DIATOMS AS INDICATORS OF HISTORICAL MACROPHYTE BIOMASS IN FLORIDA LAKES

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1991

ACKNOWLEDGMENTS

I thank Daniel E. Canfield, Jr. for suggesting the concept of this study in constructive criticisms he offered during my master's defense. Dan's challenge provided me with motivation: I chose this topic because I was determined to show him I could resolve the problem. Mark Hoyer and Christine Horsburgh were responsible for collection and management of macrophyte data, and Mark was especially helpful in providing me with this information. The Florida Museum of Natural History provided the vehicles, boats, and equipment for field work. Brian Rood, J. Daniel Bryant and Dennis Crumby assisted in the field. Silvia Ferguson gave much time and hard work in field assistance, and has been a constant source of support throughout this study.

I am grateful to Claire Schelske, Marty Fleisher, and Arthur Peplow for radionuclide assay of samples used to calculate bulk sediment accumulation rates. I thank Douglas Turley for the time and computer expertise he offered for data management. Paul Zimba gave generous assistance in computer programming during his personal time, making it possible for me to use the CANOCO statistical package. Dana Griffin provided funds for mainframe computing. Martha Love and Sarah E. Whitmore kindly helped with manuscript preparation.

This dissertation work was begun under the guidance of Edward S. Deevey, Jr., my major professor for more than 9 years. Ed's death in November 1988 was a blow to many academic disciplines, and a sad personal loss of which I am especially cognizant at this time. I have benefitted from Frank Nordlie's particulalry competent guidance through the completion of my studies. Claire Schelske generously provided the space, resources and financial support that allowed me to complete my graduate work. Joseph S. Davis and Ronald G. Wolff have been supportive members of my graduate committee for many years. It is largely due to Ron's encouragement that I pursued graduate studies at the University of Florida. No list of acknowledgements for my graduate work would be complete without expressing sincere thanks for all manner of support and encouragement to Mark Brenner, my colleague of 11-1/2 years who introduced me to paleolimnology.

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May 1991

Chairman: Frank G. Nordlie
Major Department : Zoology

Macrophytes represent an important component of primary production in lakes that is usually ignored in trophic state classification. Trophic classifications traditionally emphasize water-column nutrient concentrations and phytoplankton biomass. Predictive models have been developed from diatom assemblages to assess historical changes in lake trophic state, but these models usually infer water-column total P or chlorophyll *a* values and thus also ignore macrophyte production. Lake-sediment core samples often indicate former periods of low trophic state, although these periods may instead represent low water-level events that periodically occur in Florida lakes. Because macrophyte biomass is negatively correlated with water-column nutrients, macrophyte biomass may have been high at times when nutrient inferences suggest that lakes were unproductive.

The purpose of this study was to develop predictive models for inferring historic macrophyte biomass using diatoms, and to incorporate those models into a scheme that permits a more complete assessment of former lake trophic state than do models based solely on water-column nutrient concentrations.

Subfossil diatom assemblages were analyzed from the surface sediments of 29 Florida lakes covering a range of macrophyte abundance. Trophic-state, pH, and specific conductance formed an environmental gradient that was the principal influence on diatom communities in the limnologically diverse set of lakes. The planktonic proportion of the diatom community was positively correlated with trophic state, whereas the periphytic proportion was negatively correlated with trophic state. Sedimentary diatom concentrations, however, showed that both of these life-form communities had a positive response to increase in water-column nutrients.

Multivariate models are presented that permit estimates of former macrophyte biomass from fossil diatom assemblages. The kg of P contained in once-living macrophyte biomass can be estimated using a mean percent P value for macrophyte taxa. This mass of P divided by lake volume yields a concentration that can be added to limnetic P inferences obtained from diatom predictive models to estimate the potential total P content of the water column (WCP) Trophic state index values calculated with historic WCP will reflect both former macrophyte and phytoplankton aspects of trophic state.

CHAPTER 1

INTRODUCTION

The Concept of Trophic State in Lakes

Primary productivity in lakes can be defined as the rate at which new organic matter is formed by photosynthesis in autotrophs such as phytoplankton and macrophytes. Annual productivity is typically expressed as the number of grams of carbon fixed per unit of lake surface area per year. Lake productivity, however, has been more traditionally thought of in conceptual terms referred to as trophic state, and typologically described using categories ranging from ultraoligotrophic at the low end of productivity to hypereutrophic at the high end (cf. Shannon and Brezonik 1972).

Several trophic state indices (TSI) have been developed that permit numerical expression of trophic state using biological, physical and chemical characteristics. Shannon and Brezonik (1972), for instance, used principal components analysis to reduce seven variables including chlorophyll *a* (Chl *a*), primary productivity, and total P to a single variable that described the trophic status of lakes. Although it was inclusive, this TSI has been regarded as cumbersome, especially because of the difficulty in obtaining primary productivity values. Carlson (1977) sought a single, easily obtained measure to describe lake trophic state, and he selected

Secchi depth, a convenient variable that reflected phytoplankton standing crop in many lakes. Carlson scaled his TSI with the intention that a ten-unit increase in TSI would be equivalent to a doubling of algal biomass, but his index failed to relate in a uniform way to Chl *a*. Carlson calibrated his TSI to limnetic Chl *a* and total P for a set of north-temperate lakes and developed subindices to permit expression of TSI from these latter two variables.

Kratzer and Brezonik (1981) later modified Carlson's approach by constructing a subindex expressing TSI from water-column total N concentrations after observing N limitation in several Florida lakes located on phosphatic limestones. They proposed an averaged subindex that used mean TSI values based on Chl *a* and Secchi depth, and the lesser of the two TSI values based on total P and total N.

Baker *et al.* (1981) observed different relationships between Secchi depth, total P and Chl *a* in Florida lakes than Carlson (1977) observed in north-temperate lakes. Huber *et al.* (1982), therefore, constructed a new TSI for Florida lakes using the Florida Lakes Data Base, a large data set that is maintained at the Water Resources Research Center at the University of Florida.

Huber *et al.* based their TSI on Chl *a*, a more direct measure of phytoplankton biomass than Secchi depth, and they retained Kratzer and Brezonik's total N and averaged subindex approach because of N limitation in some Florida lakes. Huber *et al.* described lakes with total N/total P values >30 as P-limited, and calculated averaged TSI (TSI(AVG) for these lakes as the mean of TSIs based on Secchi depth (TSI(SD)), Chl *a* (TSI(Chl *a*) and total P (TSI(TP)). Lakes with total N/total P values <10 were described as N-limited, and TSI(AVG) was

calculated as the mean of TSI(SD), TSI(Chl *a*) and TSI(TN). Huber et al. regarded lakes with total N/total P values between 10 and 30 as nutrient-balanced, and noted that nutrient-Chl *a* relationships were different in these lakes than in nutrient-limited lakes. They constructed new TSI expressions for total P (TSI(TPB) and total N (TSI(TNB) for nutrient-balanced lakes, and defined TSI(AVG) for these lakes as the mean of TSI(SD), TSI(Chl *a*), TSI(TPB) and TSI(TNB). The TSI of Huber *et al.* is the only TSI developed specifically for use in Florida lakes.

All of the trophic state indices discussed above, however, share in common their bias towards phytoplankton biomass and water-column nutrient concentrations as the relevant indicators of primary production in lakes, and they give no importance to the presence of macrophytes. Porcella *et al.* (1980) constructed a multivariate index based on Carlson's (1977) subindices and included a term derived from percent-area coverage of macrophytes. Because Porcella *et al.'s* TSI was developed for north-temperate lakes that are P-limited and demonstrate hypolimnetic oxygen deficits during stratification, this TSI might be inappropriate for use in Florida. The macrophyte term also failed to quantify nutrients contained in macrophyte biomass as other TSIs using water-column total P quantify the nutrients contained in phytoplankton biomass.

Canfield *et al.* (1983a) proposed a new approach to trophic state classification of lakes that gave consideration to nutrients contained in macrophyte biomass as well as to water-column nutrient concentrations. They quantified the amount of P contained per unit of dry weight in many species of macrophytes from 6 Florida lakes.

Next they estimated the macrophyte biomass in each lake from the area covered by macrophytes and the macrophyte density in kg of wet biomass per square meter. This permitted calculation of the kg of P contained in macrophyte biomass in each lake and the amount of P that would be released to the water column assuming 100% death and decomposition of the macrophytes. Dividing this mass of P by the lake volume yielded a concentration that when added to water column total P produced an estimate of the potential total P content of the water column (WCP). This approach provided more realistic estimates of trophic state for lakes such as Fairview in Orange Co., which appeared oligotrophic based on water-column nutrients and Chl *a*, but contained a large standing crop of macrophytes. The estimate of total water-column P content brought this lake to the eutrophic range, which was edaphically consistent with other lakes in the same physiographic region. Recent evidence shows that water-column P concentration in Lake Fairview has increased to the predicted WCP level because of macrophyte removal by grass carp (Canfield pers. comm.). Canfield *et al.* (1983a) noted that the same approach may be used with N for lakes that are N-limited.

Macrophytes and the Lake Ecosystem

Despite the emphasis on water-column nutrients and phytoplankton biomass to characterize lake trophic state, macrophytes are responsible for a substantial amount of the primary production that occurs in many lakes. This is especially the case in Florida because the shallow depths of Florida lakes, the high amounts of insolation and the long growing season are conditions that support

high macrophyte standing crops (Brenner *et al.* 1990). Many Florida lakes have high nutrient concentrations because of edaphic reasons or anthropogenic loading (Canfield and Hoyer 1988), and this also stimulates macrophyte production.

Macrophyte Growth Forms

Macrophyte species are often grouped into growth-form categories that describe whether or not the plants are rooted in sediments and whether they grow laterally in the water or erect and out of the water. Submerged macrophytes are those typically rooted in sediments, growing completely under the water and usually flexible due to a lack of rigid cellular tissue. *Myriophyllum heterophyllum* Michx., *Utricularia purpurea* Walt. and *Ceratophyllum demersum* L. are three examples of submerged taxa native to Florida, while another common taxon, *Hydrilla verticillata* Royle is an introduced exotic that has proliferated widely. Many submerged taxa, when growing in dense stands, are regarded as nuisance species that have a negative effect on lake recreational uses (Brenner *et al.* 1990).

Floating-leaved plants can be divided into two categories depending on whether they are rooted in sediments or not. Rooted floating-leaved plants derive most of their nutrients from the sediments (Carignan and Kalff 1980) and often have large peltate leaves growing at the surface where they have access to sunlight and atmospheric CO_2 for photosynthesis. Common examples of these taxa found in Florida are *Nymphaea* spp. (water-lily), *Nelumbo lutea* (Willd.) Pers. (American lotus), *Nuphar luteum* (L.) Sibth. & Smith

(spadderdock), *Nymphoides aquatica* (Gmel.) O.Ktze and *Brasenia shreberi* Gmelin. A second group of floating-leaved taxa are unrooted in sediments and free-floating. These taxa, which include *Lemna minor* L. (duckweed), *Pistia stratiotes* L. (water-lettuce) and *Salvinia rotundifolia* Willd., obtain their nutrients from the water and exhibit adaptations that keep the plant afloat. *Eichhornia crassipes* (Mart.) Solms. is a floating-leaved species introduced to Florida, which because of its rapid spread and prolific growth, has become a severe economic and environmental problem (Tarver *et al.* 1979).

Emergent taxa, which grow erect in shallow aquatic areas and do not depend on the water for support, demonstrate the third growth form in macrophytes. Common examples of these taxa are *Typha* spp. (cattails), which was the macrophyte with the most extensive areal coverage in a large survey of Florida lakes (Schardt 1983), and *Sagittaria latifolia* Willd.

Some taxa exhibit growth patterns that are typical of more than one growth-form category. *Hydrocotyl umbellata* L., for instance, grows mostly as a submerged plant though leaves are frequently emergent in shallow water. Portions of *Hydrocotyl* mats occasionally break away and are redistributed as floating vegetation. *Potamogeton* spp. also exhibits extensive lateral submerged growth, but bears some floating leaves at the surface.

Environmental Factors Influencing Macrophyte Distribution

Many studies have been conducted to determine which environmental factors most affect the distribution and abundance of macrophytes, and many of these studies have come to different

conclusions. Collins *et al.* (1987), for instance, compared macrophyte biomass density with 13 different chemical, physical and biological variables at various sites in Lake George, NY. They concluded that water depth was the most important factor affecting macrophyte biomass, and that substrate type and eutrophication status were of secondary importance. Canfield and Hoyer (1988) studied the influence of light and nutrient availability on macrophytes in Florida streams, and they concluded that nutrients do not regulate the abundance of macrophytes. Shading of macrophytes was the most important factor regulating macrophytes in that study, while substrate type, water depth and current velocity had a secondary influence. Jackson and Charles (1988) studied macrophyte species composition in 31 small, unproductive lakes in New York that were low in specific conductance. They concluded that pH was the regulating factor, that area, slope and substrate composition were of secondary importance, and that macrophyte distribution bore no relation to trophic state indicators. Crowder *et al.* (1977) concluded that specific conductance was as important a macrophyte determinant as pH in their study on circumneutral to hardwater lakes. Duarte and Kalff (1990) determined that alkalinity and slope were the most important factors in their study, but they explained the discrepant conclusions between studies as the result of differences in scale of analysis. When macrophytes are compared between lakes in hardwater areas, water chemistry, including specific conductance and trophic state are bound to be important determinants of macrophyte disribution (Duarte and Kalff 1990, Jackson and Charles 1988). Surveys of unproductive, dilute lakes

cover a small range of difference along the pH-alkalinity-conductivity complex, and they are likely to conclude that pH is the important variable affecting macrophyte distribution (Jackson and Charles 1988). Surveys conducted within one or a few lakes will cover only a small range of water chemisty differences, and site characteristics, such as waves, slope and sediment type, will prove to be the most important determinants (Duarte and Kalff 1990). Within a single lake, wave exposure is likely to be a leading determinant of macrophyte biomass at shallow littoral depths, whereas water transparency will exert more influence at greater depths (Duarte and Kalff 1990).

Effect of Macrophytes on Lake Ecosystem

Macrophytes seem to exert considerable effects on the nutrient cycling, biology, sedimentation patterns and senescence of the lakes in which they occur. Rooted macrophytes obtain most of their nutrients from lake sediments and thus link the sediments with overlying water (Carpenter 1981). This provides a mechanism for the regeneration of sedimentary nutrients into the water-column. Carignan and Kalff (1982) observed that living macrophytes were responsible for a 2.2% daily increase in P that represented a net seasonal input to the littoral zone because the P was derived from sediments. While P is not released from living macrophytes at a rapid rate, substantial amounts of nutrients in the macrophyte biomass are released when macrophytes die back and shoots decay. Approximately 75% of the P released is in a soluble reactive form, and P becomes rapidly assimilated by phytoplankton, leading to an

increase in water-column Chl *a* (Carpenter and Lodge 1986). Landers (1982) estimated that approximately 18% of the annual P loading in Lake Monroe, Indiana originated from senescing macrophytes. Carpenter (1981) also concluded that most of the dissolved organic carbon and dissolved total P in Lake Wingra, Wisconsin was released during decomposition of *Myriophyllum spicatum* in the littoral zone. Filbin and Barko (1985) have concluded that the release of sedimentary nutrients into the water column by macrophytes may be more significant in lakes than in reservoirs because of the riverine nature of reservoirs.

Macrophytes have several influences on the sedimentation patterns in lakes where they are found. Macrophytes tend to intercept or modify the flow of materials such as sediment from land to the pelagic zone. By reducing water velocity and wave action, macrophytes function as sediment traps in the littoral zone. This effect was shown to be significant in historical changes in sedimentation patterns of Lough Augher, Northern Ireland (Anderson 1990b). When macrophytes die, their biomass increases sedimentary organic matter content and leads to an accretion of littoral sediment that promotes infilling of the lake basin and expansion of emergent vegetation (Carpenter 1981, Carpenter and Lodge 1986). Macrophyte presence in lakes, therefore, accelerates infilling and senescence of lakes.

Macrophytes provide a complex habitat, and their presence leads to an increase in those species commonly found in littoral areas. When macrophytes are present, epiphytic algae proliferate and an increase is observed in epiphytic grazers such as snails (Carpenter

and Lodge 1986). Zooplankton are abundant in weed beds and the habitat complexity also provides cover and protection for spawning and young fish (Carpenter and Lodge 1986). Dense infestations of submerged macrophytes, nevertheless, have been shown to have a negative effect on the presence of sport fish (Shireman and Maceina 1981).

Conflicting reports have been presented about the effects of eliminating macrophytes in lakes through chemical or biological control. Carpenter and Lodge (1986) stated that because of the macrophyte role in enhancing sedimentary P recycling, an increase in macrophyte standing crop will lead to an increase in phytoplankton standing crop, whereas the long-term effect (>3 yrs.) of killing macrophytes will lead to a decrease in water-column N and P and a decrease in phytoplankton. This positive correlation between macrophyte and phytoplankton standing crop is contrary to the negative relationship reported by Canfield *et al.* (1984) between the percent of lake volume infested with macrophytes and water-column Chl *a* for 32 Florida lakes. An increase in water-column P concentrations and phytoplankton standing crop has been shown following herbicide application to macrophytes in Florida lakes because of nutrient release by the decaying plant material (Richard *et al.* 1984). An increase in water-column P was also reported following biological control of macrophytes using the grass carp *Ctenopharyngodon idella* because of nutrient release from feces, although this increase seems less dramatic because of the retention of P in the fish biomass (Richard *et al.* 1984, Canfield *et al.* 1983b, Canfield *et al.* 1984).

The Relationship of Macrophytes With Epiphyton

Epiphytic algae growing in macrophyte beds often exhibit high concentrations of biomass and are responsible for a significant proportion of the primary production in a lake. Allen and Oceuski (1981), for instance, determined that algal epiphytic production in Lake Ohrid, Yugoslavia was higher than the production they observed in littoral or pelagic algae. Cattaneo and Kalff (1980) observed that the epiphytic algae in eutrophic portions of Lake Memphremagog, Quebec fixed more carbon than macrophytes did throughout the growing season. Fontaine and Ewel (1981) estimated that macrophytes and their associated epiphytes were responsible for 56% of the gross production in Little Lake Conway, Florida.

The question of macrophytes as a nutrient source for their epiphytic algae has been a much-debated issue often referred to as the "neutral substrate hypothesis" in the literature. Cattaneo and Kalff (1979) observed no significant difference in epiphytic production on *Potamogeton richardsonii* and artificial plants made of plastic. They concluded that macrophytes functioned as neutral support structures. Carignan and Kalff (1982) studied epiphytic algae growing on fully ^{32}P labelled *Myriophyllum spicatum* and concluded that epiphytes derived only 3.4-9.0% of their P from the labelled macrophytes, and that macrophytes were more important to epiphytes for support than as a P source. Gough and Gough (1981) took issue with Cattaneo and Kalff (1979), and cited Hutchinson's (1975) statements that macrophytes release by-products of nutrient assimilation, photosynthates and inorganic nutrients. They argued

that although some macrophytes may be neutral hosts, others affect epiphytic production or community composition. Cattaneo and Kalff (1981) replied that epiphytic biomass was mostly related to the surface area of the substrate on which the epiphytes grow, and that water chemistry exhibits a greater influence than macrophytes on epiphytic production.

Recent studies by Burkholder and Wetzel (1990) seem to offer a more definitive explanation of macrophyte influence on epiphytes. They measured alkaline phosphatase (APA), an enzyme that catalyzes hydrolysis of organic P compounds to release orthophosphate, in epiphyton growing on natural and artificial plants. They observed, as did Cattaneo and Kalff (1979), that APA concentrations were higher in epiphyton growing on artificial substrates than they were in epiphyton growing on macrophytes. Burkholder and Wetzel concluded that epiphyton on artificial substrates are P-limited and synthesize APA to provide a P source, although the epiphyton growing on macrophytes were not P-limited because of nutrient release by the macrophytes.

Epiphyton can in turn exert effects that influence the growth of their macrophyte hosts. Nutrients are usually in abundant supply to rooted macrophytes, and macrophytes generally do not seem to compete with epiphyton for this resource. When epiphyton biomass is high, however, epiphyton may shade their macrophyte hosts (Eminson and Moss 1980). Filbin and Barko (1985) observed that epiphytic biomass in Eau Galle Reservoir, Wisconsin comprised up to 33% of the macrophyte and epiphyte biomass, and they concluded that epiphyton may have limited macrophyte growth by light

attenuation. Sand-Jenson and Sondergaard (1981) studied phytoplankton and epiphyton shading effects on macrophytes in Danish lakes. In oligotrophic, silicate-poor lakes, the water was responsible for most of the light attenuation. Epiphyton were responsible for 50% of the light attenuation to macrophytes in oligotrophic, silicate-rich lakes receiving N supply. In a lake that had a high nutrient supply, they determined that epiphytes were responsible for 86% of the light attenuation to macrophytes. Sand-Jensen and Sondergaard concluded that the shading effects that epiphytes exert on macrophytes becomes a decisive factor limiting depth distribution of macrophytes in lakes with high nutrient supply.

Substrate Specificity and Growth Forms of Periphyton

Some studies have indicated a high degree of substrate specificity by epiphytic and periphytic diatoms. Round (1956) characterized diatom taxa growing on plants (epiphytic) as "attachment" types mostly of the genera *Achnanthes*, *Cymbella* and *Epithemia*, whereas diatoms found on sediments (epipelic) were actively motile and unattached, including the genera *Navicula*, *Amphora* and *Diploneis*. Round noted, however, that diatom taxa growing on stones (epilithic) were similar to epiphytic diatoms. Siver (1978) observed that the diatom genera *Achnanthes*, *Cocconeis* and *Eunotia* were the most abundant taxa growing on *Potamogeton robinsii*. Blindow (1987) stated that the composition of epiphyton on *Potamogeton* and *Chara* was different than the epiphytic composition on *Nitellopsis* that was heavily marl-encrusted. Eminson and Moss (1980) observed that host specificity of periphyton was greater in

oligotrophic lakes because of the importance of macrophyte nutrient loss to epiphytes, whereas host specificity was less pronounced in mesotrophic and eutrophic lakes because of the greater effect of water-column nutrients on periphytic taxa.

Several studies have demonstrated the importance of diatom growth form to patterns of colonization and physical structure of epiphytic diatom communities. *Achnanthes* and *Cocconeis* are solitary cells that lie adnate to the substrate and colonize horizontally, and these genera are usually the initial colonizers on new substrate (Robinson and Rushforth 1987). Later colonizers must contend with space limitations, and genera such as *Gomphonema* and *Cymbella* are at an advantage because they grow on long stalks and colonize in a vertical orientation (Roemer *et al.* 1984, Robinson and Rushforth 1987). This upward expansion of the epiphytic community improves light and nutrient availability for taxa in the higher tiers (Hudson and Legendre 1987), though some adnate forms below such as *Cocconeis placentula* var. *euglypta* (Ehr.) Cl. exhibit shade tolerance (Robinson and Rushforth 1987). Swift-moving taxa capable of complex movements including *Nitzschia* and *Navicula* can be observed within the community matrix (Hudson and Legendre 1987). As the thickness of periphyton on the substrate becomes too great, cells on the outer tiers are subject to loss by grazing or sloughing off by currents (Roemer *et al.* 1984, Hudson and Legendre 1987). Sloughed off periphytic taxa can become part of the planktonic drift and are then referred to as tychoplanktonic (Lowe 1974).

