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Development of a decision tree model for the prediction of the limitation potential of phytoplankton in Lake Okeechobee, Florida, USA

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South Florida Water Management District

With 4 figures and 4 tables

Abstract: Conducting long-term algal bioassays in large, complex systems such as Lake Okeechobee is an expensive and time-intensive undertaking, especially in comparison with physical and chemical monitoring. This paper describes a water quality-based decision tree model for predicting whether the phytoplankton in Lake Okeechobee is limited by light or nutrients. The model was developed and validated using the results of algal bioassays coupled with routinely monitored water quality data. Algal bioassays indicated that the factor most commonly limiting phytoplankton production in Lake Okeechobee for the period of October 1997 to November 2000 was light (59 %) followed by nitrogen (41 %). Limitation status of the phytoplankton was positively correlated with irradiance (in terms of Secchi depth/total depth) and phytoplankton biomass (in terms of chlorophyll-a) and negatively related to dissolved inorganic nitrogen and soluble reactive phosphorus concentrations. A cross-tabulation procedure was used to examine how the frequency of occurrence of light limitation and nutrient limitation varied as a function of these variables. The cross-tabulation procedure was also used to derive the empirical threshold values used to construct the model. This result supports both the accuracy of the derived critical threshold values and the validity of using chemical measurements in predicting whether light is limiting or nutrients are limiting in Lake Okeechobee. The model successfully predicted light limitation versus nutrient limitation in three independent validation data sets 70 % to 85 % of the time. When nutrient limiting conditions prevailed, the model did not successfully predict which nutrient (nitrogen, phosphorus, or a combination of nitrogen and phosphorus) was limiting. Our results suggest that the predictive abilities of the model could be enhanced by using time-specific data rather than averaged monthly data.

Key words: bioassay, decision tree model, nutrient limitation, light limitation, subtropical lake.

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Introduction

In 1994, a long-term ecological monitoring project was initiated in Lake Okeechobee in response to legislation that mandated restoration and protection of the lake's ecosystem (South Florida Water Management District 1989). The goal of this effort was to establish assessment techniques that would help quantify the success of restoration efforts. Because algal bioassay studies are used to examine the environmental variables that influence or limit phytoplankton growth and to evaluate the growth potential of the algae (RYTHER & DUNSTAN 1971, SCHINDLER 1975, SCHELSKE et al. 1978, SMITH 1984, ELSER & KIMMEL 1985), nutrient and light gradient algal bioassays were initiated in Lake Okeechobee.

Laboratory algal bioassays have been used widely in both freshwater and marine systems (GRANELI 1984, D'ELIA et al. 1986, ELSER et al. 1988, ZOU et al. 2001), and are popular because they are relatively easy to set up and analyze, especially in small homogeneous systems where sampling is limited to a few sites simultaneously. Lake Okeechobee, however, is the largest subtropical lake in North America and is a heterogeneous ecosystem with significant spatial and temporal variation in chemical, physical, and biological parameters (KRATZER & BREZONIK 1984, PHLIPS et al. 1993, HAVENS et al. 1994, PHLIPS et al. 1995).

Because of the lake's spatial complexity and because multi-day bioassays are required for the reliable determination of limitation status (SCHELSKE et al. 1974, GOLTERMAN 1975, DODDS & PRISCU 1990) resource and manpower constraints limited our capabilities of assessment of nutrient status to 4 sites on a bimonthly basis. In contrast, the lake has a long history of comprehensive monitoring for physical and chemical parameters at numerous sites within the pelagic region (JAMES et al. 1995). The purpose of this paper was to determine if this extensive water quality database, coupled with the algal bioassays, could be used to develop a decision tree model for predicting limitation status of the phytoplankton population in Lake Okeechobee. The goal was to provide a tool to accurately and efficiently predict limitation status of the phytoplankton at multiple sites on a regular basis throughout this complex system using routinely monitored water quality data, rather than the more expensive and time consuming algal bioassays.

This manuscript documents the framework used for the development of the simple water quality based decision tree model. The model's performance and utility in predicting limitation status are also documented.

Study site

Lake Okeechobee is a large (1730 km^2), shallow, subtropical lake located in south-central Florida, USA (FLAIG & HAVENS 1995). The surface area consists of approximately 75 % pelagic and 25 % littoral habitat depending on water level (AUMEN 1995). PHLIPS et al. (1993) identified several ecologically distinct zones in the lake, based largely on sediment type, light levels, nutrient concentrations, and phytoplankton biomass (Fig. 1). The Central pelagic region is characterized by high levels of turbidity from resuspended sediments (MACEINA & SOBALLE 1990, HANLON et al. 1998), high total phosphorus concentrations and low chlorophyll and phytoplankton biomass. The North region has high nutrient and chlorophyll concentrations over sandy sediments. The South region is shallow and clear, with low nutrient concentrations and peat sediment. Phytoplankton biomass in this region is influenced by external nutrient inputs. The West region is a transition area between the shallow near-shore region and the deeper pelagic region with water quality characteristics dependent on lake stage. Cyanobacteria currently dominate the phytoplankton community and periodically large scale surface algal blooms occur along the near shore regions of the lake (HAVENS et al. 2003).

Methods

Bioassay-field procedures

To account for the physical and chemical heterogeneity, the four sites described above were sampled on a bimonthly basis from October 1997 to August 2002 (Fig. 1). Samples for bioassays were collected using an integrated sampling tube consisting of a 40 mm inner diameter clear PVC pipe equipped with a stopper remotely operated by a long cord. Repeated samples were composited into 20-L polycarbonate carboys, covered with a tarp to exclude direct sunlight, and transported back to the laboratory where they were allowed to equilibrate in the dark overnight at room temperature (~ 25 °C) before assays were begun. In a study by MALLIN & PAERL (1992), similar overnight sample storage resulted in no significant loss in productivity (up to 24 h storage) relative to same-day tests. At the same time that water was collected for bioassays, separate samples were collected for spectrophotometric in-vitro chlorophyll analysis (APHA 1995), and station depth and Secchi transparency were measured.

