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Relations between trophic state indicators and plant biomass in Florida lakes

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Abstract

We collected quantitative data on macrophyte abundance and water quality in 319 mostly shallow, polymictic, Florida lakes to look for relationships between trophic state indicators and the biomasses of plankton algae, periphyton, and macrophytes. The lakes ranged from oligotrophic to hypereutrophic with total algal chlorophylls ranging from 1 to 241 mg m^{-3}. There were strong positive correlations between planktonic chlorophylls and total phosphorus and total nitrogen, but there were weak inverse relationships between the densities of periphyton and the trophic state indicators total phosphorus, total nitrogen and algal chlorophyll and a positive relationship with Secchi depth. There was no predictable relationship between the abundance of emergent, floating-leaved, and submersed aquatic vegetation and the trophic state indicators. It was only at the highest levels of nutrient concentrations that submersed macrophytes were predictably absent and the lakes were algal dominated. Below these levels, macrophyte abundance could be high or low. The phosphorus–chlorophyll and phosphorus–Secchi depth relationships were not influenced by the amounts of aquatic vegetation present indicating that the role of macrophytes in clearing lakes may be primarily to reduce nutrient concentrations for a given level of loading. Rather than nutrient concentrations controlling macrophyte abundance, it seems that macrophytes acted to modify nutrient concentrations.

Introduction

We have assembled a database on 319 Florida lakes containing information on quantitative estimates of macrophyte biomass, plankton chlorophyll, morphometry, and water quality. Since most of these lakes are shallow, these data provide us with an opportunity to examine current theories about shallow lakes that have been summarized in several new books on the subject (Moss et al., 1996; Scheffer, 1998; Jeppesen et al., 1998). For example, the theory of alternative stable states as outlined by Scheffer (1998), states in part that shallow lakes can shift from a clear, macrophyte-dominated state to a turbid, algal-dominated state with no change in nutrient loading. Such shifts have been observed in individual Florida lakes such as Lake Baldwin, Florida, where grass carp (*Ctenopharyngodon idella* Val.) were used to reduce submersed vegetation from 69% to 0% between 1978 and 1980 (Shireman et al., 1985). At the same time, the concentration of total phosphorus increased 3 times, plankton chlorophyll increased 5 times, and the Secchi depth decreased from 5 m to 1.5 m. We evaluated whether processes that lead to such changes in an individual lake would be apparent as patterns in the relationships between nutrients, plankton, periphyton, macrophytes, and morphometry among lakes of varying trophic states. We know of no similar study covering such a large number of lakes that looks at the factors that might influence the biomass of plants in shallow, polymictic, subtropical lakes. The objectives of this analysis are to summarize basic standing crop inform-

ation on macrophytes in several Florida lakes, to look for relationships among trophic state indicators and the biomass of plants in Florida lakes, and to examine some of the assumptions used to develop the theory of alternative stable states.

Methods

Macrophyte sampling

A total of 319 lakes were sampled between 1983 and 1999 with 230 lakes sampled once, 71 lakes twice, 13 lakes three times, 2 four times, and 3 were sampled five times. Most of these lakes are regularly sampled for water quality as a part of a citizens volunteer monitoring program, Florida LAKEWATCH, however 60 lakes were included in a research study (Canfield & Hoyer, 1992) where lakes were selected to represent a broad range of trophic states from oligotrophic to heteroeutrophic. Each separate macrophyte sampling date was treated individually yielding a total of 434 lake-years of observations. Aquatic macrophytes were sampled once during the growing season following the protocol established by Canfield et al. (1990). Transects were run across the lake with a Raytheon DE-719 recording fathometer, and the percent volume inhabited (PVI) and percent area covered (PAC) were determined from the fathometer charts (Maceina & Shireman, 1980). We also calculated a potential PAC in each lake by noting the maximum depth that submersed macrophytes were found at and determining the per cent of the lake area that was at that depth or less. The submersed, emergent, and floating-leaved plant zones were determined by the criteria of Wetzel (1983), and the width of the combined floating-leaved and emergent plant zones was measured along 5–30 transects. The average width was multiplied times the shoreline length to estimate the area covered by emergent and floating-leaved plants, and this was expressed as a per cent of the lake surface area (PACFE). On each transect, a single 0.25 m^2sample of vegetation (when present) was taken in each plant zone and each species present was recorded. The sampled vegetation was placed into nylon mesh bags,spun to remove excess water, and weighed to the nearest 0.1 kg. The average aboveground wet weights of emergent, floating-leaved, and submersed plants (kg m^{-2}) were determined for each lake. No attempt was made to rinse epiphytic algae from the plants, so all biomass estimates can be considered to be an assemblage of both macrophytes and epiphytes.

Periphyton sampling

In 60 of the lakes, periphyton biomass as mg chlorophyll kg^{-1} wet weight of host plant was estimated on the most common plants sampled along ten transects. Approximately 100 g wet weight of each macrophyte sampled was cut from 0.1 to 0.5 m below the surface of the water and placed into 500 ml of tap water in a plastic bottle and placed on ice. Periphyton was removed by shaking each bottle by hand within 7 h of sampling. Each sample was shaken manually for 30 s and the supernatant poured through a 1.0-mm screen to remove large particles. The procedure was repeated three times for each plant sample, adding 500 ml of tap water for each shaking. The supernatant water (1500 ml) was analyzed for chlorophyll spectrophotometrically following pigment extraction with 90% ethanol (Sartory & Grobbelaar, 1984). The total amount of chlorophyll was then divided by the wet weight of the macrophyte sample.

Plankton chlorophyll and water quality sampling

Water quality measurements for 60 of the lakes have been published previously (Bachmann et al., 1996). For the other lakes, we used averages of monthly samples collected by citizen volunteers as a part of the Florida LAKEWATCH program. In the field volunteers collected surface (0.5 m) water samples for total phosphorus (TP), total nitrogen (TN), and total chlorophyll (CHL) analyses and measured Secchi disk transparency (SD) from 1 to 6 evenly distributed locations on each lake. Water for the TP and TN analyses was collected in acid-washed, triple-rinsed, 250-ml Nalgene bottles while water for CHL analyses was placed into 4-l, tap water rinsed plastic bottles. On shore measured volumes of lake water from the 4-l bottles were filtered through Gelman Type A–E glass fiber filters. The filters and water samples were then frozen and sent to the water quality laboratory at the Department of Fisheries and Aquatic Sciences. TP concentrations ($\mu g \cdot l^{-1}$) were determined by the procedures of Murphy & Riley (1962) with a persulfate digestion (Menzel & Corwin, 1965). TN concentrations ($\mu g \cdot l^{-1}$) were determined by oxidizing water samples with persulfate and determining nitrate-nitrogen with second derivative spectroscopy (Bachmann & Canfield, 1996). CHL concentrations ($\mu g \cdot l^{-1}$) were determined spectrophotometrically following pigment extraction with 90% ethanol (Sartory & Grobbelaar, 1984). Most of these data have been reported in Florida LAKEWATCH (1999). In addition

our laboratory has collected color data (Pt-Co units) on 140 of the lakes during related studies. We used published values for lake mean depth and lake surface area (Bachmann et al., 1996; LAKEWATCH, 1999).

Statistical procedures

To account for heterogeneity of variance, the various measures of plant abundance, TP, TN, CHL, Secchi depth, lake area and mean depth were transformed to their base-10 logarithms prior to most analyses. Prior to taking logarithms 1 was added to zero values of PAC and PVI and 0.01 was added to zero values for macrophyte densities. JMP®, a statistical software package of the SAS Institute (1994), was used to compute all statistics. Stepwise multiple regression was used to look for possible relationships between plant abundance and TP, TN, CHL, Secchi depth, lake area, and lake mean depth. We also used stepwise multiple regression to see how various measures of plant abundance affected relationships between both chlorophyll and Secchi disk depths and plant nutrients. A probability level of 5% was used to determine statistical significance.

