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Factors affecting the maximum depth of colonization by submersed macrophytes in Florida lakes

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Abstract

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In 32 Florida lakes, Secchi depth (SD), light attenuation coefficient measured with a light meter, plant and sediment type, and slope were examined with respect to the maximum depth of plant colonization (MDC). The MDC was shown to be significantly related to light through measurements taken by SD ($R^2 = 0.46$; $p < 0.05$) and a light meter ($R^2 = 0.41$; $p < 0.05$). While both light measurements can be used to estimate MDC, SD accounted for more variance in MDC than light attenuation coefficients. Plant type, sediment type and slope did not account for more variance in MDC than light measurements for these Florida lakes. Additional unpublished data from 187 Florida Lakes (Florida LAKEWATCH, 279 lake-years of data) also showed a significant positive relationship between SD and MDC ($R^2 = 0.68$; $p < 0.05$). The best fit MDC-SD regression line in meters was: log (MDC) = 0.66 log (SD) + 0.31. A maximum MDC line relating MDC to SD in meters was also calculated and was found to be equal to: log (max MDC) = 0.53 log (SD) + 0.59. The maximum MDC line describes light limitation when the MDC response falls on or near the response curve, and when MDC values fall below the line, some other factor likely limits colonization of macrophytes.

Key words: aquatic plants, light attenuation, Secchi depth, sediment, slope

The distribution and abundance of aquatic macrophytes in lakes are affected by many forces including but not limited to pressure (Hutchinson 1975), substrate characteristics (Bachmann *et al.* 2001), lake morphology (Duarte and Kalff 1986), water column nutrient concentrations (Jupp and Spence 1977), waterfowl grazing (Weisner *et al.* 1997), and light availability (Canfield *et al.* 1985, Chambers and Kalff 1985). Given the high attenuation of irradiance through the water column, and because plants require light to photosynthesize, light availability is often considered one of the most important factors that regulate abundance and distribution of aquatic macrophytes (Zimmerman *et al.* 1994).

The maximum depth at which autotrophic aquatic plants colonize has been shown in numerous studies to be linearly related to transparency of the water (Maristo 1941, Canfield *et al.* 1985, Hudon *et al.* 2000). Chambers & Kalff (1985) found the average maximum depth of plant colonization (MDC) for charophytes at 11% of the surface incident irradiance, and MDC for angiosperms and bryophytes at 21% of the surface irradiance. However, aquatic plants have been recorded in areas receiving <1-2% of the surface irradiance (Hutchinson 1975).

Canfield *et al.* (1985) demonstrated a relationship between water transparency as measured by Secchi depth (SD) and MDC in 26 Florida lakes. They also developed an empirical model for the relationship that could provide lake managers with a first approximation of how changes in SD values caused by either natural or anthropogenic activities might affect the extent of macrophyte colonization in lakes. However, they cautioned that other environmental factors (*e.g.*, types of plants present, basin morphometry, sediment types) besides SD values need to be considered to enhance the predictive ability of the model.

To support water-resource protection, the Florida Legislature directed the state's five water management districts to establish minimum water levels for lakes (Section 373.042, Florida Statutes). The Southwest Florida Water Management District (SWFWMD) developed methods for establishing minimum lake levels (Chapter 40D-8. Florida Administrative Code), which included use of the model developed by Canfield *et al.* (1985) to assess potential changes in the coverage of submersed vegetation with changes in water transparency. For example, Hoyer *et al.* (2005) showed that potential percent area covered with aquatic plants (PAC) in individual lakes can increase or decrease with water level fluctuations, depending on lake morphology. The potential area of a lake with the presence of aquatic vegetation could be calculated at changing water levels by using models that predict MDC; the potential PAC could then be calculated by overlaying this depth on a bathymetric map. The SWFWMD, however, recognized the need to develop a more robust model from a larger number of lakes.

This study was designed based on the earlier work of Canfield *et al.* (1985) to develop more robust model/models for use by SWFWMD. The first part of the study involved the sampling of 32 Florida lakes. The main objective for the 32-lake study was to determine if photosynthetically active radiation (PAR) was more accurate at predicting MDC than SD. Plant and sediment type and bottom slopes were also measured to determine if MDC could be better predicted than relying on only SD. The second phase of this study used Florida LAKEWATCH information (Florida LAKEWATCH, unpubl.) to develop an empirical model relating SD to MDC for 279-lake-years to increase the representation of Florida lakes. A series of models was also generated to quantify the relationship of other limnological parameters (color, chlorophyll, total phosphorus [TP], total nitrogen [TN]) to MDC to supplement the limited amount of information in the existing literature. Finally, another model was developed that predicts the MDC when light limitation is the dominant factor influencing macrophyte colonization.

Materials and methods

Two data sets were used for model development. The first data set involved field sampling of 32 Florida lakes using the basic approach of Canfield *et al.* (1985). Study lakes selected were located in eight counties, with the majority located in peninsular Florida (Fig. 1). Lakes located in the SWFWMD comprised 38% of the sampled lakes. A study by Brown *et al.* (1998) compared differences of mean monthly SD readings from annual means in 209 Florida lakes and showed the mean percent difference of SD fluctuated 4-6% on either side of the annual mean. Given that mean monthly SD readings deviate little from month to month for many Florida lakes, a long sampling period between May and December of 2004 was considered to be an acceptable time frame to carry out this project. Each lake was visited once during the sampling season.