Bioassay-laboratory procedures

For comparability purposes, assay methodology was generally similar to that used in ALDRIDGE et al. (1995) and PHLIPS et al. (1997), two previous bioassay studies on Lake Okeechobee. Bioassays were conducted in triplicate at a volume of 150 ml using a dedicated set of 250 ml screw cap Erlenmeyer flasks. Assays were performed in

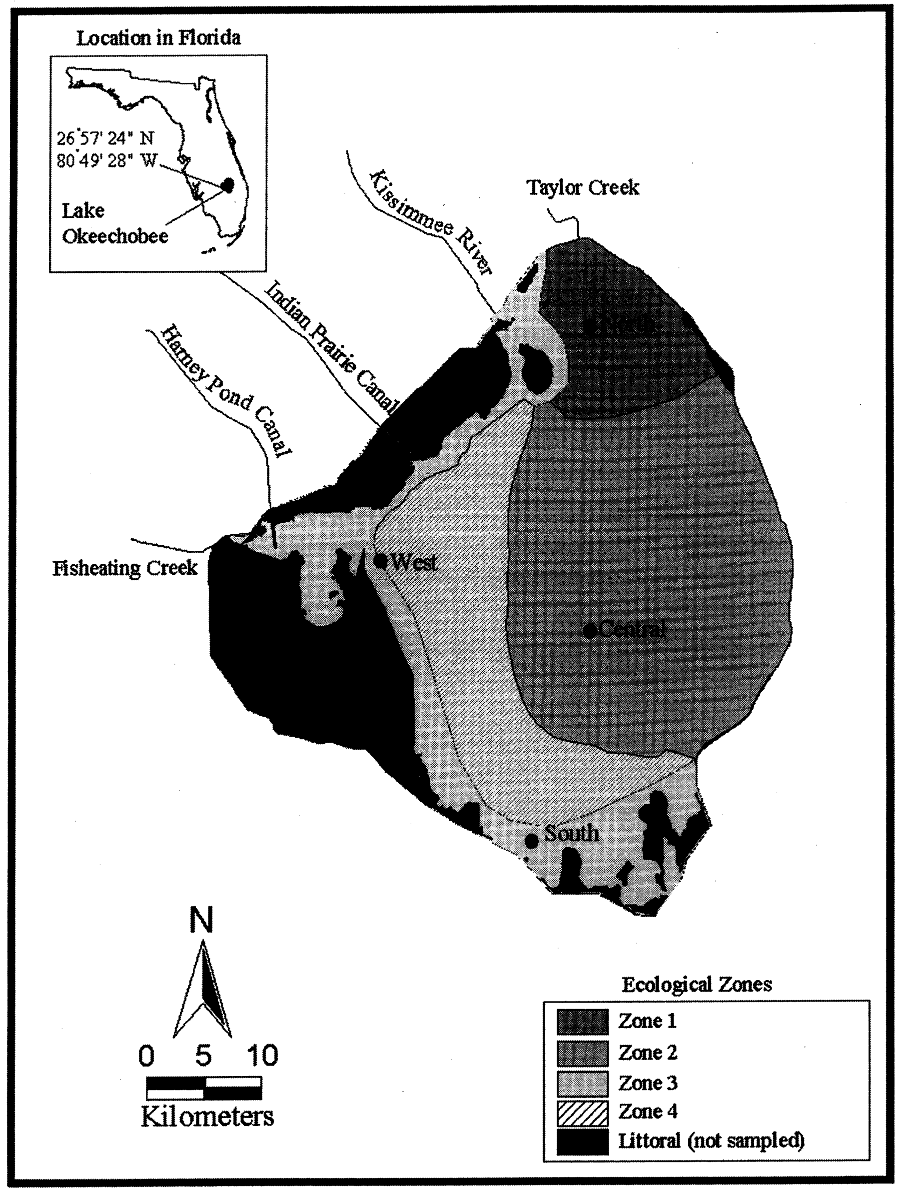

Fig. 1. Map of Lake Okeechobee, showing locations of the four bimonthly bioassay sampling sites in relation to the ecological zones defined by PHLIPS et al. (1993). Zones are characterized as follows: North (zone 1)-sand sediment, high nutrient and chlorophyll-a concentrations; Central (zone 2)-mud sediment, high turbidity, low nutrient and chlorophyll-a concentrations; South (zone 3)-peat sediment, low turbidity, low nutrient concentrations; West (zone 4)-sand sediment, nutrient and chlorophyll-a concentrations influenced by external nutrient inputs.

