

Relations between trophic state indicators and fish in Florida (U.S.A.) lakes¹

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Abstract: Total fish biomass per unit area was positively correlated with total phosphorus, total nitrogen, chlorophyll *a*, and inversely correlated with Secchi disk transparency in 65 Florida (U.S.A.) lakes selected to range from oligotrophic to hypereutrophic. Species numbers were positively related to lake surface area but not trophic state. There were some shifts in species composition with changes in trophic state, though only a few species showed significant changes in their standing crops. In particular the recreationally important centrarchids did not show important changes with trophic state, and there were no critical points on the trophic spectrum where there were dramatic changes in fish abundance or standing crops. The facts that Florida lakes do not have deep, cold hypolimnia, do not have salmonid species, and have no ice in the winter are among the possible reasons that the more eutrophic Florida lakes do not show the same changes in fish populations often described for northern lakes.

Résumé : Il y avait une corrélation positive entre la biomasse totale de poissons par unité de surface et le phosphore total, l'azote total et la chlorophylle *a*, et une corrélation inverse entre cette biomasse et la transparence mesurée à l'aide du disque de Secchi, dans 65 lacs de Floride (É.-U.) allant d'oligotrophes à hypereutrophes. Les nombres d'espèces étaient liés positivement à la superficie des lacs, mais non à leur état trophique. La composition des espèces variait quelque peu avec l'état trophique, mais seules quelques espèces accusaient des différences importantes dans le nombre d'individus. Plus particulièrement, les centrarchidés importants sur le plan récréatif n'accusaient pas d'importants changements avec l'état trophique, et le spectre trophique ne présentait aucun point critique correspondant à des changements dramatiques de l'abondance ou du nombre d'individus. L'absence d'un hypolimnion froid et profond, l'absence de salmonidés et l'absence de glace en hiver comptent parmi les raisons pouvant expliquer pourquoi les lacs de Floride plus eutrophes n'accusent pas les mêmes variations de population de poissons dont on a souvent fait état dans les lacs nordiques.

[Traduit par la Rédaction]

Introduction

Eutrophication is a concern in Florida where a growing human population and changes in land use are increasing nutrient inputs to many lakes. The impacts of excess algal populations on water transparency and the general appearance of Florida lakes are well known (Canfield and Hodgson 1983; Canfield et al. 1985); however, less information is available on the effects that changes in trophic state have on fish populations. There is special interest in Lake Okeechobee, a large (1730 km²) and shallow (mean depth = 2.7 m) lake in south Florida where total phosphorus concentrations in the lake have increased over the past 20 years (Janus et al. 1990; James et al.

1995). As Lake Okeechobee has a major recreational fishery, there is interest in knowing the potential impact of trophic state changes on fish populations in this and other Florida lakes.

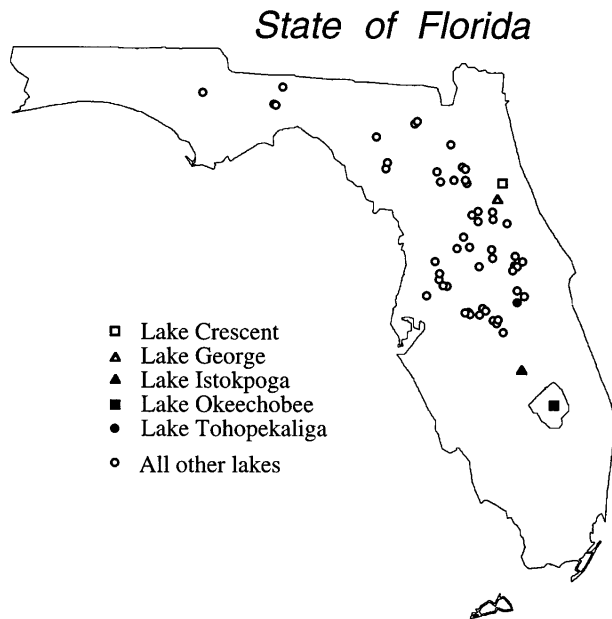
There are many quantitative studies that support the expectation that an increase in productivity at the base of food chains in a lake should translate into an increase in the abundance of fish at higher trophic levels. Oglesby (1977) found high correlations between fish yields in lakes and summer phytoplankton standing crops as measured by chlorophyll *a* and also between fish yield and annual primary productivity. Melack (1976) studied tropical lakes in Africa and India and found that fish yields increased logarithmically as primary production increased arithmetically. McConnell et al. (1977) found that fish yield and gross photosynthesis were highly correlated in six experimental ecosystems involving a variety of fishes. Yurk and Ney (1989) found a strong correlation between fish standing crops and total phosphorus in 22 southern Appalachian reservoirs. Downing et al. (1990) found that fish community production was correlated with annual phytoplankton production, mean total phosphorus concentrations, and annual average fish standing stock. Hanson and Leggett (1982) found that both fish biomass and yield were predicted by lake total phosphorus concentrations as well as by the ratio of macrobenthos biomass to lake mean depth. Lee et al (1991) reanalyzed the data of Oglesby (1977) and Hanson and Leggett (1982) and found a strong correlation between fish yield and normalized phosphorus loading to lakes. In Florida, Kautz (1980) found that total fish biomass increases with trophic state as measured

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Fig. 1. Location of lakes sampled for this study.

by total nitrogen concentrations. Bays and Crisman (1983) found a similar relationship with algal chlorophylls. The overwhelming evidence from these and other studies is that, as lakes become more eutrophic, the standing crops, productivity, and yields of fish increase. Ryding and Rast (1989) cite this as one of the positive properties of eutrophication in relation to the production of fish for food. In addition to the studies based on standing crops or commercial fish yields, Jones and Hoyer (1982) found that the yields of sport fish to angler harvest in 26 lakes and reservoirs in Iowa and Missouri were highly correlated to mean summer phytoplankton standing crop as measured by chlorophyll *a*.

Conversely, there are many observations in the literature that suggest that, as eutrophication proceeds, there is a decline in the quality of a fishery in terms of species composition. Larkin and Northcote (1969) reviewed a number of studies showing changes in fish populations as a result of eutrophication. These included changes in the fish fauna of Lake Erie coincident with eutrophication, the loss of *Coregonus* from Lake Muritz in northern Germany, and the loss of whitefish in the Bodensee. In a recent review of the literature on eutrophication and fisheries, Lee et al (1991) agree that eutrophication can significantly affect the types of fish in a water body. They cite various studies showing a decline in species richness in response to an increase in trophic state. Persson et al. (1988) showed that, in going from the least productive to the most productive in a series of Swedish lakes, there was a major decrease in the proportion of piscivorous fish. In his study of 22 lakes in Florida, Kautz (1980) concluded that sport fishes reach maximum biomass and optimum densities in mesotrophic–eutrophic lakes but suffer adverse effects with further enrichment.

Many of these previous studies have been carried out on deep, northern lakes with different fish communities from those in Florida. The results may not directly apply to shallower lakes in a warmer climate. The purpose of our study was to examine data on trophic indicators and fish populations

from a large sample of Florida lakes to determine the relationships between lake trophic state and the total biomass, species richness, species composition, and standing crops of fish.

Methods

Fish sampling

Most of the data were collected on 60 Florida lakes (Fig. 1) that were sampled specifically to develop empirical relationships between fish and trophic state variables (Canfield and Hoyer 1992). Ten to 17 lakes were sampled each year between June 1986 and June 1990. The lakes encompassed a range of trophic states and included lakes within the major trophic categories (oligotrophic, mesotrophic, eutrophic, and hypereutrophic) following the guidelines of Forsberg and Ryding (1980). Rotenone sampling for fish was conducted once during the warm season (May–November) at each lake to determine standing crop and community structure. Two to twelve 0.08-ha blocknets were set at each lake depending on lake size. The majority of lakes were sampled with six nets, but Little Fish Pond (surface area 2 ha) was sampled with only 2 nets while Lake Apopka (surface area >12 000 ha) was sampled with 12 nets. Equal numbers of blocknets were set in littoral (with one side being the shore) and limnetic habitats. Blocknet sampling followed procedures outlined by Shireman et al. (1983). Biomass (kilograms per hectare) estimates were calculated for each fish species in each net and weighted by habitat (littoral and open-water area) to obtain whole-lake estimates.

