Phytoplankton as a factor in the decline of the submersed macrophyte *Myriophyllum spicatum* L. in Lake Wingra, Wisconsin, U.S.A.

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Abstract

A dramatic decline in biomass and areal coverage of the submersed macrophyte *Myriophyllum spicatum* in Lake Wingra, Wisconsin, USA during the mid-1970's is documented using aerial photography, vegetation surveys, and quadrat biomass sampling. Over the same period, light penetration as measured by Secchi disc transparency and extinction coefficient decreased substantially. During this period, extinction coefficient was closely correlated with chlorophyll *a* levels implicating phytoplankton as the major source of decreased light penetration. A growth model for *M. spicatum* predicts a substantial decline in macrophyte biomass when extinction coefficient is increased to the levels reported since 1977. Available data do not show whether the phytoplankton increase preceeded or followed the macrophyte decline. Nonetheless it is clear that phytoplankton growth can account for a substantial portion of the decline and that macrophyte recovery will be difficult given the phytoplankton-induced decrease in water clarity.

Introduction

From the mid-1950's (following carp removal) through 1975, macrophytes were an important and productive component of the Lake Wingra littoral zone (Baumann *et al.* 1974). Beginning in the late 1960's, Eurasian water milfoil, *Myriophyllum spicatum* (hereafter referred to as *Myriophyllum*), became the overwhelmingly dominant species (Nichols & Mori 1971, Carpenter 1980). In the period 1975–77, a dramatic decline in the abundance of this species occurred. Since 1977 biomass levels for *Myriophyllum* have reached only one-third of their former values (Carpenter 1980). Although some minor species have increased slightly in importance, the net result has been an overall dramatic decrease in submersed vegetation in Lake Wingra.

The unexpected and abrupt decline of *Myriophyllum* has stimulated an active search for factors contributing to the reduced abundance. Carpenter (1980), in a thorough review of available data, assessed the role of the following factors in causing the decline: toxin accumulation, harvesting and herbicides, climate, nutrients, epiphytes, competition from other macrophytes, and parasites or pathogens. He concluded that no one factor alone could account for the decline and that a multifactor synergistic mechanism was involved. Smith (1978) also ruled out nutrients as the sole cause for the Lake Wingra *Myriophyllum* decline.

One factor which has not been sufficiently explored is competition for light from phytoplankton and attached algae. Light penetration has been shown to limit macrophyte growth in a number of studies. Peltier & Welch (1970) found that macrophytes reached nuisance proportions in Pickwick Reservoir, Alabama only in those years when springtime rainfall and resultant turbidity were low. Robel (1961) showed an inverse relationship between submersed macrophyte biomass and turbidity. Spence (1976) has shown that the depth to which macrophytes can colonize is related inversely

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to light extinction. In his Scottish lochs phytoplankton were responsible for most of the light attenuation. These results suggest that increases in phytoplankton populations with progressive nutrient enrichment could be responsible for macrophyte declines by limiting light availability. Extensive paleolimnological and historical evidence from the Norfolk Broads area of England has led Phillips *et al.* (1978) to suggest another alternative: the decline of macrophytes is coincident with increased epiphytic and filamentous algal growth; increases in phytoplankton biomass are subsequent rather than causal.

This paper will document changes which have occurred in the submersed littoral vegetation of Lake Wingra since the early 1970's. Light extinction, Secchi disc, and phytoplankton chlorophyll *a* measurements for 1978 and 1979 will be compared with pre-1975 values to test the hypothesis that increased phytoplankton biomass has caused a marked decrease in water clarity in Lake Wingra. Simulations with WEED, a macrophyte growth model designed and calibrated for Lake Wingra (Titus *et al.* 1975), will test the hypothesis that the observed changes in water clarity can account for the decline in *Myriophyllum* biomass. Available data on epiphytic and filamentous algae during the 1970's will also be examined to determine the possible role of these algae in the macrophyte decline.

