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Largemouth Bass Abundance and Aquatic Vegetation in Florida Lakes: An Empirical Analysis

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ABSTRACT

Data from 56 Florida lakes were examined for relationships between abundance of aquatic macrophytes and young-of-the-year (< 160 mm TL), subadult (161 - 240 mm TL) and adult (>250 mm TL) largemouth bass (*Micropterus salmoides*). Study lakes ranged from 2 ha to 271 ha. Trophic status ranged from oligotrophic to hypereutrophic. The percentage of lake area covered (PAC) and the percentage of lake volume infested (PVI) with aquatic macrophytes among the lakes ranged from <1% to 100%. Young-of-the-year largemouth bass abundance ranged from 0 to 5857 fish/ha. Subadult largemouth bass abundance ranged from 0 to 216 fish/ha and adult largemouth bass abundance ranged from 1 fish/ha to 75 fish/ha. There were weakly significant, direct relationships among lakes between measures of macrophyte abundance and estimates of young-of-the-year and subadult abundance. There were weakly significant inverse relationships among lakes between measures of macrophyte abundance and growth (mm/day) of age-1 and age-2 largemouth bass. There were no significant relationships among lakes between measures of macrophyte abundance and estimates of adult largemouth bass abundance or standing crop (kg/ha). Adult largemouth bass abundance and standing crop were positively correlated to lake trophic status. After accounting for lake trophic status, the abundance of young-of-the-year largemouth bass was directly related to PVI, and age-1 growth rate was inversely related to PVI but there were no significant relationships between macrophyte abundance and the abundance of subadult and adult largemouth bass. There are no strong predictable relationships between the abundance of aquatic macrophytes and the abundance of adult largemouth bass among Florida lakes < 300 ha.

Key words: Aquatic macrophytes, lake trophic status, largemouth bass, lake surface area.

INTRODUCTION

The presence of aquatic macrophytes increases the structural complexity of lake ecosystems. This complexity is reported to increase the number of young-of-the-year and subadult largemouth bass (*Micropterus salmoides*) by providing spawning substrate (Chew 1974), protection of nests from wind (Shirley and Andrews 1977), increased food from the production of epiphytic invertebrates (Moxley and Langford 1982), and reduction in predation (Strange et al. 1975, Aggus and Elliot 1975, Crowder and Cooper, 1979 Savino and Stein, 1982). Aquatic macrophytes also provide habitat for many of the forage fish that are important to the recruitment of largemouth bass to adult size (Barnett and Schneider 1974, Gutreuter and Anderson 1985). Consequently, largemouth bass anglers, fisheries biologists, and other professionals involved in lake management often

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strongly support the statement that aquatic macrophytes are essential for largemouth bass populations.

While there is a strong belief that aquatic macrophytes nurture largemouth bass populations by providing food, shelter, and spawning habitat, excessive aquatic vegetation can cause stunted fish populations and reduced fish growth and condition (Bennett 1948, Buck et al. 1975, Colle and Shireman 1980, Shireman et al. 1983). Consequently, Crowder and Cooper (1979) suggested the welfare of predatory fish increases with increasing aquatic vegetation densities up to some undefined point, after which further increases in aquatic vegetation results in decreased capture rates of prey and thus reduced growth of predators.

Aquatic plant management is important to maintain overall lake quality and anglers recognize that there can be too much vegetation in a lake (King et al. 1978). Consequently, how much aquatic vegetation is needed to support largemouth bass populations is an important question given the economic importance of largemouth bass fishing and the need to control vegetation for recreational boating, general aesthetics, and lake access. Many fisheries biologists and lake management professionals believe a moderate amount of aquatic vegetation is required, but a review of the primary literature suggests the evidence supporting the need for a moderate amount of aquatic vegetation is not definitive. Some research suggests that aquatic vegetation positively effects largemouth bass populations (Ware and Gassaway 1978, Moxley and Langford 1982, Durocher et al. 1984, Wiley et al. 1984), but other research found no predictable effects when macrophytes are controlled (Bailey 1978, Klussmann et al. 1988). We used data from 56 Florida lakes to examine relationships between the abundance of macrophytes, lake trophic status, and the abundance of young-of-the-year (< 160 mm TL), subadult (161 - 240 mm TL) and adult (>250 mm TL) largemouth bass.

METHODS

Fifty-six north and central Florida lakes were studied between June 1986 and June 1990 (Canfield and Hoyer 1992). Study lakes were selected by a stratified sampling regime based on lake trophic status and abundance of aquatic macrophytes. Eight of the study lakes were selected because submersed aquatic macrophytes had been eliminated by grass carp for at least 10 years. These lakes were considered reference lakes because the largemouth bass populations were the product of aquatic ecosystems with virtually no aquatic vegetation.

Aquatic macrophytes were sampled at each lake once in the summer. Four transects were run completely across each lake with a boat-mounted Raytheon DE-719 recording fathometer for calculating percentage of lake area covered with macrophytes (PAC), percent volume infested with aquatic vegetation (PVI), and lake mean depth following the procedures described by Maceina and Shireman (1980). Lake surface area was obtained from the Gazetteer of Florida Lakes (Shafer et al. 1986).

The above-ground standing crop of emergent, floating-leaved, and submersed vegetation was measured along ten uniformly placed transects around each lake. Plant species found along a transect were recorded. At each transect, divers cut the above-ground portions of aquatic macrophytes that were inside a plastic square (0.25 m^2) randomly thrown once in each plant zone. Vegetation was placed in nylon mesh bags, spun removing excess water to a constant weight, and weighed to the nearest 0.10 kg. Average standing crop (kg/m^2) for each vegetation zone was calculated by averaging 10 samples from each zone. The combined width (m) of the floating-leaved and emergent zones was also measured at each transect and then averaged for each lake. This information was used to calculate the total plant biomass of each lake. All lakes had at least a trace of aquatic vegetation. Lakes with more emergent and floating-leaved macrophyte coverage than submersed macrophytes were classified as emergent and floating-leaved dominated lakes, and lakes with more submersed macrophyte coverage than emergent and floating-leaved macrophytes were classified as submersed dominated lakes.