Each lake was also sampled by gillnets and electrofishing to provide additional information on fish species composition. Three experimental gillnets were fished in the majority of lakes, but six nets were set in Lake Apopka. Nets were fished along the bottom in water depths >2 m once for 24 h during the summer sampling period. Gillnets were 50 × 2.4 m and each gillnet had five 10-m panels of different mesh size (bar mesh sizes: 19, 25, 38, 51, and 76 mm). Electrofishing was conducted at each lake once during the warm season sampling period in nearshore areas in all habitats. Two to 10 electrofishing samples (10 min transects) were taken at each lake depending on lake size. Six samples were taken at most of the lakes, but only two samples were taken at Little Fish Pond (lake surface area 2 ha). Ten samples were taken from Lake Harris (lake surface area 5580 ha). Electrofishing transects were evenly spaced around each lake and electrofishing was done for 10 min with continuous current.

For Lake Okeechobee, data were obtained from fish population surveys made by the Florida Game and Fresh Water Fish Commission (Fox et al. 1992). Fish assemblages were sampled for biomass in five vegetation communities in the northern, southern, and western regions of the lake. Sampling was carried out in the fall seasons of 1989, 1990, and 1991. Three blocknets, 3.4 m deep with 3-mm bar mesh and encompassing 0.08 ha, were set in each vegetation community in each sample area during each year. Three Wegner rings (4.0 m²) (Wegner et al. 1973) were randomly placed within each blocknet to estimate abundance of fish less than 6 cm total length (Miller et al. 1990). Emulsified rotenone (5%) was applied within the net at a concentration of 2 mg·L⁻¹, and fish were picked up for 3 days. Percentages of fish collected on the second and third day in similar vegetation types were used to adjust numbers of fish collected in Wegner rings removed after the first day. Collected fish were sorted by species, divided into 2-cm size-classes (i.e., 4-cm group, 4.00–5.99 cm), enumerated, and weighed to the nearest gram. Second- and third-day weights were assigned from length–weight tables derived from first-day weights.

Although no fish biomass samples were taken from the open-water areas of Lake Okeechobee, trawl sampling data were used to check the fish species list (Fox et al. 1992). A 4.88-m, semiballoon trawl net having 35-mm stretched mesh in the wings and 25-mm stretched mesh in the bag was fished in July and January of each year beginning

Table 1. Total number of fish species, whole lake fish standing crop, littoral zone fish standing crop, total phosphorus (TP), total nitrogen (TN), chlorophyll *a* (Chl *a*), Secchi depths (SD), mean depths (Z), and surface areas (SA) for 65 Florida lakes.

Lake	No. of fish species	Standing crop		TP ($\mu\text{g}\cdot\text{L}^{-1}$)	TN ($\mu\text{g}\cdot\text{L}^{-1}$)	Chl <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	SD (m)	Z (m)	SA (ha)
		Whole lake ($\text{kg}\cdot\text{ha}^{-1}$)	Littoral zone ($\text{kg}\cdot\text{ha}^{-1}$)						
Okeechobee	41		372	92	1480	30	0.5	2.7	173 000
Crescent	44		284	30	1100	34	0.6		6 290
George	42		379	56	1400	79	0.7		18 600
Istokpoga	31		219	210	700	10	0.9	1.8	11 207
Tohopekaliga	34		507	138	1535	44	0.8	2.0	9 194
Alligator	18	112	211	371	2367	84	0.5	1.1	137
Apopka	24	24	81	140	3789	127	0.3	1.6	12 412
Baldwin	19	65	361	21	530	18	1.6	4.5	80
Barco	9	7	11	2	82	1	5.4	4.4	13
Bell	16	44	63	17	641	20	1.5	2.7	32
Bivens Arm	12	683	326	384	3256	241	0.4	1.2	76
Bonny	16	79	420	59	1858	40	0.6	2.0	143
Brim Pond	6	103	80	9	624	8	2.2	4.0	3
Bull Pond	22	69	117	11	522	3	1.4	2.3	11
Carlton	25	308	749	92	3228	173	0.4	3.6	155
Carr	15	207	8	19	874	11	1.8	1.9	254
Catherine	17	103	91	2	303	2	3.2	3.2	41
Clay	7	136	85	7	356	4	4.0	2.3	5
Clear	12	41	227	21	761	21	1.3	5.9	64
Conine	20	179	174	1043	2056	110	0.5	3.5	96
Crooked	12	106	113	7	313	5	3.1	2.3	8
Cue	6	10	44	5	91	2	5.8	3.5	59
Deep	17	88	89	2	158	1	5.1	3.0	4
Douglas	17	81	81	11	1122	2	1.5	1.2	16
Fish	21	129	210	25	935	18	1.0	1.9	89
Gate Lake	14	69	82	28	407	20	1.1	1.8	8
Grasshopper	21	135	161	6	259	1	3.7	2.7	59
Harris	34	109	206	28	1550	37	0.6	4.0	5 580
Hartridge	21	47	44	11	485	4	2.3	3.4	176
Holden	16	84	258	44	1226	64	0.5	4.5	102
Hollingsworth	16	150	1046	113	2517	135	0.3	1.5	144
Hunter	18	414	444	98	1723	82	0.5	1.7	340
Keys Pond	10	27	41	2	208	1	5.3	2.9	5
Killarny	18	230	403	21	603	22	1.0	4.7	96
Koon	23	46	45	5	687	3	1.4	1.5	44
Lawbreaker	4	32	42	1	108	1	5.5	4.3	5
Lindsey	13	78	167	19	636	6	1.9	2.2	55
Little Fish	8	240	251	21	1161	13	1.4	1.2	2
Live Oak	23	27	81	13	389	9	2.6	3.0	152
Lochloosa	29	149	160	32	1053	22	1.0	1.8	2 309
Loften	10	56	57	5	633	2	2.5	2.6	5
Marianna	21	193	244	26	1054	21	1.3	3.8	204
Mill Dam	29	42	36	11	462	4	2.7	5.7	85
Miona	24	63	62	12	867	8	1.5	2.3	169
Moore	15	42	96	5	353	3	5.3	2.9	28
Mountain	14	135	185	37	813	10	1.7	1.6	51
Mountain 2	17	47	193	17	331	2	2.4	3.3	55
Okahumpka	25	95	68	21	1033	11	1.4	0.9	271
Orienta	17	190	232	25	448	9	2.2	3.4	52
Pasadena	16	115	111	15	702	3	2.2	3.1	151
Patrick	25	170	173	10	1808	5	2.0	1.8	159
Pearl	20	84	111	28	819	228	0.9	2.0	24
Picnic	11	48	51	8	137	1	2.6	3.3	18
Round Pond	9	135	126	3	444	3	2.6	1.3	4

Table 1 (concluded).

Lake	No. of fish species	Standing crop		TP ($\mu\text{g}\cdot\text{L}^{-1}$)	TN ($\mu\text{g}\cdot\text{L}^{-1}$)	Chl <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	SD (m)	Z (m)	SA (ha)
		Whole lake ($\text{kg}\cdot\text{ha}^{-1}$)	Littoral zone ($\text{kg}\cdot\text{ha}^{-1}$)						
Rowell	30	463	615	66	910	47	0.8	1.3	147
Suggs	20	19	12	66	1249	4	0.5	2.0	73
Susannah	19	217	470	23	674	25	1.5	3.9	31
Swim Pond	15	60	61	25	1025	11	0.6	0.6	9
Thomas	13	98	147	22	759	10	1.8	3.9	55
Tomahawk	13	84	99	6	192	1	4.2	4.4	15
Turkey Pen	10	52	71	2	132	1	3.2	5.0	6
Wales	15	51	42	27	899	42	0.8	3.4	132
Watertown	18	147	290	27	777	24	1.0	3.8	19
Wauberg	22	674	464	166	1478	102	0.6	3.6	100
West Moody	18	170	220	14	584	2	2.8	3.5	39
Mean	18	131	200	60	949	32	2	3	3 733
Median	17	92	147	21	759	10	1.45	2.7	59
Maximum	41	683	1046	1043	3789	241	5.8	5.9	173 000
Minimum	4	7	8	1	82	1	0.3	0.6	1.8

Note: For lakes Okeechobee, Crescent, George, Istokpoga, and Tohopekaliga the water chemistry is based on open-water samples and for the other lakes it is an average of open-water and littoral zone samples. Sampling was done between 1986 and 1992.

Table 2. Slopes and intercepts for regression equations and Pearson's correlations (r^2) between the trophic state variables total phosphorus (TP; $\text{mg}\cdot\text{m}^{-3}$), total nitrogen (TN; $\text{mg}\cdot\text{m}^{-3}$), chlorophyll *a* (Chl *a*; $\text{mg}\cdot\text{m}^{-3}$), and Secchi disk depth (SD; m) in 65 Florida lakes.