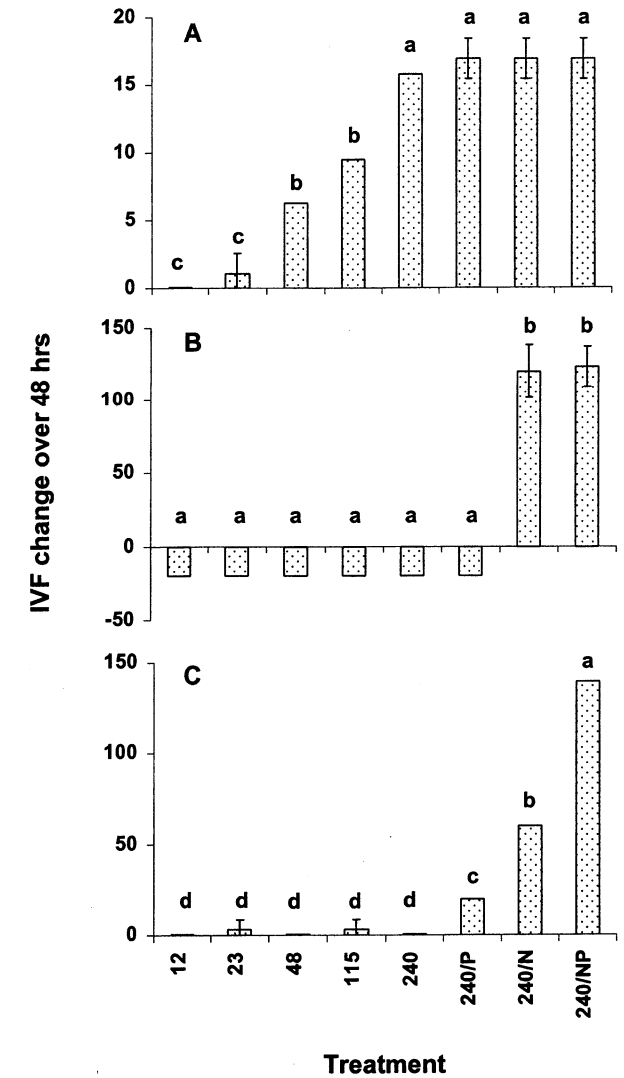

Fig. 2. Examples of bioassay results classified as **(A)** light limitation, **(B)** nitrogen limitation, and **(C)** nitrogen + phosphorus limitation. Error bars represent 1 standard deviation, letters above bars refer to Scheffe groupings. Legend on the x-axis is in the form μMoles m^{-2} s^{-1}/nutrient addition. Note different scales on y-axis.

REVCO® environmental chambers set at the ambient temperature of the water column on the day water samples were collected. Photoperiod was set at 12/12 dark/light h from October through March, and at 11/13 dark/light h from April through September. Control and nutrient enriched flasks were incubated at a PAR level of 240 μMoles m^{-2} s^{-1} as measured by a Licor® 4π quantum sensor. The light gradient consisted of radiation levels of 240, 115, 48, 23, and 12 µM m^{-2} s^{-1}. Light levels were chosen to replicate the levels used by PHLIPS et al. (1997) but nutrient enrichment and control treatments were limited to one light intensity due to resource availability. A PAR level of 240 µM m^{-2} s^{-1} was utilized because it was determined to be the lake's average maximum daily surface irradiance in the summer (PHLIPS et al. 1997) and should yield phytoplankton growth responses typical of that in the lake. Nutrient assays received either 400 µgN L^{-1}, 40 µgP L^{-1}, or 400 µgN L^{-1} plus 40 µgP L^{-1}. Enrichment levels were chosen to mimic the levels used by ALDRIDGE et al. (1995) and were consistent with the bioassay recommendations of SCHELSKE (1984). All flasks were thoroughly mixed once each day prior to sampling. Changes in algal biomass were estimated as changes in net in-vivo fluorescence of chlorophyll-a (IVF) using a Turner Design® Model 10 fluorometer with a 1 cm path length. A nutrient was considered limiting when algal biomass increased significantly in the enriched treatment but not in the control as determined by ANOVA followed by Scheffe's multiple comparison procedure (SAS 1999). Similarly, light was considered limiting when a significant light gradient response was present and no response to nutrient amendment under maximum light levels was noted. Examples of the three limitation classifications identified (light limited, N limited, and NP limited) are presented as Fig. 2. To minimize the effects of circadian rhythms and exposure to light on IVF (BERMAN 1972), fluorescence readings were taken near the end of the dark cycle. IVF was measured at the start of the assay, and after 48 hours of incubation. HAVENS et al. (1996) determined that macrozooplankton have only minimal impacts on the natural phytoplankton assemblages of Lake Okeechobee, therefore, the samples were not filtered prior to assay and grazing pressure was assumed to be equal across all treatments. Assays were not carried beyond 48 hours to limit the potential confounding effects of species succession and feedback involving other components of the system (SCHELSKE 1984, CARIGNAN & PLANAS 1994, DODDS & PRISCU 1990, DOWNING et al. 1999).

Results and discussion

Bioassay

Overall, light (L) was the most common limiting factor in Lake Okeechobee during this study accounting for 54 % of all bioassay outcomes while nitrogen (N) and nitrogen + phosphorus (NP) accounted for 29 % and 17 %, respectively (Table 1). Phosphorus-limited conditions were never documented in this study.

On a spatial scale, the deeper, more turbid North and Central sites were light-limited (L-limited) 54–85 % of the time while in the shallower, less turbid West and South nutrient limitation (N and NP) prevailed (57–67 %).

The lake oscillated between being primarily L-limited or primarily nutrient-limited seemingly as a function of irradiance related parameters, whether driven by wind, or other factors, and this in turn imparts a seasonal component to limitation status (in terms of L, N, or NP) with L-limitation being more prevalent during the windier, more turbulent winter months and nutrient limitation becoming more dominant during the summer.

Table 1. Limitation classification (status) by date and site in Lake Okeechobee based on the bioassay growth response after 48 hours. L = light limitation, N = nitrogen limitation, NP = nitrogen + phosphorus limitation. Percent values rounded to the nearest %.

Date	North	Central	West	South
Oct–97	N	L	L	N
Dec–97	N	L	NP	NP
Feb–98	L	L	–	L
Apr–98	L	L	L	L
Jun–98	L	L	NP	NP
Sep–98	L	L	NP	N
Nov–98	N	L	L	L
Feb–99	L	L	L	L
Apr–99	N	L	NP	N
Jun–99	N	N	NP	N
Aug–99	N	L	NP	N
Nov–99	L	L	NP	N
Jan–00	L	L	L	L
Mar–00	L	L	L	L
May–00	L	L	L	L
Jul–00	L	L	NP	N
Sep–00	N	N	NP	–
Nov–00	L	L	NP	N
Jan–01	NP	L	L	L
Mar–01	L	L	NP	–
May–01	N	–	NP	–
Aug–01	N	–	NP	–
Oct–01	L	L	L	L
Dec–01	L	L	NP	L
Feb–02	L	L	N	N
Apr–02	N	N	NP	N
Jun–02	N	N	N	–
Aug–02	N	L	N	N
% L	54	85	33	43
% N	43	15	11	48
% NP	3	0	56	9