Summer water samples were collected from six stations (three littoral and three open-water) on one date, and three open-water stations on two additional dates. Water samples were collected 0.5 m below the surface in acid-cleaned Nalgene bottles, placed on ice, and returned to the laboratory for analysis. Secchi depth was also measured at each water sampling station. Total phosphorus concentrations were determined (Murphy and Riley 1962) after a persulfate oxidation (Menzel and Corwin 1965). Total nitrogen was determined by a modified Kjeldahl technique (Nelson and Sommers 1975). Water was filtered through Gelman type A-E glass fiber filters for chlorophyll *a* determination. Chlorophyll *a* was determined by using the method of Yentsch and Menzel (1963) and the equations of Parson and Strickland (1963).

Nutrient content of aquatic plants in an individual lake were determined from composite samples of all plant types. Plant material was dried at 70 C to a constant weight and ground in a Wiley Mill until fragments were <0.85 mm. Dried plant material was given a persulfate digestion, diluted and analyzed for total phosphorus and total nitrogen.

An adjusted chlorophyll *a* concentration was calculated for each lake because errors in trophic state assessment can be large in macrophyte-dominated lakes (Canfield et al. 1983). Nutrient and chlorophyll *a* concentrations can be low and Secchi disc transparency can be high in eutrophic lakes where there is an abundance of macrophytes. Canfield et al. (1983) proposed the trophic status of lakes having growths of aquatic macrophytes could be assessed by adding the phosphorus in the macrophytes to the phosphorus in the water and then using the potential water column phosphorus concentration (WCP) to classify the lake's trophic status. The method, however, has serious limitations if it is applied to all Florida lakes because nitrogen is the primary limiting nutrient in many Florida lakes (Canfield 1983, Canfield and Hoyer 1988). Thus, WCP and a water column nitrogen concentration (WCN), were calculated using the same methods as Canfield et al. (1983) used for phosphorus.

The Canfield et al. (1983) method essentially adds the nutrients from plant biomass into the water column. To assess the trophic status of the study lakes, an adjusted chlorophyll *a* concentration was calculated substituting WCP and WCN for total phosphorus and total nitrogen concentrations in a multivariate regression equation relating chlorophyll *a* concentrations to total phosphorus and total nitrogen concentrations (Canfield 1983). The adjusted chlorophyll *a* values were then used with the trophic classification system of Forsberg and Ryding (1980) to assign the trophic status of each lake.

Young-of-the-year and subadult largemouth bass abundance was determined using four to six blocknets and rotenone sampling. Blocknets were set in the summer between May and October when water temperatures facilitate the use of rotenone. Nets were placed equally in littoral (with one side being the shore) and limnetic habitats. Blocknet areas were treated with 2.0 mg/L rotenone (5 percent active ingredient, Noxfish). Fish killed inside the nets were collected for three days. Fish were separated by species into 40 mm total length (TL) size groups and counted. The numbers of fish were summed by net for all three days, averaged by littoral or open-water regions and then extrapolated to a whole-lake basis (fish/ha), weighting for the area of littoral and open water regions in each lake. Littoral areas were defined by the area of the lakes with aquatic vegetation (PAC). If there was no aquatic vegetation, the littoral area was considered the width of the 0.08 hectare blocknet (28 m) around the entire lake. Average first and second year growth for largemouth bass in Florida are 153 and 254 mm TL, respectively (Hoyer and Canfield 1994). We considered largemouth bass ≤160 mm TL as young-of-the-year fish and those between 161 and 240 mm TL subadults. Because blocknet data are extremely variable (DuRant et al. 1979), adult (>250 mm TL) largemouth bass stock (fish/ha) and standing crop (kg/ha) were estimated by use of an intensive mark-recapture program.

The Mark-recapture studies were conducted during cool weather between January and June of the year after blocknet sampling, to reduce mortality from handling and tagging stress. Fish were collected with electrofishing gear and given a left pelvic fin-clip. Electrofishing and marking with left pelvic clips continued until approximately 10% of the captured fish were marked, then a recapture phase started giving those fish a right pelvic clip. Population estimates (fish/ha) were obtained by use of the Petersen method (Ricker 1975). A length was recorded for each marked fish and a frequency histogram based on the 40 mm TL size groups was determined for each lake. The standing crop of adult largemouth bass (kg/ha) was then calculated using first day weights from blocknet samples and the percentage of the total fish caught in each size class, times the recapture estimate. Mark-recapture estimates were not obtained on six lakes because low conductivity made electrofishing ineffective.

Growth rates were estimated from otoliths. Otoliths were taken from largemouth bass > 120 mm TL collected in blocknets and supplemental electrofishing at the time the blocknets were set. Otoliths were measured in whole view according to the methods of Hoyer et al. (1985b) and back-calculations for length at age determined with the Lee method. Growth rates were calculated by dividing average length obtained during a year for each lake and dividing by 365.

Adjusted chlorophyll *a* and largemouth bass population values were transformed to their logarithms (base 10) before statistical analyses to accommodate heterogeneity of variances. Because some lakes had 0 values for young-of-the-year largemouth bass and subadults, these values were transformed to their logarithms (base 10) after adding one to all values (Snedecor and Cochran 1979). Growth rates of age-1 and age-2 fish were normally distributed and were not transformed. Plant abundance as measured by PVI, instead of PAC, was used in many statistical analyses because PAC was a component of some response variables (adjusted chlorophyll *a* and weighted fish abundance). Aquatic macrophyte percentage data were transformed using the square root arcsine transformation (Snedecor and Cochran 1979).

The relationship of adjusted chlorophyll *a* concentrations and PVI to largemouth bass abundance and growth was examined using multiple regression. The overall significance of PVI and adjusted chlorophyll *a* were tested using a multivariate linear model to account for suspected correlations among the abundance and growth rate responses. The effect of multiple collinearity between the two independent variables was examined using standard regression diagnostics.