Methods

Lake Wingra is a small (137-ha) lake of glacial origin surrounded by the city of Madison, Wisconsin, USA and its immediate suburbs (43°4'N, 89° 25'W). With a maximum depth of about 4 m and a mean depth of about 2.4 m the lake seldom stratifies for more than a few days.

Chlorophyll *a* was measured during summer and fall of 1979 on phytoplankton samples from pelagic (mid-lake) and littoral stations at 0.5 m depth increments. Samples were held in the dark until filtration and extraction in DMSO-acetone. Light (PHAR) profiles were determined with a Lambda photon sensor 2–3 times per month at both pelagic and littoral stations. Light extinction coefficients were determined by linear regression of ln-transformed light levels against depth:

$$\ln I(z) = \ln I(0) - k_2 z$$

where $I(z)$ = light level at depth z
k_2 = light extinction coefficient due to water and suspended materials (m^{-1})
z = depth (m)

Secchi disc readings were taken at a mid-lake station in 1979. Macrophyte and filamentous algal coverage were determined from aerial photography taken in early September with color infra-red film.

Chlorophyll *a* levels and light extinction coefficients measured at a mid-lake station for 1970–73 were derived from Koonce & Hasler (1976). In their study phytoplankton was collected on membrane filters and ground in acetone to ensure complete extraction. Chlorophyll levels of occasional duplicate samples extracted in methanol were no higher than acetone-extracted samples (Koonce, pers. comm.). Available data indicate that methanol extracts as well as DMSO-acetone (Stauffer *et al.* 1979). Thus, these extractions with acetone are comparable to 1979 extractions with DMSO-acetone. Light levels in 1970–75 were measured in a vertical profile and the extinction coefficient k_2, calculated as described above for the 1978-79 data. Secchi disc readings for 1973 are from Gasith (1974). Each value is the mean of readings by two observers. Light extinction coefficients for 1975 are from Titus (1977).

Information on the distribution and abundance of aquatic macrophytes (1970–78) was obtained from several sources. Carpenter (1980) has summarized the available data on *Myriophyllum* biomass. Distribution of *Myriophyllum* in Lake Wingra is known from vegetation surveys conducted in 1969 (Nichols & Mori 1971) and 1977 (Johnsen & Kimble, unpublished data). Aerial photographic methods were used by Gustafson & Adams (1973) and McCracken *et al.* (1974) to assess macrophyte and filamentous algal biomass and coverage.

The macrophyte production model WEED, designed and calibrated specifically for *Myriophyllum* in Lake Wingra, was used to estimate the effects of decreased water clarity on macrophyte growth. Titus *et al.* (1975) provided an extensive description and documentation of the model. Initial biomass, temperature, and light values used in the simulations were from actual data gathered in 1977. Only light extinction coefficient, k_2 in Titus *et al.*, was varied.

Methods used by different investigators were carefully reviewed to ensure that methodological differences were not responsible for reported differences in the observed values of extinction coefficient, chlorophyll *a*, and macrophyte biomass and coverage. In all cases, the observed differences were much larger than methodological bias could account for.

Results and discussion

1. The decline of Myriophyllum

Carpenter (1980) has documented the decline of *Myriophyllum* in Lake Wingra using quadrat biomass samples collected by various investigators during the period 1969–78. *Myriophyllum* biomass in 1977 and 1978 was less than one-third of the 1970–73 biomass.

Coverage as determined by aerial photography provides dramatic documentation of the *Myriophyllum* decline. Remote sensing of macrophytes by aerial photography detects only those plants near the surface. Thus, photographs should be taken when beds are well developed and winds are calm. Since biomass is concentrated near the surface, the growth form of *Myriophyllum* is more amenable to aerial measurement than that of many submersed macrophytes. Figure 1 compares coverage by macrophytes in September 1972 with that in September 1979 in Lake Wingra's east end. Both figures are from aerial photographs taken at times of near maximal biomass and calm wind conditions around mid-day. The decline in *Myriophyllum* coverage is dramatic.