Comparisons of plant communities

In some cases, we used appropriate conversion factors to convert the biomasses of plankton, periphyton and submersed macrophytes into units of dry weight. The PAC was divided by 100 and multiplied by the average wet weight of submersed macrophytes to get an average biomass density for the lake. Dry weights of macrophytes were determined by multiplying wet weights by 0.08, a factor that represents the average ratio of dry to wet weight of submersed plants in Florida lakes (Canfield & Hoyer, 1992). Plankton and algal chlorophylls were converted to dry weights of algae by multiplying chlorophyll values by 70, a factor which has been used in other studies (Scheffer, 1998). Plankton concentrations were multiplied by the lake mean depth to get standing crops on an areal basis.

Water column phosphorus

To determine the concentration of phosphorus contained in the submersed macrophyte community, we multiplied the average dry weights per square meter times 1.41 mg TP g^{-1}dry weight, a number that represents the mean phosphorus (mg) content of dried plant material measured in 750 samples from 60 Florida lakes (University of Florida, unpublished data). This areal concentration was divided by the mean depth to get an average concentration of macrophyte phosphorus per unit volume. To find the water column, phosphorus concentration as defined by Canfield et al. (1983), the macrophyte phosphorus concentration was added to the total phosphorus concentration measured in water samples.

Comparisons between lakes

We compared the trophic indicators of lakes with submersed plants present to those where submersed plants were absent (e.g. the measured biomass was zero) and also made comparisons between macrophyte-dominated and algal-dominated lakes. Since we could find no generally accepted operational definition for these lake types, we devised our own. Macrophyte-dominated lakes were considered as those where the ratio of the dry weight of submersed macrophytes to the dry weight of plankton algae was 100 or greater. Algal-dominated lakes were those where the ratio of submersed macrophytes to plankton algae was 1 or less, and the remaining lakes were placed into an intermediate group. We also tried defining macrophyte-dominated lakes as those with a PVI $>80\%$ and algal-dominated lakes as those with a PVI $<20\%$ and found that either definition gave practically the same results. We used one-way ANOVA to determine if there were significant differences among the means of the trophic state indicators for the lake groups. Differences among trophic indicators for macrophyte-dominated, intermediate, and algal-dominated lakes were examined by performing a Tukey–Kramer HSD test at the 0.05 level of significance. To compare the groups visually with respect to the four trophic state indicators, we made frequency distributions for logarithms of TP, TN, CHL, and Secchi disk depths by forming groups based on 0.25 of a logarithmic unit. For example in the range of 10–100 mg m^{-3} TP the groupings in the untransformed units would be 10–17.9, 17.91–31.8, 31.81–53.7, and 53.71–100 mg m^{-3}.

Results

Characteristics of study lakes

Average values for several physical and chemical variables measured in our study lakes are presented in Table 1. The water quality variables include repeat measurements made in different years for some of the

lakes. In general, the lakes were shallow with an average mean depth of only 3.1 m, and 95% of them fell between 1.1 and 6.4 m. Lake surface area was much more variable ranging from 1 to 19 808 ha. Average values for chlorophyll, total phosphorus, and total nitrogen of 18.1, 32.4, and 664 mg m^{-3} respectively, indicate that the average lake was eutrophic, however the range of chlorophyll from 1 to 241 mg m^{-3} indicates that our sampled lakes ranged from oligotrophic to hypereutrophic. Water color in the 140 lakes where we had measurements was also highly variable, ranging from 0 to 295 Pt-Co units and averaging 40 Pt-Co units. In some lakes, water color most likely played a role in determining Secchi disk depths that averaged 2 m for all lakes in our sample. We found no submersed aquatic plants in lakes with more than about 150 Pt-Co units (Fig. 1A).

Some of the biological characteristics of our sample lakes are given in Table 2. The total number of macrophyte species for lakes that had macrophytes ranged from 5 to 52 per lake with an average of 23 (Table 2). While there was no significant relationship between the number of plant species per lake and the four trophic state variables, there was a significant, positive correlation ($r = 0.54$) between the number of plant species and log lake surface area, though there was considerable scatter in the relationship. More detailed information on the species composition and habitat preferences for the macrophyte species commonly found in Florida lakes are presented in Hoyer et al. (1996).

On average the emergent and floating leaved plants covered 12% of the surface areas of the study lakes with a range from 0 to 100% in individual lakes. Within these zones emergent plants averaged 4 kg m^{-2} and floating leaved plants averaged 2 kg m^{-2}wet weight (Table 2). In areas where they were present, submersed plants also averaged 2 kg m^{-2}, while the average for the entire lake area was 1.2 kg m^{-2}. The ranges in densities (wet weights) for the three plant types were similar, ranging from 0 to about 20 kg m^{-2}. On average the lakes in our sample had a PAC of 31% and a PVI of 11%, though both ranged from 0 to 100%. The density of periphyton averaged 21 mg of chlorophyll per kg of macrophytes and ranged from 1.4 to 75 mg of chlorophyll per kg of macrophytes.

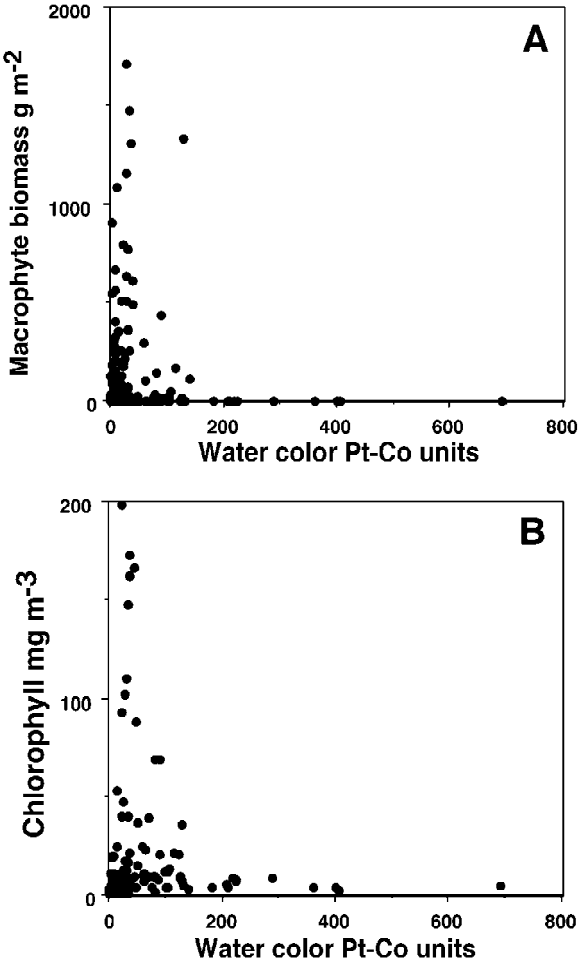

Figure 1. (A) Wet weight of submersed macrophytes and water color in 60 Florida lakes. (B) Plankton chlorophyll and water color in the same lakes.

Relationships with trophic state indicators

Emergent and floating leaved plants

The densities of stands of emergent and floating leaved macrophytes in each of the lakes are plotted against values for the four trophic state indicators examined in this study (Fig. 2). In general, there was no simple relationship between the densities of emergent and floating leaved plants and the four trophic state indicators. None of the R^2 values for TP, TN, CHL or SD exceeded 0.02 (Table 3). The per cent of the lake areas occupied by emergent and floating leaved macrophytes (PACFE) combined (Fig. 2) showed small negative correlations (Table 3) with TP ($r = -0.13$), CHL ($r = -0.22$), mean depth ($r = -0.21$) and lake area ($r = -0.27$) and also a significant relationship in a multiple regression with mean depth and lake area.

