

A MODEL TO DESCRIBE GROWTH OF THE FILAMENTOUS ALGA *PITHOPHORA OEDOGONIA* (CHLOROPHYTA) IN AN INDIANA LAKE¹

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ABSTRACT

A computer model was developed to simulate growth dynamics of the weedy filamentous alga *Pithophora* (*Pithophora oedogonia* (Mont.) Wittr.) in an Indiana lake. The model, based on a modification of the Monod function, took into account 1) temporal shifts between the growth limiting nutrients (nitrogen and phosphorus), 2) self-shading within the algal mats, and 3) washout of the free-floating mats as a result of heavy rains and winds during a 7-day period. Limitations of the model included 1) low sensitivity of washout predictions to intense rainfalls (2.5 to 5 cm) that occur within a 24 hour period, 2) competitive or allelopathic effects from blue-green algal blooms, and 3) weather induced light limitation. The model can be used to assess effects of management practices designed to reduce nutrient concentrations in the lake. Greater reduction in biomass was predicted when nitrate concentration in the lake was reduced by 50% than if a similar reduction in total phosphorus was achieved.

Key words: Aquatic weeds, macrophytes, nitrogen, phosphorus.

INTRODUCTION

Filamentous algae can dominate the littoral zones of lakes and ponds. Their accumulation and decomposition results in loss of aesthetic appeal, deterioration of water quality, and curtailment of many human uses. Investigations on the growth dynamics of *Cladophora glomerata* (L.) Kütz., the major filamentous algal nuisance species in the Great Lakes, resulted in the development of a mathematical model which relates spatial and seasonal variations in production with changes in phosphorus concentrations (Canale and Auer, 1982). Such models are not only useful in generating hypotheses regarding algal survival mechanisms but also for devising management schemes for their control.

Similar information on the growth requirements of other frequently encountered and important filamentous algae is, however, lacking. One such species, *Pithophora oedogonia* (Mont.) Wittrock, is widely distributed throughout the eastern United States (Prescott, 1962; Smith 1950).

This alga is a serious management problem because of its prolific growth in shallow lakes, boat channels, and fish culture ponds and because of its tolerance to commonly used algicides⁴. Thus, a model describing the growth of *Pithophora oedogonia* under various environmental and nutrient regimes could be a useful tool in management of the organism.

The model described here is based on modifications to the Monod function described by O'Brien (1974). O'Brien stated that growth of several algal species could be described by the Monod equation:

$$g = G_m \frac{C}{C + K_s} \quad (1)$$

where: g = the growth rate,
 G_m = the maximum growth rate,
 C = the concentration of the limiting nutrient,
 K_s = the half saturation constant (the concentration of nutrient at which the growth rate is one-half the maximum growth rate.)

O'Brien modified this equation by including a term, d , to account for algal mortality (Eq. 2) and by incorporating a second equality (Eq. 3) to decrease nutrient dynamics as growth occurred:

$$g = G_m \frac{C}{C + K_s} - d \quad (2)$$

$$\frac{dC}{dt} = R - D(N_g) \quad (3)$$

where: N_g = algal biomass produced,
 R = the rate of replacement of the limiting nutrient,
 D = the depletion factor or percent cell composition of the limiting nutrient,

O'Brien suggested that equations 2 and 3 constituted the simplest set of equations that describe the observed growth characteristics for phytoplankton.

Our initial attempts to model *Pithophora* growth were based on equations 2 and 3. However, these equations do not account for temporal shifts between limiting nutrients.

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⁴Lembi, C. A., N. L. Pearlmutter, and D. F. Spencer. 1980. Life cycle, ecology, and management considerations of the green filamentous alga, *Pithophora*. Purdue University Water Resources Research Center. No. 130. 97 pp.

Evidence from previous studies (Spencer and Lembi, 1981) indicated that nitrogen limitation is as important as phosphorus limitation in regulating the spatial distribution of *Pithophora*. Thus, our model includes a method for determining when nitrogen or phosphorus is limiting growth. Other modifications incorporated into the model take into account washout episodes and self-shading to which the free-floating, dense *Pithophora* mats are often subjected.

MATERIALS AND METHODS

The values for the terms in the model equation were estimated from laboratory growth studies. Culture studies were conducted in a growth chamber with a 16:8 L:D cycle and irradiance of $48 \pm 4 \mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Growth of *Pithophora* at various temperatures and external concentrations of nitrogen (N) and phosphorus (P) was determined. Details of the procedures are given in Spencer and Lembi (1981) and Spencer (1983). Growth rates for various N (40 to 5850 μM) and P (7 to 360 μM) concentrations were fitted to the Monod function by curvilinear regression using a computer program described by Hanson *et al.* (1967), and K_s and G_m were estimated for each temperature. Kinetic parameters for 20 C were obtained from Spencer and Lembi (1981).

Model input data (temperature, nutrients, and rainfall) were obtained by monitoring chemical and physical parameters in Surrey Lake, a small ($A = 3.9$ ha), shallow ($z = 1.4$ m) man made drainage lake near Columbus in Bartholomew County, central Indiana (Lat. $39^\circ 11' 18''$, long. $85^\circ 51' 17''$). The inflowing stream drains a watershed of approximately 1128 ha, 63% of which is used as cropland (corn and soybeans) and pasture, 21% woodland, and 16% residential. Most of the residential area is located 1.2 km upstream from Surrey Lake. Each residence is located on a septic tank-finger system which is adjacent to the stream. The major soil types in the drainage area are Fincastle silt loam and Brookston silty clay loam.

