Effects of a Large-Scale Habitat Enhancement Project on Habitat Quality for Age-0 Largemouth Bass at Lake Kissimmee, Florida

MICHEAL S. ALLEN AND KIMBERLY I. TUGEND

Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st Street, Gainesville, Florida 32653, USA

Abstract.—A habitat enhancement project was conducted from 1995–1996 to remove macrophytes and organic matter from about half of the 80-km shoreline of Lake Kissimmee, Florida. Habitat quality was evaluated in enhanced and control (i.e., debilitated areas left intact after enhancement) areas and largemouth bass density and growth in enhanced sites from 1998–2000. Control sites were characterized by low dissolved oxygen throughout the day (mean < 2 mg/L), high aquatic macrophyte biomass (> 50 kg/m^2), and the percent of coverage of aquatic macrophytes (PAC) from 100 percent. Qualitative fish sampling in control sites yielded no sportfishes. Enhanced sites generally had mean DO greater than 4 mg/L, relatively low aquatic macrophyte biomass (mean < 5 kg/m^2), and intermediate PAC (5–90%). Mean density of age-0 largemouth bass in enhanced sites averaged about 100 fish/ha from May–August of both years and was positively related to PAC in block nets in 1998. Growth rates of age-0 largemouth bass in 1998 and 1999 were rapid compared to historical records at Lake Kissimmee and a database some records of 56 Florida lakes. Diet analysis of age-0 largemouth bass revealed that fish were important prey (> 30% of diets by weight) from June–March of both years. Early piscivory of age-0 largemouth bass probably resulted in rapid growth rates. The habitat enhancement project created quality habitat for age-0 largemouth bass at Lake Kissimmee, and benefits were prolonged relative to previous enhancement efforts at another lake.

Introduction

Altered hydrology of many Florida lakes and rivers, primarily for flood control, has reduced the extent of natural water-level fluctuations compared to historic hydrologic regimes. Williams et al. (1985) noted that diminished water-level fluctuations have reduced maximum lake surface areas of some Florida lakes by about 20–50 percent. More stable water levels have resulted in "permanent" stands of very dense emergent plants in the narrow zone of lake fluctuation, which lead to excessive deposition of organic matter and eventual loss of littoral habitat (Moyer et al. 1995). Macrophyte species that commonly dominate the littoral region following water stabilization include pickerelweed *Pontederia cordata*, cattail *Typha* spp., smartweed *Polygonum* spp., and water primrose *Ludwidgia* spp. These vegetation communities are characterized as dense (percent-area coverage of 100%), with extremely high plant biomass and poor habitat for sportfishes including largemouth bass *Micropterus salmoides* (Moyer et al. 1995).

Habitat enhancement in Florida lakes (via lake drawdowns and muck removal) has been effective in improving sportfish abundance. Moyer et al. (1995) found that an extreme drawdown and sediment removal project at Lake Tohopekaliga, Florida resulted in increased electrofishing catch-per-effort of largemouth bass, bluegill *Lepomis macrochirus* and redear sunfish *L. microlophus*. Habitat enhancement also provided angler access to areas of the lake that were formerly inaccessible.

Habitat enhancement efforts, however, are costly, and benefits sometimes can be short-lived. The 1987 Lake Tohopekaliga habitat enhancement project cost about US$450,000, but enhanced sites debilitated to previous conditions within three years (Moyer et al. 1995). Moyer et al. (1995) documented higher densities of age-0 largemouth bass in enhanced versus control areas of Lake Tohopekaliga in the first year following habitat enhancement, but density estimates of age-0 largemouth bass were zero for both enhanced and control habitats in the second year.

Thus, past habitat enhancement efforts have not yielded long-term benefits to sportfish populations. Given the costs associated with enhancement, strategies to optimize benefits to sportfish populations and to lengthen the period of fishery benefit are essential. The objectives of this study were to: compare habitat quality, e.g., dissolved oxygen concentration, macrophyte biomass, in enhanced and control areas of Lake Kissimmee following a large-scale habitat enhancement project; measure age-0 largemouth bass density in enhanced sites and evaluate factors related to age-0 largemouth bass density; and use modal total length (TL) of age-1 fish to compare growth rates to historical data from the lake prior to enhancement.

Methods

Study Site

Lake Kissimmee is a 19,808-ha eutrophic lake (Florida Lakewatch 2000) located in Osceola County, Florida. Although historical annual water-level fluctuations sometimes exceeded 3 m (Moyer et al. 1993), however, water levels have been regulated via a series of locks since the 1960s, resulting in annual water-level fluctuations less than 1.5 m (Moyer et al. 1993). Subsequently, large expanses of high-density emergent macrophytes dominated inshore areas of the lake during 1990–1995.

A large-scale habitat enhancement project was conducted at Lake Kissimmee in 1995–1996 (Figure 1). Drawdown of the lake began in November 1995, and organic matter and plant biomass was removed from about half of the 80-km shoreline using bulldozers, front-end loaders, and dump trucks. Enhanced areas contained bare sand substrate after enhancement. The lake was refilled beginning in June 1996, and total cost of the project was $5–6 million. Unlike previous enhancement efforts in Florida (Moyer et al. 1995), pickerelweed in enhanced areas at Lake Kissimmee was targeted for annual herbicide treatments by the Florida Fish and Wildlife Conservation Commission to prevent rapid plant expansion. Airboats were used for application of herbicides (e.g., primarily Weedar and Rodeo) in enhanced areas each spring or summer from 1997 to 1999.

Inshore areas left unenhanced contained relatively homogeneous stands of pickerelweed and smartweed. These dense macrophyte and muck-dominated areas are termed “control” type habitats in this paper (Figure 1). Control areas remained relatively unchanged from conditions found throughout the inshore areas of the lake prior to the habitat enhancement project (M. Hulon, Florida Fish and Wildlife Conservation Commission, personal communication).