Table 1. Limnological characteristics of Florida lakes sampled in this study

Variable	*N*	Median	Mean	Geometric mean	Standard deviation	Minimum	Maximum
Surface area (ha)	275	70	473	75	1736	1	19808
Mean depth (m)	318	2.7	3.1	2.7	1.4	0.4	9.9
Secchi depth (m)	417	1.7	2.0	1.6	1.4	0.3	8.1
Color (Pt-Co units)	140	21.1	40	20	54	0	295
Total phosphorus (mg m^{-3})	433	16	32	18.4	68	1	1043
Total nitrogen (mg m^{-3})	433	664	806	645	598	43	3789
Chlorophyll (mg m^{-3})	434	8	18	8.6	29	1	241

Table 2. Measures of macrophyte abundance in Florida lakes sampled in this study. The densities of the three macrophyte communities are based on wet weights

Variable	*N*	Median	Mean	Geometric mean	Standard deviation	Minimum	Maximum
Number of species	362	23	23	21	9	5	52
Density emergent (kg m^{-2})	434	3.3	4	2.6	3.4	0	27
Density floating leaved (kg m^{-2})	434	1.1	2	0.6	2.9	0	19
Density submersed (kg m^{-2})	434	0.9	2	0.4	3.2	0	22
PACFE	325	7.2	11.6	6.3	17.4	0	159
PAC	434	22	31	15	29z	0	100
PVI	434	3.5	10.7	3.6	18.2	0	100
Periphyton mg Chl kg^{-1} plants	65	16.1	20.7	13.2	16.6	1.42	74.7
Average dry wt submersed plants (g m^{-2})	434	12.5	92.1	3.8	218	0	1731
Dry wt plankton algae (g m^{-2})	434	1.5	3.7	1.8	5.7	0.1	51

Table 3. Coefficients of determination (R^2) between various measures of plant abundance and several trophic state indicators and lake morphometric values for 434 lake-years. The last column represents the R^2 value for a multiple regression with both mean depth and Secchi depth as independent variables

	TP	TN	CHL	Secchi	Mean depth	Area	Depth & Secchi
Emergent	0.01	0.02**	0.00	0.00	0.00	0.00	–
Floating leaved	0.00	0.01**	0.01	0.00	0.01*	0.05**	–
Submersed density	0.12**	0.03**	0.09**	0.13**	0.00	0.00	0.18**
Average sub density	0.15**	0.05**	0.11**	0.14**	0.00	0.00	0.21**
PAC	0.05**	0.02**	0.05**	0.07**	0.05**	0.00	0.21**
PVI	0.01*	0.00	0.02**	0.01*	0.17**	0.00	0.25**
PACFE	0.02**	0.00	0.05**	0.00	0.05**	0.07**	0.09**
Algal chlorophyll	0.68**	0.50**	–	0.58**	0.04**	0.01	–

**Significant at the 0.01 level. *Significant at the 0.05 level.

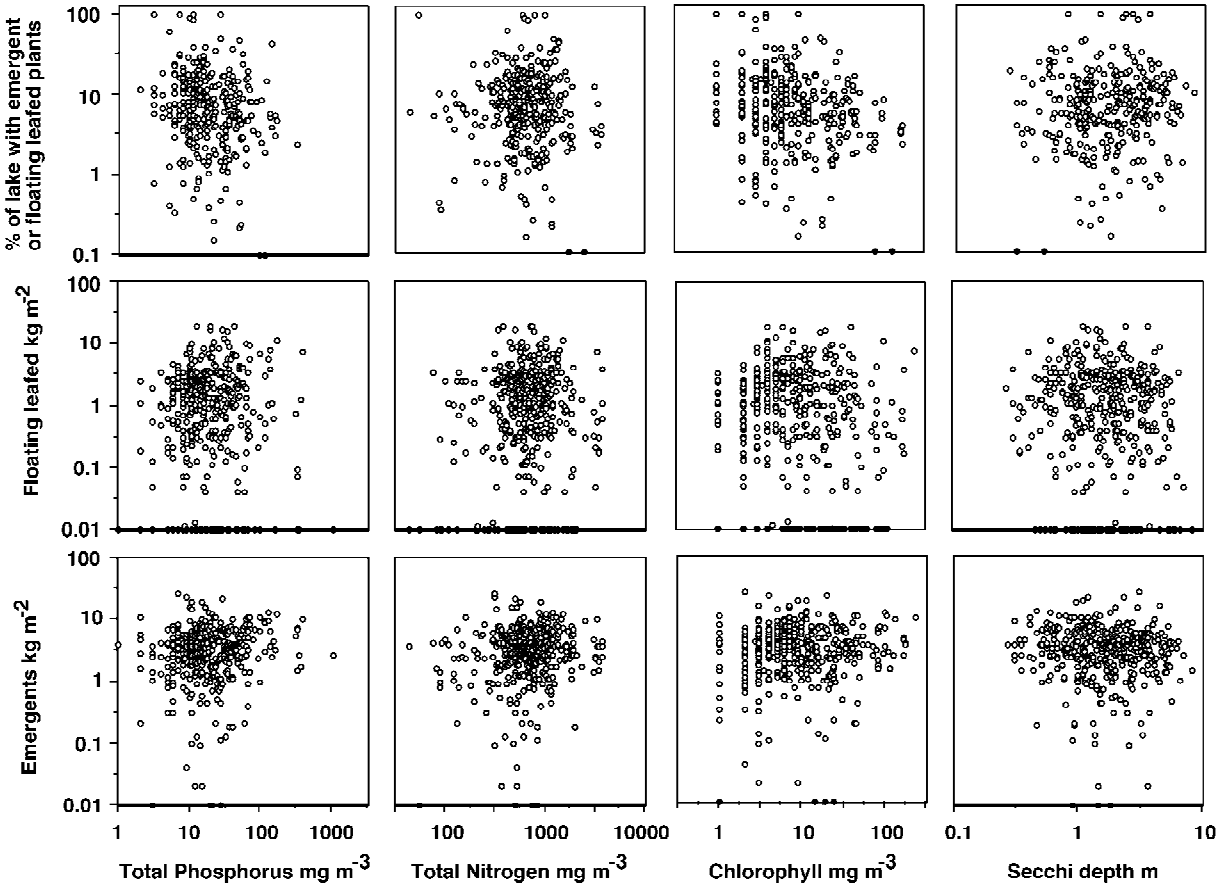

Figure 2. Wet weights of emergent plants and floating leaved plants and % of lake areas occupied by emergent and floating leaved plants (PACFE) as functions of total phosphorus, total nitrogen, chlorophyll and the Secchi disk depth. Zero values of biomass are plotted as 0.01 kg m^{-2} and zero% covered as 0.1%.

Submersed plants

Densities of stands of submersed plants, PAC and PVI, are plotted against the trophic state indicators in Figure 3. In general, there were no simple relationships between these measures of submersed plants and trophic state indicators, however, there were some weak but statistically significant correlations (Table 3). The density of submersed macrophytes showed a positive correlation with Secchi depth (r = 0.36) and a negative relationship with total phosphorus (r = −0.34), chlorophyll (r = −0.29) and total nitrogen (r = −0.18) (Table 3). Similarly, when submersed plants were represented by average lake density, the coefficients of determination for Secchi depth, total phosphorus, chlorophyll, and total nitrogen were 0.14, 0.15, 0.11, and 0.05 (Table 3). These are very weak relationships and cannot be used to predict the abundance of aquatic macrophytes from knowledge of trophic state indicators.