Water samples for nutrient analyses were collected at stations along a north-south transect parallel to the long axis of Surrey Lake. Samples were taken at irregular intervals (generally 2 to 4 weeks) from February 1979 through December 1981. Sampling stations 2 to 7 (Spencer and Lembi, 1981) were located in the shallow cove area (mean $z = 0.42$ m) that receives the stream inflow. Stations 8 to 12 were located in the deeper open lake area (mean $z = 2.0$ m). Previous studies indicate that *Pithophora* growth occurs primarily in the cove area of Surrey Lake (Spencer and Lembi, 1981). Therefore, environmental measurements utilized in the model were limited to those taken at the cove stations.

Water samples were collected 0.1 to 0.5 m from the surface depending on the depth of the station. Nitrate was determined by the cadmium reduction method (APHA, 1975); ammonia by Nesslerization (APHA, 1975). Total phosphorus was determined on unfiltered aliquots following perchloric acid digestion (APHA, 1975). Temperature was measured with a YSI Model 33 S-C-T meter. Additional information on chemical and physical characteristics of Surrey Lake are provided in Spencer and Lembi (1981). Precipitation data from Columbus, Indiana and wind

speed and direction from Cincinnati, Ohio were obtained from the National Weather Service.

Biomass density of *Pithophora* in Surrey Lake was monitored over a 3-year-period and used to verify model predictions of biomass changes. *Pithophora* biomass was sampled at the cove stations using a 30.48 cm diameter, open-ended aluminum tube. Samples were rinsed to remove sediments and *Lemna minor* L. and dried for 48 h at 110 C. Samples were weighed and biomass ($\text{g dry wt}\cdot\text{m}^{-2}$) was calculated for each of the cove stations. A portion of dried material was ground to a fine powder in a mortar and pestle and utilized to determine tissue nitrogen and phosphorus (nutrient depletion factor, D; Eq. 3). Ground samples (10 to 20 mg) were digested with potassium persulfate at 120 C for 2 h (Raveh and Avnimelech, 1979). Aliquots of the digested samples were adjusted to pH of 7 and phosphorus was measured by the ascorbic acid technique. The remainder of the digested sample was treated with Devarda alloy to reduce all nitrogen species to ammonia which was measured with the phenol-hypochlorite method (Wetzel and Likens, 1979).

RESULTS AND DISCUSSION

Environmental parameters. Water temperature in the cove ranged from 0 to 35 C during the study period (Fig. 1A). Cumulative rainfall (7 day) for Columbus, IN indicate that episodes of heavy rainfall (7-day totals > 5 cm) occurred during all 3 years of the study (Fig. 1B). High concentrations of nitrate occurred in the winter and early spring and generally declined during May and June (Fig. 1C). Nitrate concentrations recovered in July but returned to lower levels from August through October. Ammonia concentrations were generally much lower than nitrate concentrations and usually accounted for less than 15% of the total soluble inorganic nitrogen. Total phosphorus levels varied considerably over the 3-year-period (Fig. 1D). Total phosphorus increased during the period of late May to late July in all 3 years of the study. Tissue concentrations of nitrogen ranged from 2.6 to 4.6% with a mean of 3.7% ($n = 15$; $\text{SD} = \pm 1.6\%$). Tissue phosphorus ranged from 0.3 to 0.6% with a mean of 0.5% ($n = 15$; $\text{SD} = \pm 0.3\%$).

Culture studies. The effect of temperature on maximum growth rate, G_m , for *P. oedogonia* grown in laboratory culture was described by Spencer (1983). G_m increased as temperature increased to 30 C. The relationship can be summarized by the following Arrhenius equation:

$$G_m = (6.6 \times 10^6) e^{-5187/T} \quad (4)$$

where: e = the base of the natural logarithm,
 T = temperature in degrees Kelvin.

It was noted that maximum rates of net photosynthesis measured in the field were substantially higher than rates for laboratory cultures (O'Neal *et al.* 1985). It is likely that such differences between field and laboratory cultured *Pithophora* would result in higher *in situ* growth rates. A linear equation was developed that relates the ratio of field/laboratory photosynthesis to temperature and the temperature dependent ratios were multiplied by the G_m predicted by Eq. 4 to obtain a corrected G_m . A similar proce-