At each study lake, four straight transects across the lake (*e.g.*, north to south, east to west, southwest to northeast, and southeast to northwest) were established to provide an assessment of macrophyte coverage. The MDC was found along each transect using a Raytheon DE-719 fathometer and was considered to be the last or deepest plant detected on the chart paper for either side of the littoral zone. Buoys were placed at locations of measured macrophyte MDC. After all transects were completed, the three-to-four deepest buoy stations were checked with a toothed hook (18 × 18 cm) for the presence of submersed aquatic macrophytes.

At stations where MDC was identified, measurements were made for SD, light attenuation (E), true color, sediment type, bottom slope, and the plant species present were identified. In some lakes with sparse plant growth, fewer than three stations were found harboring submersed aquatic macrophytes. At these lakes, open water stations were sampled for SD, light attenuation (E), true color, and sediment type. Variables with quantitative values (*i.e.*, SD, E, color, and slope) were averaged by lake for the day sampled, and because lakes were visited only once during the study, each lake was considered the experimental unit for the quantitative variables. Conversely, the experimental unit for qualitative variables (*i.e.*, plant and sediment type) was considered to be the lake stations. At the occurrence of MCD in each of the 32 study lakes, water transparency was measured with a Secchi disk on the shady side of the boat. If the Secchi disk was visible on the bottom for all 3 stations, an additional Secchi reading was taken in a deeper location to use for analysis. Surface and corresponding underwater light irradiance were measured (in quanta units) on the sunny side of the boat using a photometer (LI-COR model LI-1400 data logger) with a quantum sensor placed both above (LiCor 193) and below (LiCor 192) the water. Light meter readings were taken at two-to-three depths. If possible, light measurements at each station were made at depths of 1, 2, and 3 m to better represent light attenuation for the entire water column. An additional open-water light reading was taken in deeper water at some lakes where all three stations were shallow (<3 m) or when sun coverage was fading and no stations had yet been sampled for light. Light readings were averaged over 10 sec to mitigate instantaneous fluctuations with light intensity. The downward attenuation coefficient values for each station were calculated as the slope of the graph of the natural logarithm of the irradiance values, corrected for changes in incident irradiance on the y-axis, against depth on the x-axis (Lind 1974). The percent of surface irradiance penetrating at MDC was calculated using the relationship:

$$I_Z/I_o = 100e^{-Ez}$$

where I_Z/I_o = percent of subsurface irradiance, E = light attenuation coefficient, and z = MDC (Scheffer 1998).

Water samples were collected at the surface (0.5 m) with 250-mL, acid-cleaned, triple-rinsed Nalgene bottles and immediately placed on ice until they could be put in a freezer for later analysis. True color values were determined following filtration through a Gelman type A/E glass fiber filter, centrifugation of the filtrate, and using the platinum-cobalt standard technique determined by spectroscopy (Bowling *et al.* 1986).

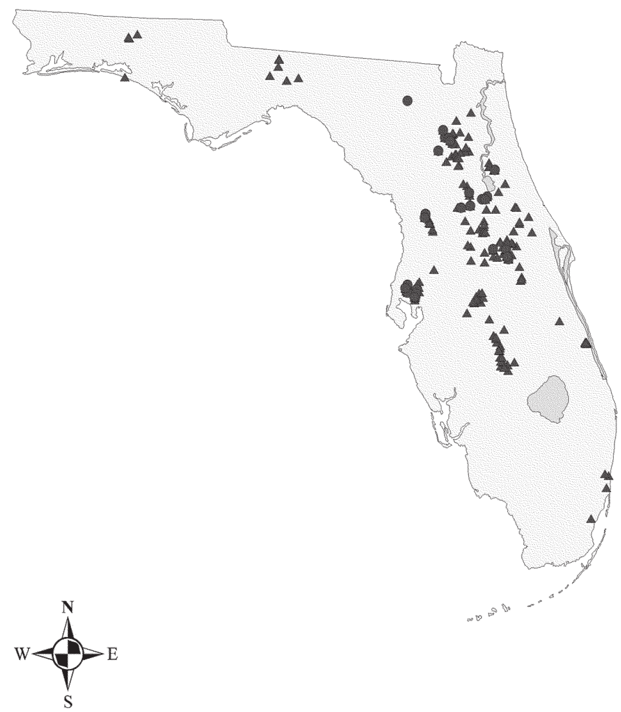

Figure 1.-Locations of lakes sampled for both studies. Triangles represent lake locations from the 279-lake-year study and circles represent lake locations from the 32-lake study.

A ponar dredge with a 15-cm opening was used to obtain sediment samples. Sediment type was classified as one of three types: sandy, organic, or mixed. Sediment samples that were dark colored and slippery to the touch were classified as organic; white, granular sediment samples were classified as sandy; and a blend of organic and sandy sediments was categorized as a mixed sediment.

