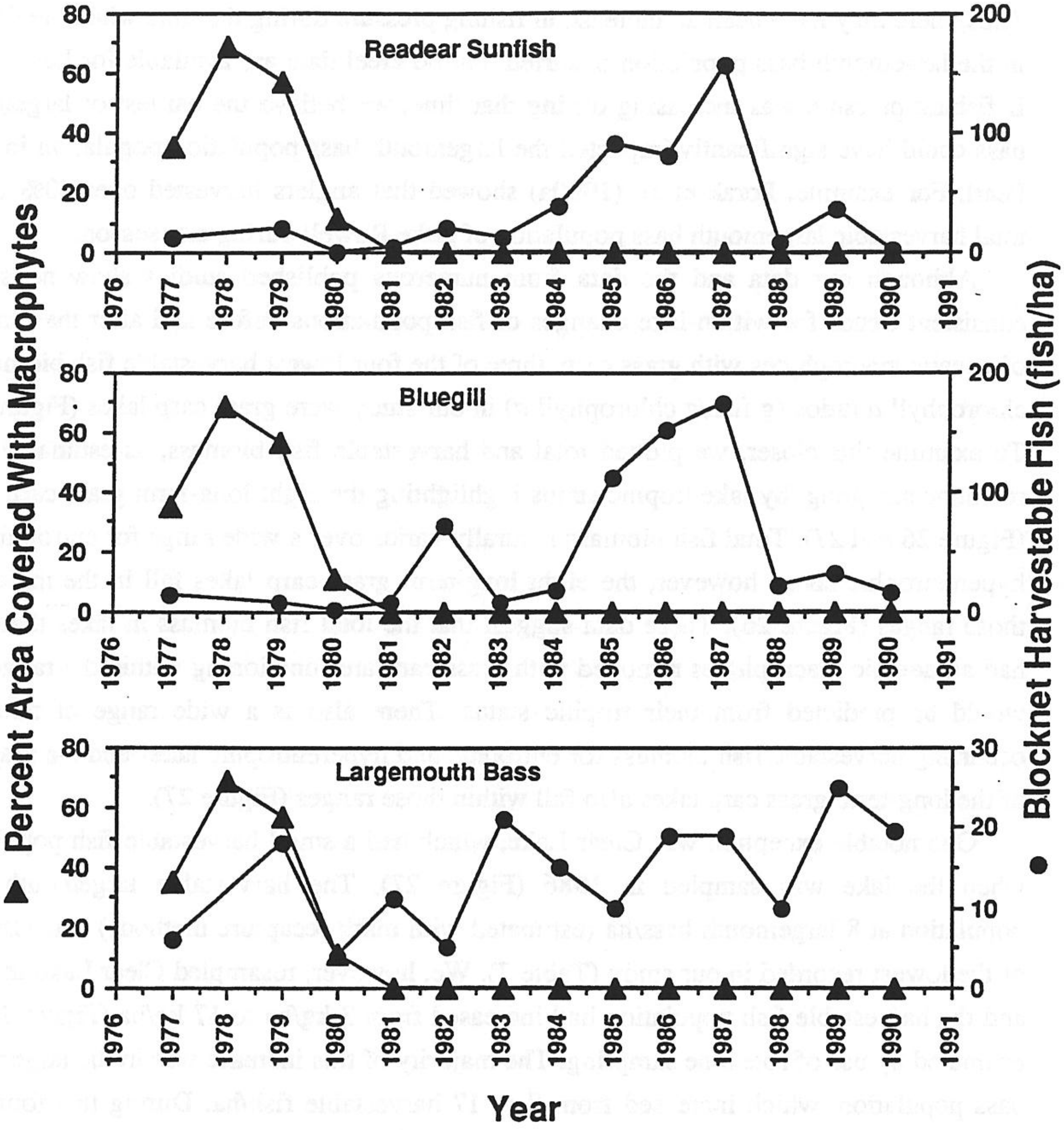


Figure 25. Long-term blocknet harvestable bluegill, redear sunfish and largemouth bass and macrophyte coverage data for Lake Baldwin, Florida (Colle and Shireman, unpublished data).

Thus, there may have been an increase in fishing pressure during the time when the decline in the largemouth bass population occurred, but no creel data are available for Lake Pearl. If fishing pressure was increasing during that time, we believe the harvest of largemouth bass could have significantly impacted the largemouth bass population population in Lake Pearl. For example, Porak et al. (1990a) showed that anglers harvested over 40% of the total harvestable largemouth bass population of Lake Rowell during one season.

Although our data and the data from numerous published studies show no strong consistent trends for within-lake changes of fish populations before and after the removal of aquatic macrophytes with grass carp, three of the four lowest harvestable fish biomass to chlorophyll *a* ratios (g fish/g chlorophyll *a*) in our study were grass carp lakes (Figure 15). To examine this closer, we plotted total and harvestable fish biomass, as estimated with rotenone sampling, by lake trophic status highlighting the eight long-term grass carp lakes (Figure 26 and 27). Total fish biomass naturally varies over a wide range for eutrophic and hypereutrophic lakes, however, the eight long-term grass carp lakes fall in the middle of those ranges (Figure 26). These data suggest that the total fish biomass in lakes that have had all aquatic macrophytes removed with grass carp are functioning within the range that would be predicted from their trophic status. There also is a wide range of naturally occurring harvestable fish biomass for eutrophic and hypereutrophic lakes and the majority of the long-term grass carp lakes also fall within those ranges (Figure 27).

One notable exception was Clear Lake, which had a small harvestable fish population when the lake was sampled in 1986 (Figure 27). The harvestable largemouth bass population at 8 largemouth bass/ha (estimated with mark recapture methods) was also one of the lowest recorded in our study (Table 7). We, however, resampled Clear Lake in 1990 and the harvestable fish population had increased from 3 kg/ha to 17 kg/ha (Figure 27), as estimated by use of rotenone sampling. The majority of this increase was in the largemouth bass population, which increased from 8 to 17 harvestable fish/ha. During this four year period, there was also no aquatic vegetation reestablished in Clear Lake. Thus, unless the reader of this report is willing to give us the credit for improving the harvestable fish population of Clear lake, some naturally occurring event must have happened to improve this fish population.

We believe that there is the potential for a decreased fish population in lakes that have had total removal of aquatic macrophytes with grass carp, but fish populations in these

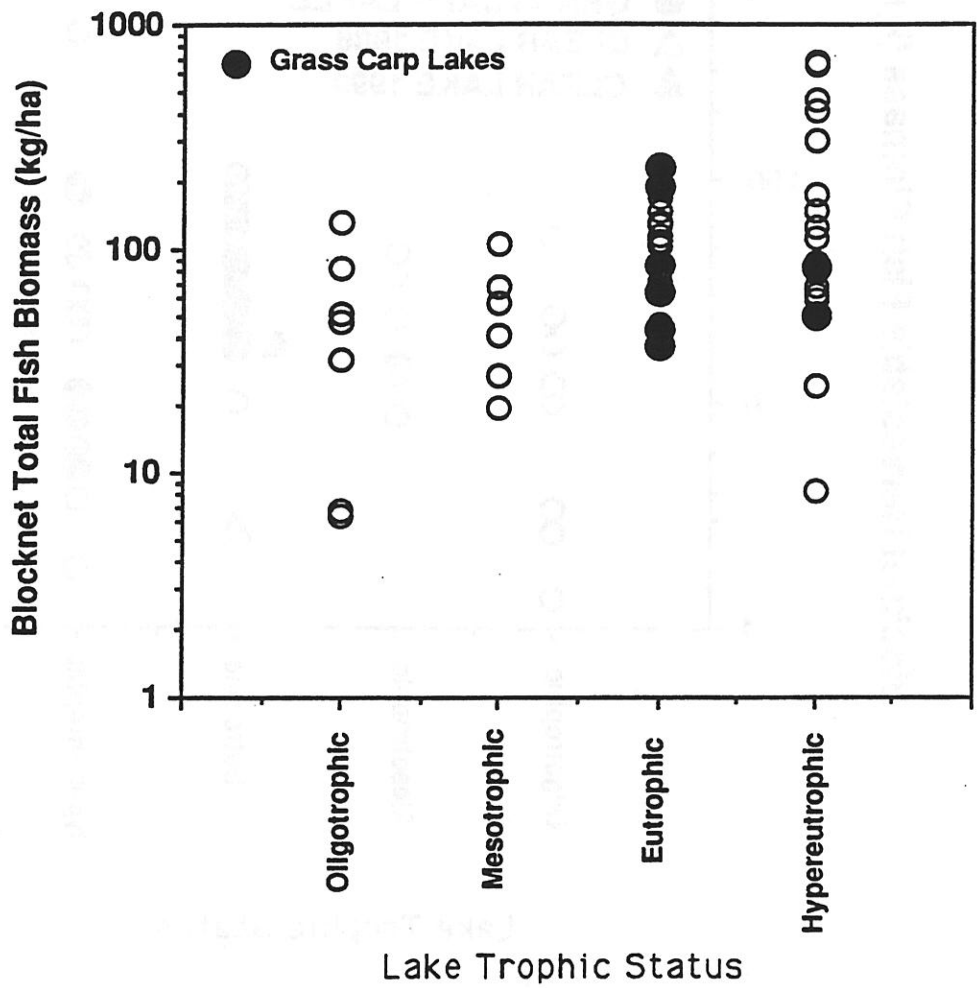


Figure 26. The relation between lake trophic status and total fish biomass (kg/ha), as estimated with blocknets, for 60 Florida Lakes. Eight lakes that have had all aquatic macrophytes removed with grass carp for 10 to 15 years have been highlighted.

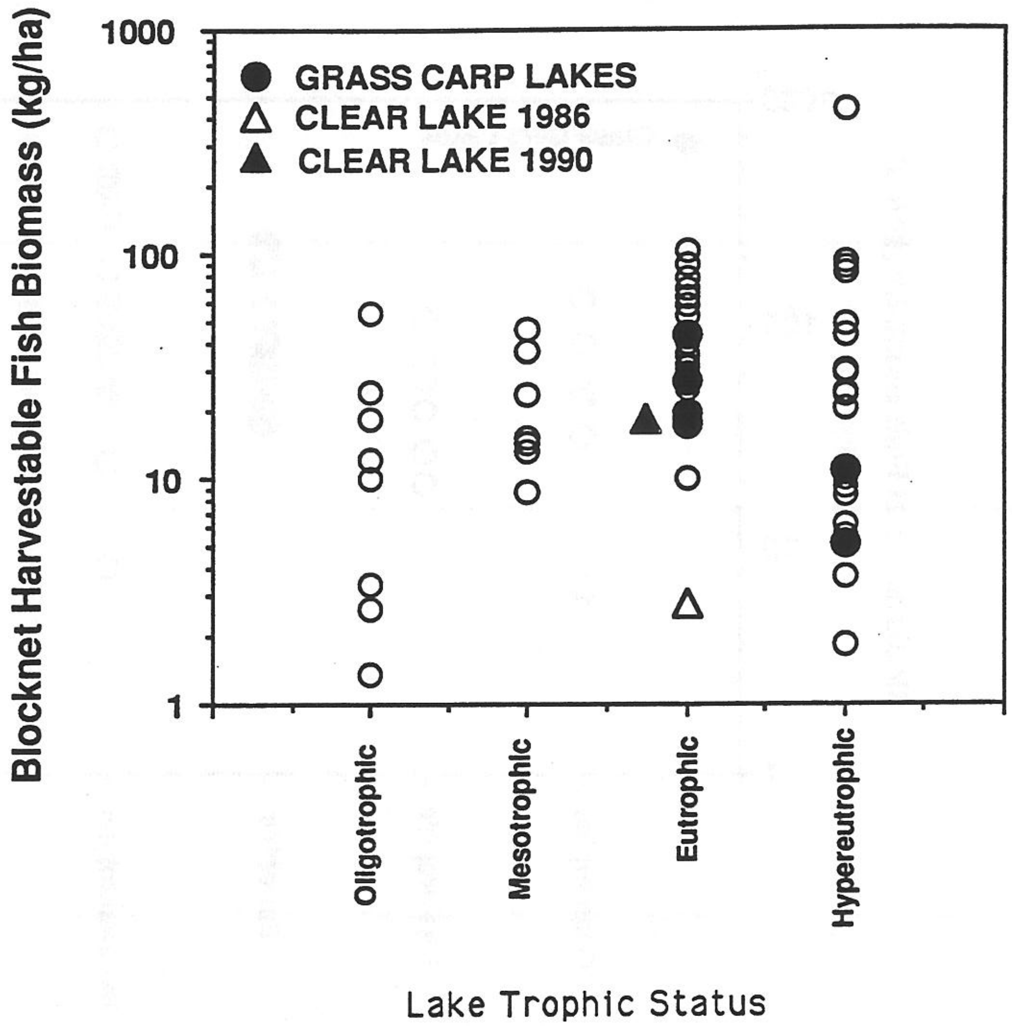


Figure 27. The relation between lake trophic status and harvestable fish biomass (kg/ha), as estimated with blocknets, for 60 Florida Lakes. Eight lakes that have had all aquatic macrophytes removed with grass carp for 10 to 15 years have been highlighted.

lakes fluctuate naturally and can be equivalent to other Florida lakes of equal trophic status. A consistent trend in lakes with complete control of aquatic macrophytes, however, was a primary production shift from a macrophyte-periphyton base to a phytoplankton-based system. Concurrent with this change, we found (Table 251) as have others (Ware and Gasaway 1978; Klussmann et al. 1988) that there is an increase in the abundance of open-water fish species (e.g., gizzard shad and threadfin shad) and a decrease in macrophyte-associated species (e.g., bluespotted sunfish and golden topminnow). This trend has led many individuals to ask if the introduction of the grass carp will eliminate any native fish populations.

Sample area and species richness relations have been reported for many flora and fauna (Flessa and Sepkoski 1978; Connor and McCoy 1979). Williamson (1988) suggested that there were several possible explanations for species area relations including: 1) an increase in area may simply increase the sampling size, resulting in more species; 2) an increase in area may correlate with an increase in habitat heterogeneity; and 3) MacArthur and Wilson, theory of island biogeography may be a factor (see MacArthur and Wilson 1967). Determining the exact mechanism for these relations is beyond the scope of this report, but there is a strong lake area-fish species relation for the 60 Florida lakes sampled in our study (Figure 28). The eight long-term grass carp lakes fall within the range of the lake area-species richness relation for these 60 Florida lakes. Although the total abundance of macrophyte-oriented species decreases, the long-term removal of aquatic macrophytes with grass carp has not eliminated fish species from these systems. This finding was reported earlier for Lake Baldwin (Shireman and Hoyer 1986) and has also been reported for Lake Conroe, Texas (Klussmann et al. 1988) where complete control of aquatic macrophytes was achieved with grass carp. Thus, the shift from a macrophyte dominated system to a phytoplankton dominated system may produce a change fish species composition, but it apparently will not by itself eliminate fish species from a lake.

Table 251. Mean fish species percent composition (by weight) of the total fish biomass estimated with blocknets. The values are listed by species for the percent area covered with aquatic macrophytes groups. N represents the number of lake samples in which a species was found and r is the correlation coefficient for the relation between percent area covered with aquatic macrophytes and percent composition for each species in those lakes.

			Percent Area Covered With Aquatic Macrophytes			
Fish Species	n	r	0 - 25%	26 - 50%	51 - 75%	75 - 100%
Species with decreasing percent composition with increasing macrophyte coverage:						
Gizzard shad	21	-0.44[a]	28.12	11.21	0.25	0.93
Threadfin shad	28	-0.32[a]	15.48	19.06	6.98	1.99
Species with increasing percent composition with increasing macrophyte coverage:						
Bluespotted sunfish	27	0.34[a]	0.93	0.85	3.60	2.13
Bowfin	17	0.59[a]	2.48	3.69	.	7.77
Dollar sunfish	22	0.47[a]	0.11	1.17	0.81	3.72
Golden topminnow	32	0.33[a]	0.11	0.51	0.61	0.61
Least killifish	17	0.45[a]	0.00	0.01	.	0.02
Mosquitofish	52	0.32[a]	0.06	0.10	0.07	0.57
Sailfin molly	11	0.74[a]	0.12	0.10	.	0.45
Tadpole madtom	13	0.46[a]	0.08	0.27	0.78	0.49
Warmouth	65	0.67[a]	2.89	16.89	10.33	20.25
White catfish	11	0.55[a]	0.77	0.02	.	10.56
Yellow bullhead	35	0.41[a]	0.69	1.75	3.18	1.75
Species with no trend in percent composition with increasing macrophyte coverage:						
Black crappie	40	-0.13	5.20	4.19	2.72	3.13
Bluegill	65	-0.15	30.34	31.96	31.43	22.23
Blue tilapia	14	0.05	9.47	2.80	15.41	.
Bluefin killifish	28	0.11	0.61	0.08	0.91	0.77
Brook silverside	44	-0.21	0.38	0.05	0.10	0.07
Brown bullhead	32	0.01	2.65	0.27	2.61	3.58
Chain pickerel	9	0.14	.	4.97	.	6.41
Everglades pygmy sunfish	11	0.08	0.02	0.10	.	0.03
Flagfish	5	0.24	.	0.79	0.04	0.91
Florida gar	20	0.29	2.39	1.34	1.00	4.59
Golden shiner	47	-0.10	4.18	4.26	5.94	1.57
Lake chubsucker	39	0.01	11.85	8.75	6.65	14.13
Largemouth bass	65	0.12	14.71	18.16	18.64	18.60
Lined topminnow	19	0.07	0.18	0.39	.	0.35
Longnose gar	3	0.31	0.01	.	.	0.02
Pirate perch	4	-0.60	0.10	0.07	.	0.05
Redbreast sunfish	8	0.38	0.84	0.13	.	.
Redear sunfish	51	0.04	10.68	15.70	7.86	11.29
Redfin pickerel	11	0.16	1.19	0.57	.	2.40
Seminole killifish	33	0.03	0.56	2.10	0.02	0.37
Spotted sunfish	23	0.35	0.30	1.77	3.01	0.87
Swamp darter	43	0.12	0.03	0.06	0.08	0.05
Taillight shiner	11	-0.05	0.27	1.01	.	0.05

a = significant at $p \leq 0.10$

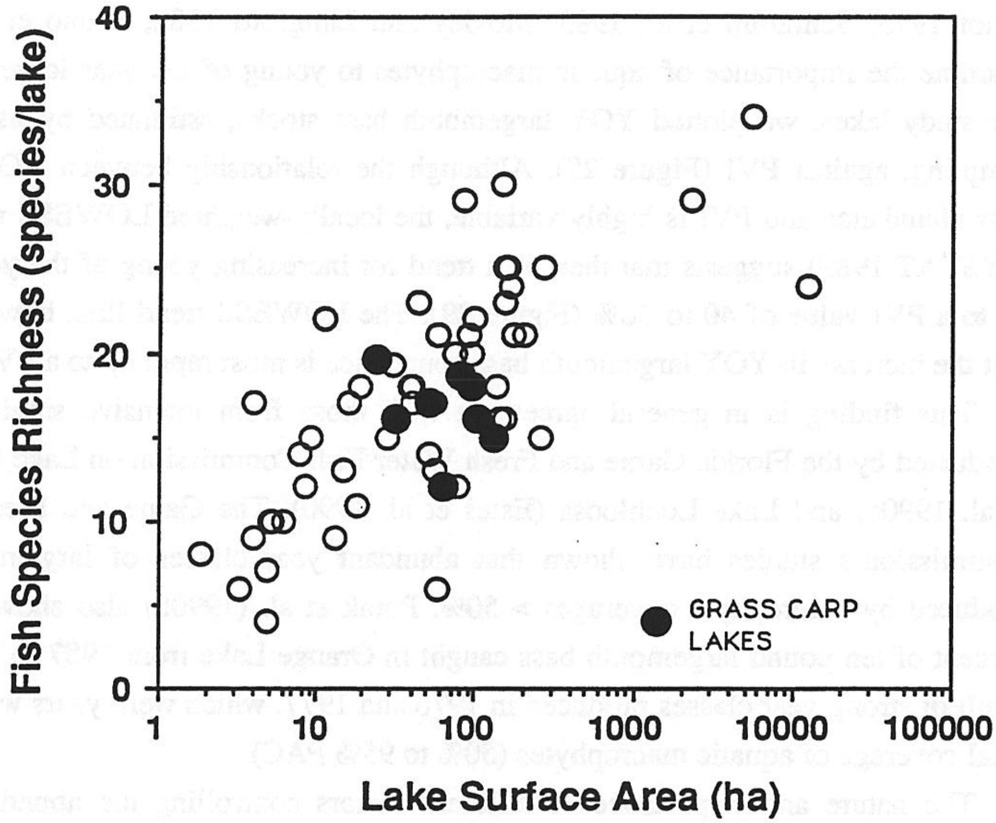


Figure 28. Relation between fish species richness (species/lake) and lake area for 60 Florida lakes. Eight lakes that have had all aquatic macrophytes removed, with grass carp for 10 to 15 years have been highlighted.