Y-variable	X-variable	Slope	Intercept	r^2
Log ₁₀ Chl <i>a</i>	Log ₁₀ TP	0.887	-0.174	0.73
Log ₁₀ Chl <i>a</i>	Log ₁₀ TN	1.405	-2.985	0.69
Log ₁₀ TN	Log ₁₀ TP	0.498	2.180	0.66
Log ₁₀ SD	Log ₁₀ Chl <i>a</i>	-0.466	0.617	0.78
Log ₁₀ SD	Log ₁₀ TP	-0.473	0.779	0.75
Log ₁₀ SD	Log ₁₀ TN	-0.790	2.394	0.78

in July 1987 and continuing through January 1991. In July 1987, one 10-min haul was taken at each of 25 open-water sites. In all subsequent sampling periods, two 10-min hauls were made at 27 sites, although some stations were missed during low-water periods in July 1990.

To add more large lakes to the data set, we also used fish biomass data (Eisenhauer et al. 1993; Moxley et al. 1993; Moyer et al. 1992, 1993) collected by the Florida Game and Fresh Water Fish Commission in the littoral areas of lakes Crescent, George, Istokpoga, and Tohopekaliga (Fig. 1). In the fall of both 1990 and 1991, eight littoral, standard rotenone blocknet samples (0.1 ha) were taken from Lake Crescent and four from Lake George. Data for species composition were also obtained from two fall 0.4-ha limnetic blocknet samples taken in both years on Lake George. Fish biomass data from Lake Istokpoga and Lake Tohopekaliga were obtained from six (0.4 ha) littoral rotenone blocknet sites taken from August 1988 through August 1991 and fall 1990, 1991, and 1992, respectively. Additional information on species composition was obtained by electrofishing, gill nets, and Wegner rings.

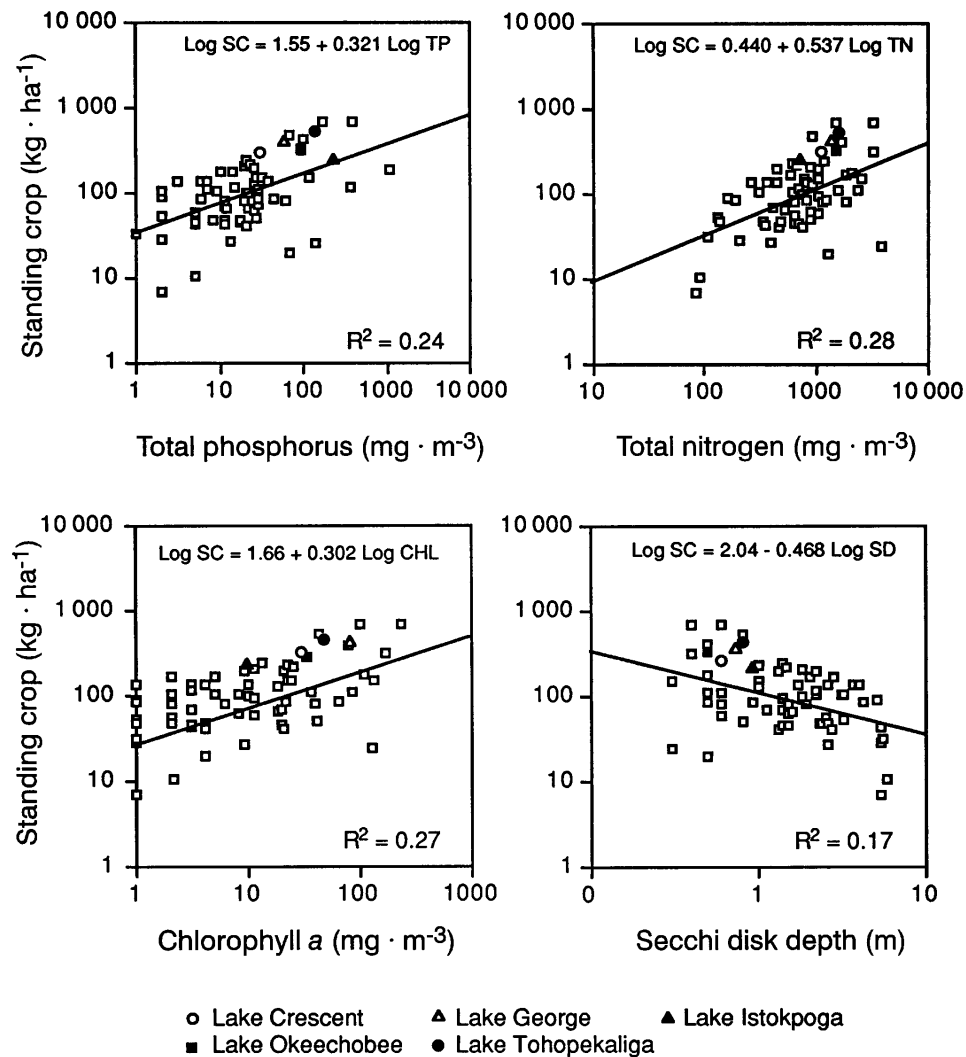
We examined the potential effect of increasing lake trophy on species richness, defined as the number of different species of fish collected in each lake. First, we examined the cumulative number of fish species encountered in each lake as fishing effort increased to assess the likelihood that more sampling would add additional species. For the 60 lakes sampled by Canfield and Hoyer (1992), we constructed curves showing the cumulative numbers of fish species obtained as progressively more blocknets were fished. For each spe-

cies in each lake, we used our catch records to determine the number of nets in which the species was found out of the total number of nets set. We then determined the probability that the species would be encountered for the first time in the first, second, third, and other nets set following the basic laws of probability (Dietrich and Kearns 1986). The expected frequencies for each species for each net were then summed to derive a curve of species found versus sampling effort. In each case the greatest increases in numbers of species found are in the first few nets with relatively little increase in the number of species caught as the last net is fished. As a measure of the flatness of the right-hand portion of the curve, the numbers of species seen after the next to last net was fished were expressed as a percentage of the number of species found after the last net was examined. In 41 of the 60 lakes, 95–100% of the species found in all nets were found by the next-to-last net. In only three cases was the value less than 90%. However, in addition to the species found in these blocknets, fish were also collected by gillnets and electroshocking to search for species that may have been missed.

For the five lakes sampled by the Florida Game and Freshwater Fish Commission, we compiled the cumulative numbers of species collected by all means for each year of sampling. For lakes Okeechobee, Istokpoga, and Tohopekaliga, 40 of 41, 30 of 31, and 32 of 34, respectively, of the species found were noted before the last year of sampling. Lakes Crescent and George were only sampled in 2 years with 36 of 44 and 38 of 42 of the species being found in the first year. We might expect to find a few more species in the latter two lakes with more sampling. It is noted that several marine species were found in these two lakes as a result of their close connection with the St. Johns River estuary and that they had more fish species than any of the other lakes in our study.

To assess whether trophic state played a role in determining the presence or absence of a fish species in lakes of a particular trophic state, we divided our lakes into four groups based on chlorophyll *a* concentrations in the water following the guidelines of Forsberg and Ryding (1980). Oligotrophic lakes had less than 3 $\text{mg}\cdot\text{m}^{-3}$ of chlorophyll *a* ($n = 14$); mesotrophic, 3–7 $\text{mg}\cdot\text{m}^{-3}$ ($n = 12$); eutrophic, 7–40 $\text{mg}\cdot\text{m}^{-3}$ ($n = 26$); and hypereutrophic, >40 $\text{mg}\cdot\text{m}^{-3}$ ($n = 13$). A chi-square test was used to determine if trophic state played a significant role in determining fish distribution in lakes. Many of the fish were found in fewer than 20 lakes, making the sample size too small for a valid chi-square test. Thus, we further grouped the lakes

Fig. 2. Fish standing crops ($\text{kg}\cdot\text{ha}^{-1}$) in relation to total phosphorus, total nitrogen, chlorophyll *a*, and Secchi disk transparency for 65 Florida lakes. The regression lines and r^2 values are based on the 60 lakes with whole-lake estimates of standing crops. The points for the five large lakes represent littoral fish standing crops only and are included for comparative purposes.



into oligotrophic-mesotrophic lakes and eutrophic-hypereutrophic lakes and tested to see if the frequencies of presence or absence were randomly distributed between the two groups. If any of the expected frequencies were less than five, we used the Fisher exact probability test (Siegel 1956) to test for significant differences in distributions.

