because large beds of vascular plants persisted in sheltered bays and behind islands. The plants in these beds had grown to the water surface in 2002 and were able to continue net growth despite rather deep water in 2003.

The taxonomic composition of SAV changed over the 5 years of study (Fig. 3(c)). In 1999, when biomass was low, it was nearly all due to vascular plants, in particular *Potamogeton*, *Vallisneria*, and *Hydrilla*. When the biomass and spatial extent of SAV increased in 2000 and 2001, it was almost exclusively *Chara*, which formed uniform lawns of 10–30 cm height over much of the shoal area. After water levels increased in 2002, the community structure switched to strong dominance by vascular plants, with *Vallisneria* and *Hydrilla* accounting for most of the biomass, followed by *Potamogeton* and a variety of other taxa (*Najas*, *Utricularia*, and *Ceratophyllum*). The loss of *Chara* occurred in fall 2001, and was attributed to the effects of a wind storm that may have uprooted *Chara* but not the vascular plants, which subsequently colonized the shoal area in spring 2002 (Havens et al., 2004). In 2003 the SAV continued to be dominated by vascular plants, although there was some increase in *Chara* relative biomass. The dominant species in 2003 were *Vallisneria*, followed by *Potamogeton*, and then *Hydrilla*.

Of the three dominant emergent plants observed in this study (Table 1), only *Scirpus* was present along the northwest and southwest shoreline of the lake during 1999–2001. However, when lake stages increased to moderate levels in 2002, after the drought period, there was wide-spread growth of *Eleocharis* and *Paspalidium*, totaling 375 and 437 ha, respectively. The development of *Eleocharis* in that particular region of the lake was of considerable interest, because it had been documented in that same area during a survey conducted in 1973 (Pesnell & Brown, 1976), at a time when mean water levels were considerably lower than what they typically had been in the highly managed system of the 1980s and 1990s. Quantitative data are not yet available for emergent plant cover in 2003, however our preliminary analysis of aerial photographs and our field observations indicate that *Eleocharis* and *Paspalidium* both displayed reduced spatial extent in that year compared to 2002.

Table 1. Spatial extent (hectares) of three dominant emergent vegetation taxa along the northwest and southwest shoreline areas of Lake Okeechobee, based on aerial photography taken in summer 1999–2003. The symbol (–) indicates no data for that location/year

	Northwest			Southwest		
Year	*Scirpus*	*Eleocharis*	*Paspalidium*	*Scirpus*	*Eleocharis*	*Paspalidium*
1999	91	0	0	–	0	0
2000	–	0	0	111	0	0
2001	113	0	0	–	0	0
2002	56	221	193	117	154	244
2003*	–	–	–	–	–	–

*Maps are being produced in GIS at this time – preliminary results are described in text.

Largemouth bass recovery

There were changes in both the density and population size structure of largemouth bass during this study (Fig. 4), coinciding with the onset of the diverse community of SAV and emergent shoreline plants in 2002. During the bass surveys conducted in 1999–2001, common features were low CPUE values, ranging from 0.11 to 0.18 fish min^{-1}, and a near absence of juvenile fish, indicating failed recruitment. In contrast, the CPUE in 2002 was 0.41 fish min^{-1}, and there was successful recruitment, as evidenced by large numbers of 10–22 cm fish in the population. In 2003, the CPUE remained high, at 0.48 fish min^{-1}, and there again was successful recruitment of young fish.

Discussion

We documented changes in SAV, emergent vegetation, and population density and size structure of largemouth bass in response to a period of low water level in Lake Okeechobee, Florida's largest lake. The results indicate that despite several years of stress from high water, and a large scale loss of vegetation (Havens et al., 2001), the ecosystem was able to recover many of its natural habitat values. However, duration of recovery was approximately 3 years, rather than happening immediately in the year when high water stress was removed. This somewhat low resilience existed despite the fact that the lake occurs in the subtropics, where water temperatures and solar radiation remain quite high in winter, so that year-round growth (albeit somewhat reduced, due to shorter photoperiod than in summer) of plants and animals can occur.