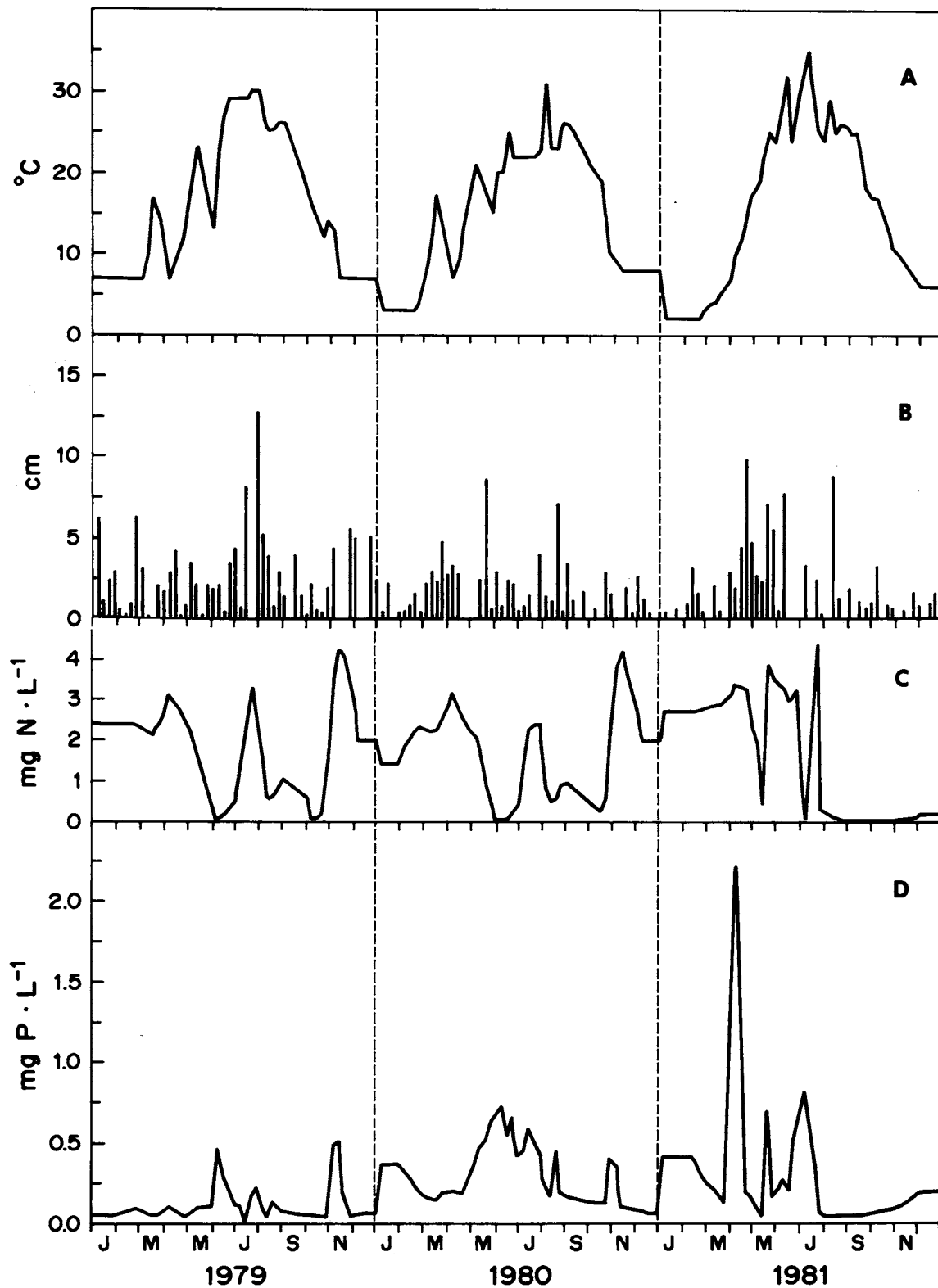


Figure 1. Selected environmental parameters measured in Surrey Lake cove area. A. Water temperature. B. Precipitation, cumulative 7 day totals. C. Nitrate. D. Total phosphorus.

dure was employed by Canale and Auer (1982) in their *Cladophora* growth model.

Half-saturation constants, K_s , relating growth to external N and P concentrations at different temperatures were

also determined (Figs. 2A and 2B). The relationship between K_s for nitrate and temperature can be summarized by:

$$K_{s(\text{NO}_3)} \mu\text{M} = -640.126 + (45.6 \times T \text{ (C)}) \quad (5)$$

The coefficient of determination for this equation was 0.75. A similar equation relating K_s for phosphate to temperature is:

$$K_{s(\text{PO}_4)} \mu\text{M} = 3.12 - (0.1 \times T \text{ (C)}) \quad (6)$$

The coefficient of determination for this equation was 0.12.

The model. A computer program written in BASIC combined the results of the field and laboratory studies with equations 2 and 3 to simulate growth of *Pithophora* in Surrey Lake. The program used the Surrey Lake data on water temperature and nitrate and total phosphorus concentrations collected during the course of this project. Missing data were estimated by linear interpolation of existing data. Although algae appear able to use both nitrate and

ammonia for growth (Morris, 1974), nitrate was clearly the most abundant inorganic nitrogen species entering Surrey Lake. We therefore chose to incorporate it into the *Pithophora* growth model. The relationship between total phosphorus and algal growth within a lake appears to be strong (Wetzel, 1975); therefore this parameter was also chosen for the growth model.