Lakes were separated into five groups. Grass carp lakes were combined as reference lakes because the largemouth bass populations in those lakes were the product of a submersed vegetation free environment for a minimum of 10 years. The remaining lakes were grouped into quartiles based on PAC (1st quartile = PAC ≤ 6.7%, 2nd quartile = PAC 6.8 - 40%, 3rd quartile = PAC 41 - 87%, and 4th quartile = PAC > 87%). This allowed comparisons between average largemouth bass population parameters in lakes having low, intermediate and high levels of aquatic vegetation and the grass carp lakes. The significance of differences between the reference lakes and the quartile groups was determined using Dunnett's test. Computations were performed using various procedures in SAS and JMP statistical packages (SAS Institute Inc. 1985, SAS Institute Inc. 1989). Unless otherwise stated, statements of statistical significance imply $P \leq 0.05$.

RESULTS AND DISCUSSION

Young-of-the-year, subadult, and adult largemouth bass abundance varied considerably among lakes (Table 1). Average abundance of young-of-the-year (< 160 mm TL) largemouth bass ranged from none captured (Lake Barco and Clay Lake) to 5857 fish/ha (Watertown). Subadult (161 mm TL - 240 mm TL) largemouth bass abundance ranged from none captured (Lake Suggs) to 216 fish/ha (Lake Susannah). Adult (>250 mm TL) largemouth bass abundance ranged from 1 fish/ha to 75 fish/ha and average standing crop ranged from < 1 kg/ha to 47.2 kg/ha (Lake Barco and Little Fish, respectively).

The lakes in this study reflect a wide range of limnological conditions (Table 2). Surface areas ranged from 2 ha to 271 ha, mean total phosphorus concentrations ranged from 2 µg/L to 1043 µg/L, and average total nitrogen concentrations ranged from 82 µg/L to 3256 µg/L. Average chlorophyll *a* concentrations ranged from 1 µg/L to 241 µg/L and average Secchi disc transparency ranged from 0.3 m to 5.8 m. Lake trophic status among the lakes ranged from oligotrophic to hypereutrophic. PAC and PVI ranged from < 1% to 100%. Eighty-seven species of aquatic macrophytes were identified in the 56 lakes, 28 of the lakes were dominated by floating-leaved and emergent vegetation and 28 were domi-

TABLE 1. LARGEMOUTH BASS DATA FROM 56 FLORIDA LAKES (CANFIELD AND HOYER 1992). YOY = YOUNG OF THE YEAR LARGEMOUTH BASS AND AN ASTERISK INDICATES LAKES STOCKED WITH GRASS CARP HAVING NO AQUATIC VEGETATION FOR A MINIMUM OF 10 YEARS.

Lake Name	County	Largemouth bass >250 mm TL (fish/ha)	Largemouth bass >250 mm TL (kg/ha)	YOY (Fish/ha)	Subadult (Fish/ha)	First year growth (mm/day)	Second year growth (mm/day)
Barco	Putnam	1	0.6	0	13	0.48	0.26
Bonny	Polk	6	5.9	101	34	0.51	0.23
Keys-pond	Putnam	6	2.4	250	67	0.39	0.19
Picnic	Putnam	6	1.6	27	27	0.37	0.19
Cue	Putnam	7	4.2	5	28	0.44	0.23
Mill Dam	Marion	8	5.7	97	44	0.39	0.25
Clear*	Pasco	8	5.3	67	38	0.44	0.35
Carlton	Orange	8	7.8	25	3	0.45	0.29
Holden*	Orange	10	9.3	31	29	0.35	0.31
Tomahawk	Marion	11	6.2	168	53	0.39	0.20
Bull Pond	Putnam	12	8.1	537	13	0.39	0.23
Wales*	Polk	12	7.1	24	10	0.42	0.37
Bivens-arm	Alachua	13	13.6	18	4	0.52	0.37
Suggs	Putnam	13	11.0	9	0	0.39	0.15
Thomas	Polk	13	6.7	5	26	0.38	0.24
Okahumpka	Sumter	13	7.9	619	38	0.41	0.20
Grasshopper	Lake	13	8.6	54	25	0.39	0.25
Killarny*	Orange	14	15.6	25	9	0.45	0.28
Hollingsworth	Polk	14	10.0	8	10	0.47	0.31
Moore	Leon	14	7.8	314	14	0.38	0.22
Round-pond	Marion	16	21.1	625	72	0.31	0.21
Wauberg	Alachua	17	15.6	548	27	0.42	0.33
Mountain 2	Polk	17	9.1	161	18	0.41	0.26
Fish	Osceola	17	10.9	12	64	0.42	0.33
Miona	Sumter	18	8.7	188	38	0.36	0.23
Catherine	Marion	18	14.2	107	76	0.38	0.21
Swim Pond	Marion	19	10.0	9	58	0.44	0.27
Baldwin*	Orange	19	24.9	159	19	0.42	0.39
Hunter	Polk	20	10.9	48	57	0.54	0.22
Sanitary	Polk	22	17.1	280	37	0.36	0.31
Clay	Lake	23	12.0	0	6	0.46	0.21
Gate Lake	Polk	23	12.4	29	36	0.55	0.25
Hartridge	Polk	24	11.1	285	74	0.34	0.22
Live-oak	Osceola	24	15.4	346	69	0.40	0.26
Watertown	Columbia	26	19.2	5857	33	0.46	0.33
Mountain	Hernando	26	15.6	1458	30	0.46	0.31
Alligator	Columbia	28	34.7	491	1	0.49	0.37
West Moody	Pasco	28	17.6	2600	56	0.40	0.32
Pearl*	Orange	30	26.9	28	23	0.47	0.30
Deep	Putnam	32	15.5	88	13	0.34	0.24
Bell*	Pasco	34	21.2	12	2	0.47	0.24
Patrick	Polk	34	11.6	243	27	0.47	0.22
Orienta*	Seminole	37	18.8	222	39	0.43	0.33
Brim-pond	Putnam	38	17.3	4268	36	0.44	0.29
Conine	Polk	40	28.4	96	9	0.47	0.30
Pasadena	Pasco	42	27.7	1136	51	0.41	0.35
Susannah	Orange	44	43.6	250	216	0.43	0.29
Rowell	Bradford	48	34.3	55	31	0.42	0.30
Crooked	Lake	56	25.5	1052	27	0.40	0.24
Little Fish	Putnam	75	47.2	601	60	0.42	0.33
Douglas	Lake	•	•	653	20	0.43	0.32
Carr	Leon	•	•	510	27	0.35	0.33
Turkey-pen	Calhoun	•	•	23	20	0.30	0.23
Lindsey	Hernando	•	•	233	15	0.40	0.27
Loften	Leon	•	•	219	50	0.34	0.26
Koon	Lafayette	•	•	60	6	0.40	0.33