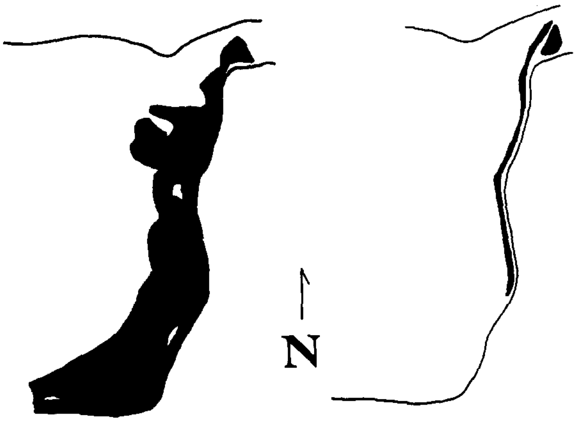

Fig. 1. Lake surface coverage by *Myriophyllum spicatum* in Lake Wingra's east end as determined by aerial photography during September. Left is 1972, right is 1979.

Additional evidence for the decline comes from transect studies conducted in 1969 and 1977. Workers in the 1977 study contacted the earlier investigators and made every effort to duplicate their procedures. In each study transects were laid out perpendicular to the shore at 100 m intervals. The abundance of each species relative to a four-point scale was determined for 5 m intervals. The results of these two studies are compared in Fig. 2. Large areas of once dense *Myriophyllum* have thinned to lower densities. The decline as shown for 1977 continued into 1978 when no *Myriophyllum* could be found in the previously heavily infested east end of the lake.

2. The decrease in water clarity and the increase of the phytoplankton

Extinction coefficients measured by several investigators over the years 1970–79 are shown in Fig. 3. The increase in light extinction in 1978–79 over the period 1970–75 is obvious in the summer months. Summertime (June-September) light extinction coefficients (k_2) exceeded 2.00 m^{-1} only twice in 46 measurements during the years 1970–75 whereas k_2 never fell below 2.20 in 17 measurements in 1978–79. April and May, critical periods for early macrophyte growth, showed similar extinction coefficients during both periods. Secchi disc readings, which were made more sporadically than light profiles, bear out the 1978–79 decrease in water clarity (Table 1).

Several lines of evidence point to phytoplankton as a major cause of the increased turbidity. First, like the extinction coefficient, phytoplankton biomass as measured by chlorophyll *a* increased dramatically from 1972–73 to 1979 (Fig. 4). During the period 1972–73, chlorophyll *a* never exceeded 40 $\mu g \cdot l^{-1}$ whereas samples taken from June to September of 1979 show 50–120 $\mu g \cdot l^{-1}$ chlorophyll *a*. Second, the variation in extinction coefficient was closely and significantly related to variations in phytoplankton chlorophyll *a* ($r = 0.95$, $p < .01$). This close relationship indicates that phytoplankton are indeed the major source of increased turbidity in Lake Wingra. During 1979 the cyanobacterium *Mycrocystis* dominated the summer phytoplankton.