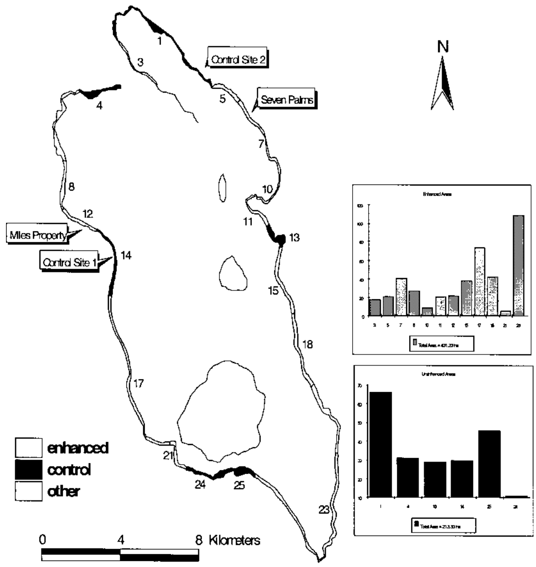

Figure 1. Enhanced and control (macrophyte dominated) areas at Lake Kissimmee based on habitat mapping in September 1998. Enhanced and control sample sites are shown. White areas indicate habitats that were not enhanced, but did not harbor high densities of macrophytes. Numbers adjacent to each section correspond to surface areas indicated on bar graphs. Total area of enhanced and control habitats was estimated by summation. Offshore macrophytes are not indicated on this map.

Mapping

A digital map depicting locations of lake-wide enhanced and control areas of Lake Kissimmee was constructed during September 1998. Lake Kissimmee was circled twice in an airboat equipped with a Trimble GeoExplorer Global Positioning Systems (GPS) receiver with differential correction. The first pass around the lake was used to map the lake boundary (outside edge of the lake). The lakeward edges of enhanced and control areas were mapped on the second pass. Enhanced and control areas around the lake were categorized according to a visual estimate of percent area covered with aquatic macrophytes (PAC). ArcInfo software was used to confirm that all coordinates lay within the historic lake boundary based on an existing digital map of the lake (Florida Geographic Database, University of Florida). Total area of enhanced and control areas in the lake were estimated by summing all control and enhanced areas (ha) from the digital map. To evaluate lake-wide changes in PAC between years, enhanced areas were surveyed again in September 1999.

Sampling for this project occurred bimonthly from May 1998 to March 2000 (starting about two years after completion of the enhancement project). Two enhanced sites (Miles Property and Seven Palms) and adjacent control sites were sampled for habitat characteristics and qualitative fish samples (Figure 1).

Dissolved oxygen concentrations (mg/L) (DO) were measured in control and enhanced sites during May–October of 1998 and 1999 with a model 85 Yellow Springs Instrument (YSI) meter. Measurements of DO were taken at about 40 percent of the depth at 8–10 randomly selected locations within each sample site. Because no differences in DO were found between the two control or the two enhanced sites across sample months in either year, dissolved oxygen data were grouped as "enhanced" and "control" habitats for each sample month. Dissolved oxygen data were analyzed with a three-way analysis of variance (ANOVA) with time period (morning (5:30–9 a.m.) and daytime (9 a.m.–3 p.m.) as blocks and habitats (control and enhanced), months, and study year (1998 and 1999) as factors. Interaction effects included in the analysis were month × habitat, year × habitat, and year × month × habitat. Variation attributed to the year*month interaction was not of interest and was not included in the analysis. We used the LSMEANS procedure (SAS 1996) to separate means if an interaction or a single factor was significant.

Age-0 largemouth bass were sampled with block nets during May, June, and August 1998 and May, July, and August of 1999 at both enhanced sites. Sample sizes varied among months, but the Miles Property site was usually sampled with six block nets, whereas the Seven Palms site, which was about twice as large, was usually sampled with 10–12 block nets. A 68.8-m block net (1-cm bar mesh) was pursed around the shore in a semicircle (total area = 0.075 ha), and rotenone was applied at 3 mg/L. Fish were collected by three to four people for 30–45 minutes. All fish collected were placed in 10 percent formalin and returned to the laboratory where they were identified as to species, measured to the nearest mm total length (TL) and weighed to the nearest 0.1 g. Age-0 largemouth bass were separated from other fishes and saved for diet analysis (described below). The number of age-0 largemouth bass collected in each net was divided by the area sampled (0.075 ha) to obtain density (fish/ha). To assess changes in age-0 largemouth bass density in enhanced sites between years, we used a repeated-measures ANOVA (Procedure MIXED, SAS 1997) with year as the fixed effect, enhanced sites as subjects, and month nested within year as the time variable. Density values were $\log_{10}$ transformed after adding one to all values to homogenize the variance. The LSMEANS procedure (SAS 1996) was used to separate means if the month effect was significant. Density of age-0 largemouth bass was also compared to a statewide database (Hoyer and Canfield 1996) to assess whether densities were relatively high or low compared to statewide averages.

Electrofishing transects (each 10 minutes) were used to sample largemouth bass in both enhanced sites during August, October, January, and March of each year. Seven Palms and Miles Property enhanced sites were sampled with 12 and 6 transects, respectively, each month. All electrofishing transects were conducted at night except for August 1998 samples, which were collected during daytime.

We used length frequencies were used to evaluate growth of 1998 and 1999 year-class largemouth bass, i.e., whether length frequencies of age-1 fish collected in March of 1999 and 2000 differed using a Kolmogorov-Smirnov test (both year classes approximately age-1). Modal total length of 1998 and 1999 year-class largemouth bass were compared to historical data at the lake (Moyer et al. 1993) to assess growth of fish before and after the habitat enhancement. Modal TLs were also compared to a statewide database (Hoyer and Canfield 1996) to assess growth at Lake Kissimmee compared to a statewide average.

Diet analysis was conducted on 1998 and 1999 year-class largemouth bass. Fish were returned to the laboratory where stomach contents were removed from up to 60 fish for each sample site. If large numbers of fish were collected (e.g., 80–150), the stomach contents were removed from a random sample of 60 fish per sample site each month. Fish in the diets were identified to the lowest possible taxon, and macroinvertebrates were identified to order, except for grass shrimp *Palaemonetes* spp., which were identified to genus. Stomach contents were counted and weighed (nearest mg). Frequency of occurrence was used to assess percent occurrence of fish and invertebrates in largemouth bass diets for each sample month, and mean percent composition by weight of invertebrates and fish in the diets was used to evaluate the relative importance of fish versus invertebrates for each sample month.