Model development and testing

Database construction

Many factors can limit phytoplankton growth, but in order to be considered for inclusion in our model the variable had to meet two criteria. First, the variable had to be considered a key factor for algal growth in Lake Okeechobee. In unstratified shallow systems such as Lake Okeechobee, phytoplankton growth is generally regulated by the concentration and relative ratios of N and P (as either total or soluble forms) and irradiance levels. In two previous short term experimental bioassay studies on Lake Okeechobee, algal production was most often limited by N availability (ALDRIDGE et al. 1995) with L. limitation frequently encountered in areas with unconsolidated and flocculent mud sediments, regardless of the availability of dissolved nutrients (PHLIPS et al. 1997). PHLIPS et al. (1997) also determined that a very strong inverse relationship exists between dissolved inorganic nitrogen (DIN) concentrations and the occurrence of N-limitation, the rates of N-fixation, and the occurrence of heterocysts on cyanobacterial filaments. Overall growth was limited by light regardless of availability of soluble reactive phosphorus (SRP) or DIN under turbid conditions, and the occurrence of certain taxa of cyanobacteria (those requiring high levels of irradiance for N-fixation) were growth limited by light.

Second, the variable had to be relatively easy to measure because our objective was to develop a simple model, both in design and utility. One could argue that the examination of phytoplankton species composition would be a good indicator of L- or N-limiting conditions because heterocystic cyanobacteria typically dominate in N-limiting conditions while non-heterocystic cyanobacteria can sustain net growth in L-limiting conditions (PAERL et al. 2001, VAN DUIN et al. 1995). However, taxonomic identification of phytoplankton is labor-intensive and therefore was not considered for inclusion in the model.

Consequently, variables that were considered for possible inclusion in the model were limited to DIN, SRP, the ratio of DIN to SRP, Secchi depth to total depth ratio (SD : TD), and chlorophyll-a (CHLA) concentrations. The SD : TD ratio was employed as a surrogate for underwater irradiance and CHLA was employed as a surrogate for phytoplankton biomass.

For each station, the bimonthly bioassay limitation results were combined with the averaged monthly water quality data. The water quality data were obtained from the South Florida Water Management District's comprehensive hydrologic and water quality data base (DBHYDRO). The data included monthly (October–April) or twice monthly (May–September) measurements for the above mentioned variables. Standard methods for parameter collection and analysis were used in the field and laboratory, and are described in detail in JAMES et al. (1995).

The resulting data base was arbitrarily divided into two separate and independent data sets to eliminate problems associated with calibration and validation of a model with the same data set. The data from October 1997–November 2000 were used as the calibration data set and the data from January 2001–August 2002 were used as a validation data set.

Model construction

To determine which of the variables from those considered for possible inclusion in the model were significantly related to phytoplankton growth in Lake Okeechobee, and should therefore be included in our model, Pearson correlation coefficients were generated between the variables and the limitation classification, or status, (in terms of either light limited or nutrient limited based on the bioassay results) using the calibration dataset. Limitation status of the phytoplankton in Lake Okeechobee was positively correlated with mean monthly light levels (SD : TD, $r = 0.50$, $p < 0.001$) and mean monthly phytoplankton biomass (CHLA, $r = 0.29$, $p = 0.015$) and negatively related to mean monthly dissolved nutrient concentrations (DIN, $r = -0.45$, $p = 0.002$ and SRP, $r = -0.49$, $p < 0.001$). No significant relationships were found to exist between limitation status and the ratio of dissolved nutrient concentrations (DIN : SRP).

The relationships of the significantly correlated variables with limitation status were subsequently examined using principle component analysis (PCA). Results from the PCA indicate that nearly 70 % of the variability can be explained by axis 1, which was directly related to SD : TD and CHLA, and inversely related to DIN (Table 2). This axis was considered to be the major driving force in determining limitation status and when limitation status was considered as a function of axis 1, two distinct groupings were elucidated (Fig. 3). L-limitation occurred most often when both light level and phytoplankton standing crop were low while N-limitation (as both N and NP) occurred most often when both light level and phytoplankton standing crop were high but dissolved inorganic nitrogen was low. Axis 2, accounting for only about 21 % of the variability (Table 2), was considered a minor driving force and no discernable patterns in the data were evident (Fig. 3).

The conditions necessary for the separation of N and NP could not be determined from this analysis and P-limitation was never encountered in the bioassays. Consequently, subsequent reference to N-limitation describes the con-

Table 2. Correlation of Eigenvectors for the first and second principal components with major limnological variables considered to be key factors in algal growth. These two axes accounted for 88 % of the variability in the data set. SD : TD = Secchi Depth to Total Depth ratio; CHLA = Chlorophyll-a (mg m^{-3}); DIN = Dissolved Inorganic Nitrogen (mg L^{-1}); SRP = Soluble Reactive Phosphorus (mg L^{-1}).

Variable	Axis 1	Axis 2
SD:TD	0.77	0.58
CHLA	0.41	−0.76
DIN	−0.46	0.29
SRP	−0.13	0.06

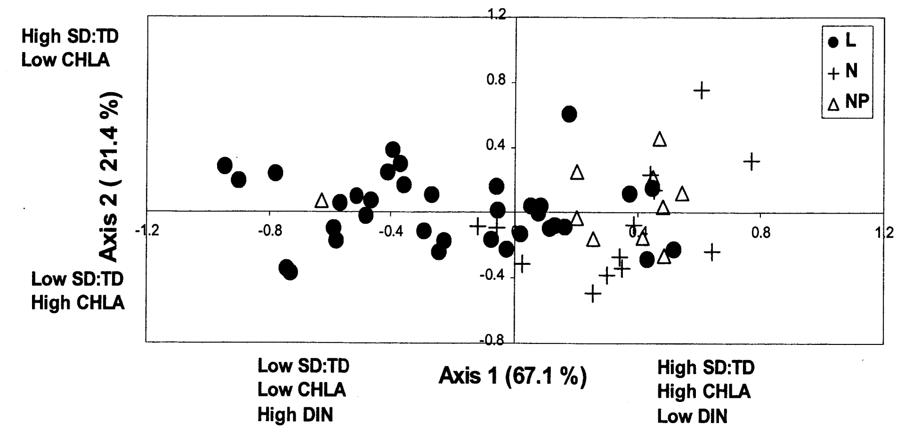

Fig. 3. Limitation status (L = Light, N = Nitrogen, NP = Nitrogen + Phosphorus) derived from bioassays plotted against the first two principal components of the limnological variables matrix. SD : TD = Secchi Depth to Total Depth ratio; CHLA = Chlorophyll-a (mg m^{-3}); DIN = Dissolved Inorganic Nitrogen (mg L^{-1}).