nated by submersed vegetation. Cattail (*Typha* spp.) was the dominant emergent plant in seven lakes and spatterdock (*Nuphar luteum*) was the dominant floating-leaved vegetation in five lakes. Hydrilla (*Hydrilla verticillata*) and bladderwort (*Utricularia* spp.) were dominant submersed plants in 10 and six lakes respectively.

Numerous studies have been conducted to determine the environmental factors that regulate fish abundance in lakes and to develop models that predict fish yields (Rounsefell 1946, Rawson 1952, Carlander 1955, Moyle 1956, Ryder 1965). Lake trophic status is an important determinant of fish abundance (Melack 1976, McConnell et al. 1977,

Table 2. Physical and chemical data from 56 Florida lakes (Canfield and Hoyer 1992). PAC = percent area covered with aquatic macrophytes, PVI = percent volume infested with aquatic macrophytes, Secchi = Secchi depth, TP = total phosphorus, TN = total nitrogen, CHLA = chlorophyll *a*, and ACHLA = adjusted chlorophyll *a*. An asterisk indicates lakes stocked with grass carp having no aquatic vegetation for a minimum of 10 years.

Lake	Lake trophic status	PAC (%)	PVI (%)	Surface area (ha)	Secchi (m)	TP (µg/L)	TN (µg/L)	CHLA (µg/L)	ACHLA (µg/L)
Barco	Oligotrophic	36.7	1.3	13	5.4	2	82	1	1
Bonny	Hypereutrophic	10.0	6.5	143	0.6	59	1858	40	51
Keys-pond	Mesotrophic	40.0	7.9	5	5.3	2	208	1	4
Picnic	Oligotrophic	86.7	5.4	18	2.6	8	137	1	2
Cue	Oligotrophic	1.0	0.5	59	5.8	5	91	2	2
Mill Dam	Mesotrophic	33.3	9.1	85	2.7	11	462	4	6
Clear*	Eutrophic	1.0	1.0	64	1.3	21	761	21	21
Carlton	Hypereutrophic	1.0	0.5	155	0.4	92	3228	173	173
Holden*	Hypereutrophic	1.0	0.5	102	0.5	44	1226	64	64
Tomahawk	Oligotrophic	43.3	12.1	15	4.2	6	192	1	3
Bull Pond	Mesotrophic	20.0	11.4	11	1.4	11	522	3	4
Wales*	Hypereutrophic	3.4	0.3	132	0.8	27	899	42	42
Bivens-arm	Hypereutrophic	6.7	1.4	76	0.4	384	3256	241	268
Suggs	Mesotrophic	1.0	0.5	73	0.5	66	1249	4	4
Thomas	Eutrophic	6.7	0.5	55	1.8	22	759	10	10
Okahumpka	Hypereutrophic	100.0	98.1	271	1.4	21	1033	11	350
Grasshopper	Oligotrophic	80.0	17.2	59	3.7	6	259	1	2
Killarny*	Eutrophic	1.0	0.5	96	1.0	21	603	22	22
Hollingsworth	Hypereutrophic	1.0	0.5	144	0.3	113	2517	135	136
Moore	Mesotrophic	40.0	13.9	28	5.3	5	353	3	5
Round-pond	Hypereutrophic	100.0	79.4	4	2.6	3	444	3	47
Wauberg	Hypereutrophic	1.0	0.5	100	0.6	166	1478	102	112
Mountain 2	Oligotrophic	13.3	4.6	55	2.4	17	331	2	2
Fish	Eutrophic	3.3	1.4	89	1.0	25	935	18	19
Miona	Hypereutrophic	96.6	86.0	169	1.5	12	867	8	62
Catherine	Eutrophic	48.4	9.3	41	3.2	2	303	2	12
Swim Pond	Hypereutrophic	86.7	77.8	9	0.6	25	1025	11	118
Baldwin*	Eutrophic	3.9	1.3	80	1.6	21	530	18	18
Hunter	Hypereutrophic	1.0	0.5	40	0.5	98	1723	82	83
Sanitary	Eutrophic	53.3	35.7	204	1.3	26	1054	21	22
Clay	Hypereutrophic	100.0	76.3	5	4.0	7	356	4	97
Gate Lake	Eutrophic	36.7	17.5	8	1.1	28	407	20	20
Hartridge	Eutrophic	60.0	11.5	176	2.3	11	485	4	28
Live-oak	Eutrophic	100.0	55.1	152	2.6	13	389	9	18
Watertown	Eutrophic	6.7	0.8	19	1.0	27	777	24	24
Mountain	Eutrophic	40.0	20.7	51	1.7	37	813	10	21
Alligator	Hypereutrophic	10.2	10.0	137	0.5	371	2367	84	84
West Moody	Eutrophic	100.0	89.3	39	2.8	14	584	2	19
Pearl*	Eutrophic	2.6	1.7	24	0.9	28	819	22	22
Deep	Hypereutrophic	96.7	20.5	4	5.1	2	158	1	100
Bell*	Eutrophic	1.0	0.5	32	1.5	17	641	20	20
Patrick	Eutrophic	93.3	42.1	159	2.0	10	1808	5	15
Orienta*	Eutrophic	1.0	0.5	52	2.2	25	448	9	9
Brim-pond	Eutrophic	3.4	1.2	3	2.2	9	624	8	9
Conine	Hypereutrophic	1.0	0.5	96	0.5	1043	2056	110	110
Pasadena	Eutrophic	73.3	61.6	151	2.2	15	702	3	13
Susannah	Eutrophic	6.7	1.1	31	1.5	23	674	25	26
Rowell	Hypereutrophic	43.3	10.3	147	0.8	66	910	47	47
Crooked	Mesotrophic	26.7	2.8	8	3.1	7	313	5	13
Little Fish	Eutrophic	80.0	30.7	2	1.4	21	1161	13	32
Douglas	Eutrophic	96.7	67.3	16	1.5	11	1122	2	12
Carr	Hypereutrophic	100.0	100.0	254	1.8	19	874	11	201
Turkey-pen	Oligotrophic	16.7	2.6	6	3.2	2	132	1	1
Lindsey	Eutrophic	100.0	79.6	55	1.9	19	636	6	36
Loften	Mesotrophic	86.7	21.9	5	2.5	5	633	2	4
Koon	Eutrophic	96.7	92.6	44	1.4	5	687	3	16