Lake area alone showed no significant correlation with any of the measures of macrophyte abundance except for a small positive correlation (r = 0.23) with the density of floating-leaved plants (Table 3), however mean depth did show some statistically significant negative correlations with PVI (r = −0.41), PAC (r = −0.22), and the concentration of floating-leaved plants (r = −0.09). Again the relationships were weak. The correlation between PVI and mean depth most likely reflects the fact that if plant height is held constant, the shallower waters will have a higher percentage of their volume occupied by plants. In stepwise multiple regressions of PAC, PVI, and the two measures of submersed plant density, the first two variables to make significant contributions to the coefficients of determination were lake mean depth and the Secchi disk depth (Table 3), with depth having a negative effect and Secchi disk a positive effect.

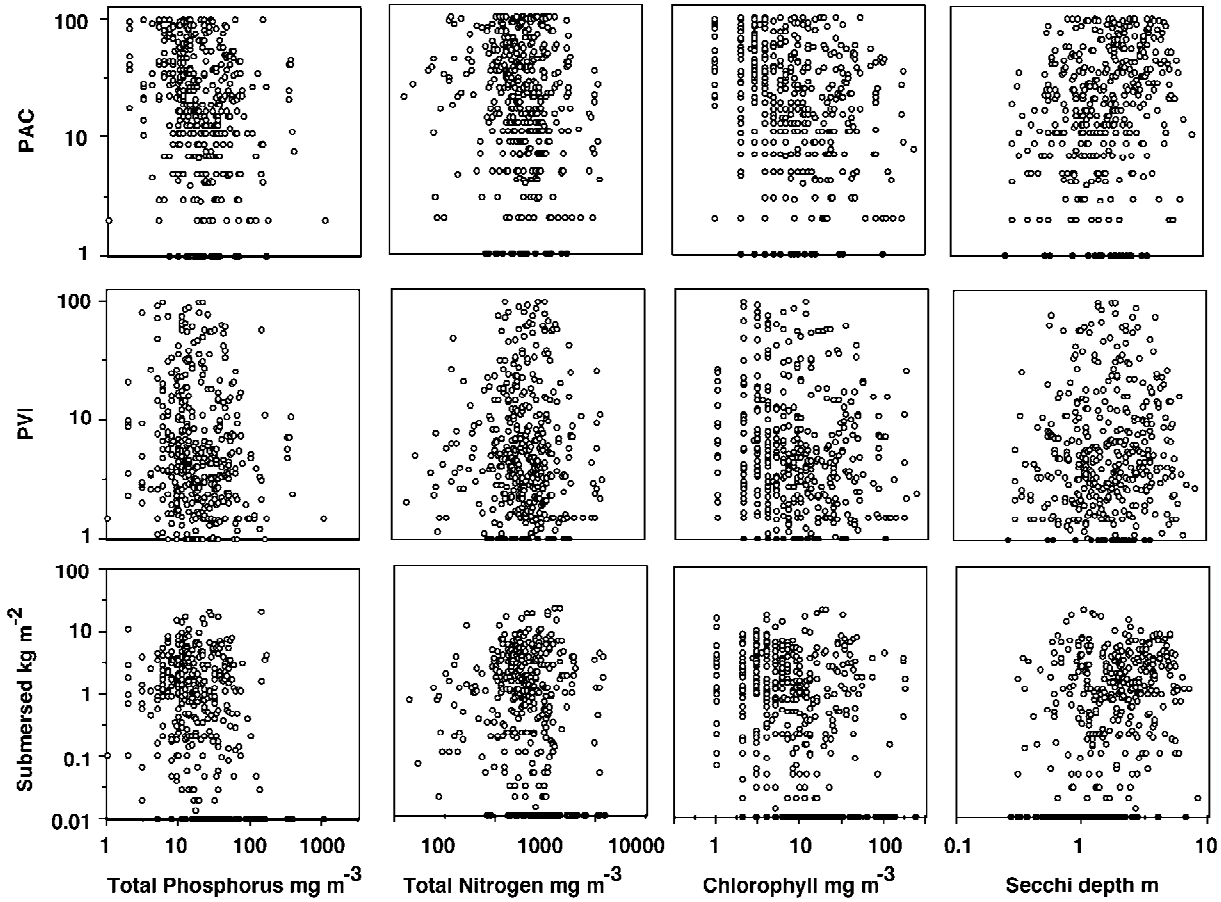

Figure 3. Wet weight, PVI and PAC of submersed plants as functions of total phosphorus, total nitrogen, chlorophyll, and the Secchi disk depth. Zero values of biomass are plotted as 0.01 kg m^{-2} and zero values of PVI and PAC as 1%.

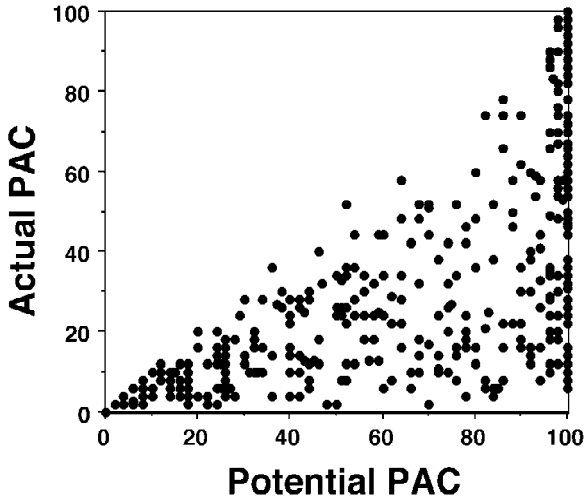

Figure 4. Actual PAC and potential PAC in the study lakes. The potential PAC is based on the area of the lake equal to or less than the maximum depth of plant colonization in a lake.

There was a poor relationship between the measured PAC values for the lakes and the potential PAC values (Fig. 4). The potential PAC was based on the assumption that the greatest depth that any macrophytes are found at in a lake represents the depth of light limitation; so that if light reaching the lake bed was the sole limiting factor for submersed macrophyte abundance, the PAC would be equal to the area of the lake with depths equal to or less than that depth. We found that for almost all of the lakes there were significant areas of lake bed that could have had submersed vegetation based on the maximum depth of colonization that did not have plants present.

We did not find submersed plants in 85 of the lakes we sampled, many of which had been stocked with herbivorous grass carp. A comparison of the trophic state indicators in the lakes with and without submersed macrophytes (Fig. 5) showed that in general the lakes without submersed plants present had

higher average levels of total phosphorus, total nitrogen, and chlorophyll but lower Secchi disk depths. The differences between the means were statistically significant (all $p < 0.05$) in one-way ANOVAs. For lakes with submersed plants present the highest total phosphorus concentration was 166 mg m-^{3}, the highest total nitrogen concentration 3750 mg m^{-3}, the highest chlorophyll concentration 182 mg m^{-3} and the lowest Secchi depth 0.3 m. For lakes with submersed plants absent, the lowest total phosphorus concentration was 8 mg m^{-3}, for total nitrogen 261 mg m^{-3}, chlorophyll 2 mg m^{-3} and the highest Secchi depth with submersed absent was 6.6 m. The important point illustrated by the distributions (Fig. 5) is the great overlap in the trophic state indicators for lakes with and without submersed plants present. Except for the extreme end of their ranges, none of these variables can be used with any accuracy to predict whether submersed plants will be present or absent in a given Florida lake.

Periphyton

Periphyton standing crops measured as the amount of periphyton chlorophyll per unit weight of macrophytes showed an inverse relationship with trophic state indicators (Fig. 6). Periphyton chlorophyll concentrations decreased with increasing phytoplankton chlorophyll ($r = -0.50$), decreasing Secchi depth ($r = 0.43$), increasing total phosphorus ($r = -0.37$), and increasing total nitrogen ($r = -0.28$). Again there is considerable scatter in the distribution of the points in each plot, so the accuracy of predictions is limited. On a dry-weight basis periphyton accounted for about 1.8% of the total dry weight of the submersed macrophytes with their attached algae.