dition when N or NP limitation exists and the focus of the model validation will be restricted to L-limitation versus N-limitation (as N or NP). All statistical analyses were performed using SAS version 8 (SAS 1999).

Model threshold values

A simple cross-tabulation procedure was employed to examine how the frequency of L-limitation and N-limitation varied as a function of each significantly correlated variable and to derive the empirical values used to construct the model. This is a non-parametric data reduction procedure that makes no assumptions about the underlying distribution of the data and can be used on categorical data such as limitation status (Walker 1987). The steps involved in this procedure were as follows:

1. The calibration data set was sorted based on the most highly correlated variable; records with missing values for this variable were deleted;
2. Records were divided into equal sized intervals; a division of 7 intervals with 10 observations per interval was chosen because it was the only combination that achieved the highest amount of variability within an interval, the smallest between interval differential, and equal number of observations per interval;
3. Mean values were calculated for each variable in each interval;
4. Percent frequency of occurrence of each limitation status (L, or N/NP) was calculated for each interval.

Table 3. Mean values by interval for the significantly correlated variables. These values, derived from the cross-tabulation procedure, were considered to be threshold values and were used to construct the decision tree model. SD : TD = Secchi Depth to Total Depth ratio; CHLA = Chlorophyll-a (mg m^{-3}); DIN = Dissolved Inorganic Nitrogen (mg L^{-1}); DIN : SRP = Dissolved Inorganic Nitrogen to Soluble Reactive Phosphorus ratio; L = Light limitation; N = Nitrogen limitation; NP = Nitrogen + Phosphorus co-limitation. Bold interval number signifies major breakpoint.

	Cross-Tabulation Means				
Interval	SD : TD	CHLA	DIN	% L	% N/NP
1	**0.029**	9.4	0.487	**100**	0
2	0.058	13.1	0.291	80	20
3	0.090	19.4	0.264	80	20
4	**0.126**	**26.6**	**0.119**	**50**	**50**
5	0.167	37.1	0.118	60	40
6	0.257	28.8	0.034	20	80
7	0.560	17.5	0.128	20	80

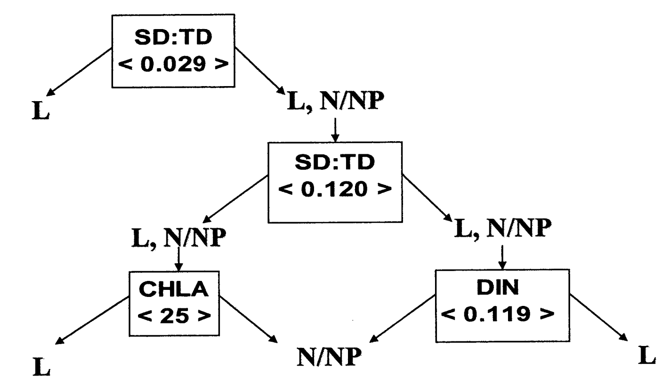

Fig. 4. Decision tree model for the determination of limitation status in Lake Okeechobee. Values were derived from the examination of the results of the cross tabulation procedure. SD : TD = Secchi Depth to Total Depth ratio; CHLA = Chlorophyll-a (mg m^{-3}); DIN = Dissolved Inorganic Nitrogen (mg L^{-1}); L = Light limitation; N = Nitrogen limitation; NP = Nitrogen + Phosphorus co-limitation.

The values derived for each variable in an interval were considered to be threshold values for that variable. These threshold values were then used to construct a decision tree model.

Because it was the most highly correlated variable, the data set was sorted by SD : TD. The resulting threshold values for each key variable and the % frequency of occurrence of each limitation status in each interval are given in Table 3. Two major breakpoints were evident in the cross-tabulation results. The first major breakpoint occurred at interval 1 where L-limitation occurred 100 % of the time when the SD : TD threshold value was less than or equal to 0.029.

Thus, when SD : TD is below 0.029 L-limitation prevails and when SD : TD is above 0.029 limitation status is dependent on factors other than light levels. The second major breakpoint occurred in interval 4 with SD : TD of 0.126, CHLA of 26 mg m^{-3} and DIN of 0.119 mg L^{-1}. At this light level either L-limitation or N-limitation occurred (50/50 chance) so determination of limitation status was accomplished by examination of CHLA and DIN levels at light levels greater than and less than the SD : TD threshold value of 0.126. When SD : TD is less than or equal to 0.126, but greater than 0.029, and CHLA is less than 26 mg m^{-3} L-limitation occurs 80 % of the time and N-limitation occurs 20 % of the time. When SD : TD is greater than 0.126 and DIN concentrations are less than 0.119 mg L^{-1} N-limitation usually prevails. The decision tree model was then constructed using the derived breakpoint threshold values of SD : TD = 0.029 and 0.126, CHLA = 26 mg m^{-3}, and DIN = 0.119 mg L^{-1} (Fig. 4).