During summer of 1998 and 1999, aquatic macrophytes were sampled for biomass, and percent area coverage (PAC) was estimated visually within each block net. A total of five to eight 0.25-m^2 quadrats were placed randomly within each block net, and aquatic macrophytes were removed, identified to the lowest possible taxon, and weighed (wet) to the nearest 10 g with Pesola Inc. hanging scales. Quadrats were then averaged to obtain mean macrophyte biomass for each block net. We assessed changes in macrophyte biomass between years and enhanced sample sites with a repeated-measures ANOVA (Procedure MIXED, SAS 1997) using year, site (Miles Property and Seven Palms), and the year × site interaction as fixed effects, enhanced sites as subjects, and sample month nested within year as the time variable. The LSMEANS procedure (SAS 1996) was used to separate means if the year or site effects were significant. Correlation analysis was used to assess relations between PAC and age-0 largemouth bass density in 1998 and 1999. Macrophyte biomass in control sites was measured with five quadrats in the Miles Property site in 1998 and 1999 and five quadrats in the Seven Palms site in 1999.

Quantitative fish sampling occurred only in the enhanced sites because extremely high macrophyte biomass in control sites prevented boat operation and deployment of block nets or standard electrofishing. Qualitative fish samples were collected in both control sites during October 1999. Rotenone was applied to two areas (each about 0.04 ha) in each control site and fish were collected for 30–45 minutes. Fish collected were then identified to species, which provided presence / absence data of fishes for those areas.

Results

The digital map revealed an estimated 431 ha of enhanced habitat and 213 ha of remaining control habitat in 1998 (Figure 1). Visual estimates of PAC in lake-wide enhanced areas ranged from 0 to 50 percent in September 1998 and from 10 to 90 percent in September 1999. Thus, PAC generally increased in enhanced areas around the lake from 1998 to 1999. All control areas contained PAC of 100 percent in both years.

Mean DO concentrations were higher in enhanced areas than control areas in both morning and daytime samples during both years (Figure 2). The block effect (early morning versus daytime)

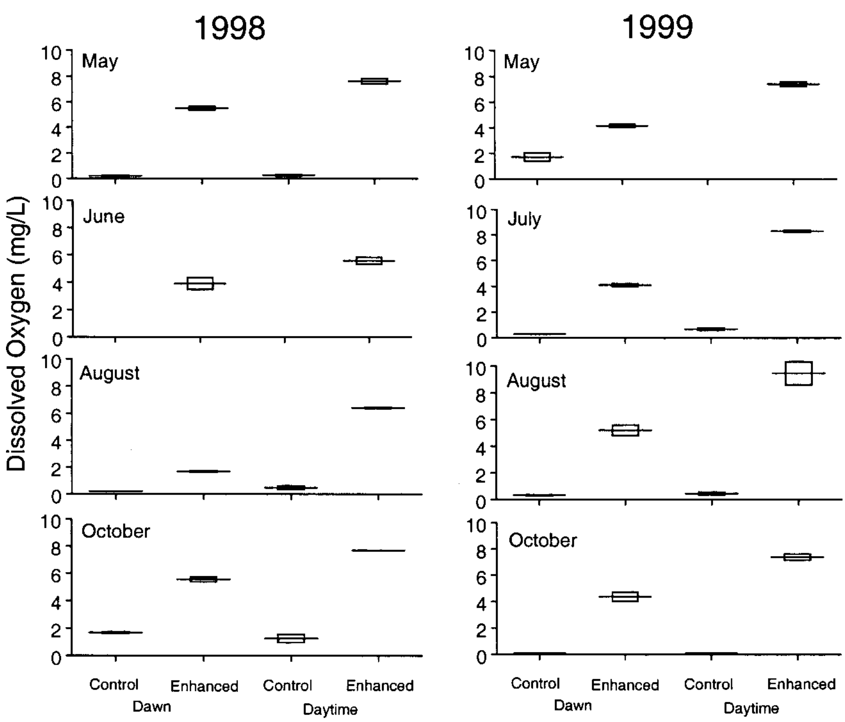

Figure 2. Mean dissolved oxygen concentrations ± 1 SE collected during dawn (5:30–9 a.m.) and daytime (9 a.m.–3 p.m.) in control and enhanced sample sites in 1998 (left panels) and 1999 (right panels). Sample months are shown. Missing values for control sites in June 1998 and May 1999 resulted from equipment failure. Three-way ANOVA found a significant years*month*sample area interaction ($P < 0.01$).

Table 1. Mean density (fish / ha), standard error (SE), coefficient of variation (CV = SD / 0 × 100%), the range (minimum and maximum observations), and sample size (*N* = number of block nets) of age-0 largemouth bass collected from two restored sites at Lake Kissimmee during 1998. Months of collection are indicated.

Year	Month	Site	Mean	SE	CV	Range	*N*
1998	May	Miles Property	91	54	130	0–290	5
1998	May	Seven Palms	80	49	120	0–200	4
1998	June	Miles Property	91	40	110	13–250	6
1998	June	Seven Palms	150	66	150	0–770	12
1998	August	Miles Property	140	64	110	0–350	6
1998	August	Seven Palms	160	37	74	0–320	10
1999	May	Miles Property	73	24	81	27–170	6
1999	May	Seven Palms	93	24	89	0–270	12
1999	July	Miles Property	280	120	110	40–870	6
1999	July	Seven Palms	93	20	76	0–210	12
1999	August	Miles Property	130	28	50	2–213	6
1999	August	Seven Palms	88	33	128	0–290	12

accounted for significant variation in the analysis ($P < 0.001$). The month × year × habitat interaction was significant ($F_{2,\,396} = 47$, $P < 0.001$), suggesting that differences in DO between habitats varied among months and between years after accounting for time period (block factor). Values of DO averaged less than 2 mg / L in control sites for both time periods in all months (Figure 2). Morning DO values in enhanced sites were below 2 mg / L in August 1998, but averaged above 3 mg / L in morning samples collected in the other sample months. Enhanced areas had mean DO over 6 mg / L in all daytime samples (Figure 2). Although DO levels varied among months and years, DO was much lower in control habitats than in enhanced habitats (Figure 2).