Plankton

Algal chlorophylls were strongly related to total phosphorus ($r = 0.82$) and total nitrogen ($r = 0.70$) and the Secchi depths were inversely related to chlorophyll concentrations ($r = -0.76$). These relationships have been shown many times in Florida lakes (Brown et al., 2000). We also found that water color seems to place a limit on the biomass of plankton algae in lakes with colors of about 150 Pt-Co units or more (Fig. 1B). This was similar to the relationships for submersed macrophytes and probably represents light limitation.

Macrophyte-dominated versus algal-dominated lakes

In Figure 7, we show the distributions of values for the four trophic state indicators for macrophyte-dominated, intermediate, and algal-dominated lakes. In going from macrophyte-dominated to algal-dominated lakes, there was an increase in average values for total phosphorus, total nitrogen, and chlorophyll, with a decrease in average Secchi disk depth. For each of the trophic state indicators, the means for each of the three lake groups are significantly different from each other (all $p < 0.05$) with the exception of the average values for total nitrogen in the macrophyte-dominated lakes verses the intermediate lakes. The highest total phosphorus concentration for a macrophyte-dominated lake was 139 mg m^{-3} and the highest chlorophyll was 32 mg m^{-3}. Similar to the distributions for lakes with and without submersed macrophytes, there was considerable overlap in the ranges of trophic state indicators for these three lake groups, so that again an accurate prediction is not possible from knowledge of the values for the trophic state indicators. Moss et al. (1996, Fig 0.4) also note the broad overlap in total phosphorus concentrations between lakes dominated by plants and those dominated by phytoplankton.

To make a visual determination of whether macrophytes influenced the phosphorus–chlorophyll and the phosphorus–Secchi depth relationships, we followed the example of Faafeng & Mjelde (1998) and plotted phytoplankton chlorophyll levels and Secchi disk depths against total phosphorus concentrations in Figure 8A, B with different symbols used for lakes that we classified as algal-dominated, intermediate, and macrophyte-dominated. For a given level of phosphorus, there was no obvious effect of macrophyte or algal dominance on the chlorophyll levels or Secchi disk depths as the points for the three different lake groups are scattered amongst each other.

For a statistical test that was independent of our method of determining algal or macrophyte dominance, we ran stepwise multiple regressions with chlorophyll and Secchi depths as dependent variables and total phosphorus, total nitrogen, PAC, PVI and mean depth, as independent variables (Table 4). For the prediction of chlorophyll, total phosphorus, total nitrogen, and mean depth were the only independent variables that improved the R^2 value, indicating that the macrophytes had no significant effect on the phosphorus chlorophyll relationship in this sample of lakes. Previously Canfield et al. (1984) using a sample of

Table 4. Results of stepwise multiple regressions for chlorophyll and Secchi depth versus logarithms of total phosphorus, total nitrogen, PAC, PVI, and lake mean depth using data from 432 lake-years. Numbers in table represent coefficients of determination (R^2). Only variables that made a statistically significant ($p<5\%$) reduction in R^2 are listed. Depths are in units of m and concentrations in mg m^{-3}

Dependent variable	Independent variable(s)	R^2
Log chlorophyll	TP	0.68
	TP, TN	0.70
	TP, TN, mean depth	0.72
[a]Log CHL = −1.47 + 0.852 Log TP + 0.425 Log TN + 0.300 Log MD		
Log Secchi depth	TP	0.65
	TP, mean depth	0.70
	TP, mean depth, TN	0.73
	TP, mean depth, TN, PAC	0.76
Log SD = 1.13 − 0.355 Log TP − 0.274 Log TN + 0.407 Log MD+ 0.098 Log PAC		

[a]For comparison (Canfield et al. 1984) previously found with 32 lakes
Log CHL = −2.08 + 0.28 Log TP + 1.02 Log TN – 0.005 Log PVI.

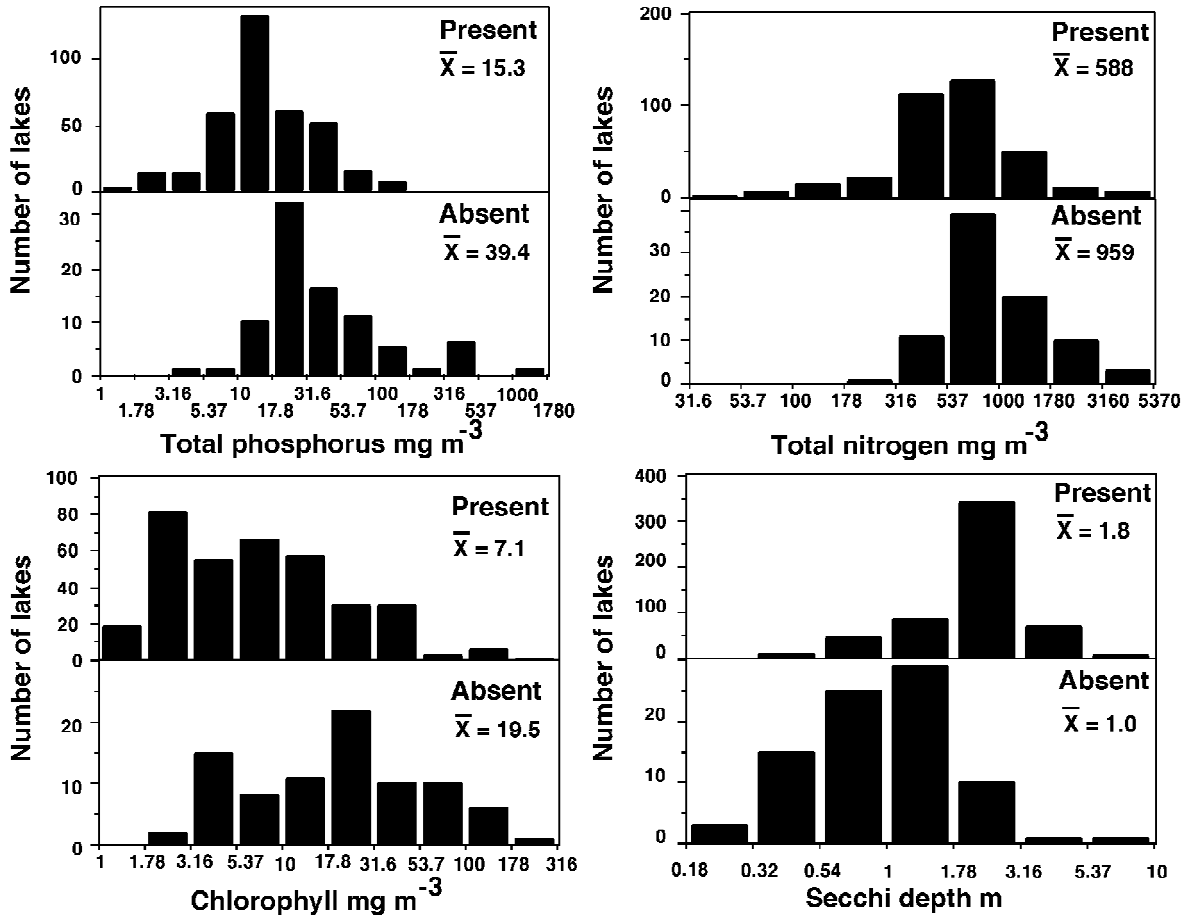

Figure 5. Frequency distributions of total phosphorus, total nitrogen, chlorophyll and Secchi disk depths in lakes with and without submersed macrophytes present. Note a logarithmic scale is used for the variables.