A flow diagram of the model is shown in Figure 3. An important feature of the model is the method for determining whether N or P limits growth for a given time interval. This is done by calculating the appropriate temperature dependent K_s values for N- and P-limited growth. Next, the ratio of N:P in the water is determined. Tilman (1977) suggested that in a chemostat at steady state an alga would be simultaneously limited by two nutrients when the ratio of the nutrient concentrations is equal to the ratio of the K_s values for those nutrients (Eq. 7).

$$N/P = K_{s(N)}/K_{s(P)} \quad (7)$$

If, however, $N/P > K_{s(N)}/K_{s(P)}$, then P is the limiting nutrient. Conversely, N limits growth when $N/P < K_{s(N)}/K_{s(P)}$. While it is unlikely that steady state growth of *Pithophora* occurs in Surrey Lake, there is evidence that this approach may be useful in predicting nutrient limitation for

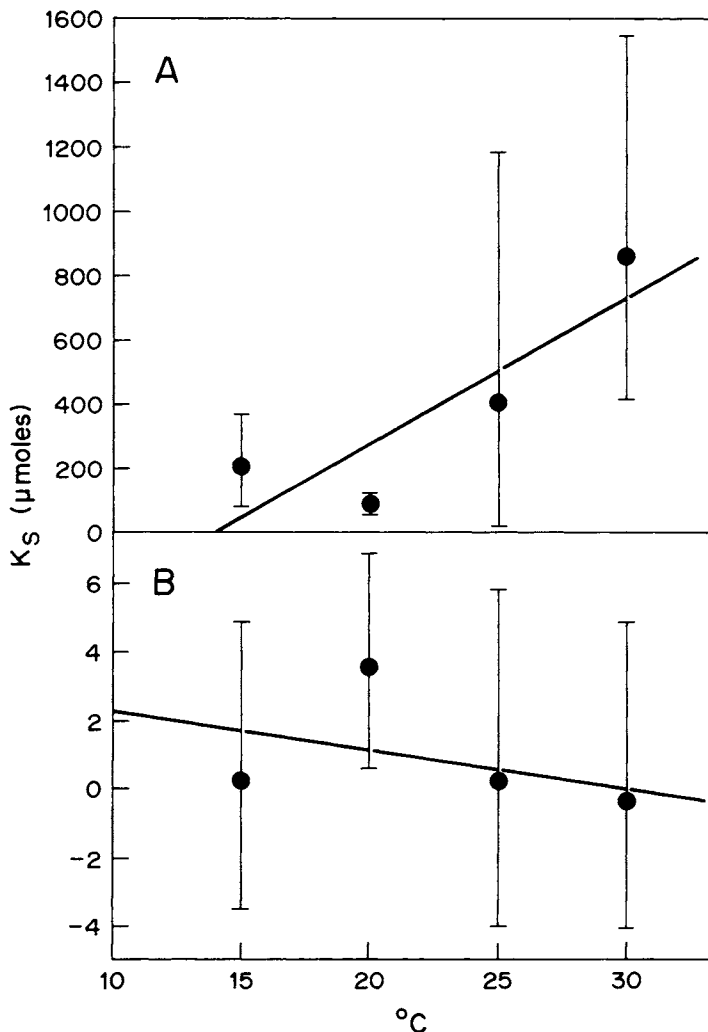


Figure 2. K_s for nutrient-limited growth versus temperature for laboratory cultures of *Pithophora*. A. Nitrogen-limited growth. B. Phosphorus-limited growth. Error bars represent 1 standard error.

NUTRIENT, TEMPERATURE, AND RAINFALL DATA

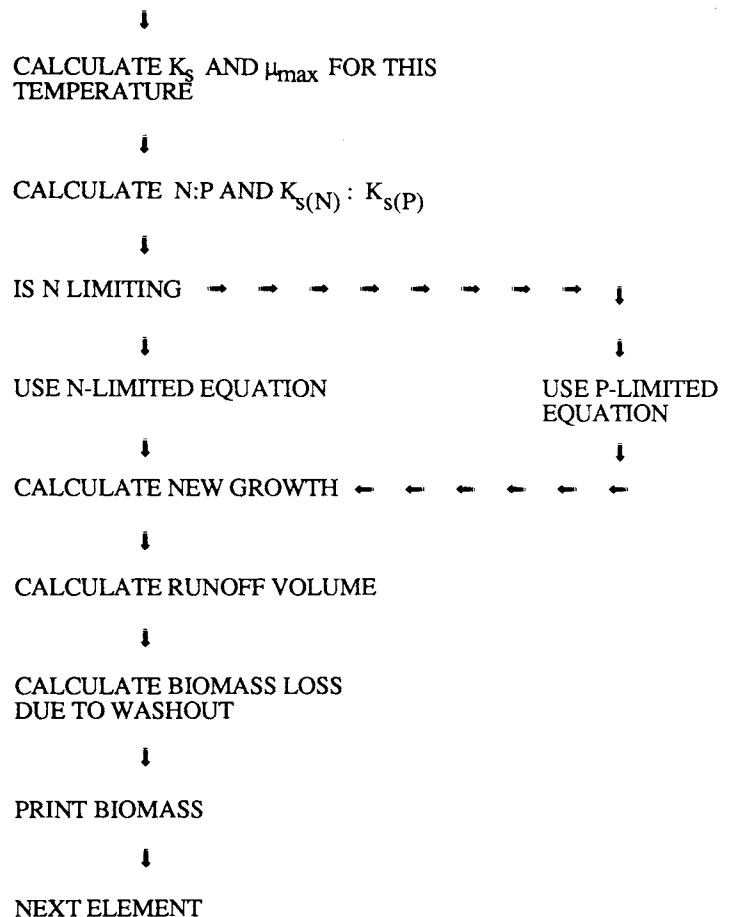


Figure 3. Flow diagram for the *Pithophora* growth model.