Influence of Aquatic Macrophytes on Largemouth Bass Populations

Aquatic macrophytes have been linked to the survival and well-being of largemouth bass populations in lakes, especially young of the year (YOY) largemouth bass (Horel 1951; Barnett and Schneider 1974; Chew 1974; Wegener and Williams 1974b; Aggus and Elliot 1975; Schramm et al. 1983; Moxley and Langford 1982; Bruno et al. 1990). To examine the importance of aquatic macrophytes to young of the year largemouth bass in our study lakes, we plotted YOY largemouth bass stocks, estimated by use of rotenone sampling, against PVI (Figure 29). Although the relationship between YOY largemouth bass abundance and PVI is highly variable, the locally-weighted LOWESS regression line (SYSTAT 1989) suggests that there is a trend for increasing young of the year abundance up to a PVI value of 40 to 50% (Figure 29). The LOWESS trend line, however, suggests that the increase in YOY largemouth bass abundance is most rapid up to a PVI of 15%.

This finding is in general agreement with those from intensive single lake studies conducted by the Florida Game and Fresh Water Fish Commission on Lake Rowell (Porak et al. 1990a) and Lake Lochloosa (Estes et al. 1990). The Game and Fresh Water Fish Commission's studies have shown that abundant year classes of largemouth bass are produced by macrophyte coverages > 50%. Porak et al. (1990b) also showed the largest percent of ten pound largemouth bass caught in Orange Lake from 1987 to 1989 were the result of strong year classes produced in 1976 and 1977, which were years with the highest areal coverage of aquatic macrophytes (50% to 95% PAC).

The nature and importance of different factors controlling the abundance of YOY largemouth bass, however, can change with the scale of analysis (also see Duarte and Kalff 1990). In our study, we examined the variance in YOY largemouth abundance among lakes where the studies by the Florida Game and Fresh Water Fish Commission examined the variance in abundance within a single lake. Although the fluctuation of vegetation abundance within a lake can produce a strong year class of largemouth bass in years of high vegetation (Estes et al. 1990; Porak et al. 1990a), YOY largemouth bass will not be as abundant in the years following the crash of vegetation because of cannibalism from the previous strong year class (Porak et al. 1990a). Lakes with little vegetation also have the potential for large year classes of YOY largemouth bass (Figure 29). For example, Watertown Lake and Brim Pond had the two largest standing stocks of YOY largemouth

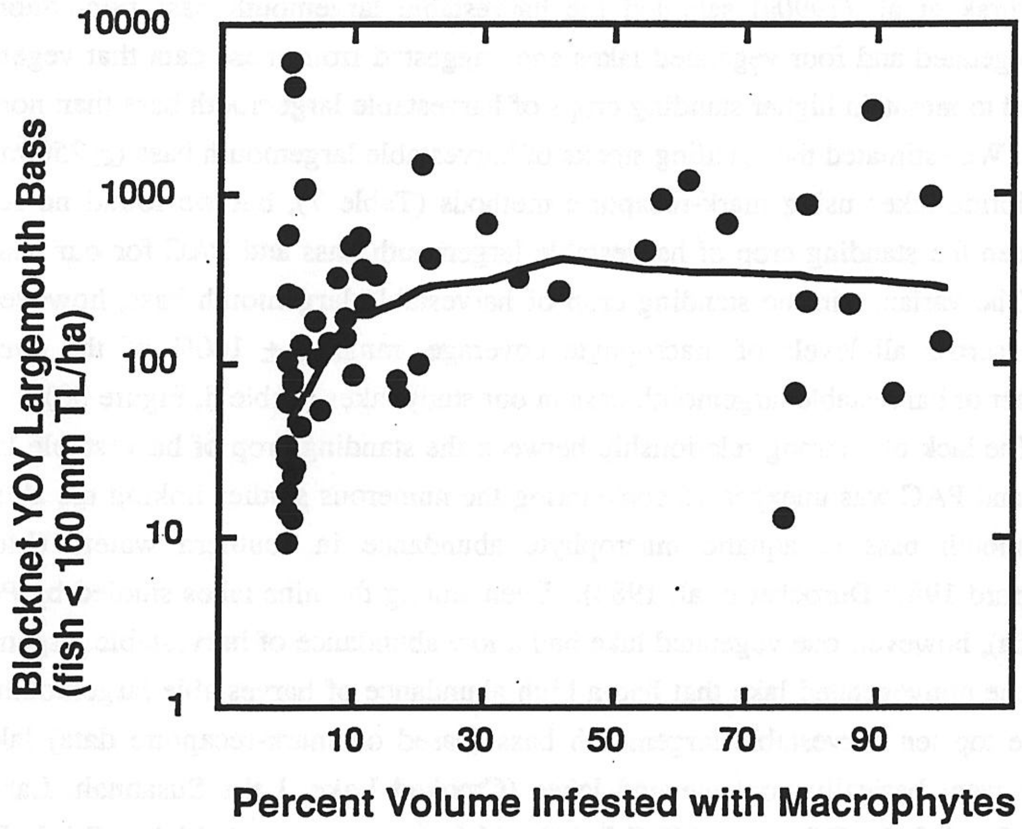


Figure 29. Relation between young of year (YOY) largemouth bass, estimated with rotenone sampling, and the percent volume infested with aquatic vegetation for 60 Florida lakes. The plotted line is a locally weighted regression trend line (LOWESS, Cleveland 1979, 1981).

bass (5,800 and 4,200 fish/ha, respectively) sampled during our study and each lake had virtually no macrophytic vegetation for several years prior to our sampling. Thus, removing all macrophytic vegetation from a lake does not guarantee that the standing crops of YOY largemouth bass will be low, but maintaining a minimum PVI value of 15% in lakes seems to increase the probability of having a strong year class of largemouth bass.

Porak et al. (1990a) sampled the harvestable largemouth bass populations in five nonvegetated and four vegetated lakes and suggested from these data that vegetated lakes tended to maintain higher standing crops of harvestable largemouth bass than nonvegetated lakes. We estimated the standing stocks of harvestable largemouth bass (≥ 250 mm TL) for 51 Florida lakes using mark-recapture methods (Table 7), but we found no relationship between the standing crop of harvestable largemouth bass and PAC for our lakes (Figure 30). The variance in the standing crop of harvestable largemouth bass, however, was the same across all levels of macrophyte coverage, ranging ± 100% of the overall mean number of harvestable largemouth bass in our study lakes (Table 8, Figure 30).

The lack of a strong relationship between the standing crop of harvestable largemouth bass and PAC was unexpected considering the numerous studies linking the abundance of largemouth bass to aquatic macrophyte abundance in southern waters (Moxley and Langford 1982; Durocher et al. 1984). Even among the nine lakes studied by Porak et al. (1990a), however, one vegetated lake had a low abundance of harvestable largemouth bass and one nonvegetated lake that had a high abundance of harvestable largemouth bass. Six of the top ten harvestable largemouth bass (based on mark-recapture data) lakes in our study were basically nonvegetated lakes (Crooked Lake, Lake Susannah, Lake Conine, Brim Pond, Lake Orienta and Bell Lake) and four were vegetated lakes (Little Fish Pond, Lake Rowell, Lake Pasadena, and Lake Patrick). The standing stock of harvestable (> 250 mm TL) largemouth bass in these lakes ranged from 35 to 75 fish/ha, which is well above the average of 22 fish/ha for all 51 Florida lakes that we measured. We, therefore, believe that the larger data base of our study fills in the complete range of conditions that Porak et al. (1990a) were not able to sample and we conclude that there is no strong relationship between the percent area covered with aquatic macrophytes and harvestable largemouth bass standing stocks in lakes.

The size structure of largemouth bass populations is sometimes more important to the fisheries of lakes then the standing stock of harvestable fish. To examine the size structure

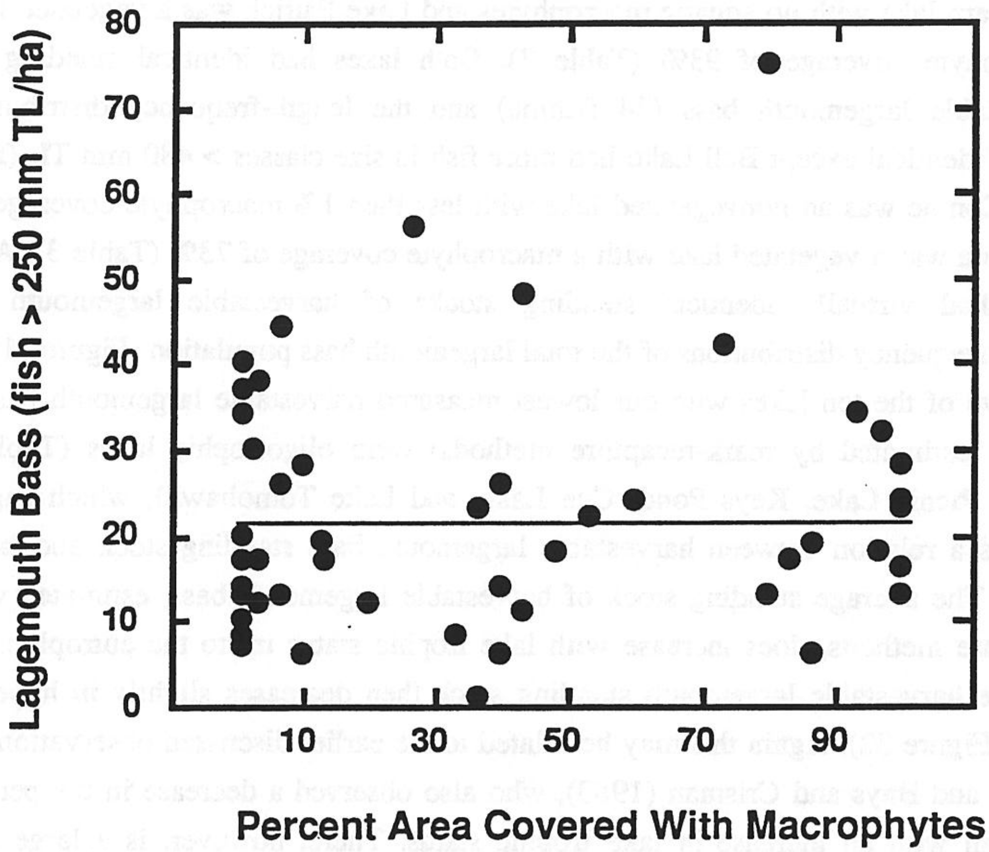


Figure 30. Relation between percent area covered with macrophytes and harvestable largemouth bass (fish > 250 mm TL/ha), estimated with mark-recapture methods. The line on the graph represents the average of 22 harvestable largemouth bass/ha for all the lakes sampled in this study.

of largemouth bass populations in the top ten harvestable largemouth bass lakes, we made length-frequency charts using all largemouth bass > 160 mm TL captured during the same week in the warm-water season using rotenone sampling, experimental gillnets and electrofishing (Figure 31). No trend was found between the size distribution of largemouth bass populations and the abundance of aquatic macrophytes. Bell Lake was a long-term grass carp lake with no aquatic macrophytes and Lake Patrick was a vegetated lake with a macrophyte coverage of 93% (Table 3). Both lakes had identical standing stocks of harvestable largemouth bass (34 fish/ha) and the length-frequency distributions were almost identical except Bell Lake had more fish in size classes > 480 mm TL (Figure 31). Lake Conine was an nonvegetated lake with less then 1% macrophyte coverage and Lake Pasadena was a vegetated lake with a macrophyte coverage of 73% (Table 3). Again, both lakes had virtually identical standing stocks of harvestable largemouth bass and length-frequency distributions of the total largemouth bass population (Figure 31).

Five of the ten lakes with our lowest measured harvestable largemouth bass standing stocks (estimated by mark-recapture methods) were oligotrophic lakes (Table 7; Lake Barco, Picnic Lake, Keys Pond, Cue Lake, and Lake Tomohawk), which suggests that there is a relation between harvestable largemouth bass standing stock and lake trophic status. The average standing stock of harvestable largemouth bass, estimated with mark-recapture methods, does increase with lake trophic status up to the eutrophic range, but average harvestable largemouth standing stock then decreases slightly in hypereutrophic lakes (Figure 32). Again this may be related to the earlier discussed observations of Kautz (1980) and Bays and Crisman (1983), who also observed a decrease in the percentage of sportfish with an increase in lake trophic status. There, however, is a large amount of variance in the standing stock of harvestable largemouth bass in the hypereutrophic lakes with Lake Rowell, Lake Conine, and Alligator Lake having more than 30 harvestable largemouth bass/ha and Lake Carlton, Lake Wales and Lake Holden having less then 10 harvestable largemouth bass/ha (Table 7). Lake Apopka was too large to estimate largemouth bass standing stock with mark recapture methods, but rotenone and electrofishing sampling indicated the largemouth bass population was extremely low in this hypereutrophic lake (Table 33).

Why there is a depression in largemouth bass populations in some hypereutrophic lakes, but not others is not known. Some investigators have suggested that the large amount

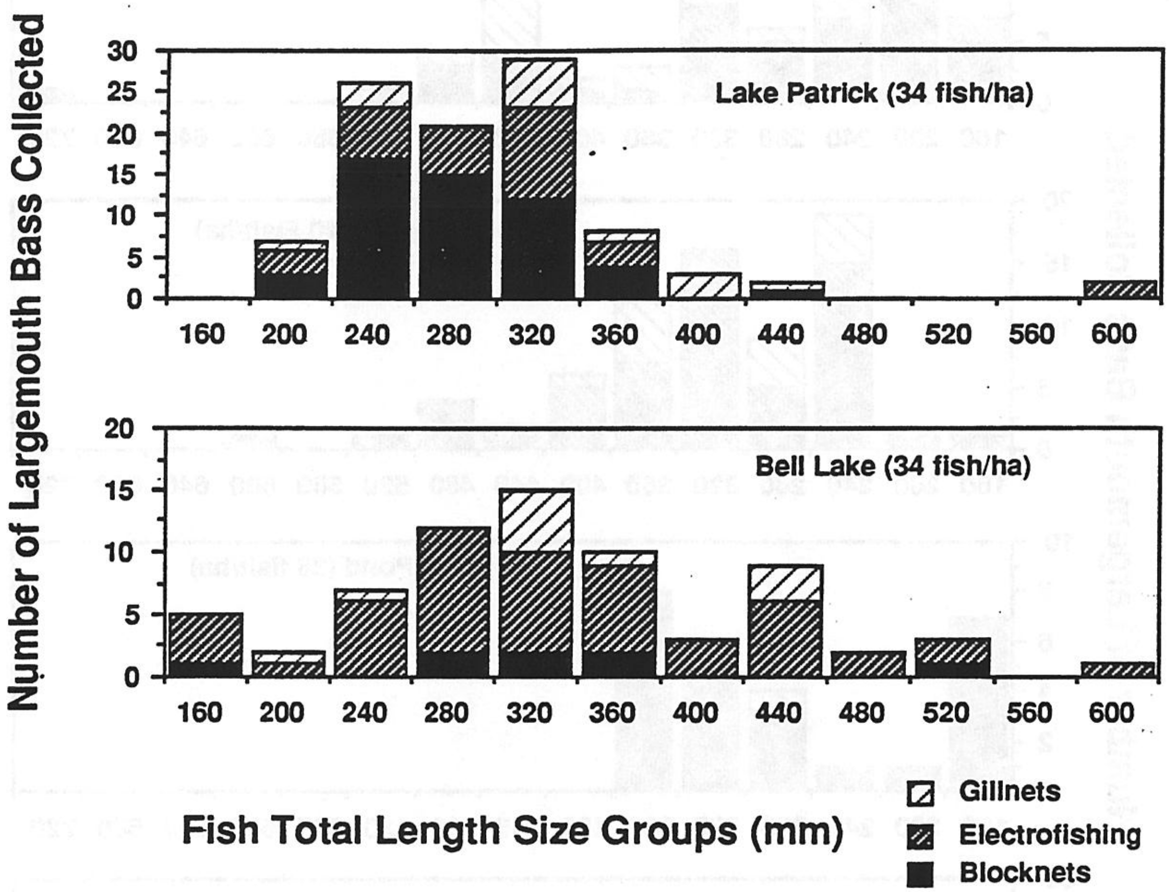


Figure 31. Length frequency distribution of all largemouth bass > 160 mm TL caught in gillnets, electroshocking transects, and blocknets for the 10 lakes with the largest harvestable largemouth bass standing crop estimates. The standing crop of harvestable (> 250 mm TL) largemouth bass, estimated with mark-recapture methods, is listed in parentheses after the lake name.