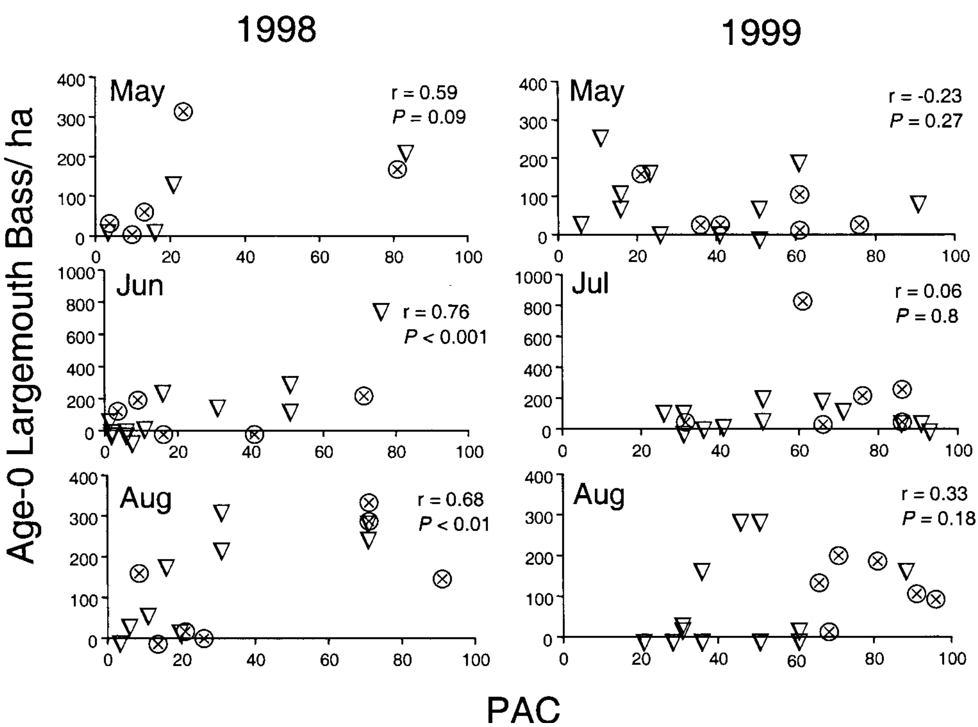

Figure 3. Relationship between age-0 largemouth bass density in block nets and percent coverage of aquatic macrophytes (PAC) during 1998 (left panels) and 1999 (right panels). Sample month is indicated. Block nets from the Miles Property site are indicated by circles, and block nets from the Seven Palms site are indicated with triangles. Correlation coefficients and significance levels are shown.

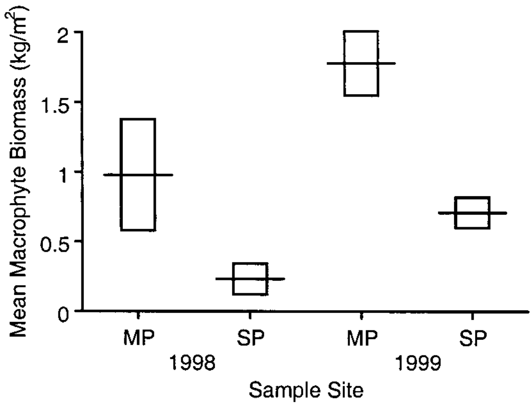

Figure 4. Length frequencies of 1998 (black bars) and 1999 (gray bars) year-class largemouth bass from May 1998 to March 2000. Fish were collected with block nets in May, electrofishing and block nets in August, and electrofishing in March of each year.

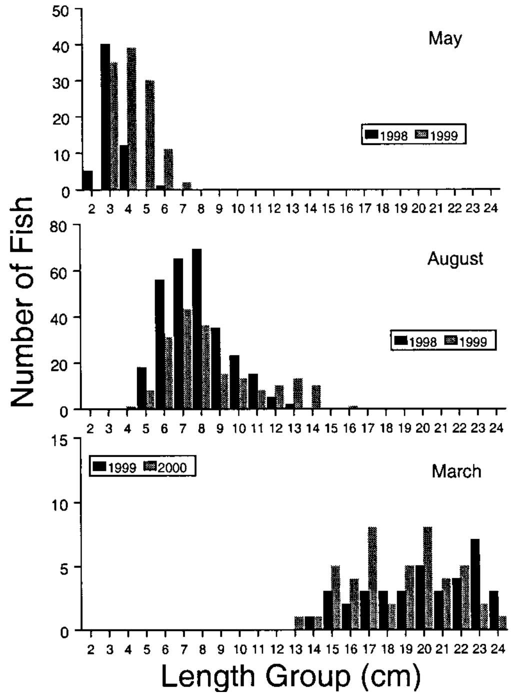

Figure 5. Frequency of occurrence of food items (i.e., percent of fish containing each prey type) in diets of 1998 (black bars) and 1999 (gray bars) year-class largemouth bass. Sample month is indicated, and sample size (*N*) is the number of fish diets examined in each year and month.

Mean density of age-0 largemouth bass in enhanced areas was similar in 1998 and 1999. Mean density ranged from 80 to 160 age-0 fish / ha in 1998 and 73–280 fish / ha in 1999 (Table 1). Least-squares mean density of age-0 largemouth bass across all months was 128 in 1998, and 115 in 1999. Repeated-measures ANOVA found no significant differences in $\log_{10}$ mean density between years ($F_{1,95} = 0.28$, $P = 0.29$). Hoyer and Canfield (1996) found mean age-0 largemouth bass densities of 106 fish / ha (range 0–5,857) for 56 Florida lakes. Thus, densities of age-0 largemouth bass in enhanced areas of Lake Kissimmee were similar to average values for Florida lakes.

Mean age-0 largemouth bass density in enhanced sites was positively related to PAC in block nets in June and August 1998 and was marginally significant in May 1998, likely due to a smaller sample size (Figure 3). Fish density, however, was not related to PAC in any month during 1999 (Figure 3). Most block nets contained PAC less than 20 percent in 1998, and age-0 largemouth bass appeared concentrated in areas with higher PAC (e.g., 20–80%). Conversely, few block nets contained PAC below 20 percent in 1999 (Figure 3), and age-0 largemouth bass densities were not related to PAC, likely because most areas contained intermediate levels (i.e., 20–80%) of PAC (Figure 3).

Size structures of the 1998 and 1999 year-class largemouth bass were similar. Age-0 largemouth bass length frequencies showed modal lengths of 3 and 4 cm in May of 1998 and 1999, respectively (Figure 4). Modal lengths of 1998 year-class largemouth bass in March 1999 were 20 and 23 cm (Figure 4). The 1999 largemouth bass year-class had modal lengths of 17 and 20 cm in March of 2000. The Kolmogorov-Smirnov test was not significant ($K = 1.16$, $P = 0.14$) between March 1999 and 2000, indicating that growth rates to age-1 were similar between the year classes.