Oglesby 1977, Jones and Hoyer 1982 Hanson and Leggett 1982, Bays and Crisman 1983). Consequently, any study attempting to elucidate relationships between the abundance of aquatic macrophytes and the abundance of largemouth bass must consider the effect of lake trophic status (Hoyer et al. 1985a).

Young-of-the-year largemouth bass abundance and the abundance of subadult largemouth bass in our study lakes averaged (geometric mean) 106 fish/ha and 25 fish/ha, respectively. Young-of-the-year largemouth bass abundance (fish/ha) was not correlated with average lake total phosphorus concentrations, total nitrogen concentrations, chlorophyll *a* concentrations, Secchi disc values, or adjusted chlorophyll *a* concentrations (Table 3). Young-of-the-year largemouth bass abundance was, however, significantly correlated to PVI (r = 0.26) but not PAC. The abundance of subadult largemouth bass (fish/ha) was correlated with total phosphorus concentrations (r = -0.39), total nitrogen concentrations (r = -0.27), chlorophyll *a* concentrations (r= -0.26) and Secchi depth (r= 0.35). The abundance of subadult largemouth bass was not correlated to adjusted chlorophyll *a* concentrations. The abundance of subadult largemouth bass, however, was correlated to both PAC (r = 0.33) and PVI (r = 0.29). Only a small fraction of the variance in Young-of-the-year largemouth bass abundance (R^2 = 0.08) and the abundance of subadult largemouth bass (R^2= 0.06) was explained by a combination of adjusted chlorophyll *a* concentrations and PVI (Table 4). In these multiple linear regressions PVI caused a significant effect for young-of-the-year largemouth bass but not for subadult largemouth bass, after accounting for lake trophic status.

The growth of age-1 and age-2 fish averaged 0.42 and 0.27 (mm/day), respectively. Growth of age-l and age-2 fish were correlated (Table 3) with average lake total phosphorus concentrations (r = 0.51 and r = 0.50, respectively), total nitrogen concentrations (r = 0.38 and r = 0.42, respectively), chlorophyll *a* concentrations (r = 0.52 and r = 0.57, respectively), Secchi disc values (r = -0.44 and r = -0.42, respectively), and adjusted chlorophyll *a* concentrations (r = 0.25 and r = 0.33, respectively). Growth of age-l fish was also correlated with both PAC (r = - 0.40) and PVI (r = -0.28). Growth of age-2 fish was correlated with PAC (r = -0.36) but not PVI. Only a small fraction of the variance in the age-1 growth (R^2 = 0.22) and age-2 growth (R^2 = 0.15) was explained by a combination of adjusted chlorophyll *a* concentrations and PVI (Table 4). In these multiple linear regressions PVI caused a significant effect for age-1 growth but not for age-2 growth, after accounting for lake trophic status.

The stock (fish/ha) and standing crop (kg/ha) of adult largemouth bass averaged (geometric mean) 18 fish/ha and 11.6 kg/ha, respectively. The stock (fish/ha) of adult largemouth bass was not correlated with average lake total phosphorus concentrations chlorophyll *a* concentrations or Secchi disc values (Table 3) but was correlated with total nitrogen concentrations (r = 0.30) and adjusted chlorophyll *a* concentrations (r = 0.33). The standing crop (kg/ha) of adult largemouth bass was correlated with total phosphorus (r = 0.38), total nitrogen (r = 0.45), chlorophyll *a* (r = 0.40), adjusted chlorophyll *a* (r = 0.45) and Secchi depth (r= -0.31). The stock (fish/ha) and standing crop (kg/ha) of adult largemouth bass were not correlated with PAC or PVI. Only a small fraction of the variance in the stock (R^2 = 0.12) and standing crop (R^2 = 0.22) of adult largemouth bass was explained by a combination of adjusted chlorophyll *a* concentrations and PVI with only adjusted chlorophyll *a* being significant (Table 4).

Aquatic macrophytes have been linked to the survival and abundance of young-of-the-year, subadult, and adult largemouth bass in Florida (Wegener and Williams 1974, Barnett and Schneider 1974, Moxley and Langford 1982, Shireman et al. 1983). Young-of-the-year, and subadults do show weak positive relations with PAC and PVI in the 56 study lakes. The growth rates of these fish (age-1 and age-2 growth rates) show inverse trends with PAC and PVI, which is similar to studies showing reduced fish growth and condition in lakes with excessive aquatic vegetation (Bennett 1948, Buck et al.