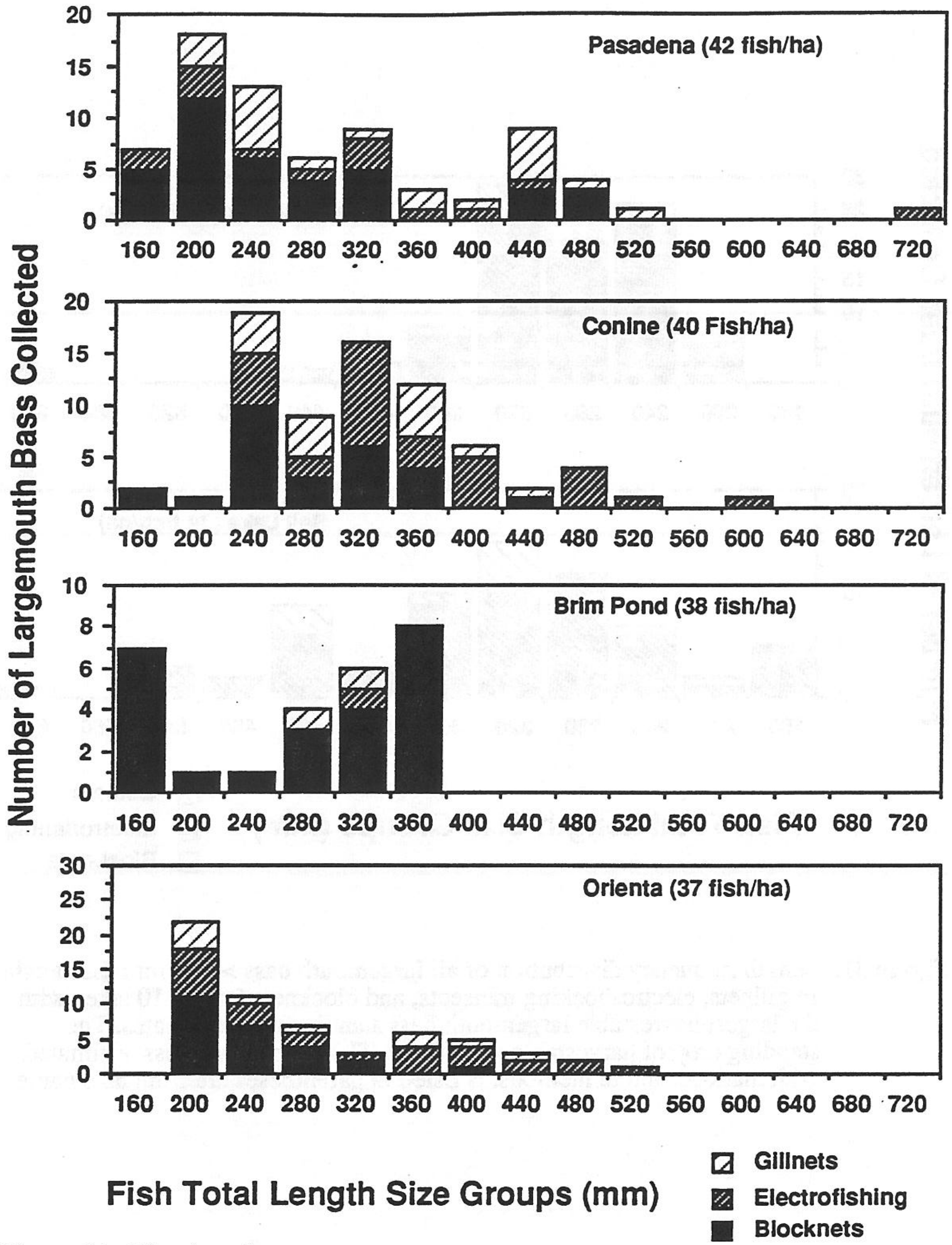
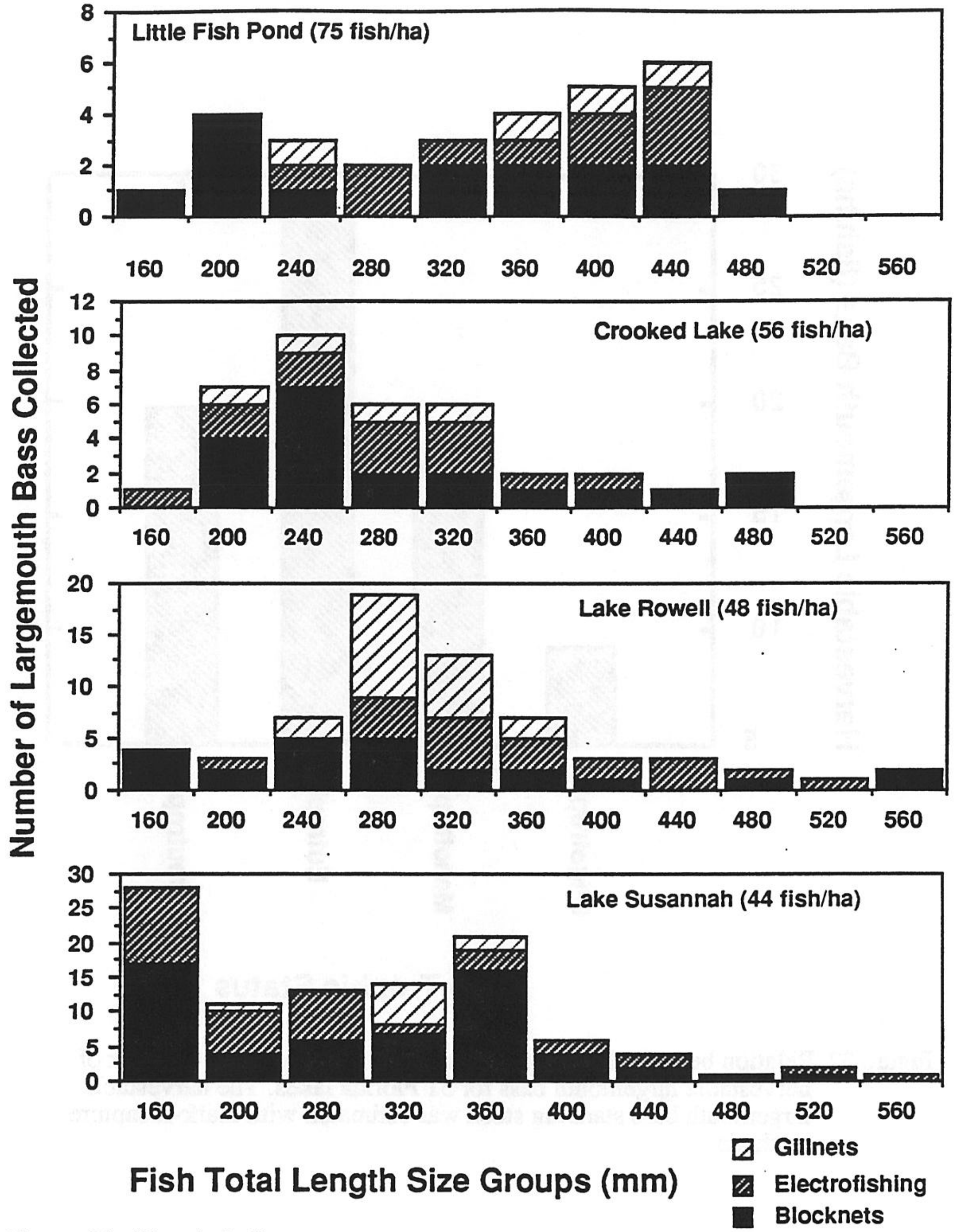


Figure 31. (Continued)



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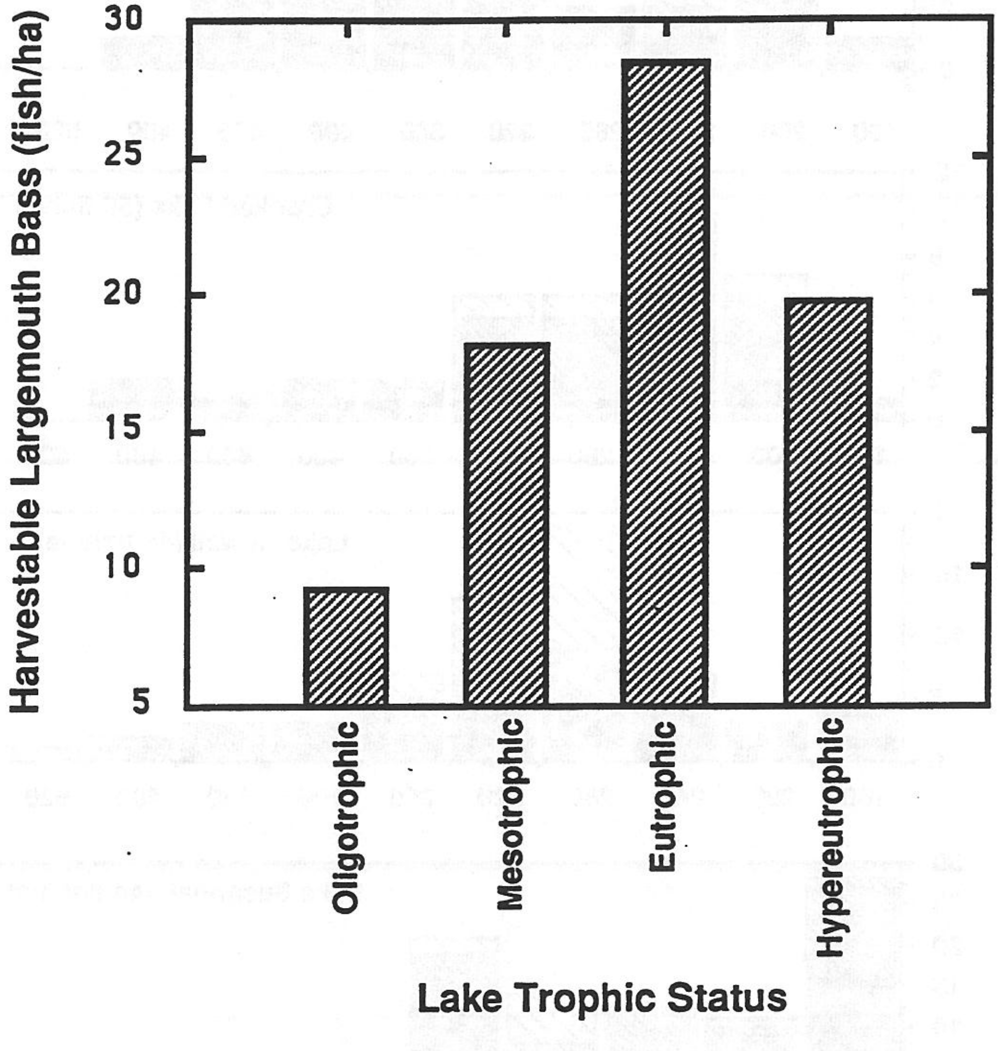

Figure 32. Relation between lake trophic status and average standing stock of harvestable largemouth bass for 51 Florida lakes. The harvestable largemouth bass standing stock was estimated with mark-recapture methods.

of organic sediment typically found in hypereutrophic lakes interferes with the spawning activities of largemouth bass (Chew 1974). Anaerobic conditions in the sediments of hypereutrophic lakes have also been reported to decrease benthic invertebrate populations (Jonasson 1964), which may decrease food supplies for YOY largemouth bass. Dense populations of algae with a large percentage of blue-greens may also give rough fish and commercial fish some competitive advantage over sportfish (Kautz 1980), but the fact that some hypereutrophic lakes have good populations of largemouth bass suggests that we may be able to manage largemouth bass populations in these lakes. For example, Lake Hollingsworth in 1974 had a severely depressed largemouth bass population with little or no reproduction occurring (Chew 1974). When we sampled Lake Hollingsworth in 1987, our littoral blocknets estimated over 150 kg/ha of largemouth bass. YOY largemouth bass were also present, which demonstrated that reproduction was occurring in the lake (Table 88). Understanding the mechanisms responsible for depressed populations of sportfish in hypereutrophic lakes and what occurred in Lake Hollingsworth between 1974 and 1987 may lead to the restoration of sportfish populations in several hypereutrophic Florida lakes (e.g., Lake Apopka).

Large fluctuations in the percent area covered with aquatic macrophytes (< 10% to > 60% PAC) have been linked to large standing stocks of harvestable largemouth bass (Estes et al. 1990; Porak et al. 1990a). One concern that needs to be discussed here is the potential side effects of fluctuating large amounts of aquatic vegetation in lakes as a management strategy for largemouth bass populations. The fluctuation of large amounts of hydrilla in Lake Rowell (Porak et al. 1990a) and Lochloosa Lake (Estes et al. 1990) produced abundant populations of harvestable largemouth bass. This management procedure, however, may accelerate organic sedimentation and the aging of lakes because the accumulation of refractory macrophyte detritus in lake sediments has important long-term effects on succession (Wetzel 1979; Carpenter and Lodge 1986). Whitmore (1991) measured the sedimentation rate in 26 Florida lakes and these rates averaged 0.04 $g/cm^2/year$. Lake Rowell had a sedimentation rate in 1988 that was 5 times the average of all lakes (Whitmore 1991) and was the highest sedimentation rate measured (0.21 $g/cm^2/year$). Joyce (1992) also found a direct relation between percent area covered with hydrilla and organic sedimentation rates in experimental tanks. Thus, more information about the effect of macrophyte management on organic matter sediment accumulation rates should be obtained before a statewide program of massive fluctuation in aquatic macrophyte abundance is initiated as a management strategy for largemouth bass populations.

Limnological Factors Affecting Bird Populations On Florida Lakes

The main objective of our research project was to examine the relationships between limnology, fisheries and aquatic macrophytes in Florida's lakes. After our research project was initiated, concerns were raised regarding the potential effects of aquatic plant management programs on bird populations utilizing Florida lakes. Because it became evident that bird populations utilizing our study lakes could be quantified and the relations among limnology, aquatic bird populations, and aquatic macrophytes examined with a little extra work, we initiated a sampling program in 1988 that counted and identified birds using our study lakes. In November 1990, a preliminary analysis of our bird data from 33 lakes was presented at the 10th annual international symposium of the North American Lake Management Society (NALMS). A paper entitled "*Limnological Factors Influencing Bird Abundance and Species Richness on Florida lakes*" was published after this meeting in NALMS' journal, Lake and Reservoir Management (Appendix I).

In August 1991, a second paper titled "*Bird Abundance and Species Richness on Florida Lakes: Influence of Trophic Status, Lake Morphology, and Aquatic Macrophytes*" was presented at an international symposium titled "Aquatic Birds in the Trophic Web of Lakes". The symposium was held at Mount Allison University in Sackville, New Brunswick. The paper, which used data from 44 Florida lakes and included more comprehensive data analyses, was selected along with other papers presented at the symposium for publication as a special issue in Hydrobiologia in 1992. The complete paper is presented below.

Abstract

Data from 46 Florida lakes were used to examine relationships between bird abundance (numbers and biomass) and species richness, and lake trophic status, lake morphology and aquatic macrophyte abundance. Average annual bird numbers ranged from 7 to 800 birds km^{-2} and bird biomass ranged from 1 to 465 kg km^{-2}. Total species richness ranged from 1 to 30 species per lake. Annual average bird numbers and biomass were positively correlated to lake trophic status as assessed by total phosphorus ($r=0.61$), total nitrogen ($r=0.60$) and chlorophyll *a* ($r=0.56$) concentrations. Species richness was positively correlated to lake area ($r=0.86$) and trophic status ($r=0.64$ for total phosphorus concentrations). The percentage of the total annual phosphorus load contributed to 14 Florida lakes by bird populations was low averaging 2.4 %. Bird populations using Florida lakes, therefore, do not significantly impact the trophic status of the lakes under natural situations, but lake trophic status is a major factor influencing bird abundance and species richness on lakes. Bird abundance and species richness were not significantly correlated to other lake morphology or aquatic macrophyte parameters after the effects of lake area and trophic status were accounted for using stepwise multiple regression. The lack of significant relations between annual average bird abundance and species richness and macrophyte abundance seems to be related to changes in bird species composition. Bird abundance and species richness remain relatively stable as macrophyte abundance increases, but birds that use open-water habitats (e.g., double-crested cormorant, *Phalacrocorax auritus*) are replaced by species that use macrophyte communities (e.g., ring-necked duck, *Aythya collaris*).

Introduction

Florida has more than 7700 lakes that range in size from 0.4 ha to over 180,000 ha (Shafer *et al.* 1986). The majority of the research and lake management conducted on these lakes involves investigations of eutrophication related problems and aquatic macrophyte management (Shireman *et al.* 1983; Joyce 1985; Canfield & Hoyer 1988a; Dierberg *et al.* 1988). This work is done primarily for the purposes of providing potable water, flood control, navigation, recreational boating, swimming, and fishing. Consequently, consideration is seldom given to the bird populations that utilize these lakes and very little information is available to determine how different lake management actions may affect bird populations.

Hoyer & Canfield (1990) provided a preliminary examination of the relations among bird abundance and species richness and lake trophic status, morphology, aquatic macrophytes for 33 Florida lakes. In this paper, data from 13 additional Florida lakes have been added to the earlier data. Our purpose, here, is to further examine relationships between limnological factors and bird numbers, biomass and species richness. Many factors have been shown to influence aquatic bird populations including geographic location, habitat condition in nesting and wintering areas, and climatic factors (Weller & Spatcher 1965). We, however, focused our study on three major habitat characteristics that have previously been shown to be important to bird populations: lake trophic status (Nilsson & Nilsson 1978; Murphy *et al.* 1984;), lake morphology (MacArthur & Wilson 1967; Brown & Dinsmore 1986) and aquatic macrophyte abundance (Johnson & Montalbano 1984; Montalbano *et al.* 1979). Because there are also concerns that birds can contribute to eutrophication problems in lakes (Manny *et al.* 1975 ; Nordlie 1976), we examined the potential of the bird populations to contribute to the nutrient load of Florida lakes.

Methods

Birds counts for this study were obtained by counting birds that were observed on or feeding from aquatic habitats during a survey of 46 Florida lakes. The counts were conducted between November 1988 and September 1990. Birds were counted on each lake once in the winter (November to February), once in the spring (March to May) and once in the summer (July to September). Birds were counted by observers who motored once around the perimeter of each lake in a small boat. Birds were identified to species except gulls, terns, and crows, and care was taken not to count birds twice that flushed ahead of the boat.

Species richness was defined as the total number of bird species observed throughout the entire sampling period. Average annual bird abundances (birds km^{-2}) were calculated by averaging all three counts for each lake. Average annual bird biomass (kg km^{-2}) was calculated by multiplying the average live weight of a given species, taken from Terres (1980), by annual average bird abundance values for that species and summing by lake. The annual total phosphorus load excreted by bird populations was calculated by multiplying the average annual bird biomass by the total phosphorus defecation rates calculated by Manny *et al.* (1975) for canada geese (*Branta canadensis*).

Aquatic macrophytes were sampled at each lake once during the summer. The percent lake volume infested with aquatic macrophytes (PVI) and the percent lake area covered by macrophytes (PAC) were determined according to the methods of Maceina & Shireman (1980). The above-ground standing crop of emergent, floating-leaved, and submerged vegetation (Canfield et al. 1990) was measured along ten uniformly-placed transects around the lake. At each transect, divers cut the above ground portions of aquatic macrophytes that were inside a 0.25 m^2 plastic square randomly thrown once in each plant zone. The vegetation was placed in nylon mesh bags, spun to remove excess water, 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.

Composite samples of all plant types present in a lake were collected for phosphorus content analysis. 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 then given a persulfate digestion, diluted and analyzed for total phosphorus (see below).

Lake area (km^2) was obtained from Shafer *et al.* (1986) and shoreline length (km) was measured from aerial photographs with a 1:20,000 or 1:40,000 reduction. Mean depth (m) was calculated from the fathometer transects used for PVI and PAC calculations. Shoreline development was calculated according to the methods of Wetzel (1975).

Summer water samples were collected from six stations (three littoral and three open-water) and three open-water samples were collected from each lake on two additional dates during the year. Water samples were collected 0.5 m below the surface in acid-cleaned

Nalgene bottles, placed on ice, returned to the laboratory, and analyzed. Secchi depth (m) was measured at each station where water was collected.

Total phosphorus was analyzed (Murphy & Riley 1962) after a persulfate oxidation (Menzel & Corwin 1965). Total nitrogen was determined by a modified Kjeldahl technique (Nelson & Sommers 1975). Water was filtered through Gelman type A-E glass fiber filters for chlorophyll *a* determinations. Chlorophyll *a* was determined by using the method of Yentsch & Menzel (1963) and the equations of Parson & Strickland (1963).

Measured planktonic chlorophyll *a* values are often not good indicators of lake trophic status when large amounts of aquatic macrophytes are present because aquatic macrophytes and associated epiphytic algae can compete for nutrients that would otherwise be used by planktonic algal cells (Canfield *et al.* 1983). Thus, we also assessed the trophic status of each lake by calculating a total water column phosphorus concentration (WCP) value for each lake (see Canfield *et al.* 1983). WCP values were obtained by adding the measured total phosphorus in the water to the phosphorus incorporated in plant tissue.

Statistical analyses were conducted using SYSTAT (Wilkinson 1987). Because the data values spanned orders of magnitude and variances were proportional to the means, all data were transformed to their logarithms (base 10), except PVI and PAC which are percent values. For the logarithmic transformation, a value of 0.001 kg was added to the plant biomass values that were measured as 0 values. Unless stated otherwise, statements of statistical significance imply $P \leq 0.05$.

Results and Discussion

The lakes included in this study encompassed a wide range of limnological conditions (Table 1). The size of the lakes ranged from 0.02 to 2.71 km^2 and lake trophic status, based on the classification system of Forsberg & Ryding (1980), ranged from oligotrophic to hypereutrophic. The lakes, however, are representative of Florida lakes (Canfield & Hoyer 1988b) and therefore provide the range of conditions needed to examine the effects of lake trophic status, aquatic macrophyte abundance and lake morphology on Florida bird populations.

