Hydrobiologia **297/280**: 107–119, 1994.
J. J. Kerekes (ed.), Aquatic Birds in the Trophic Web of Lakes.

Bird abundance and species richness on Florida lakes: influence of trophic status, lake morphology, and aquatic macrophytes

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Key words: Florida, bird populations, trophic status, lakes, water quality, aquatic macrophytes

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 180000 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 1:20000 or 1:40000 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 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 equa-

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 leaf 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 leaf 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	1.00	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

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

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

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

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

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 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

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
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.

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

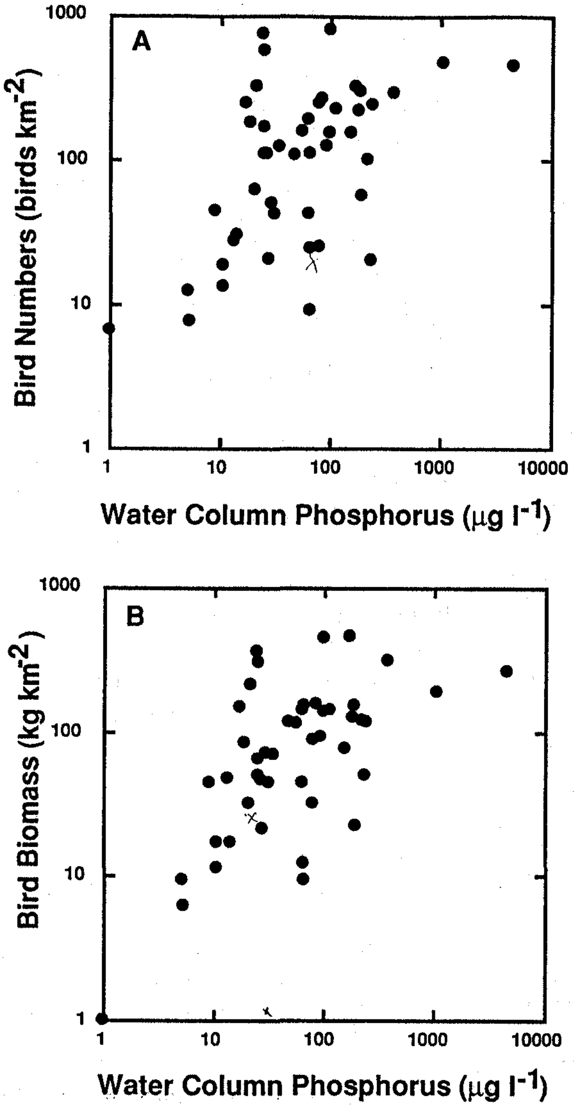


Fig. 1. Relation between annual average bird numbers (A, birds km^{-2}) and biomass (B, kg km^{-2}) and water column phosphorus concentration (WCP, $\mu g\, l^{-1}$) for 46 Florida lakes. WCP values are calculated by adding the phosphorus incorporated in aquatic macrophyte and epiphytic algae tissue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

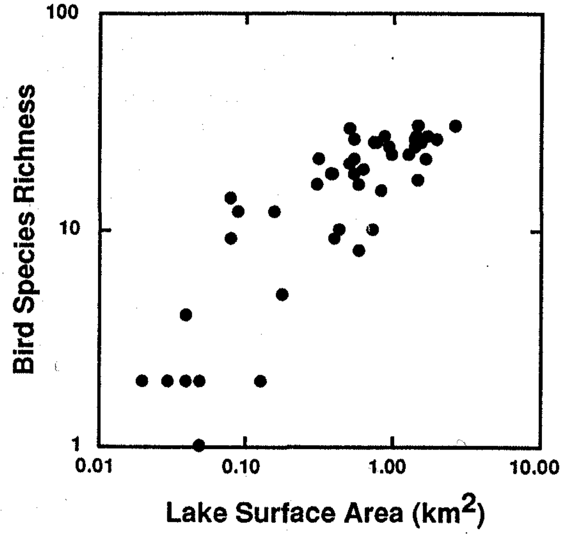


Fig. 2. Relation between lake species richness (total species) and surface area (km^2).