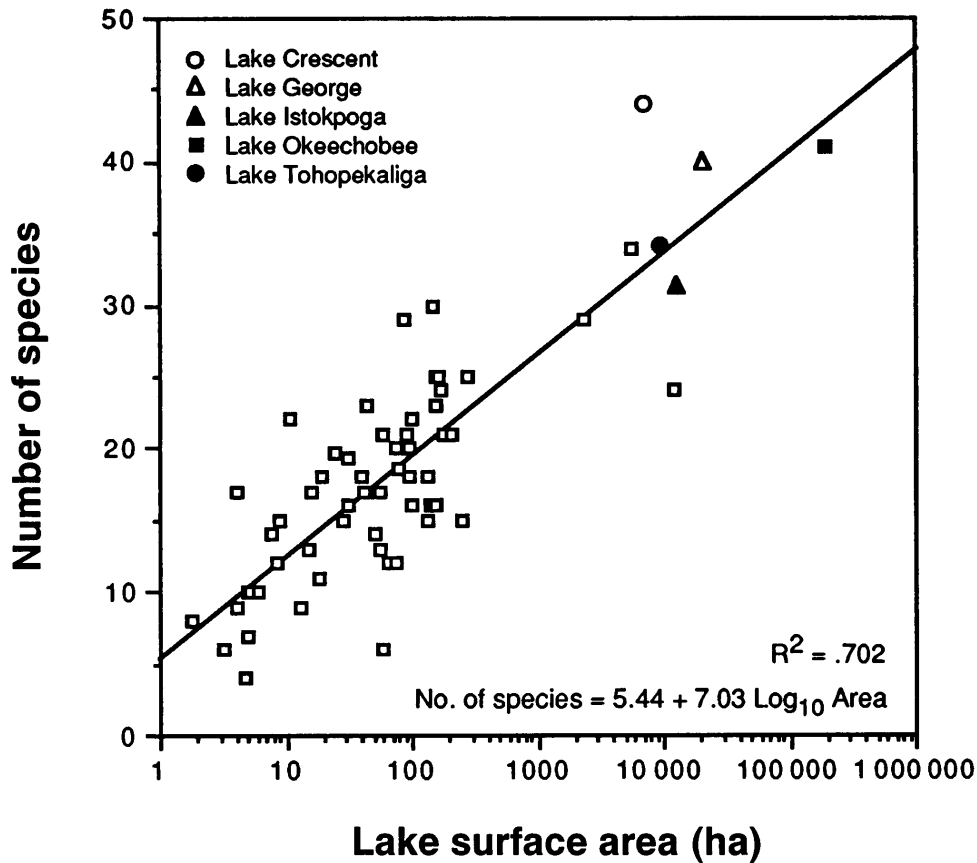
To determine the effects of lake trophic state on the standing crops of individual fish species in the 60 lakes with weighted averages for fish standing crops, we determined the average standing crop for each species in each of the four trophic state categories. If a species was missing in a lake, its standing crop was included as zero. A one-way analysis of variance was used to determine if there were significant differences in the standing crops among the four trophic categories.

To test the idea that the proportion of piscivorous species declines with increasing trophic state (Persson et al. 1988), we calculated the percent of the total fish biomass that consisted of piscivorous fish for the 60 lakes that had both littoral and open-water samples. Those fish considered piscivorous as adults were classified on the basis of the works by Pflieger (1975), Lee et al. (1981), and Becker (1983) and included Florida gar (*Lepisosteus platyrhincus*), longnose gar (*Lepisosteus osseus*), bowfin (*Amia calva*), chain pickerel (*Esox niger*), redbfin pickerel (*Esox americanus americanus*), Atlantic

needlefish (*Strongylura marina*), black crappie (*Pomoxis nigromaculatus*), and largemouth bass (*Micropterus salmoides*). Proportions should be useful in detecting relative changes in piscivorous activity; whereas absolute values would be overestimates because these species also feed on other food items.

Because of their importance to the sport fishery, we also calculated the weight of all centrarchids and largemouth bass in each lake's sample (as kilograms per hectare and as percentages of the total fish weight). For five important sport fish species we used the length-frequency data from the blocknet samples from the 60 lakes with weighted means of open-water and littoral fish to calculate relative stock densities (RSD-Q) for quality or larger fish following Gabelhouse (1984). For the warmouth (*Lepomis gulosus*) in each lake we divided the number of fish in the sample 15 cm or greater in length by the number greater than 8 cm long. The resulting RSD-Q value represents the proportion of the stock fish (those fish greater than 8 cm) that are of quality size (15 cm) or greater. The same lengths were used for the bluegill (*Lepomis macrochirus*) calculations. For the redear sunfish (*Lepomis microlophus*) we divided the number of fish larger than 18 cm by those greater than 12 cm; for the black crappie, the number greater than 20 cm by those greater than 12 cm;

Fig. 3. Relationship between the number of species of fish per lake and the logarithm of lake surface area.



and for the largemouth bass, the number of fish greater than 32 cm by those greater than 20 cm. These are the same or close to the minimum sizes suggested by Gabelhouse (1984).

Water quality

For the 60 Florida lakes sampled by Canfield and Hoyer (1992), six water-quality sampling stations were established at each lake. Summer water samples were collected from six stations (three each in the littoral and pelagic zones) on a single date at the time the fish populations were sampled. Additional samples were collected from the three pelagic stations on two subsequent dates. Secchi disk measurements were made only at the open-water stations. Water was collected from just below the surface (0.5 m) in acid-cleaned Nalgene bottles. Samples were placed on ice and returned to the laboratory for analysis. The measurements that are used in this analysis included total phosphorus, determined with the methods of Murphy and Riley (1962) after persulfate oxidation (Menzel and Corwin 1965); total nitrogen, determined by a modified Kjeldahl technique (Nelson and Sommers 1975); and total chlorophyll *a* concentrations (uncorrected for phaeophytins), determined by filtering a measured portion of lake water through a Gelman type A-E glass fiber filter and then following the method of Yentsch and Menzel (1963) and the equations of Parsons and Strickland (1963).

Surface water samples (0.5 m) were collected from eight open-water stations in Lake Okeechobee. Secchi disk readings were made at the same time and sample analyses included total phosphorus, total nitrogen, and chlorophyll *a*. The station locations and analytical methods are discussed in James et al. (1995). The stations were sampled at least monthly and sometimes twice a month. For this study we calculated monthly averages for each variable for each station and then averaged the station means to find a lake average for each

month. The lake average was taken as the mean of the monthly averages for the years 1989 through 1991. Water-quality data from the open waters of the other four large lakes were based on records and published reports of the Florida Game and Fresh Water Fish Commission (Moyer et al. 1992, 1993; Lange et al. 1993).

Statistical analysis

For tests of the effects of trophic state on fish standing crops in regression analyses, logarithms of total phosphorus, total nitrogen, algal chlorophyll *a*, and Secchi disk depth were used because these variables span several orders of magnitude and their expected errors increase with magnitude. Both linear and curvilinear fits were tried. The parametric statistical analyses (paired *t*-tests, bivariate correlation coefficients, and analysis of variance) were run according to Snedecor and Cochran (1980) using the JMP statistical package (SAS Institute 1994). Multiple regressions were run with the stepwise, forward selection mode (SAS Institute Inc. 1985). Chi-square analyses followed the procedures given in Siegel (1956). The 5% level of confidence was used to reject null hypotheses in all cases.

Results

Two-way analysis of variance showed no differences ($p < 0.05$) in concentrations of total phosphorus, total nitrogen, and chlorophyll *a* from open-water samples, littoral area samples, and averages of the two for the 60 original lakes. No differences ($p < 0.05$) were found in a comparison of our open-water samples from Lake Okeechobee and littoral samples (Phlips et al. 1993) from that lake. Thus, either littoral samples

Table 3. Fish species collected in 65 Florida lakes ranked by frequency of occurrence.