Fifty bird species were observed during the study period, but some species occurred on only one lake (Table 2). These rare species included the american white pelican (*Pelecanus erythrorhynchos*), canada goose, and fulvous whistling duck (*Dendrocygna bicolor*). Some species, however, occurred on as many as 38 of the 46 study lakes. The most common

Table 1. Summary statistics for trophic state, aquatic macrophyte (plant biomasses are live weight estimates), lake morphology, and bird population parameters estimated in 46 Florida lakes. The annual average (MEAN) is listed with the minimum (MIN), and maximum (MAX) values, and the standard error of the mean (SE).

PARAMETERS	MEAN	MIN	MAX	SE
TROPHIC STATE:				
Total phosphorus ($\mu g\ l^{-1}$)	57	1.0	1043	24
Water column phosphors ($\mu g\ l^{-1}$)	196	1	4538	99
Total nitrogen ($\mu g\ l^{-1}$)	882	82	3256	110
Chlorophyll *a* ($\mu g\ l^{-1}$)	27	1	241	7
Secchi depth (m)	2.0	0.3	5.8	0.2
AQUATIC MACROPHYTES:				
Percent volume infested with macrophytes (%)	25	0	98	5
Percent area covered with macrophytes (%)	43	1	100	6
Emergent biomass (kg m^{-2})	3.9	0.3	26.8	0.7
Floating-leaved biomass(kg m^{-2})	1.3	0.0	11.2	0.4
Submergent biomass(kg m^{-2})	1.8	0.0	16.6	0.5
Emergent and floating-leaved width (m)	29.3	0.4	162.8	4.7
LAKE MORPHOLOGY:				
Lake surface area (km^2)	0.74	0.02	2.71	0.10
Shoreline length (km)	3.49	0.60	8.40	0.30
Shoreline development	1.34	0.65	2.45	0.06
Mean depth (m)	2.8	0.6	5.9	0.2
BIRD POPULATION:				
Bird numbers (bird km^{-2})	174	7	803	28
Bird biomass (kg km^{-2})	114	1	465	17
Species richness (total species)	17	1	30	1

Table 2. List of bird species identified and counted on 46 Florida lakes between November 1988 and September 1990. N is the number of lakes on which a bird was observed. Annual average bird numbers (MEAN, birds km^{-2}) for each species is listed with the minimum (MIN) and maximum (MAX) values, and the standard error of the mean (SE).

Common Name	Scientific Name	N	MEAN	MIN	MAX	SE
Pied-billed Grebe	*Podilymbus podiceps*	23	1.1	0.1	2.6	0.2
American White Pelican	*Pelecanus erythrorhynchos*	1	0.9	0.9	0.9	
Double-crested Cormorant	*Phalacrocorax auritus*	30	9.5	0.2	66.7	2.8
Anhinga	*Anhinga anhinga*	32	10.8	0.4	71.9	2.6
Least Bittern	*Ixobrychus exilis*	12	0.6	0.2	1.2	0.1
Great Blue Heron	*Ardea herodias*	38	5.6	0.7	20.6	0.8
Great Egret	*Casmerodius albus*	34	5.9	0.2	43.7	1.7
Snowy Egret	*Egretta thula*	22	3.0	0.2	8.7	0.5
Little Blue Heron	*Egretta caerulea*	25	2.4	0.6	8.3	0.5
Tricolored Heron	*Egretta tricolor*	20	2.1	0.3	8.3	0.5
Cattle Egret	*Bubulcus ibis*	20	14.4	0.2	129.2	6.7
Green-backed Heron	*Butorides striatus*	28	4.3	0.2	16.7	0.8
Black-crowned Night-heron	*Nycticorax nycticorax*	7	3.7	0.2	12.3	2.0
White Ibis	*Eudocimus albus*	23	8.7	0.2	78.0	3.4
Glossy Ibis	*Plegadis falcinellus*	2	0.7	0.7	0.7	0.0
Wood Stork	*Mycteria americana*	6	1.8	0.2	3.2	0.6
Canada Goose	*Branta canadensis*	1	0.6	0.6	0.6	
Fulvous Whistling Duck	*Dendrocygna bicolor*	1	0.1	0.1	0.1	
Wood Duck	*Aix sponsa*	18	7.5	0.4	33.3	2.1
Mottled Duck	*Anus fulvigula*	6	2.1	0.7	5.2	0.7
Mallard	*Anas platyrhynchos*	11	42.4	1.7	183.9	18.9
Blue-winged Teal	*Anas discors*	3	4.9	1.8	9.2	2.2
Ring-necked Duck	*Aythya collaris*	11	31.6	0.4	220.8	19.7
Turkey Vulture	*Cathartes aura*	11	7.6	0.2	41.7	3.9
Black Vulture	*Coragyps atratus*	19	5.6	0.2	34.5	2.4
Bald Eagle	*Haliaeetus leucocephalus*	15	1.7	0.2	7.4	0.5
Osprey	*Pandion haliaetus*	28	2.1	0.2	6.7	0.3
Northern Harrier	*Circus cyaneus*	8	0.4	0.2	0.8	0.10
Red-tailed Hawk	*Buteo jamaicensis*	7	1.0	0.1	4.2	0.5
Red-shouldered Hawk	*Buteo lineatus*	11	1.0	0.2	3.7	0.3
American Kestrel	*Falco sparverius*	5	0.4	0.1	0.6	0.10
Sora	*Porzana carolina*	1	0.7	0.7	0.7	
Purple Gallinule	*Porphyrula martinica*	10	2.0	0.2	10.3	0.9
Common Moorhen	*Gallinula chloropus*	28	26.2	0.3	146.4	6.7
American Coot	*Fulica americana*	19	32.8	0.2	292.9	18.4
Limpkin	*Aramus guarauna*	6	0.8	0.2	1.5	0.2
Sandhill Crane	*Grus canadensis*	4	1.1	0.2	1.7	0.3
Semipalmated Plover	*Charadrius semipalmatus*	7	1.0	0.2	3.3	0.4
Killdeer	*Charadrius vociferus*	11	3.7	0.6	11.1	1.0

Table 2. Continued.

Common Name	Scientific Name	N	MEAN	MIN	MAX	SE
Lesser Yellowlegs	*Tringa solitaria*	3	1.6	0.4	3.7	1.1
Common Snipe	*Gallinago gallinago*	10	7.5	0.2	51.9	5.0
Gulls	*Laridae Larinae*(1)	21	20.4	0.2	98.3	6.7
Terns	*Laridae Sterninae*(1)	18	5.0	0.2	39.6	2.2
Belted Kingfisher	*Ceryle alcyon*	31	3.1	0.2	22.2	0.8
Purple Martin	*Progne subis*	14	12.6	0.2	138.9	9.8
Tree Swallow	*Tachycineta bicolor*	4	9.1	0.6	15.2	3.3
Bank Swallow	*Riparia riparia*	1	1.3	1.3	1.3	
Crows	*Corvidae*(2)	37	15.6	0.6	304.3	8.2
Red-winged Blackbird	*Agelaius phoeniceus*	33	19.4	0.8	92.3	4.1
Boat-tailed Grackle	*Quiscalus major*	30	43.1	0.4	156.4	7.4

(1) Listed as subfamily.
(2) Listed as family.species observed were counted on more than 65% of the lakes sampled,

and included the great blue heron (*Ardea herodias*), great egret (*Casmerodius albus*), and anhinga (*Anhinga anhinga*). The species occurring with the highest densities (birds km^{-2}) were mallard (*Anas platyrhynchos*), american coot (*Fulica americana*), and red-winged blackbird (*Agelaius phoeniceus*). Least numerous birds included american white pelican, sora (*Porzana carolina*), and limpkin (*Aramus guarauna*).

All trophic state variables in our study were significantly correlated to bird abundance (numbers and biomass), and species richness (Table 3). The strongest correlations were with total phosphorus concentrations (r=0.61, r=0.61, and r=0.64, respectively). Similar correlations were reported between bird abundance, species richness and lake trophic state variables for 33 Florida lakes (Hoyer & Canfield 1990). Hoyer & Canfield (1990), however, suggested that chlorophyll *a* rather than total phosphorus should be used as the major trophic state variable for predicting bird abundance and species richness in lakes because chlorophyll *a* is a convenient estimator of the organic base upon which aquatic bird populations depend. Because chlorophyll *a* values can greatly underestimate the trophic status of lakes with large biomasses of aquatic vegetation, we choose to use WCP concentrations to assess lake trophic status in this study (see Canfield *et al.* 1983).

Regression analyses yielded the following statistically significant regression equations for

Table 3. Correlation matrix for all parameters sampled on 46 Florida lakes. All absolute r values equal to or greater then 0.30 are significant at a $p \leq 0.05$ level.

Variables	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14	X15	Y1	Y2	Y3
Trophic State:																		
X1..Total phosphorus ($\mu g\ l^{-1}$)	1.00	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
X2..Water column phosphorus ($\mu g\ l^{-1}$)	0.54	1.00	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
X3..Total nitrogen ($\mu g\ l^{-1}$)	0.81	0.59	1.00	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
X4..Chlorophyll *a* ($\mu g\ l^{-1}$)	0.87	0.41	0.82	1.00	.	.	.	.	.	.	.	.	.	.	.	.	.	.
X5..Secchi depth (m)	-0.86	-0.47	-0.88	-0.87	1.00	.	.	.	.	.	.	.	.	.	.	.	.	.
Aquatic Macrophytes:																		
X6..PVI (%)	-0.21	0.48	0.06	-0.25	0.13	1.00	.	.	.	.	.	.	.	.	.	.	.	.
X7..PAC (%)	-0.40	0.35	-0.17	-0.47	0.34	0.85	1.00	.	.	.	.	.	.	.	.	.	.	.
X8..Emergent ($kg\ m^{-2}$)	0.06	0.35	0.08	0.19	-0.07	-0.04	-0.13	1.00	.	.	.	.	.	.	.	.	.	.
X9..Floating-leaved ($kg\ m^{-2}$)	0.08	0.47	0.25	0.03	-0.12	0.46	0.44	0.24	1.00	.	.	.	.	.	.	.	.	.
X10..Submerged ($kg\ m^{-2}$)	-0.49	0.16	-0.30	-0.49	0.50	0.51	0.61	0.28	0.26	1.00	.	.	.	.	.	.	.	.
X11..Width (m)	-0.12	0.26	0.05	-0.26	0.12	0.46	0.52	0.05	0.38	0.60	1.00	.	.	.	.	.	.	.
Lake Morphology:																		
X12..Surface area (km^2)	0.50	0.37	0.46	0.45	-0.41	-0.03	-0.16	-0.01	-0.06	-0.16	0.04	1.00	.	.	.	.	.	.
X13..Shore line length (km)	0.43	0.35	0.39	0.38	-0.35	-0.02	-0.11	0.06	0.02	-0.09	0.04	0.90	1.00	.	.	.	.	.
X14..Mean depth (m)	-0.15	-0.03	-0.16	-0.13	0.11	0.02	0.11	0.16	0.18	0.14	0.00	-0.20	0.24	1.00	.	.	.	.
X15..Shoreline development	-0.20	-0.46	-0.40	-0.18	0.41	-0.47	-0.39	0.01	-0.36	-0.01	-0.37	0.10	0.06	-0.09	1.00	.	.	.
Bird Population:																		
Y1..Bird numbers (birds km^{-2})	0.61	0.55	0.59	0.56	-0.51	0.10	-0.11	0.05	0.08	-0.09	-0.07	0.40	0.45	0.12	-0.19	1.00	.	.
Y2..Bird biomass ($kg\ km^{-2}$)	0.61	0.61	0.60	0.56	-0.52	0.13	-0.01	0.07	0.24	-0.06	-0.04	0.31	0.40	0.22	-0.30	0.92	1.00	.
Y3..Species richness (total species)	0.64	0.47	0.59	0.56	-0.53	-0.01	-0.16	-0.06	0.02	-0.18	0.01	0.86	0.82	-0.07	-0.08	0.70	0.62	1.00

predicting bird abundance (numbers and biomass) and species richness from WCP concentrations:

$$\text{Log (Bird numbers)} = 1.14 + 0.48 \text{ Log (WCP)} \qquad R^2 = 0.30 \qquad (1)$$

$$\text{Log (Bird biomass)} = 0.91 + 0.53 \text{ Log (WCP)} \qquad R^2 = 0.38 \qquad (2)$$

$$\text{Log (Species richness)} = 0.57 + 0.31 \text{ Log(WCP)} \qquad R^2 = 0.22 \qquad (3)$$

There is a large amount of variance in bird numbers and biomass at any given level of WCP (Figs, 1A and 1B) and the total variance in bird numbers (Equation 1) and biomass (Equation 2) accounted for by WCP concentrations alone was low 30 and 38%, respectively. We, therefore, used the WCP values and all aquatic macrophyte and lake

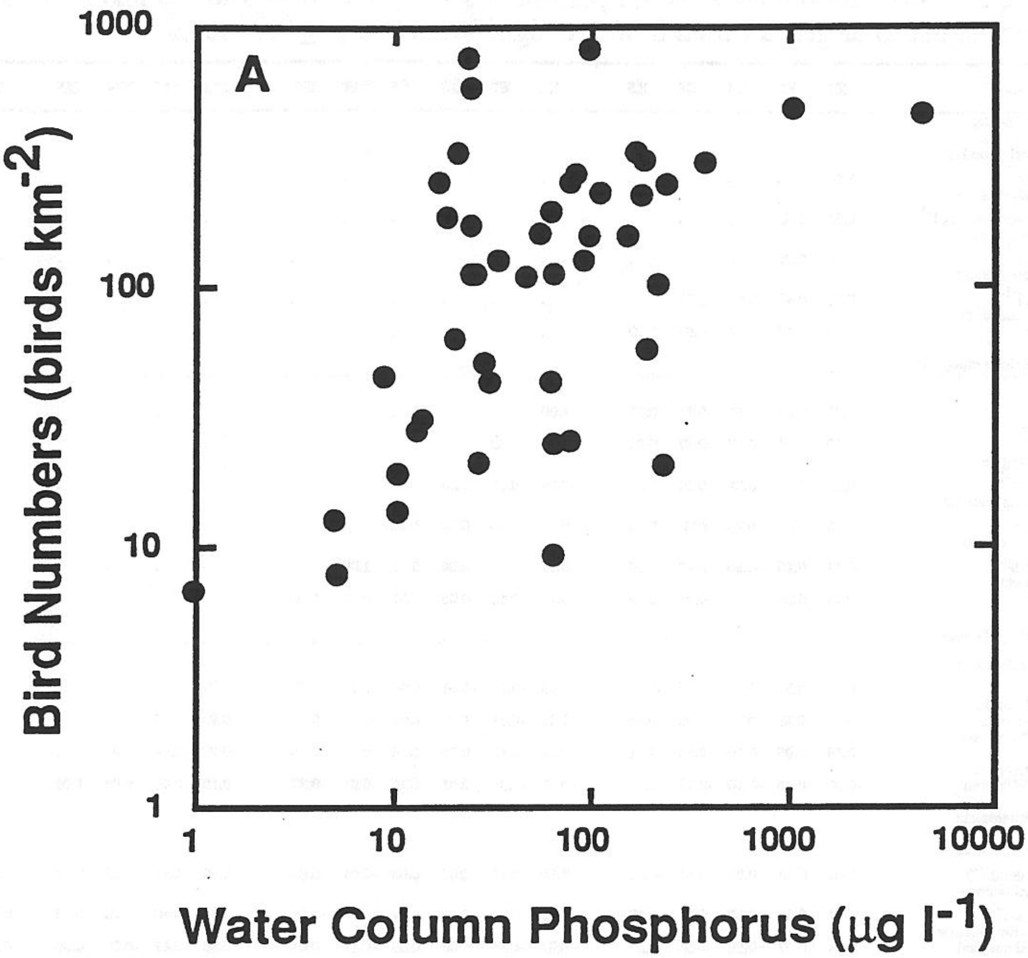

Fig. 1. Relation between annual average bird numbers (A, birds km^{-2}) and biomass (B, kg km^{-2}) and water column phosphorus concentration (WCP, µg l^{-1}) for 46 Florida lakes. WCP values are calculated by adding the phosphorus incorporated in aquatic macrophyte and epiphytic algae tissue to the measured total phosphorus concentration according to the methods of Canfield *et al.* (1983) and Canfield & Hoyer (1991).

morphology parameters as independent variables in stepwise multiple regressions to try to account for more variance in bird numbers and biomass. An alpha-to-enter and an alpha-to-remove of 0.05 was used for the analyses (Wilkinson 1987) and we used only WCP as a trophic state parameter because all trophic state parameters were intercorrelated. No aquatic macrophyte or lake morphology parameters, however, accounted for significantly more variance after WCP values were entered into the multiple regression models.

Although there was a significant correlation between species richness and WCP values, species richness was most strongly correlated to lake area (r=0.86; Table 3; Fig. 2).

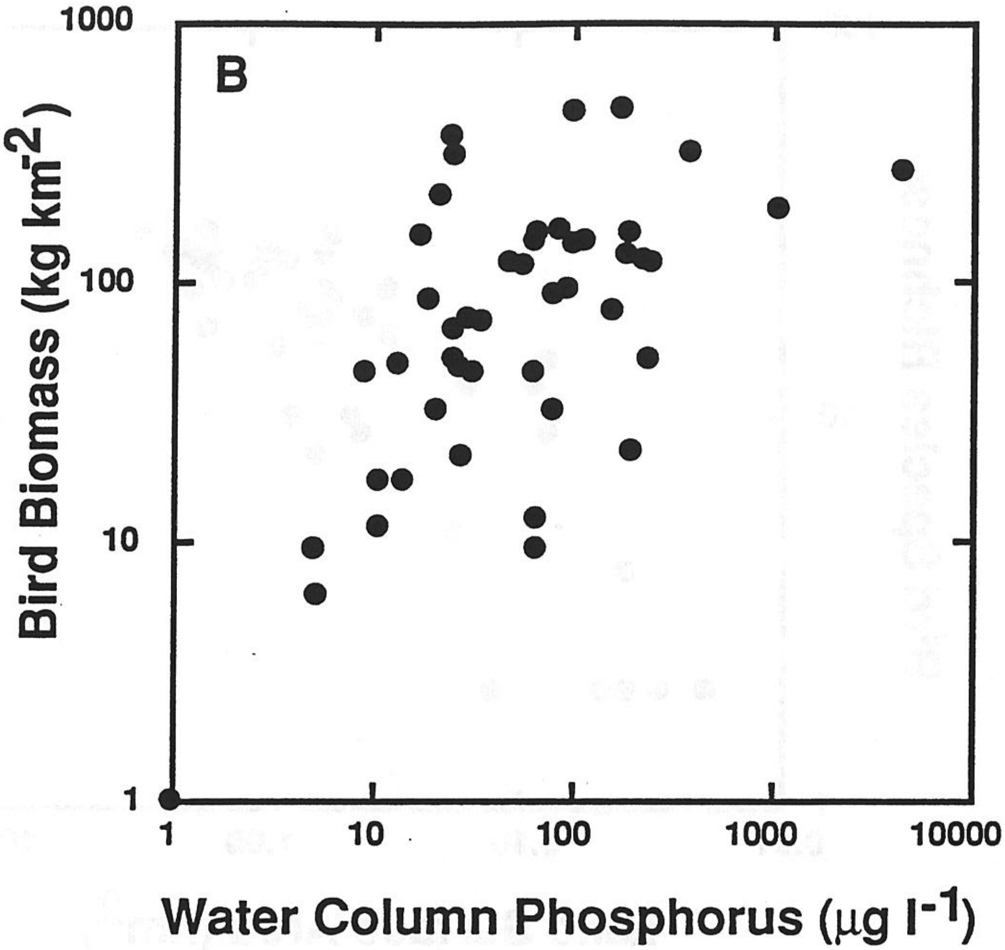

Fig. 1. Continued.