Methods for Reconstructing Historical Macrophyte Communities

Historical macrophyte presence has been traditionally determined from lake sediments by methods that do not yield quantitative estimates of standing crop. Macrophyte presence has been assessed historically from macrophyte remains, pollen and seeds that are found in lake sediment. Davis (1985) studied historical macrophyte presence in upper Chesapeake Bay and summarized many of the biological and diagenetic factors that obscure accurate reconstruction of former macrophyte communities. Seed preservation is poor in some taxa (e.g. *Vallisneria* and *Potamogeton*) and seed dispersal is poor in others (e.g. *Myriophyllum*) leading to under-representation of these taxa in sediments. Pollen and seed production is variable among species of macrophytes (Yeo 1966, Birks 1980), and plants producing larger quantities of these may be over-represented in the sedimentary record. Seeds and pollen also may be unreliable indicators of macrophyte standing crop because a large number of species reproduce vegetatively by budding, fragmentation and by plants arising from stolons and rhizomes (Tarver *et al.* 1979).

Seed representation in the sedimentary record may be affected by differential transport and palatability (Birks 1980). Birks (1973) and Watts (1978) have shown that seed dispersal is often localized for macrophyte taxa. Dispersal patterns, therefore, can cause a high degree of spatial variability of macrophyte indicators in lake sediment. Sampling from many littoral sediment cores is required to obtain a reliable reconstruction of macrophyte history.

To summarize, traditional methods of macrophyte community reconstruction tend to over-represent, under-represent or miss entire portions of the macrophyte community. No single method has been developed that will provide reasonably accurate quantitative estimates of historical macrophyte standing crop.

Diatom Methods in Paleolimnology

Some Quantitative Diatom Methods Used in pH Reconstructions

Most quantitative work using diatoms to reconstruct past limnological conditions has been concerned with lake acidification due to anthropogenically induced acid precipitation. The large number of lake acidification studies recently funded (Davis 1987) indicates that lake acidification has occupied an important place on the agenda of national and international environmental concerns. The high costs of implementing more rigid air pollution standards necessitated statistical rigor to determine if atmospheric loadings of sulfur and N oxides were having significant fallout effects on aquatic ecosystems. As a consequence, lake acidification studies received priority funding and were numerous. Davis (1987) reviewed many such studies that used diatoms to infer historical pH trends.

The earliest quantitative index relating diatom assemblages to pH of lakewater was the α index described by Nygaard (1956), a ratio of acidic to alkaline diatoms in a sample based on the pH autecological classifications (Hustedt 1937-38) of the individual taxa. Renberg and Hellberg (1982) developed the somewhat more sophisticated index B that was also a ratio of the percentage of diatoms in pH autecological categories. These authors regressed log-

transformed index B values with pH for a set of 30 Swedish lakes and produced a model with which they assessed lake acidification due to atmospheric deposition in Sweden. Index B is somewhat statistically dubious, however, because coefficients for the autecological terms could not have been calculated by a simple linear regression between pH and log index B as indicated by Renberg and Hellberg (Whitmore 1989).

Cluster analysis has been used to identify diatom assemblages characteristic of various pH conditions (e.g. Davis and Anderson 1985). Charles (1985) used cluster analysis to group diatom species with similar pH requirements and he performed a multiple regression of these clusters with pH values of 38 Adirondack lakes. His model explained approximately 90% of the variance in pH in his calibration data set.

Davis and Berge (1980) performed a stepwise multiple regression of 33 taxa in a set of Norwegian lakes and produced a model consisting of 7 taxa that explained 93% of the variance in pH (unadjusted R^2). Dixit and Evans (1986) have shown, however, that particularly in lakes with spatial variability in diatom assemblages, the use of indicator assemblages rather than individual taxa in predictive models will greatly reduce the error term. Hustedt's (1937-38) pH autecological categories have also been used in multiple regression equations to develop pH predictive models based on diatom assemblages (Davis and Berge 1980, Charles 1984, 1985).

Ordination techniques, which reduce the number of diatom variables in a model, have been used to construct pH predictive equations. Principal components analysis is an indirect ordination

technique that was used to develop models for assessing lake acidification in Maine and Norway (Davis and Berge 1980, Davis and Anderson 1985). Davis and Anderson (1985) found that principal component models were less sensitive than multiple regression models using individual taxa to variation in the frequencies of taxa caused by environmental factors other than pH. Van dam *et al.* (1980) also used a principal components procedure to calibrate diatom models and assess the effects of acid precipitation on Dutch moorland pools.

Reciprocal averaging (RA) is another indirect ordination technique that has been used in diatom-based models. Charles (1985) used reciprocal averaging to ordinate diatom data and he correlated RA axes with environmental variables in a set of Adirondack lakes. pH was a primary determinant of diatom assemblage composition in that set of lakes and a regression equation predicting pH from Charles' first RA axis explained 90% of the variance in pH. In other environmental applications, Servant-Vildary and Roux (1990) have used reciprocal averaging to determine the effects of ionic elements on diatom species composition in saline lakes of the Bolivian Altiplano.

Canonical correspondence analysis (CANOCO) is a direct ordination technique that has been used in pH reconstructions to define axes that are combinations of taxa responding directly to pH. The axes have then been regressed with pH and the resulting models used to document historical trends in lake acidification. Battarbee *et al.* (1988), for example, used CANOCO to assess the acidification of

Scottish lochs and their recovery following abatement of atmospheric sulfate emissions in the United Kingdom.

Diatom Methods for Reconstructing Trophic State

Historical trophic state studies generally have not received the degree of quantitative treatment that studies of lake acidification have. Diatom/trophic reconstructions have often relied heavily on autecological information of specific taxa for qualitative interpretation of diatom percentage diagrams from lake sediment cores. Brugam (1978), for instance, documented the eutrophication of Linsley Pond in Connecticut and Bradbury (1975) used diatoms to interpret the history and eutrophication of Minnesota lakes. Battarbee (1978) observed the influence of land use and sewage effluent on the eutrophication of Lough Neagh, Northern Ireland. Håkansson (1982) presented an excellent ecological analysis of the diatom flora from Håvgårdssjön in Sweden and documented eutrophication after 1900 due to agricultural activity. Qualitative studies have provided understanding of gross trends in the trophic trajectory of lakes because of climatic patterns and anthropogenic influence, but they have lacked ability to discern subtle trophic differences, assess rates of change or demonstrate statistical significance.

Ratios have been proposed that quantitatively describe lake productivity using the percentages of diatom species separated at high taxonomic levels. Nygaard's (1949) C/P index was a ratio of the number of valves in the diatom orders Centrales and Pennales. High C/P values were thought to indicate eutrophic conditions because of

the supposed eutrophic preference of Centrales, a notion refuted by the wide range of trophic preferences actually observed for centric taxa (Battarbee 1979). Stockner and Benson (1967) studied historic trends in Lake Washington and proposed the A:C index, a ratio of the number of valves in the tribe Araphidiniae to the number of valves in the order Centrales. Centrales were assumed to be oligotrophic rather than eutrophic indicators in this scheme. Stockner (1971) later qualified the conditions under which this index would accurately indicate trophic state, but subsequent studies (e.g. Brugam 1979, Battarbee 1979, Carney 1982, Charles 1985, Whitmore 1985) have shown that the A:C index is not a useful indicator of lake trophic status. The essential problem with these indices is that they assume ecological uniformity of diatom species over broad taxonomic groupings, whereas the individual species actually have ecologically diverse requirements (C. Reimer pers. comm.).

Schelske *et al.* (1983) examined concentrations of biogenic silica in sediment cores from the Great Lakes. Increases in biogenic silica were shown over time in the sediments of all of the Great Lakes because eutrophication led to a more rapid production and sequestering to sediments of diatom valves. The peak in sedimentary storage of biogenic silica in Lakes Ontario and Erie occurred in the 1800's and was followed by a decline that resulted from silica limitation (Kilham 1971) as these lakes continued to eutrophicate. Sedimentary biogenic silica increased after 1940 in Lake Michigan and reached a maximum abundance in 1964, after which it declined. Stoermer *et al.* (1990) used cluster analysis to delineate diatom zonation in a sediment core from Lake Michigan

and determined that changes in diatom species composition support the eutrophication inferences of sedimentary biogenic silica. Schelske (1988) demonstrated that recent declines in sedimentary biogenic silica are consistent with historic water concentration data that showed a decline in dissolved silica in Lake Michigan.

Whitmore (in press) studied the relationship in Florida lakes between sedimentary diatom concentrations and accumulation rates and lake trophic state as indicated by a TSI based on water-column Chl *a*. Both periphyton and planktonic diatom concentrations were positively correlated with water-column Chl *a*. Because diatom accumulation rates were determined by three order of magnitude differences in sedimentary diatom concentrations rather than by the small range in bulk sediment accumulation rates, sedimentary diatom concentrations were shown to be more expedient predictors of Chl *a* than diatom accumulation rates. Sedimentary concentrations were found to be unreliable predictors of trophic state when factors such as silica limitation or blue-green bacterial inhibition limit phytoplankton production, or when post-depositional changes affect preservation of diatom valves.

Bailey and Davis (1978) used a multiple regression of diatom taxa to predict water-column total P in a set of 19 lakes in Maine. The best model explained 96% of the variance of total P in these lakes, but contained only a few species of *Fragilaria* as independent variables. Such models based on a limited number of taxa may prove unreliable when applied to lakes outside of their calibration data sets because of the large number of environmental factors that can influence the distribution and abundance of species (Patrick

1973). Predictive approaches that utilize groups of taxa are generally more reliable than those based on a limited number of taxa (Battarbee 1979).

Diatom indices have been proposed that used trophic autecological classifications of taxa for lakes in Florida (Whitmore 1985, 1989) and in Canada (Agbeti and Dickman 1989). In both of these studies, diatoms were classified into 5 autecological categories, and their percentages were structured into an index similar to indices used for pH reconstructions (Nygaard 1956, Renberg and Hellberg 1982). Log-transformed values of the indices were regressed with log-transformed total P and Chl *a* in the Canadian lakes and with TSI(TP) and TSI(Chl *a*) in Florida lakes. Log-transformed values of the diatom inferred trophic index (D.I.T.I.) (Agbeti and Dickman 1985) explained 71% of the variance in log-transformed total P in the Canadian lakes, and the TROPH 1 index (Whitmore 1989) explained 83% of the variance in TSI(TP) in Florida lakes. Agbeti and Dickman concluded that the D.I.T.I. diatom index was influenced by unspecified environmental factors. Whitmore showed that pH was an important covariable affecting diatom assemblages in the Florida lakes, though partial correlations demonstrated that the predictive model using the TROPH 1 diatom index was not statistically confounded by pH. Despite the fact that silica limitation or cyanobacterial inhibition may affect paleoproductivity inferences based on diatom accumulation rates (Anderson 1990c), the TROPH 1 index still seems useful because diatom assemblages are qualitatively distinct at the high nutrient conditions where their populations are limited (Whitmore in press).

Canfield (pers. comm.) pointed out that while diatom indices such as TROPH 1 may be accurate predictors of water-column total P, they are not comprehensive indicators of lakewide trophic state because they ignore the important component of primary production that is in macrophytes.

Anderson *et al.* (1990) used the reciprocal averaging (RA) indirect ordination method to study historical changes in lake trophic state in Lough Augher, Northern Ireland resulting from loading and later re-direction of nutrients from point sources. Anderson *et al.* did not correlate RA axes with water quality indicators to quantitatively assess trophic state changes, but instead plotted RA axes against each other to graphically depict assemblage similarity and ecological change.

Charles (1985) investigated the relationship between lake-water characteristics and sedimentary diatom assemblages in 38 Adirondack lakes. Charles used reciprocal averaging to determine which environmental variables influenced the diatom assemblages, and found that total P was a weak correlate with the first RA axis. He concluded that pH proved a more important determinant of diatom assemblage composition in the Adirondack lakes because those lakes spanned a wider range of pH than of trophic state.

Huttunen and Meriläinen (1986) used detrended correspondence analysis, another indirect ordination method, to interpret historical limnological trends in a Finnish lake and were able to demonstrate eutrophication following deforestation and the inception of agriculture, as well as recent lake acidification.

Fritz (1990) used the canonical correspondence option of CANOCO (ter Braak 1987) in a constrained ordination of 127 diatom taxa in 64 lakes of the northern Great Plains. The ordination axis was constrained by the variable salinity, which resulted in a predictive model that Fritz used in reconstructing historical changes in the salinity of Devils Lake.

In recent studies of Canadian lakes (Christie and Smol 1990, Hall and Smol 1990), attempts to construct trophic predictive models have involved canonical correspondence analysis as an explanatory ordination method to identify limnological variables affecting diatom assemblages in lakes having a wide range of trophic state but a narrow range of pH. Weighted averaging calibration (Line and Birks 1990) was then used as the regression method to construct transfer functions and determine historical changes in trophic variables. Anderson (1990c) examined the weighted averaging approach to quantitative trophic-state reconstruction and warned that weighted averaging studies largely utilize open water phytoplankton and v chemical data, and that they ignore littoral community production and chemistry. Anderson suggested that modeling methods should be coupled with the use of multiple cores to calculate whole-basin diatom accumulation rates that would give a reliable measure of both plankton and periphytic paleoproduction.

Comments on Statistical Methods

Cluster analysis is a statistical method that groups observations into clusters that reflect their similarity without *a priori* consideration of which factors are influencing the similarities.

Cluster analysis of diatom assemblages from a set of lakes, for instance, would result in clusters of diatom species that demonstrate a similar response to the environmental variables responsible for between-lake variance in the assemblages.

Indirect ordination techniques, which include reciprocal averaging, principal components analysis and detrended correspondence analysis, reduce the number of variables (e.g. diatom taxa) by combining the variables into a series of linear combinations of the original variables called ordination axes. With indirect ordination methods, ordination axes are just particular combinations of variables that are uncorrelated and appear in the order that best explains the variance within the data set. The relationship between indirect ordination axes and environmental variables that influence the data set can then be determined by correlating axes with environmental variables. Other ordination axes, however, may be more suitable for establishing the relationship between the taxa and specific environmental variables influencing diatom assemblages.

Canonical correspondence analysis (CCA), included in canonical community ordination (CANOCO), is a direct ordination technique in which variables are combined into ordination axes that are constrained by specific environmental variables (ter Braak 1987). Ordination axes are independent and uncorrelated, and are created in order of their variance explained by the environmental variables. CANOCO, therefore, effectively inserts a regression model into the ordination model. When a single environmental variable is specified in the CCA procedure, CANOCO can be used to obtain eigenvectors to

construct a calibration model for that environmental variable (ter Braak 1987).

Principal components analysis is a linear ordination method in which species demonstrate a linear response over the ordination axes and species coefficients, called eigenvectors, are calculated as slopes of those lines. In weighted averaging methods, which include detrended correspondence analysis (DCA), species are assumed to respond in a modal fashion over the ordination range, and coefficients are equal to the center or optimum of their distribution curve along the range of ordination values (ter Braak 1987). CANOCO is an extension of DCA that also assumes a modal species distribution over ordination axes (ter Braak 1987).

Reciprocal averaging (RA), or factor correspondence analysis, is an extension of principal components. Hill and Gauch (1980) compared RA and DCA and concluded that DCA was a better method. A main fault they cite with RA is that the second ordination axis demonstrates an 'arch effect' that is a mathematical artifact relating to no real structure in the data. Charles (1985), for instance, observed this arch effect in his study of diatom communities of Adirondack lakes and found it made ecological interpretations difficult. A second fault of RA is that it does not preserve ecological distances between species along the ordination axes (Hill and Gauch 1980). Anderson *et al.* (1990) have presented, on the other hand, an argument that RA is a preferred method over DCA because DCA destroys spatial relationships between successive samples that is necessary to demonstrate a time trajectory of community response in

sediment cores, and it interferes with assessment of the importance of species on samples.

Effects of Spatial Variation on Diatom Assemblages

In paleolimnological work, there is frequently an implicit assumption that diatom assemblages have been homogenized by resuspension prior to deposition so that a single surface-sediment sample or a sediment core reflects lakewide mean limnological conditions. If spatial variability exists in species composition of diatom assemblages in surficial sediments, variance is introduced into the calibration data sets used for models describing diatom/limnological relationships. Spatial variability in diatom assemblages from sediment cores may also affect the precision of historical inferences.

Anderson (1990a) studied variability in diatom concentrations and accumulation rates in 10 sediment cores from Lough Augher and found that diatom accumulation rates and concentrations were not spatially uniform. Differences resulted partly from variance in bulk sediment accumulation rates that was not related in a predictable way to water depth (Anderson 1990b). Factors including localized resuspension, stream inputs, slumping and the effects of macrophytes on wind circulation patterns were responsible for the spatial differences in sedimentation rates. Anderson concluded that no single sediment core reflected the mean accumulation rate of the whole basin.

Studies on the spatial heterogeneity of species composition in surficial sediment samples have shown that no single sample

represents an "average" lakewide diatom assemblage (Earle *et al.* 1988). Variance due to site seems to increase when habitat specificity of taxa is considered, i.e. when planktonic and periphytic taxa are separated (Dixit and Evans 1986, Anderson 1990a). Planktonic taxa typically show greater representation in deeper water, whereas periphytic taxa show relatively little redistribution and are more abundant in the littoral zone. With respect to spatial variation within a lake basin, periphyton contribute a substantial amount of the variance observed in diatom assemblages because their substrate preferences lead to patchy distributions (Earle *et al.* 1988). In a sediment core from any particular site in a lake, however, periphytic diatoms tend to demonstrate more even accumulation rates than do planktonic taxa (Anderson 1990a, 1990b).

Spatial variation in subfossil diatom assemblages does not seem to invalidate construction of calibration data sets using single samples from each lake when lakes are sampled over a limnological range. Earle *et al.* (1988) have shown that single-sample, between-lake differences are high enough to indicate that the comparison of diatom assemblages between lakes is valid if samples are retrieved from deeper areas with gentle slopes rather than from steep-sloped areas.

Spatial variation does not preclude meaningful application of predictive models to historical samples provided that the effects of sample variance on inferences are understood. Anderson (1990a) showed that sediment cores retrieved from deeper water sites consistently demonstrated greater resolution of historical changes in

limnology than cores taken in littoral areas. Although taxon resolution varied with sediment core site, each core from Lough Augher gave fundamentally the same record of eutrophication. Dixit and Evans (1986) concluded that when time or financial constraints are important, a sediment core from the deepest site on a lake will provide a reliable indication of historical trends in pH. Because of differences in pH inferences from various sites, however, Dixit and Evans indicate that it is important to analyze several sediment cores and demonstrate replicability for absolute inferences.

Purpose

The purpose of this study is to develop methods that would permit quantitative assessment of historical macrophyte biomass in lakes using sedimentary indicators. Macrophyte standing crop has been documented to be high (Canfield *et al.* 1983a) in lakes such as Fairview in Orange Co., Florida that appear oligotrophic and have been used for calibration of diatom/trophic state models (Whitmore 1989). Conventional paleolimnological reconstructions of trophic state have focused on inferring water-column nutrient concentrations principally from planktonic diatom assemblages, but they have ignored the often substantial component of primary production occurring in macrophytes.

Historical inferences of lower water-column nutrient concentrations obtained with existing diatom predictive models don't necessarily indicate that lakes were formerly less productive. A negative correlation has been shown between water-column nutrient concentration or phytoplankton biomass as measured by Chl *a* and

macrophyte biomass (Canfield *et al.* 1983a, Canfield *et al.* 1984). Historic samples indicating low water-column nutrient concentrations may represent times of high macrophyte production, especially if the cyclic changes in water level of Florida's shallow lakes (Deevey 1988) promote a periodic lakeward expansion of macrophyte beds. If the trophic trajectory of lake ecosystems over time is to be fully understood, a more holistic consideration of historical trophic state is required, one that includes the macrophyte component of production.

Conventional sedimentary indicators of macrophytes are not appropriate for quantitative reconstructions for a variety of reasons:

1) pollen and seed production is species specific quantitatively and is often absent in plants such as *Hydrilla* that largely undergo vegetative reproduction. Models predicting historical macrophyte standing crop from sedimentary pollen or seeds would have to be calibrated for each individual species;
2) there are no known photosynthetic pigments that would be preserved in sediments and that are specific to macrophytes;
3) diagenesis often affects the preservation of macrophyte remains.

Diatoms are considered as potential macrophyte indicators in this study because diatoms are usually well-preserved in lake sediments and they are ecologically specific. Life-form classifications are available (Lowe 1974) that permit separate consideration of planktonic and periphytic taxa. Sedimentary concentrations and accumulation rates of periphytic taxa might be expected to demonstrate a positive correlation with the amount of submerged macrophyte biomass for 2 reasons. First, a positive relationship exists between periphytic biomass and the increased substrate area afforded by macrophytes with many small or finely-dissected leaves such as *Hydrilla* (Cattaneo and Kalff 1981). Secondly, evidence also

indicates that diatom biomass might be stimulated by nutrient release from macrophyte substrates (Burkholder and Wetzel 1990).

The specific objectives of this study are to:

1) obtain information on diatom assemblages in a calibration set of Florida lakes that represent a wide range of macrophyte presence;
2) identify periphyton and planktonic components of the assemblages;
3) perform explanatory analyses to determine which variables influence diatom assemblages over the range of macrophyte presence;
4) construct predictive models that could be used to quantitatively assess historical macrophyte standing crop using percentages, sedimentary concentrations or accumulation rates of diatoms; and
5) derive a plan to assimilate historic macrophyte inferences into a scheme that permits a more complete assessment of former lake trophic state than models restricted to concentrations of water column nutrients.

I propose to develop new multivariate models predicting historical macrophyte presence in the following manner. For explanatory analyses of diatom communities, a cluster analysis will be used to identify diatom taxa with similar ecological responses. An indirect (unconstrained) ordination method, such as PCA, will be used to ordinate taxa in linear combinations that best explain the variance between assemblages. The ordination axes will then be correlated with environmental variables to determine which variables exert the greatest influence on diatom assemblages. Multivariate predictive models will be constructed by stepwise linear regression of taxa and by the direct ordination method canonical correspondence analysis, in which the linear combinations of diatom taxa are constrained in a manner best explained by the limnological variables of interest.

CHAPTER 2

METHODS

Collection of Sediment Samples

Sediment samples were collected from the sediment-water interface of 30 Florida lakes. Lakes chosen for study were those named in data sets (Canfield and Duarte 1988, Canfield unpub. data) that contained data on macrophyte abundance. Lakes were selected to cover the range of macrophyte presence as uniformly as possible. Sediment samples were collected in two sets of field surveys. Survey Set 1 consisted of samples from 10 lakes collected in the Spring of 1982. Samples were collected at a mid-lake station using an Ekman dredge. Volumetric portions were removed with a pipette and transferred to 125-ml Nalgene bottles. Sediment samples in Survey Set 2 were collected between November 1987 and May 1988 from 20 additional Florida lakes. These samples were collected with a 77-cm long, 8.8-cm diameter acrylic piston corer that was driven into the sediment with 1 m long sections of magnesium-zirconium coring rods. Water above the sediment-water interface was removed by aspiration. The top 2 cm of sediment was collected with a syringe and transferred to 125 ml Nalgene bottles.

Laboratory Analyses

Sediment samples were subdivided in the Paleoecology Laboratory of the Florida Museum of Natural History for diatom analyses, estimation of bulk sediment accumulation rates by ^{210}Pb assay, and determination of percent organic matter.

Sediment samples for diatom analyses were cleaned using hydrogen peroxide and potassium dichromate (Van der Werff 1955). Digested samples were diluted with deionized water in 400-ml beakers and settled overnight. The supernatant solutions were removed by vacuum aspiration and the process of dilution, settling and aspiration was repeated until the dichromate color was no longer visible. Cleaned samples were suspended in 60 ml of water and settled onto coverslips in evaporation trays (Battarbee 1973). Dried coverslips were mounted on glass slides using Hyrax mounting medium.