Aquatic vegetation recovery

The recovery sequence for SAV is described in detail with monthly data by Havens et al. (2004), and therefore it will be discussed at a more general level in this synthesis paper, where multiple components of the community are being considered. A key feature of the SAV recovery, in comparison to patterns documented in temperate lakes, was early colonization of the lake bottom by *Chara*, and subsequent replacement of that macro-alga by vascular SAV. In a similar study, following community succession in Lake Veluwemeer, the Netherlands, Van den Berg et al. (1999) concluded that *Chara* was a superior competitor to the dominant vascular plant, *Potamogeton*, and that *Chara* lawns were a stable endpoint in plant community succession following recovery from periods of reduced light penetration. In an earlier study, Blindow (1992) documented the replacement of *Potamogeton* by *Chara* in a Swedish lake, and both Scheffer (1998) and Van Nes et al. (2002) described *Chara* lawns as part of a stable clear water state.

We suspect that a reason for *Chara* success during 2000–2001 in Lake Okeechobee was the occurrence of a massive bank of oospores in the lake sediments that germinated under relatively low irradiance conditions, and then were able to maintain net growth even when the water had not yet cleared of suspended sediments and algal blooms (Havens et al., 2004). Harwell & Havens (2003) showed that when sediments from the shoal

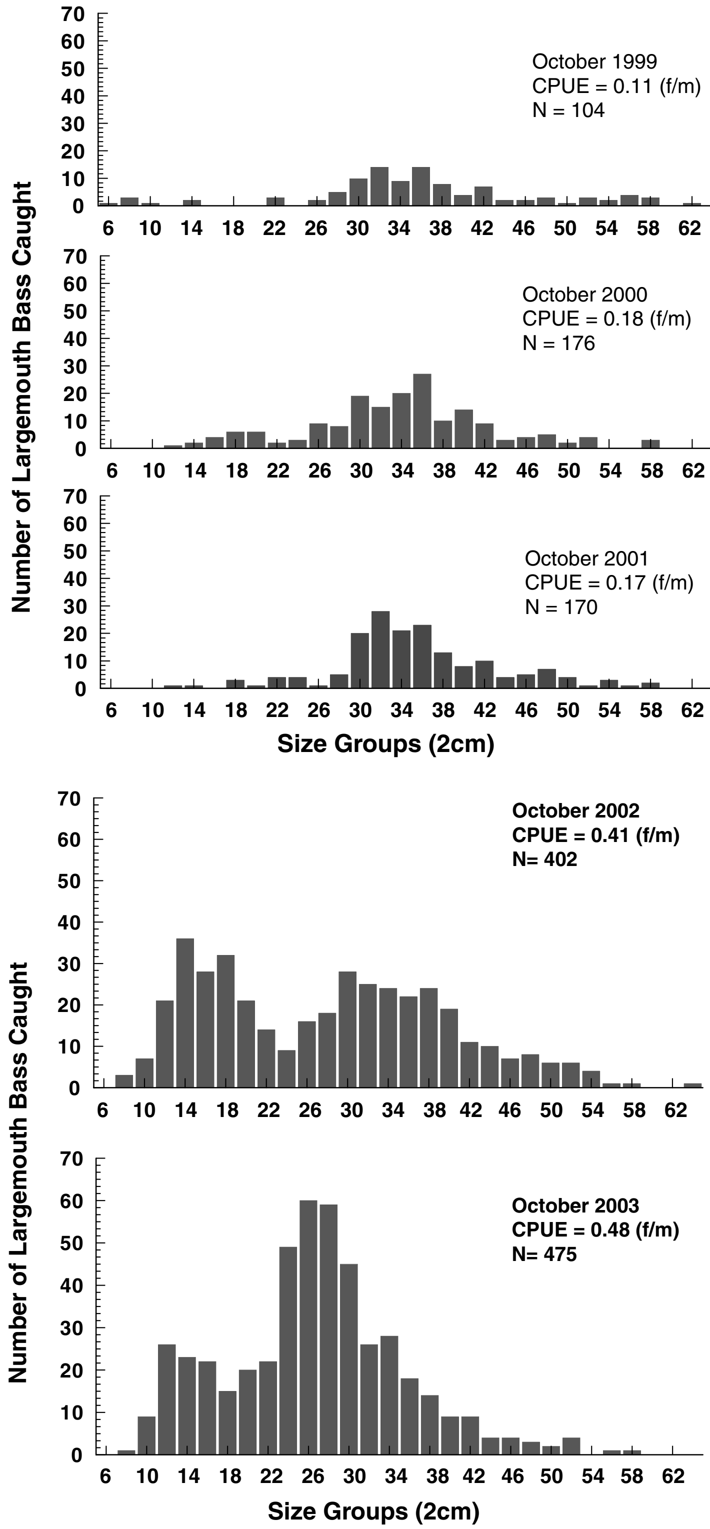

Figure 4. Population size structure of largemouth bass in Lake Okeechobee, determined from electro-shocking in October 1999 to 2003. In each year the annual sampling effort was 990 min (22 sites, three 15 min repetitions at each site).