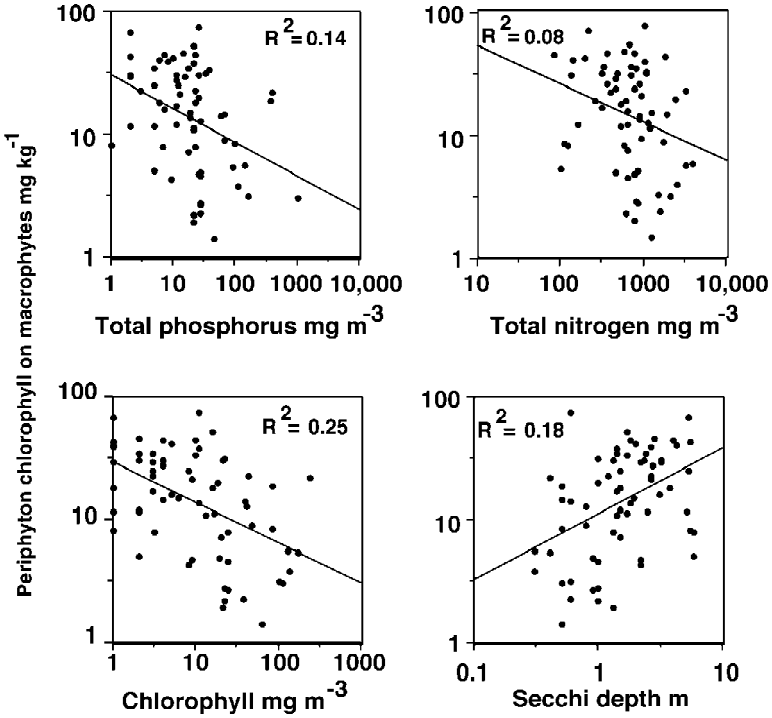

Figure 6. Density of periphyton chlorophyll on macrophytes from Florida lakes in relation to total phosphorus, total nitrogen, chlorophyll and the Secchi disk depth.

32 Florida lakes found that after taking into account TN and TP the addition of PVI to the multiple regression raised the R^2 value by 0.04. In either case the macrophyte effect is very small. These findings strongly suggest that macrophytes are not producing substances that inhibit the phytoplankton in these lakes as has been suggested in other studies (Hasler & Jones, 1949).

For the prediction of Secchi depth, after total phosphorus, total nitrogen, and mean depth were taken into account, the R^2 increased by only 0.03 when PAC was added (Table 4). While the effect was statistically significant ($p<5\%$), the reduction in the variance was relatively small. As an example of the potential effect we calculated expected Secchi disk depths with the multiple regression equation (Table 4) using values for TP (18 mg m^{-3}), TN (645 mg m^{-3}), and mean depth (2.7 m) representing averages for our lake sample (Table 1) and various values for PAC. With a PAC of 100% the calculated Secchi depth would be 1.9 m, at 50% 1.8 m, and at 20% PAC it would be 1.7 m. The absolute differences are small by the calculation. Because there was no statistical effect of macrophytes on chlorophyll, it is possible that the effect of macrophytes on Secchi depth represents sediment resuspension.

Figure 8C is similar to Figure 8B except that we used water column phosphorus instead of total phosphorus as the independent variable and thus included the phosphorus contained in and on the submersed macrophytes as well as that in the water and suspended matter. Here, there are two distinct groups of points with deeper Secchi depths for macrophyte-dominated lakes than for algal-dominated lakes with the same amount of water column phosphorus. This relationship is important to our discussion of the theory of alternative trophic states.

Relative biomass of plankton, periphyton, and submersed macrophytes

The average dry standing crop of submersed macrophytes of 92 g m^{-2} exceeded that of the plankton algae at 3.7 g m^{-2} (Table 2). The periphyton made up about 1.8% of the dry weight of the combined macrophytes and their attached algae, so that on average the plankton and periphyton biomasses (1.6 g m^{-2}) are about the same. On the other hand, the averages are not too useful, since the biomasses of both

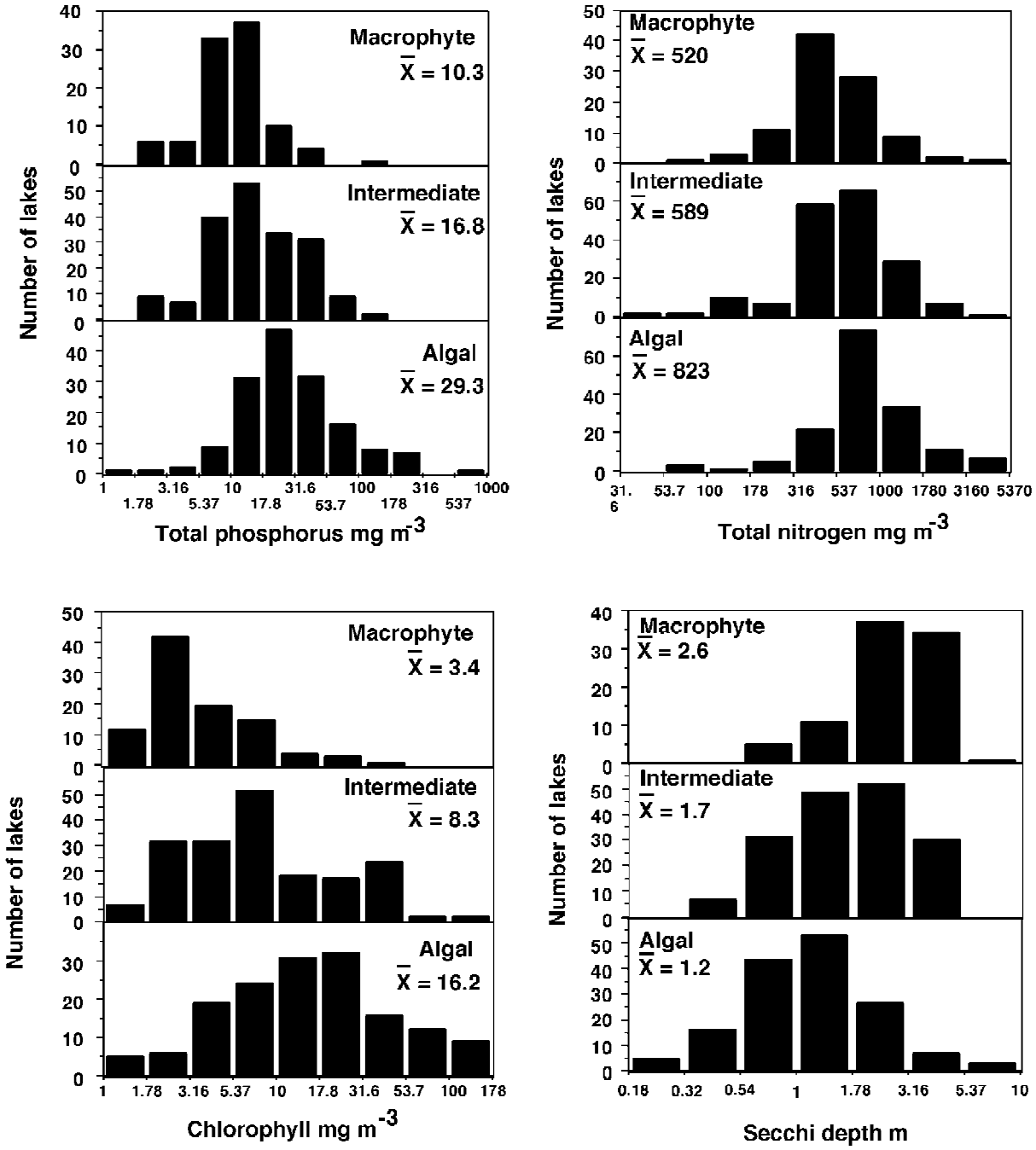

Figure 7. Frequency distributions of total phosphorus, total nitrogen, chlorophyll and Secchi disk depths in macrophyte-dominated, algal-dominated, and intermediate lakes. Note a logarithmic scale is used for the variables.