Similar species-area relations have been reported for many flora and fauna (Flessa & Sepkoski 1978; Connor & McCoy 1979). The best-fit multiple linear regression, however, indicated that lake area and WCP could account for 77% of the variance in species richness:

$$\text{Log (Species richness)} = 1.12 + 0.56 \text{ Log (Lake area)} + 0.12 \text{ Log (WCP)} \qquad R^2 = 0.77 \qquad (4)$$

No other lake morphology or aquatic macrophyte variables significantly accounted for additional variance.

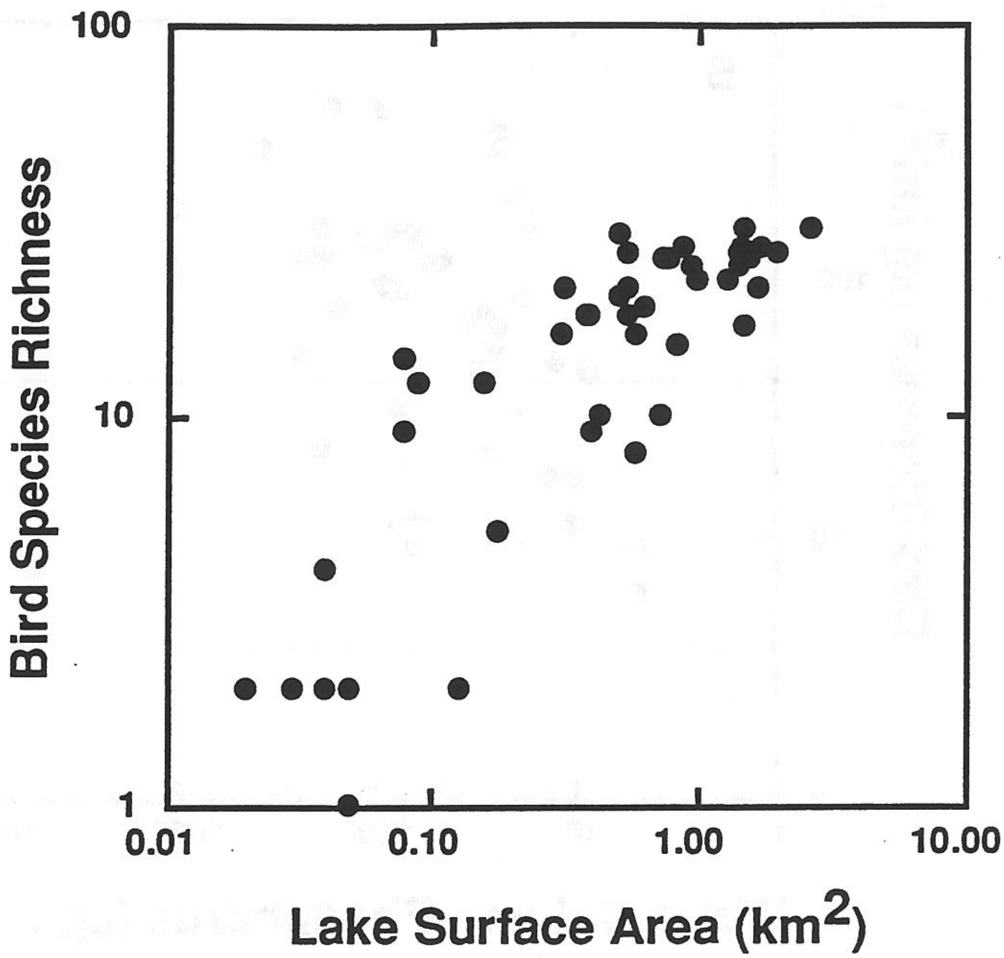

Fig. 2. Relation between lake species richness (total species) and surface area (km^2).

We anticipated significant correlations between the lake morphology variables other than lake area and bird abundance and species richness because previous studies had linked shoreline development and mean depth with bird abundance and species richness (Nilsson & Nilsson 1978; Murphy *et al.* 1984). Shoreline development for our lakes, however, averaged only 1.34 and the values only ranged from 0.65 to 2.45 (Table 1). This makes it very difficult to detect a significant effect when other variables are strongly correlated. Lake mean depth values in our study ranged 0.6 to 5.9 m (Table 1), but many of the aquatic birds counted in our study were limited to shallow shoreline areas where they could forage for food. Because these birds can not wade in limnetic portions of a lake system, it is not surprising that mean depth values were not significantly related to bird abundance, and species richness (Table 3). The width of the immediate shoreline that can used by many wading birds, however, is potentially important. This width would be related to the slope of a lake system, out from the shoreline, which would determine the maximum depth at which many bird species could wade and forage for food. The slope of a lake has also been related to patterns in aquatic macrophyte biomass and coverage (Canfield & Duarte 1988), thus slope rather than shoreline development or mean depth may be the most important factor influencing bird abundance and species richness after the effects of lake trophic status are accounted for.

Birds use aquatic macrophytes for nesting, resting and refuge sites. Macrophytes are also used as food by birds and the plants provide substrate for invertebrate food items (Odum *et al.* 1984; Engel 1990). Bird abundance, biomass and species richness, however, were not significantly correlated with any aquatic macrophyte parameters that were measured in this study (Table 3; Figs, 3A, 3B, and 3C). This is surprising considering the reported association between aquatic birds and aquatic macrophytes. Individual bird species, however, may require different types and quantities of aquatic macrophytes (Weller & Spatcher 1965; Weller & Fredrickson 1974). For example, ring-neck ducks (*Aythya collaris*) were observed on 11 lakes. These were the only lakes in which *Hydrilla verticillata* , a major food source for ring-neck ducks, was found. This relation has also been observed by other researchers in Florida (Gassaway *et al.* 1977; Johnson & Montalbano 1984). Of the 12 lakes on which least bitterns (*Ixobrychus exilis*) were observed, 11 had extensive stands of cattails (*Typha* sp.), which is reported to be a primary habitat for the species (Palmer 1962).

To examine the relation between individual bird species and percent area covered with aquatic macrophytes, we calculated the frequency of detection for each species in lakes with low (< 26%, n=20), moderate (26 to 75%, n=11), and high (> 75%, n=15) areal coverages of aquatic macrophytes (Table 4). We divided the individual bird species into three different groups using the frequency of detection values: (1) species with a decreasing frequency of detection as aquatic macrophyte coverage increases, (2) species with an increase in the frequency of detection with an increase in aquatic macrophyte coverage, and (3) species that show a random frequency of detection with an increase in aquatic macrophytes. The double-crested cormorant (*Phalacrocorax auritus*) and anhinga showed a much higher frequency of detection in lakes with low aquatic macrophyte coverage (Table 4). These bird species are fish eaters and they can have difficulty capturing prey in lakes full of aquatic vegetation; thus cormorants and anhingas are less likely to inhabit lakes with large coverages of aquatic macrophytes. In a similar situation, largemouth bass

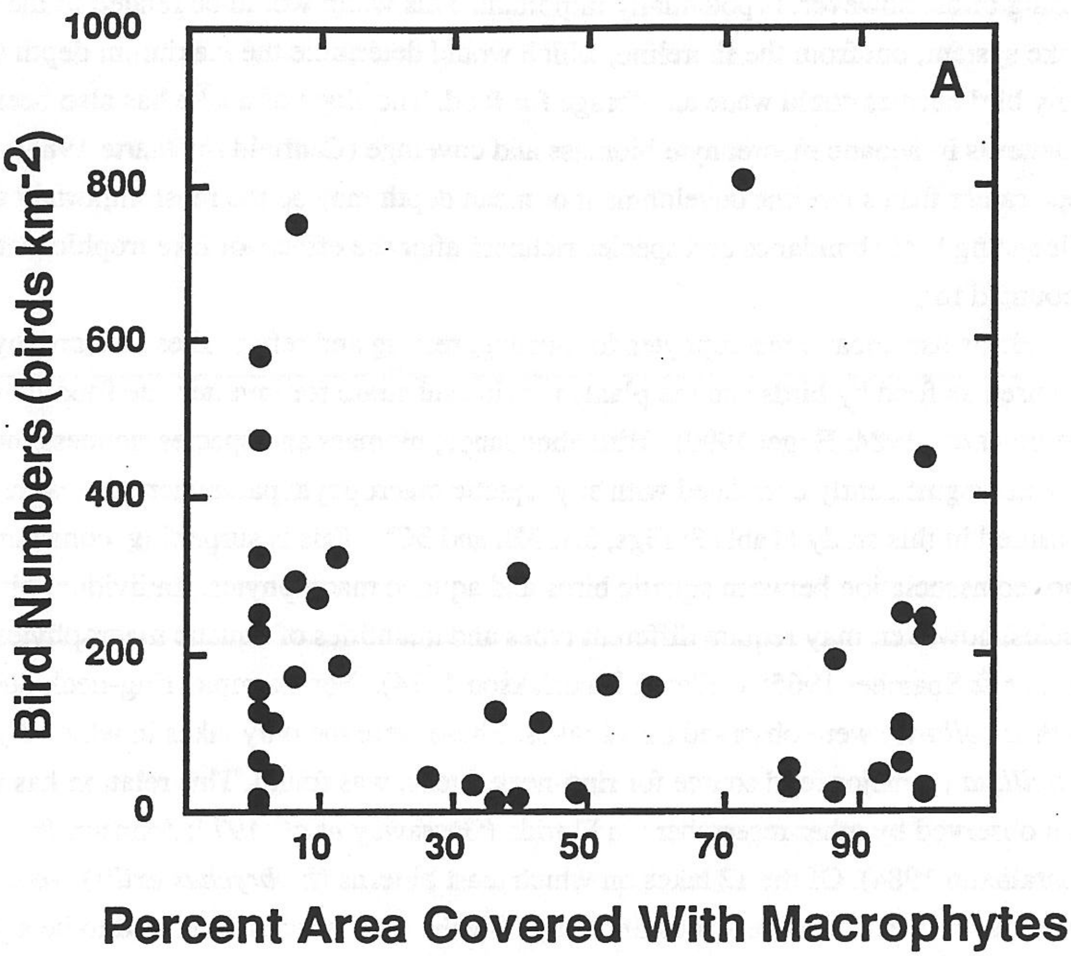

Fig. 3. The relation between bird numbers (A, birds km^{-2}), biomass (B, kg km^{-2}), and species richness (C, total species) and percent area covered with aquatic macrophytes for 46 Florida lakes.

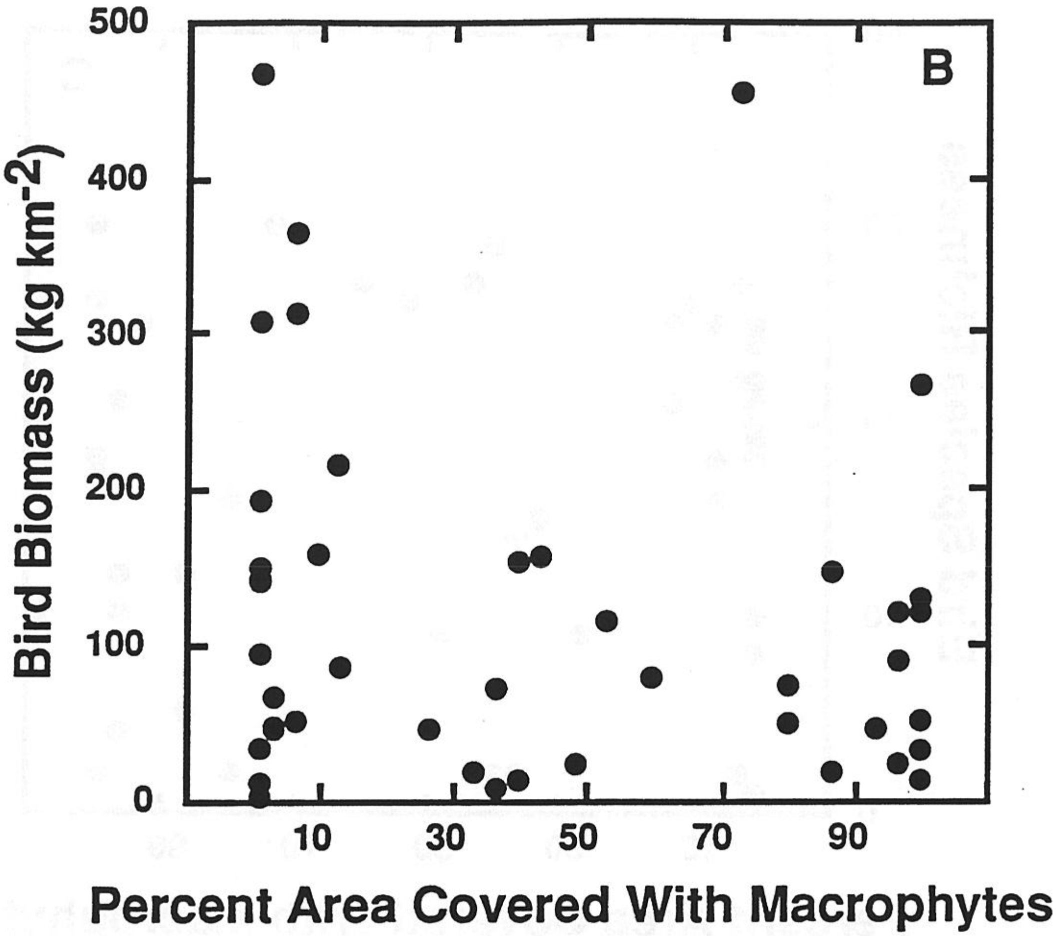

Fig. 3. Continued.

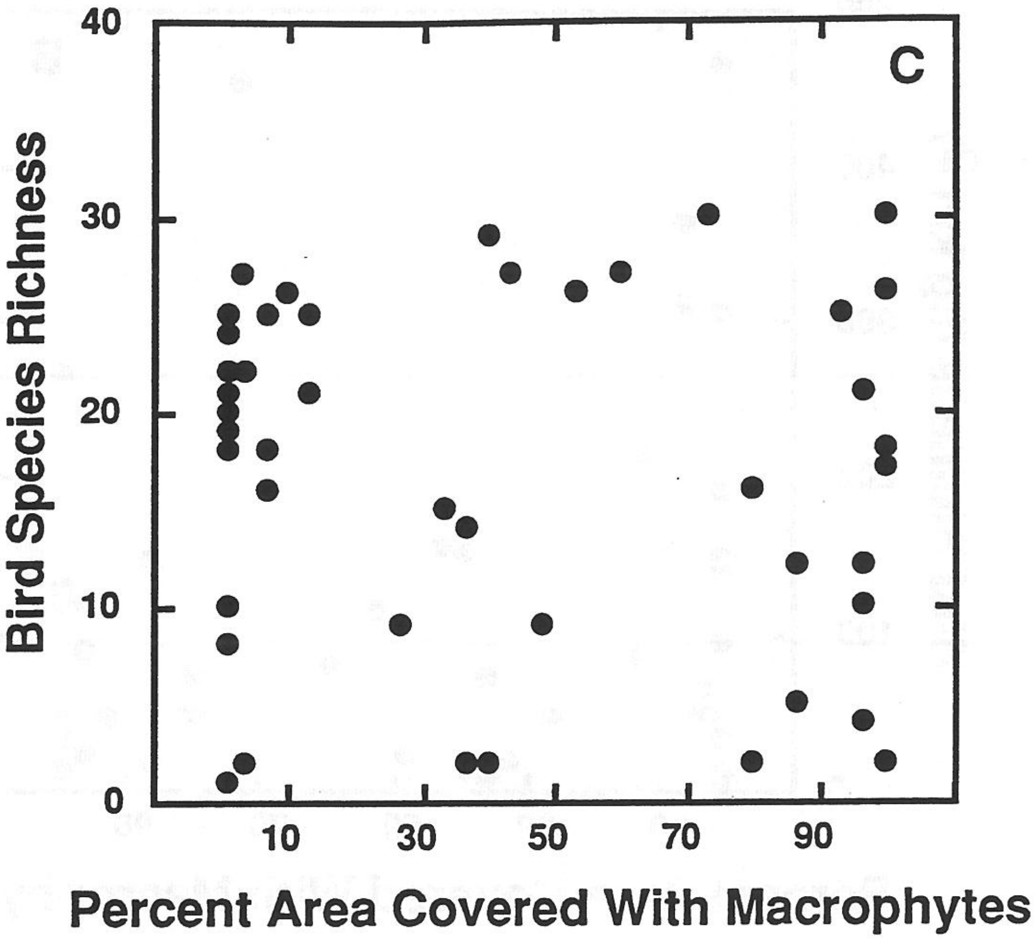

Fig. 3. Continued.

Table 4. Frequency of detection (%) of bird species using Florida lakes with low (< 26 %), moderate (26 to 75 %), and high (> 75 %) percent area coverage of aquatic macrophytes. The number of lakes in each group is listed in parentheses. Bird species are grouped by those increasing, decreasing and having no relation to aquatic macrophytes.

Species relation to increasing aquatic macrophyte coverage	Percent area covered with aquatic macrophytes		
	Low (n=20)	Moderate (n=11)	High (n=15)
Decreasing frequency of detection:			
Double-crested Cormorant	85	54	46
Anhinga	80	73	53
Great Egret	85	73	60
Snowy Egret	85	73	60
Little Blue Heron	65	55	40
Tricolored Heron	55	55	20
Green-backed Heron	75	55	47
Black-crowned Night-heron	20	18	7
White Ibis	60	55	33
Wood Stork	20	18	0
Wood Duck	20	18	0
Mallard	45	18	0
Osprey	70	73	40
Northern Harrier	20	18	13
Common Moorhen	70	64	47
Semipalmated Plover	25	18	0
Gulls	65	55	13
Terns	55	36	20
Belted Kingfisher	80	64	53
Purple Martin	55	18	7
Crows	90	82	67
Red-winged Blackbird	80	73	60
Boat-tailed Grackle	80	55	53
Increasing frequency of detection:			
Pied-billed Grebe	40	55	60
Ring-necked Duck	5	36	40
Turkey Vulture	10	18	47
Red-shouldered Hawk	15	27	33
American Coot	35	45	47

Table 4. Continued.

Species relation to increasing aquatic macrophyte coverage	Percent area covered with aquatic macrophytes		
	Low (n=20)	Moderate (n=11)	High (n=15)
Random frequency of detection:			
Least Bittern	35	36	7
Great Blue Heron	80	73	93
Cattle Egret	45	55	33
Black Vulture	45	45	33
Bald Eagle	35	45	20
Red-tailed Hawk	10	18	20
Purple Gallinule	25	27	13
Limpkin	10	18	13
Killdeer	20	18	33
Common Snipe	15	36	20

populations have difficulty capturing prey in lakes with large coverages of aquatic vegetation (Colle & Shireman 1980; Savino & Stein 1982). Ring-necked duck and american coot use aquatic vegetation as a direct food source and show a high frequency of detection in lakes with high aquatic macrophyte coverages (Table 4). These birds probably are attracted to matted vegetation as a food source (Johnson & Montalbano 1984) and have a higher probability of occurring on a lake with large populations of aquatic macrophytes. Least bittern is an example of a bird species that shows a random frequency of detection at all levels of aquatic macrophyte coverages. The least bittern, however, shows a strong relation with *Typha* sp. (Palmer 1962). This suggests that this species may show little or no relation to the total aquatic macrophyte population but requires *Typha* sp. or plant species with a similar structure to be present on a lake system.

Part of the variance in the bird abundance and species richness relations and the lack of significance by other variables that we assumed a priori would influence bird abundance and species richness could be the result of our survey sampling strategy. Constraints imposed on our study allowed only three bird counts during a year-long period. Changes in bird abundance over an annual cycle are quite prevalent in lake systems (Johnson & Montalbano 1989), especially those in Florida (Hoyer & Canfield 1990). Our study, however, supports other published studies that have indicated lake trophic status is a major factor determining bird abundance and species richness on lake systems (Nilsson & Nilsson 1978; Murphy *et al.* 1984; Hoyer & Canfield 1990).