Common name	Scientific name	No. of lakes	TP ($\mu\text{g}\cdot\text{L}^{-1}$)	CHL <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	TN ($\mu\text{g}\cdot\text{L}^{-1}$)	Surface area (ha)	Standing crop		Lake size effect	Trophic state effect
							Whole lake ($\text{kg}\cdot\text{ha}^{-1}$)	Littoral only ($\text{kg}\cdot\text{ha}^{-1}$)		
Bluegill	<i>Lepomis macrochirus</i>	64	57	29	938	413	38.102		None	None
Largemouth bass	<i>Micropterus salmoides</i>	64	57	29	938	413	15.102		None	None
Warmouth	<i>Lepomis gulosus</i>	63	57	28	934	418	8.639		None	None
Mosquitofish	<i>Gambusia holbrooki</i>	51	68	33	1023	504	0.274		None	None
Redear sunfish	<i>Lepomis microlophus</i>	50	73	37	1132	537	15.067		More	More
Golden shiner	<i>Notemigonus crysoleucas</i>	47	76	38	1177	571	5.321		More	More
Brook silverside	<i>Labidesthes sicculus</i>	47	53	27	939	542	0.138		None	None
Lake chubsucker	<i>Erimyzon sucetta</i>	42	27	12	735	284	11.751		None	Less
Black crappie	<i>Pomoxis nigromaculatus</i>	42	84	42	1192	634	4.840		More	More
Swamp darter	<i>Etheostoma fusiforme</i>	40	31	14	724	283	0.033		None	None
Brown bullhead	<i>Ictalurus nebulosus</i>	34	95	43	1229	784	2.802		More	More
Yellow bullhead	<i>Ictalurus natalis</i>	33	32	29	961	737	1.290		None	None
Seminole killifish	<i>Fundulus seminolis</i>	32	79	42	1142	822	0.628		None	More
Golden topminnow	<i>Fundulus chrysotus</i>	32	22	11	688	156	0.344		None	Less
Bluespotted sunfish	<i>Enneacanthus gloriosus</i>	29	22	17	846	407	1.779		More	None
Bluefin killifish	<i>Lucania goodei</i>	29	26	20	814	414	0.729		More	None
Threadfin shad	<i>Dorosoma petenense</i>	26	82	40	1195	1 003	20.940		More	More
Gizzard shad	<i>Dorosoma cepedianum</i>	25	123	67	1599	1 104	66.074		More	More
Florida gar	<i>Lepisosteus platyrhincus</i>	25	47	23	883	480	2.682		More	None
Spotted sunfish	<i>Lepomis punctatus</i>	24	107	40	1169	522	2.626		More	More
Dollar sunfish	<i>Lepomis marginatus</i>	24	23	15	795	366	1.212		None	None
Bowfin	<i>Amia calva</i>	20	57	26	1015	240	4.830		More	None
Least killifish	<i>Heterandria formosa</i>	19	40	12	712	173	0.084		None	None
Lined topminnow	<i>Fundulus lineolatus</i>	19	10	6	422	43	0.190		Less	Less
Blue tilapia	<i>Tilapia aurea</i>	18	152	80	1818	1 380	12.731		More	More
Tadpole madtom	<i>Noturus gyrinus</i>	16	43	28	1128	1 468	0.279		More	None
White catfish	<i>Ictalurus catus</i>	15	122	40	1353	1 760	1.085		More	More
Taillight shiner	<i>Notropis maculatus</i>	15	67	61	1598	1 915	0.673		More	More
Sailfin molly	<i>Poecilia latipinna</i>	15	44	42	1316	1 919	0.085		More	More
Chain pickerel	<i>Esox niger</i>	13	17	11	728	332	4.232		None	None
Grass carp	<i>Ctenopharyngodon idella</i>	12	44	39	1170	1 096	17.211		None	None
Redfin pickerel	<i>Esox americanus americanus</i>	12	16	7	649	572	1.035		None	Less
Everglades pygmy sunfish	<i>Elassoma evergladei</i>	11	54	19	619	45	0.033		None	Less
Atlantic needlefish	<i>Strongylura marina</i>	8	87	112	2856	6 049	0.906		More	More
Flagfish	<i>Jordanella floridae</i>	8	20	7	800	136	0.347		More	None
Redbreast sunfish	<i>Lepomis auritus</i>	7	53	66	1570	1 176	1.419		None	None
Bream	<i>Lepomis</i> sp.	6	180	96	1976	156	1.267		None	None
Shiners	<i>Notropis</i> sp.	6	75	27	1094	993	0.120		None	None
Longnose gar	<i>Lepisosteus osseus</i>	5	81	102	2942	4 242	0.016		More	None
Pygmy killifish	<i>Leptolucania ommata</i>	5	9	4	503	31	0.002		None	None
Pirate perch	<i>Aphredoderus sayanus</i>	4	42	19	975	643	0.106		None	None
Striped mullet	<i>Mugil cephalus</i>	3	161	48	2477	65 963		52.537	None	None
Channel catfish	<i>Ictalurus punctatus</i>	3	144	24	2227	63 499		5.447	None	None
American eel	<i>Anguilla rostrata</i>	3	27	24	777	19	3.211		None	None
Sunshine bass	<i>Morone chrysops</i> × <i>Morone saxatilis</i>	3	87	112	2856	6 049	0.466		None	None
Flier	<i>Centrarchus macropterus</i>	3	22	16	853	792	0.185		None	None
Ladyfish	<i>Elops saurus</i>	2	195	56	2975	12 445		0.450	None	None
Hogchoker	<i>Trinectes maculatus</i>	2	195	56	2975	12 445		0.350	None	None
Clown goby	<i>Microgobius gulosus</i>	2	111	32	2990	89 645		0.211	None	None
Bay anchovy	<i>Anchoa mitchilli</i>	2	195	56	2975	12 445		<0.100	None	None
Sheepshead minnow	<i>Cyprinodon variegatus</i>	1	92	30	1480	173 000		0.310	None	None
Snook	<i>Centropomus undecimalis</i>	1	92	30	1480	173 000		0.179	None	None

Table 3 (concluded).

Common name	Scientific name	No. of lakes	TP ($\mu\text{g}\cdot\text{L}^{-1}$)	CHL <i>a</i> ($\mu\text{g}\cdot\text{L}^{-1}$)	TN ($\mu\text{g}\cdot\text{L}^{-1}$)	Surface area (ha)	Standing crop			Trophic state effect
							Whole lake ($\text{kg}\cdot\text{ha}^{-1}$)	Littoral only ($\text{kg}\cdot\text{ha}^{-1}$)	Lake size effect	
Blackbanded sunfish	<i>Enneacanthus chaetodon</i>	1	11	4	462	85	0.104		None	None
Grey snapper	<i>Lutjanus griseus</i>	1	130	34	4500	6 290		0.100	None	None
Naked goby	<i>Gobiosoma bosc</i>	1	130	34	4500	6 290		0.100	None	None
Inland silversides	<i>Menidia beryllina</i>	1	92	30	1480	173 000		0.092	None	None
Pugnose minnow	<i>Opsopoeodus emiliae</i>	1	92	30	1480	173 000		0.006	None	None
Opossum pipefish	<i>Micropphis brachyurus</i>	1	92	30	1480	173 000		0.002	None	None
Walking catfish	<i>Clarias batrachus</i>	1	92	30	1480	173 000		0.002	None	None
Atlantic croaker	<i>Micropogonias undulatus</i>	1	130	34	4500	6 290		<0.100	None	None
Silver jenny	<i>Eucinostomus gula</i>	1	130	34	4500	6 290		<0.100	None	None
American shad	<i>Alaso sapidissima</i>	1	260	79	1450	18 600		<0.100	None	None
Atlantic stingray	<i>Dasyatis sabina</i>	1	260	79	1450	18 600		<0.100	None	None
Gulf pipefish	<i>Syngnathus scovelli</i>	1	260	79	1450	18 600		<0.100	None	None
Pugnose shiner	<i>Notropis anogenus</i>	71	260	79	1450	18 600		<0.100	None	None

Note: For the lakes in which they were found, average values are given for the trophic state indicators total phosphorus (TP), chlorophyll *a* (Chl *a*), total nitrogen (TN), lake surface areas and whole lake standing crops (based on both littoral and open-water blocknets). For six of the lakes only littoral standing crop data are available. Chi-square or Fisher exact probability tests were used to determine if fish species were more or less abundant in larger rather than smaller lakes or in eutrophic-hypertrophic lakes rather than oligotrophic-mesotrophic lakes. More, significant increase; less, significant decrease; none, no difference.

or a combination of littoral and open-water samples can be used to characterize lakes in a broad survey of this type.

Total phosphorus, total nitrogen, and chlorophyll *a* concentrations ranged over two or three orders of magnitude (Table 1). For example, chlorophyll *a* ranged from 1 to 241 $\text{mg}\cdot\text{m}^{-3}$. There were no significant correlations between the trophic state indicators and lake mean depth. This probably results from the very small range of mean depths in these Florida lakes (0.6–5.8 m; Table 1). There was a tendency for the larger lakes to be more eutrophic. We found weak positive correlations ($p < 0.05$) between total phosphorus, total nitrogen, and chlorophyll *a* with the logarithms of surface area ($r^2 = 0.09, 0.26, \text{ and } 0.09$, respectively) and a negative correlation with Secchi disk depth ($r^2 = 0.22$).