A minimum of 500 diatom valves was counted and identified on a single slide of each sample using an American Optical Microstar microscope at 1500X with a dark-phase condenser. Each diatom valve was identified to the lowest taxonomic level possible using standard diatom floras including those of Patrick and Reimer (1966-1975) and Hustedt (1930,1930-1966).

The concentration of diatoms (D CONC) in the sediment samples was calculated with the following formula:

$$D\text{-}CONC = C(PVD)^{-1}$$

where D-CONC = number of frustules g^{-1} dry weight of sediment
C = number of valves counted
P = proportion of settling tray area counted

V = cm^3 of sediment in initial sample
D = g dry weight of sediment cm^{-3} of initial sample.

Life-form autecological information for the majority of diatom taxa was obtained from the literature (Lowe 1974, Patrick and Reimer 1966-1975, Hustedt 1930). The concentrations of periphytic valves (PERICONC) and euplanktonic valves (PLNKCONC) were calculated by multiplying the concentration of diatoms in the samples by the proportion of periphyton and euplankton in each sample. Tychoplanktonic diatoms normally show a periphytic life-form, though are often suspended with the plankton (Lowe 1974). Tychoplanktonic taxa were arbitrarily assumed to be 1/3 euplanktonic for these calculations.

Bulk-sediment accumulation rates were measured for each sediment sample using the Binford and Brenner (1986) dilution tracer method based on ^{210}Pb assay. ^{210}Pb assay for 8 lakes from Survey Set 1 was performed by a modification of the Eakins and Morrison (1978) method that involved estimating ^{210}Pb recovery of samples from the proportion of recovery onto copper planchettes of a ^{208}Po spike. Atmospherically derived (unsupported) ^{210}Pb activity was calculated as the difference between total residual ^{210}Pb activity in the samples and an average supported ^{210}Pb activity (0.80 pCi g^{-1}) that was estimated from sediment cores of nine other Florida lakes (Binford and Brenner 1986).

Sediment samples for ^{210}Pb assay of Survey Set 2 lakes were dried, ground with mortar and pestle and weighed. These samples were sealed in polypropylene tubes for greater than 3 weeks to permit ingrowth of ^{226}Ra daughter products. Radionuclide activity

was then measured using an ORTEC Intrinsic Germanium Detector connected to a 4096-channel multichannel analyzer. The unsupported activity was obtained by difference between total residual ^{210}Pb activity and supported activity of each sample as assessed from ^{214}Bi.

Bulk-sediment accumulation rates (SEDACCUM) were estimated for samples from lakes in both survey sets using the following formula:

$$SEDACCUM = F^{210}PbA^{-1}$$

where SEDACCUM = g dry sedimentcm^{-2} yr^{-1}
$F^{210}Pb$ = flux of ^{210}Pb fallout (pCi cm^{-2} yr^{-1})
A = unsupported ^{210}Pb activity in sediment (pCi g^{-1}).

Annual diatom accumulation rates (D-ACCUM) were estimated as follows:

$$D\text{-}ACCUM = (D\text{-}CONC)(SEDACCUM)$$

where D-ACCUM = valves cm^{-2} yr^{-1}.

The annual accumulation rates of periphytic valves (PERIACCM) and euplanktonic valves (EUPLACCM) were obtained by multiplying the periphyton and euplankton proportions of each sample by the total diatom accumulation rates.

Subsamples of 1.001 cm^3 wet sediment were dried at 60 °C in a drying oven. Dry weight per unit volume (rho) was then measured for each sample by weighing the dry material on an Ainsworth 24N analytical pan balance. Percent loss on ignition (% L.O.I.), a measure of sedimentary organic matter content, was determined for each sample by weighing the sediment samples before and after

combustion in a muffle furnace for 1 hr at 550 °C. Percent loss on ignition was then calculated as:

% L.O.I. = 100 x (1- (sample weight before combustion/sample weight after combustion)).

Organic matter accumulation rates (ORGACCUM) were calculated with the following equation:

ORGACCUM = SEDACCUM x (% L.O.I./100)

where ORGACCUM = g dry organic matter cm^{-2} yr^{-1}.

Quantifying Macrophyte Presence

Researchers from the Department of Fisheries and Aquaculture at the University of Florida obtained quantitative macrophyte data for the survey lakes in field work conducted between 1982 and 1988. The percentage of the lake area covered by macrophytes (percent-area coverage) was obtained for 23 lakes by planimetry on morphometric maps. The area covered by submergent vegetation as estimated from recording fathometer transects (Canfield and Duarte 1988) was added to the area covered by emergent and floating-leaved vegetation. The percentage of the lake volume filled with macrophytes (percent-volume infestation) was also estimated morphometrically for 30 lakes using the percent areal coverage of submerged macrophytes and the height of submerged vegetation as indicated by fathometry (Maceina and Shireman 1980).
Morphometric data including lake surface area, shoreline length, shoreline development and mean depth were available for 24 of the survey lakes.

The average wet-weight biomass per unit area of submerged, emergent and floating-leaved macrophytes was determined from 0.25 m^2 quadrats randomly sampled from 10 transects through the littoral zones of 23 lakes. Above-ground biomass in each quadrat was collected by divers, spun to remove excess water and weighed to the nearest 0.1 kg (Canfield and Duarte 1988).

Water Chemistry Data

Median water chemistry values for the lakes in Survey Set 1 were obtained from the Florida Lakes Data Base of the Water Resources Research Center at the University of Florida. Water quality variables selected from this data set included median values for total P, total N, Chl *a*, Secchi depth, specific conductance and pH.

Mean water chemistry values were obtained by the Department of Fisheries and Aquaculture for each lake in Survey Set 2 by averaging data from 3 mid-lake stations (M. Hoyer, pers. comm.). Total P analyses were performed following persulfate digestion (Murphy and Riley 1962, Menzel and Corwin 1965), and total N was measured using a modified Kjeldahl technique (Nelson and Sommers 1975). Water samples were filtered through a Gelman type A-E glass fiber filter and Chl *a* was measured using the Yentsch and Menzel (1963) method and Parson and Strickland (1963) equations. Secchi depth was measured with a 20-cm black and white Secchi disk. Trophic state index (TSI) values (Huber *et al.* 1982) were calculated using the mean or median values of total P, total N, Chl *a* and Secchi depth for each lake in Survey Sets 1 and 2. Specific conductance was measured with a Yellow Springs Instrument Company model 31

conductivity bridge. pH was measured with an Orion 601A pH meter.

Statistical Analyses

Data for diatom, macrophyte and water chemisty variables were stored as Statistical Analysis System (SAS Inst., Inc. 1985) data sets using the University of Florida's Northeast Regional Data Center. I plotted the percent-area coverage, percent-volume infestation, and submerged, emergent and floating-leaved biomass for macrophytes against the percentage, concentration and accumulation rates of diatom species to identify taxa responding to macrophyte presence. Pearson product-moment correlation coefficients were obtained between percent loss on ignition, organic-matter accumulation rates and macrophyte variables using the SAS CORR procedure (SAS Inst., Inc. 1985). I also obtained correlation coefficients between macrophyte variables and the percentages, concentrations and accumulation rates of planktonic and periphytic diatoms. Correlation coefficients were calculated between the macrophyte variables and log-transformed concentrations and accumulation rates of diatoms. In order to determine whether morphometric and chemical variables have covariable effects on diatom-macrophyte relationships, I obtained correlation coefficients between macrophyte, morphometric and water chemistry variables.

For purposes of multivariate statistical analyses, it was essential to reduce the number of diatom species from the 223 diatom taxa observed. I examined plots of diatom percentages versus percent-area coverage and percent-volume infestation, and selected forty-seven taxonomic groups, several of which were the sum of taxa in

the same genus. Because of the large number of rare taxa present, this preserved most of the diatom information in each sample (mean = 96.6%) while substantially reducing the number of species.

Hierarchical cluster analysis was performed on the 47 taxonomic groups using the SAS VARCLUS procedure (SAS Inst., Inc. 1985). I applied this procedure to the percentages, concentrations and accumulation rates of the taxonomic groups, and repeated the procedures after partialling out the effects of TSI(AVG) and pH. Tree diagrams of the hierarchical clusters from each analysis were constructed using the SAS TREE procedure (SAS Inst., Inc. 1985). Scores for diatom clusters were obtained for each lake in the survey using standardized scoring coefficients from the cluster analyses and the SAS SCORE procedure (SAS Inst., Inc. 1985). I then correlated the scores for each cluster with macrophyte, chemical and morphometric variables using the SAS CORR procedure to determine which variables most influenced each cluster of taxa.

Principal components analyses of the percentages, concentrations and accumulation rates of the 47 diatom taxonomic groups were performed using the SAS PRINCOMP procedure (SAS Inst., Inc. 1985). I repeated the PRINCOMP procedure for each of the three models while partialling out the effects of TSI(AVG) and pH. The standardized principal component scores of the first 8 principal components in each test were calculated for the diatom assemblages in the survey lakes using the SAS SCORE procedure. I then correlated the principal component scores with macrophyte, water chemistry and morphometric variables to identify the environmental variables influencing each principal component.

Canonical correspondence analysis (CCA) was performed on the percentage data for 47 diatom taxonomic groups using the canonical community ordination (CANOCO) statistical package developed by ter Braak (1987). In the first set of computations, the diatom groups were ordinated in an axis constrained by the environmental variable percent-volume infestation. In a second set of computations, 47 diatom taxa were ordinated into an axis constrained by percent-area coverage.

Multivariate models that predict percent-volume infestation, percent-area coverage and biomass for submerged, emergent and floating-leaved plants were derived using the maximum R^2 improvement method of the SAS STEPWISE procedure (SAS Inst., Inc. 1985). I reduced the number of independent diatom variables in each stepwise regression to 20 or less, a recommended maximum for this procedure (SAS Inst., Inc. 1985), after examining plots of diatom taxonomic groups versus macrophyte variables. Regressions were performed for each macrophyte variable using percentage data for the diatom groups. The regressions for percent-area coverage and percent-volume infestation were repeated using concentration and accumulation rate data for the diatom groups.

I selected the best model in each STEPWISE regression procedure by plotting Mallows' Cp statistic versus the number of variables in each model (p) and selecting the model in which Cp was approximately equal to p (Daniel and Wood 1971). Adjusted R^2s, which show the coefficient of determination after removing the inflating effect of dependent variables, were calculated using the SAS RSQUARE procedure (SAS Inst., Inc. 1985).

Partial correlations (Ott 1977) were used to determine if predictive models were statistically free from confounding effects of environmental variables correlated with their dependent variables. I accomplished this by calculating multiple correlation coefficients as the square root of the coefficients of determination for the multivariate models. The multivariate models were then regressed with the covariant dependent variables using the SAS GLM procedure (SAS Inst., Inc. 1985), and I calculated multiple correlation coefficients for these confounded forms of the model. Partial correlation coefficients were calculated using the multiple correlation coefficients to assess whether models with correct dependent variables were significant when the effects of the covariables were held constant.

Diatom-index values (TROPH 1) (Whitmore 1989) were calculated for the subfossil diatom assemblages in the survey lakes. A predictive model was developed to yield water-column total P estimates from subfossil diatom assemblages for historic WCP (Canfield *et al.* 1983a) inferences. The 51 lakes used to construct this model were the lakes included in the present study, lakes in Whitmore's (1989) study, and Lake Francis in Highlands County. Water-column total P values for the lakes outside of the present study were median values obtained from the Florida Lakes Data Base. TROPH 1 values for subfossil diatom assemblages were regressed with water-column total P values using the SAS GLM procedure (SAS Inst., Inc. 1985).

Because of the significant negative correlation between macrophyte presence and water-column nutrient concentrations

(Canfield *et al.* 1984), it was important to assess whether macrophyte presence would have a significant confounding effect on the model for predicting water-column total P. Log-transformed TROPH 1 index values were correlated with log-transformed total P and percent-area coverage values for the survey lakes.

CHAPTER 3

RESULTS

Thirty lakes were sampled in the surface-sediment survey (Table 1). Lake Miona was removed from the data set prior to statistical analyses because the lake was observed to contain virtually no macrophytes despite a percent-volume infestation value of 86% measured by Canfield (unpub. data). Triploid grass carp had been introduced to Lake Miona by the Florida Game and Freshwater Fish Commission in the time between the macrophyte and surface-sediment surveys in order to control aquatic vegetation (M. Hoyer, pers. comm.).

Many correlation coefficients were used in this study to assess relationships between morphometric, water-chemistry and macrophyte variables and to determine which environmental variables influenced specific groups of diatoms. The criterion for significance of all correlation coefficients discussed below is the $\alpha = 0.05$ level of significance.

Water-chemistry values (Table 2a) showed that survey lakes ranged from ultraoligotrophic to hypereutrophic (TSI(AVG): 4.1 to 88.5) as determined by water-column nutrient concentrations, and from acidic to alkaline conditions (pH: 4.61 to 9.03). Total N/total P ratios suggested that Lakes Wauberg and Alligator were N-limited (Huber *et al.* 1982). Log-transformed water-column total P was

Table 1. Lake, county and sampling dates for macrophyte and diatom surveys.

Lake	County	Macrophyte date	Diatom date
Alligator	Columbia	2 Jun 1987	19 Dec 1988
Apopka	Orange	Sep 1981	27 Jul 1982
Bonny	Polk	22 Sep 1987	17 Dec 1988
Carr	Leon	7 Jul 1987	15 Jan 1989
Catherine	Marion	8 Sep 1987	8 Dec 1988
Clay	Lake	15 Jul 1986	20 Jan 1989
Crooked	Lake	9 Jun 1987	17 May 1989
Deep	Putnam	16 Jun 1987	1 Feb 1989
Fairview	Orange	Oct 1982	28 Jul 1982
Harris	Lake	12 Oct 1987	25 Mar 1989
Hartridge	Polk	11 Aug 1987	17 Dec 1989
Keys Pond	Putnam	9 Jun 1986	2 Feb 1989
Lindsey	Hernando	10 May 1988	16 Nov 1988
Live Oak	Osceola	24 May 1988	12 Jan 1989
Lochloosa	Alachua	22 Aug 1988	9 Nov 1988
Loften Ponds	Leon	16 May 1988	14 Jan 1989
Miona	Sumter	19 Aug 1986	6 Jan 1989
Moore	Leon	18 May 1988	15 Jan 1989
Mystic	Madison	Jul 1982	4 May 1982
Ocean Pond	Baker	Aug 1982	3 May 1982
Okahumpka	Sumter	Aug 1981	26 May 1982
Orange	Alachua	Oct 1982	15 Aug 1982
Patrick	Polk	21 Jun 1988	18 Dec 1988
Rowell	Bradford	9 Aug 1988	5 Dec 1988
Stella	Putnam	Sep 1981	10 Aug 1982
Tomohawk	Marion	18 Jul 1988	8 Dec 1988
Townsend	Lafayette	Jul 1981	4 May 1982
Watertown	Columbia	Aug 1982	3 May 1982
Wauberg	Alachua	22 Jul 1986	7 Nov 1988
Wildcat	Lake	Aug 1982	3 Aug 1982

Table 2a. Summary water chemistry data for survey lakes. Sources of data were Canfield (unpub. data) and Florida Lakes Data Base.

Lake	Water-column total P (mg l^{-1})	TSI(AVG)	TN/TP	pH	Specific conductance (µS/cm)
Alligator	0.320	74.9	7.4	7.9	144.0
Apopka	0.192	88.5	21.0	8.0	395.0
Bonny	0.050	71.2	37.2	7.7	255.8
Carr	0.015	42.4	58.0	6.3	25.3
Catherine	0.003	16.6	100.0	4.7	48.3
Clay	0.001	7.4	360.0	4.8	52.0
Crooked	0.007	24.3	47.1	4.6	44.3
Deep	0.002	4.1	80.0	4.6	37.0
Fairview	0.015	27.4	33.3	8.1	198.8
Harris	0.028	66.4	55.4	8.5	247.7
Hartridge	0.010	33.6	48.0	7.8	219.3
Keys Pond	0.002	6.7	85.0	5.4	42.7
Lindsey	0.017	41.2	38.2	6.8	34.0
Live Oak	0.014	35.3	25.0	7.0	131.0
Lochloosa	0.032	61.0	32.8	7.7	87.7
Loften Ponds	0.004	20.5	97.5	4.8	19.0
Moore	0.005	19.7	70.0	5.8	16.3
Mystic	0.015	25.7	34.7	6.7	28.0
Ocean Pond	0.040	46.0	10.5	5.0	45.5
Okahumpka	0.020	47.2	47.5	9.0	201.7
Orange	0.040	59.4	27.8	7.2	82.5
Patrick	0.010	35.5	147.0	8.1	320.3
Rowell	0.069	66.0	11.7	7.7	289.7
Stella	0.010	25.1	43.0	7.1	240.0
Tomohawk	0.004	15.7	52.5	4.9	34.7
Townsend	0.009	29.5	64.4	5.2	23.4
Watertown	0.062	51.7	16.9	7.4	153.3
Wauberg	0.158	77.1	9.9	7.4	80.0
Wildcat	0.008	20.9	23.9	4.8	33.0

Table 2b. Summary data for macrophyte variables of survey lakes. Source of data was Canfield (unpub. data).

Lake	Percent area coverage	Percent volume infestation	Floating -leaved biomass ($kg\ m^{-2}$)	Submerged biomass ($kg\ m^{-2}$)	Emergent biomass ($kg\ m^{-2}$)
Alligator	10	10	1.2	0.0	1.7
Apopka	3	0	1.1	0.0	2.5
Bonny	10	7	0.0	3.0	8.1
Carr	100	100	7.0	9.9	12.7
Catherine	48	9	1.1	2.9	4.6
Clay	100	76	4.5	6.8	8.1
Crooked	27	2	3.8	2.4	26.8
Deep	97	21	2.5	11.7	10.6
Fairview		33			
Harris	27	2	0.8	0.9	2.4
Hartridge	60	11	0.0	8.0	4.9
Keys Pond	40	8	0.0	1.0	2.8
Lindsey	100	80	1.3	1.8	3.0
Live Oak	100	55	0.3	1.6	2.0
Lochloosa	83	57	0.6	2.6	2.2
Loften Ponds	87	22	0.6	0.7	0.3
Moore	40	14	0.2	1.3	1.7
Mystic		78			
Ocean Pond		0			
Okahumpka	100	95	8.8	16.6	11.9
Orange		79			
Patrick	93	42	0.4	1.3	1.1
Rowell	43	10	0.3	0.0	0.4
Stella		39			
Tomohawk	43	12	0.5	1.0	1.4
Townsend		65			
Watertown	7	1	0.0	0.0	1.0
Wauberg	0	1	11.2	4.4	12.1
Wildcat		2			

Table 2c. Summary morphometric data for survey lakes. Sources of data were Canfield (unpub. data) and Florida Lakes Data Base.

Lake	Mean depth	Lake area	Shoreline length	Shoreline development
Alligator	1.1	137	5.3	1.3
Apopka	1.6	12412	54.9	1.4
Bonny	2.0	143	6.4	1.5
Carr	1.9	254	5.1	
Catherine	3.2	41	4.5	2.0
Clay	2.3	5	0.9	1.2
Crooked	2.3	8	2.0	2.0
Deep	3.0	4	1.6	2.3
Fairview		163		
Harris	4.0	5580	61.3	2.3
Hartridge	3.4	176	5.5	1.2
Keys Pond	2.9	5	1.0	1.3
Lindsey	2.2	55	3.2	1.2
Live Oak	3.0	152	5.0	1.1
Lochloosa	1.8	2309	22.6	1.3
Loften Ponds	2.6	5	2.0	2.6
Moore	2.9	28	1.8	
Mystic		19		
Ocean Pond		722		
Okahumpka		394		
Orange	1.8	5142		
Patrick	1.8	159	4.65	1.04
Rowell	1.3	147	5.18	1.21
Stella				
Tomohawk	4.4	15	4.01	2.92
Townsend	1.5	44	3.58	1.52
Watertown	3.8	19	1.64	1.06
Wauberg	3.6	100	8.35	2.36
Wildcat		94		

found to be highly correlated with specific conductance and pH (Table 3, Fig. 1). Macrophyte variables were not significantly correlated with water chemistry or morphometric variables, except for percent-area coverage, that had a significant negative correlation with TSI(AVG) (Fig. 2) and log-transformed total P (Table 3).

Two hundred twenty-three diatom taxa were found in the recent sediments of the survey lakes (Appendix 1). Initially, 125 taxa had life-form preferences described in the literature (Lowe 1974, Patrick and Reimer 1966-1975), but the average percentage of valves with unknown life-form preference was 15.04%. Life-form preferences were assumed for 28 additional taxa (Appendix 1) based on valve morphology. Taxa with a raphe that belonged to genera known to be largely periphytic were assumed to have a periphytic life-form preference. Two small species of *Cyclotella* and the long, lineate *Nitzschia romana* and *Synedra filiformis* var. *exilis* were assumed to be tychoplanktonic. These assumptions were discussed with Rex L. Lowe (pers. comm.), who believed them to be correct. The new life-form assignments reduced the mean percentage of valves with unknown life-form preference in survey samples to 2.03%.