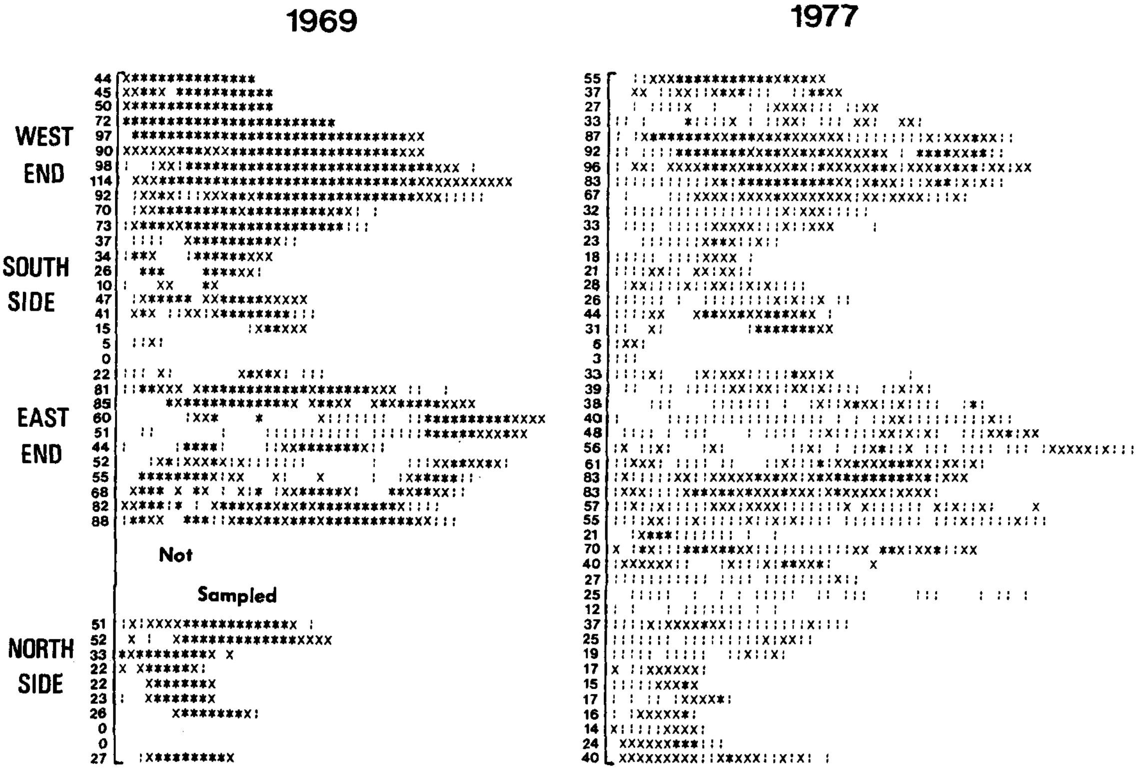

Fig. 2. Relative abundance of *Myriophyllum spicatum* in Lake Wingra as determined by vegetational surveys, 1969 and 1977. Shoreline is stretched out along left margin of plots, with transects extending into the lake perpendicular to the shore. Each point represents 5 m distance along the transect. Transects are 100 m apart★: continuous; x: not continuous, but > 5 plants · 5 m^{-1}; ¦: < 5 plants · 5 m^{-1}; blank, absent. Values along left margin of transect represent total relative abundance of macrophytes in each transect. Each point along the transect was given a score (★: 3, x: 2, ¦: 1) and these were summed along the transect.

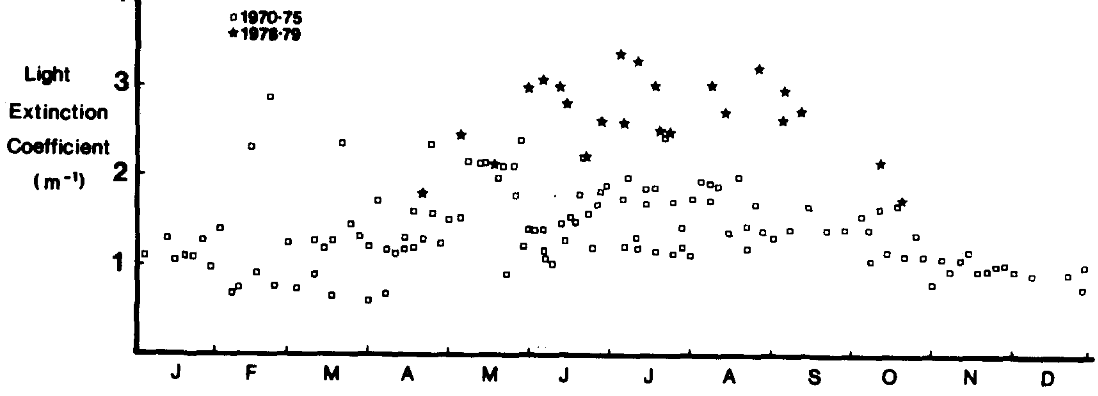

Fig. 3. Light extinction coefficients for Lake Wingra, open water region, 1970–79.

Table 1. Secchi disc readings at mid-lake site, Lake Wingra.