Age-0 largemouth bass in enhanced areas of Lake Kissimmee exhibited rapid growth relative to historical data both from Lake Kissimmee and from statewide averages. Modal lengths of age-1 largemouth bass (identified from length frequencies) in Lake Kissimmee were 12–16 cm in spring electrofishing samples from 1988 to 1992 (Moyer et al. 1993). Modal lengths from the 1998 and 1999 year-class fish collected in this study were 20–23 cm in March at both enhanced areas, suggesting that fish growth was higher in enhanced sites than samples collected prior to the habitat enhancement. Hoyer and Canfield (1996) surveyed 56 Florida lakes and found that mean TL-at-age 1 was 153 mm across all lakes. These comparisons indicate that the 1998 and 1999 largemouth bass year classes exhibited rapid growth with few fish less than 150 mm by March of each year (Figure 4).

Stomach contents from 1,131 largemouth bass were examined in this study. Age-0 largemouth bass consumed fish as early as May (Figure 5). Frequency of fish in the diets generally increased from May through March for both year classes (Figure 5). Invertebrates in the diets were composed mostly of insects in May 1998, but grass shrimp was the most frequent invertebrate in fish diets for all other months in both years. Fish became the dominant portion of age-0 largemouth bass diets by August in both years. Of the fish containing prey, mean percent composition by weight of fish increased from 20 percent and 30 percent in May and June of 1998 and 1999, respectively, to over 70 percent and 85 percent by March of 1999 and 2000, respectively. Common fishes in largemouth bass diets throughout the study period included killifish *Fundulus* spp., *Gambusia* spp., and inland silverside *Menidia beryllina*, which were common in diets. Shads *Dorosoma* spp. and sunfishes *Lepomis* spp. became common prey items from October through March of each year.

Macrophyte biomass increased in enhanced sites from 1998 to 1999. Mean monthly biomass in enhanced sites ranged from 0.12 to 1.58 kg / m^2 in 1998 and 0.26–2.18 kg / m^2 in 1999 (Table 2). Macrophyte communities were diverse in enhanced areas and included up to 22 plant species in a single block net. The most common plants found in enhanced areas were *Hydrilla verticillata*, *Hydrocotyle* spp., pickerelweed, *Bacopa* spp., spikerush *Eleocharis* spp., torpedograss *Panicum repens*, knotgrass *Paspalum* spp., dwarf arrowhead *Sagittaria subulata*, and eel grass *Vallisneria americana*. The repeated-measures ANOVA found significant differences in mean macrophyte biomass between years ($F_{1, 84}$ = 10.77, P = 0.001) and sites ($F_{1, 84}$ = 21.8, P < 0.001) (Figure 6). The year × site interaction was not significant (P > 0.4). Thus, the Miles Property site had higher macrophyte biomass than the Seven Palms site, but biomass in both sites increased from 1998 to 1999 (Figure 6).

Plant and fish sampling in control sites indicated differences in plant biomass and fish com-

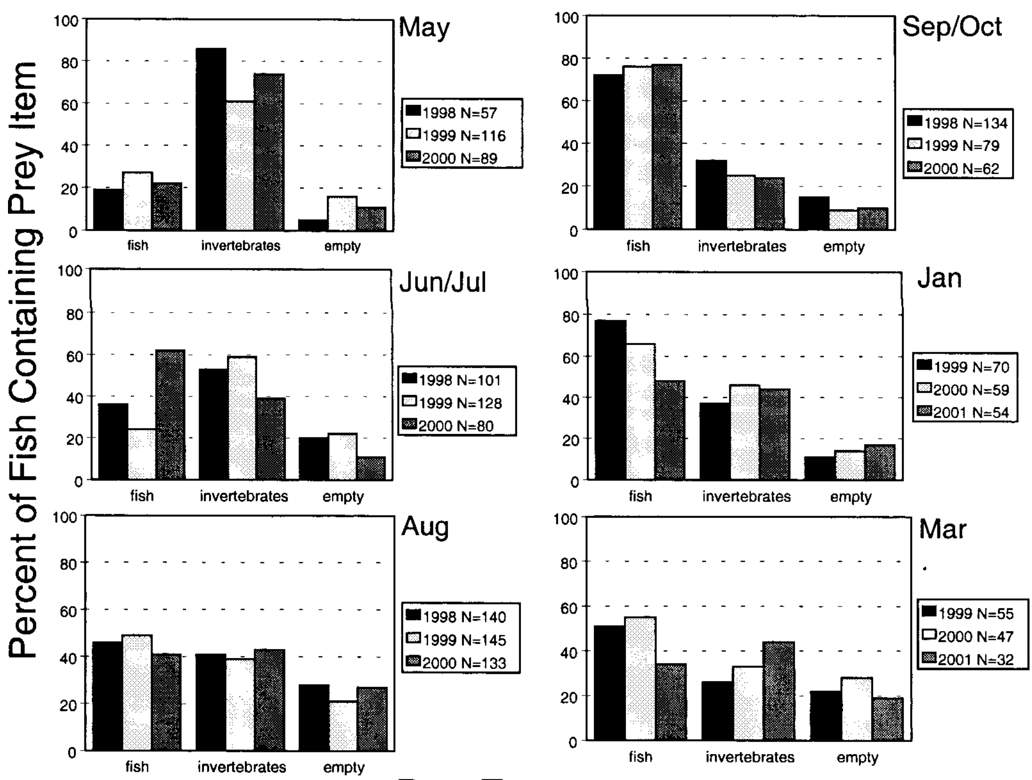

Figure 6. Mean macrophyte biomass (kg / m^2) ± 1 SE from Miles Property (MP) and Seven Palms (SP) enhanced sites during 1998 and 1999. Mean biomass increased at both sites from 1998 to 1999, and biomass was significantly higher at the Miles Property site than at the Seven Palms site in both years.

Table 2. Mean, standard deviation (SD), coefficient of variation (SD / 0 × 100%) and range of macrophyte biomass (kg / m²) collected in 0.25-m² quadrats from enhanced and control sites of Lake Kissimmee each month. Sample size for biomass estimates in enhanced areas represents the number of block nets each month. Sample size for pickerelweed-dominated areas represents the number of 0.25-m² quadrats. Biomass values for the control habitats illustrate the magnitude of differences between enhanced and control habitats.