Chlorophyll *a* concentrations in these lakes were highly correlated ($p < 0.01$) with both total phosphorus and total nitrogen (Table 2). Because total phosphorus and total nitrogen were both correlated ($p < 0.01$) with each other (Table 2), these data do not indicate which is the limiting element. The Secchi disk transparency is highly correlated with chlorophyll *a*, total phosphorus, and total nitrogen ($p < 0.01$; Table 2). For these lakes as a group the chlorophyll *a* concentration largely determines the water transparency rather than suspended solids and humic materials, although there are exceptions in some individual lakes.

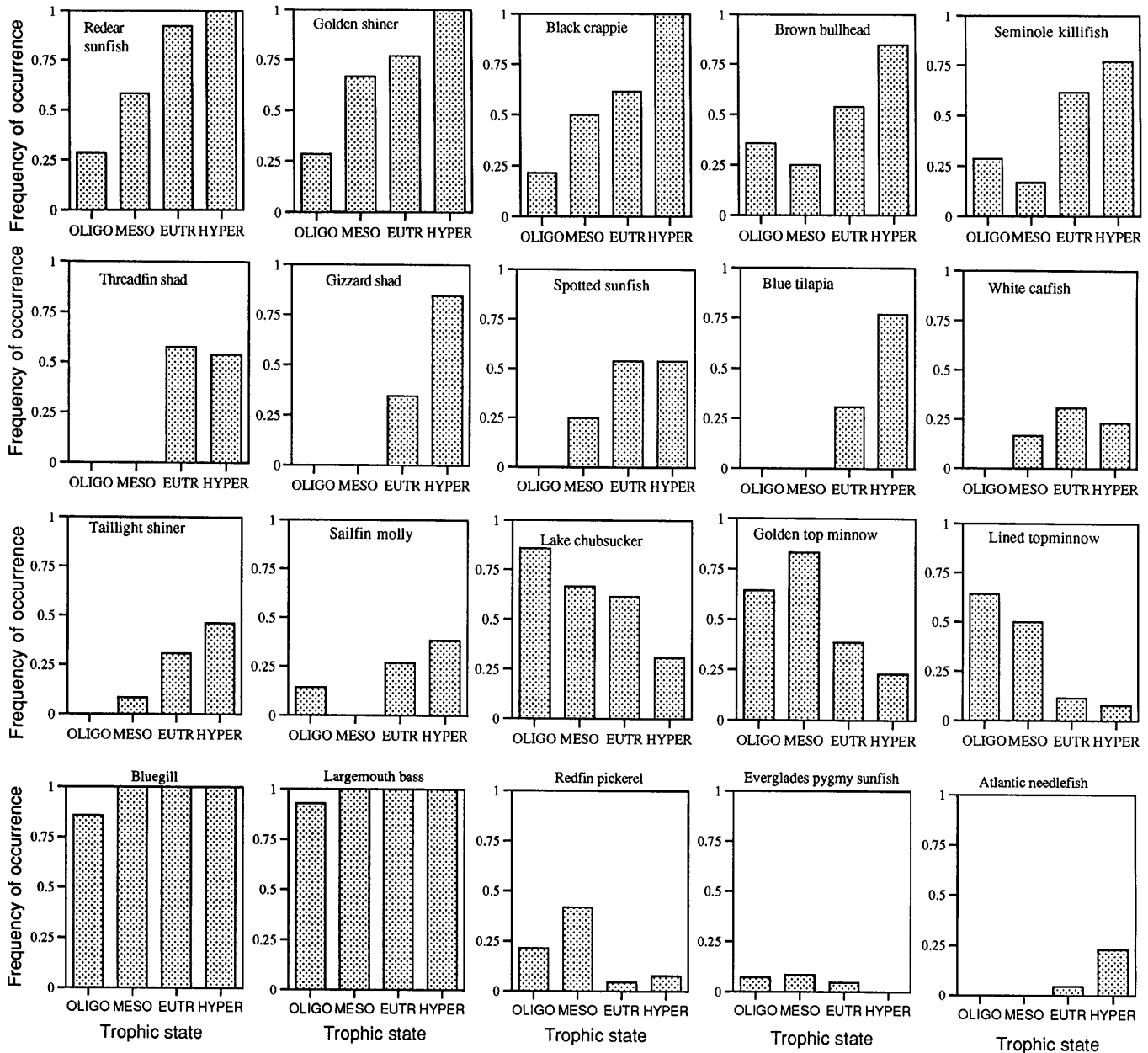
The standing crop of fish based on a weighted average of catches in both littoral and open-water blocknets averaged 131 $\text{kg}\cdot\text{ha}^{-1}$ (range 7–683 $\text{kg}\cdot\text{ha}^{-1}$). For the 60 lakes with both littoral and open-water data the standing crops of fish increased with increases in chlorophyll *a*, total phosphorus, and total nitrogen and decreased with increases in Secchi disk transparency (Fig. 2). The correlations were significant ($p < 0.01$) though the r^2 values (0.27, 0.24, 0.28, and 0.27, respectively) indicated that trophic state explained only about one fourth of the variance in fish crops. There was no significant correlation between the standing crop of fish and lake surface

area. Other factors and experimental error in sampling may be responsible for a great portion of the observed variance in the standing crop estimates. Five lakes only had estimates of littoral fish standing crops, so they were not included in the correlation analysis. The points for littoral fish crops in those five lakes are plotted in the same graphs, however, to illustrate that they fall within the same scatter as the points for the other 60 lakes (Fig. 2).

On average there were 18 species of fish in each lake (range 4–44 species; Table 1). The larger the lake the more species of fish that were found. Lake surface area (Fig. 3) explained 70% of the variance in species numbers. A number of marine species (e.g., Atlantic stingray (*Dasyatis sabina*), bay anchovy (*Anchoa mitchilli*), Atlantic croaker (*Micropogonias undulatus*), etc.) occurred in some of the larger lakes with oceanic connections. A reanalysis with those species removed still yielded an r^2 of 0.67. Species richness was weakly correlated with total phosphorus, total nitrogen, chlorophyll *a*, and Secchi depth ($r^2 = 0.05, 0.20, 0.03, \text{ and } 0.25$, respectively) with a positive relationship for the first three variables and a negative relationship for the Secchi disk transparency. However, in a stepwise, multiple regression in the forward mode using logarithms of surface area, total phosphorus, total nitrogen, chlorophyll *a*, and Secchi disk transparency as independent variables, log surface area was the only significant variable selected. There was no indication that the number of fish species declined with increasing trophic state in these lakes.

Sixty-five fish species were collected in the study lakes (Table 3). Bluegill, largemouth bass, warmouth, mosquitofish (*Gambusia holbrooki*), and redear sunfish were found in 75–98% of the lakes, whereas 15 other species were collected in only a single lake. Significant differences in their distributions between lakes of different trophic states were found for 18 species (Fig. 4). Thirteen of the fish species were more likely to be present in lakes of higher trophic states while only

Fig. 4. Fraction of lakes of different trophic state in which various species of fish were present. For each of these species, except the bluegill and largemouth bass, there was a significant difference between the fraction found in oligotrophic–mesotrophic lakes and the fraction found in eutrophic–hypereutrophic lakes.