Bottom slope was calculated around MDC stations, not the entire littoral area. Slope was calculated from the Raytheon DE-719 fathometer chart by dividing the rise (the change in water depth) by the horizontal distance across the station.

The second data set involved obtaining information on 187 lakes with macrophyte communities sampled by Florida LAKEWATCH between 1991 and 2004. Although most lakes were sampled only once, some lakes were sampled multiple times providing 279-lake-years of information. The 187 lakes were located in 24 counties (Fig. 1), and 35% of the lakes were in the SWFWMD.

For the 279-lake-year study, Florida LAKEWATCH provided fathometer chart papers examined later for MDC. Four to ten transects were taken on each lake, and the MDC was recorded as the last or deepest observable plant on the fathometer charts. The 279-lake-year data included 29 lakes from the 32 lakes studied.

Florida LAKEWATCH is a volunteer citizens' lake monitoring program in which volunteers measure SD, chlorophyll, TP, TN, usually on a monthly basis, at 3 mid-lake locations (Canfield *et al.* 2002). Secchi depth readings and true color samples were obtained using the same procedures as the 32-lake study. Surface (0.5 m) water samples for measuring chlorophyll were collected in 4-L, tap-water rinsed, plastic milk jugs and placed in coolers until the samples could be filtered. A measured volume of water was filtered through a Gelman Type A-E glass fiber filter. Filters where folded and placed inside a larger paper filter and then stored inside a silica gel desiccant bottle in a freezer. Chlorophyll was extracted from the filters in hot ethanol (Sartory and Grobbelarr 1984). The trichromatic equation for chlorophyll *a* was used to calculate the concentrations of chlorophyll with the hot ethanol method (Method 10200H; APHA 1992).

Water samples for TP and TN were collected at the surface (0.5 m) with 250-mL, acid-cleaned, triple-rinsed, Nalgene bottles. Water samples were immediately placed on ice and held until returned at the end of the sampling day to the Florida LAKEWATCH water quality laboratory in Gainesville, Florida, where they were frozen until analysis by Florida LAKEWATCH staff. Total phosphorus concentrations were determined using the methods of Murphy and Riley (1962) with a persulfate digestion (Menzel and Corwin 1965). Total nitrogen concentrations were determined by the oxidization of water samples using persulfate and determining nitrate-nitrogen with second derivative spectroscopy (D'Elia *et al.* 1977).

Data obtained from Florida LAKEWATCH (SD, color, chlorophyll, TP, and TN) were averaged for the year in which plants were inventoried at each lake. For each lake, Florida LAKEWATCH means were first averaged for the day of the month sampled, and these monthly means were averaged for a yearly mean for the lake. Some lakes were represented in the data set more than once if they were sampled multiple years.

If Florida LAKEWATCH was missing water chemistry data for the corresponding year that MDC was measured, long-term water chemistry means for that lake were used. Long-term means were computed by averaging all yearly means for a lake. For the 279-lake-year study, long-term values used represented 5% of SD readings, 43% of color measurements, and 2.5% of chlorophyll, TP, TN values.

Table 1.-Descriptive statistics for the maximum depth of plant colonization (MDC in m), Secchi depth (SD in m), light attenuation coefficient (E in m^{-1}), percent (%) of subsurface irradiance penetration (I_Z / I_o x 100), color (PCU), and slope (%) for the 32-lake study.

Parameter	n	Minimum	Maximum	Mean	Standard deviation
MDC	32	0.7	9.2	3.1	1.8
SD	32	0.3	5.8	1.8	1.2
E	32	0.2	6.8	1.8	1.5
Color	32	2	385	50	70
I_Z / I_o	32	0.008	47	11	14
I_Z / I_o hydrilla	9	0.43	99	19	33
I_Z / I_o Non-hydrilla	72	0.0003	78	10	16
I_Z / I_o Angiosperm	68	0.0003	99	12	20
I_Z / I_o Charophyte	13	0.02	19	7	6
Slope	31	0.3	13	4	3

Data analysis

To predict MDC for the 32-lake study, regression equations and coefficient of determination values (R^2) were calculated using SD and E readings as independent variables. The coefficient of correlation (r) was used to measure the strength of the relationship between E and SD. Multiple linear regression analysis was used to relate SD, E, and MDC (dependent variables) to both color and chlorophyll (independent variables). Best-fit linear regressions were calculated between SD and E and vice versa. A t-test was used to test for significant differences in the average percent of incident light at the MDC between stations with hydrilla (*Hydrilla verticillata* Royle) versus non-hydrilla, and between stations harboring angiosperms versus charophytes. To investigate sediment influence on MDC, a multiple linear regression was run on MDC and SD, adding sediment type as the second variable. Also, the coefficient of determination was calculated for the relationship between slope and MDC (McClave and Sincich 2000).