Date	1973	1979
May 16	-	0.60 m
May 27	0.70 m	-
June 14	-	0.40 m
June 18	0.82 m	-
June 25	0.68 m	-
June 27	-	0.40 m
July 25	-	0.45 m
July 30	0.58 m	-
Aug. 6	0.67 m	-
Sept. 5	-	0.50 m
Sept. 6	0.73 m	-

3. Predicting the effect of reduced water clarity on macrophyte growth

The macrophyte production model WEED can be used to simulate the effects of reduced water clarity on *Myriophyllum* biomass development. A major input parameter for WEED is the extinction coefficient k_2. During April and May in all years, k_2 varied from 1.8 to 2.5 m^{-1}. Thus a value of $k_2 = 2.1$ was chosen for the period of April 15 to May 25 in the simulation. For the remainder of the growing season, May 26 to September 15, k_2 was set at 2.8, typical of the increased 1978-79 summertime light extinction. Temperature and light data for 1977 were the same as in Carpenter (1980). Resulting biomass predictions are shown in Fig. 5. Also shown are a simulation with k_2 decreased to 1.5 after May 26 to simulate pre-1977 conditions and the observed 1977 biomass values. Note the large decrease in predicted biomass caused by the increased extinction coefficient. The increased light extinction can account for about half of the decline in macrophyte biomass.

By concentrating most of its photosynthetic tissue in the upper few decimeters of the water column, *Myriophyllum* exhibits a midsummer growth form which should make it less susceptible to phytoplankton-induced light stress (Titus & Adams 1979). However, growth is initiated each spring from very short, overwintering shoot stock which must grow upward through the water column to reach the surface. The onset of elevated turbidity coincides with the period during which *Myriophyllum* is making its growth surge upward (Titus *et al.* 1975, Jones 1980). At this critical period *Myriophyllum* may well be vulnerable to decreased light penetration. Titus *et al.* (1975) concluded that if the extinction coefficient were increased to 2.5 m^{-1} for the entire growing season, growth would not

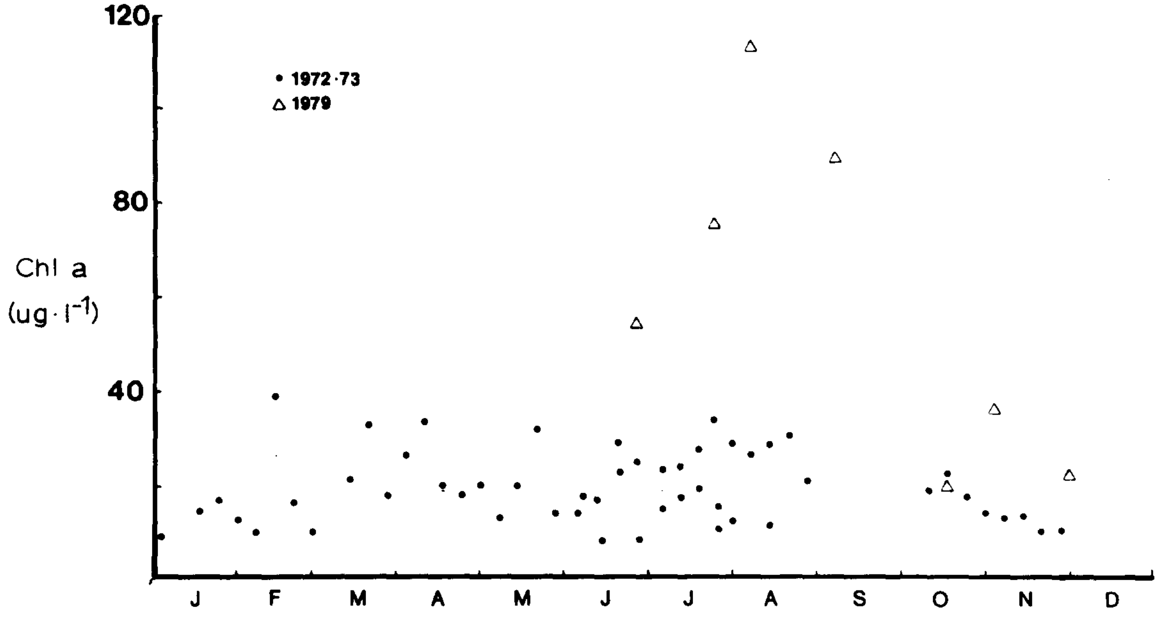

Fig. 4. Chlorophyll *a* in Lake Wingra, 1972-73 and 1979.