Year	Month	Habitat	Sample Area	Mean kg / m²	SD	CV	Range	*N*
1998	June	Enhanced	Miles Property	0.47	0.46	97	0.1–1.39	6
1998	June	Enhanced	Seven Palms	0.12	0.21	170	0–0.68	12
1998	August	Enhanced	Miles Property	1.50	1.83	121	0–4.64	6
1998	August	Enhanced	Seven Palms	0.36	0.71	197	0–2.32	10
1999	May	Enhanced	Miles Property	1.19	0.73	61	0.26–2.22	6
1999	May	Enhanced	Seven Palms	0.26	0.28	109	0.01–0.88	12
1999	July	Enhanced	Miles Property	1.95	1.12	57	0.76–4.03	6
1999	July	Enhanced	Seven Palms	0.73	0.29	39	0.46–1.27	12
1999	August	Enhanced	Miles Property	2.18	0.94	38	0.87–3.57	6
1999	August	Enhanced	Seven Palms	1.15	0.96	84	0.22–3.79	12
1998	August	Control	Miles Property	56.8	8.10	14	48.4–66.8	5
1999	August	Control	Miles Property	171	48	14	117–223	5
1999	August	Control	Seven Palms	87.0	29	34	50–114	5

munities. Mean macrophyte biomass in control sites ranged from 56.8 to 171 kg / m² in 1998 and 1999 (Table 2), depicting biomass at least two orders of magnitude higher in control versus enhanced sites. Control sites contained very little open water and relatively homogeneous stands of pickerelweed and smartweed. Qualitative fish samples in control habitats yielded few species. Fishes collected in control areas were least killifish *Heterandria formosa*, tadpole madtom *Noturus gyrinus*, *Gambusia* spp., flagfish *Jordanella floridae*, and sailfin molly *Poecilia latipinna*. No largemouth bass or other centrarchids (family Centrarchidae) were collected.

Discussion

Control areas were probably not suitable habitat for age-0 largemouth bass because of unfavorable macrophyte biomass and DO concentrations. Control areas contained extremely high plant biomass (mean > 50 kg / m²) relative to enhanced sites (mean < 3 kg / m²). Control areas also contained high amounts of organic material in the interstitial spaces between plant stems and very little open water. Most warmwater fishes die when exposed to DO levels less than 2.0 mg / L (Moss and Scott 1961; Smale and Rabeni 1995), which were common in morning and daytime samples at control sites from May through August of each year. Cech et al. (1979) found that mortality of adult largemouth bass was likely at prolonged exposure to DO levels less than 2.9 mg / L.

No centrarchids were collected in the qualitative fish samples in control habitats. Dense macrophyte habitats contained Poecilids and Cyprinodontids (Moyer et al. 1993) at Lake Tohopekaliga, Florida, which was similar to the community found in these habitats at Lake Kissimmee. Lewis (1970) noted that Cyprinodontoids (including Poecilids and Cyprinodontids) are well adapted for aquatic surface respiration (e.g., upturned mouth and flattened head) and can inhabit oxygen-deficient waters by utilizing oxygenated surface water. Conversely, *Lepomis* spp. and golden shiner *Notemigonus crysoleucas* are marginally adapted for surface respiration (e.g., terminal mouths, must orient vertically to access surface layers), and largemouth bass (both juvenile and adult) are not adapted for surface respiration because their large mouth precludes selectively drawing water from the surface (Lewis 1970; Miranda et al. 2000).

Our fish sampling methods differed between habitats, with qualitative rotenone samples in control sites and quantitative block net samples in enhanced sites. Qualitative samples in control sites were required because the complexity of these habitats precluded the deployment of a block net. These habitats contained thick mats of vegetation and detrital matter that made securing the block net lead line on the bottom nearly impossible. Nevertheless, due to the complexity of these habitats with high macrophyte biomass, very little open water, and mean DO concentrations below 2 mg / L throughout the day, we surmise that age-0 largemouth bass density in control sites was likely very low or nil. Our qualitative fish samples supported this supposition; no centrarchids were collected from control habitats.

Age-0 largemouth bass densities in enhanced sites were similar to a statewide average of fish for Florida lakes (Hoyer and Canfield 1996), with mean densities around 100 fish / ha during both years. Our samples were collected with only one day of fish pick-up, which was similar to methods described by Timmons et al. (1978) except that our net encompassed 0.075-ha instead of 0.01-ha. Conversely, our density estimates represent incomplete recovery of fish compared to Hoyer and Canfield (1996), who collected fish for three days, and the actual density values at Lake Kissimmee were probably higher than our estimates. Our sampling methods allowed sampling a variety of macrophyte densities each sample month, which would not be possible by leaving each block net in place for two to three days (Timmons et al. 1978).

The habitat enhancement project opened substantial littoral areas that were probably not available to age-0 largemouth bass prior to the project and likely increased age-0 largemouth bass abundance at Lake Kissimmee. Copeland and Noble (1994) found that age-0 largemouth bass seldom moved greater than 500 m from release sites in a North Carolina reservoir. Thus, most fish collected from enhanced sites in this study were probably spawned within the same enhanced sites.

Age-0 largemouth bass in enhanced areas of Lake Kissimmee exhibited rapid growth relative both to fish collected prior to enhancement at Lake Kissimmee and those in a statewide database. Although diet data for Lake Kissimmee age-0 largemouth bass from 1988 to 1992 were unavailable, and we were unable to compare pre- and postenhancement diets, early piscivory likely caused the rapid growth rates found in this study. Fish were a common prey for age-0 largemouth bass by June 1998 and 1999. Based on modal TL, fish became important prey items in May–June, when fish reached 30–70 mm TL and comprised greater than 50 percent of largemouth bass diets by weight from August to March of both years, likely resulting in rapid growth through age-1. Cailteux et al. (1996) found that age-0 largemouth bass in unvegetated Florida lakes consumed fish at 60 mm TL, whereas age-0 fish from vegetated lakes did not consume fish until they reached 120 mm TL. Bettoli et al. (1992) found a similar trend in Lake Conroe, Texas, where age-0 largemouth bass became piscivorous at a smaller size and had faster growth after elimination of hydrilla. The habitat enhancement project at Lake Kissimmee may have increased piscivory and growth rates of age-0 largemouth bass by reducing macrophyte density compared to preenhancement conditions.