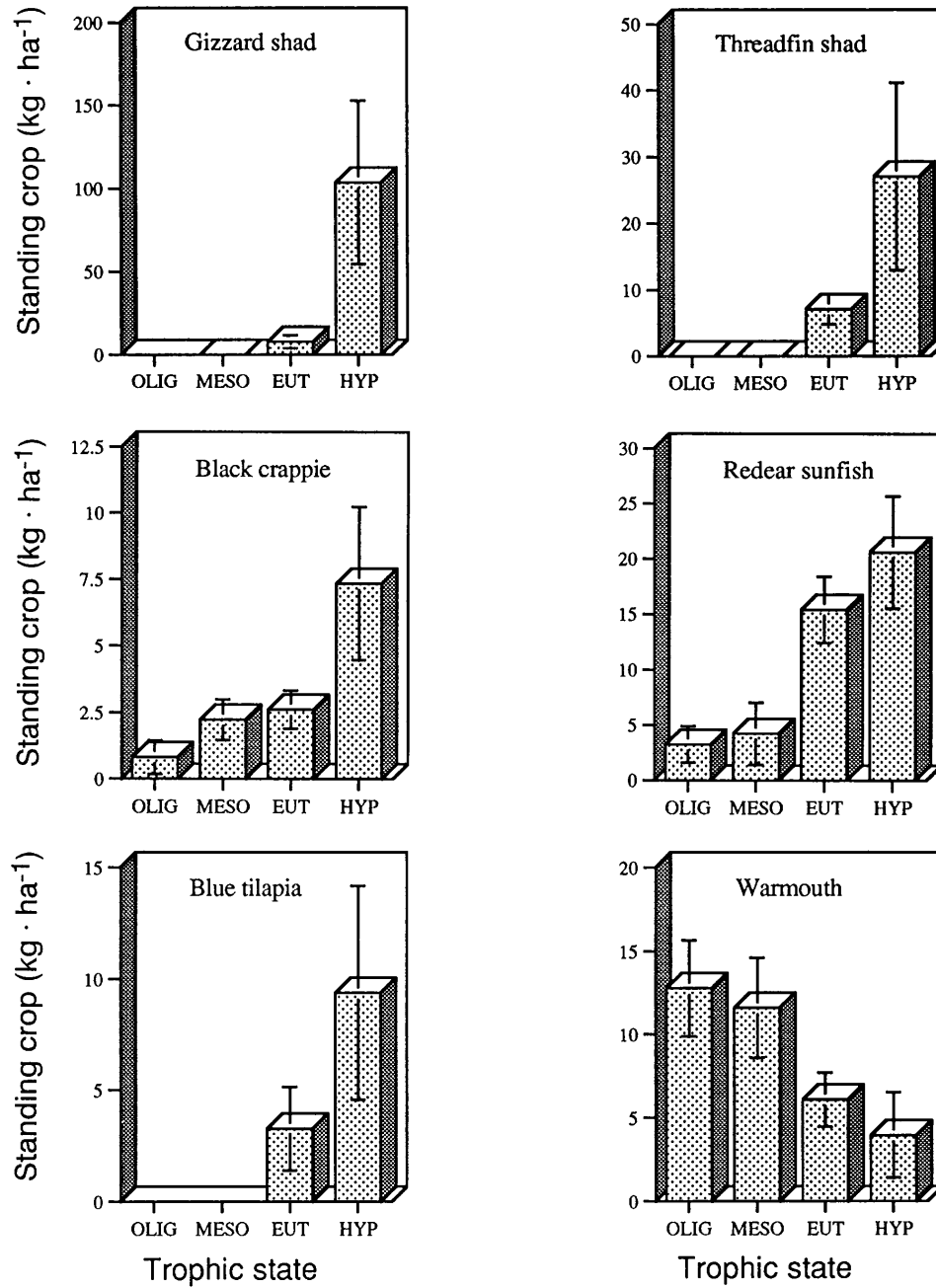


five species, the lake chubsucker (*Erimyzon sucetta*), golden topminnow (*Fundulus chrysotus*), lined topminnow (*Fundulus lineolatus*), redbfin pickerel, and Everglades pygmy sunfish (*Elassoma evergladei*), were less likely to be found in eutrophic–hypereutrophic lakes than oligotrophic–mesotrophic lakes (Table 3). Another indication of the trophic state preferences for these species can be derived by looking at the average values for the trophic state indicators for the lakes in which they were found (Table 3) relative to the averages for the entire sample (Table 1). For example, the redbfin pickerel was most commonly found in lakes with low nutrient concentrations while the blue tilapia (*Tilapia aurea*) was more likely to be in lakes with higher nutrient concentrations.

A similar test was made of the effect of lake size on the distribution of individual fish species. The lakes were divided into small lakes (<100 ha) and large lakes (>100 ha), and a chi-square or Fisher exact probability test (Siegel 1956) was used to test the distribution of presence or absence. Nineteen species were more likely to be found in large lakes while only one was more likely to be found in small lakes (Table 3). In most cases the fish most likely to be found in eutrophic–hypereutrophic lakes were the same species that were more likely to be found in large lakes. Because our larger lakes tended to be more eutrophic, it is not possible to sort out completely the effects of lake size and trophic state.

Standing crops of individual species increased with trophic

Fig. 5. Average standing crops with standard errors for fish in groups of lakes of different trophic state. For each of these species a one-way analysis of variance showed significant differences ($p < 0.05$) among standing crops for the four trophic categories.



state ($p < 0.05$) for the gizzard shad (*Dorosoma cepedianum*), threadfin shad (*Dorosoma petenese*), black crappie, redeer sunfish, and blue tilapia while the warmouth tended to have higher standing crops in lakes of lower productivity (Fig. 5). The increases in biomass for the gizzard shad, the threadfin shad, and the blue tilapia are particularly noteworthy. All were practically absent from oligotrophic–mesotrophic lakes (Fig. 4) but increased in both frequency of occurrence and average standing crop in eutrophic and especially hypereutrophic lakes (Fig. 5). The average standing crop for the gizzard shad for lakes in which it was found ($66 \text{ kg}\cdot\text{ha}^{-1}$) was the highest for all species encountered while the standing crop for

the threadfin shad ($21 \text{ kg}\cdot\text{ha}^{-1}$) ranked third behind the bluegill ($38 \text{ kg}\cdot\text{ha}^{-1}$). The blue tilapia showed a similar pattern in both frequency of occurrence (Fig. 4) and average standing crop (Fig. 5) as the two shad species.

The piscivorous species as a group averaged about 22% of the total fish biomass in our lakes and ranged from 0 to 73%. The absolute weights of the piscivore group tended not to change with increasing trophic state (Table 4). However, when expressed as a percentage of the total biomass the relative importance of this group declined as the lakes became more productive, though the r^2 values are quite small (0.03–0.12). On average the percentages of piscivorous species for

Table 4. Pearson's correlations (r^2) between several indices of lake trophic state and several measures of fish population composition and quality for the 60 Florida lakes with data on both open-water and littoral fish.

	Log total phosphorus	Log total nitrogen	Log chlorophyll <i>a</i>	Log Secchi depth
Total biomass minus shad	0.14**	0.14**	0.14**	(-) 0.07*
Weight of piscivores	0.01	0.06*	0.02	(-) 0.01
Weight of centrarchids	0.14**	0.14**	0.13**	(-) 0.06*
Weight of largemouth bass	(-) 0.01	(-) 0.00	(-) 0.00	0.00
Percentages based on total biomass				
Piscivores	(-) 0.09*	(-) 0.03	(-) 0.12**	0.07*
Centrarchids	(-) 0.10*	(-) 0.06*	(-) 0.19**	0.16**
Largemouth bass	(-) 0.21**	(-) 0.14**	(-) 0.17**	0.17**
Percentages based on total biomass minus biomass of shad				
Piscivores	(-) 0.02	(-) 0.00	(-) 0.02	0.01
Centrarchids	0.01	0.01	0.00	0.00
Largemouth bass	(-) 0.14**	(-) 0.10*	(-) 0.09*	0.11**
RSD-Q				
Black crappie	(-) 0.27**	(-) 0.35**	(-) 0.23**	0.23**
Bluegill	(-) 0.01	(-) 0.03	(-) 0.01	0.02
Largemouth bass	0.12**	0.16**	0.22**	(-) 0.10*
Redear sunfish	0.01	(-) 0.00	0.00	(-) 0.02
Warmouth bass	0.08*	0.04	0.14**	(-) 0.13**

Note: The percentages were calculated on both the total weight of fish and the total weight minus the weights of gizzard shad and threadfin shad. The minus signs in parentheses indicate negative relationships. The RSD-Q represents the proportion of the fish stock greater than a minimum size (see text). Curvilinear regressions were also tried, but they did not result in improved fits for these data.

*Significant at the 5% level.

**Significant at the 1% level.

oligotrophic, mesotrophic, eutrophic, and hypereutrophic lakes were 25, 28, 21, and 11%, respectively, of the total biomass. One of the most important piscivores, the largemouth bass, on average, made up 15% of the fish biomass with a range of from 0 to 69%. The absolute biomass of the largemouth bass showed no changes with trophic state (Table 4), though their percentage of the total biomass became less abundant at higher trophic states. On average the percentages of largemouth bass by weight in oligotrophic, mesotrophic, eutrophic, and hypereutrophic lakes were 20, 17, 16, and 4%, respectively, of the total biomass. The centrarchids, on average, made up 66% of the total biomass with a range from 15 to 99%. They likewise showed a pattern of increasing absolute biomass with increases in trophic state (Table 4) but decreasing in percent biomass in lakes of higher trophic states.