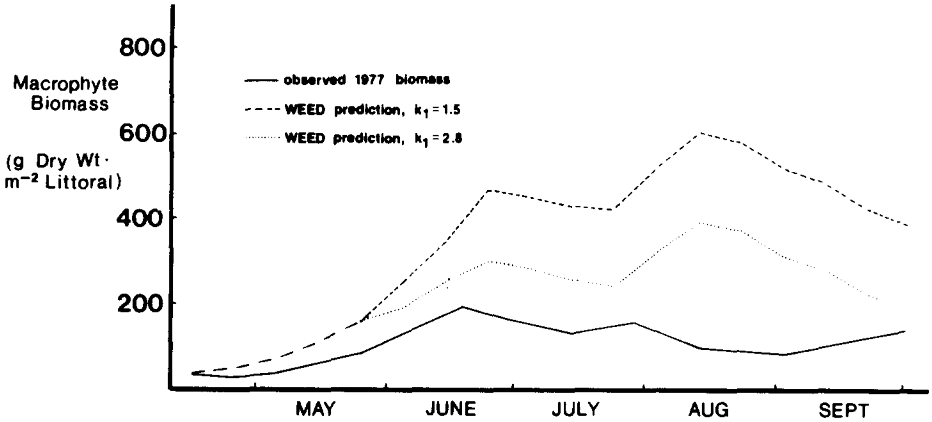

Fig. 5. Predicted (WEED) *vs.* observed macrophyte biomass.

occur at a rooting depth of 1.5 m. In the present study k_2 was not increased to 2.8 m^{-1} until May 25 allowing the development of at least some of the macrophyte canopy. However, these latter simulations also show that while *Myriophyllum* maintains much of its structural carbon with decreased light penetration, its non-structural carbohydrate reserves at year's end fall drastically from 172.4 g·m^{-2} with $k_2 = 1.5$ m^{-1} to 8.2 g·m^{-2} at $k_2 = 2.8$. Since this pool supports overwintering metabolism, its low level would foreshadow greatly reduced vigor the following year.

During the early 1970's, the *Myriophyllum* canopy was often overtopped by dense growths of the filamentous alga *Oedogonium* (McCracken *et al.* 1974). These growths probably inhibited macrophyte growth by shading, thus possibly contributing to decreased biomass levels. However, those weedbeds most densely colonized (west end) by *Oedogonium* are now among the healthiest. Furthermore, some weedbeds which disappeared were never overtopped by *Oedogonium*. Epiphytic algae and associated bacteria and non-living particulates lushly coat the *Myriophyllum* now (Jones 1980). However, no pre-decline studies are available to assess the possible correlation of this epiphytic coating with the macrophyte decline. Thus, this aspect of the hypothesis of Phillips *et al.* (1978) cannot be rigorously tested.

Summary

We have demonstrated that increased phytoplankton biomass causing decreased light penetration has occurred concurrently with the decline of submersed macrophytes in Lake Wingra. Furthermore, we have shown that the decrease in available light can explain a large part of the drop in biomass production by submersed macrophytes. The causal mechanisms remain in doubt. Our data are insufficient to prove that increases in phytoplankton caused the decline of the plants or, conversely, that the decline of the plants was responsible for increases in the phytoplankton. However, we can conclude that given the phytoplankton-created low water clarity, macrophyte growth will be inhibited. Thus, regardless of its original cause, the present situation of high phytoplankton biomass and reduced littoral macrophytes will tend to be self-perpetuating. Any trend toward rejuvenation by littoral macrophytes will encounter a much less favorable light environment than existed before the decline.

Acknowledgements

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