Pithophora (Spencer and Lembi, 1981) and other algae (Tilman, 1977). The model calculates the appropriate ratios and uses the equation for N- or P-limited growth as indicated.

Another factor limiting *Pithophora* growth is self-shading within the massive mats. O'Neal and Lembi (1983) found that light was reduced to the compensation point for photosynthesis less than 1 cm beneath layers of *Pithophora* filaments. Such intense self-shading would result in a photosynthetically active outer layer of mat surrounding a light limited core with new growth occurring primarily in the outer layer of filaments. Based on general observations, the geometry of a *Pithophora* mat approximated an ellipsoid with the photosynthetically active layer limited to the outer 4 cm. Biomass density ($\text{g}\cdot\text{cm}^{-3}$ of mat) was measured on mat segments collected at Surrey Lake and were used to convert calculated mat volumes to biomass. The proportion of the mat illuminated was regressed on the log of the biomass. The photosynthetically active biomass was calculated using the resulting equation:

$$N_p = N_{\text{tot}} (1.631 - (0.185 \times \text{LOG}(N_{\text{tot}}))) \quad (8)$$

where: N_p = photosynthetically active biomass,
 N_{tot} = total mat biomass.

Light penetration was assumed to be reduced to 1 cm at very high biomass densities ($> 240 \text{ g}\cdot\text{m}^{-2}$) and a relationship similar to Eq. 8 was derived on this assumption. The calculated photosynthetically active biomass (N_p) was utilized in the growth calculations.

The relationship between *Pithophora* mortality (loss rate) and temperature was estimated by plotting the negative growth rates for cultures grown without nitrate as a function of temperature (Fig. 4). The linear regression equation was:

$$\text{loss rate (doubling } d^{-1}) = e^{-7.081 + 0.162 \times T} \quad (9)$$

where: T = temperature (C).

The coefficient of determination of the regression was 0.69. The maximum loss rate for *Pithophora* (-0.11 d^{-1}) was assumed to occur during the autumn period of akinete formation. Akinetes are resting spores formed by the direct modification of vegetative cells. Intercalary cells between the akinetes senesce resulting in the break-up of the filaments. One factor that appears related to akinete inducement is a regime of declining temperatures such as that observed late in the growing season at Surrey Lake (unpublished data). This temperature regime was used to predict akinete formation and its associated increase in loss rate.

Loss of *Pithophora* from the cove area after heavy rains was an important biomass loss factor. Strong winds originating from a southerly direction and traveling down the long axis of Surrey Lake could blow the floating algal mats out of the cove and into the deep area of the lake. This information combined with the fact that *Pithophora* forms floating mats of filaments suggested that perhaps loss of biomass due to washout was important and that winds blowing from the appropriate direction would enhance the washout effect.

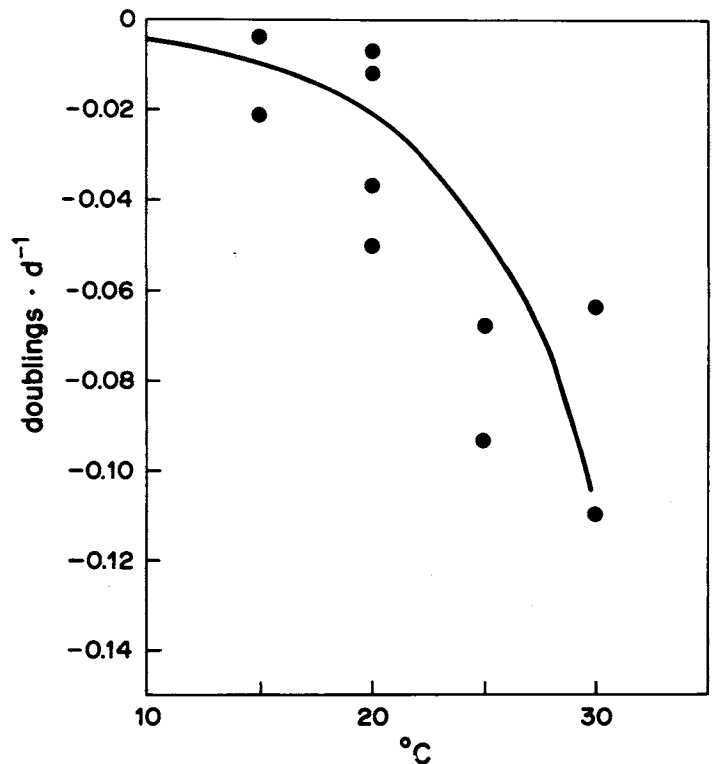


Figure 4. Mortality rate for N-starved, laboratory cultures of *Pithophora* versus temperature.