Nutrient imports from bird populations can contribute significantly to the annual nutrient load of some lake systems (Manny *et al.* 1975; Nordlie 1976). We, therefore, estimated the annual phosphorus load of the bird populations to determine if the bird populations on our study lakes could be significantly influencing the trophic status of the lakes. Because detailed nutrient budgets were not available for most of the study lakes, we first expressed the estimated phosphorus load from the birds as a percentage of the lake's WCP value. The percentage of the total phosphorus in each lake's water column that could be attributed to the annual bird phosphorus load averaged 6%, but values ranged from < 1% to 25%. Four lakes had values exceeding 20%. To examine bird phosphorus loading rates in more detail, we used annual total phosphorus loading data (Huber *et al.* 1982) for 14 lakes that were included in our study. The percentage of the annual phosphorous load that could have been contributed by the bird populations utilizing these lakes ranged from < 1% to 9% and averaged 2.4% (Table 5). Our calculated phosphorus contributions by bird populations to the annual phosphorus imports, however, are probably overestimates because the majority of the birds are getting their nutrients from the lake by feeding on organisms that live in the lake. Thus, the annual contribution of nutrients by bird populations to Florida lakes is generally low and the trophic status of these lakes is probably not significantly affected by bird populations. There, however, remains the potential for birds to contribute significantly to the nutrient loading rates of lakes, especially if large populations of birds feed outside the lake and roost on the lake (Manny *et al.* 1975; Nordlie 1976).

Table 5. Annual total phosphorus load (mg m^{-2} yr^{-1}) for 14 Florida lakes, from Huber *et al.* (1982) and corresponding annual total phosphorus load (mg m^{-2} yr^{-1}) contributed from bird populations utilizing these lakes. The annual total phosphorus load was calculated by multiplying the annual average bird biomass by the total phosphorus defecation rate for waterfowl calculated by Manny *et al.* (1985).

Lake	County	Annual load	Bird load	Bird load (% of total)
Okahumpka	Putnam	1790	16.5	0.9
Bivens Arm	Alachua	800	19.4	2.4
Wales	Polk	370	2.9	0.8
Clear	Pasco	270	2.0	0.7
Susannah	Orange	250	22.6	9.1
Hollingsworth	Polk	150	8.8	5.9
Hartridge	Polk	130	4.8	3.7
Bell	Pasco	2150	9.2	0.4
Bonny	Polk	420	9.8	2.3
Lindsey	Hernando	730	7.4	1.0
Koon	Lafayette	1310	7.4	0.6
Orienta	Seminole	690	19.1	2.8
Rowell	Bradford	8030	9.6	0.1
Marianna	Polk	290	7.1	2.5

Conclusions

Aquatic bird populations are influenced by many limnological factors. Our study and others, however, have suggested that a water body's trophic status is a major factor influencing species abundance (numbers and biomass) and richness (Nilsson & Nilsson 1978; Murphy *et al.* 1984; Brown & Dinsmore 1986). Productive aquatic ecosystems are able to support a greater number and biomass of organisms and more specialized species (Hutchinson 1959; MacArthur 1970; Wright 1983). For many lakes, eutrophication control is a major management objective and current lake management strategies generally include attempts to reduce nutrient concentrations through lake drawdowns, alum treatments, and nutrient diversions (Canfield & Hoyer 1988a; Dierberg *et al.* 1988). Successful eutrophication control programs, however, have resulted in reductions in fish (Yurk & Ney 1989) and similar reductions in bird abundance and species richness could be expected based on the results of this study. Eutrophication abatement programs should therefore be planned with full consideration of the potential trade-off between cleaner water and reduced fish and bird populations.

Bird populations have the potential to significantly contribute to the nutrient load of lake systems if large numbers of birds feed outside the lake and then roost on the lake. The percentage of the total phosphorus load contributed to 14 Florida lakes by bird populations, however, was low averaging 2.4 %. These values are also inflated because the majority of the nutrient load contributed by these bird populations comes from the lake through feeding activities of the birds. Thus, bird populations using Florida lakes, under normal situations, do not significantly impact the trophic status of the lakes and this is probably true of most other lakes. Bird abundance and species richness is increased on eutrophic lakes because productive lakes have greater food resources.

Aquatic macrophytes are important to bird populations that use lakes and the management of aquatic macrophytes has the potential to affect bird populations. Our study, however, strongly suggests that the removal of aquatic macrophytes from lakes may have no effect on annual average bird abundance (numbers or biomass) or total species richness. The bird species composition, however, will change as aquatic macrophytes are removed from the lake system. Birds that use aquatic macrophytes (e.g., ring-necked duck) will be replaced by species that use open-water habitats (e.g., double-crested cormorant). Some bird species may also require specific type of aquatic vegetation and the removal of that type may exclude an individual bird species from a lake system. Our analyses therefore suggest the importance of examining bird species as functional groups in more detailed studies.

The majority of the birds counted during this study were observed using near-shore areas. These areas were where the water depth was shallow enough to allow wading birds to forage for food and where terrestrial vegetation provides cover and roosting areas. Future studies of bird populations using lakes systems should carefully examine near-shore areas, and determine the importance of terrestrial vegetation to bird populations. As shorelines are developed for homes or parks, much of the terrestrial vegetation is often removed so people can see the lake. This could have a major effect on not only how many birds are present on the lake, but the species composition and distribution. We, therefore, suggest that whole-lake bird counts be conducted with a description of individual bird habitat use, nesting locations, and feeding activities. Studies should include a minimum of monthly counts because of the seasonal changes that can occur in bird populations.

CONCLUSIONS and RECOMMENDATIONS

Aquatic Macrophytes and Lake Trophic State Parameters

Are aquatic macrophytes an important component of lake ecosystems? The answer to this question is simply, yes. Our findings and those of numerous other published studies from throughout the world have demonstrated that aquatic macrophytes can influence not only biogeochemical cycles in lakes, but the biological functioning and structure of lakes. The more difficult question to answer relates to how many aquatic macrophytes are needed in a lake to be a beneficial component of lake ecosystems? We conclude that the answer to this question depends totally on the management objectives for a particular lake.

Aquatic macrophytes can significantly affect the water quality of a lake. For example, we have demonstrated like many others (Hasler and Jones 1949; Hogetsu et al. 1960; and Canfield et al. 1984) that there is a significant inverse relationship between phytoplankton biomass as measured by chlorophyll *a* concentrations and the abundance of aquatic macrophytes. We have also shown that there is a significant positive relationship between water clarity as measured by use of a Secchi disc and the abundance of aquatic macrophytes. Aquatic macrophytes, however, do not significantly affect whole-lake water clarity and phytoplankton biomass of a lake until macrophytes are extremely abundant. Our analyses suggest that significant changes in whole-lake algal biomass and water clarity can only occur when aquatic macrophyte coverage exceeds values of 30% to 50% and PVI values exceed 40%.

Aquatic macrophytes coverages between 30% and 50% are usually considered an "aquatic weed" problem by many lake users. Although the presence of large amounts of aquatic macrophytes in a lake does not insure that there will be no algal blooms, reducing macrophyte coverage by over 40% will insure a significant change in water quality as measured by chlorophyll *a* concentrations and water clarity. For example, this can happen by reducing aquatic macrophyte coverage from 60% to 20% or from 40% to 0%. User groups, therefore, must be informed that they should expect increased phytoplankton biomass and reduced water clarity when large amounts of aquatic macrophytes are removed from a lake system. They can not get rid of their "aquatic weeds" and still maintain their existing water clarity.

The magnitude of any water quality changes in an individual lake, however, depends upon the abundance of aquatic macrophytes and the lake's trophic status. Large reductions in macrophyte coverage, therefore, may cause unacceptable changes in phytoplankton biomass and water clarity in some lakes, but not others. We suggest that a preliminary assessment of the potential changes in nutrient concentrations in the lake be made according to the methods of Canfield et al. (1983a) and that an adjusted chlorophyll *a* concentration be calculated for the lake as we did in this study. An assessment also should be made of the water quality of other lakes located in the same aquatic ecoregion (see Canfield and Hoyer 1988a) because lakes having similar aquatic macrophyte coverages in the same ecoregion often have similar water quality.

Leaving a small fringe of aquatic macrophytes along the shoreline has been advocated as a means for improving whole-lake water quality. Our study clearly demonstrated that this is not the case if water quality is defined solely in terms of nutrient concentrations, phytoplankton biomass and water clarity. A fringe of aquatic macrophytes can not remove sufficient nutrients to reduce whole-lake nutrient concentrations and phytoplankton biomass. A simple mass balance calculation will demonstrate that the nutrients in a shoreline fringe of macrophytes represent a small fraction of not only the annual nutrient input, but the total pool of available nutrients in a lake. It is also important to note that rooted aquatic macrophytes derive most of their nutrients from the sediments. Small amounts of aquatic macrophytes in an individual lake, however, may have a significant effect on phytoplankton biomass and water clarity in localized areas. For example, many of Florida's large lakes (e.g., Lake Okeechobee) have whole-lake macrophyte coverages < 30%, but these lakes have large areas of adjoining marshes or bays with large amounts of macrophytes. Water in these marshes and bays is typically clearer than that found in open-water areas. The presence of these clear waters may have a significant aesthetic value to some user groups as well as some wildlife values. Thus, aquatic macrophyte beds may be an important microhabitat in some lakes even though the lake's total macrophyte coverage is < 30%.

Large coverages of aquatic macrophytes can influence other limnological properties of lakes that may be as important if not more important than water quality. For example, rooted aquatic macrophytes stabilize the bottoms of many shallow Florida lakes, which reduces turbidity by retarding the wind resuspension of bottom sediments. Large macrophyte beds can also retard the development of large waves, which can prevent shoreline erosion and enhance the habitat of some wildlife species (Carpenter and Lodge 1986). Macrophytes, however, produce large amounts of refractory macrophyte detritus, which has important long-term effects on lake succession (Wetzel 1979).

Accretion of sediments causes expansion of the littoral zone. As the littoral zone increases, greater dominance by emergent macrophytes such as *Typha* spp. accelerates sediment accretion and lake succession (Wetzel 1979; Carpenter 1981). This process hastens the eventual filling in of lakes. Although the control of aquatic macrophytes will encourage the growth of phytoplankton, the deposition of organic matter by algae is significantly less than that of aquatic macrophytes, especially emergent aquatic macrophytes. Recent studies have also shown that maintenance control of aquatic macrophytes by use of herbicides reduces the deposition of organic matter (e.g., Joyce 1985; Joyce et al. 1992). Thus, the control of extensive growths of aquatic macrophytes can retard the eventual transition of an open-water lake to a marsh system.

Aquatic Macrophytes and Fish Populations

The effect aquatic macrophytes have on fish populations has been debated in the literature for many years. Our research clearly shows that over a wide range of lake conditions, lake trophic status is the most important factor influencing fish populations. We demonstrated that there are a significant relationships between total and harvestable fish biomass (kg/ha) and lake trophic status , when fish were collected by use of rotenone sampling, experimental gillnets or electrofishing. Chlorophyll *a* concentrations in Florida lakes, however, accounted for 50% less variance in fish biomass than did similar relations presented by Oglesby (1977) and Jones and Hoyer (1982). This variance could be due to the presence of large amounts of aquatic vegetation in many Florida lakes.

We found no significant correlation between total or harvestable fish biomass (kg/ha), estimated by use of rotenone sampling, and any of the aquatic macrophyte parameters measured during this study. Some lakes with few macrophytes supported high fish biomass whereas others did not. Lakes with both moderate and high macrophyte coverage also supported both high and low fish biomass. A direct comparison of total and harvestable fish biomass to the percent area covered with aquatic macrophytes, however, does not directly consider lake trophic status, which is a major factor determining total and harvestable fish biomass in a wide range of lake systems. To account for lake trophic status, we calculated a fish biomass to adjusted chlorophyll *a* ratio (e.g., g fish biomass/g chlorophyll *a*). Fish biomass per unit of chlorophyll *a* ratios for both total and harvestable fish tend to be low at both low and high aquatic macrophyte abundances. The maximum fish biomass to chlorophyll *a* ratios tended to occur in lakes with PVI values ranging from 20% to 40%, suggesting as others have found (Cooper and Crowder 1979; Savino and Stein 1982; Wiley et al. 1984), that fish abundance is optimized at intermediate aquatic vegetation levels. The lowest total and harvestable fish biomass per unit of chlorophyll *a* ratios measured occurred in lakes with PVI values < 20% and > 75%.

The depressed fish biomass per unit of chlorophyll *a* ratios in lakes with PVI values > 75% is consistent with the findings of other studies that have shown excessive aquatic vegetation results in stunted fish populations (Shireman et al. 1983) and reduced fish growth and condition (Bennett 1948; Buck et al. 1975; Colle and Shireman 1980; Maceina and Shireman 1985). The depressed total and harvestable fish biomass to chlorophyll *a* ratios for lakes with PVI values < 20% would also seem to support the need for at least some aquatic vegetation in lakes for fish populations. Several of our study lakes with PVI values < 20% and > 75%, however, had high total and harvestable fish biomass to chlorophyll *a* ratios. Thus, there is only an increased probability of having depressed fish populations at both low and high levels of aquatic macrophytes.

The largemouth bass is an important sportfish to the State of Florida and aquatic macrophytes have been linked to the survival and well-being of largemouth bass populations in lakes. Studies have shown that aquatic macrophytes can provide spawning substrates (Horel 1951; Chew 1974; Bruno et al. 1990), abundant epiphytic macroinvertebrates that are important to the diet of juvenile largemouth bass (Moxley and Langford 1982; Schramm et al. 1983), abundant small forage fish for adult largemouth bass (Barnett and Schneider 1974) and reduce predation on juvenile largemouth bass by providing refuge (Aggus and Elliot 1975; Wegener and Williams 1974b). We found that there is a trend for increasing young of the year abundance with an increase in aquatic macrophyte coverage up to about 40 to 50% PVI. We, however, found no relation between the standing crop of harvestable largemouth bass and the percent area covered with aquatic macrophytes.

The majority of this report was done examining trends in total and harvestable fish populations. This was intentional because many studies like ours concentrate most of their effort on the high profile species like the largemouth bass and virtually no effort is directed towards other species. Although the largemouth bass is an important sportfish to the State of Florida, the average fishing effort directed toward the largemouth bass estimated from creel census data for 9 Florida lakes (Wegener and Williams 1977; Johnson et al. 1982; Estes 1990; Porak et al. 1990) was only 36% of the total fishing effort. For these 9 lakes, the percentage of the total fishing effort directed toward the largemouth bass ranged from 14% in Lake Carlton (Johnson et al. 1982) to 73% in Lake Rowell (Porak et al. 1990). Thus, we suggest that in addition to largemouth bass populations, future research and management programs need to consider other fish populations that attract an average of 64% of the fishing effort in Florida lakes.

Aquatic Macrophytes and Bird Populations

It has long been recognized that aquatic macrophytes have value as habitat for wildlife, especially birds (Weller and Spatcher 1965; Weller and Fredrickson 1974; Johnson and Montalbano 1984), but we found no strong relationships between the abundance of aquatic macrophytes and total bird abundance and species richness for our study lakes. We did, however, find positive relationships between lake trophic status and average annual bird abundance and total species richness. Individual bird species require different types and quantities of aquatic macrophytes (Weller and Spatcher 1965; Weller and Fredrickson 1974). For example, of the 11 lakes on which ring-neck ducks (*Aythya collaris*) were observed, 10 maintained extensive mats of hydrilla, indicating a possible relation between ring-necked ducks and hydrilla. This relation has also been observed by other researchers in Florida (Gassaway et al. 1977; Johnson and Montalbano 1984). We also found that lakes with virtually no aquatic macrophytes were used extensively by birds such as the anhinga (*Anhinga anhinga*) and double-crested cormorant (*Phalacrocorax auritus*) that feed on fish. We, therefore, conclude that bird abundance and species richness remains relatively stable as aquatic macrophyte abundance decrease, but birds that use macrophyte communities (e.g., ringnecked duck) are replaced by birds that use open-water habitats (e.g., double-crested cormorant).

There are concerns that birds can contribute to eutrophication problems in lakes (Manny et al. 1975; Nordlie). The percentage of the annual total phosphorus that could have been contributed by the bird populations to fourteen lakes in this study, ranged from <

1% to 9% and averaged 2.4%. These percentages are probably overestimates because the majority of the birds are getting their nutrients from the lake by feeding on organisms that live in the lake. Thus, the annual contribution of nutrients by bird populations to Florida lakes is generally low and the trophic state of these lakes is probably not significantly affected by bird populations.

We also believe that near-shore terrestrial vegetation may be very important to bird populations using lakes because we observed the majority of birds near shoreline areas. Thus, future studies of bird populations using lakes systems should not only investigate species specific relations between birds and aquatic macrophytes, but determine the importance of terrestrial vegetation near lakes to bird populations because this vegetation is often cleared by property owners to observe a lake.

Management Considerations

Lakes are important resources and they often must be managed for a variety of purposes including flood control, water supply, fishing, and general recreation. A lake, however, cannot be all things to all people and not all management objectives are compatible. Desirable uses, even obtainable ones, can conflict and lake user groups invariably would like to see their lake do everything (Olem and Flock 1990). They want aesthetic pleasure, great fishing, clean water, sandy shorelines and bottoms, and a healthy wildlife population - all without pests, insects, or weeds. Unfortunately, no lake can meet all these demands. It also is not always possible to optimize each management objective in multiuse water bodies. For example, the objective of maintaining crystal clear water is not compatible with producing large populations of sportfish because there is a direct relation between lake trophic status and harvestable fish populations. Waterfowl hunting in Florida lakes is better with large abundances of aquatic vegetation, which may not be compatible with home owners who enjoy sailing. Thus, those charged with managing lakes must work with the public to determine what priority uses of the water body will be and how much money should be spent to maintain these uses.

We have attempted in this study to describe the relations among aquatic macrophytes, water quality, fish populations and bird populations in order to give those individuals or agencies charged with managing Florida's lake systems a quantitative basis on which to base their management decisions. We strongly urge that lake management programs ascertain what are the desired uses of each lakes. The lake management programs, however, must also reflect the limnological properties of lakes. Oligotrophic lakes with their low biological productivity certainly have attributes that make them more desirable than hypereutrophic lakes for many uses, but there are only a limited number of geographic regions in Florida where oligotrophic lakes can occur. Regional lake management strategies, therefore, must be developed based on specific aquatic ecoregions rather than on statewide standards for lake quality. For example, it would be foolish to set oligotrophic water quality standards for a region that has nutrient rich soils and naturally occurring eutrophic lakes (e.g., Polk County). It also must be recognized that although aquatic macrophytes can be beneficial for lakes, the complete removal of aquatic macrophytes by use of plant management techniques such as grass carp will not necessarily destroy the long-term viability of the lake.

We suggest, as others have, that a moderate amount of aquatic macrophytes would be beneficial to most Florida lakes. A macrophyte coverage of at least 15% with any combination of emergent, floating-leaved, and submersed vegetation seems to reduce the probability of adverse fisheries problems so this may be a reasonable aquatic plant management goal for many lakes. The presence of aquatic macrophytes in a Florida lake, however, will require a long-term commitment to manage the aquatic plant community. Non-native species such as hydrilla and water hyacinth will continue to be a problem and maintenance control of these plants should be a major goal of most aquatic plant management programs to prevent these plants from totally taking over a lake. We advocate maintenance control rather than complete elimination because these plants like any plant can have beneficial effects for some lakes. For example, hydrilla could be important for reestablishing the fisheries of hypereutrophic lakes where light limitation has eliminated most native plant species (Moxley and Langford 1982). It, however, should also be recognized that many native plant species including those like Vallisneria that have been classified as desirable aquatic plants can also cause weed problems and will need to be managed in some lakes. Extensive growths of emergents such as cat-tails can also be problematic, especially in lakes that experience large fluctuations in water level.