plankton and macrophytes vary over several orders of magnitude (Table 2). The plot of plankton standing crop *versus* submersed macrophyte standing crop on a linear scale (Fig. 9A) indicates that at the extremes we have lakes that are primarily algal-dominated or macrophyte-dominated. The highest standing crops of submersed macrophytes are found at the lowest standing crops of plankton algae and the highest algal crops tend to be found at low densities of submersed macrophytes. When we look at a double logarithmic plot

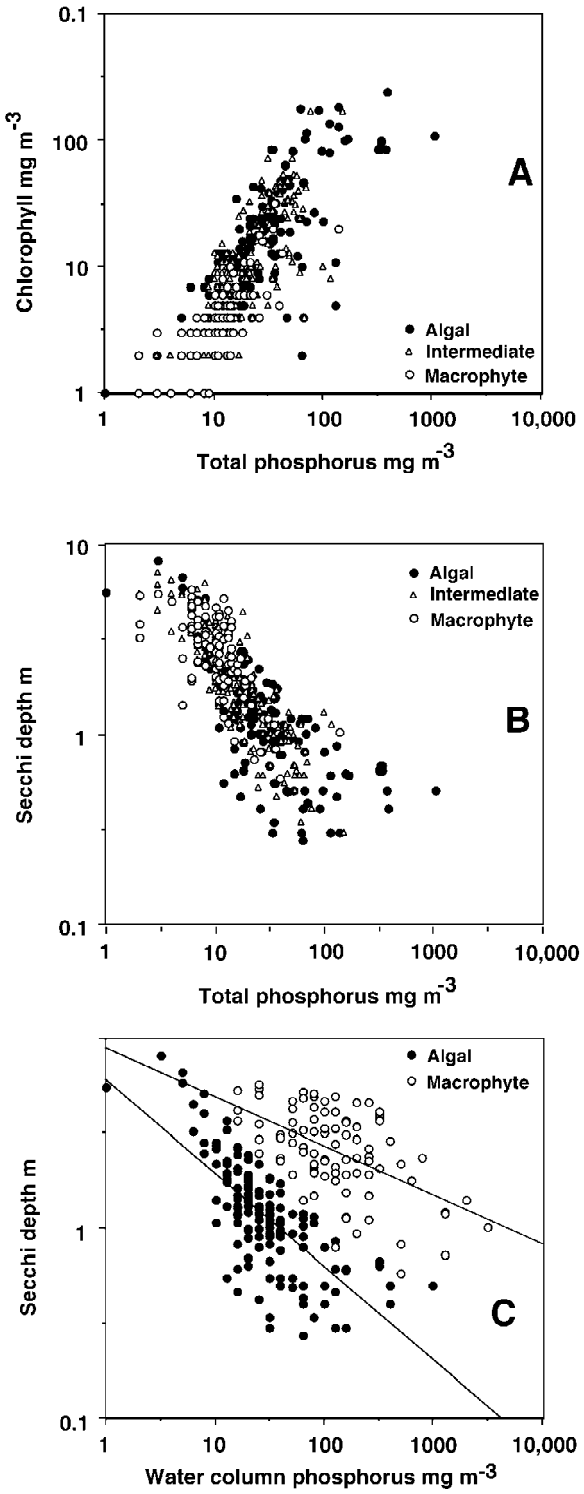

Figure 8.

Figure 8. (A) Relationship between algal chlorophylls and total phosphorus with different symbols for algal-dominated, macrophyte-dominated and intermediate lakes. (B) Relationship between Secchi disk depth and total phosphorus with different symbols for algal-dominated, macrophyte-dominated and intermediate lakes. (C) Relationship between Secchi disk depth and water column phosphorus with different symbols for algal-dominated and macrophyte-dominated lakes. Fitted regression lines are shown for the two lake types. Water column phosphorus includes phosphorus in and on the submersed aquatic plants plus total phosphorus measured in the water and suspended matter.

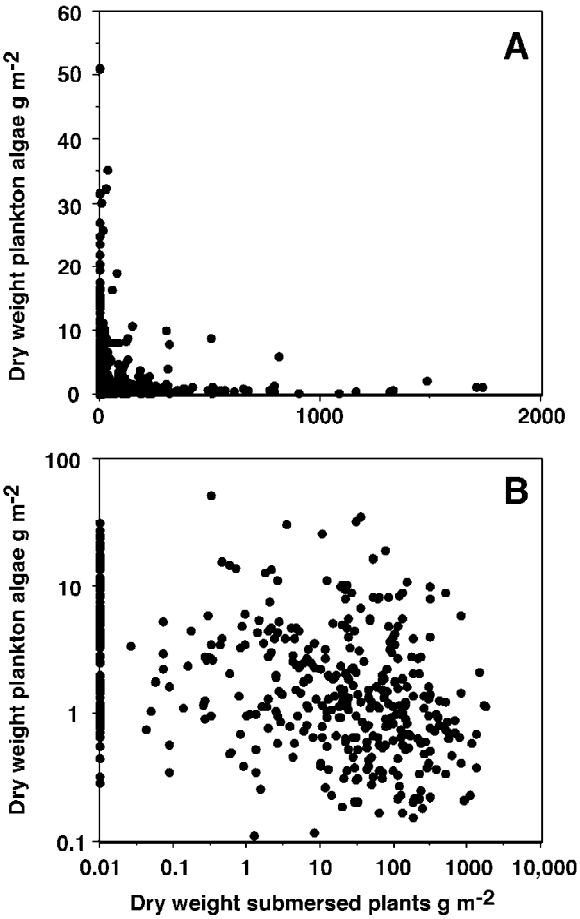

Figure 9. (A) Dry weight of plankton algae vs dry weight of submersed plants in Florida lakes on a linear scale. (B) Same data as A but on a logarithmic scale. Zero values of submersed plant biomass are plotted as 0.01 g m^{-2}.

of the same data (Fig. 9B), we can see that most of the lakes do not have extreme values for either variable and there is no relationship between the two. The biomass of submersed macrophytes exceeds that of the plankton algae in 278 out of our sample of 434 lake-years.

Discussion

What is the relationship between macrophyte abundance and trophic state?

Unlike the phytoplankton that showed strong correlations with trophic state indicators such as TP and TN, there was no predictable relationship between the abundance of macrophytes and trophic state in our sample of Florida lakes. This was true for the measured densities of emergent, floating leaved, and submersed plants as well as for more general measures of plant density and coverage like PVI and PAC. The same was true for the presence or absence of submersed plants in these lakes. It was only at the highest levels of nutrient concentrations that submersed macrophytes were predictably absent and the lakes were algal-dominated. Below these nutrient levels the macrophyte abundance could be high or low. This is probably due to the fact that many macrophytes can obtain their nutrients from the sediments rather than from the water, so that a low nutrient content in the open water does not necessarily mean that the sediments have not accumulated sufficient nutrients to support a significant biomass of macrophytes. Water color, however, was one environmental variable that had a decided effect on plant biomass. All lakes with water color values of about 150 CO-Pt units and above showed a distinct depression in the biomass of plankton algae and macrophytes. This is most likely due to reductions in light penetration caused by the stained water.

We considered if the lack of good correlations between various measures of aquatic plant abundance and trophic state indicators might be due to sampling errors in estimating plant biomass, since a previous examination of our sampling methods showed average coefficients of variation for the individual lake-average standing crops of emergent, floating leafed, and submersed macrophytes were 60%, 120%, and 86%, respectively (Canfield et al., 1990). These errors should not result in the observed lack of correlation, however, since in our surveys the various measures of aquatic plant abundance varied by from 2 to 3 orders of magnitude (Figs 2 and 3), a range much larger than the errors of measurement in the individual lakes.

We also found no relationship between the number of species of macrophytes in a lake and the values for the trophic state indicators. The best indicator of species numbers was lake area though the relationship was weak. Other studies have shown that species numbers of birds (Hoyer & Canfield, 1990) and fish (Bachmann et al., 1996) also increase with lake size in Florida lakes.