Based on growth rates and diet composition, survival of age-0 largemouth bass inhabiting enhanced areas was likely high. Survival of age-0 largemouth bass through winter is positively related to growth rate, fish size (Aggus and Elliot 1975; Miller and Storck 1984; Maceina and Isely 1986; Miranda and Hubbard 1994a; Garvey et al. 1998), and amount of lipid reserves accumulated through fall (Keast and Eadie 1985; Wicker and Johnson 1987; Miranda and Hubbard 1994b; Ludsin and DeVries 1997). Wicker and Johnson (1987) found high mortality of age-0 largemouth bass in Lake Dora, Florida in May and June, when fish attempted to switch to fish as prey. In this study, densities of age-0 largemouth bass did not decline through summer, and fish were important prey items from June–March of each year. Given the rapid growth rates, early piscivory, and large fish size of 1998 and 1999 year-class largemouth bass, survival was likely high.

Age-0 largemouth bass density increased with aquatic macrophyte coverage in enhanced sites during summer 1998, but was not related to PAC in 1999. Intermediate amounts of cover (e.g., aquatic macrophytes) provide quality habitat for largemouth bass (Aggus and Elliot 1975; Durocher et al. 1984; Wiley et al. 1984; Miranda and Hubbard 1994a; Miranda and Pugh 1997). Aquatic macrophytes provide high amounts of invertebrate and fish prey and protection from predation (Crowder and Cooper 1982; Savino and Stein 1982; Miranda and Pugh 1997). Macrophytes in enhanced areas during 1998 were clumped, with many areas having PAC below 10 percent. Conversely, no block net samples in 1999 contained PAC below 15 percent. Although age-0 largemouth bass density was similar in both years, the fish appeared to congregate around the existing patches of macrophytes in 1998, but were distributed more evenly throughout the more abundant macrophytes in 1999.

Rapid colonization of aquatic macrophytes in newly-enhanced areas could provide cover for age-0 largemouth bass and accelerate fishery benefits relative to low macrophyte coverage for one to two years after enhancement. Conversely, high plant densities reduce fish feeding efficiency (Savino and Stein 1982; Bettoli et al. 1992) and growth (Borawa et al. 1979; Shireman et al. 1985). Increases in macrophyte abundance could reduce growth rates or eventually result in lost habitat due to establishment of highly-dense plant communities (i.e., control sites). Thus, fishery managers are presented with a trade off, where slow macrophyte colonization in enhanced areas would delay benefits of enhancement (i.e., produce lower densities of age-0 largemouth bass in initial years), yet rapid plant expansion would quickly debilitate the habitats to control site conditions. Variable levels of macrophyte colonization were observed at our enhanced sample sites, with more rapid plant accumulation at the Miles Property site than at the Seven Palms sample site, indicating a need to identify factors related to colonization of enhanced habitats by aquatic plants (e.g., exposure of enhanced sites to wind and wave action). By understanding which factors are related to macrophyte expansion, fishery managers could potentially predict sites that are prone to rapid or delayed macrophyte colonization. Future enhancement sites could then be chosen based on the desired rate of macrophyte expansion.

Nevertheless, the 1995–1996 Lake Kissimmee habitat enhancement project has had more prolonged benefits than to a previous effort in Florida. Moyer et al. (1995) found that at Lake Tohopekaliga enhanced sites returned to preenhancement conditions within about two years. In the current study, enhanced sites contained abundant and rapidly growing age-0 largemouth bass in both the second and third year following enhancement. Colonization by macrophytes in enhanced areas of Lake Kissimmee was slower than that found in enhanced areas of Lake Tohopekaliga (Moyer et al. 1995). This result may be due to the selective herbicide treatments by the Florida Fish and Wildlife Conservation Commission to reduce pickerelweed density in enhanced areas of Lake Kissimmee.

Habitat enhancement efforts will likely become an even more important tool for largemouth bass conservation and management in the future. Most U. S. reservoirs were constructed during the 1950s and 1960s (Miranda 1996), and loss of natural habitat (e.g., woody debris) in reservoirs will increasingly challenge fishery managers (e.g., Kimmel and Groeger 1986). Efforts to establish native aquatic macrophytes in reservoirs have increased in recent years in an attempt to improve fish habitat (Smart et al. 1996). In Florida, stabilized water levels have led to excessive macrophyte biomass in littoral regions of many lakes. Thus, in both reservoirs and natural lakes, current habitat management focuses on attempting to establish or maintain intermediate levels of aquatic macrophytes. The large-scale habitat enhancement we evaluated in the current study created intermediate levels of macrophytes and improved habitat for age-0 largemouth bass. Benefits to the adult largemouth bass population at Lake Kissimmee were not identified in this study and should be evaluated in future assessments of habitat enhancement projects. By assessing fish-population responses, fishery managers can develop enhancement strategies that maximize fishery benefits.

Acknowledgments

We thank M. Duncan, C. Hanson, B. Hujik, J. Lamb, E. Nagid, W. Pine, W. Porak, T. Tuten, P. Wheeler, and D. Van Genechten for help with field work, and K. Dockendorf, M. Duncan, and M. Bledsoe for processing samples. K. Bennett constructed the digital maps. We thank W. Porak for sharing information from a concurrent research project on Lake Kissimmee, and D. Canfield and R. Bachmann for conversations regarding the lake. We appreciate the hospitality shown by Leo and Joanne Cosce (Lester's Fish Camp) throughout our field work. B. Johnson, M. Hulon, M. Mann, W. Porak, and R. Myers provided helpful comments on a previous draft of this manuscript. This study was funded by the Florida Fish and Wildlife Conservation Commission.

References

Aggus, L. R., and G. V. Elliot. 1975. Effects of cover and food on year-class strength of largemouth bass. Pages 317–322 *in* R. H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C..

Bettoli, P. W., M. J. Maceina, R. L. Noble, and R. K. Betsill. 1992. Piscivory in largemouth bass as a function of aquatic vegetation abundance. North American Journal of Fisheries Management 12:509–516.

Borawa, J. C., J. H. Kerby, M. T. Huish, and A. W. Mullis. 1979. Currituck Sound fish populations before and after infestation by Eurasian watermilfoil. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 32(1978):520–528.