An empirical model was developed using the Florida LAKEWATCH database for 279-lake-years of information relating SD to MDC to increase the representation of Florida lakes. Furthermore, a maximum MDC line was developed following the techniques of Brown *et al.* (2000) who created a maximum chlorophyll line that described the maximum response of chlorophyll across levels of the potentially limiting factor (TP). The Law of Limiting Factors is an ecological principle that implies that the speed of growth of an organism is governed by the slowest or most limiting factor (Blackman 1905). The maximum line relating MDC and SD was determined by sorting the 279 SD values from lowest to highest and then dividing these into 10 groups. Because 279 is not divisible by 10, there were 28 SD values in each of the first nine groups, and one group of 27 SD readings. The maximum MDC value in each group with its associated SD value was then used to run a regression through the 10 pairs of points. Linear and multiple regression models were created to quantify the relationship of MDC to color and chlorophyll because these two light-reducing variables have been shown to be hyperbolically related to SD depth (Canfield and Hodgson 1983). Furthermore, because TP and TN have been shown to be positively related to chlorophyll concentrations (Canfield 1983), these nutrients were also examined mathematically with respect to the MDC.

To meet the assumption of normality, all distributions for both data sets were transformed to a base-10 logarithm for regression analysis prior to statistical analysis. A software program, Kaleidagraph version 3.6, was used to generate figures and JMP version 4.0 was used to perform statistical tests. The alpha level of rejection was set at 0.05.

Results and discussion

Canfield *et al.* (1985) sampled 26 Florida lakes with SD ranging from approximately 1-6.3 m. The 32-lake study had a similar range in SD from 0.3 m to 5.8 m. The mean transparency for all lakes was 1.8 m. The other measured limnological parameters in the 32-lake study also varied considerably. Measured light extinction coefficients ranged from 0.2 m^{-1} to 6.8 m^{-1} (mean for all lakes 1.8 m^{-1}). True color ranged from 2 PCU to 385 PCU (mean color 50 PCU). The calculated bottom slopes ranged from 0.3% to 13% (mean slope 4%). The MDC ranged from 0.7 m to 9.2 m, with mean depth of aquatic macrophyte colonization at 3.1 m (Table 1).

Canfield *et al.* (1985) found a significant positive relationship, represented by Equation 1 (Table 2), between the MDC

Table 2.-Regression equations of the maximum depth of submersed plant colonization (MDC in m) related to Secchi depth (SD in m), light attenuation coefficient (E in m^{-1}), color (PCU), chlorophyll (CHL in µg/L), total phosphorus (TP in µg/L), and total nitrogen (TN in µg/L).

Eq. #	Input variable	N	Eq.	R^2	p value	Region	Reference
1	SD	108	log(MDC) = 0.61 log(SD) + 0.26	0.49	<0.05	Finland, Florida, Wisconsin	Canfield *et al.* (1985)
2	SD	32	log(MDC) = 0.64 log(SD) + 0.30	0.46	<0.05	Florida	na
3	E	32	log(MDC) = -0.51 log(E) + 0.48	0.41	<0.05	Florida	na
4	SD	279	log(MDC) = 0.66 log(SD) + 0.31	0.68	< 0.05	Florida	na
5	SD	10	log(max MDC) = 0.53 log(SD) + 0.59	0.97	< 0.05	Florida	na
6	COLOR	262	log(MDC) = -0.29 log(COLOR) + 0.85	0.40	< 0.05	Florida	na
7	CHL	279	log(MDC) = -0.28 log(CHL) + 0.71	0.30	< 0.05	Florida	na
8	TP	279	log(MDC) = -0.43 log(TP) + 0.99	0.43	< 0.05	Florida	na
9	TN	279	log(MDC) = -0.47 log(TN) + 1.76	0.32	< 0.05	Florida	na
10	COLOR & CHL	262	log(MDC) = -0.22 log(COLOR) - 0.18 log(CHL) + 0.93	0.51	< 0.05	Florida	na
11	SD	160	$(MDC)^{0.5}$ = 0.53 ln(SD) + 1.51	0.51	< 0.05	Wide Variety	Duarte & Kalff (1987)
12	SD	90	$(MDC)^{0.5}$ = 1.33 log(SD) + 1.40	0.58	< 0.05	Quebec & the World	Chambers & Kalff (1985)
13	SD	68	(MDC) = 0.62(SD) + 2.12	0.34	< 0.05	Wisconsin	Nichols (1992)

Table 3.-Multiple linear regression equations relating Secchi depth (SD in m), light attenuation coefficient (E in m^{-1}) and the maximum depth of plant colonization (MDC in m) to color (PCU) and chlorophyll (CHL in µg/L).

n	Equation	R^2	p value
29	log(SD) = -0.25 log(COLOR) – 0.39 log(CHL) + 0.88	0.71	< 0.05
29	log(E) = 0.52 log(COLOR) + 0.22 log(CHL) – 0.82	0.74	< 0.05
29	log(MDC) = -0.27 log(COLOR) -0.35 log(CHL) + 1.11	0.65	< 0.05

and SD depth ($R^2 = 0.49$) using data from Finnish, Florida, and Wisconsin lakes. The 32 Florida lakes sampled during this study also showed a significant positive relationship between the MDC and SD depth ($R^2 = 0.46$; $p < 0.05$; Fig. 2a), represented by Equation 2 (Table 2). The equation between MDC and SD for the 32 Florida lakes was very similar to Canfield *et al.* (1985) study, and the similarity of equations (1) and (2) provides significant data that suggests the positive relationship between MDC and SD is repeatable.