The periphyton on the other hand did show a weak pattern of decreasing abundance in terms of density as trophic state indictors like phosphorus, nitrogen, phytoplankton chlorophyll, and especially Secchi depth indicated increasing trophic state. This may be a reflection of lowered light intensities in the water column with increasing trophic state. Since the periphyton are attached to one spot and cannot move in the water column like suspended phytoplankton, they are going to be subject to decreases in available light. It has been theorized that the loss of macrophytes with eutrophication in some lakes is due to the shading effects of increasing loads of periphytic algae on the surface of the plants (Phillips et al., 1978). Our results would indicate that this is not likely in our Florida lakes, because we did not find a predictable increase in periphyton with increases in nutrient concentrations. We note, however, that we did not find large growths of filamentous algae on the macrophytes that have been noted in other studies (Phillips et al., 1978).

Alternative stable states

We examined the concept that macrophyte-dominated lakes are clear and that algal-dominated lakes are turbid. When we compared what we considered to be macrophyte-dominated lakes with algal-dominated lakes, we did indeed find that there was a difference in the average Secchi disk depth, however there was a broad range of overlap between the two groups. macrophyte-dominated lakes were not necessarily clear and algal-dominated lakes were not necessarily turbid. On the other hand individual lakes that make the switch from the macrophyte state to the algal state do show a decrease in water clarity while those switching from the algal state to the macrophyte state show an increase in transparency. This implies that in the theory of alternative stable states (Scheffer 1998), the concept of a clear or turbid lake is a relative one that applies to a single lake and not to aggregations of macrophyte or algal-dominated lakes.

We also examined Scheffer's theoretical explanation for the phenomenon of alternative stable states. His basic model (Scheffer, 1998) starts with three assumptions about the behavior of shallow lakes: (1) Turbidity increases with nutrient level, (2) Vegetation reduces turbidity, and (3) Vegetation disappears entirely when a critical turbidity is exceeded.

Our results support his first assumption. In the Florida lakes as the concentration of nutrients increased, the turbidity increased as evidenced by the inverse relationship between total phosphorus and Secchi disk depth. The second assumption cannot be tested directly, since our study looks at a cross-section of many lakes rather than following individual lakes that have significant increases or decreases in macrophyte abundance through time. Even so, we can make an indirect test by starting with a figure that Scheffer (1998, Fig. 5.34) uses to illustrate this assumption. His plot has turbidity on the vertical axis and nutrients on the horizontal axis with two parallel lines. The upper line shows turbidity increasing with nutrients for lakes without vegetation while the lower line is for lakes with vegetation. Our data did not show any significant effect of macrophyte biomass on the relationships between total phosphorus concentration and algal chlorophyll and only a very small effect of macrophytes on the relationship between phosphorus and Secchi disk transparency. On the other hand, when we plotted Secchi disk depth versus water column phosphorus (Fig 8C), we did find two different lines, one for algal-dominated lakes and the other for macrophyte-dominated lakes. Because the water column phosphorus is defined as the sum of total phosphorus in the water column and the phosphorus contained in and on the macrophyte community, these two lines reflect the partitioning of phosphorus between the plankton community and the macrophytes with their associated periphyton. When there are few macrophytes, the phosphorus is concentrated in the plankton with a subsequent increase in turbidity. When macrophytes dominate, there is relatively less phosphorus to support the plankton community and transparency is higher.

Our data would also be consistent with Scheffer's figure if the nutrient axis was taken to be nutrient loading rate rather than nutrient concentration. In other words, for a given loading, the amount of total phosphorus in the water would be less if a large amount of macrophytes were present in the lake. Janse (1997) reached a similar conclusion using simulation models of shallow lakes with and without macrophytes. Since turbidity is proportional to TP concentration in our lakes, the macrophytes would reduce the turbidity as well. The mechanisms by which macrophytes reduce phosphorus concentrations might be due to reduced resuspension of phosphorus-bearing sediments, settling of phytoplankton to the lakebed due to reduced turbulence within the plant beds, nutrient uptake by macrophytes or by periphyton growing on their surfaces, or a change in the fish population with a reduction in the sediment-disturbing benthivorous fish in the macrophyte-dominated lakes. The Lake Baldwin example supports this idea, since a change in macrophyte coverage resulted in increases in total phosphorus and chlorophyll and a decrease in water transparency with no known change in nutrient loading. The use of vegetation-filled marshes to reduce nutrient concentrations is well documented and also supports this approach. It would be desirable to test this hypothesis with nutrient budget studies for lakes with and without macrophytes or for lakes that have undergone major changes in macrophyte abundance. Currently, we do not have such data for the Florida lakes.

We could not use our data to establish a critical turbidity at which all macrophytes would be lost and above which macrophytes would be abundant. While we did find some relationships between plant abundance and Secchi depth, the correlations were weak and did not indicate a definite cutoff point. This is probably due in part to differences in morphometry, for the critical extinction coefficient would be less for a deeper lake than for a shallower one, so there will be differences from lake to lake. But even when we ran multiple regressions with both Secchi depth and mean depth as independent variables, the correlations were weak. Based on other studies showing that the maximum depth of plant colonization can be related to Secchi disk depth (Canfield et al., 1985), we had expected to find better relationships between light and macrophyte abundance. The problem with this approach is illustrated by our finding that the coverage of our lakebeds by plants did not necessarily correspond with that predicted by the maximum depth at which those plants were found. The macrophytes do not necessarily grow in all areas where there is sufficient light reaching the bottom. Scheffer et al. (1992) had reached the same conclusion after studying the submersed vegetation in a chain of shallow, eutrophic lakes. They found that it was only possible to use environmental factors to predict where macrophytes would not grow in a lake, not where they would grow. This fact makes it very difficult to develop predictive models for macrophyte coverage in shallow lakes.

Cause and effect relationships

We started our analysis to see if plant nutrients measured in lake water determined the abundance of macro-

phytes in the way that plant nutrients determine levels of plankton algae. We failed to find such a relationship most likely because the sediments can play an important role as a nutrient source to the macrophytes independent of the water concentrations. Our results suggest that we were looking at the problem from the wrong direction. It is more likely that the macrophytes were playing a role in modifying the nutrient concentrations and other trophic indicators in the lakes. Our Figures 5 and 7 illustrate decreases in trophic state indicators as the relative amounts of macrophytes in the lakes increase. In the previous section, we noted several mechanisms by which significant macrophyte growths can reduce nutrient concentrations and lead to reduced plankton and increased transparency.

It is important to note that throughout our discussion, we have used the traditional definition of trophic state, which is based on only those plants that are suspended in the water column and ignores the biomass of the macrophytes. An argument can be made that the macrophytes should be included in trophic state classifications (Canfield et al., 1983), since their productivity also provides energy and materials to support the lake ecosystem.

Application to other lake regions

The Florida lakes in our study are primarily shallow and polymictic, so that our results should be useful for other shallow lake regions. However, our lakes are also subtropical and have no freezing period in the winter that can cause a major setback to the macrophytes each winter. This may make the Florida lakes less likely to switch from a macrophyte state to an algal state than northern lakes during the spring period when algal shading may be a critical factor in preventing the regrowth of macrophytes.

Our results may also not reflect what happens in regions with much higher levels of plant nutrients. For example when Jeppesen et al. (1990) made plots of Secchi disk depths against total phosphorus concentrations for several Danish lakes with and without macrophytes, they found greater Secchi disk transparencies for a given total phosphorus concentration for lakes with macrophytes than for those without substantial aquatic vegetation. Our Florida lakes differed in this respect, perhaps because the Danish lakes studied by Jeppesen et al. (1990) tended to have much higher levels of total phosphorus than our Florida lakes.

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