TSI(AVG) and pH were negatively correlated with the proportion of periphytic diatoms (Fig. 3) and positively correlated with the proportion of planktonic diatoms (Fig. 4) in surficial samples (Table 4). Diatom concentrations and accumulation rates were found to vary as much as 4 orders of magnitude within the study lakes. Log-transformed accumulation rates produced more significant correlation coefficients with environmental variables than

Table 3. Pearson product-moment correlation coefficients between water quality and macrophyte variables for survey lakes. * = $p < 0.05$.

	correlation coefficient prob. > | r | under Ho: rho = 0 sample size			
	log_{10} total P	TSI(AVG)	pH	Specific conductance
Percent area coverage	*-0.558 0.007 22	*-0.518 0.014 22	-0.185 0.410 22	-0.298 0.177 22
Percent volume infestation	-0.169 0.380 29	-0.131 0.497 29	0.136 0.482 29	-0.212 0.269 29
Floating-leaved biomass	0.124 0.582 22	0.134 0.552 22	0.072 0.750 22	-0.194 0.388 22
Submerged biomass	-0.252 0.258 22	-0.219 0.327 22	0.033 0.883 22	-0.136 0.546 22
Emergent biomass	-0.124 0.582 22	-0.121 0.592 22	-0.253 0.256 22	-0.251 0.260
pH	*0.679 <0.001 29	*0.713 <0.001 29	---	*0.755 <0.001 29
Specific conductance	*0.493 0.007 29	*0.569 0.001 29	---	---

Table 3 cont'd.

	correlation coefficient prob. > | r | under Ho: rho = 0 sample size			
	Lake surface	Mean depth	Shoreline length	Shoreline develop.
Percent area coverage	-0.322 0.145 22	-0.137 0.553 21	-0.314 0.165 21	-0.173 0.452 21
Percent volume infestation	-0.106 0.593 28	-0.396 0.062 23	-0.230 0.304 22	-0.401 0.064 22
Floating-leaved biomass	-0.11 0.626 22	0.043 0.852 21	-0.084 0.717 21	0.184 0.426 21
Submerged biomass	-0.2107 0.347 22	0.0739 0.750 21	-0.238 0.299 21	-0.007 0.976 21
Emergent biomass	-0.165 0.462 22	-0.035 0.880 21	-0.175 0.449 21	0.168 0.467 21
pH	0.343 0.074 28	-0.196 0.371 23	*0.508 0.016 22	-0.370 0.090 22
Specific conductance	*0.51 0.005 28	-0.216 0.322 23	*0.563 0.006 22	-0.241 0.281 22

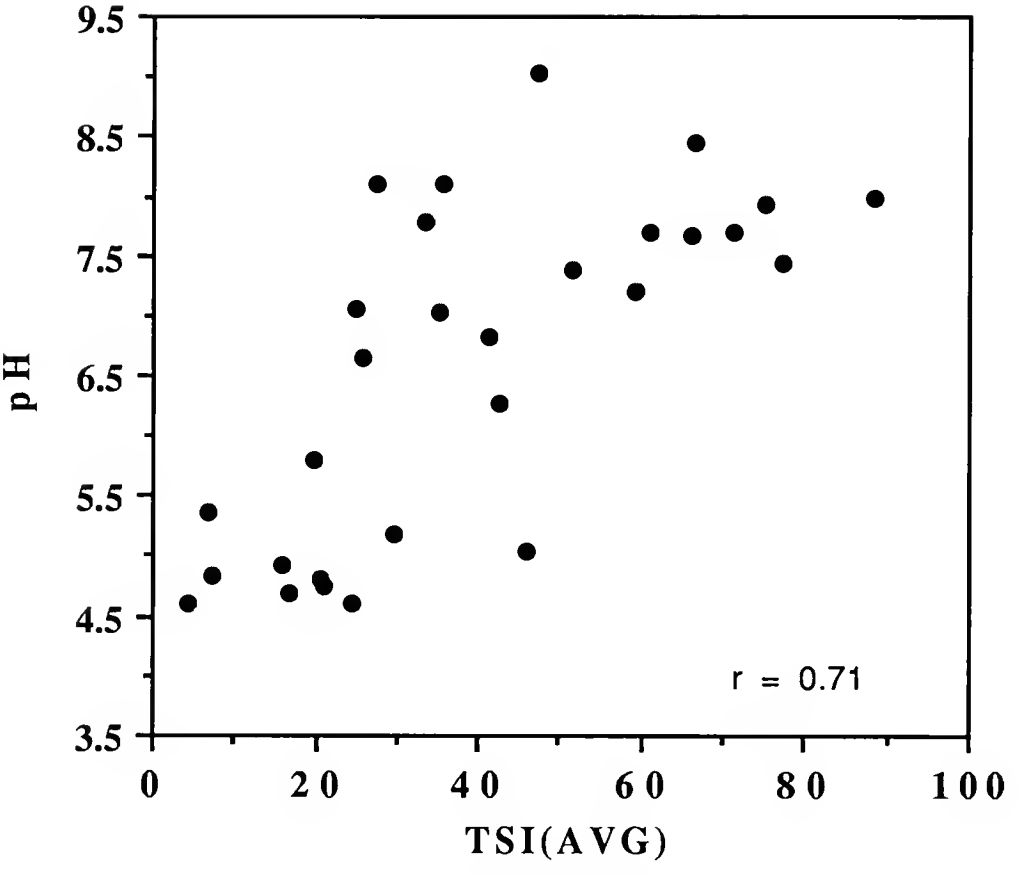

Figure 1. Plot of pH versus TSI(AVG) for 29 lakes in synoptic survey.

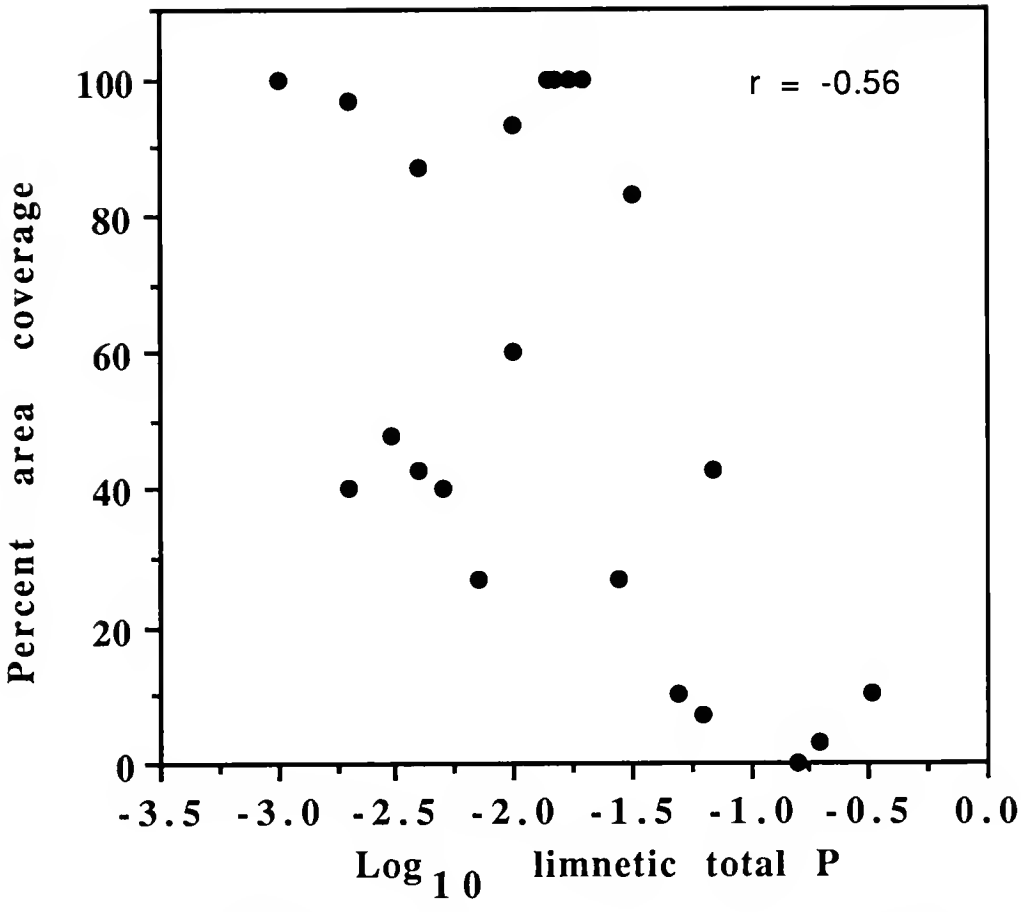

Figure 2. Plot of percent area coverage versus log-transformed limnetic total P for 29 survey lakes.

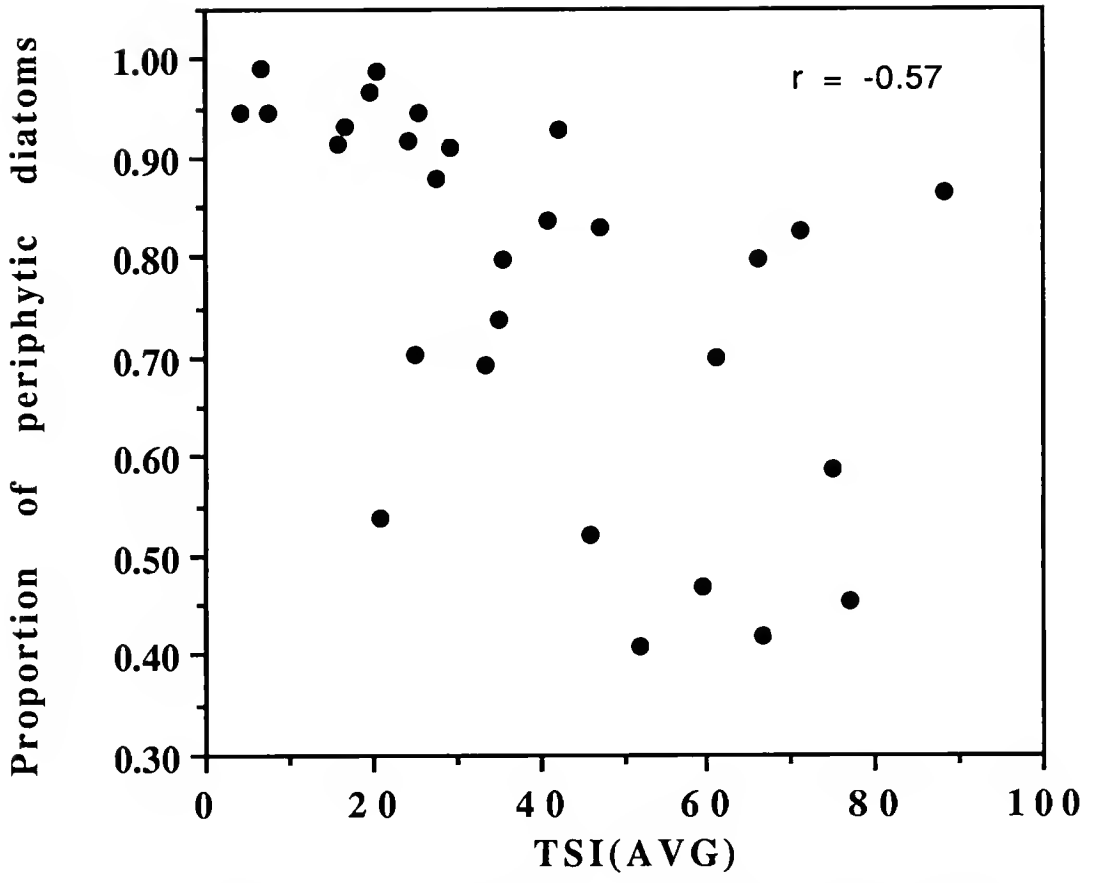

Figure 3. Proportion of diatom assemblage that periphyton represent versus TSI(AVG) for 29 lakes in survey.

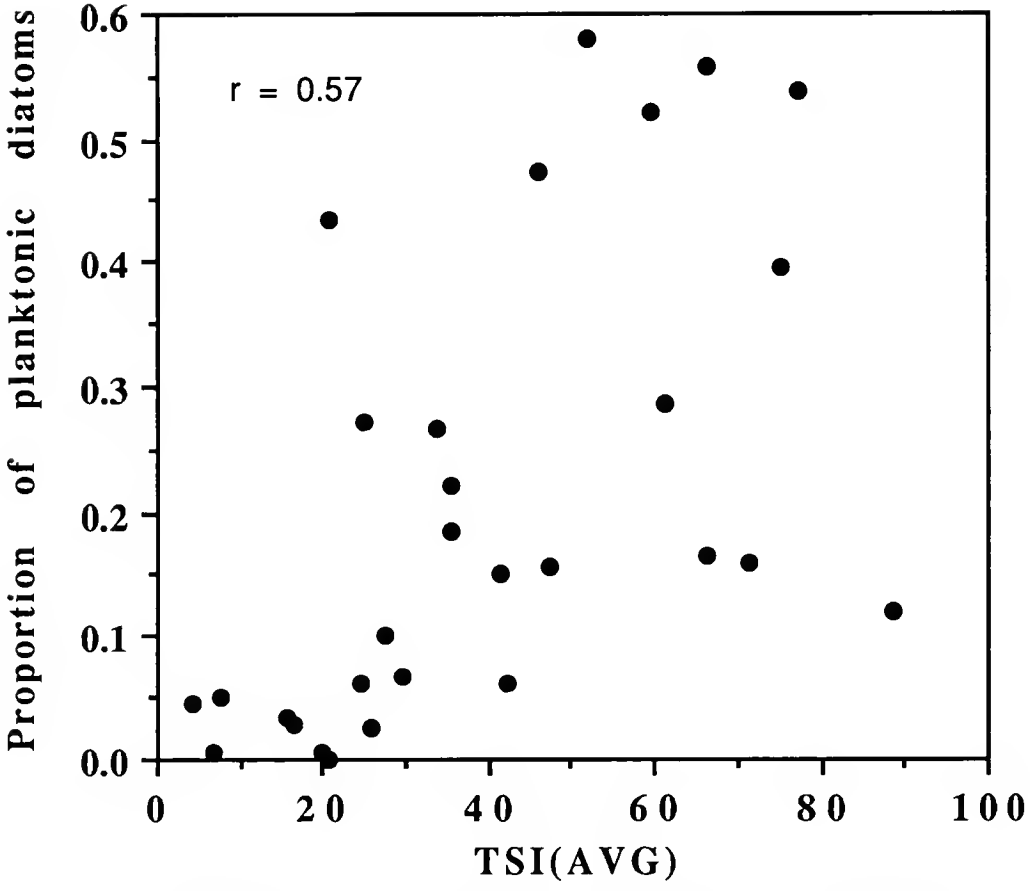

Figure 4. Proportion of diatom assemblage that plankton represent versus TSI(AVG) for 29 lakes in survey.

Table 4. Correlation coefficients for diatom variables, which are based on proportions, sedimentary concentrations and annual accumulation rates of periphyton and plankton, with water quality, macrophyte and morphometric variables. Keys Pond was removed from periphyton concentration data because of an anomalously high diatom concentration value (see Fig. 5). * = $p < 0.05$.

correlation coefficient
prob. > | r | under Ho: rho = 0
sample size

	PERI-PROP	PLNK-PROP	PERI-CONC	log PLNK-CONC	log PERI-ACCM	log PLNK-ACCM
log_{10} total P	*-0.610 <0.001 29	*0.613 <0.001 29	*0.410 0.030 28	*0.644 <0.001 29	0.377 0.053 27	*0.630 <0.001 27
TSI(AVG)	*-0.566 0.001 29	*0.573 0.001 29	*0.507 0.006 28	*0.656 <0.001 29	0.347 0.076 27	*0.578 0.002 27
pH	*-0.404 0.030 29	*0.402 0.031 29	0.309 0.109 28	*0.492 0.007 29	0.300 0.130 27	*0.517 0.006 27
Specific conductance	-0.223 0.244 29	0.215 0.262 29	0.204 0.298 28	*0.387 0.038 29	*0.392 0.041 27	*0.480 0.011 27
Percent-area coverage	*0.445 0.038 22	*-0.438 0.042 22	-0.220 0.339 21	-0.353 0.107 22	-0.180 0.422 22	-0.280 0.206 22
Percent-volume infestation	0.258 0.176 29	-0.243 0.204 29	-0.105 0.596 28	-0.186 0.333 29	-0.280 0.158 27	-0.203 0.311 27

Table 4 cont'd.

correlation coefficient
prob. > l r l under Ho: rho = 0
sample size

	PERI-PROP	PLNK-PROP	PERI-CONC	log PLNK-CONC	log PERI-ACCM	log PLNK-ACCM
Floating-leaved biomass	-0.097 0.668 22	0.126 0.576 22	0.221 0.336 21	0.088 0.695 22	*-0.205 0.360 22	0.019 0.932 22
Submerged biomass	0.193 0.391 22	-0.173 0.440 22	-0.106 0.647 21	-0.140 0.534 22	-0.311 0.159 22	-0.137 0.543 22
Emergent biomass	0.165 0.463 22	-0.143 0.525 22	0.028 0.904 21	-0.005 0.982 22	-0.278 0.211 22	-0.113 0.616 22
Mean depth	-0.195 -0.372 22	0.169 0.440 22	-0.096 0.669 22	-0.059 0.789 22	-0.246 0.270 22	-0.108 0.633 22
Shoreline length	-0.372 0.088 22	0.371 0.089 22	0.131 0.572 21	0.337 0.125 22	0.155 0.492 22	0.315 0.154 22
Shoreline develop-ment	-0.002 0.992 22	-0.013 0.955 22	-0.273 0.232 21	-0.272 0.220 22	-0.413 0.056 22	-0.330 0.133 22

untransformed values did. Table 4 shows that concentrations and log-transformed accumulation rates of both periphyton (Fig. 5) and plankton (Fig. 6) were positively correlated with TSI(AVG). pH, an important correlate of TSI, was found to be negatively correlated with the proportion of periphyton and positively correlated with the proportion of plankton in recent sediments of survey lakes. pH was also positively correlated with the log-transformed concentrations and accumulation rates of plankton. Chl a, total N and Secchi depth values used to calculate TSI(AVG) are shown in Appendix 4. Appendix 6 lists the proportions, sedimentary concentrations and accumulation rates of periphyton and plankton in the survey lakes.

The only macrophyte variable that demonstrated significant correlation coefficients with diatom life-form variables was percent-area coverage, which was positively correlated with the proportion of periphyton, and negatively correlated with the proportion of plankton (Table 4). Percent-area coverage was also negatively correlated with the concentration of planktonic diatoms. Coefficients of determination indicate that the 3 diatom life-form variables correlated with percent-area coverage would each explain only 19-24% of the variance in that variable. Percent loss on ignition and organic matter accumulation rates (Table 5) were not significantly correlated with any of the water chemistry or macrophyte variables.

Appendix 2 lists the 47 taxonomic groupings that were used in multivariate analyses. Individual taxa were combined into groupings based on taxonomic and ecological affinities, and selected for multivariate analyses based on the results of plots of their percentages versus macrophyte variables.

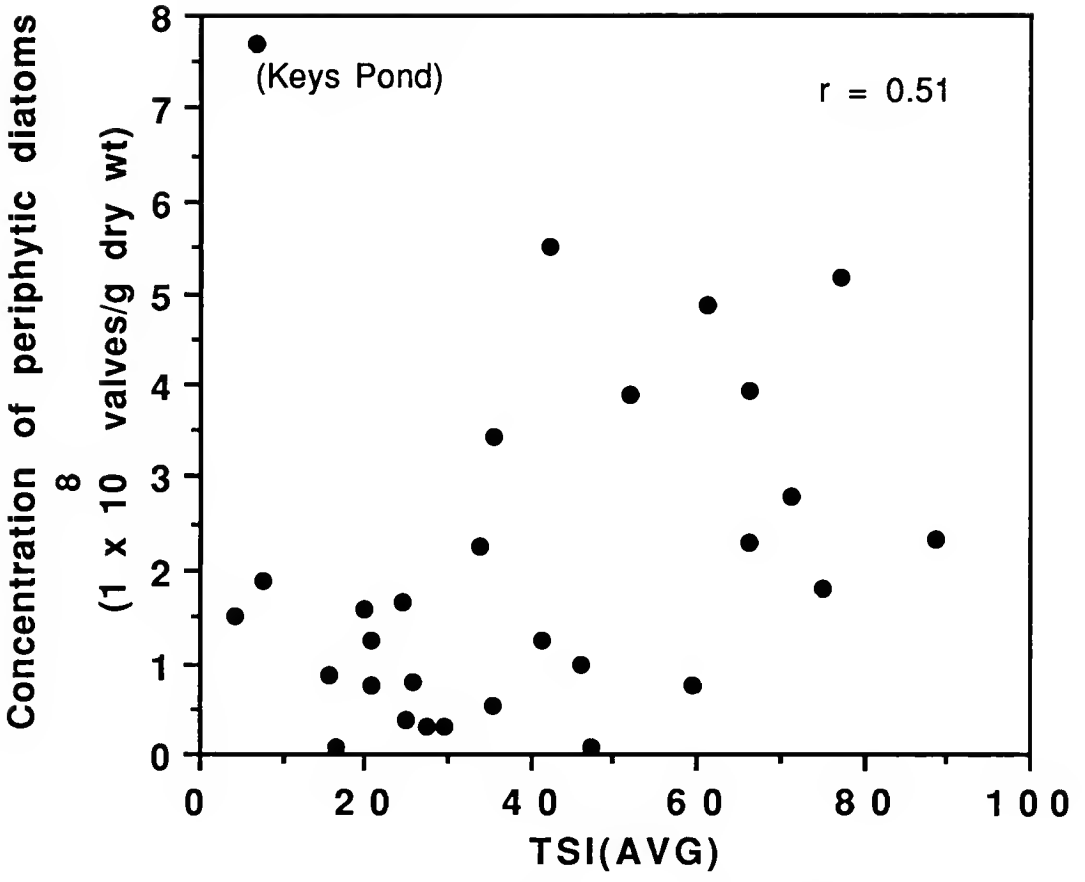

Figure 5. Concentration of periphytic diatoms in surface sediments versus TSI(AVG) for 29 lakes.

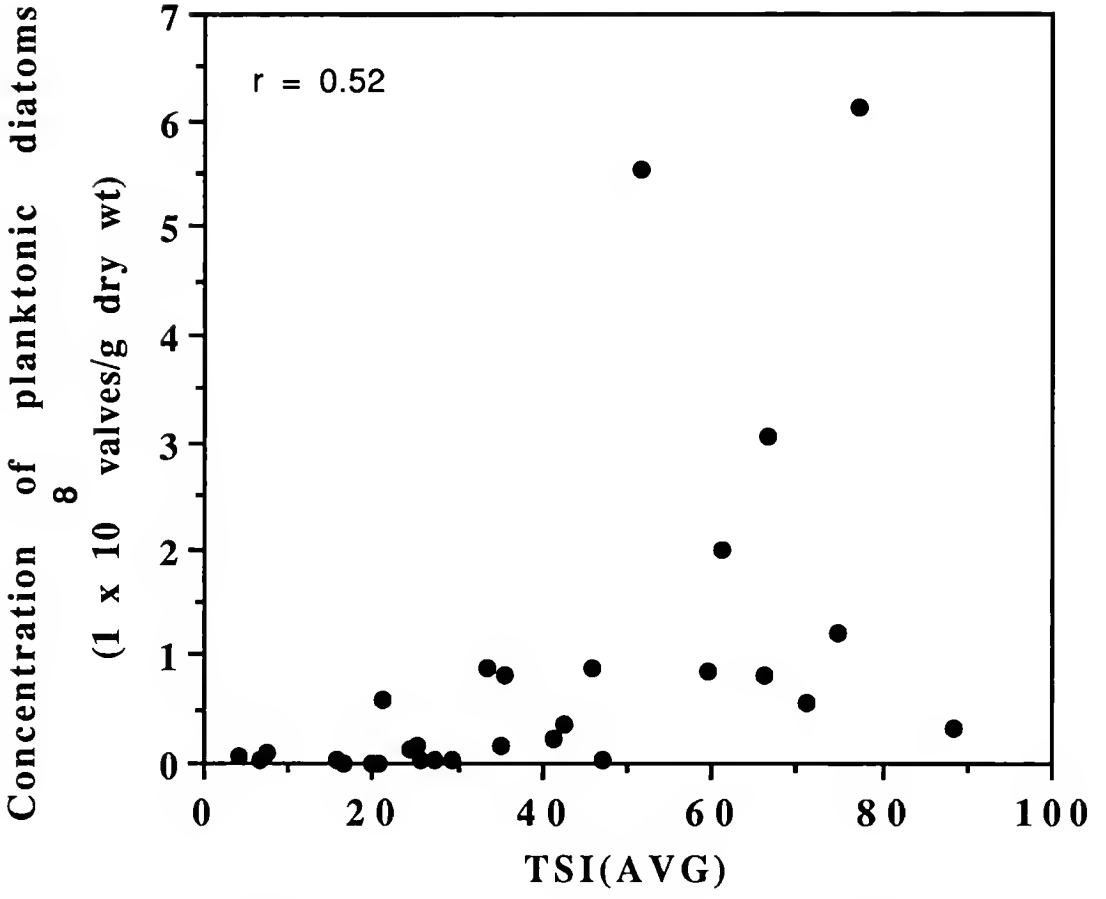

Figure 6. Concentration of planktonic diatoms in surface sediments versus TSI(AVG) for 29 lakes.

Table 5. Percent loss on ignition, bulk sediment accumulation rates, and organic mater accumulation rates for lakes in synoptic survey.