Table 3. Correlation matrix for all parameters sampled on 56 Florida lakes. Mark recapture estimates were conducted for adult largemouth bass (>250 mm TL) in only 50 lakes. Absolute r values equal to or greater than 0.25 for all correlations are significant at a P ≤0.05 level, except ones with adult largemouth bass. Absolute r values equal to or greater than 0.27 are significant for correlations with adult largemouth bass.

Variable	X1	X2	X3	X4	X5	X6	X7	X8	Y1	Y2	Y3	Y4	Y5	Y6
Lake Trophic Status:														
X1. Total Phosphorus (μg/L)	1.00	•	•	•	•	•	•	•	•	•	•	•	•	•
X2. Total Nitrogen (μg/L)	0.83	1.00	•	•	•	•	•	•	•	•	•	•	•	•
X3. Chlorophyll *a* (μg/L)	0.86	0.84	1.00	•	•	•	•	•	•	•	•	•	•	•
X4. Adjusted Chlorophyll *a* (μg/L)	0.58	0.71	0.73	1.00	•	•	•	•	•	•	•	•	•	•
X5. Secchi (m)	-0.88	-0.88	-0.89	-0.64	1.00	•	•	•	•	•	•	•	•	•
Lake morphology:														
X6. Surface area (ha)	0.48	0.46	0.43	0.23	-0.42	1.00	•	•	•	•	•	•	•	•
Aquatic macrophyte:														
X7. PAC (%)	-0.49	-0.30	-0.53	0.05	0.48	-0.21	1.00	•	•	•	•	•	•	•
X8. PVI (%)	-0.27	-0.05	-0.32	0.24	0.26	-0.06	0.89	1.00	•	•	•	•	•	•
Largemouth Bass:														
Y1. YOY (Fish/ha)	-0.03	0.10	-0.08	0.03	0.12	-0.05	0.20	0.26	1.00	•	•	•	•	•
Y2. Recruits (Fish/ha)	-0.39	-0.27	-0.26	-0.11	0.35	-0.15	0.33	0.29	0.39	1.00	•	•	•	•
Y3. Largemouth > 250 mm TL (no/ha)	0.23	0.30	0.20	0.33	-0.12	-0.09	0.12	0.19	0.48	0.14	1.00	•	•	•
Y4. Largemouth > 250 mm TL (kg/ha)	0.38	0.45	0.40	0.45	-0.31	0.03	-0.03	0.11	0.44	0.03	0.91	1.00	•	•
Y5. First year growth (mm/day)	0.51	0.38	0.52	0.25	-0.44	0.05	-0.40	-0.28	-0.24	-0.27	0.00	0.05	1.00	•
Y6. Second year growth (mm/day)	0.50	0.42	0.57	0.33	-0.42	0.25	-0.36	-0.22	0.18	-0.04	0.26	0.42	0.28	1.00

Table 4. Multiple linear regression models relating dependent variables number of YOY largemouth bass (<160 mm TL), number of subadult largemouth bass (160-240 mm TL), age 1 and age 2 largemouth bass growth rates, stock and standing crop of adult (>250 mm TL) largemouth bass to independent variables adjusted chlorophyll *a* concentration and percent volume infested with aquatic macrophytes (PVI %). An asterisk denoted a significant effect at p≤0.05.

Dependent variables	Lakes	Intercept	Independent variables	Slope	F Ratio	Probability >F	R^2
Log 10 YOY (fish/ha)	56	1.81	Adjusted chlorophyll *a*	-0.0146	0.01	0.94	
			PVI	0.5583	4.40	0.04*	0.08
Log 10 subadult (fish/ha)	56	1.44	Adjusted chlorophyll *a*	-0.1144	1.44	0.23	
			PVI	0.2237	2.54	0.12	0.06
age 1 growth rates (mm/day)	56	0.4	Adjusted chlorophyll *a*	0.0330	9.29	<0.01*	
			PVI	-0.0494	9.56	<0.01*	0.22
age 2 growth rates (mm/day)	56	0.24	Adjusted chlorophyll *a*	0.0349	8.79	<0.01*	
			PVI	-0.0218	1.59	0.21	0.15
Log 10 adult bass > 250 mm TL (fish/ha)	50	1.00	Adjusted chlorophyll *a*	0.1626	4.79	0.03*	
			PVI	0.0946	0.61	0.44	0.12
Log 10 adult bass > 250 mm TL (kg/ha)	50	0.72	Adjusted chlorophyll *a*	0.2599	11.33	<0.01*	
			PVI	-0.0051	0.00	0.97	0.20

1975, Colle and Shireman 1980). Stock (fish/ha) and standing crop (kg/ha) of adult largemouth bass showed no relation with PAC and PVI and only weak positive trends with lake trophic status. Other positive relations between trophic state variables (Secchi depth and chlorophyll *a*) and largemouth bass standing crop and yield have also been reported (Ploskey et al. 1986, Hoyer et al. 1985). Results of the individual multiple linear regressions show overall low R^2 values ranging from 6% to 22%. The multivariate analysis indicated marginal significance for adjusted chlorophyll *a* ($p<0.05$) overall, and nonsignificance overall for PVI and the interaction of PVI and adjusted chlorophyll. Thus, the small amount of variance accounted for in all of these relations suggest that neither lake trophic status or macrophyte abundance seem to be major determinants of largemouth bass growth rates or abundance (fish/ha) among the Florida lakes sampled.

The lakes with the ten lowest adult largemouth bass stock estimates (Barco, Bonny, Keys-pond, Picnic, Cue, Mill Dam, Clear, Carlton, and Holden) had mean total phosphorus and total nitrogen concentrations of 25 µg/L and 820 µg/L, respectively. The lakes with the highest largemouth bass stock estimates (Bell, Patrick, Orienta, Brim-pond, Conine, Pasadena, Susannah, Rowell, Crooked, Little Fish) had average total phosphorus and total nitrogen concentrations of 120 µg/L and 930 µg/L, respectively. The ten lakes with the lowest adult largemouth bass stock estimates and the lower nutrient concentrations had PAC values ranging from 1 to 87%, while the lakes with the ten highest adult largemouth bass stock estimates and the higher average nutrient concentrations had PAC values ranging from 1 to 93% (Table 1 and 2). Again, lakes with higher nutrient concentrations tended to have more adult largemouth bass, but there was no apparent relationship between adult largemouth bass stock and abundance of aquatic macrophytes among these lakes.