Model validation

The predictive abilities of the model were tested on the validation data set as well as on data sets obtained from two independent bioassay studies previously conducted on Lake Okeechobee. ALDRIDGE et al. (1995) performed nutrient enrichment bioassays at stations similar to this study from January 1990 through December 1992 and PHLIPS et al. (1997) performed comparable bioassays from May 1994 through April 1995. The construction of the data sets from these two additional sources was identical to the procedures used in the construction of our calibration and validation data sets. The quantitative basis for evaluating the performance of the model was the percentage of time the model correctly predicted whether the phytoplankton would potentially be limited by light or nutrients (as N or NP) based on the water quality data when compared to the actual limitation results obtained from the bioassays. A total of 159 comparisons between the models predicted limitation results and the actual bioassay limitation results were performed on the three validation data sets (Table 4). Of the 159 comparisons, 32 were performed on this study's validation data set, 20 were performed on the PHLIPS et al. (1997) data set, and 107 were performed on the ALDRIDGE et al. (1995) data set. For all three data sets combined, the model successfully predicted whether the phytoplankton would potentially be L-limited or N-limited between 70 % and 85 % of the time, resulting in an overall success rate of 75 %. Prediction success rate was greatest for the PHLIPS et al. (1997) data set and lowest for the ALDRIDGE et al. (1995) data set.

The ability of our model to predict L-limitation vs. N-limitation in all three validation data sets was high. This performance strongly supports the accuracy of the derived critical threshold values in predicting L- vs. N-limitation. However, when nutrient limitation was prevalent, the model could not accurately predict which nutrient (N or NP) was limiting.

Table 4. Percent success rates for predicting Light limitation (L) versus Nitrogen limitation (N/NP) using the decision tree model for the three validation data sets and the supplemental instantaneous date- and time-specific data set in Lake Okeechobee. Percent values rounded to the nearest %, (n = number). This study = data from January 2001 – August 2002, PHLIPS et al. (1997) = data from May 1994 – April 1995, ALDRIDGE et al. (1995) = data from January 1990 – December 1992, Instantaneous = February 2003 – April 2004, used parameter values collected and recorded concurrently with the bioassay samples instead of using averaged monthly parameter values.

	Validation Data Sets									
	This Study		PHLIPS et al. (1997)		ALDRIDGE et al. (1995)		Overall		Instantaneous	
	%	(n)	%	(n)	%	(n)	%	(n)	%	(n)
Correct	84	(27)	85	(17)	70	(75)	75	(119)	92	(22)
Incorrect	16	(5)	15	(3)	30	(32)	25	(40)	8	(2)

The major strength of the proposed model, however, is that the parameters are biologically and physically interpretable. The variables that were most highly correlated with limitation status were, light (SD : TD), phytoplankton biomass (CHLA) and DIN concentration, so from an ecological standpoint, what the model describes is that in Lake Okeechobee, at very low irradiance levels (SD : TD < 0.029) there is a high probability that phytoplankton cells will be L-limited regardless of the concentrations of phytoplankton or DIN. When irradiance levels are above the threshold value (SD : TD > 0.029) the occurrence of L- or N-limitation depends on the amount of phytoplankton in the water column or the concentration of DIN. At intermediate light levels (SD : TD between 0.029 and 0.126) limitation status is mediated by the amount of phytoplankton in the water column. At low chlorophyll levels, cells are L-limited while at higher chlorophyll levels (a threshold of about 26 mg m^{-3}), there is sufficient phytoplankton biomass to take up and deplete the available N so cells become N-limited. Finally, at very high light levels, limitation status is determined by dissolved inorganic nitrogen concentrations. When DIN concentrations are low, cells are N limited and when DIN concentration are higher, cells are L-limited.

MAKI et al. (2004) determined that there is a shift in the photosynthetic behavior of the phytoplankton in response to changing water levels. At high water levels, the phytoplankton photosynthetic characteristics were similar among the ecological zones while the photosynthetic behavior became spatially heterogeneous when water levels are lower. This would suggest that water level is important in the function and ecology of the phytoplankton. The model was calibrated using data collected during average to relatively high water levels (> 3.7 m). Only ~ 16 % of the observations in the calibration data set were obtained during low water conditions (< 3.7 m), and no observations were obtained below 3.6 m. Therefore, low lake conditions were not well represented in the model and lower success rates would be expected. However, the validation success rate was still quite high in the two data sets containing observations collected when low water level, and/or drought, conditions were encountered. In both the ALDRIDGE et al. (1995) data set and in this study, between 14 % and 28 % of the observations were collected during low water levels but success rates were still between 70 % and 84 %. Somewhat lower success rates were obtained in these two data sets when compared to the PHLIPS et al. (1997) data set which had the highest model predictive success rate (85 %) and no instances when low water level conditions were encountered. Therefore, incorporating more extremely low lake level data (< 3.7 m) into the calibration data set should result in an increased predictive success rate.

Additionally, our model correctly predicted L-limitation vs. N-limitation with a high degree of accuracy (70 %–85 %) using mean monthly or bimonthly water quality data for all parameters. The rational for using averaged monthly monitoring data was that they presumably encompass both episodic and chronic events. However, improvement to the model might be achieved by using instantaneous date- and time-specific data, especially with regards to the nutrient data. To explore the possibility of improvement to the model, from February 2003 to January 2004 instantaneous data for all of the model parameters were collected in conjunction with the bioassay samples. A supplemental data set containing these instantaneous date- and time-specific data was then constructed and utilized as an additional validation data set. When the bioassay results were compared to the model results the model correctly predicted whether or not light was limiting 22 out of 24 observations resulting in a 92 % success rate (Table 4). While this data set is quite small, these results suggest that the potential exists for enhanced predictive abilities when instantaneous data are used rather than averaged monthly data.