Lake	% Loss on ignition @ 550 °C	bulk sediment accumulation (g cm^{-2} yr^{-1})	Organic matter accumulation (g cm^{-2} yr^{-1})
Alligator	59.14	0.07	0.04
Apopka	64.10	0.09	0.06
Bonny	53.46	0.03	0.02
Carr	26.53	0.02	0.01
Catherine	55.21	0.03	0.02
Clay	43.98	0.03	0.01
Crooked	50.11	0.02	0.01
Deep	69.65	0.10	0.07
Fairview	8.20	0.22	0.02
Harris	80.93	0.04	0.03
Hartridge	53.56	0.05	0.03
Keys Pond	30.49	0.02	0.01
Lindsey	17.12	0.03	0.01
Live Oak	86.06	0.16	0.13
Lochloosa	36.10	0.04	0.01
Loften Ponds	33.60	0.02	0.01
Moore	17.21	0.04	0.01
Mystic			
Ocean Pond	39.00	0.10	0.04
Okahumpka	67.10	0.06	0.04
Orange			
Patrick	44.30	0.25	0.11
Rowell	69.00	0.31	0.21
Stella	14.00	0.17	0.02
Tomohawk	63.00	0.03	0.02
Townsend	79.60	0.04	0.03
Watertown	60.30	0.07	0.04
Wauberg	72.40	0.04	0.03
Wildcat			

Results of Cluster Analyses

Cluster analysis based on the percentage data for 47 taxonomic groups produced 16 clusters of taxa. Nine of these clusters demonstrated significant correlation coefficients with TSI(AVG), and six clusters showed significant correlations with pH (Table 6). Four clusters that were correlated with TSI(AVG) and pH also showed significant correlations with specific conductance. Three clusters were correlated with both lake surface area and shoreline length. Mean depth and shoreline development were each correlated with single separate clusters. Of the 80 correlation coefficients between diatom clusters and macrophyte variables, only two were significant, one with percent-volume infestation, and one with emergent biomass. *Navicula pupula* vars. (S-NAVPU) and *Stauroneis* spp. (S-STAU) were the taxonomic groups in the cluster correlated with percent-volume infestation, and these were included among the pool of independent variables (Appendix 3.1) in a stepwise procedure to construct a model that predicts percent-volume infestation. *Caloneis* sp. A and *Navicula seminulum* vars. (S-NAVSEM) were the taxonomic groups correlated with emergent biomass, but this correlation was driven by a single datum because both species showed anamalously high percentages in Crooked Lake.

Due to the overwhelming influence TSI(AVG) and pH had on composition of taxonomic clusters, cluster analysis using taxonomic percentages was repeated while partialling out the effects of pH and TSI(AVG). Fourteen diatom clusters resulted from this procedure. Seven of the clusters still demonstrated a significant correlation with TSI(AVG), and six of these had significant correlations with pH. Two

Table 6. Pearson product-moment correlation coefficients for clusters based on percentage data for diatom taxonomic groups with macrophyte and water quality variables. * = $p < 0.05$.

	CLUS1	CLUS2	CLUS3	CLUS4	CLUS5
	correlation coefficient prob. > | r | under Ho: rho = 0 sample size				
TSI(AVG)	*-0.691 <0.001 29	0.163 0.397 29	*0.547 0.002 29	-0.173 0.368 29	*0.528 0.003 29
pH	*-0.692 <0.001 29	*0.322 0.009 29	*0.409 0.0276 29	-0.356 0.058 29	*0.389 0.037 29
Specific conduc-tance	*-0.531 0.003 29	0.212 0.269 29	0.218 0.257 29	-0.253 0.185 29	0.154 0.426 29
Percent-area coverage	0.145 0.519 22	-0.084 0.710 22	-0.358 0.102 22	0.193 0.388 22	-0.271 0.215 22
Percent-volume infestation	-0.124 0.521 29	-0.083 0.671 29	-0.194 0.313 29	-0.165 0.392 29	-0.120 0.536 29
Floating-leaved biomass	-0.149 0.508 22	-0.116 0.607 22	-0.092 0.685 22	-0.019 0.934 22	0.408 0.060 22
Submerged biomass	-0.024 0.916 22	0.121 0.591 22	-0.279 0.209 22	-0.113 0.617 22	-0.106 0.640 22
Emergent biomass	-0.045 0.843 22	-0.096 0.670 22	-0.233 0.297 22	0.404 0.062 22	0.040 0.859 22

Table 6 cont'd.

	correlation coefficient prob. > | R | under Ho: rho = 0 sample size				
	CLUS6	CLUS7	CLUS8	CLUS9	CLUS10
TSI(AVG)	-0.081 0.677 29	*0.485 0.008 29	*0.387 0.038 29	-0.101 0.603 29	-0.044 0.819 29
pH	-0.124 0.521 29	*0.545 0.002 29	0.304 0.109 29	*0.381 0.041 29	0.250 0.191 29
Specific conduc-tance	-0.150 0.437 29	*0.415 0.025 29	0.209 0.276 29	*0.392 0.036 29	0.335 0.075 29
Percent-area coverage	-0.058 0.797 22	-0.006 0.980 22	-0.296 0.180 22	0.226 0.312 22	-0.018 0.935 22
Percent-volume infestation	-0.009 0.963 29	0.276 0.147 29	-0.151 0.435 29	0.107 0.582 29	0.018 0.927 29
Floating-leaved biomass	0.1768 0.431 22	0.213 0.341 22	-0.225 0.312 22	-0.249 0.262 22	-0.103 0.645 22
Submerged biomass	0.059 0.793 22	0.362 0.097 22	-0.190 0.396 22	-0.097 0.666 22	-0.225 0.313 22
Emergent biomass	*0.724 <0.001 22	0.0731 0.746 22	-0.251 0.259 22	-0.109 0.626 22	-0.259 0.245 22

Table 6 cont'd.

	correlation coefficient prob. > | R | under Ho: rho = 0 sample size					
	CLUS11	CLUS12	CLUS13	CLUS14	CLUS15	CLUS16
TSI(AVG)	*-0.471 0.009 29	0.006 0.971 29	*0.413 0.025 29	0.205 0.284 29	*-0.4032 0.0301 29	*-0.368 0.048 29
pH	*-0.515 0.004 29	0.112 0.559 29	0.318 0.092 29	0.142 0.459 29	-0.335 0.075 29	-0.330 0.079 29
Specific conduc-tance	-0.310 0.100 29	-0.208 0.278 29	0.201 0.295 29	0.363 0.052 29	*-0.398 0.032 29	-0.331 0.078 29
Percent-area coverage	0.097 0.667 22	0.246 0.268 22	*-0.462 0.030 22	-0.190 0.396 22	0.303 0.170 22	0.334 0.128 22
Percent-volume infestation	-0.185 0.335 29	*0.439 0.017 29	-0.227 0.234 29	-0.096 0.618 29	0.341 0.063 29	0.265 0.163 29
Floating-leaved biomass	-0.099 0.659 22	-0.015 0.947 22	0.004 0.985 22	0.070 0.755 22	0.227 0.309 22	-0.175 0.435 22
Submerged biomass	0.140 0.532 22	-0.043 0.847 22	-0.001 0.995 22	0.080 0.722 22	0.262 0.237 22	0.008 0.968 22
Emergent biomass	-0.011 0.958 22	0.021 0.925 22	0.044 0.843 22	-0.038 0.864 22	0.363 0.096 22	-0.003 0.989 22

of the three clusters that were significantly correlated with specific conductance were also correlated with TSI(AVG) and pH. Among the morphometeric variables, two clusters were signifcantly correlated with mean depth, and one cluster was correlated with shoreline development. Two clusters were significantly correlated with both lake surface area and shoreline length. Of the 70 correlation coefficients between macrophyte variables and diatom clusters, only three correlation coefficients were significant. One cluster that was composed of *Caloneis* sp. A and *Navicula seminulum* vars. demonstrated a significant correlation with emergent biomass as in the unpartialled analysis, and this again appeared spurious because the correlation was driven by anomalously high percentages of both taxa in Crooked Lake. The second cluster, which consisted of *Anomoeneis* spp. (S-ANOM), *Gomphonema* spp. (S-GOMA), *Navicula pupula* vars., and *Stauroneis* spp. (S-STAU), was correlated with both percent-area coverage and percent-volume infestation. Taxonomic groups in this cluster that showed a directional change in abundance over the range of percent-area coverage and percent-volume infestation were included among the independent variables in the stepwise regression procedures to predict these macrophyte variables (Appendix 3.1 and 3.4).

Cluster analysis based on sedimentary concentrations of diatoms produced 12 clusters, 4 of which were significantly correlated with TSI(AVG), and 5 of which were correlated with pH. The morphometeric variables lake-surface area and shoreline length were each significantly correlated with 2 separate clusters. Of 60 correlation coefficients between diatom clusters and macrophyte

variables, 4 were significant. A cluster that was composed of the taxon *Caloneis* sp. A was significantly correlated with emergent biomass, but this correlation was driven by a single datum point because of the unusually high percentage of this taxon in Crooked Lake. Another cluster consisted of *Fragilaria brevistriata* and *Gomphonema* spp. (S-GOMA) and was signifcantly correlated with percent-volume infestation. This correlation did not appear meaningful because *F. brevistriata* was represented by only two data points, and *G.* spp. was correlated with percent-volume infestation only because of anamalously high values in Lake Carr. In addition, *F. brevistriata* and *G* spp. showed different slopes over the range of percent-volume infestation. A third cluster, which seemed spuriously correlated with emergent biomass, consisted of two euplanktonic and two periphytic taxa. *Asterionella* spp. (S-AST) and *Aulacoseira islandica* were the two euplanktonic taxa in this cluster and they showed high values only in Crooked Lake. *Tabellaria flocculosa* and *T. fenestrata* were the periphytic taxa in this cluster and their slopes were different over the range of emergent biomass. A fourth cluster was positively correlated with floating-leaved biomass ($r = 0.554$, $p = 0.008$, $n = 22$) and contained 9 taxonomic groups (Appendix 3.7), seven of which were euplanktonic. These taxa were used as independent variables in a stepwise regression procedure to predict floating-leaved biomass.

When the clustering procedure was repeated partialling out the effects of TSI(AVG) and pH, a cluster composed of the 7 euplanktonic taxa last mentioned was again positively correlated with floating-leaved biomass. Four clusters were still significantly correlated with

TSI(AVG) and 5 were correlated with pH. *Eunotia* spp. (S-EUN) and *Gomphonema* spp. (S-GOMA) composed a cluster that was significantly correlated with percent-volume infestation, but plots revealed that both of these taxonomic groups had low sedimentary concentrations except for unusually high concentrations in Lake Carr. Emergent biomass was significantly correlated with a cluster composed of *Asterionella* spp., *Aulacoseira islandica, Tabellaria flocculosa* and *T. fenestrata* as it was prior to partialling covariant effects. Another cluster composed of *Caloneis* sp. A and *Nitzschia capitellata* was correlated with emergent biomass, but these taxa demonstrated opposite slopes over the range of emergent biomass. None of the 66 remaining correlation coefficients between diatom clusters and macrophyte variables was significant.

Cluster analysis of diatom taxonomic groups based on annual diatom accumulation rates produced 11 clusters. Four of these clusters were significantly correlated with TSI(AVG), and three of these plus a fourth cluster were significanly correlated with pH. Four clusters were correlated with shoreline length and two clusters were correlated with specific conductance. Of the 55 correlation coefficients between diatom clusters and macrophyte variables, only one correlation coefficient was significant. Floating-leaved biomass was found to be negatively correlated with a cluster composed of 4 periphytic and 3 planktonic taxonomic groups (Appendix 3.8). These diatom groups were used in a stepwise regression procedure to predict floating-leaved biomass.

The last cluster analysis was based on diatom accumulation rates with the effects of TSI(AVG) and pH partialled out, and it produced

12 clusters of diatom taxa. TSI(AVG), pH and specific conductance had 3 significant correlations each with diatom clusters. Shoreline development and lake surface area were correlated with 2 clusters each, and mean depth was correlated with one cluster. Of 60 correlation coefficients related to the macrophyte variables, only two were statistically significant. Seven of the 9 taxa in one cluster that was correlated with floating-leaved biomass were the same taxa used in the stepwise multiple regression procedure described above for unpartialled effects of TSI(AVG) and pH. Another cluster consisted of *Fragilaria crotonensis*, a euplanktonic taxon occurring in lakes high in water-column nutrients, that had an apparently spurious correlation with floating-leaved biomass.

Results of Principal Components Analyses

Principal components analysis seems to be an appropriate indirect ordination method to apply because species distributions were observed to be linear or curvilinear, though not modal, over the range of percent-area coverage and percent-volume infestation. Correlation coefficients were examined between the first 8 principal components based on percentage data for 47 diatom taxonomic groups and environmental variables. Eigenvalues, which are equal to the variances of the components, indicate that the first 3 principal components account for 15.9%, 8.5% and 7.2% of the variance in diatom assemblages, respectively. The first principal component was found to be highly correlated with TSI(AVG), pH and specific conductance (Table 7), indicating that these environmental variables were responsible for most of the variance in the diatom assemblages.

Table 7. Correlation coefficients for principle components based on diatom percentage data with water quality and macrophyte variables. * = $p < 0.05$.

	correlation coefficient prob. > | r | under Ho: rho = 0 sample size			
	1st. principle comp.	2nd. principle comp.	3rd. principle comp.	1st. principle comp. TSI(AVG) and pH partialled out
Percent volume infestation	-0.556 0.774 29	0.130 0.500 29	*0.395 0.034 29	-0.134 0.653 29
Percent area coverage	-0.322 0.144 22	0.132 0.557 22	0.298 0.176 22	-0.171 0.444 22
Floating-leaved biomass	0.102 0.649 22	0.064 0.776 22	-0.146 0.515 22	0.086 0.703 22
Submerged biomass	-0.108 0.632 22	-0.163 0.467 22	0.168 0.453 22	-0.185 0.409 22
Emergent biomass	-0.144 0.521 22	0.114 0.612 22	0.082 0.714 22	-0.081 0.720 22
TSI(AVG)	*0.753 <0.001 29	-0.023 0.901 29	0.029 0.880 29	*0.414 0.026 29

Table 7 cont'd.

	correlation coefficient prob. > l r l under Ho: rho = 0 sample size			
	1st. principle comp.	2nd. principle comp.	3rd. principle comp.	1st. principle comp. TSI(AVG) and pH partialled out
pH	*0.775 <0.001 29	-0.132 0.494 29	*0.374 0.045 29	*0.411 0.026 29
Specific conductance	*0.539 0.003 29	-0.283 0.135 29	*0.373 0.045 29	0.187 0.330 29
Mean depth	-0.170 0.437 23	*-0.437 0.037 23	-0.154 0.481 23	-0.105 0.633 23
Shoreline length	0.200 0.369 22	*-0.457 0.032 22	0.446 0.037 22	-0.192 0.390 22
Lake surface area	0.150 0.445 28	*-0.454 0.015 28	0.314 0.103 28	-0.260 0.180 28

The second principal component was significantly correlated with with the morphometric variables mean depth, shoreline length and lake surface area. The third principal component was significantly correlated with pH, specific conductance and percent-volume infestation. A coefficient of determination indicates that the third principal component would explain 16.0% of the variance in percent-volume infestation, which is not sufficiently robust for predictive purposes. None of the remaining 60 correlation coefficients between principal components 4-8 and the environmental variables was statistically significant.

Principal components analysis of percentage data was repeated while TSI(AVG) and pH were partialled out. The first principal component, which accounted for 11.8% of the variance in diatom taxa still showed significant correlations with TSI(AVG) and pH (Table 7). The second principal component explained 9.5% of the variance in the diatom assemblages and was significantly correlated with mean depth. The third principal component explained 8.6% of the variance in the diatom assemblages and was not correlated with any of the macrophyte or environmental variables considered. The fourth principal component explained 7.5% of the variance, and was negatively correlated with floating-leaved biomass ($r = -0.442$, $p = 0.040$, $n = 22$). A model based on this principal component would explain approximately 19.5% of the variance in floating-leaved biomass. None of the correlation coefficients between principal components 5-8 and the environmental variables was significant.

Principal components analysis was performed on sedimentary diatom concentrations for the 47 diatom taxonomic groups. The first

principal component explained 18.3% of the variance and was significantly correlated with TSI(AVG) ($r = 0.648$, $p < 0.001$, $n = 29$) and pH ($r = 0.499$, $p = 0.006$, $n = 29$). The second principal component explained 10.3% of the variance in the diatom assemblages and was not significantly correlated with any of the environmental or macrophyte variables. The third principal component explained 9.9% of the variance in the diatom assemblages. This component had a significant negative correlation with floating-leaved biomass ($r = -0.536$, $p = 0.010$, $n = 22$), and a positive correlation with pH ($r = 0.400$, $p = 0.032$, $n = 29$) and shoreline length. Scores obtained for survey lakes using eigenvectors of the third principal component (Table 8) were used to construct the following model:

$$\text{floating-leaved biomass} = 2.419 - 0.750(\text{PRIN3}) \qquad 3.1$$

$$R^2 = 0.287,\ p = 0.010,\ n = 22$$

where PRIN3 is the sum of the products between eigenvectors and sedimentary concentrations of the 47 diatom groups.

The majority of the taxa in Table 8 that show large, positive eigenvectors (*e.g. Fragilaria construens, F. pinnata, Navicula lanceolata, N. pupula* and vars., *N. radiosa* and vars., *N. cuspidata, Nitzschia amphibia, N. capitellata, Cocconeis placentula* var. *lineata*), have a periphytic life form. Many of the taxa with smaller, negative eigenvectors (*e.g. Asterionella* spp., *Aulacoseira islandica, Cyclostephanos dubius, Fragilaria crotonensis*) have a euplanktonic life form. It appears that samples with large numbers of periphytic diatoms and few planktonic diatoms would have large values of PRIN3, and it would be reasonable to expect that large PRIN3 values would be associated with greater floating-leaved biomass. Equation

Table 8. Eigenvectors of third principle component based on sedimentary concentrations of 47 diatom taxonomic groups. Taxonomic acronyms are defined in Appendix 2.

Taxonomic group	Eigenvector	Taxonomic group	Eigenvector
S-ACH	0.081	NAVGOT	0.061
S-ANOM	0.089	NAVLAN	0.261
S-AST	-0.177	S-NAVPU	0.209
AULAAM	0.186	S-NAVRA	0.320
AULADIS	-0.025	S-NAVSEM	0.192
S-AULAGR	-0.096	NAVSUBT	0.122
AULAISL	-0.141	NITZAM	0.235
AULAITAL	0.039	NITZCAP	0.195
CALSPA	-0.013	NITZFONT	-0.139
COCPLACL	0.138	NITZFRUS	0.193
CYCMEN	0.124	NITZPAL	-0.128
CYCPSEUD	-0.023	S-PIN	0.109
CYCSTEL	0.013	S-STAU	0.101
CYCSTELO	0.005	S-SUR	-0.037
S-CYM	0.034	SYNDEL	0.269
CYSTEPDU	-0.177	SYNFILEX	0.123
S-EP	0.035	S-SYNRUM	-0.014
S-EUN	0.007	TABFEN	-0.098
ACTPUNC	-0.075		
NAVCUS	0.137		
NAVCONF	0.115		
TABFLOC	-0.168		
S-NEI	0.103		
FRAGBREV	0.069		
S-FRAGCO	0.298		
FRAGCROT	-0.166		
FRAGPIN	0.225		
S-FRUSRH	0.096		
S-GOMA	0.006		

3.1 shows a negative coefficient for PRIN3, however, which is contrary to the expectation that periphytic taxa would demonstrate greater representation in lakes with greater floating-leaved biomass.

Partial correlation coefficients showed that the 3rd principal component was significantly correlated with floating-leaved biomass ($r = -0.618$, $p = 0.003$, $n = 22$) when the effect of pH was held constant. Despite the non-significant correlation between pH and floating-leaved biomass (Table 3), partial correlations showed that pH was significantly correlated with the 3rd principal component ($r = 0.521$, $p = 0.016$, $n = 29$) when floating-leaved biomass was held constant. This implies that the model predicting floating-leaved biomass is confounded by the effect of pH, and should only be applied historically when it can be demonstrated that significant changes in pH have not occurred.

When the principal components analysis based on the sedimentary concentration of diatom groups was repeated partialling out the effects of TSI(AVG) and pH, the first principal component explained 16.0% of the variance in the diatom assemblages and was positively correlated with floating-leaved biomass ($r = 0.460$, $p = 0.031$, $n = 22$) and with TSI(AVG). This correlation with floating-leaved biomass was less robust than in the previous correlation with unpartialled effects. None of the remaining principal components in the partialled analysis had significant correlations with macrophyte variables.

The principal components procedure was repeated using log-transformed sedimentary diatom concentrations. The first principal component accounted for 30.4% of the variance in the diatom

assemblage and demonstrated stronger correlations with TSI(AVG) ($r = 0.783$, $p < 0.001$, $n = 29$) and pH ($r = 0.885$, $p < 0.001$, $n = 29$) than the procedure with untransformed concentration data. None of the correlation coefficients between principal components and macrophyte variables were significant in this procedure, even when the effects of TSI(AVG) and pH were partialled out.

Principal components analysis using annual diatom accumulation rates produced a first principal component that explained 21.4% of the variance and was again significantly correlated with TSI(AVG) ($r = 0.460$, $p = 0.012$, $n = 29$), pH ($r = 0.464$, $p = 0.011$, $n = 29$), and specific conductance ($r = 0.501$, $p = 0.006$, $n = 29$). The only significant correlation coefficient involving a macrophyte variable was with the fourth principal component that was significantly correlated with percent-area coverage ($r = -0.448$, $p = 0.036$. $n = 22$) and more strongly correlated with TSI(AVG) ($r = 0.501$, $p = 0.006$, $n = 29$). A predictive model using eigenvectors of this principal component would not be useful for predicting percent-area coverage because it would be confounded by TSI(AVG).

Principal components based on diatom accumulation rates with the effects of TSI(AVG) and pH partialled out produced a single significant correlation with a macrophyte variable. The sixth principal component, which accounted for 5.5% of the variance in the diatom assemblages, had a significant negative correlation with floating-leaved biomass ($r = -0.574$, $p = 0.005$, $n = 22$). A predictive model using the eigenvectors for this principal component would explain 33.0% of the variance in floating-leaved biomass but could

only be applied historically to lakes that had not undergone changes in trophic state or pH.

Results of Stepwise Multiple Regression

Percent-Volume Infestation

The maximum R^2 method of the SAS STEPWISE procedure (SAS Inst., Inc. 1985) was applied to percentage data for 17 diatom taxonomic groups selected from plots of their abundance versus percent-volume infestation (Appendix 3.1). The plot of Mallows' Cp statistic versus the number of variables in each model is shown in Figure 7. Models with larger Cp values have larger total error than models with smaller Cp values (Daniel and Wood 1971). Models in which Cp is larger than the number of independent variables plus the intercept (p) are subject to bias error. Models with Cp values less than p are subject to random errors. Figure 7 shows that the model for predicting percent-volume infestation that consisted of one diatom taxon (p = 2) showed substantial bias. All other multivariate models predicting percent-volume infestation from percentage data were subject to random error.