($r = 0.86$; Table 3; Fig. 2). 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:

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

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

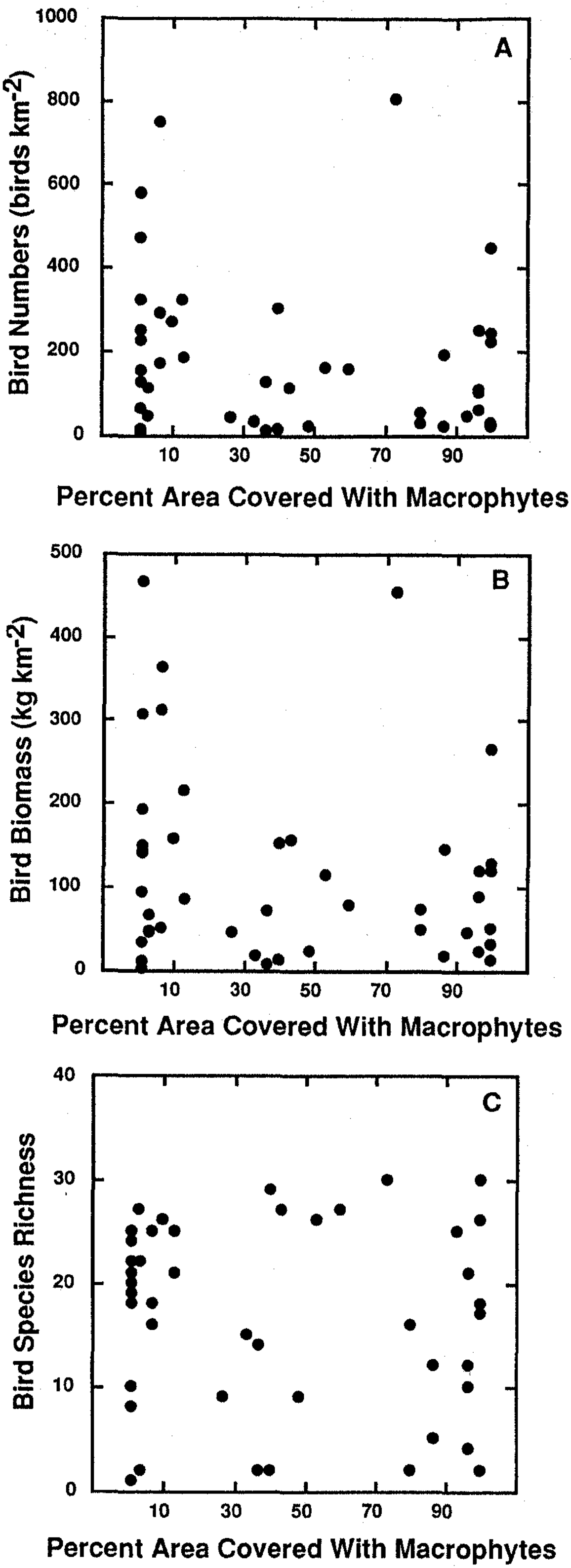
We anticipated significant correlations between the lake morphology variables other than lake area and bird abundance and species richness because previous studies had linked shoreline development and mean depth with bird abundance and species richness (Nilsson & Nilsson, 1978; Murphy *et al.*, 1984). Shoreline development for our lakes, however, averaged only 1.34 and the values only ranged from 1.00 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 5). 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.

Table 4. 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



The double-crested cormorant (*Phalacrocorax auritus*) and anhinga showed a much higher frequency of detection in lakes with low aquatic macrophyte coverage (Table 5). 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 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 5). 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 fac-

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.

Table 5. 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
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

tor 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 4). 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).

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.

Acknowledgements

We thank S. F. Mitchell and an anonymous reviewer for their many constructive comments on this manuscript. Christy Horsburgh, Phillip Lawson, and Mark Jennings were instrumental in collection of data and conducting bird counts. We thank Mary Stonecipher for conducting chemical analyses. This research was funded in part by the Bureau of Aquatic Plant Management (Contract number C 3748), Florida Department of Natural Resources.

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