Canfield *et al.* (1985) found light meter readings were highly correlated (r = 0.96) to concurrently measured SD values. Most light reaching the water surface is reflected, turned to heat, or absorbed by objects in the water column as well as by the water itself (Cole 1983). The intensity of light in the water column (I_z) decreases exponentially with depth (z) depending on the vertical attenuation coefficient (E) of the water and the starting surface illumination (I_o), using the relationship set forth in Beers law: $I_z = I_o e^{-Ez}$ (Scheffer 1998). Wavelengths are absorbed differentially in the water column with infrared light, and many of the visible reds being absorbed mostly in the first meter and with blues penetrating the deepest (Cole 1983). Additional substances in the water, such as dissolved organics (color), algae, and non-algal suspended solids, influence the amount of light penetration through the water column (Havens 2003) and potential SD values.

Light availability at a depth in the water column can be measured directly by the use of a light meter or indirectly by the use of SD. For the English Channel, the relationship between light attenuation (E) and SD measurements was E = 1.7/SD (Poole and Atkins 1929). However, the relationship between E and SD varies among studies, and many alternatives have been reported (Holmes 1970, Walker 1980). For the 32 study lakes, the correlation between the measured light attenuation coefficients and SD was significant (r = 0.81), but not as strong as that reported by Canfield *et al.* (1985; r = 0.96). Using multiple linear regression analysis, color and chlorophyll concentrations as input variables were also highly related to the output variables SD ($R^2 = 0.71$; $p < 0.05$), light attenuation ($R^2 = 0.74$; $p < 0.05$), and MDC ($R^2 = 0.65$; $p < 0.05$) (Table 3). Secchi depth, however, can be predicted reasonably well from measured light attenuation coefficients (Fig. 3a), and light attenuation coefficient (E) can be predicted from SD (Fig. 3b).

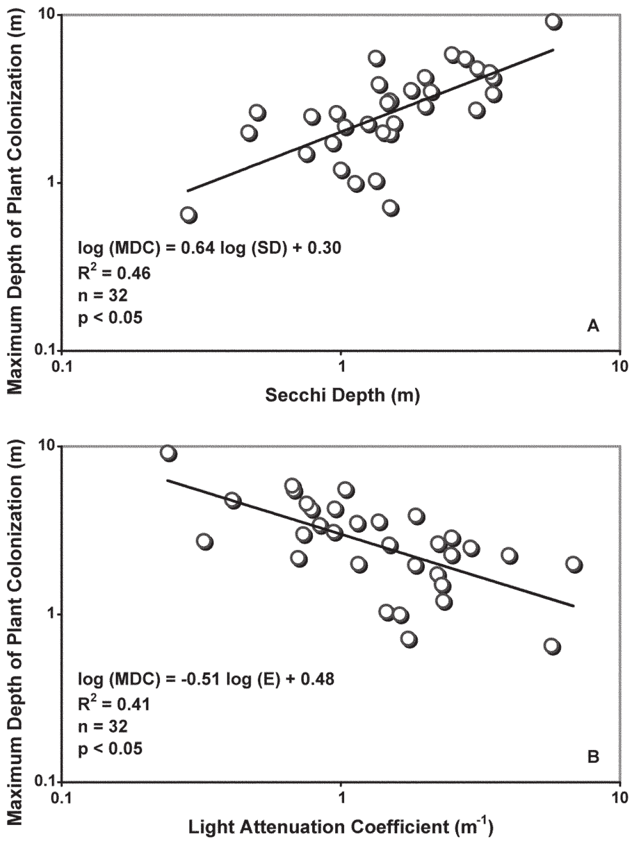

Figure 2.-Relationship between the mean maximum depth of submersed macrophyte colonization and mean Secchi depth (A) and mean light attenuation (B) for the 32-lake study.

Although E and SD are highly correlated, the large 95% confidence limit associated with the MDC-SD model published by Canfield *et al.* (1985; 46-236%) lead to speculation that the use of light meter readings could lead to the development of a more robust model. The MDC of macrophytes in the 32-lake study was negatively related to the mean light attenuation coefficient (Fig. 2b), represented by Equation 3 (Table 2).

Light attenuation, however, did not predict MDC any better than SD and actually had a slightly lower coefficient of determination ($R^2 = 0.41$) than SD readings ($R^2 = 0.46$). This finding demonstrated SD, an easily measured and inexpensive index of water transparency, is as useful if not better for