area are covered with water in the laboratory and provided with 100 μmol photons m^{-2} s^{-1} irradiance, germination of *Chara* greatly exceeds germination of vascular SAV. Furthermore, in controlled tank studies performed with *Chara* and *Vallisneria* from Lake Okeechobee, Grimshaw et al. (2002, 2004) established that the minimum irradiance required for net growth is lower in *Chara* than in the vascular plant.

When water clarity improved in areas of the lake where *Chara* lawns expanded (Havens et al., 2001, 2004), this may have created conditions conducive to vascular plant germination and growth. The plants may not have expanded in 2000 or 2001 due to competition by the dense *Chara*, and the switch to vascular plant dominance in 2002 may have been the result of a strong physical forcing function – high wave energy. At this time we know the following, based on field observations. There was a strong wind storm in fall 2001, coincident with the switch from *Chara* to vascular SAV dominance, and a substantial amount of *Chara* was observed uprooted in the water column of the lake coincident with that event. We suggest that in Lake Okeechobee, with its very long fetch and periods of high wind/wave energy (Havens et al., 2001), *Chara* cannot survive for long periods as the dominant species, because it is easily uprooted. When this occurs, vascular plants can become dominant in the community if they previously have been able to colonize areas with *Chara*.

We compared Lake Okeechobee, where *Chara* dominance is ephemeral, with a typical Dutch lake where *Chara* is a stable dominant, by considering their dynamic ratios (Hakanson, 1982). Dynamic ratio is the square root of lake surface area divided by mean depth. Lakes with higher ratios are more susceptible to sediment resuspension by wind. The dynamic ratio of Lake Okeechobee is approximately 14, compared to a ratio of 4 in Lake Veluwemeer, where Van den Berg et al. (1999) documented the stable dominance of *Chara*. The interplay between wind, wave energy, and relative dominance of *Chara* vs. vascular plants in shallow subtropical lakes certainly merits additional study, to rule out that it is not some other feature of the subtropics that precludes stable *Chara* dominance.

The development of dense stands of *Eleocharis* and *Paspalidium* along the lake's western shoreline in 2002 was consistent with results of earlier research that documented a dense seed bank of wetland plants in the sediments (Williges & Harris, 1995). This is typical of shallow aquatic ecosystems (e.g., Van der Valk & Davis, 1978; Cronk & Fennessy, 2001). As indicated, a 1973 vegetation survey (Pesnell & Brown, 1976), when water levels were lower, indicated stands of *Eleocharis* in the same locations where they appeared in 2002. Prior to 2000 germination may have been suppressed by high water, which probably also was responsible for the loss of adult plants from this area in the years since that survey was conducted. Milleson (1987) reported that *E. cellulosa* requires a dry period for seed germination, and Williges & Harris (1995) documented that when sediments were collected from the shoreline and littoral areas of Lake Okeechobee and submerged under 2–3 cm of water, *E. cellulosa* germinated in 58% of experimental samples. Another commonly emerging species was *Paspalum acuminatum*, which is quite similar in its appearance to *Paspalidum geminatum*, the taxon we observed in the shoal area in 2002. Williges & Harris (1995) did not find the later species, and we cannot confirm or refute their identification.

The continued survival of emergent aquatic plants in the shoal area of Lake Okeechobee will depend on water levels in upcoming years. Prolonged deep flooding of wetland plants can ultimately lead to stress if photosynthetic tissues are below the photic depth (Van der Valk, 1994), which is quite low in this lake (Havens & James, 1999) due to algal blooms and suspended sediment material. This situation occurred to some extent in 2003, when water depths exceeded 1 m in the shoreline shoal area for >14 months, and as noted, there were declines in density of *Paspalidium* and *Eleocharis*.