Stepwise regression to predict percent-volume infestation was attempted by using sedimentary concentration data for 17 diatom taxonomic groups (Appendix 3.2). All models demonstrated random error. Better results were obtained when log-transformed sedimentary concentrations were used in the stepwise procedure. Figure 8 is the plot of Cp versus p for models using log-transformed diatom concentrations. The model using 2 diatom taxonomic groups (p = 3) shows bias. The model using 3 taxonomic groups (p = 4)

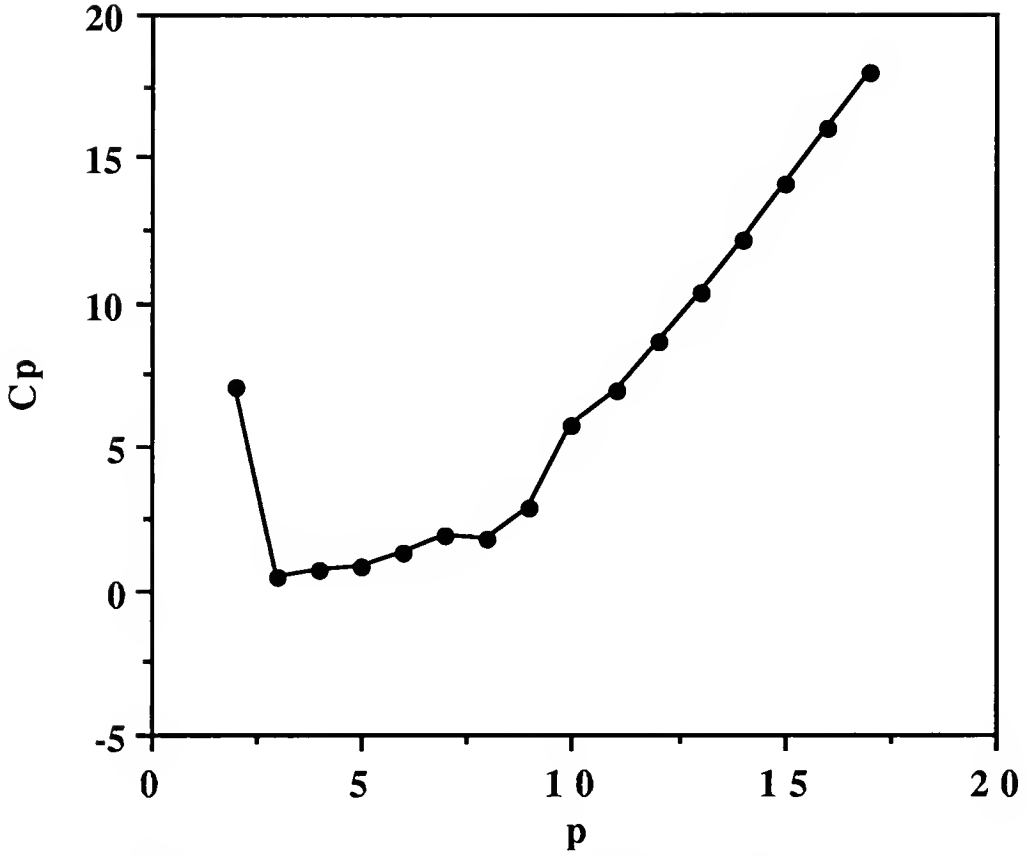

Figure 7. Mallows' Cp statistic versus p for model predicting percent volume infestation from percentage data. P is number of dependent variables + 1.

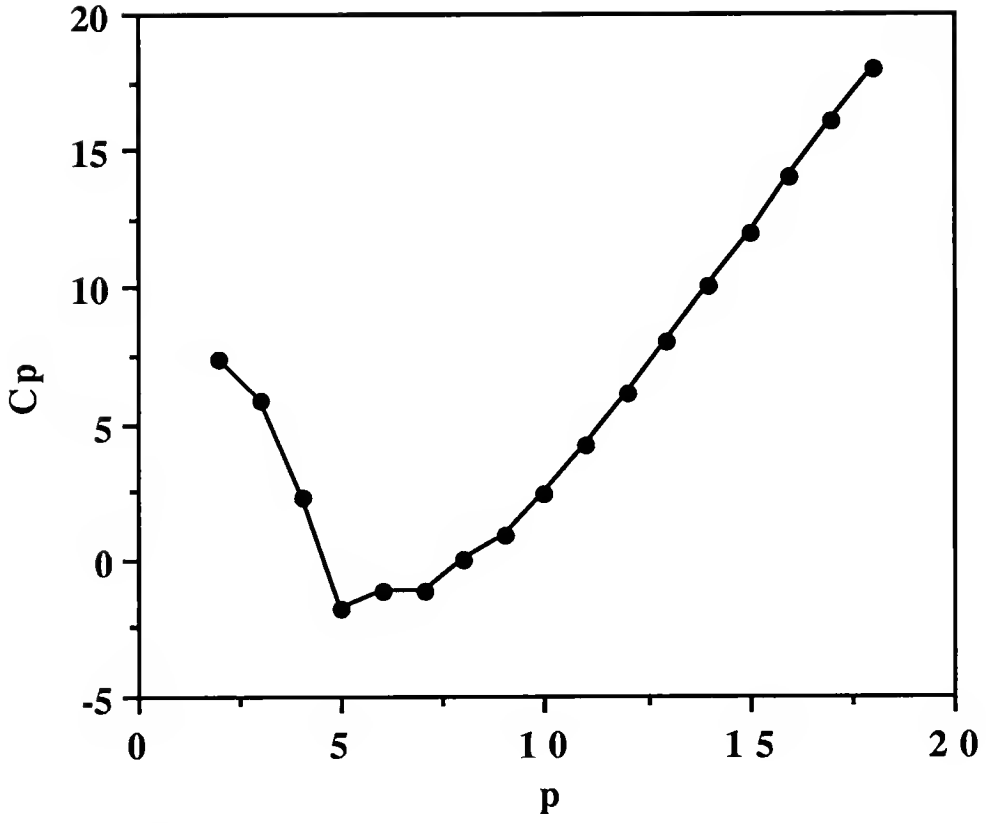

Figure 8. Mallows' Cp statistic versus p for model predicting percent volume infestation from log-transformed diatom concentrations.

shows a slight random error, but a lower total error term. The best model for predicting percent-volume infestation (PVI) from sedimentary concentrations of diatom groups is therefore:

$$PVI = 36.960 - 4.217\log(ACHEX) + 7.833\log(STAUPH) - 3.641\log(SYNFILEX) \quad 3.2$$

$R^2 = 0.519$, $p < 0.001$, $n = 29$

where values for the 3 taxa, whose acronyms are defined in Appendix 1, are expressed in valves g^{-1} dry weight of sediment. The adjusted R^2 value for this model is 0.461.

The stepwise procedure was applied to log-transformed annual accumulation rate values for 17 diatom taxonomic groups (Appendix 3.3). The best model utilized 2 diatom taxa and showed an R^2 of 0.312. The adjusted R^2 for this model was 0.259. The model was less robust than the model based on log-transformed sedimentary diatom concentrations.

Percent-Area Coverage

Eleven diatom taxonomic groups (Appendix 3.4) selected from plots were used in the stepwise procedure to construct models predicting percent-area coverage from diatom percentage data. The best model, as determined from Cp values was:

$$\text{percent-area coverage} = 27.294 + 3.971(\text{S-CYM}) + 0.871(\text{S-FRUSRH}) + 50.967(\text{STAUPH}) \quad 3.3$$

$R^2 = 0.502$, $p = 0.005$, $n = 22$

where values for the 3 taxonomic groups, which are defined in Appendices 1 and 2, are expressed as a percentage of each diatom

assemblage. The adjusted R^2 for this model was 0.419. This multivariate model was significantly confounded with TSI(AVG) (R^2 = 0.665, $p < 0.001$) and would therefore be unsuitable for predictive purposes.

The stepwise procedure was applied to sedimentary diatom concentration data for 8 taxonomic groups (Appendix 3.5). Cp statistics indicated that the best model was;

PAC = 44.408 + 2.14 x 10-6(ACHLIN) - 2.7 x 10-7(S-AULAGR) + 9.53 x 10-5(EUNINC) + 1.91 x 10-5 (STAUPH) 3.4

R^2 = 0.607, p = 0.002, n = 22, adj. R^2 = 0.514.

Acronyms for taxonomic groups are defined in Appendices 1 and 2.

The best model produced by the stepwise procedure using log-transformed sedimentary diatom concentration data showed an R^2 = 0.422, that was less robust than the model based on untransformed data.

The stepwise procedure was applied to annual diatom accumulation rates for 11 diatom taxonomic groups (Appendix 3.6). The procedure was also used for log-transformed accumulation rate data of these taxa. The best model included 3 diatom taxonomic groups and showed an R^2 = 0.415 (p = 0.006). This model bore a stronger relationship with TSI(AVG) (R^2 = 0.480, $p < 0.001$), and was therefore significantly confounded by this trophic state variable.

Floating-Leaved Biomass

Stepwise multiple regression was performed on sedimentary concentration and log-transformed sedimentary concentration of

valves of 9 diatom taxonomic groups (Appendix 3.7) that were correlated with floating-leaved biomass in the cluster analysis procedure. All models that resulted from these stepwise attempts demonstrated random errors. Stepwise regression was also performed on the 7 diatom taxa in the annual-accumulation rate cluster analysis that were correlated with floating-leaved biomass. The best model, as indicated by the Cp statistic, included a single diatom taxon, and this model explained only 28.7% of the variance in floating-leaved biomass.

Better results were obtained by stepwise regression of 12 diatom taxonomic groups (Appendix 3.9) that were selected from plots of percentage data for diatom taxa versus floating-leaved biomass. The best model obtained was the following:

$$\text{FLOATING} = 5.105 - 3.455\log10(\text{ACHS}) - 2.493\log10(\text{CYMMUEL}) + 0.264(\text{CYSTEPDU}) - 0.281(\text{S-NAVS}) - 3.297\log10(\text{S-NITZS}) \quad 3.5$$

$R^2 = 0.866$, $p < 0.001$, $n = 22$, adj. $R^2 = 0.825$

where FLOATING = floating-leaved biomass in kg wet mass m^{-2}
ACHS = ACHEX + ACHLIN + ACHLINCU + ACHMIN
S-NAVS = NAVGOT + NAVLAN + S-NAVPU + S-NAVRA +NAVSUBTS
NITZS = NITZAM + NITZCAP + NITZFRUS.

The values for all taxonomic groups, whose acronyms are defined in Appendices 1 and 2, are expressed as a percentage of the diatom assemblages. This model appeared to have a significant relationship with submerged biomass ($R^2 = 0.502$, $p = 0.034$). Partial correlation coefficients showed that floating-leaved biomass was significantly correlated with the model ($r = 0.882$, $p < 0.001$, $n = 22$) when the

effect of submerged biomass was held constant. The model was not significantly correlated with submerged biomass ($r = 0.431$, $p = 0.051$, $n = 22$), however, when the effect of floating-leaved biomass was held constant. This indicates that the above model predicting floating-leaved biomass is not confounded by the variable submerged biomass. The correlation coefficient between submerged biomass and the model, however, failed to be significant at the $\alpha = 0.05$ level of significance by a marginal amount, and the model may prove to be confounded in certain applications.

Submerged Biomass

Stepwise multiple regression was performed on percentage data for 20 diatom taxonomic groups (Appendix 3.10) to predict submerged macrophyte biomass. Cp statistic values indicated that the best model contained 11 diatom taxon variables and explained 91.6% of the variance in submerged biomass ($p < 0.001$, $n = 22$). The adjusted R^2 for the model was 0.824. This model, however, also explained 86.9% of the variance in floating-leaved biomass ($p = 0.004$, $n = 22$) and seems to be confounded by that variable. The partial correlation coefficient between the model and submerged biomass was significant ($r = 0.960$, $p < 0.001$) when the effect of floating-leaved biomass was held constant. The partial correlation coefficient between the model and floating-leaved biomass ($r = 0.938$, $p < 0.001$) was also significant when the effect of submerged biomass was held constant. The model to predict submerged biomass, therefore, is not a useful predictive model because it is significantly confounded by floating-leaved biomass.

Sum of Floating and Submerged Biomass

Because submerged macrophyte biomass could not be separated from floating-leaved biomass in predictive models, an attempt was made to combine these macrophyte variables in a single predictive model. Sixteen diatom taxonomic groups (Appendix 3.11) were selected that appeared to show response to both of these macrophyte variables. The stepwise multiple regression procedure was applied to these groups and it produced the following best model:

$$\text{FLOAT-SUB} = 13.292 - 0.384(\text{S-ACH}) - 1.159(\text{S-AULA}) - 23.126(\text{EUNPEC}) + 0.921(\text{S-FRUSRH}) - 0.912(\text{S-NAVS}) + 7.115(\text{S-STAU}) + 2.492(\text{EUNVAN}) \quad 3.6$$

$R^2 = 0.592$, $p = 0.042$, $n = 22$

in which FLOAT-SUB = sum of floating-leaved and submerged macrophyte biomass in kg wet mass m^{-2}. Acronyms for the taxonomic groups are defined in Appendices 1 and 2. The adjusted R^2 for this model was 0.389.

Emergent Biomass

The stepwise multiple regression procedure was performed on percentage data of 17 diatom taxonomic groups (Appendix 3.12) to predict emergent biomass. Cp values of all models with significant R^2 values were much less than the p values, which indicated that these models were subject to substantial random error.

Results of Canonical Correspondence Analysis

The canonical correspondence analysis option of CANOCO (ter Braak 1987) produced eigenvectors (Table 9) ordinating the 47

Table 9. Eigenvectors for percentage data of 47 diatom taxonomic groups in CANOCO Axis1 constrained by percent-volume infestation. Eigenvectors are presented in descending order. Taxonomic acronyms are defined in Appendix 2.

Taxonomic group	Eigenvector	Taxonomic group	Eigenvector
S-GOMA	1.78	AULAAM	-0.40
S-STAU	1.34	ACTPUNC	-0.44
S-NAVPU	1.32	NAVCUS	-0.45
FRAGPIN	1.20	NITZAM	-0.52
S-FRAGCO	1.14	CYCPSEUD	-0.60
S-EUN	1.00	NITZCAP	-0.61
S-ANOM	0.77	S-AULAGR	-0.70
S-NAVSEM	0.54	AULAISL	-0.76
S-CYM	0.50	NAVSUBT	-0.76
TABFEN	0.45	S-SUR	-0.81
NITZFRUS	0.43	AULAITAL	-0.85
S-EP	0.31	SYNDEL	-0.90
S-ACH	0.10	AULADIS	-0.96
CYCSTEL	0.06	NAVCONF	-0.96
TABFLOC	-0.02	CYSTEPDU	-0.99
S-SYNRUM	-0.02	CALSPA	-1.04
S-NAVRA	-0.06	SYNFILEX	-1.10
NITZFONT	-0.08	S-AST	-1.55
CYCMEN	-0.10	FRAGBREV	-1.55
NAVGOT	-0.10		
FRAGCROT	-0.11		
COCPLACL	-0.21		
S-FRUSRH	-0.21		
NAVLAN	-0.23		
S-NEI	-0.26		
CYCSTELO	-0.27		
S-PIN	-0.32		
NITZPAL	-0.35		

diatom taxonomic groups into an axis constrained by percent-volume infestation. When axis scores for the 29 survey lakes were regressed with percent-volume infestation values using the SAS GLM procedure (SAS Institute, Inc. 1985), the following predictive equation was obtained:

$$\text{percent-volume infestation} = 33.8 + 0.7(\text{Axis 1}) \qquad 3.7$$

$r^2 = 0.600$, $p < 0.001$, $n = 29$

where Axis 1 is the sum of products of eigenvectors and percentages of the 47 diatom taxonomic groups.

When canonical correspondence was invoked to produce eigenvectors ordinating the 47 diatom taxonomic groups into an axis constrained by percent-area coverage, CANOCO returned eigenvectors ordinating 45 of the taxonomic groups (Table 10). *Tabellaria fenestrata* and *T. floccolosa* may have been eliminated by CANOCO in this ordination because of under-representation. Axis scores for the 22 survey lakes with percent-area coverage values were regressed with percent-area coverage using the SAS GLM procedure (SAS Institute, Inc. 1985). The resulting equation was:

$$\text{percent-area coverage} = 53.6 - 0.5(\text{Axis 1}) \qquad 3.8$$

$r^2 = 0.447$, $p < 0.001$, $n = 22$

where Axis 1 is the sum of products of the percentages and eigenvectors of the 45 diatom taxonomic groups shown in Table 10.

A New Predictive Model for Water-Column Total P

Because inferences from Whitmore's (1989) TSI(TP) predictive model cannot detransformed to yield total P values for WCP (Canfield *et al.* 1983a) estimates, a new model is presented here using the

Table 10. Eigenvectors for percentage data of 45 diatom taxonomic groups in CANOCO Axis1 constrained by percent-area coverage. Eigenvectors are presented in descending order. Taxonomic acronyms are defined in Appendix 2.

Taxonomic group	Eigenvector	Taxonomic group	Eigenvector
FRAGBREV	2.11	S-NEI	-0.17
FRAGCROT	1.49	S-ACH	-0.18
NAVCONF	1.47	S-PIN	-0.19
S-NAVPU	1.26	S-STAU	-0.25
CYCPSEUD	1.17	S-FRAGCO	-0.28
CYSTEPDU	1.16	NAVSUBT	-0.30
NITZPAL	1.15	CYCSTELO	-0.31
CALSPA	1.06	FRAGPIN	-0.35
SYNFILEX	1.01	S-SUR	-0.48
AULAAM	1.00	S-FRUSRH	-0.71
NITZFONT	0.88	S-ANOM	-0.73
S-AULAGR	0.86	S-GOMA	-0.84
AULAITAL	0.86	S-EP	-0.86
S-AST	0.85	S-EUN	-1.08
COCPLACL	0.84	S-CYM	-1.18
NITZCAP	0.59	ACTPUNC	-1.29
NAVCUS	0.55		
CYCMEN	0.53		
NITZAM	0.53		
AULAISL	0.43		
S-NAVRA	0.42		
NAVGOT	0.25		
NAVLAN	0.21		
S-SYNRUM	0.19		
S-NAVSEM	0.18		
CYCSTEL	-0.07		
NITZFRUS	-0.10		
SYNDEL	-0.15		
AULADIS	-0.16		

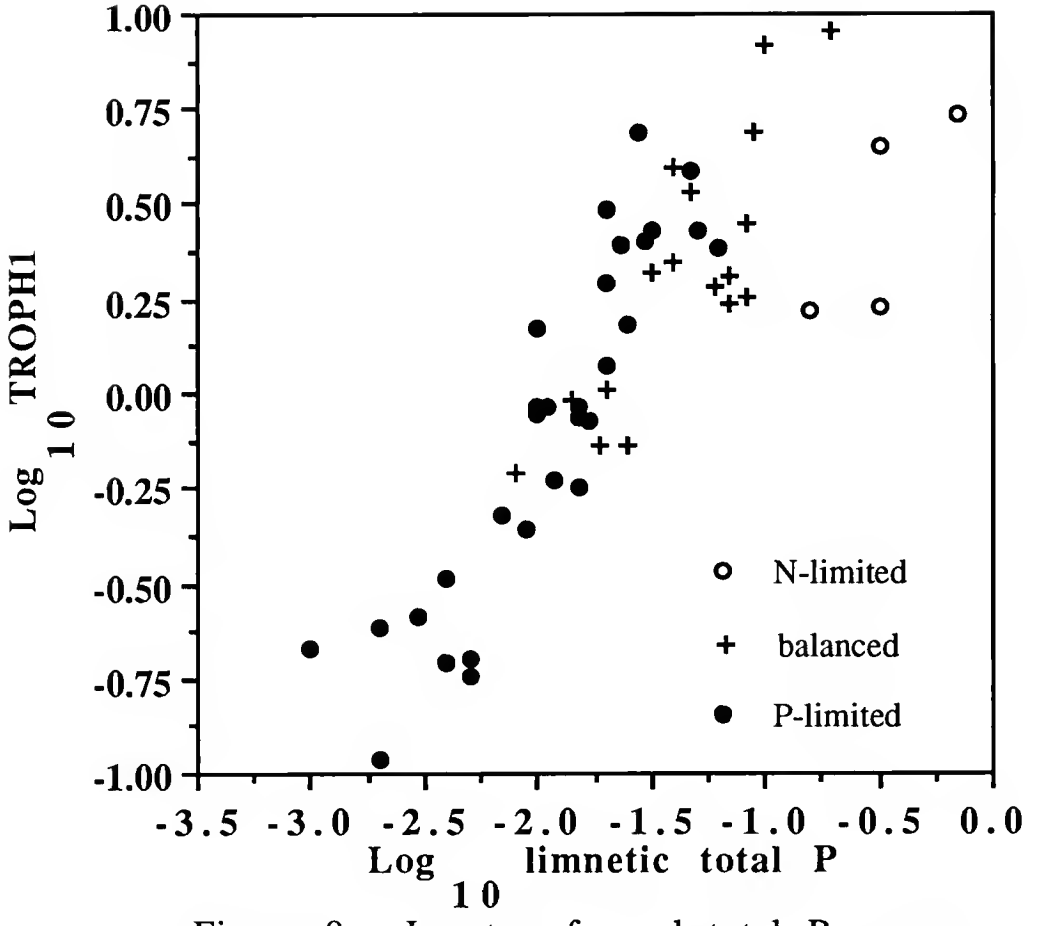

Figure 9. Log-transformed total P versus log-transformed TROPH1 diatom index for 51 lakes.

TROPH 1 diatom index (Whitmore 1989) to predict log-transformed water-column total P. Figure 9 shows a plot of log-transformed water-column total P versus the TROPH1 diatom index for 51 Florida lakes. The four nitrogen-limited lakes shown demonstrated anomalously low diatom index values for their total P values, and were removed from the regression data set. The resulting predictive model was:

$$\log_{10}(\text{total P}) = -1.795 + 0.973(\log_{10}(\text{TROPH 1})) \qquad 3.9$$

$r^2 = 0.807$, $p < 0.001$, $n = 47$.

Assessing Confoundedness in the Water-Column Total P Predictive Model

The significant negative correlation coefficient that was observed between log-transformed total P and percent-area coverage (Table 11) confirmed the inverse relationship previously observed (Canfield *et al.* 1984) between macrophyte presence and water-column nutrient concentrations. The correlation coefficient between the log-transformed TROPH 1 diatom index and percent-area coverage, however, was not significant (Table 11). The model for predicting water-column total P from the TROPH 1 diatom index is not confounded by the macrophyte variable percent-area coverage.

Table 11. Correlation coefficients between TSI(TP), percent area coverage and the log-transformed diatom index TROPH 1. * = $p < 0.05$.

correlation coefficient
prob. > l r l under Ho: rho = 0
sample size

	Water-column total P	Percent-area coverage
log(TROPH 1)	*0.838	-0.359
	<0.001	0.101
	29	22
Percent-area coverage	*-0.537	
	0.010	
	22	

CHAPTER 4

DISCUSSION

Dominant Environmental Variables and Scale of Analysis

The purpose of this study was to identify diatom taxa that are indicators of macrophyte presence in lakes. Despite an appropriate sampling design, macrophytes were not found to be a primary determinant of diatom assemblages. A trophic-state/pH/specific-conductance environmental gradient was the principal influence on the diatom communities.

I sampled lakes along a wide gradient of macrophyte abundance in order to develop predictive models with broad application for inferring historical macrophyte standing crop, and by necessity I transgressed the trophic-state gradient that is present among Florida lakes. A negative correlation exists between macrophyte abundance and water-column Chl *a* (Canfield *et al.* 1984) in Florida lakes. I also observed a negative correlation between percent-area coverage of macrophytes and water-column total P in the present study. Lakes that were low in percent-area coverage (< 10%) were high in water-column nutrients, whereas several lakes that were high in percent-area coverage (>80%) were low in water-column nutrients.

pH, trophic state and specific conductance were mutually correlated in this study as in other studies of Florida lakes (Canfield

1981, Brenner *et al.* 1990, Whitmore 1989). The majority of Florida lakes are soft-water, acidic and low in alkalinity (Brenner *et al.* 1990). Nevertheless, many lakes on phosphatic sands or carbonate-rich bedrock are naturally high in productivity and dissolved solutes (Canfield 1981). Because the present survey spanned a wide range of limnological conditions, trophic state, pH and specific conductance formed a dominant environmental gradient that emerged as the principal determinant of diatom community composition.