It is important to state here that a lake can be managed at 0% or 100% aquatic macrophyte coverage and it will not be a "dead" lake. Fish and wildlife populations will survive in a lake at some level with or without aquatic macrophytes. Different lake uses, however, are optimized at different aquatic macrophyte coverages. Thus, we state again that the determination of whether aquatic macrophytes are beneficial to a lake system is determined totally on the management objectives for a particular lake.

We believe that there are a number of future research needs if we are to optimize aquatic plant management in Florida lakes. A method is needed to manage the number of grass carp in lakes once desired levels of aquatic plant abundance are achieved. There is also a strong need to determine what aquatic macrophytes should be in a specific lake. Aquascaping and the revegetation of lakes are major components of some lake management programs. The manipulation of living organisms for lake management, however, must be compatible with the biology of the organism. Wild rice is an aquatic plant that has value to wildlife, but it only occurs naturally in Florida's river systems. Using wild rice, in a revegetation program for lake systems would, therefore not be compatible with the biology of wild rice. Thus, we suggest that the environmental ranges of individual species of aquatic macrophytes be determined so that the potential survival of each plant type will be known. Our study and others suggest that water chemistry has a major influence on the type of plants found in each lake. We, therefore, suggest an investigation of relations between water chemistry and the macrophyte species composition of lakes might be fruitful.

Lake management is an active ongoing process and better information is needed on how best to educate and involve the public in determining specific management objectives for each water body. For example, education of the general public will be needed to better inform them on how Florida lakes function and of the value of aquatic macrophytes. Education will also be needed to inform the public of the attributes of different aquatic plant management programs such as aquatic herbicide management programs that might be employed to maintain a desirable aquatic macrophyte community. Reaching a consensus on specific lake uses also may prove difficult if more than one organization is involved in the management of the lake, especially if conflicting uses are already established. Olem and Flock (1990), however, have suggested several approaches that can be used to reach a consensus on desired lake uses and to identify various lake problems. These approaches should be further investigated and studies should be made of how statewide agency policies affect aquatic plant management programs for individual lakes. Informed citizens, however, must become involved if desired and attainable lake uses are to be achieved.

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APPENDIX I

LIMNOLOGICAL FACTORS INFLUENCING BIRD ABUNDANCE AND SPECIES RICHNESS ON FLORIDA LAKES

LAKE AND RESERVOIR MANAGEMENT, 1990 6(2): 133-141

Limnological Factors Influencing Bird Abundance and Species Richness on Florida Lakes

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ABSTRACT

Forty-six bird species were observed on 33 Florida lakes with some species occurring on only one lake and others on as many as 26 lakes. Average annual bird abundance ranged from seven to 750 bird/km^2 and total species richness ranged from two to 30 species per lake. Regression analyses were used to examine the effects of lake trophic status, aquatic macrophyte abundance, and lake morphology on average annual bird abundance and total species richness. All trophic state parameters (total phosphorus, total chlorophyll *a*, etc.) accounted for significant portions of the variance in average annual bird abundance, but total chlorophyll *a* concentrations (µg/L) accounted for the highest percentage (47 percent) of the variance. The best fit regression equation was: Log Bird Abundance = 1.35 + 0.56 Log Total Chlorophyll *a*. Lake area, shoreline length, and all trophic state parameters accounted for significant portions of the variance in total species richness. Multiple regression analyses indicated that lake area (km^2) and total chlorophyll *a* (µg/L accounted for the highest percentage (87 percent) of the variance in total species richness (species/lake). The best-fit multiple regression equation was: Log Species Richness = 1.10 + 0.47 Log Lake Area + 0.17 Log Total Chlorophyll *a*. After accounting for lake trophic status and lake area, neither aquatic macrophyte abundance nor lake morphology accounted for additional variances in average annual bird abundance or total species richness.

Introduction

Florida has more than 7,700 lakes that range in size from 0.4 ha to over 180,000 ha (Shafer et al. 1986). Most of the research and lake management conducted on these lakes involves nutrient and aquatic macrophyte management (Shireman et al. 1983; Canfield and Hoyer, 1988a; Dierberg et al. 1988; Joyce, 1989). This work is done primarily for the purposes of potable water supply, flood control, navigation, recreational boating, swimming, and fishing. Often little or no consideration is given to the bird populations that use these lakes and may be affected by lake management actions.

Aquatic bird studies in Florida generally are done in marsh systems; only a few studies have examined factors affecting bird populations in lakes (Gasaway et al. 1977; Gasaway and Drda, 1977; Montalbano et al. 1979; Johnson and Montalbano, 1984; Jenni, 1969). Consequently, there is limited information on the factors influencing bird abundance and species richness in Florida's lakes. The purpose of this exploratory study is to present baseline data on bird populations that use Florida's lakes and to examine relationships between limnological factors and bird abundance and species richness. Many factors have been shown to influence bird populations including geographic location, habitat condition in nesting and wintering areas, and climatic factors. However, we focused our study on the following three major habitat characteristics that have been shown important to bird populations in other studies: lake trophic status (Nilsson and Nilsson, 1978; Murphy et al.

1984;), lake morphology (MacArthur and Wilson, 1967; Brown and Dinsmore, 1986) and aquatic macrophyte abundance (Johnson and Montalbano, 1984; Montalbano et al. 1979).

Methods

Data for this study were collected from 33 Florida lakes (Table 1). Birds observed utilizing aquatic habitats were counted while we motored once around the perimeter of each lake in a boat. Birds were identified to species except gulls, terns, and crows, which were counted in their respective groups. Care was taken not to count twice birds that flushed ahead of the boat. Birds were counted once on each lake in three different seasons: winter (November 1, 1988 to February 28, 1989), spring (March 29, 1989 to May 24, 1989) and summer (July 25, 1989 to September 29, 1989). In addition to individual seasonal counts, average annual bird numbers (number/km^2) were calculated by averaging all three counts for each lake. Species richness (species per lake) was calculated seasonally for each lake. Total species richness equalled the sum of all bird species counted throughout the entire sampling period for each lake.

Summer water samples were collected from six stations (three littoral and three open water), and three open water samples were collected from each lake once in the winter (November – February), and once in the spring (March – May). Water samples were collected 0.5 m below the surface in acid cleaned Nalgene bottles, placed on ice, returned to the laboratory, and analyzed for total phosphorus (TP, µg/L), total nitrogen (TN, µg/L), total chlorophyll *a* (TCHLA, µg/L), total alkalinity (TALK, mg/L as $CaCO_3$) and specific conductance (COND, µS/cm^2 at 25°C). Secchi depth (m) was also measured at each station where water was collected.

Total phosphorus was analyzed (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 TCHLA determinations. Total chlorophyll *a* was determined by using the method of Yentsch and Menzel (1963) and the equations of Parsons and Strickland (1963). Total alkalinity was determined by titrations with 0.02 N sulfuric acid (Stand. Methods, 1981). Specific conductance was measured by using a Yellow Springs Instrument Company Model 31 conductivity bridge. Lake averages for these parameters were calculated by date and then lake.

Table 1.—Name and location of 33 Florida lakes sampled with average annual bird abundance and total species richness listed for each lake.

LAKE NAME	COUNTY	LATITUDE	LONGITUDE	BIRD ABUNDANCE (BIRDS/km^2)	SPECIES RICHNESS (SPECIES/LAKE)
Wauberg	Alachua	29.31	−82.18	320	22
Bivens arm	Alachua	29.37	−82.20	290	25
Rowell	Bradford	29.55	−82.09	110	27
Lindsey	Hernando	28.37	−82.21	240	26
Koon	Lafayette	30.02	−83.06	110	10
Clay	Lake	29.02	−81.27	20	3
Lawbreaker	Lake	29.10	−81.37	7	2
Round pond	Lake	29.04	−81.49	25	3
Crooked	Lake	29.09	−81.36	40	9
Catherine	Marion	29.11	−81.49	20	9
Susannah	Orange	28.33	−81.19	750	16
Baldwin	Orange	28.34	−81.19	320	25
Carlton	Orange	28.45	−81.39	120	25
Live oak	Osceola	28.13	−81.14	24	17
Fish	Osceola	28.16	−81.20	110	27
Clear	Pasco	28.20	−82.15	60	19
Bell	Pasco	28.13	−82.27	250	21
Hunter	Polk	28.01	−81.58	150	18
Bonny	Polk	28.02	−81.55	270	26
Patrick	Polk	27.48	−81.30	40	25
Hartridge	Polk	28.03	−81.44	150	28
Conine	Polk	28.03	−81.43	470	24
Hollingsworth	Polk	28.01	−81.56	220	24
Wales	Polk	27.54	−81.34	110	22
Barco	Putnam	29.40	−82.00	8	2
Deep	Putnam	29.43	−82.57	100	4
Keys pond	Putnam	29.31	−81.58	10	3
Brim pond	Putnam	29.31	−81.59	40	3
Suggs	Putnam	29.41	−82.01	9	10
Cue	Putnam	29.40	−82.58	10	8
Orienta	Seminole	28.39	−81.22	580	20
Okahumpka	Sumter	28.45	−82.05	450	30
Miona	Sumter	28.54	−82.00	60	21

The percentage of lake volume infested with aquatic macrophytes (PVI) and the percentage of lake area covered by macrophytes (PAC) were determined with a Raytheon DE 719 fathometer (Maceina and Shireman, 1980). The aboveground standing crop of emergent (EMERG), floating leaf (FLOAT) and submergent (SUBMERG) vegetation (kg wet wt/m^2) was measured along 10 uniformly placed transects around the lake. A 0.25 m^2 sample of vegetation was taken in each plant zone (when present), placed in nylon mesh bags, spun to remove excess water, and weighed to the nearest 0.10 kg. Average standing crop for each vegetation zone was calculated by averaging 10 samples from each zone.

Lake area (LA) was obtained from the Gazetteer of Florida Lakes (Shafer et al. 1986). Shoreline length (SL, km), the distance to the nearest lake (DLAKE, km), and the number of lakes within 5 km (NO5KM) were measured or counted using aerial photographs with a 1:20,000 or 1:40,000 reduction. Mean depth (MEANZ, m) was calculated from the fathometer transects used for PVI and PAC calculations. Shoreline development (SD) was calculated according to the methods of Wetzel (1975).

Before statistical analyses, data were transformed to base 10 logarithms where needed to meet the requirements of parametric statistical analysis.

Statistical analyses were performed by using the SYSTAT computer package (SYSTAT, 1987). Unless stated otherwise, statements of significance imply phosphorus ≤ 0.05.

Results and Discussion

A wide range of limnological conditions existed in the 33 Florida lakes sampled (Table 2). Mean total phosphorus concentrations ranged from 1 to 1040 µg/L and total chlorophyll *a* concentrations ranged from 0.7 to 240 µg/L. Water clarity ranged from 0.3 to 5.7 m and total nitrogen concentrations ranged from 100 to 4900 µg/L. Lake area ranged from 0.032 to 2.71 km^2 and percentage area covered with aquatic macrophytes ranged from 0 to 100 percent (Table 2). The ranges of these limnological parameters are similar to those reported by Canfield and Hoyer (1988b) for 165 Florida lakes. Thus, these lakes range from oligotrophic to hypereutrophic (Forsberg and Ryding, 1980), and they should represent Florida lakes for the purpose of examining the effect of lake trophic status, aquatic macrophyte abundance, and lake morphology on bird populations.

Forty-six bird species were observed during the study period with some occurring on only one lake

Table 2.—Summary statistics for trophic state, aquatic macrophyte, lake morphology, and bird population parameters estimated in 33 Florida lakes.

PARAMETERS	MEAN	RANGE	STANDARD DEVIATION
TROPHIC STATE:			
Total phosphorus (µg/L)	72	1–1040	189
Total nitrogen (µg/L)	1100	100–4900	1100
Total chlorophyll *a* (µg/L)	36	0.7–240	57
Secchi depth (m)	2.0	0.3–5.7	1.6
Specific conductance (µS/cm^2 25°C)	138	29–384	99
Total alkalinity (mg/L as $CaCO_3$)	28	0–105	30
AQUATIC MACROPHYTES:			
Percent volume infested with macrophytes	21	0–98	33
Percent area covered with macrophytes	36	0–100	42
Emergent biomass (kg wet wt/m^2)	6.6	0.9–26.8	5.1
Floating leaf biomass (kg wet wt/m^2)	2.0	0–11.2	2.8
Submergent biomass (kg wet wt/m^2)	2.8	0–16.6	3.9
LAKE MORPHOLOGY:			
Lake surface area (km^2)	0.796	0.032–2.710	0.666
Shoreline length (km)	3.6	0.7–8.4	2.0
Mean depth (m)	2.8	0.9–5.9	1.2
Shoreline development	1.3	1–2.4	0.4
Distance to nearest lake (km)	0.4	0.2–1.5	0.3
Number of lakes within 5 km	27	3–53	13
BIRD POPULATION:			
Bird abundance (number/km^2)			
Winter	250	0–1300	321
Spring	130	0–840	168
Summer	120	0–650	131
Annual Average	170	7–750	180
Species richness (species/lake)			
Winter	11.2	1–25	7.8
Spring	9.7	0–20	6.3
Summer	9.8	1–20	6.1
Annual Total	16.8	2–30	9.4

and others occurring on as many as 26 lakes (Table 3). Thirty-two species occurred on more than 20 percent of the lakes sampled (Table 4). Seasonal bird abundance and species richness were greatest in the winter averaging 250 birds/km^2 and 11 species per lake (Table 2), which is expected due to the migratory bird populations utilizing Florida lakes during that season. Eight of the 32 species occurring on at least 20 percent of the lakes sampled could be grouped as strong winter migrants (i.e., birds occurring on significantly more lakes in the winter than spring or summer, Table 4). Additionally, an unknown percentage of winter bird abundances are probably from birds grouped as migrant residents (i.e., birds occurring on equal number of lakes in all seasons, Table 4) supplementing resident populations during winter months.

The correlations between seasonal bird population parameters and trophic state, aquatic macrophyte, or lake morphology parameters are similar for all seasons (Table 5). Therefore, the remainder of analyses were done using average annual bird abundance and total species richness. Average annual bird abundance and total species richness for these lakes ranged seven to 750 birds/km^2 and two to 30 species per lake, respectively (Tables 1 and 2). Both average annual bird abundance and total species richness were significantly correlated with total phosphorus ($r = 0.63$ and $r = 0.69$, respectively), total chlorophyll *a* ($r = 0.68$ and $r = 0.73$, respectively), and

Table 3.—List of bird species identified and counted on 33 Florida lakes between November 1988 and September 1989. N is the number of lakes on which a bird was observed and the average abundance of a given bird species is listed with the standard error of the mean (STDERR).

COMMON NAME	SCIENTIFIC NAME	N	BIRDS/km^2	STDERR
Pied-billed Grebe	*Podilymbus podiceps*	14.0	1.0	0.2
American White Pelican	*Pelecanus erythrorhynchos*	1.0	0.9	0.0
Double-crested Cormorant	*Phalacrocorax auritus*	21.0	12.6	3.9
Anhinga	*Anhinga anhinga*	24.0	11.5	3.3
Least Bittern	*Ixobrychus exillis*	9.0	0.6	0.1
Great Blue Heron	*Ardea herodias*	25.0	5.8	0.9
Great Egret	*Casmerodius albus*	25.0	5.0	1.7
Snowy Egret	*Egretta thula*	17.0	2.9	0.7
Little Blue Heron	*Egretta caerulea*	18.0	2.2	0.5
Tricolored Heron	*Egretta tricolor*	15.0	1.8	0.4
Cattle Egret	*Bubulcus ibis*	14.0	8.3	3.7
Green-backed Heron	*Butorides striatus*	1.0	3.4	0.7
Black-crowned Night-heron	*Nycticorax nycticorax*	5.0	5.0	2.6
White Ibis	*Eudocimus albus*	16.0	9.4	4.8
Glossy Ibis	*Plegadis falcinellus*	2.0	0.7	0.0
Wood Stork	*Mycteria americana*	5.0	1.9	0.7
Canada Goose	*Branta canadensis*	2.0	0.7	0.1
Fulvous Whistling Duck	*Dendrocygna bicolor*	1.0	0.1	0.0
Wood Duck	*Aix sponsa*	11.0	5.0	1.5
Mottled Duck	*Anas fulvigula*	3.0	2.6	1.4
Mallard	*Anas platyrhynchos*	10.0	45.5	20.6
Blue-winged Teal	*Anas discors*	1.0	3.8	0.0
Ring-necked Duck	*Aythya collaris*	7.0	8.7	5.9
Black Vulture	*Coragyps atratus*	14.0	6.9	3.2
Turkey Vulture	*Cathartes aura*	8.0	9.9	5.2
Osprey	*Pandion haliaetus*	20.0	2.3	0.4
Bald Eagle	*Haliaeetus leucocephalus*	8.0	1.3	0.5
Northern Harrier	*Circus cyaneus*	7.0	0.4	0.1
Red-shouldered Hawk	*Buteo lineatus*	8.0	0.6	0.2
Red-tailed Hawk	*Buteo jamaicensis*	6.0	1.0	0.6
American Kestrel	*Falco sparverius*	5.0	0.4	0.1
Sora	*Porzana carolina*	1.0	0.7	0.0
Purple Gallinule	*Porphyrula martinica*	8.0	2.3	1.2
Common Moorhen	*Gallinula chloropus*	19.0	16.7	4.4
American Coot	*Fulica americana*	14.0	27.1	20.6
Limpkin	*Aramus guarauna*	6.0	0.8	0.2
Sandhill Crane	*Grus canadensis*	1.0	0.2	0.0
Semipalmated Plover	*Charadrius semipalmatus*	7.0	1.0	0.4
Killdeer	*Charadrius vociferus*	6.0	3.3	1.1
Lesser Yellowlegs	*Tringa flavipes*	2.0	0.5	0.1
Common Snipe	*Gallinago gallinago*	5.0	1.9	1.1
Gulls (Larinae)		16.0	20.5	7.9
Terns (Sterninae)		14.0	6.0	2.8
Belted Kingfisher	*Ceryle alcyon*	25.0	3.0	0.8
Purple Martin	*Progne subis*	11.0	14.3	12.5
Tree Swallow	*Tachycineta bicolor*	1.0	15.2	0.0
Bank Swallow	*Riparia riparia*	1.0	1.3	0.0
Crows (Corvidae)		26.0	20.0	11.6
Red-winged Blackbird	*Agelaius phoeniceus*	22.0	18.2	5.0
Boat-tailed Grackle	*Quiscalus major*	21.0	48.0	9.4

Table 4.—List of bird species identified and counted on at least 20% of the Florida Lakes (n = 33) sampled, with the number of lakes on which a bird was observed in winter (November 1, 1988 to February 28, 1989), spring (March 29, 1989 to May 24, 1989) and summer (July 25, 1989 to September 29, 1989) listed.