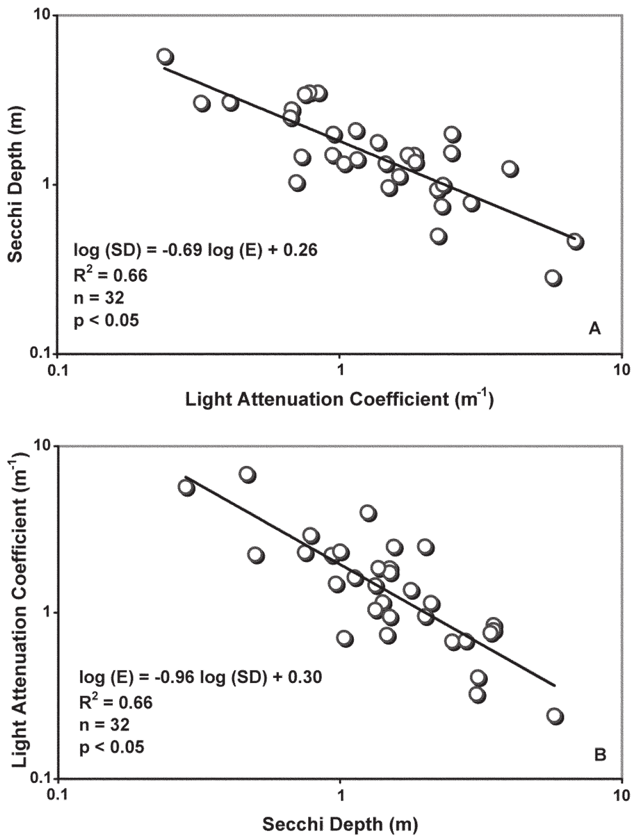

Figure 3.-Relationships between mean Secchi depth and mean light attenuation (A, B) for the 32-lake study.

assessing MDC as E values that require the use of complex and expensive equipment.

Canfield *et al.* (1985) suggested the major factor contributing to the variability in the MDC-Secchi relationship is the type of plant colonizing the lake bottom because different species of plants have different light requirements. The amount of surface light penetrating to MDC in the 32 study lakes ranged from <1% to 47%. The mean percent of incident light at MDC was 11%, which was in agreement with much of the literature (Table 1). For example, Hoyer *et al.* (2004) found that when the percent of incident light at the surface reaching the substrate of 3 Florida rivers was <10%, there was little or no submersed aquatic vegetation biomass. Sheldon and Boylen (1977) found MDC to correspond to 10% of the light intensity hitting the surface. The mean percent of incident light at MDC for stations with hydrilla, non-hydrilla, angiosperms, and charophytes present in this study was 19%, 10%, 12%, and 7%, respectively (Table 1). Although hydrilla has been shown to have a low light compensation point in laboratory conditions (15 μeinstein/m^2/sec; Van *et al.* 1976), it was not found at low light levels for the 32 lakes examined in natural conditions. There was no significant difference in percent of incident light at MDC between hydrilla and non-hydrilla species (p = 0.2). Similarly, there was no significant difference of mean percent surface penetration present at MDC between angiosperms and charophytes (p = 0.4). This indicates that for this group of Florida lakes, differences in the light requirements of individual plant types can not be invoked as the major factor contributing to the variability in the MDC-Secchi relationship.

Lake-bottom sediment serves not only as a physical anchor for submersed vegetation but also as a source of nutrients, and it exerts a major influence on macrophyte productivity (Barko *et al.* 1991). Bachmann *et al.* (2001) suggested the flocculent organic sediments in Lake Apopka were deleterious for root anchorage and limited the colonization of submersed aquatic macrophytes. When MDC was related to SD and sediment type through multiple linear regression analysis, sediment type was not shown to significantly influence MDC (p = 0.24). Sediment type, therefore, was not shown to have a significant effect on MDC and could not be used to improve the SD-MDC model.

As early as 1924, H. W. Rickett (Rickett 1924) noticed that aquatic vegetation grew deeper in lakes possessing gentle slopes and shallower in lakes having steeper slopes. Duarte and Kalff (1986) demonstrated a strong influence of littoral bottom slope on the maximum biomass of aquatic macrophyte communities. However, they pointed out that the model generated in their study did not reflect turbid lakes (*i.e.*, Secchi depth readings <2 m), where irradiance rather than slope is pre-eminent. Mean SD for the 32 lakes was 1.8 m; therefore, littoral bottom slope according to Duarte and Kalff (1986) should not greatly influence MDC in Florida lakes. Another study by Duarte and Kalff (1990) found that when lakes had more gently sloped bottoms of <15%, plant growth was possible, and that 15% was the steepest slope at which aquatic macrophytes were present and able to grow. All lakes in the 32-lake study had slopes <15%, with a mean lake bottom slope of 4%. Lake bottom slope was not significantly related to MDC (R^2 = 0.03; p = 0.35; Table 4), so slope is unlikely to be a useful variable to improve the MDC-Secchi relationship in these Florida lakes. Although slope has been found to affect aquatic plant colonization in other studies, it seems plausible that slope has a minimal influence on MDC for many of Florida lakes because they are generally shallow, with a majority of them having mean depths <5 m (Florida LAKEWATCH 2003).

Much of the variability in the MDC-SD model is possibly due to fluctuations in lakes levels that prevent plant depth from attaining a state of equilibrium. Furthermore, light regimes fluctuate through time causing oscillation in the depth at which plants colonize. For the 279-lake-year study, the use of yearly average SD readings helped account for changing light regimes in which plants were responding that year, whereas only daily SD readings were used in the 32-lake study. When yearly SD transparency values from the Florida LAKEWATCH database were used to replace the daily SD values for the 32-lake study, the yearly SD-MDC model accounted for more variability ($R^2 = 0.57$) than the model using daily SD values ($R^2 = 0.46$).