Jackson and Charles (1988) observed the effect of a similar environmental gradient on macrophyte distribution in the Adirondack lakes of New York. They found that alkalinity, pH and ionic composition were interrelated factors that determined the distribution and species composition of aquatic vegetation. Jackson and Charles stated:

> We conclude that the chemical gradient underlying compositional variation among our Adirondack softwater sites is the tail end of a broad pH complex-gradient that extends to highly alkaline waters. At the scale of environmental variation observed in Adirondack lakes, the main factors associated with vegetation variation are pH, alkalinity, Ca, Mg, and perhaps Al. In regions where the gradient is broader, or at least where the hardwater portion is represented, conductivity and trophic status become more important (Jackson and Charles 1988, p. 1456-1457).

Because Florida lakes exhibit a wide scale of variation from softwater to hardwater conditions, the resulting chemical gradient determined diatom community composition in the same manner that the chemical gradient in Adirondacks lakes determined macrophyte composition. The fact that diatom community composition was

determined mostly by trophic-state, pH, and specific conductance rather than by macrophyte presence was thus the result of the scale of analysis as discussed by Duarte and Kalff (1990). The dominant effects of trophic state and pH may have overridden differences in community structure that resulted from the influence of macrophytes. In addition, most lakes in the survey were shallow (mean depth < 3.0 m), and periphytic diatom communities may be less specific about substrate types than previous qualitative studies (e.g. Round 1956) have suggested.

Future studies might minimize error variance in macrophyte predictive models by focusing on a calibration set of lakes that covers a narrower range of trophic state and pH. This approach would sacrifice generality but improve the precision of prediction for lakes with a limited range of macrophyte standing crop. Duarte and Kalff warn, however, that "There is no reason to expect that patterns found at any one scale are transferable to other scales" (Duarte and Kalff 1990, p. 362). A problem of scale arises when any predictive model derived from a set of limnologically diverse lakes is applied historically to a single lake that has remained comparatively constant in character over time. Confidence intervals are inappropriately large for historical predictions because fewer factors affect the error variance within a single basin than within a calibration data set.

Negative Relationship Between Chl. a and Macrophytes

Lower water-column total P values may occur in lakes with high macrophyte standing crop for the following possible reasons invoked by Canfield *et al.* (1984) to explain macrophytic influence on Chl *a*:

1) The phytoplankton community competes with macrophytes, especially floating macrophytes (e.g. *Eichhornia*), and their associated epiphyton for dissolved nutrients in the water column. High macrophyte standing crop could therefore depress water-column nutrient concentrations;
2) Macrophytes minimize wind mixing and resuspension of nutrients from bottom sediments leading to a reduction in nutrient cycling.

Other possible explanations for the negative correlation include:

1) Rooted macrophytes may proliferate in lakes that are naturally low in water-column total P concentrations because they don't depend on the water for their nutrient supply. Most of the P they utilize is derived from the sediments (Carignan and Kalff 1980);
2) When water-column nutrient concentrations are high, phytoplankton and epiphyton standing crop increases and may limit submerged macrophytes by shading (Sand-Jensen and Sondergaard 1981).

Response of Periphyton to Water-Column Nutrients

TSI variables demonstrated positive correlations with the proportion of planktonic diatoms, and negative correlations with the proportion of periphytic diatoms in the survey lakes. This suggests that planktonic diatom populations assume greater importance relative to periphyton populations in lakes that are higher in trophic state. The positive correlations between water-column total P and the concentrations and log-transformed accumulation rates of periphytic diatoms, however, show that even if plankton assume greater inportance at higher water-column nutrient concentrations, periphyton production also increases with increasing trophic state.

A positive response of periphyton biomass to higher water-column nutrients has been demonstrated in previous experimental studies and lake surveys (Stockner and Armstrong 1971, Ennis 1975, Shortreed *et al.* 1984). Sand-Jensen and Sondergaard (1981) came to the unusual conclusion that epiphyton biomass increased more than phytoplankton biomass in response to increased nutrient loading. Other studies, which appear less conclusive, have shown that periphytic biomass may be unaffected or even decline with increasing water-column P concentrations. Cattaneo (1987) concluded that periphytic biomass showed a low and variable response to water-column total P in his survey of 10 Canadian lakes, but admitted that wave intensity may have altered periphytic biomass on the surface of the large stones in shallow water where he obtained his samples. Hansson (1988) found a weak, negative correlation between log-transformed periphytic algal biomass, as assessed from colonization rates on nylon net, and log-transformed total P in 20 Swedish lakes.

Hansson speculated that in lakes of higher trophic state, plankton may limit periphyton populations to some extent by shading. Hansson noted, however, that cold temperatures in the subalpine lakes of his survey may have affected colonization rates and led to some underestimates of periphyton standing crop.

One study of periphyton and plankton communities in a Florida lake demonstrated a strong negative relationship between the biomass of these groups over a 5-month period (Hodgson *et al.* 1986). This negative correlation, however, reflected seasonal variation in community dominance within a single, closed system.

In the present study, subfossil assemblages integrated over several recent years showed a clear positive correlation between periphyton production and trophic state for a limnologically diverse set of Florida lakes. Log-transformed values of planktonic and periphytic diatom concentrations were positively correlated ($r = 0.643$, $p < 0.001$, $n = 28$), as were log-transformed planktonic and periphytic diatom accumulation rates ($r = 0.717$, $p < 0.001$, $n = 26$). A positive response of both periphyton and plankton communities to water-column nutrient concentrations was observed in another study in Florida that examined sedimentary diatom concentrations and accumulation rates along a trophic gradient (Whitmore in press). Although phytoplankton and periphyton may be negatively correlated within a lake (Hodgson *et al.* 1986), this interpretation is also influenced by the scale of analysis: they are both positively affected by water-column nutrient concentrations when considered over a broad scale of trophic state.

Recommended Predictive Models for Macrophyte Variables

During construction of the predictive models in this study, particular attention was paid to the potential covariant effects non-target environmental variables might have on the predictive models. Equation 3.1, for example, which predicted floating-leaved biomass, was shown to be confounded by pH. Equation 3.3 was a multivariate regression equation predicting percent-area coverage that was confounded by TSI(AVG). In general, I do not recommend historical application of diatom predictive models that might relate to more

than one dependent variable because of the risk of error caused by unassessed changes in the covariable.

None of the multiple regression methods produced a useful model for predicting emergent biomass. All stepwise multiple regression models for emergent biomass were subject to random error. The reason that diatom taxa related so poorly to emergent vegetation might be that the stems of emergent vegetation do not provide the large surface areas for periphyton attachment that submerged and floating-leaved macrophytes provide. Surface area has been shown to be a primary factor influencing epiphytic biomass (Cattaneo and Kalff 1980). Plants with many small or finely-dissected leaves and more lateral growth patterns such as *Hydrilla*, *Valisneria* and *Myriophyllum* would, therefore, demonstrate clearer relationships with periphytic biomass than would emergent macrophytes having vertical growth forms. Hoyer and Canfield (1986), in addition, have shown that the mean surface area to biomass ratio of submerged plants is higher than for emergent plants, which permits a greater biomass of periphyton to be supported on submerged plants than on an equal weight of emergent plants.

The best model for predicting percent-volume infestation was equation 3.7 that was derived by canonical correspondence analysis and explained 60% of the variance in that macrophyte variable. Equation 3.2, a mutlivariate equation that was based on three diatom taxa, also explained 52% of the variance in percent volume infestation. Percent-area coverage is best predicted with equation 3.4 that was based on 4 diatom taxa and explained approximately

61% of the variance in areal macrophyte coverage. Another good model for predicting percent-area coverage was the canonical correspondence equation 3.8 that explained 45% of the variance in this variable. I prefer the use of the canonical correspondence analysis models over the multiple regression models because many environmental factors may affect species' distributions (Patrick 1973), and interpretations based on a few species are less likely to be reliable. None of these 4 models was statistically confounded by covariant environmental or macrophyte variables.

Macrophyte predictive models should prove useful for assessing historical patterns in macrophyte standing crop that resulted from changes in nutrient loading (Purohit and Singh 1985). Historical water level changes might also be inferred from macrophyte predictive models because macrophyte standing crop will increase when lower water levels permit a lakeward expansion of rooted macrophytes (Landers 1982), or when higher water levels permit macrophyte colonization of a shallow littoral shelf (Anderson 1990).

Floating-leaved biomass is best predicted using equation 3.5 that explains approximately 87% of the variance in this variable using 5 diatom taxonomic groups. Partial correlations showed that the floating-leaved biomass model was marginally unconfounded by submerged biomass. None of the models for predicting submerged biomass was useful, however, because of statistical confoundedness with floating-leaved biomass. Perhaps this confoundedness occurs because periphytic taxa are not specific in their attachment sites with respect to floating versus submerged vegetation, and planktonic taxa are negatively affected to an equal degree by both types of

vegetation. Combined floating and submerged biomass can be assessed historically using equation 3.6. Despite an R^2 of approximately 0.60, the adjusted R^2 indicates that this model, which is based on 7 diatom taxonomic groups, explains about 39% of the variance in floating and submerged biomass.

Applying Predictive Models to Obtain Historical TSI Estimates

The predictive models shown above can be used to determine the historical trophic state classification of lakes taking the nutrients in macrophyte biomass into account (Canfield *et al.* 1983a). The floating-leaved and submerged biomass model (equation 3.6) can be used in conjunction with equations 3.4 or 3.8, predicting percent-area coverage, in order to estimate the total submerged and floating-leaved biomass for historical samples. Total floating-leaved and submerged biomass (TFSB) is calculated as:

$$TFSB = SA \times (PACi / 100) \times Bi$$

where SA = lake surface area (m^2)
PACi = inferred percent-area coverage
Bi = inferred floating-leaved and submerged biomass (kg m^{-2}).

Canfield *et al.* (1983a) report different percent P values for the dry weight of individual macrophyte taxa, though variation is shown between lakes in those values. It is difficult to calculate accurately the amount of P contained in the inferred total biomass because the biomass of individual macrophyte taxa cannot be determined from the diatom predictive models, and inferences are for wet weight of macrophyte biomass. If an overall mean percent P value (0.234%) is

used, however, and we assume that plant water content is 90% of fresh weight (Canfield and Duarte 1988), it is possible to multiply mean percent P by the total dry weight of floating-leaved and submerged biomass to obtain an estimate of the kg of P that would be released to the water column assuming 100% decomposition of macrophyte biomass. Dividing this mass of P by the volume of the lake produces a water-column P concentration that represents the macrophyte component of trophic state. This P concentration can be added to water-column total P inferences obtained using equation 3.9 to estimate the potential total P content of the water column (WCP, Canfield *et al.* 1983a). Historical WCP estimates should take macrophyte nutrients into account and thereby provide a more complete assessment of historical trophic state than inferences based solely on water-column total P.

Whitmore's (1989) model for predicting TSI(TP) from the TROPH 1 diatom index is useful for historically assessing changes in lake trophic state, but inferred TSI(TP) values cannot be detransformed to yield the water-column total P inferences necessary to calculate WCP. Two separate equations are used to derive TSI(TP) from total P values, depending on whether a given lake is P-limited or nutrient-balanced (Huber *et al.* 1982). In historical applications, a lake may have undergone changes in nutrient limitation over time, especially if the lake received agricultural runoff, or if sewage effluent had been directed into the lake. It would be difficult, therefore, to select the appropriate equation to detransform an historic TSI(TP) inference. Equation 3.9 in the present study will provide inferences of log-transformed water-column total P, however, and these

inferences can be detransformed to provide the necessary water-column total P values for WCP estimates.

Because of the long growing season and mild climate in Florida, the annual dieback of macrophytes and nutrient release is not likely to occur to the degree in Florida that it does in winter in cold-temperate areas. Death and decomposition of macrophytes in warm-temperate and subtropical Florida lakes are less synchronized and dramatic than in colder regions. The nutrients present in macrophytes are derived from the sediment, and their release to the water column, however slow, does represent a source of nutrient loading to lakes. Although nutrients in macrophytes of Florida lakes may be less apt to appear in the water column in a seasonal pulse, macrophytes represent a substantial component of primary production and their nutrients are as germane to the concept of trophic state as the water-column nutrients contained in phytoplankton.

APPENDIX 1

SPECIES NAMES, ACRONYMS AND
LIFE-FORM CLASSIFICATIONS

Key to Appendix

Life-form classifications

e = euplanktonic
t = tychoplanktonic
p = periphytic
u = unknown
* = assumed based on valve morphology

Species name	Acronym	Life-form class.
Achnanthes biasolettiana (?Kütz.) Grun.	ACHBIAS	u
Achnanthes exigua Grun. var. *exigua*	ACHEX	p
Achnanthes exigua var. *constricta* (Grun.) Hust.	ACHEXCO	p
Achnanthes exigua var. *heterovalva* Krasske	ACHEXHE	p
Achnanthes kryophila Pet.	ACHKRY	u
Achnanthes lanceolata (Bréb.) Grun. var. *lanceolata*	ACHLAN	p
Achnanthes lanceolata var. *dubia* Grun.	ACHLANDU	p
Achnanthes linearis (W. Sm.) Grun. var. *linearis*	ACHLIN	p*
Achnanthes linearis f. *curta* H.L. Sm.	ACHLINCU	p*
Achnanthes microcephala (Kütz.) Grun. var. *microcephala*	ACHMIC	p*
Achnanthes minutissima Kütz. var. *minutissima*	ACHMIN	p
Achnanthes pinnata Hust. var. *pinnata*	ACHPIN	u
Achnanthes sp.	ACHSP	u
Actinella punctata Lewis var. *punctata*	ACHPUNC	p*

Amphora ovalis Kutz. var. *ovalis*	AMPOV	p
Amphora ovalis var. *affinis* (Kütz.) V.H. *ex* Det.	AMPOVAF	p
Amphora ovalis var. *pediculus* (Kütz.) V.H. *ex* Det.	AMPOVPED	p
Anomeoneis serians (Bréb. *ex* Kütz.) Cl. var. *serians*	ANOMSE	u
Anomeoneis serians var. *acuta* Hust.	ANOMSEAC	p
Anomeoneis serians var. *apiculata* Boyer	ANOMSEAP	p
Anomeoneis serians var. *brachysira* (Bréb. *ex* Kütz.) Hust.	ANOMSERB	p
Anomeoneis vitrea (Grun.) Ross var. *vitrea*	ANOMVIT	p
Asterionella formosa Hass. var. *formosa*	ASTFOR	e
Asterionella ralfsii W. Sm. var. *ralfsii*	ASTRAL	e
Aulacoseira ambigua (Grun.) Sim. var. ambigua	AULAAM	e
Aulacoseira distans (Ehr.) Sim. var. *distans*	AULADIS	p
Aulacoseira granulata (Ehr.) Sim. var. granulata	AULAGR	e
Aulacoseira granulata (Ehr.) Sim. var. angustissima O. Müll.	AULAGRAN	e
Aulacoseira islandica (O. Müll.) Sim. var. *islandica*	AULAISL	e
Aulacoseira italica (Ehr.) Sim. var. *italica*	AULAITAL	t-p
Aulacoseira sp.	AULASP	u
Caloneis bacillum (Grun.) Cl. var *bacillum*	CALSP	p
Caloneis latiuscula (Kütz.) Cl.	CALLAT	p
Caloneis sp. A	CALSPA	p*
Caloneis ventricosa (Ehr.) Meist. var. *ventricosa*	CALVEN	p
Capartogramma crucicula (Grun. *ex* Cl.) Ross var. *crucicula*	CAPCRU	u
Cocconeis placentula Ehr. var. *placentula*	COCPLAC	p
Cocconeis placentula var. *lineata* (Ehr.) V.H.	COCPLACL	p
Cocconeis sp.	COCSP	p
Cyclostephanos dubius (Fricke) Round	CYSTEPDU	e
Cyclotella meneghiniana Kütz. var. *meneghiniana*	CYCMEN	e-p
Cyclotella pseudostelligera Hust. var. *pseudostelligera*	CYCPSEUD	t*
Cyclotella radiosa (Grun.) Lemmerman	CYCRAD	e
Cyclotella stelligeroides Hust.	CYCSTELO	t-p
Cyclotella sp.	CYCSP	u
Cyclotella sp. A	CYCSPA	u
Cyclotella stelligera Cl. u. Grun. var. *stelligera*	CYCSTEL	t-p
Cymbella angustata (W.Sm.) Cl. var. *angustata*	CYMANG	p
Cymbella lunata W. Sm. var. *lunata*	CYMLUN	p*
Cymbella microcephala Grun. var. *microcephala*	CYMMIC	p
Cymbella minuta Hilse *ex* Rabh. var. *minuta*	CYMMIN	p
Cymbella minuta var. *silesiaca* (Bleisch *ex* Rabh.) Reim.	CYMMINSI	p

Cymbella muelleri Hust. var. *muelleri*	CYMMUEL	p
Cymbella sp.	CYMSP	p
Diploneis elliptica (Kütz.) Cl. var. *elliptica*	DIPEL	p
Diploneis sp.	DIPSP	p
Epithemia adnata (Kütz.) Bréb. var. *adnata*	EPAD	p
Epithemia argus var. *alpestris* Grun.	EPARGAL	p*
Epithemia sp.	EPSP	p
Eunotia bidentula W. Sm. var. *bidentula*	EUNBIDT	u
Eunotia carolina Patr. var. *carolina*	EUNCARO	u
Eunotia curvata (Kütz.) Largerst. var. *curvata*	EUNCUR	t-p
Eunotia diodon Ehr. var. *diodon*	EUNDIOD	p
Eunotia flexuosa Bréb. *ex* Kütz. var. *flexuosa*	EUNFLEX	p
Eunotia formica Ehr. var. *formica*	EUNFOR	p
Eunotia incisa W. Sm. *ex* Greg. var. *incisa*	EUNINC	p
Eunotia indica Grun. var. *indica*	EUNIND	p
Eunotia luna Enr. var. *luna*	EUNLUNA	u
Eunotia maior (W. Sm.) Rabh. var. *maior*	EUNMAI	p
Eunotia monodon Ehr. var. *monodon*	EUNMON	p
Eunotia naegeli Migula var. *naegeli*	EUNNAE	p
Eunotia pectinalis (O.F. Müll.?) Rabh. var. *pectinalis*	EUNPEC	p
Eunotia pectinalis var. *minor* (Kütz.) Rabh.	EUNPECM	p
Eunotia sp.	EUNSP	p
Eunotia vanheurckii Patr. var. *vanheurckii*	EUNVAN	p
Eunotia vanheurckii var. *intermedia* (Krasske ex. Hust.) Patr.	EUNVANIN	p*
Fragilaria brevistriata Grun. var. *brevistriata*	FRAGBREV	p
Fragilaria brevistriata var. *inflata* (Pant.) Hust.	FRAGBRIN	p
Fragilaria construens (Ehr.) Grun. var. *construens*	FRAGCON	t-p
Fragilaria construens var. *pumila* Grun.	FRAGCONP	t-p
Fragilaria construens var. *venter* (Ehr.) Grun.	FRANCONV	t-p
Fragilaria crotonensis Kitton. var. *crotonensis*	FRAGCROT	e
Fragilaria pinnata Ehr. var. *pinnata*	FRAGPIN	p
Fragilaria virescens Ralfs. var. *virescens*	FRAGVIR	u
Frustulia rhomboides (Ehr.) DeT. var. *rhomboides*	FRUSRH	p
Frustulia rhomboides var. *capitata* (A. Mayer) Patr.	FRUSRHCA	p
Frustulia rhomboides var. *saxonica* (Rabh.) DeT.	FRUSRHSA	p*
Gomphonema affine Kütz. var. *affine*	GOMAAF	p
Gomphonema gracile Ehr. var. *gracile*	GOMAGRAC	t-p
Gomphonema grunowii Patr. var. *grunowii*	GOMAGRUN	p
Gomphonema intricatum Kütz. var. *intricatum*	GOMAIN	p
Gomphonema parvulum (Kütz.) var. *parvulum*	GOMAPAR	p
Gomphonema parvulum var. *lanceolata* Grun.	GOMAPARL	p
Gomphonema sp.	GOMASP	p

Gopmphona truncatum var. *turgidum* (Ehr.) Patr.	GOMATRUT	p
Gyrosigma obscurum (W. Sm.) Griff. & Henfr. var. *obscurum*	GYROOBS	u
Hantzschia amphioxys (Ehr.) Grun. var. *amphioxys*	HANTAMP	p
Mastogloia smithii var. *lacustris* Grun.	MASTSMLA	p
Navicula accomoda Hust. var. *accomoda*	NAVACCOM	u
Navicula anglica var. *subsalsa* (Grun.) Cl.	NAVANGSU	u
Navicula arvensis Hust. var. *arvensis*	NAVARV	p*
Navicula confervacea (Kütz.) Grun. var. *confervacea*	NAVCONF	p
Navicula confervacea var. *peregrina* (W. Sm.) Grun.	NAVCONFP	p
Navicula cuspidata (Kütz.) Kütz. var. *cuspidata*	NAVCUS	p
Navicula exigua Greg. ex. Grun. var. *exigua*	NAVEX	p
Navicula exigua var. *capitata* Patr.	NAVEXCA	p
Navicula gottlandica Grun. var. *gottlandica*	NAVGOT	p*
Navicula halophila (Grun.) Cl. var. *halophila*	NAVHAL	u
Navicula hustedtii Krasske var. *hustedtii*	NAVHUST	p*
Navicula kriegeri Krasske	NAVKRIEG	u
Navicula lanceolata (Ag.) Hust. var. *lanceolata*	NAVLAN	p
Navicula minima Grun. var. *minima*	NAVMIN	p
Navicula mutica Kütz. var. *mutica*	NAVMUT	t-p
Navicula oblonga (Kütz.) var. *oblonga*	NAVOBL	p
Navicula pupula Kütz. var. *pupula*	NAVPU	p
Navicula pupula var. *elliptica* Hust.	NAVPUEL	p
Navicula pupula var. *rectangularis* (Greg.) Grun.	NAVPURE	p
Navicula radiosa Kütz. var. *radiosa*	NAVRA	p
Navicula radiosa var. *parva* Wallace	NAVRAPA	p
Navicula rhyncocephala Kütz. var. *rhyncocephala*	NAVRHY	p
Navicula rhyncocephala var. *germainii* (Wallace) Patr.	NAVRHYGE	u
Navicula seminuloides Hust.	NAVSE	u
Navicula seminulum Grun. var. *seminulum*	NAVSEM	p*
Navicula seminulum var. *hustedtii* Patr.	NAVSEMHU	u
Navicula seminulum var. *intermedia* Hust.	NAVSEMIN	p*
Navicula sp.	NAVSP	p
Navicula sp. F	NAVSPF	u
Navicula subtilissima Cl. var. *subtilissima*	NAVSUBT	p*
Navicula tripunctata (O. Müll.) Bory var. *tripunctata*	NAVTRI	p
Navicula viridula var. *linearis* Hust.	NAVVIRL	p
Neidium affine (Ehr.) Pfitz. var. *affine*	NEIAF	p
Neidium affine var. *amphirhyncus* (Ehr.) Cl.	NEIAFAMP	p
Neidium affine var. *ceylonicum* (Skv.) Reim.	NEIAFCEY	p*
Neidium apiculatum Reim. var. *apiculatum*	NEIAP	p
Neidium dubium (Ehr.) Cl. var. *dubium*	NEIDUB	u