Two of the ten lakes with the highest (Bell and Orienta) and two of the ten lakes with the lowest estimates (Clear and Holden) of adult largemouth bass stocks were grass carp lakes (Table 1). Adult largemouth bass abundance in the eight grass carp lakes (Clear, Holden, Wales, Killarny, Baldwin, Pearl, Bell, and Orienta) averaged (geometric mean) 18 fish/ha, which is identical to the overall average for all the study lakes. The grass carp lakes were all eutrophic or hypereutrophic lakes (Table 2). As a group, the eutrophic lakes had an average standing stock of adult largemouth bass of 28 fish/ha and the hypereutrophic lakes averaged 18 fish/ha (Figure 1). Adult largemouth bass abundance (fish/ha) in the grass carp lakes was only statistically different from the adult largemouth bass abundance in the oligotrophic lakes

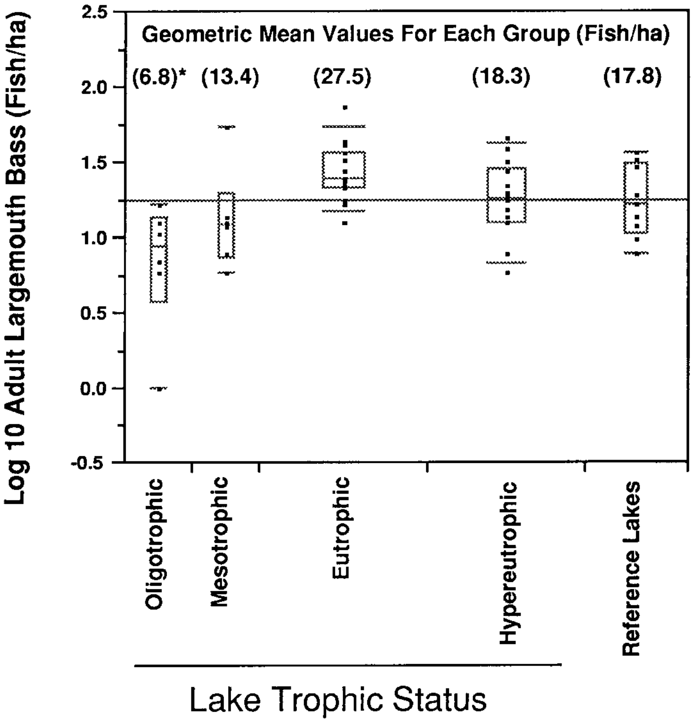

Figure 1. Geometric mean values of adult largemouth bass stocks (fish>250 mm TL/ha) of four lake trophic states and grass carp lakes (reference lakes). An asterisk denotes that Dunnett's test suggests a group is significantly different from the reference lakes. The line represents the grand mean of all values. The quantile box plots show the median as a line across the middle of the box, the 25th and 75th quantiles are the ends of the box and the 10th and 90th quantiles are the lines above and below the box.

(Figure 1), and adult largemouth stock was not significantly different from any of the four PAC groups (Figure 2).

MANAGEMENT AND RESEARCH CONCERNS

Durocher et al. (1984) suggested, based on an empirical analysis of data from 30 large Texas reservoirs, that any reduction below 20% coverage of submerged vegetation will result in a concurrent reduction in largemouth bass recruitment and standing crop. The Florida Game and Fresh Water Fish Commission suggests that 30% plant coverage represents a healthy balance for fish in small water bodies (Anonymous 1994). We, however, conclude for Florida lakes < 300 ha that there are no strong predictable relationships between the abundance (fish/ha) of adult largemouth bass and the abundance of aquatic macrophytes as measured by either PAC or PVI.

Although macrophytes can provide food, shelter, and spawning sites for largemouth bass, our study demonstrates that largemouth bass in small Florida lakes exist without submersed, floating-leaved, and/or emergent aquatic vegetation. For example, the grass carp lakes have been virtually free of aquatic macrophytes for ten or more years and all the lakes supported > 8 adult largemouth bass/ha. Lakes Bell, Orienta, and Pearl supported ≥ 30 adult largemouth bass/ha. Thus, attempts to use empirical field evidence to justify the need for a specific level (e.g., 20% to 30% PAC) of aquatic vegetation to support largemouth bass populations in Florida lakes < 300 ha will remain controversial.