Florida lakes display a wide range of limnological conditions (Canfield and Hoyer 1988). Information on MDC, SD, and other water chemistries were obtained from Florida LAKEWATCH to examine the MDC-Secchi relationship for a wide range of lakes. For the 279-lake-year study, MDC ranged from 0.7 m to 9.2 m. The mean MDC depth was 3.4 m. Secchi depth ranged from 0.2 m to 8.2 m (mean of 2.2 m). Color values ranged from 0 PCU to 430 PCU, with the mean color for all lakes equal to 50 PCU. The minimum and maximum chlorophyll concentrations were 0.5 µg/L and 292 µg/L, respectively, and the overall mean was 17 µg/L. Total phosphorus and TN concentrations ranged from 2.1 µg/L to 402 µg/L and 43 µg/L to 4550 µg/L, respectively, and averaged 28 µg/L and 764 µg/L, respectively (Table 5).

The 279-lake-year study showed a significant positive relationship between SD and MDC ($R^2 = 0.68$; $p < 0.05$; Fig. 4) represented by Equation 4 (Table 2). Equation 4 is similar to the regression equations developed by Canfield *et al.* (1985; Equation 1) and by the 32-lake study (Equation 2) and would generate approximately equivalent estimates of MDC for any given SD. The two MDC-SD models created in this study are also similar to regression equations generated in other studies. For example, for a Secchi depth of 5 m, Equation 2, Equation 4 and regression models developed by Canfield *et al.* (1985), Duarte and Kalff (1987), Chamber and Kalff (1985), and Nichols (1992) predict MDC values at 5.6, 5.8, 4.9, 5.6, 5.4, and 5.2 m, respectively (Table 2). This strongly suggests the MDC-SD relationship is applicable to a wide range of lakes and repeatable among a wide range of lakes.

For a given SD, considerable variability is clearly shown in the measured maximum depth of macrophyte colonization

Table 4.-Mean maximum depth of plant colonization (MDC in m) and mean slope (%) values by lake and relationship between MDC and mean slope.

Lake	County	MDC	Slope
Alligator	Lake	2.6	4
Alto	Alachua	2.5	2
Bay	Marion	1.97	2
Beakman	Lake	3.4	1
Bellamy	Citrus	0.72	4
Brant	Hillsborough	1	3
Church	Hillsborough	2	6
Conway North	Orange	5.5	5
Conway South	Orange	5.83	4
Dodd	Citrus	1.03	10
Doe	Marion	4.23	3
Farles Prairie	Lake	4.57	5
Grasshopper	Lake	2.25	2
Hampton	Bradford	1.73	1
Hernando	Citrus	2.27	3
Ivanhoe East	Orange	2.17	7
Little Conway	Orange	5.57	3
Little Santa Fe	Alachua	2	1
Magdalene	Hillsborough	3.57	2
Maurine	Hillsborough	1.2	4
Melrose Bay	Alachua	2.87	7
Mill Dam	Marion	2.73	3
Newnan	Alachua	0.65	0.3
Osceola	Hillsborough	3.5	7
Santa Fe	Alachua	3.87	2
Sellers	Lake	9.2	missing data
Starke	Orange	1.5	13
Stella	Putnam	4.27	3
Taylor	Hillsborough	3.1	3
Twin	Hillsborough	2.65	4
Weir	Marion	3	1
White Trout	Hillsborough	4.8	7

$\log(MDC) = 0.12 \log(SLOPE) + 0.34$
$R^2 = 0.03$
$n = 31$
$p = 0.35$

Table 5.-Descriptive statistics for maximum depth of plant colonization (MDC in m), Secchi depth (SD in m), color (PCU), chlorophyll (µg/L), total phosphorus (TP in µg/L), and total nitrogen (TN in µg/L).

Parameter	N	Minimum	Maximum	Mean	Standard deviation
MDC	279	0.7	9.2	3.4	1.8
SD	279	0.2	8.2	2.2	1.5
Color	263	0	430	50	69
Chlorophyll	279	0.5	292	17	34
TP	279	2.1	402	28	40.5
TN	279	43	4550	764	601.2

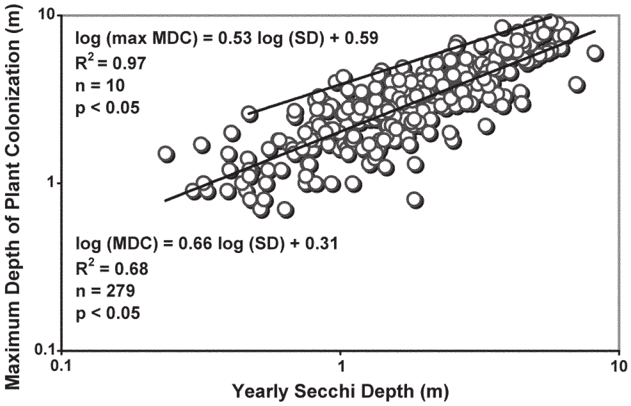

Figure 4.-Comparison of a calculated maximum line to the best-fit line relating yearly Secchi depth to the maximum depth of plant colonization for the 279-lake-year study.