Model application

In Lake Okeechobee, two current management strategies include a substantial reduction in external phosphorus inputs and lake stage management to improve light conditions by reducing the occurrence of high water levels. Reliably predicting the response of phytoplankton to nutrient and light conditions is important in determining the success of these management strategies. The performance of the model developed in this study suggests that it is an effective tool for evaluating the impact of lake stage management strategies on light limitation of phytoplankton standing crop. However, because the model was not able to distinguish between N and NP limitation when nutrient limiting conditions prevailed, and because P-limited conditions were never encountered in this study, it's usefulness in evaluating phytoplankton responses to phosphorus load reduction strategies remains uncertain. If the current phosphorus reducing efforts are successful and P-limited conditions become dominant again in the lake, it may be possible to incorporate P-limited conditions into the model through continued bioassays and model enhancements.

The performance of the model demonstrated here also suggests that this simple derivation technique may be suitable for use on a broad range of systems or regional monitoring programs once sufficient data is available to identify the system-specific parameters that are relevant to the description of the systems trophic state. Furthermore, the basic ecology that our model describes, that light and nutrient availability set the fundamental constraints on phytoplankton production, has been identified in numerous other shallow, turbid, tropical and subtropical systems. In Lake Chapala, nutrient control of phytoplankton is secondary to light control due to high inorganic turbidity (DAVALOS et al. 1989, LIND et al. 1992). CARIGNAN & PLANAS (1994) identified both light and nitrogen limitation, depending on prevailing conditions, in six shallow lakes in the Parana floodplain. CLOERN (1987) indicated that for a number of nutrient replete estuaries, photic zone productivity could be estimated as a function of the phytoplankton biomass and the mean irradiance of the photic zone. PHLIPS et al. (2000) found that variations in phytoplankton standing crop in certain regions of the nutrient-rich St. Johns River are related to light availability. The application of this technique in these and other similar systems could result in the development of similarly successful models.

Conclusions

Long-term bioassay experiments on the factors that limit phytoplankton standing crops in large, complex systems such as Lake Okeechobee are expensive and time-consuming, especially in comparison with physical and chemical analysis. The goal of this research was to develop a reliable model for accurately and efficiently predicting limiting status using routine monitoring data rather than nutrient bioassays.

The results of the model validation demonstrates its ability to distinguish between light limited conditions and non-light limited conditions, but currently has limitations in discerning N, P, or NP limited conditions. It should be emphasized that the development of our model was dependent upon an extensive sampling program involving frequent sampling during varying physical and environmental conditions. Because validation of the model was accomplished using bioassay results, the model should be considered a complement to, and not a surrogate for, bioassay measurements.

The model derivation process developed in this study is potentially useful and economical for a wide range of lakes. Further demonstrations of the successful application of this framework to other lakes and reservoirs with both similar and different trophic status would offer further validation for the use of this model for management purposes.

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References

ALDRIDGE, F. J., PHLIPS, E. J. & SCHELSKE, C. L. (1995): The use of nutrient enrichment bioassays to test for spatial and temporal distribution of limiting factors affecting phytoplankton dynamics in Lake Okeechobee, Florida. – Arch. Hydrobiol. Beih. Ergebn. Limnol. **45:** 177–190.

APHA (American Public Health Association) (1995): Standard methods for the examination of water and wastewater. – 19th edition. American Public Health Association, Washington DC.

AUMEN, N. G. (1995): The history of human impacts, lake management, and limnological research on Lake Okeechobee, Florida (USA). – Arch. Hydrobiol. Beih. Ergebn. Limnol. **45:** 1–16.

BERMAN, T. (1972): Profiles of chlorophyll concentration by the in vivo fluorescence: some limnological applications. – Limnol. Oceanogr. **17:** 616–618.

CARIGNAN, R. & PLANAS, D. (1994): Recognition of nutrient and light limitation in turbid mixed layers: Three approaches compared in the Parana floodplain (Argentina). – Limnol. Oceanogr. **39:** 580–596.

CLOERN, J. E. (1987): Turbidity as a control on phytoplankton biomass and productivity in estuaries. – Cont. Shelf Res. **7:** 1367–1381.

DAVALOS, L. O., LIND, O. T. & DOYLE, R. D. (1989): Evaluation of phytoplankton-limiting factors in Lake Chapala, Mexico: Turbidity and the spatial and temporal variation in algal assay response. – Lake Res. Manage. **5:** 99–104.

D'ELIA, C. F., SANDERS, J. G. & BOYNTON, W. R. (1986): Nutrient enrichment studies in a coastal plain estuary: Phytoplankton growth in large-scale, continuous cultures. – Can. J. Fish. Aquat. Sci. **43:** 397–406.

DODDS, W. K. & PRISCU, J. C. (1990): A comparison of methods for the assessment of nutrient deficiency of phytoplankton in a large oligotrophic lake. – Can. J. Fish. Aquat. Sci. **47:** 2328–2338.

DOWNING, J. A., OSENBERG, C. W. & SARNELLE, O. (1999): Meta-analysis of marine nutrient-enrichment experiments: variation in the magnitude of nutrient limitation. – Ecology. **80:** 1157–1167.

ELSER, J. J., ELSER, M. M., MACKAY, N. A. & CARPENTER, S. R. (1988): Zooplankton-mediated transitions between N and P limited algal growth. – Limnol. Oceanogr. **33:** 1–14.

ELSER, J. J. & KIMMEL, B. L. (1985): Nutrient availability for phytoplankton production in a multiple-impoundment series. – Can. J. Fish. Aquat. Sci. **42:** 1359–1370.

FLAIG, E. G. & HAVENS, K. E. (1995): Historical trends in the Lake Okeechobee ecosystem I. Land use and nutrient loading. – Arch. Hydrobiol. Suppl. **107:** 1–24.

GOLTERMAN, H. L. (1975): Physiological limnology. – Elsevier, Amsterdam.

GRANELI, E. (1984): Algal growth potential and limiting nutrients for phytoplankton production in Oresund water of Baltic and Kattegat origin. – Limnologica **15:** 563–569.

HANLON, C. G., MILLER, R. L. & MCPHERSON, B. F. (1998): Relationship between wind velocity and underwater irradiance in a shallow lake (Lake Okeechobee Florida, USA). – J. Amer. Water Res. Assoc. **34:** 951–961.