COMMON NAME	SCIENTIFIC NAME	WINTER	SPRING	SUMMER
Migrant-Resident:				
Anhinga	*Anhinga anhinga*	19	17	20
Great Blue Heron	*Ardea herodias*	21	22	22
Great Egret	*Casmerodius albus*	22	17	23
Snowy Egret	*Egretta thula*	12	7	16
Little Blue Heron	*Egretta caerulea*	13	9	12
Tricolored Heron	*Egretta tricolor*	12	4	12
White Ibis	*Eudocimus albus*	11	9	9
Wood Duck	*Aix sponsa*	3	8	8
Mallard	*Anas platyrhynchos*	8	8	10
Black Vulture	*Coragyps atratus*	8	6	7
Turkey Vulture	*Cathartes aura*	3	1	5
Osprey	*Pandion haliaetus*	8	18	10
Northern Harrier	*Circus cyaneus*	3	1	3
Purple Gallinule	*Porphyrula martinica*	4	3	5
Common Moorhen	*Gallinula chloropus*	17	18	18
Terns	*Laridae Sterninae*	10	5	7
Crows	*Corvidae*	15	24	17
Red-winged Blackbird	*Agelaius phoeniceus*	13	20	16
Boat-tailed Grackle	*Quiscalus major*	19	20	17
Winter Migrants:				
Pied-billed Grebe	*Podilymbus podiceps*	12	2	1
Ring-necked Duck	*Aythya collaris*	7	1	1
Bald Eagle	*Haliaeetus leucocephalus*	6	5	2
Red-shouldered Hawk	*Buteo lineatus*	6	1	1
Double-crested Cormorant	*Phalacrocorax auritus*	18	14	10
American Coot	*Fulica americana*	14	6	3
Gulls	*Laridae*	16	7	1
Belted Kingfisher	*Ceryle alcyon*	23	4	13
Spring Migrants:				
Semipalmated Plover	*Charadrius semipalmatus*	0	7	0
Purple Martin	*Progne subis*	0	9	3
Summer Users:				
Least Bittern	*Ixobrychus exilis*	0	6	5
Green-backed Heron	*Butorides striatus*	7	16	17
Cattle Egret	*Bubulcus ibis*	2	7	10

Secchi depth (r = -0.59 and r = -0.68, respectively) as well as other trophic state parameters (Table 5). Average annual bird abundance and total species richness were significantly correlated to lake surface area (r=0.48 and r=0.89, respectively) and shoreline length (r=0.55 and r=0.86, respectively).

Regression equations are listed in Table 6 to allow estimates of average annual bird abundance on lakes with one of six different trophic state parameters. Linear regression analyses, however, showed that the best-fit regression equation was with total chlorophyll *a*, which accounted for 47 percent of the total variance in average annual bird abundance (Table 6). Stepwise multiple regression analyses revealed that, after accounting for lake trophic status (as estimated with chlorophyll *a* concentrations), no multivariate model using aquatic macrophyte or lake morphology parameters accounted for significantly more variance in average annual bird abundance.

Where possible, we suggest using chlorophyll *a* rather than other trophic state parameters to estimate bird abundance on lakes because total chlorophyll *a* seems a convenient estimator of the organic base upon which aquatic bird populations depend. Total chlorophyll *a* alone accounts for a large portion of the variance in total bird abundance (Figure 1). Chlorophyll *a* also relates to nutrient concentrations (Canfield, 1983), and already has been successfully used to model other vertebrate populations in lakes (Oglesby, 1977; Jones and Hoyer, 1982). In certain situations nutrient concentrations and Secchi depth measurements can result in misclassifications of lake trophic status. For example, inorganic suspended solids in Missouri reservoirs and Lake Okeechobee, Florida, have been shown to reduce algal biomass per unit of phosphorus by causing light limitation (Hoyer and Jones, 1983; Canfield and Hoyer, 1988a).

Eight linear regression equations presented in Table 6 indicate that all trophic state parameters and two lake morphology parameters individually accounted for over 45 percent of the variance in total species richness. Lake area, however, accounted for the largest portion of the variance (R^2 = 0 .80) in total species richness (Table 6 and Fig. 2). Multivariate regression analyses, with lake area as a primary variable, showed that only the six trophic

Table 5.—Correlation matrix for all parameters sampled on 33 Florida lakes (see methods for parameter units). All absolute r values equal to or greater than 0.35 are significant at a p ≤ 0.05 level.

VARIABLES	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12	X13	X14	X15	X16	X17
Trophic state:																	
X1..Total phosphorus	1.00																
X2..Total nitrogen	0.78	1.00															
X3..Total chlorophyll *a*	0.91	0.85	1.00														
X4..Secchi depth	−0.88	−0.87	−0.91	1.00													
X5..Specific conductance	0.68	0.72	0.73	−0.63	1.00												
X6..Total alkalinity	0.59	0.77	0.72	−0.66	0.63	1.00											
Aquatic macrophytes:																	
X7..PVI	−0.29	−0.08	−0.28	0.20	−0.28	0.01	1.00										
X8..PAC	−0.47	−0.22	−0.46	0.40	−0.32	−0.06	0.88	1.00									
X9..Emergent biomass	0.20	0.00	0.13	−0.08	−0.08	0.00	0.14	0.15	1.00								
X10..Floating biomass	0.08	0.16	0.12	−0.16	−0.12	0.18	0.47	0.42	0.25	1.00							
X11..Submergent biomass	−0.52	−0.42	−0.52	0.47	−0.42	−0.24	0.54	0.64	0.47	0.33	1.00						
Lake morphology:																	
X12..Surface area	0.59	0.60	0.59	−0.60	0.66	0.63	0.02	−0.08	0.00	−0.03	−0.19	1.00					
X13..Shoreline	0.54	0.52	0.55	−0.53	0.54	0.52	−0.01	−0.07	0.06	0.02	−0.15	0.91	1.00				
X14..Mean depth	−0.19	−0.32	−0.20	0.35	−0.08	−0.23	−0.50	−0.38	−0.09	−0.44	−0.03	−0.22	−0.20	1.00			
X15..Shoreline development	−0.11	−0.20	−0.09	0.16	−0.26	−0.26	−0.08	0.01	0.14	0.12	0.11	−0.24	0.20	0.04	1.00		
X16..Distance to nearest lake	0.23	0.26	0.23	−0.26	0.30	0.22	0.09	−0.02	−0.24	0.05	−0.30	0.54	0.44	−0.31	−0.24	1.00	
X17..Number of lakes within 5 km	−0.35	−0.40	−0.33	0.37	−0.38	−0.21	−0.23	−0.16	0.07	−0.31	0.10	−0.46	−0.41	0.49	0.11	−0.57	1.00
Bird abundance:																	
Y1..Winter abundance	0.60	0.64	0.65	−0.54	0.51	0.71	−0.12	−0.24	0.16	0.00	−0.24	0.51	0.54	−0.12	0.07	0.25	−0.18
Y2..Spring abundance	0.50	0.62	0.59	−0.51	0.46	0.56	0.08	−0.02	0.05	0.20	−0.26	0.42	0.49	−0.30	0.15	0.12	−0.14
Y3..Summer abundance	0.54	0.49	0.55	−0.53	0.45	0.46	−0.11	−0.20	0.05	−0.05	−0.27	0.50	0.56	−0.03	0.12	0.32	−0.18
Y4..Annual abundance	0.63	0.66	0.68	−0.59	0.52	0.67	−0.04	−0.16	0.16	0.05	−0.26	0.48	0.55	−0.17	0.16	0.21	−0.16
Bird species richness:																	
Y5..Winter species	0.72	0.76	0.77	−0.68	0.77	0.76	−0.01	−0.15	0.02	0.02	−0.32	0.84	0.79	−0.23	−0.12	0.49	−0.44
Y6..Spring species	0.53	0.65	0.62	−0.56	0.56	0.56	0.05	−0.08	−0.02	0.20	−0.26	0.62	0.65	−0.27	0.07	0.30	−0.27
Y7..Summer species	0.68	0.69	0.67	−0.67	0.67	0.70	−0.10	−0.19	−0.05	−0.08	−0.32	0.90	0.85	−0.11	−0.15	0.47	−0.37
Y8..Total species	0.69	0.74	0.73	−0.68	0.70	0.76	−0.04	−0.14	0.02	0.07	−0.29	0.89	0.86	−0.24	−0.09	0.47	−0.40
Bird abundance:	Y1	Y2	Y3	Y4	Y5	Y6	Y7	Y8									
Y1..Winter abundance	1.00																
Y2..Spring abundance	0.58	1.00															
Y3..Summer abundance	0.68	0.45	1.00														
Y4..Annual abundance	0.92	0.72	0.83	1.00													
Bird species richness:																	
Y5..Winter species	0.79	0.67	0.67	0.79	1.00												
Y6..Spring species	0.56	0.91	0.46	0.63	0.76	1.00											
Y7..Summer species	0.70	0.54	0.75	0.72	0.89	0.65	1.00										
Y8..Total species	0.72	0.71	0.66	0.74	0.96	0.81	0.93	1.00									

Table 6.—Regression models relating average annual bird abundance (birds/km²) and total species richness (species/lake) to six trophic state parameters and multivariate regression models relating total species richness to lake area and six trophic state parameters. All listed regressions are significant at p ≤ 0.05. Data were collected from 33 Florida Lakes.

DEPENDENT VARIABLE	MODEL	STANDARD ERROR OF ESTIMATE	R^2
average annual bird Abundance (birds/km²):			
	= 1.23 + 0.54 Log (total phosphorus)	0.47	0.39
	= −0.64 + 0.90 Log (total nitrogen)	0.46	0.44
	= 1.35 + 0.56 Log (total chlorophyll *a*)	0.44	0.47
	= 2.09 − 0.94 Log (Secchi depth)	0.48	0.34
	= 0.09 + 0.91 Log (specific conductance)	0.51	0.27
	= 1.70 + 0.29 Log (total alkalinity)	0.44	0.44
Total Species Richness (species/lake):			
	= 0.61 + 0.40 Log (total phosphorus)	0.29	0.47
	= −0.74 + 0.65 Log (total nitrogen)	0.27	0.53
	= 0.71 + 0.39 Log (total chlorophyll a)	0.27	0.53
	= 1.24 − 0.72 Log (Secchi depth)	0.29	0.46
	= −0.52 + 0.81 Log (specific conductance)	0.28	0.49
	= 0.94 + 0.22 Log (total alkalinity)	0.26	0.57
	= 1.31 + 0.59 Log (lake area)	0.17	0.80
	= 0.55 + 1.17 Log (lake shoreline)	0.20	0.75
Total Species Richness (species/lake):			
	= 1.10 + 0.49 Log (lake area) + 0.14 Log (total phosphorus)	0.16	0.84
	= −0.49 + 0.47 Log (lake area) + 0.27 Log (total nitrogen)	0.15	0.86
	= 1.10 + 0.47 Log (lake area) + 0.17 Log (total chlorophyll a)	0.15	0.87
	= 1.32 + 0.50 Log (lake area) − 0.23 Log (Secchi depth)	0.16	0.83
	= 0.83 + 0.51 Log (lake area) + 0.22 Log (specific conductance)	0.17	0.83
	= 1.20 + 0.46 Log (lake area) + 0.09 Log (total alkalinity)	0.15	0.86

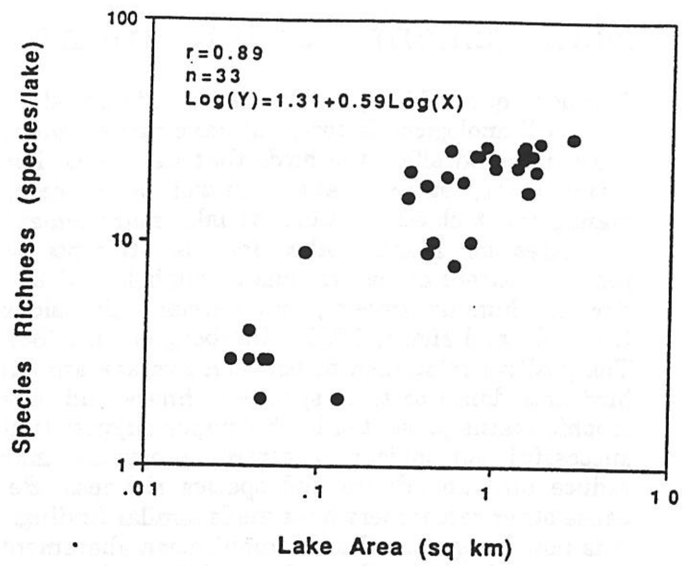

Figure 1.—Relation between average annual bird abundance (birds/km²) and total chlorophyll *a* (µg/L) for 33 Florida lakes.

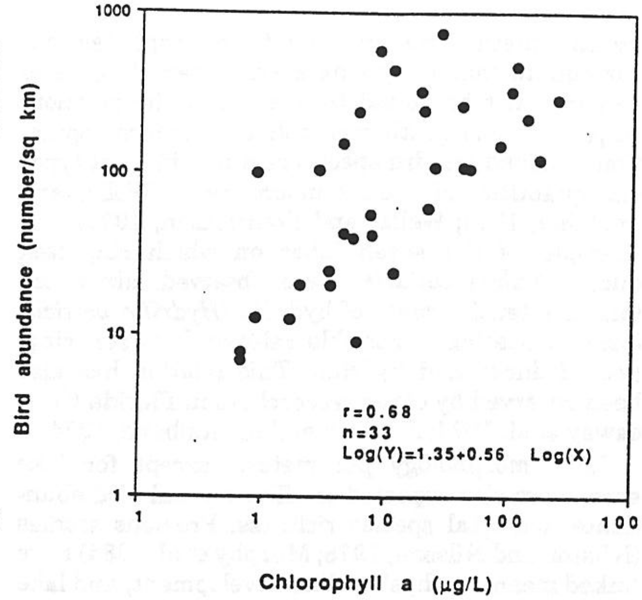

Figure 2.—Relation between total species richness (species/lake) and lake area (km²) for 33 Florida lakes.

state parameters accounted for significantly more variance in total species abundance (Table 6) than lake area alone. The following best-fit multiple linear regression indicated that lake area and total chlorophyll *a* accounted for 87 percent of the variance in species richness:

$$\text{Log Species Richness} = 1.10 + 0.47 \text{ Log Lake Area} + 0.17 \text{ Log Total Chlorophyll } a \quad (1)$$

Similar species-area relations have been reported for many flora and fauna (Flessa and Sepkoski, 1978; Connor and McCoy, 1979). Williamson (1988) suggested that there are several possible explanations for species area relations: (1) an increase in area may simply increase the sampling size, resulting in more species; (2) an increase in area may correlate with an increase in habitat heterogeneity; and (3) MacArthur and Wilson, theory of island biogeography may be a factor (see MacArthur and Wilson, 1967).

We found that as lake size in our study lakes increased so did the sampling area and the near shore terrestrial and aquatic habitat heterogeneity (personal observation). No effect related to the MacArthur–Wilson theory of island biogeography was found (see later discussion), but the relative importance of each mechanism discussed by Williamson (1988) may differ under different ecological conditions. Separating the mechanisms that determine species-area relations, however, is beyond the scope of this paper.

The direct relation between total chlorophyll *a* and species richness supports the suggestion of several investigators (Hutchinson, 1959; MacArthur 1970; Wright, 1983) that more productive systems can support more specialized species, thus yielding greater species richness. Relations between species richness and trophic state parameters also have been reported for vascular plants, snails, fish and birds in marsh, pond, and lake systems (Nilsson and Nilsson, 1978; Murphy et al. 1984; Brown and Dinsmore, 1986). However, Nilsson and Nilsson (1978) suggest that lakes suffering from cultural eutrophication will have fewer species than lakes of equal size and natural trophic status.

Two lakes in our data set (Lake Rowell, Bradford County, and Lake Conine, Polk County, Table 1) currently receive point source nutrient enrichment and can be considered culturally eutrophic. Using lake area and total chlorophyll *a* concentrations for these two lakes and the corresponding equation in Table 6, the number of species that would be predicted in each lake was calculated and compared to the observed number of species. At Lake Rowell and Lake Conine, the observed number of species (27 and 24, respectively) was similar to the predicted number of species (22 and 29, respectively). This suggests that lakes suffering from cultural eutrophication can have bird species richness that equals the richness of lakes of equal trophic status and size that have not received anthropogenic additions of nutrients.

Birds use aquatic macrophytes for nesting, resting, and refuge sites. Macrophytes are also food for birds, and the plants provide substrate for invertebrate food items (Odum et al. 1984). However, multivariate regression analyses indicated that no aquatic macrophyte parameters related significantly to average annual bird abundance or total species richness in the Florida lakes after the effects of trophic state and lake area were accounted for. This is surprising considering the reported association between aquatic birds and aquatic macrophytes, but our aquatic macrophyte data are extremely general and may not be suited to examining the relationships between aquatic macrophytes and bird populations. Individual bird species require different types and quantities of aquatic macrophytes (Weller and Spatcher, 1965; Weller and Fredrickson, 1974). For example, of the seven lakes on which ring-neck ducks (*Aythya collaris*) were observed, six maintained extensive mats of hydrilla (*Hydrilla verticillata*), indicating a possible relation between ring-necked ducks and hydrilla. This relation has also been observed by other researchers in Florida (Gassaway et al. 1977; Johnson and Montalbano, 1984).

Lake morphology parameters, except for lake area, were also expected to affect annual bird abundance and total species richness. Previous studies (Nilsson and Nilsson, 1978; Murphy et al. 1984) have linked mean depth, shoreline development, and lake isolation parameters with bird population abundance and species richness.

After accounting for trophic status and lake area, no lake morphology parameters related significantly to annual bird abundance or total species richness, but there were significant correlations between two lake isolation parameters (distance to the nearest lake, r = 0.47 and number of lakes within a 5 km radius, r = -0.40) and total species richness (Table 5). Similar isolation parameters have also been shown significantly related to species richness in other aquatic systems (Murphy et al. 1984; Brown and Dinsmore, 1986). However, according to island biogeography theory (MacArthur and Wilson, 1967), as the distance to another lake increases the number of species present should decrease, and as the number of lakes within a 5 km radius increases the number of species present should increase, which is the exact opposite of what we observed. Therefore, we believe our correlations are spurious. Nilsson and Nilsson (1978) also found no relationship between isolation parameters and species richness in areas where lakes are relatively close and abundant. This is the case for our Florida lakes, which have an average distance to the nearest lake of 0.4 km and an average number of lakes within 5 km of 27 (Table 2).

Another explanation for our observed lack of relations between bird populations and both aquatic macrophyte and lake morphology parameters may be that the majority of birds were counted near shoreline areas in shallow littoral zones. This suggests that many aquatic birds may be limited to shoreline areas where water is shallow and food for birds may be concentrated. Nearshore areas may also be where preferred aquatic and terrestrial vegetation is found. Thus, whole lake parameters (e.g., percentage area covered with macrophytes and lake mean depth) may show no relation to bird populations simply because many birds are limited to shoreline areas.

Management Considerations

Because aquatic bird populations are influenced by several limnological factors, any lake management program could affect the birds that use lakes. For many lakes, eutrophication control is a major management objective. Current lake management strategies for Florida lakes include attempts to reduce nutrient concentrations through lake drawdowns, alum treatments, and nutrient diversions (Canfield and Hoyer, 1988a; Dierberg et al. 1988). The positive relationships between average annual bird abundance or total species richness and lake trophic status presented in this paper suggest that successful eutrophication control programs may reduce bird abundance and species richness. Because other researchers have made similar findings, it is now recognized that eutrophication abatement programs should be planned with full consideration of the potential trade-off between cleaner water and reduced fish populations (Yurk and Ney, 1989).

Nuisance growths of aquatic macrophytes are common in many of the world's lakes. Mechanical harvesting, chemical treatments, and biological control of aquatic macrophytes are major lake management strategies used in Florida lakes (Shireman et al. 1983). The effect of aquatic vegetation management programs on bird populations, however, is not clear. Many studies suggested strong relationships between aquatic vegetation and bird populations (Weller and Spatcher, 1965; Weller and Fredrickson, 1974; Johnson and Montalbano, 1984), but data presented in this study indicate that removal of aquatic vegetation in lakes may have no effect on total bird abundance or species richness. However, we believe that the relations between aquatic macrophyte and bird populations may be species-specific and confined to shoreline areas where water depths are shallow and food for birds may be concentrated and easily available. Reductions from 80 to 100 percent coverage of aquatic macrophytes (a common occurrence in Florida lakes) toward 40 percent coverage, which is a common target level for fisheries management (Wiley et al. 1984), should not affect average annual bird abundance or total species richness. We also believe that near shore terrestrial vegetation may be very important to bird populations using lakes because most of the birds we observed were near shoreline areas. Thus, future studies of bird populations using lakes should not only investigate species-specific relations between birds and aquatic macrophytes but also determine the importance of terrestrial vegetation near lakes to bird populations because this vegetation is often cleared by property owners to observe a lake.

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KEYWORDS: Florida; bird populations; lakes; water quality.

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