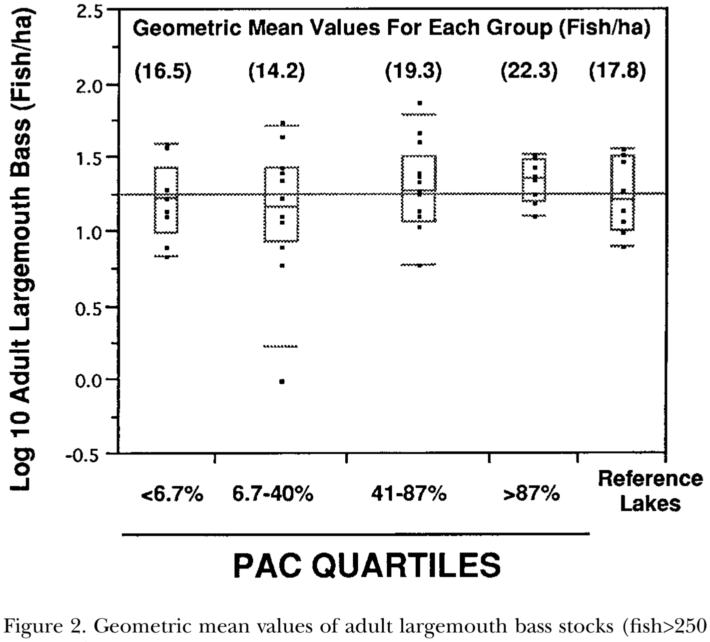

Figure 2. Geometric mean values of adult largemouth bass stocks (fish>250 mm TL/ha) of four quartiles based on percent area covered with aquatic vegetation (first quartile = PAC<6.7%, second quartile = PAC 6.7-40%, third quartile = PAC 41-87%, and fourth quartile = PAC>87%), and grass carp lakes (reference lakes). An asterisk denotes that Dunnett's test suggests a group is significantly different from the reference lakes. The line represents the grand mean of all values. The quantile box plots show the median as a line across the middle of the box, the 25th and 75th quantiles are the ends of the box and the 10th and 90th quantiles are the lines above and below the box.

Our study addressed the effect of aquatic macrophytes on largemouth bass populations, not the effect of aquatic macrophytes on largemouth bass fishing. Additional research is needed to determine if the loss of aquatic macrophytes adversely affects largemouth bass catches on lakes < 300 ha. Anglers tend to use aquatic vegetation to find fish and fishing aquatic vegetation is part of the largemouth bass fishing experience. Thus, anglers will continue to perceive aquatic plant management in a negative context unless it can be demonstrated that the loss of vegetation does not adversely affect largemouth bass fishing. From a practical lake management standpoint, it seems reasonable to try to leave some aquatic macrophytes for anglers, but we suggest that the 20-30% PAC currently being recommended for largemouth bass is not needed in small Florida lakes.

The statistical importance of different factors controlling the abundance of largemouth bass can change with the scale of analysis (e.g., Duarte and Kalff 1989). We examined the effect of lake trophic status on the abundance of young-of-the-year, subadult, and adult largemouth bass because Hoyer et al. (1985a) and Ploskey et al. (1986) found a positive relationship between lake trophic status as assessed by chlorophyll *a* concentrations and largemouth bass standing crop and yield. Although lake trophic status has some direct effect on largemouth bass standing crop and growth in small Florida lakes, it is not a particularly strong determinant of the number of young-of-the-year, subadult, or adult largemouth bass per hectare. Carlander (1955), after compiling information on lakes and reservoirs from different regions of the United States, reported that largemouth bass standing crops ranged from 0.22 kg/ha to 74 kg/ha. The average standing crop for largemouth bass for lakes and reservoirs was 12 kg/ha. The standing crop estimates of adult largemouth bass in our study lakes ranged from 0.64 kg/ha to 68 kg/ha and averaged 15 kg/ha (coefficient of variation = 68%). Why largemouth bass numbers and standing crops in lakes are relatively constant across trophic status and lakes with diverse limnological conditions is an area where additional research is needed.

One factor that may contribute to largemouth bass surviving in lakes of different trophic status and in lakes with and without aquatic vegetation is the opportunistic feeding behavior of largemouth bass (Shireman and Hoyer 1986, Porak et al. 1990, Bettoli et al. 1992, 1993). These studies suggest that as aquatic macrophytes are removed from a system largemouth bass food habits shift from macrophyte oriented species (e.g., small Centrarchids) to open-water oriented species (e.g., Clupeids).

Angler harvest may also be a key influence on the abundance of largemouth bass. Williams et al. (1988) found largemouth bass exploitation rates of up to 35% did not constitute overharvest or affect the size distribution of largemouth bass populations in Florida's Kissimmee Chain of Lakes. Exploitation rates in some small Florida lakes, however, can exceed 35%. Anglers harvested an estimated 20 largemouth bass/hectare (42% of the estimated population) in lake Rowell, Florida during a three-month spring creel (Porak et al. 1990). The exploitation rates in our study lakes, however, probably bracket 35% by a considerable margin. Little Fish in our study, is a lake with an expected low exploitation rate because it is located on private property and has limited fishing pressure. This lake also had the highest standing crop of adult largemouth bass at 75 fish/ha. Thus, research is needed to examine the possibility of differential angler mortality between lakes with and without aquatic macrophytes and harvest of largemouth bass may have to be managed more intensely in some lakes to support quality fishing.

We examined the variance in largemouth abundance among lakes having a surface area < 300 ha. Although lakes < 300 ha constitute 97% of Florida's lakes (Shafer et al. 1986), most of Florida's better known fishing lakes are substantially larger (e.g., Lake Kissimmee, 14,143 ha Lake Tohopekaliga, 7,612 ha Lake Okeechobee, 181,000 ha). Large Florida lakes without aquatic vegetation may have a bottleneck related to the survival of largemouth bass to adult size because shoreline habitat may be the only available refuge from predation. In Florida, most lakes are near circular and the abundance of shoreline habitat per surface area of these lakes decrease dramatically as the surface area of a lake increases. Large lakes, therefore, may need aquatic macrophytes as refuge for young-of-the year and subadult largemouth bass more so than small lakes due to the reduced shoreline to surface area ratio. For example, if the fish management goal for a Florida lake is to produce an average population of 22 adult largemouth bass per hectare (Hoyer and Canfield 1994), a circular 10-ha lake without vegetation has 112 m of shoreline habitat to save a minimum 22 young-of-the year or subadult largemouth bass. A circular 10,000-ha lake without vegetation, however, would have to produce a minimum 22 young-of-the year or subadult largemouth bass for every 3.5 m of shoreline habitat. This does not hold true for large lakes or reservoirs that have a high shoreline development and may be the reason why Bailey (1978) found no predictable impact on largemouth bass populations in reservoirs, after the removal of aquatic macrophytes with grass carp. Therefore, we suggest that additional research is needed to determine the relations among aquatic macrophytes, shoreline development and largemouth bass populations in large lake systems (i.e., lakes > 300 ha).

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