HAVENS, K. E., EAST, T. L. & BEAVER, J. R. (1996): Experimental studies of zooplankton-phytoplankton-nutrient interactions in a large subtropical lake (Lake Okeechobee, Florida, U.S.A.). – Freshwat. Biol. **36:** 579–597.

HAVENS, K. E., HANLON, C. & JAMES, R. T. (1994): Seasonal and spatial variation in algal bloom frequencies in Lake Okeechobee, Florida, U.S.A. – Lake Res. Managem. **10:** 139–148.

HAVENS, K. E., JAMES, R. T., EAST, T. L. & SMITH, V. H. (2003): N:P ratios, light limitation, and cyanobacterial dominance in a subtropical lake impacted by non-point source nutrient pollution. – Environ. Pollut. **122:** 379–390.

JAMES, R. T., SMITH, V. H. & JONES, B. L. (1995): Historical trends in the Lake Okeechobee ecosystem III. Water Quality. – Arch. Hydrobiol. Suppl. **107:** 49–69.

KRATZER, C. R. & BREZONIK, P. L. (1984): Application of nutrient loading models to the analysis of trophic condition in Lake Okeechobee. – Florida Environ. Managem. **8:** 109–120.

LIND, O. T., DOYLE, R., VODOPICH, D. S., TROTTER, B. G., LIMON, J. G. & DAVALOS-LIND, L. (1992): Clay turbidity:regulation of phytoplankton production in a large, nutrient-rich tropical lake. – Limnol. Oceanogr. **37:** 549–565.

MACEINA, M. J. & SOBALLE, D. M. (1990): Wind related limnological variations in Lake Okeechobee Florida. – Lake Res. Managem. **6:** 93–100.

MAKI, R. P., SHARFSTEIN, B., EAST, T. L. & RODUSKY, A. J. (2004): Phytoplankton photosynthesis-irradiance relationships in a large, managed, eutrophic, subtropical lake: The influence of lake stage on ecological homogeneity. – Arch. Hydrobiol. **161:** 159–180.

MALLIN, M. A. & PAERL, H. W. (1992): Effects of variable irradiance on phytoplankton productivity in shallow estuaries. – Limnol. Oceanogr. **37:** 54–62.

PEARL, H. W., FULTON, R. S., MOISANDER, P. H. & DYBLE, P. H. (2001): Harmful freshwater algal blooms, with and emphasis on cyanobacteria. – The Sci. World J. **1:** 76–113.

PHLIPS, E. J., ALDRIDGE, F. J., HANSEN, P., ZIMBA, P. V., IHNAT, J., CONROY, M. & RITTER, P. (1993): Spatial and temporal variability of trophic state parameters in a shallow subtropical lake (Lake Okeechobee, Florida, USA). – Arch. Hydrobiol. **128:** 437–458.

PHLIPS, E. J., ALDRIDGE, F. J. & HANSEN, P. (1995): Patterns of water chemistry, physical and biological parameters in a shallow subtropical lake (Lake Okeechobee, Florida, USA). – Arch. Hydrobiol. Beih. Ergebn. Limnol. **45:** 117–135.

PHLIPS, E. J., CICHRA, M., HAVENS, K. E., HANLON, C., BADYLAK, S., RUETER, B., RANDALL, M. & HANSEN, P. (1997): Relationships between phytoplankton dynamics and the availability of light and nutrients in a shallow sub-tropical lake. – J. Plankton Res. **19:** 319–342.

PHLIPS, E. J., CICHRA, M., ALDRIDGE, F. J., JEMBECK, J., HENDRICKSON, J. & BRODY, R. (2000): Light availability and variation in phytoplankton standing crops in a nutrient-rich blackwater river. – Limnol. Oceanogr. **45:** 916–929.

RYTHER, J. H. & DUNSTAN, W. M. (1971): Nitrogen, phosphorus, and eutrophication in the coastal marine environment. – Science **171:** 1008–1013.

SAS (1999): Statistical analysis system, version 8. – SAS Institute. Cary, NC.

SCHELSKE, C. L. (1984): In situ and natural phytoplankton assemblage bioassays. – In: SHUBERT, L. E. (ed.): Algae as ecological indicators. – Academic Press. London, pp. 15–47.

SCHELSKE, C. L., ROTHMAN, E. C., STOERMER, E. R. & SANTIAGO, M. A. (1974): Responses of phosphorus limited Lake Michigan phytoplankton to factorial enrichments with nitrogen and phosphorus. – Limnol. Oceanogr. **19:** 409–419.

SCHELSKE, C. L., ROTHMAN, E. C. & SIMMONS, M. S. (1978): Comparison of bioassay procedures for growth-limiting nutrients in the Laurentian Great Lakes. – Mitt. Internat. Verein. Limnol. **21:** 65–80.

SCHINDLER, D. W. (1975): Whole-lake eutrophication experiments with phosphorus, nitrogen, and carbon. – Verh. Internat. Verein. Limnol. **19:** 3221–3231.

SMITH, S. V. (1984): Phosphorus versus nitrogen limitation in the marine environment. – Limnol. Oceanogr. **29:** 1149–1160.

South Florida Water Management District (1989): Surface water improvement and management (SWIM) plan for Lake Okeechobee. – South Florida Water Management District, West Palm Beach, FL, USA.

VAN DUIN, E. H. S., AALDERINK, R. H. & LIJKLEMA, L. (1995): Light adaptation of *Oscillatoria agardhii* at different time scales. – Water Sci. Tech. **32:** 35–48.

WALKER, W. W. (1987): Cross-tabulation as a tool for analyzing large monitoring data bases. Monitoring, Modeling, and Mediating Water Quality. – Proc. American Water Resources Association Conference, Syracuse, New York.

ZOU, L., ZHANG, J., PAN, W. & ZHAN, Y. (2001): In situ nutrient enrichment experiment in the Bohai and Yellow Sea. – J. Plank. Res. **23:** 1111–1119.

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