Washout effects were incorporated into the model by using the Soil Conservation Service runoff equation (USDA, 1975) to calculate the amount of runoff that would result for a given amount of rainfall in the Surrey Lake drainage area. Resultant wind direction and resultant wind speed associated with each 24 h rainfall were examined. If the resultant wind direction was between 170° and 240° , wind was assumed to enhance washout. The degree of washout enhancement was dependent on wind speed. An effective rainfall (RF_e) was calculated based on a derived, linear relationship (Eq. 9).

$$\text{RF}_e = \text{RF} \times (1.0 + (0.2 \times \text{WS}_r)) \quad (10)$$

where: RF = 24 h rainfall (cm),

WS_r = resultant wind speed (mph),

When the resultant wind direction was not within the critical range, the effective rainfall was equal to the 24 h rainfall amount. Cumulative totals (7 d) of RF_e were normalized to 2-yr 24 h rainfall assuming that the highest value measured during the year was the 2-yr 24 h rainfall. A daily average was calculated and divided by the maximum value and the resulting fraction multiplied by the 2-yr 24 h rainfall of 7.6 cm to give the relative effective rainfall during a 1 week interval. The volume of runoff predicted in the watershed was divided by the volume of Surrey Lake and this ratio multiplied by the *Pithophora* biomass to estimate the amount of biomass washed out of the lake.

Model verification and limitations. In order to check the validity of the model, Surrey Lake environmental data from 1979, 1980 and 1981 were used to predict biomass

levels. The model's predictions were compared to measured *Pithophora* biomass for these three years (Fig. 5). The model's predictions in 1979 and 1980 coincided closely with actual biomass. Regressions of predicted biomass levels generated by the model against measured biomass levels in Surrey Lake resulted in coefficients of determination (R^2) of 0.666 for 1979 and 0.368 for 1980. Since the 1979 data were used in the development and initial calibration of the model, the correlation coefficient for this year

is probably inflated relative to the 1980 value. The 1979 predictions accurately show biomass maxima in mid July and late September that were separated by a midsummer decline that followed a heavy rainfall of approximately 10 cm on July 28-29. A similar pattern of *Pithophora* biomass was predicted and observed for 1980. A minor biomass peak occurred in mid July and was followed by a washout in late July that reduced biomass levels. Biomass subsequently recovered and reached the main biomass maxima in late September, 1980. Predicted biomass maxima in both years were within the range monitored in the lake. Furthermore, the model accurately reflects the lower biomass levels achieved in 1980 (under $200 \text{ g}\cdot\text{m}^{-2}$) compared with 1979 (over $200 \text{ g}\cdot\text{m}^{-2}$). This between-year difference appears related to more extensive washout of biomass in May and early June of 1980 (Fig. 6) and higher nitrogen levels in August-September, 1979. It is also apparent that washout of biomass from Surrey Lake is a major factor shaping the annual distribution of biomass and the magnitude of the biomass maxima.

The model did not accurately reflect biomass changes during 1981 (Fig. 5) as indicated by a coefficient of deter-