(Fig. 4), demonstrating that other environmental factors besides water transparency influence MDC. However, a clear upper limit for MDC at various SD levels represents the depth where light is most likely the limiting environmental factor, described by Equation 5 (Table 2). When MDC values fall below the line, some environmental factor other than light is inhibiting plant growth.

Because SD readings were related to the measured color ($R^2 = 0.49$) and chlorophyll samples ($R^2 = 0.59$), these two light reducing variables were quantifiably related to MDC. Moreover, because chlorophyll readings were related to TP ($R^2 = 0.69$) and TN ($R^2 = 0.53$), regression models were developed to relate these nutrients to MDC. Therefore, MDC was also significantly inversely related to color ($R^2 = 0.40$; $p < 0.05$), chlorophyll ($R^2 = 0.30$; $p < 0.05$), TP ($R^2 = 0.43$; $p < 0.05$), and TN ($R^2 = 0.32$; $p < 0.05$). The light-attenuating substances, color and chlorophyll, were inversely related to MDC through multiple regression analysis ($R^2 = 0.51$; $p < 0.05$; Table 2). Given the significant relationships between MDC and color, chlorophyll, TP, and TN, it is possible to provide a basic assessment of the potential effects of these variables on macrophyte colonization in Florida lakes even without measurements of SD or E.

Conclusion

For this study, the maximum depth inhabited by an angiosperm was 9.2 m. This was similar to the findings of Hutchinson (1975), who concluded that most angiosperms in lakes are limited to depths of 9 m. A few exceptions of extreme deepwater expansion by freshwater angiosperms have been noted. For example, Sheldon and Boylen (1977) found *Elodea canadensis* growing to depths of 12 m in Lake George, New York and *Hydrilla verticillata* has been found growing to a depth of 15 m in Crystal River (Langeland 1996).

This study has confirmed the findings of Canfield *et al.* (1985) that MDC can be predicted using SD transparency. Furthermore, MDC can be predicted reasonably well by light meter measurements. The mean percent of incident light at MDC was 11% for the Florida lakes studied, which is in agreement with much of the primary literature. Although plant species, sediment type, and slope have been shown to influence aquatic plant colonization on an individual lake basis, no significant influences on MDC were found in this study when looking for trends among lakes. When those variables (plant species, sediment types, slope) where taken into account, they did not increase the predictive capabilities of the SD-MDC model.

Although this study represents a more comprehensive research effort than those of Canfield et al (1985) to identify and quantify the environmental determinants of MDC, it offers no improvement on the predictive value offered by the SD measurements reported in that study. This suggests that light attenuation, as quantified by SD sampling, is the most important environmental factor in determining MDC. Nevertheless, there is substantial variability in SD-MDC correlates from one site to another, suggesting that other factors play a causal role.

There are many possible combinations of environmental variables for a specific site over the course of time, and this introduces the element of unquantifiable chance into any predictive value for response by a resident organism. The inability of this research effort to isolate other specific factors as core determinants makes it likely that the range of variation in MDC response from site to site is to be expected. In the final analysis, this simply represents a measurable variation in response to an immeasurably complex interaction of environmental factors.

An upper limit line relating MDC to SD was developed and describes light limitation when the MDC response falls on or near the response curve. MDC values that fall below the line indicate some other limiting environmental factor. The maximum MDC model predicts the upper limit of deepwater plant expansion, but other factors will routinely result in an actual depth of plant colonization less than predicted.

The other water chemistry parameters examined (color, chlorophyll, TP, and TN) were found to provide reasonable estimates for predicting the potential depth of macrophyte colonization and could be particularly useful when SD or E of a lake is unknown. Water-resource managers should assess each lake independently and consider which water chemistry variable is the dominant factor influencing plant colonization. For example, true color would be the best tool to use for predicting MDC for a dystrophic lake.

Hoyer *et al.* (2005) found no overall relations between trophic state variables (SD, chlorophyll, TP, and TN) and water lake level fluctuations among 84 Florida lakes. When examined on an individual lake basis, direct, inverse, or no significant relations were found between lake trophic state variables and water level fluctuations. Mechanisms, such as sediment resuspension and aquatic macrophyte abundance, that can impact nutrient and chlorophyll concentrations and water clarity were also shown to increase or decrease with changing water levels, depending on lake bathymetry. The data suggest that predicting impacts of water level fluctuations on trophic state variables among populations will be difficult, but that examination of mechanisms within a lake could be more useful for predicting lake response to changes in water level. The potential area of a lake covered with submersed aquatic vegetation can be calculated for a lake by using any of the models generated in this study that predict MDC; potential PAC could then be calculated by overlaying this depth to a bathymetric map. The potential PAC could also be calculated at different contours to examine how PAC will change with decreasing water level.

Submersed aquatic macrophytes play an integral role in the functioning of lake processes; therefore, it is important to understand the response of submersed plants to changes in lake conditions, such as eutrophication or altered water levels. These models allow assessment of potential changes in plant coverage that might result from changes in light and water chemistry variables and manipulation of lake water level.

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