Cailteux, R. L., W. F. Porak, S. Crawford, and L. L. Conner. 1996. Differences in largemouth bass food habits and growth in vegetated and unvegetated north-central Florida lakes. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 50:201–211.

Cech, J. J., Jr., C. G. Campagna, and S. J. Mitchell. 1979. Respiratory responses of largemouth bass (*Micropterus salmoides*) to environmental changes in temperature and dissolved oxygen. Transactions of the American Fisheries Society 108:166–171.

Copeland, J. R., and R. L. Noble. 1994. Movements by young-of-year and yearling largemouth bass and their implications for supplemental stocking. North American Journal of Fisheries Management 14:119–124.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interactions between bluegills and their prey. Ecology 63:1802–1813.

Durocher, P. P., W. C. Provine, and J. E. Kraii. 1984. Relationship between abundance of largemouth bass and submersed vegetation in Texas reservoirs. North American Journal of Fisheries Management 4:84–89.

Florida Lakewatch. 2000. Long-term fish population trends in Florida Lakes: 1999. data. Department of Fisheries and Aquatic Sciences, University of Florida, Institute of Food and Agricultural Sciences. University of Florida, Gainesville, Florida.

Garvey, J. E., R. A. Wright, and R. A. Stein. 1998. Overwinter growth and survival of age-0 largemouth bass (*Micropterus salmoides*): revisiting the role of body size. Canadian Journal of Fisheries and Aquatic Sciences 55:2414–2424.

Hoyer, M. V., and D. E. Canfield, Jr. 1996. Largemouth bass abundance and aquatic vegetation in Florida Lakes: and empirical analysis. Journal of Aquatic Plant Management 34:23–32.

Keast, A., and J. M. Eadie. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. Transactions of the American Fisheries Society 114:204–213.

Kimmel, B. L., and A. W. Groeger. 1986. Limnological and ecological changes associated with reservoir aging. Pages 103–109 *in* G. E. Hall and M. J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. American Fisheries Society, Reservoir Committee, Southern Division, Bethesda, Maryland.

Lewis, W. M., Jr. 1970. Morphological adaptations of cyprinodontoids for inhabiting oxygen deficient waters. Copeia 1970:319–326.

Ludsin, S. A., and D. R. DeVries. 1997. First-year recruitment of largemouth bass: the inter-dependency of early life stages. Ecological Applications 9(3):1024–1038.

Maceina, M. J., and J. J. Isely. 1986. Factors affecting growth of an initial largemouth bass year class in a new Texas reservoir. Journal of Freshwater Ecology 3:485–492.

Miller, S. J., and T. Storck. 1984. Temporal spawning distribution of largemouth bass and young-of-year growth, determined from daily otolith rings. Transactions of the American Fisheries Society 113:571–578.

Miranda, L. E. 1996. Development of reservoir fisheries management paradigms in the twentieth century. Pages 3–16 *in* L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society, Symposium 16, Bethesda, Maryland.

Miranda, L. E., and W. D. Hubbard. 1994a. Winter survival of age-0 largemouth bass relative to size, predators, and shelter. North American Journal of Fisheries Management 14:773–780.

Miranda, L. E., and W. D. Hubbard. 1994.b. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Transactions of the American Fisheries Society 123:80–87.

Miranda, L. E., and L. L. Pugh. 1997. Relationship between vegetation coverage and abundance, size, and diet of juvenile largemouth bass during winter. North American Journal of Fisheries Management 17:601–610.

Miranda, L. E., M. P. Driscoll, and M. S. Allen. 2000. Transient microhabitats allow fish survival in inhospitable plant stands. Freshwater Biology 44:617–628.

Moss, D. D., and D.C. Scott. 1961. Dissolved-oxygen requirements of three species of fish. Transactions of the American Fisheries Society 90:377–393.

Moyer, E. J., and seven coauthors. 1993. Completion report for Kissimmee Chain of lakes studies, study II: Lake Kissimmee investigations (1988–1993). Florida Game and Fresh Water Fish Commission, Tallahassee, Florida.

Moyer, E. J., M. W. Hulon, J. J. Sweatman, R. S. Butler, and V. P. Williams. 1995. Fishery responses to habitat restoration in Lake Tohopekaliga, Florida. North American Journal of Fisheries Management 15:591–595.

SAS. 1996. User's guide, version 6. SAS Institute Inc., Cary, North Carolina.

SAS. 1997. SAS / STAT software: changes and enhancements through release 6.12. SAS Institute Inc., Cary, North Carolina.

Savino, J. F., and R. A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated submersed vegetation. Transactions of the American Fisheries Society 111:255–266.

Shireman, J. V., M. V. Hoyer, M. J. Maceina, and D. E. Canfield, Jr. 1985. The water quality and fishery of Lake Baldwin, Florida: 4 years after macrophyte removal by grass carp. Lake and Reservoir Management 1:201–206.

Smale, M. A., and C. F. Rabeni. 1995. Hypoxia and hyperthermia tolerances of headwater stream fishes. Transactions of the American Fisheries Society 124:698–710.

Smart, R. M., R. D. Doyle, J. D. Madsen, and G. O. Dick. 1996. Establishing native submersed aquatic plant communities for fish habitat. Pages 347–356 *in* L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society, Symposium 16, Bethesda, Maryland.

Timmons, T. J., W. L. Shelton, and W. D. Davies. 1978. Sampling of reservoir fish populations in littoral areas with rotenone. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 32:474–485.

Wicker, A. M., and W. E. Johnson. 1987. Relationships among fat content, condition factor, and first-year survival of Florida largemouth bass. Transactions of the American Fisheries Society 116:264–271.

Wiley, M. J., R. W. Gorden, S. W. Waite, and T. Powless. 1984. The relationship between aquatic macrophytes and sport fish production in Illinois ponds: a simple model. North American Journal of Fisheries Management 4:111–119.

Williams, V. P., D. E. Canfield, Jr., M. M. Hale, W. E. Johnson, R. S. Kautz, J. T. Krummrich, F. H. Langford, K. Langland, S. P. McKinney, D. M. Powell, and P. L. Shafland. 1985. Lake habitat and fishery resources in Florida. Pages 43–119 *in* W. E. Seaman, Jr. Florida aquatic habitat and fishery resources. American Fisheries Society, Florida Chapter, Bethesda, Maryland.