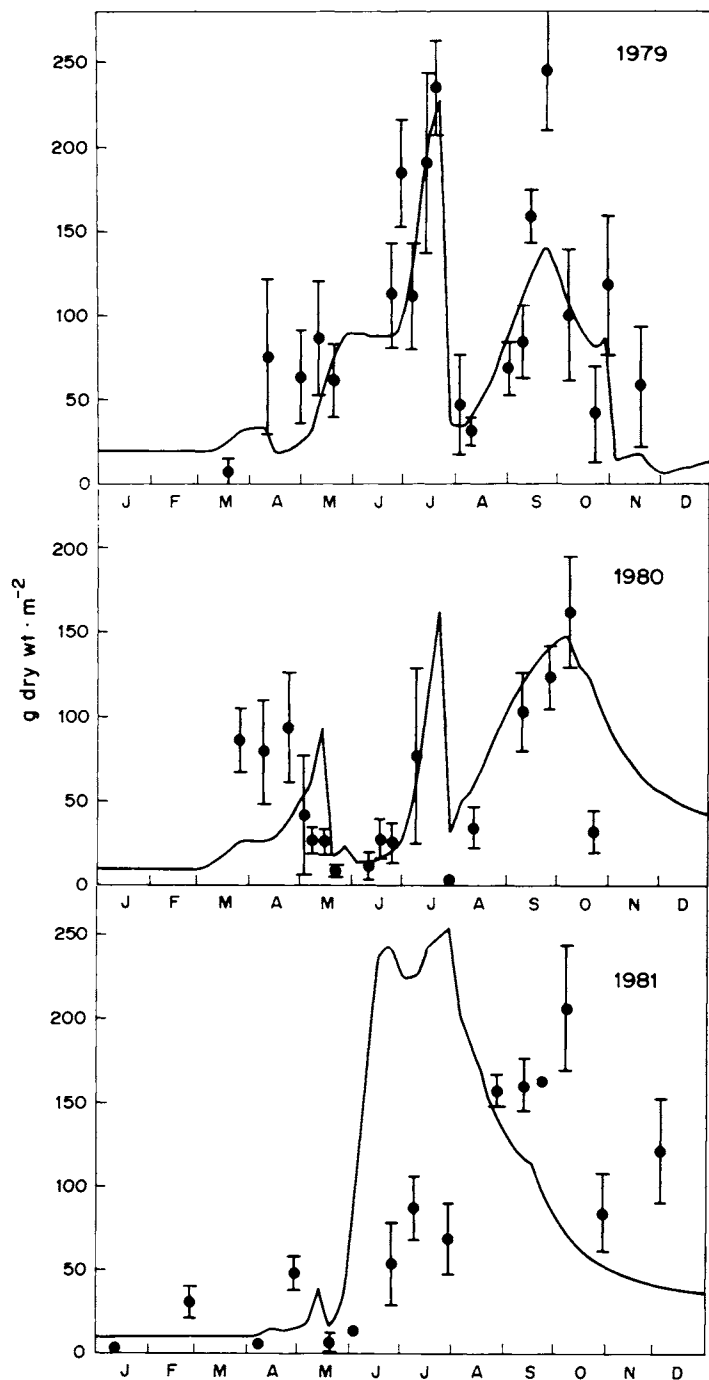


Figure 5. Model estimates (solid line) of *Pithophora* biomass in Surrey Lake during 1979, 1980 and 1981. (●) indicate measured biomass levels in the cove area. Error bars represent 1 standard error.

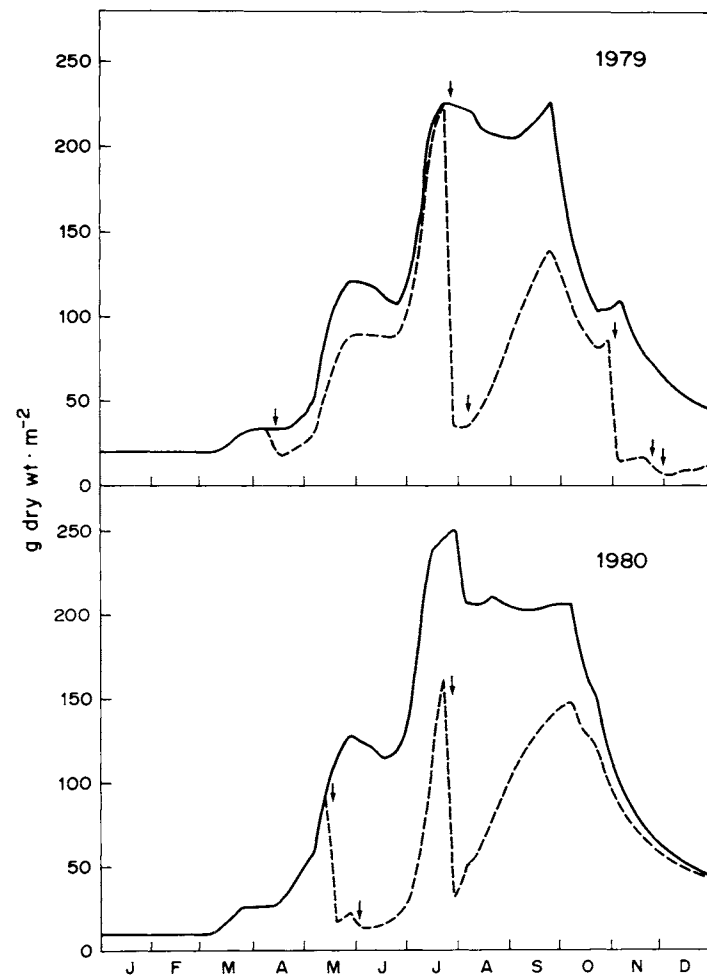


Figure 6. Effect of washout episodes on model estimates of *Pithophora* biomass for 1979 and 1980. Biomass predictions are presented with washout (dashed line) and without washout episodes (solid line). Arrows indicate washout episodes.

mination of 0.004 for regressions of predicted biomass against actual biomass. Sustained growth in Surrey Lake began in June, 1981 and the maxima ($206 \text{ g} \cdot \text{m}^{-2}$) occurred in late September and early October. Model predictions for 1981 indicated rapid biomass increases in May and June with a predicted maximum that extends from early June to mid July. Although the predicted maximum occurred 2 to 3 months prior to the actual biomass maximum, the magnitude predicted ($254 \text{ g} \cdot \text{m}^{-2}$) for the maximum was in relatively good agreement. Nutrient levels and temperatures were conducive for rapid growth early in the growing season in 1981, but actual *Pithophora* growth was much less than model predictions. The delay in actual biomass development is not explained by washout since rainfall was relatively light during the June through August period. However, the washout equation is relatively insensitive when most of the week's rainfall occurs in a brief event (e.g., within a 24 h period). Such intense, short-term rainfalls could produce significant washout but escape detection by the model. In fact, this situation occurred on June 10, 1981 when 6.9 cm of rain fell in a 24 h period. Another possible factor in the delay in actual biomass development in Surrey Lake is the occurrence of blooms of the blue-green alga *Aphanizomenon*. During July, exactly when biomass levels should have peaked according to the model predictions, Surrey Lake developed a heavy *Aphanizomenon* bloom. Blooms of this planktonic blue-green alga were recorded in both 1980 and 1981 and appeared to negatively interact with *Pithophora* photosynthetic metabolism (O'Neal *et al.* 1985). Although the bloom was greater in 1980 than in 1981, its effect may have been less due to masking by simultaneous washouts. By the beginning of September, 1981 the bloom had subsided and accumulation of *Pithophora* was again noted. The allelopathic effects of *Aphanizomenon* and other blue-green bloom formers on chlorophyte species are well documented (Boyd, 1973; Lefevre *et al.* 1950; Tassigny *et al.* 1971). The bloom of *Aphanizomenon* may also have adversely affected *Pithophora* growth through shading and/or competition for nutrients. In addition, the model does not take into account light limitation caused by periods of heavy cloud cover and (or) turbidity resulting from sediment influx. Such light limitation could reduce *Pithophora* growth in Surrey Lake relative to model predictions.