Because of the large increase in standing crops of gizzard shad and threadfin shad found in eutrophic and hypereutrophic lakes, we analyzed the data to see if these increases might be responsible for the drops in the relative proportions of the piscivores, centrarchids, and largemouth bass. The biomasses of these two shad species were subtracted from the total fish biomass to derive a new biomass total that did not include the shad species. This new total also showed increases with increases in trophic state (Table 4); however, both the percent piscivores and percent centrarchids now showed no correlation with trophic state while the percent largemouth bass continued to decrease in lakes at higher trophic levels. This suggests that the addition of large standing crops of gizzard and threadfin shad to the total fish biomass was responsible for the decrease in the proportions of the piscivores and centrarchids as groups.

The largemouth bass is one of the most important fish spe-

cies in terms of occurrence because it was found in 64 of 65 of our study lakes and ranked fifth in average standing crop for the lakes in which it was found (Table 2). It showed no pattern of change in standing crop with changes in lake trophic state for this group of lakes but did show a decline in percentage of total biomass as lakes became more eutrophic. At the same time, however, the proportion by number of largemouth bass of quality size or greater as defined by Gablehouse (1984) increased with increasing trophic state (Table 4). Two other fish, the bluegill and warmouth, were also very common, being found in 64 and 63 of our lakes, respectively. The bluegill showed no changes in average standing crops or in proportions of larger fish with increases in trophic state (Table 4) while the warmouth showed decreases in standing crop (Fig. 5) but increases in the proportion of larger sized individuals with increases in trophic state (Table 4). The redear sunfish showed increases in frequency of occurrence (Fig. 4) and increases in average standing crop (Fig. 5) but no change in RSD-Q (Table 4) as lakes increased in productivity. The other important centrarchid, the black crappie, also became more common (Fig. 4) and had larger standing crops (Fig. 5) in more eutrophic lakes but had a smaller proportion of quality-sized fish (Table 4) in the richer lakes.

Discussion

The fish populations in the Florida lakes in this study fit some of the patterns found for other lakes discussed in the fisheries literature. There is an increase in the total standing crops of fish as the concentrations of total phosphorus, total nitrogen, and chlorophyll *a* increase and as the Secchi depth decreases. Similar results were found by Bays and Crisman (1983) for 30

Florida lakes. Canfield and Hoyer (1992) also found correlations between fish standing crops and trophic state for 60 Florida lakes when they took into account the standing crops of aquatic macrophytes in addition to phytoplankton in determining trophic state. On average the standing crops increased about one order of magnitude from the oligotrophic to the hypereutrophic Florida lakes in this study with no sign of a decrease in the most hypereutrophic lakes. There is considerable unexplained variance (about 75%) in these relationships due in part to other factors influencing fish crops and the practical sampling problems of estimating the biomass of wild fish populations. For this reason, predictions based on these relationships are imprecise; however, holding all other things constant, the standing crop of fish in Florida lakes should increase as they become more eutrophic.

Increases in trophic state did not result in a decrease in the number of fish species per lake. The lake surface area accounted for most of the variance in total species numbers, and once area was taken into account, there was no correlation between the number of fish species per lake and the various trophic state indices. The finding that larger lakes have a greater species richness than smaller lakes has been documented in comparisons of lakes throughout the world, including North America and Africa (e.g., Barbour and Brown 1974) and in Florida (Keller and Crisman 1990). A number of studies have documented this species–area relationship and tested hypotheses such as equilibria related to colonization and extinction, as suggested by theories of island biogeography and habitat diversity (Browne 1981; Barbour and Brown 1974; Eadie et al. 1986; Magnuson 1976; Tonn and Magnuson 1982). Studies investigating species diversity and fish community assemblages have also looked at factors such as size, pH, plant nutrients, latitude, and insularity and applied statistical techniques to determine the factors that influence species richness (Connor and McCoy 1979; Tonn and Magnuson 1982; Keller and Crisman 1990). Results of regression analyses for lakes in Florida and on data from other parts of North America by Keller and Crisman (1990) show that lake area explains the largest proportion of the variance in fish species richness.

Only five species showed decreases in frequency of occurrence with increasing trophic state, while all other species either stayed the same or increased in frequency of occurrence as lakes became more eutrophic. A similar pattern was found for average standing crops of individual species in lakes of different trophic states. Most species showed no significant change in biomass with changes in trophic state, while one species, the warmouth, decreased. Five species, the gizzard shad, threadfin shad, black crappie, redear sunfish, and blue tilapia, showed increases in standing crops with increasing trophic state. Bays and Crisman (1983) also noted the increased standing crops of shad in Florida lakes. For the recreationally important centrarchids the only negative changes noted with higher trophic states were lower standing crops of warmouth and lower proportions of larger sized black crappie. On the positive side the centrarchids as a group increased in biomass, the redear sunfish and black crappie increased in average standing crop, and the largemouth bass had a higher proportion of larger fish in the more eutrophic lakes.

Persson et al. (1988) found that the piscivorous fish in 15 Swedish lakes they had studied decreased in relative abundance as their lakes became more eutrophic. The piscivores

made up about 70% of the biomass in their oligotrophic lakes and dropped to about 7% in lakes of mesotrophic or higher trophic state. They thought that in very productive lakes with decreased habitat heterogeneity their primary piscivore, the perch (*Perca fluviatilis*), faced increased competition from cyprinids and that this had a negative effect on the recruitment of perch. We also found declines in the relative proportions of piscivores to other fish groups when we looked at lakes of increasing trophic state; however, the magnitude of the decrease was not as great as that found for the Swedish lakes. In our case there was no decrease in the absolute standing crop of the piscivores, but rather higher standing crops of gizzard shad and threadfin shad in eutrophic and hypereutrophic lakes reduced the relative importance of the piscivores.

We could only study the relationships between fish and trophic state over a cross section of lakes of varying trophic state rather than in individual lakes undergoing eutrophication over time. This places a limit on predictions that can be made for Lake Okeechobee or other lakes that may show changes in trophic state due to changes in nutrient inputs resulting from land use changes in their watersheds. Because of the scatter in our data, due in part to the many unexplained factors influencing fish populations and the problems in obtaining precise standing crop information for fish, we would have a problem in making a precise prediction of fish standing crops for an unknown Florida lake given information on basic water chemistry. On the other hand there were some general patterns in the relationships between lake trophic state and the total biomass, species richness, species composition, and species standing crops of fish in Florida lakes that should be useful in a predictive manner. First, the number of fish species in a lake seemed to be determined primarily by the size of the lake and not the trophic state, so we should not expect dramatic changes in total species numbers as lakes become more or less eutrophic. Second, there might be shifts in species composition with changes in trophic state, though only a few species showed significant changes in their standing crops. In particular the recreationally important centrarchids did not show dramatic changes over the trophic spectrum. Third, we did not identify any critical points on the trophic spectrum that caused dramatic changes in fish abundance and standing crops; there was nothing comparable with the loss of dissolved oxygen in the hypolimnion of a eutrophying northern lake. Last, the trophic indicators for our sample of lakes ranged over 2 or 3 orders of magnitude. The expected change in trophic state of a Florida lake that is already in the eutrophic to hypereutrophic category will likely be much less, so changes in the fish population due to changes in trophic status are likely to be small, and any changes in fish populations brought upon by changes in trophic state will be overshadowed by the many other variables that influence fish populations from year to year.

Since these findings do not fit the expectations of several earlier studies in the literature, it is worth looking at how these Florida lakes might differ from the lakes in those earlier studies. One major difference is that many of the lakes where eutrophication has been cited as the cause for changes in fish populations have been deep, stratified lakes in temperate regions where salmonid populations have been reduced or eliminated (Larkin and Northcote 1969). The loss of dissolved oxygen in the hypolimnion of stratified lakes is an important factor in reducing the available habitat for these species of fish

and their preferred foods (Colby et al. 1972). Florida lakes, however, are shallow, do not have cold hypolimnia, and lack salmonid species. Winterkills under the ice in the winter are also related to the impacts of eutrophication on fish community structure (Lee et al. 1991), but again this situation would not be relevant in Florida's climate. Lastly, in the case of the 22 lakes studied by Kautz (1980), his plot of sport fish biomass versus trophic state as determined by total nitrogen content did indicate a downward trend for hypereutrophic lakes. However, when he grouped the lakes by trophic state he found that the standing crops of sport fishes for oligotrophic, mesotrophic–eutrophic, and hypereutrophic lakes were 52, 89, and 65 kg·ha⁻¹, respectively, but these values were not statistically different from each other. Thus, those data did not support the contention that sport fish biomass declined with increasing trophic state in Florida lakes. According to our study, Florida lakes with up to 240 mg·m⁻³ of algal chlorophyll *a* show no significant decrease in biomass of important sport fish except the warmouth.

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