Neidium floridanum Reim. var. *floridanum*	NIEFL	p
Neidium iridis (Ehr.) Cl. var. *iridis*	NEIIR	p
Neidium iridis var. *amphigomphus* (Ehr.) A. Mayer	NEIIRAMH	p
Neidium iridis var. *ampliatum* (Ehr.) Cl.	NEIIRAML	p
Neidium ladogense var. *densestriatum* (Østr.) Foged	NEILADDE	p
Neidium sp.	NEISP	p
Nitzschia amphibia Grun. var. *amphibia*	NITZAM	p
Nitzschia capitellata Hust. var. *capitellata*	NITZCAP	t-p
Nitzschia fonticola Grun. var. *fonticola*	NITZFONT	p
Nitzschia frustulum Kütz. var. *frustulum*	NITZFRUS	e-p
Nitzschia gracilis Hantz.	NITZGRAC	u
Nitzschia Hantzschiana Rabh.	NITZHANT	u
Nitzschia linearis (W. Sm.) var. *linearis*	NITZLIN	p
Nitzschia obtusa W. Sm. var. *obtusa*	NITZOBT	u
Nitzschia palea (Kütz.) W. Sm. var. *palea*	NITZPAL	t-p
Nitzschia romana Grun.	NITZROM	t*
Nitzschia scalaris (Ehr.) W. Sm.	NITZSCAL	u
Nitzschia sigma (Kütz.) W. Sm. var. *sigma*	NITZSIG	p
Nitzschia sp.	NITZSP	p
Nitzschia tryblionella var. *levidensis* (W. Sm.) Grun.	NITZTRYL	t-p
Opephora americana M. Perag. var. *americana*	OPEAM	p
Opephora martyi Herib. var. *martyi*	OPEMAR	p
Pinnularia abaujensis (Pant.) Ross var. *abaujensis*	PINABA	p
Pinnularia abaujensis var. *linearis* (Hust.) Patr.	PINABAL	p
Pinnularia abaujensis var. *rostrata* (Patr.) Patr.	PINABAR	p
Pinnularia appendiculata (Ag.) Cl. var. *appendiculata*	PINAP	p*
Pinnularia biceps Greg. var. *biceps*	PINBI	p
Pinnularia biceps var. *petersenii* Ross	PINBIPET	u
Pinnularia borealis var. *rectangularis* Carlson	PINBORRE	p
Pinnularia braunii (Grun.) Cl. var. *braunii*	PINBR	u
Pinnularia braunii var. *amphicephala* (A. Mayer) Hust.	PINBRAMP	p*
Pinnularia caudata (Boyer) Patr. var. *caudata*	PINCAUD	u
Pinnularia dactylus Ehr. var. *dactylus*	PINDAC	p
Pinnularia latevittata Cl. var. *latevittata*	PINLAT	p
Pinnularia latevittata var. *domingensis* Cl.	PINLATDO	p
Pinnularia legumen (Ehr.) Ehr. var. *legumen*	PINLEG	p
Pinnularia sp.	PINSP	p
Pinnularia sp. B	PINSPB	p*
Pinnularia subcapitata Greg. var. *subcapitata*	PINSUB	p
Pinnularia subcapitata var. *paucistriata* (Grun.) Cl.	PINSUBPA	p
Pinnularia viridis (Nitz.) Ehr. var. *viridis*	PINVIR	p
Pinnularia viridis var. *minor* Cl.	PINVIRMI	p

Rhopalodia gibba (Ehr.) O. Müll. var. *gibba*	RHOPGIB	p
Stauroneis anceps Ehr. var. *anceps*	STAUANC	p
Stauroneis obtusa Lagerst. var. *obtusa*	STAUOBT	u
Stauroneis pachycephala Cl. var. *pachycephala*	STAUPACH	u
Stauroneis palustris Hust.	STAUPAL	u
Stauroneis phoenocenteron (Nitz.) Ehr. var. *phoenocenteron*	STAUPH	p
Stauroneis phoenocenteron f. *gracilis* (Ehr.) Hust.	STAUPHGR	p
Stauroneis smithii Grun. var. *smithii*	STAUSM	u
Stauroneis sp.	STAUSP	p
Stenopterobia intermedia (Lewis) V.H. var. *intermedia*	STENINT	u
Stephanodiscus niagarae Ehr. var. *niagarae*	STEPNI	u
Stephanodiscus rotula var. *minutula* (Kütz.) Ross & Sims	STEPROMI	e
Surirella biseriata Bréb. var. *biseriata*	SURBIS	t-p
Surirella delicatissima Lewis	SURDEL	p*
Surirella linearis W. Sm. var. *linearis*	SURLIN	p*
Surirella linearis var. *constricta* (Ehr.) Grun.	SURLINCO	p*
Surirella robusta Ehr. var. *robusta*	SURROB	u
Surirella robusta var. *splendida* (Ehr.) V.H.	SURROBSP	p
Surrirella sp.	SURSP	u
Surirella tenera Greg. var. *tenera*	SURTEN	u
Synedra acus Kütz. var. *acus*	SYNACUS	t-p
Synedra delicatissima W. Sm. var. *delicatissima*	SYNDEL	e
Synedra delicatissima var. *angustissima* Grun	SYNDELAN	e
Synedra filiformis var. *exilis* Cl.-Eul.	SYNFILEX	t*
Synedra incisa Boyer var. *incisa*	SYNINC	u
Synedra miniscula Grun. var. *minuscula*	SYNMIN	u
Synedra parasitica (W. Sm.) Hust. var. *parasitica*	SYNPAR	p
Synedra pulchella Ralfs *ex.* Kütz. var. *pulchella*	SYNPUL	p
Synedra pulchella var. *lanceolata* O'Meara	SYNPULLA	p
Synedra radians Kütz. var. *radians*	SYNRAD	e
Synedra rumpens Kütz. var. *rumpens*	SYNRUM	p
Synedra rumpens var. *familiaris* (Kütz.) Grun.	SYNRUMFA	p
Synedra rumpens var. *fragiliariodes* Grun.	SYNRUMFR	u
Synedra sp.	SYNSP	u
Synedra sp. A	SYNSPA	u
Synedra ulna (Nitz.) Ehr. var. *ulna*	SYNUL	e
Synedra ulna var. *amphirhyncus* (Ehr.) Grun.	SYNULAMP	e
Tabellaria fenestrata (Lyngb.) Kütz. var. *fenestrata*	TABFEN	p
Tabellaria flocculosa (Roth) Kütz. var. *flocculosa*	TABFLOC	t-p
Triceratium sp.	TRICSP	p*

APPENDIX 2

FORTY-SEVEN DIATOM TAXONOMIC GROUPS USED IN MUTLIVARIATE ANALYSES

Acronym for taxonomic group	group composed of: (see Appendix 1 for species acronyms)
S-ACH	ACHBIAS + ACHEX + ACHEXCON + ACHEXHE + ACHKRY + ACHLAN+ ACHLANDU + ACHLIN + ACHLINCU + ACHMIC ACHMIN +ACHPIN + ACHSP
ACTPUNC	ACTPUNC
S-ANOM	ANOMSE + ANOMSEAC + ANOMSEAP + ANOMSERB + ANOMVIT
S-AST	ASTFOR + ASTRAL
AULAAM	AULAAM
AULADIS	AULADIS
S-AULAGR	AULAGR + AULAGRAN
AULAISL	AULAISL
AULAITAL	AULAITAL
CALSPA	CALSPA
COCPLACL	COCPLACL
CYCMEN	CYCMEN
CYCPSEUD	CYCPSEUD
CYCSTEL	CYCSTEL
CYCSTELO	CYCSTELO
S-CYM	CYMLUN + CYMMIC + CYMMIN + CYMMINSI + CYMMUEL
CYSTEPDU	CTSTEPDU
S-EP	EPARGAL + EPAD + EPSP
S-EUN	EUNBIDT + EUNCARO + EUNCUR + EUNDIOD + EUNELEG + EUNEXIG + EUNFLEX + EUNFOR + EUNINC + EUNIND + EUNLUNA + EUNMAI + EUNMON + EUNNAE + EUNPEC + EUNPECM + EUNSP + EUNVAN + EUNVANIN
FRAGBREV	FRAGBREV
S-FRAGCO	FRAGCON + FRAGCONP + FRAGCONV

FRAGCROT	FRAGCROT
FRAGPIN	FRAGPIN
S-FRUSRH	FRUSPH + FRUSRHCA + FRUSRHSA
S-GOMA	GOMAAF + GOMAGRAC + GOMAGRUN + GOMAIN + GOMAPAR + GOMAPARL + GOMASP
NAVCONF	NAVCONF
NAVGOT	NAVGOT
NAVCUS	NAVCUS
NAVLAN	NAVLAN
S-NAVPU	NAVPU + NAVPUEL + NAVPURE
S-NAVRA	NAVRA + NAVRAPA
S-NAVSEM	NAVSEM + NAVSEMIN
NAVSUBT	NAVSUBT
S-NEI	NEIIR + NEIIRAMH + NEIIRAML + NEIAP + NEIDUB + NEIFL + NEISP + NEILADDE
NITZAM	NITZAM
NITZCAP	NITZCAP
NITZFONT	NITZFONT
NITZFRUS	NITZFRUS
NITZPAL	NITZPAL
S-PIN	PINABA + PINABAL + PINABAR + PINBI + PINBIPET + PINBORRE + PINBR + PINBRAMP + PINCAUD + PINDAC + PINLAT + PINLATDO + PINLEG + PINSP + PINSPB + PINSUB + PINSUBPA + PINVIR + PINVIRMI + PINAP
S-STAU	STAUANC + STAUPACH + STAUOBT + STAUPAL + STAUPH + STAUPHGR + STAUSM + STAUSP
S-SUR	SURBIS + SURDEL + SURLIN + SURLINCO + SURROB + SURROBSP + SURSP + SURTEN
SYNDEL	SYNDEL
SYNFILEX	SYNFILEX
S-SYNRUM	SYNRUM + SYNRUMFA
TABFEN	TABFEN
TABFLOC	TABFLOC

APPENDIX 3

TAXONOMIC GROUPS USED IN STEPWISE REGRESSION PROCEDURES

(Taxonomic acronyms are defined in Appendices 1 and 2.)

Key to trend in diatom representation over range of macrophyte variable

i = increasing over range
ic = increasing in curvilinear fashion
d = decreasing over range
dc= decreasing in curvilinear fashion
u = uniform over range

3.1. Predicting percent-volume infestation from diatom percentage data beginning with 17 diatom taxonomic groups.

Acronym of taxonomic group	Trend
ACHEX	d
S-AST	d
S-AULAGR	d
AULAITAL	d
CYMLUN	i
EUNCUR	i
FRAGBREV	d
S-GOMA	i
S-NAVPU	i
NAVLAN	d
NAVRA	d
NAVSUBT	d
NITZAM	d
S-PIN	d
S-STAU	i
S-SUR	d
SYNDEL	d

3.2. Predicting percent-volume infestation from diatom concentration data beginning with 17 diatom taxonomic groups.

Acronym of taxonomic group	Trend
ACHEX	dc
ACHMIN	dc
ANOMSERB	d
AULAAM	dc
S-AULAGR	dc
CALSPA	dc
COCPLACL	d
CYCSTEL	d
CYCPSEUD	d
NAVLAN	d
S-NEI	dc
NITZCAP	dc
NITZFONT	dc
S-PIN	dc
STAUPH	i
SYNFILEX	d
SYNRUM	dc

3.3. Predicting percent-volume infestation from log-transformed diatom accumulation rates beginning with 17 diatom taxonomic groups.

Acronym of taxonomic group	Trend
ACHEX	d
ACHMIN	d
ANOMSERB	d
AULAAM	d
S-AULAGR	d
CALSPA	d
COCPLACL	d
CYCSTEL	d
CYCPSEUD	dc

NAVLAN	d
S-NEI	d
NITZCAP	d
NITZFONT	d
S-PIN	d
STAUPH	u
SYNFILEX	dc
SYNRUM	dc

3.4. Predicting percent-area coverage from diatom percentage data beginning with 11 diatom taxonomic groups.

Acronym of taxonomic group	Trend
$\log_{10}$(ACHLIN)	i
S-ANOM	i
AULAAM	d
$\log_{10}$(AULAGRAN)	d
CYCPSEUD	d
S-CYM	ic
S-EUN	i
S-FRUSRH	i
NAVRA	d
STAUPH	i
TABFEN	i

3.5. Predicting percent-area coverage from diatom concentration data beginning with 8 diatom taxonomic groups.

Acronym of taxonomic group	Trend
ACHLIN	ic
AULAAM	d
S-AULAGR	dc
CYCPSEUD	d
CYCSTEL	d
EUNINC	ic
STAUPH	ic
SYNFILEX	d

3.6. Predicting percent-area coverage from log-transformed diatom accumulation rates beginning with 11 diatom taxonomic groups.

Acronym of taxonomic group	Trend
ANOMSERB	i
AULAGRAN	d
CYCPSEUD	d
CYMLUN	ic
CYMMIN	i
S-EUN	i
FRUSRHCA	i
S-GOMA	i
NAVPU	d
STAUPH	i
SYNFILEX	d

3.7. Predicting floating-leaved biomass beginning with 9 diatom taxonomic groups identified in cluster analysis of diatom concentration data.

Acronym of taxonomic group	Trend
S-AULAGR	dc
CYCMEN	d
CYCPSEUD	u
CYSTELO	u
CYSTEPDU	i?
FRAGCROT	i?
NITZFONT	u
NITZPAL	u?
S-SYNRUM	u

3.8. Predicting floating-leaved biomass beginning with 7 diatom taxonomic groups identified from cluster analysis of diatom accumulation rates.

Acronym of taxonomic group	Trend
S-AST	u?
AULAISL	d?
TABFLOC	d
S-NEI	d
S-NAVRA	dc
SYNFILEX	dc
TABFEN	dc

3.9. Predicting floating-leaved biomass from log-transformed diatom percentage data beginning with 12 taxonomic groups.

Acronym of taxonomic group	Trend
$\log_{10}$(ACHEX + ACHLIN + ACHLINCU + ACHMIN)	d
$\log_{10}$(S-ANOM)	d
$\log_{10}$(AULAGR + AULAITAL + AULAISL + AULAAM)	d
$\log_{10}$(CYMMUEL)	d
$\log_{10}$(CYSTEPDU)	i
$\log_{10}$(EUNPEC)	d
$\log_{10}$(S-FRUSRH)	d
$\log_{10}$(NAVGOT + NAVLAN + S-NAVPU + S-NAVRA + NAVSUBT)	d
$\log_{10}$(NITZAM + NITZCAP + NITZFRUS)	d
$\log_{10}$(SYNDEL + SYNRUM)	d
$\log_{10}$(S-STAU)	d
$\log_{10}$(S-SUR)	d

3.10. Predicting submerged biomass from diatom percentage data beginning with 20 taxonomic groups.

Acronym of taxonomic group	Trend
S-ACH	dc
S-ANOM	d?
AULAAM	d?
S-AULAGR	d
(AULAISL + AULAITAL)	d
(CYCMEN + CYCPSEUD + CYCSTEL + CYSTELO)	d
S-CYM	d
CYSTEPDU	d?
EUNPEC	d
EUNVAN	d
FRAGCROT	d?
S-FRUSRH	dc
S-NAVRA	d
NAVSUBT	d
S-NEI	d
S-NITZ	d
S-PIN	d
S-STAU	d
S-SUR	d
(SYNDEL + S-SYNRUM)	d

3.11. Predicting floating + submerged biomass from diatom percentage data beginning with 16 taxonomic groups.

Acronym of taxonomic group	Trend	
	Floating	Submerged
S-ACH	d	d
S-ANOM	d	d
(AULAISL + AULAITAL)	d	d
S-CYM	dc	dc
CYSTEPDU	d?	i?

EUNPEC	d	d
S-FRUSRH	dc	dc
(NAVGOT + NAVLAN + S-NAVPU + S-NAVRA + NAVSUBT)	d	d
S-NITZ	u	d
S-STAU	d	d
S-SUR	d	d
(SYNDEL + SYNRUM)	d	d
FRAGCROT	d?	i?
EUNVAN	d	d
S-AULAGR	u	d
AULAAM	d	d

3.12. Predicting emergent biomass from diatom percentage data beginning with17 taxonomic groups.

Acronym of taxonomic group	Trend
(ACHEX + ACHLIN + ACHLINCU + ACHMIN)	d
(AULAM + AULAGR + AULAITAL)	dc
CYCMEN	d
CYCPSEUD	d
CYCSTEL	d
S-CYM	d
EUNPEC	d
FRAGCONV	d
S-FRUSRH	d
FRAGPIN	d?
S-NAVRA	d
NAVSUBT	d
S-NITZ	d?
S-PIN	d
S-SUR	d
TABFEN	d
S-SYNRUM	d

APPENDIX 4

CHL *A*, TOTAL N, AND SECCHI DEPTH VALUES USED TO CALCULATE TSI(AVG)

Lake	Chl *a* ($\mu g\ l^{-1}$)	Total N ($mg\ l^{-1}$)	Secchi depth (m)
Alligator	25.4	2.37	0.46
Apopka	59.3	4.03	0.20
Bonny	36.5	1.86	0.58
Carr	7.0	0.87	1.81
Catherine	1.5	0.30	3.20
Clay	2.1	0.36	4.00
Crooked	1.8	0.33	3.13
Deep	0.9	0.16	
Fairview	2.4	0.50	4.80
Harris	37.2	1.55	0.60
Hartridge	3.7	0.48	2.32
Keys Pond	1.0	0.17	5.25
Lindsey	5.2	0.65	1.95
Live Oak	5.3	0.35	2.55
Lochloosa	26.5	1.05	0.97
Loften Ponds	1.2	0.39	2.48
Moore	3.5	0.35	5.28
Mystic	3.6	0.52	7.00
Ocean Pond	3.9	0.42	1.10
Okahumpka	5.1	0.95	1.20
Orange	16.8	1.11	0.80
Patrick	4.0	1.47	2.00
Rowell	37.8	0.81	0.65

Stella	2.0	0.43	4.10
Tomohawk	1.2	0.21	4.00
Townsend	5.1	0.58	3.80
Watertown	15.9	1.05	1.90
Wauberg	114.7	1.57	0.57
Wildcat	1.2	0.19	3.61

APPENDIX 5

SUBJECTIVE TROPHIC STATE CLASSIFICATION OF LAKES IN SURVEY

Key to Trophic Classification categories:

U = ultraoligotrophic
O = oligotrophic
M = mesotrophic
E = eutrophic
H = hypereutrophic

	Classification based on:		
Lake	water-column nutrients	macrophyte presence	overall
Alligator	H	O	H
Apopka	H	O	H
Bonny	E	O	H
Carr	M	H	H
Catherine	U	M	M
Clay	U	H	H
Crooked	O-M	O-M	O-M
Deep	U	E	E
Fairview	M	M	M
Harris	M	O-M	M
Hartridge	O	M	M
Keys Pond	U	M	M
Lindsey	M	H	H
Live Oak	M	H	H
Lochloosa	E	E	E
Loften Ponds	U	M-E	M-E
Moore	O	M	M

Mystic	M	H	H
Ocean Pond	E	U	E
Okahumpka	M	H	H
Orange	E	H	H
Patrick	M	H	H
Rowell	E	M	E
Stella	M	E	E
Tomohawk	U	M	M
Townsend	O	H	H
Watertown	E	O	E
Wauberg	H	U	H
Wildcat	O	U	O

APPENDIX 6

PROPORTIONS, SEDIMENTARY CONCENTRATIONS, AND ANNUAL ACCUMULATION RATES OF PERIPHYTIC AND PLANKTONIC DIATOMS

Lake	proportion of		sedimentary concentration of		accumulation rate of	
	periphyton	plankton	periphyton (valves g^{-1} dry wt.)	plankton	periphyton (valves cm^{-2} yr^{-1})	plankton
Alligator	0.589	0.396	121100000	179900000	12510980	8418825
Apopka	0.864	0.121	32570000	233500000	21346251	2976821
Bonny	0.826	0.160	53870000	278200000	8590952	1663516
Carr	0.929	0.063	35180000	551900000	12891190	879094
Catherine	0.932	0.027	249700	8650000	275007	7940
Clay	0.946	0.050	9864000	187100000	5007004	264036
Crooked	0.917	0.063	11490000	166100000	2709780	187405
Deep	0.944	0.046	7447000	151700000	15611878	766160
Fairview	0.877	0.100	3253000	28390000	6152316	704900
Harris	0.418	0.559	305900000	228900000	8459550	11304190
Hartridge	0.693	0.267	87880000	227700000	11040351	4261654
Keys Pond	0.990	0.005	3558000	769600000	14336580	66276
Lindsey	0.835	0.151	22720000	125700000	3766963	681188
Live Oak	0.738	0.221	15940000	53360000	8310804	2483256
Lochloosa	0.700	0.286	198600000	485100000	19189076	7856724
Loften Ponds	0.986	0.001	82270	123900000	2112018	1402
Moore	0.966	0.005	836600	158300000	7106080	37550
Mystic	0.945	0.025	2061000	79150000		

Ocean Pond	0.520	0.473	89050000	97880000	10101995	9190420
Okahumpka	0.830	0.156	1728000	9189000	562356	105759
Orange	0.467	0.522	86230000	77040000		
Patrick	0.797	0.186	79880000	342600000	85213324	19870675
Rowell	0.797	0.166	81420000	391000000	119924146	24974864
Stella	0.704	0.272	15010000	38870000	6584954	2543414
Tomohawk	0.913	0.035	3320000	87080000	2729599	104071
Townsend	0.911	0.068	2257000	30420000	1329103	98631
Watertown	0.408	0.580	555000000	390400000	25688546	36517243
Wauberg	0.453	0.538	613200000	516400000	18105581	21501135
Wildcat	0.540	0.435	59450000	73820000	38164329	30736411

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BIOGRAPHICAL SKETCH

Thomas J. Whitmore was born in Bridgeport, Connecticut on July 27, 1955. Tom graduated from the University of Connecticut in 1977 with a Bachelor of Science degree from the Biology Department. His studies emphasized geology and paleontology, and included a 12-credit independent study on the paleoecology of the Miocene and Pliocene sediments of the South Carolina coastal plain. Tom completed a graduate course in micropaleontology at Western Connecticut State College and entered the University of Florida for graduate work in 1979.

Though intending research in invertebrate paleontology, Tom met Edward S. Deevey, Jr. and began studies with Ed on the paleolimnology of Florida lakes. Tom studied the "Ecology and Systematics of Diatoms" with Charles Reimer at Iowa Lakeside Laboratory in the summer of 1981, and submitted his master's thesis entitled "Diatom Transfer Functions for Assessing the Cultural Eutrophication of Florida Lakes" in 1985.

Tom continued graduate work in Ed Deevey's laboratory at the Florida Museum of Natural History until Ed's death in 1988. In 1990, Ed's lab relocated to join Claire Schelske in the Department of Fisheries and Aquaculture at the University of Florida. Tom continued graduate studies under the guidance of Frank Nordlie, Chairman of the Department of Zoology. He also participated in field

work and research in 1989-90 on the paleolimnology of the Yunnan Plateau of China under the direction of Mark Brenner, his long-time friend and colleague.

Tom's professional interests include further research on assessing the trophic trajectories of lakes, reconstructing climatic and anthropogenic influences on lakes in southern China, and interpreting long-term climatic patterns in Florida from lake sedimentary indicators.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Frank G. Nordlie, Chairman
Professor of Zoology

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May 1991

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