The model predicts a steady decline in biomass from August through October, 1981 when actual biomass was peaking in Surrey Lake. This predicted decline is related to extremely low nitrate concentrations measured during this period. However, fewer nutrient measurements were taken during this period of 1981 than in 1979 and 1980, and model predictions based on them should be viewed with caution. In addition, utilization of internal nitrogen reserves could sustain growth for short periods during which external nitrate was scarce.

Model simulations. Although there are limitations to its use, the model generally provides an accurate assessment of overall growth patterns and biomass maxima of *Pithophora* in the field. The model is also useful in assessing *Pithophora* response to reductions in nutrient concentrations such as might be achieved with a lake management program. Simulations in which either nitrate or total phosphorus were reduced by 50% were executed.

The results (Fig. 7) show that a greater reduction in biomass would result if nitrate were reduced by 50% than for a similar reduction in total phosphorus. Nitrate reduction resulted in predicted biomass decreases of 49% (1979) and 41% (1980) whereas total phosphorus reductions resulted in biomass reductions of only 7% (1979) and 3% (1980). This is in agreement with earlier studies (Spencer and Lembi, 1981) which indicated that nitrate was an important factor limiting the distribution of *Pithophora* in Surrey Lake. The relative insensitivity of *Pithophora* growth to phosphorus limitation appears related to the fact that phosphorus limiting conditions occur during periods when maximum growth rates are severely reduced by low temperatures. As a result, further reductions in growth rate by phosphorus limitation have only a minor impact on predicted biomass levels.

These results suggest that management actions designed to prevent entry of nitrate into Surrey Lake would lead to the greatest decrease in *Pithophora* growth. Nitrate input from the Surrey Lake drainage system could be reduced by replacing the septic tank-finger systems of the residential area with a sewer and by utilizing best management practices such as nitrogen fertilizer injection on sur-

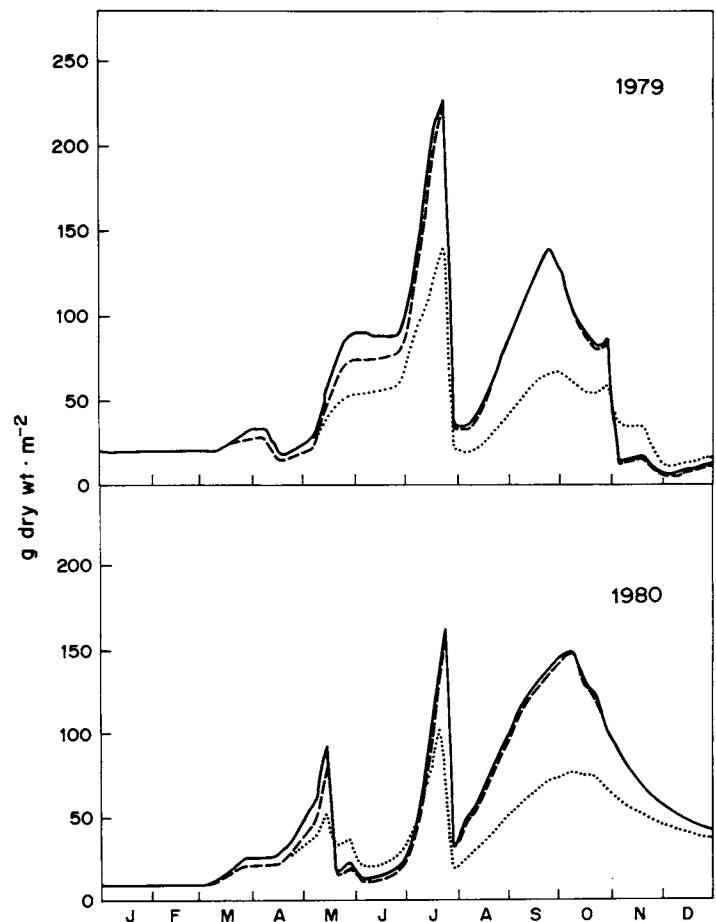


Figure 7. Effect of nutrient reductions on model estimates of *Pithophora* biomass for 1979 and 1980. Nutrient reduction scenarios presented are 1) no reduction (solid line), 2) 50% phosphorus reduction (dashed line), and 3) 50% nitrogen reduction (dotted line).

rounding agricultural lands⁵. In a more general sense, however, the real value of a computer model such as the one described here is that it provides the rationale for considering management strategies other than algicide treatments that, to this point, have been relatively ineffective for the control of this noxious aquatic weed.

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