Largemouth bass recovery

There is a large literature related to the population dynamics, feeding habits, habitat requirements, and other aspects of the reproductive biology and ecology of largemouth bass. In the USA largemouth bass are one of the most economically important sport fishes. For example, an early 1990s survey indicated that over 50% of all anglers in the USA targeted largemouth bass in their fishing on freshwater systems (U.S. Department of Interior, 1996). Lake Okeechobee is known locally as the 'bass capital of the USA,' and there are over 500 permitted bass fishing tournaments annually on this lake. Thus an understanding of factors critical to the reproductive success of this fish is important both locally and regionally.

Hoyer & Canfield (1996) note that there are four key factors influencing recruitment of young bass into the adult population, all of which can be related to the presence of a complex vascular plant community: (1) availability of favorable spawning substrate; (2) protection of nests from wind; (3) availability of epiphytic invertebrates, forage fish, and other food resources; and (4) protection from predators. These authors examined the SAV and bass fisheries of 56 Florida lakes, and found that after factoring out effects of trophic state, there was a significant increase in the abundance of young largemouth bass with increasing percent volume infestation (PVI) of SAV. Our results were similar but more pronounced, perhaps because we compared extreme conditions (1999 vs. 2002–2003) and focused on just one lake, which reduces variability. Most interesting was Hoyer & Canfield's (1996) finding that abundance of young largemouth bass was not correlated with percent area covered (PAC) by SAV. This suggests that it was not just the presence of SAV, but its physical structure that is important for controlling bass population dynamics. Our results confirm this conclusion, and similar results have been obtained in reservoirs elsewhere in the USA, though they did not find such a close linkage between bass recruitment and SAV community structure as documented here. Sammons et al. (1999), for example, found that in Normandy Reservoir, Tennessee, USA, the survival of young bass was positively related to water level, and suggested that this was due to inundation of peripheral wetland habitat.

There are factors other than SAV structure that influence survival of young largemouth bass. Maceina & Bettoli (1998) found that in four reservoirs along the Tennessee River, survival was best correlated with water residence time, presumably because at short residence times, there was reduced production at lower trophic levels (i.e., the plankton), and subsequent food limitation of forage fish. Ludsin & DeVries (1997) concluded that survival of young bass was largely controlled by first winter mortality, which in turn, was a function of the amount of lipid reserves in the fish tissue, and ultimately, the date of hatch and shift to piscivory. This situation is not expected to apply to south Florida lakes, where winter water temperatures remain above 15 °C. In this study, there was no significant relationship between water temperature and bass recruitment or catch success, regardless of whether we considered yearly average temperatures, winter temperatures, spawning season temperatures, or temperature at the time of fish sampling.

The factor responsible for the improved recruitment of largemouth bass in Lake Okeechobee during 2002–2003 appears to be the increased structural complexity of the aquatic vegetation community that developed that year. However, we cannot determine from this study to what extent the bass response was due to protection of young fish from predation, vs. better conditions for nesting and increased food availability – all of these go hand in hand with the SAV changes we observed.

Some of the year-to-year variation in bass population attributes, especially catch success for adult fish, might be related to sampling efficiency and/or migration from the pelagic zone. In 2000 and 2001, greater numbers of large bass were caught than in 1999, despite poor recruitment. This might be explained by increased catch success when the water was shallow in the later two years. Likewise, the increased number of adult bass caught in 2002 and 2003 could reflect migration, since adult bass in this lake are known to actively move between the pelagic and littoral zone (Fry et al., 1999). Importantly, however, these factors cannot explain the substantial increase in catch of young fish that occurred in 2002 and 2003, when deeper water and dense vegetation would be expected to reduce catch success, not cause it to increase.

Synthesis

A conceptual diagram (Fig. 5) summarizes events that occurred in Lake Okeechobee from 1999 to 2003, from the perspective of hydrologic changes, aquatic plant succession, and largemouth bass recruitment. The plant community initially was

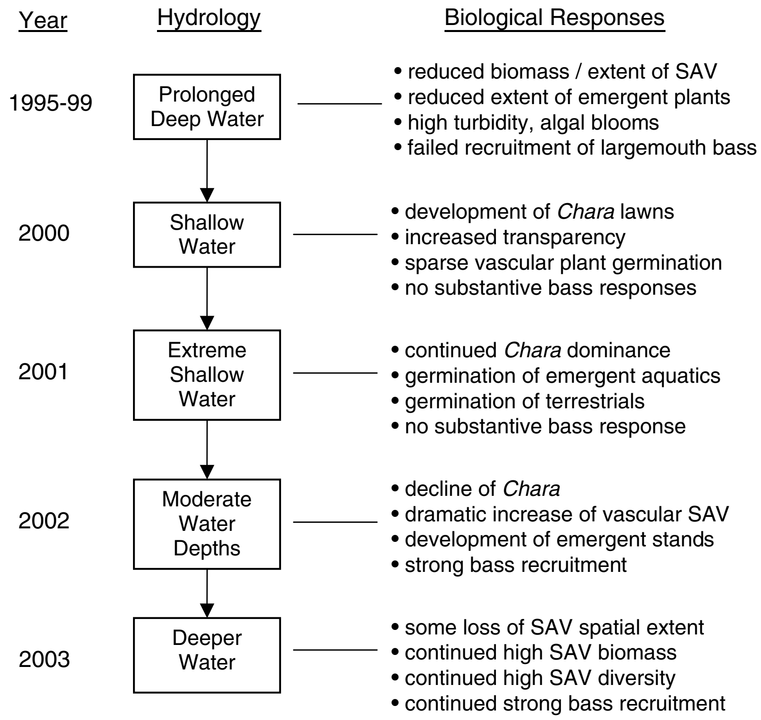

Figure 5. Conceptual diagram of hydrologic changes and ecosystem responses in Lake Okeechobee from 1999 to 2003, as described in detail in the text.

sparse and the FWC documented failed recruitment of the lake's largemouth bass population. The SFWMD carried out a managed recession of the lake in spring 2000, which when combined with a drought, dropped water depths by approximately 1 m. During summer 2000, widespread lawns of *Chara* developed in the South and West shoal areas, and water transparency increased. There was some germination of vascular plants, but their biomass and spatial extent remained relatively low. The community had a low and uniform vertical structure, resembling a lawn. In that year there was not a successful recruitment of young largemouth bass. This may have been due to a lack of cover for young fish to hide from predators, lack of suitable spawning habitat, or insufficient food resources to support young fish. As the drought progressed, extreme low water occurred in summer 2001, and large shoal areas were exposed. In areas that remained inundated, *Chara* continued to dominate the SAV in terms of both biomass and spatial extent. During that year, there was germination of emergent plants on the exposed lake bottom, much of it being terrestrial vegetation (authors' personal observations), but also emergent aquatic plants.

In summer 2002, when moderate water levels returned following increased rainfall and runoff from the watershed, *Eleocharis* and *Paspalidium* expanded along the western shore. At the same time, the SAV switched to dominance by vascular SAV, including *Vallisneria*, *Hydrilla*, and *Potamogeton*, which provided a more complex structure than *Chara* lawns. The loss of *Chara* near the end of 2001 may have been due to a wind storm that uprooted the fragile macro-alga, leaving vascular plants behind to colonize the landscape. When *Chara* was lost in November, water temperatures were relatively low and photoperiod relatively short, and perhaps for this reason there were no algal blooms in the shoreline areas. This timing may have facilitated the rapid expansion of the vascular plant community. With a highly structured habitat present in 2002, there was successful recruitment of young fish into the population. Bass recruitment continued to be good in

2003, when spatial extent of SAV was reduced, but large beds with high biomass and diversity persisted around the lake shore.

These findings suggest a link between the structure of aquatic vegetation and population dynamics of a sport fish in a subtropical lake, and agree with results previously documented for temperate systems, in particular reservoirs where there is marked variation in water level. In Lake Okeechobee, the temporal dynamics of plants and fish are likely to continue as long as the lake functions as the major storage location for water in the regional flood control system of South Florida. As water managers work towards regional restoration efforts to alleviate some of the extremes in water level in this lake, research results such as those obtained in this study will be used to identify optimal hydrologic variation to sustain a diverse community of aquatic vegetation and successful recruitment of bass and other fish, vs. the wildly fluctuating community that occurred in recent decades. This is a challenge locally, and for any large lake ecosystem that has multiple uses for flood protection, water supply, and wildlife habitat.

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