

Predicted impact of zebra mussel (*Dreissena polymorpha*) invasion on water clarity in Lake Mendota

Tara Reed-Andersen, Stephen R. Carpenter, Dianna K. Padilla, and Richard C. Lathrop

Abstract: Lake Mendota, which is plagued by periodic cyanobacterial blooms, is typical of many lakes in the Laurentian Great Lakes region that are vulnerable to zebra mussels (*Dreissena polymorpha*) but have yet to be invaded. We coupled removal estimates with chlorophyll production estimates in a dynamic model to predict the likely impact of mussel-mediated removal of phytoplankton on water clarity across a range of hypothetical zebra mussel densities. Models were fit to chlorophyll and temperature data collected biweekly from Lake Mendota during 1977–1993. When we assumed daily epilimnetic circulation, the percentage of days when the chlorophyll concentration exceeded $50 \mu\text{g}\cdot\text{L}^{-1}$ was decreased threefold at mussel densities as low as $1000 \text{ mussels}\cdot\text{m}^{-2}$. When we assumed less frequent epilimnetic circulation, the density of mussels required to substantially improve water clarity increased dramatically. We predict that zebra mussel invasion would lead to increased water clarity in Lake Mendota. Cyanobacterial blooms would be reduced but not eliminated. Negative impacts on other lake processes following zebra mussel invasion could outweigh the benefits of lower phytoplankton concentrations.

Résumé : Le lac Mendota, affecté par le fléau des efflorescences périodiques de cyanobactéries, est caractéristique de nombreux lacs de la région des Grands Lacs laurentiens qui sont vulnérables aux moules zébrées (*Dreissena polymorpha*) mais qui n'ont pas encore été envahis par cette espèce. Nous avons jumelé des estimations de l'absorption des cyanobactéries aux estimations de la production de chlorophylle dans un modèle dynamique pour prévoir l'impact probable de l'absorption du phytoplancton par les moules sur la transparence de l'eau à diverses densités hypothétiques de moules zébrées. Les modèles ont été ajustés aux données sur la chlorophylle et la température recueillies toutes les deux semaines dans le lac Mendota, de 1977 à 1993. Lorsque nous avons supposé une circulation épilimnétique quotidienne, le pourcentage de jours où la concentration de chlorophylle dépassait $50 \mu\text{g}\cdot\text{L}^{-1}$ a été trois fois moindre à des densités de moules atteignant à peine $1000 \text{ moules}\cdot\text{m}^{-2}$. Lorsque nous avons supposé une circulation épilimnétique moins fréquente, la densité de moules requises pour augmenter sensiblement la transparence de l'eau a augmenté de façon spectaculaire. Nous sommes d'avis qu'une invasion de moules zébrées augmenterait la transparence de l'eau du lac Mendota. Les efflorescences de cyanobactéries seraient réduites, mais pas éliminées. Des effets négatifs pour d'autres processus lacustres suite à une invasion de moules zébrées pourraient l'emporter sur les avantages d'une réduction des concentrations phytoplanctoniques.

[Traduit par la Rédaction]

Introduction

Since their introduction into North America in the late 1980s (Hebert et al. 1989), zebra mussels (*Dreissena polymorpha*) have spread throughout the Great Lakes region. Factors controlling the ability of zebra mussels to invade lakes include limnological properties such as calcium concentration and pH (Ramcharan et al. 1992) and the presence

of vectors for transport, most commonly recreational boat trailers (Padilla et al. 1996a). While zebra mussels have spread throughout the region, a large number of lakes have yet to be invaded. Lake Mendota serves as an icon for eutrophic lakes not yet invaded. An extensive time series of phytoplankton data make this lake ideal for forecasting the impacts of zebra mussel invasion of eutrophic lakes in the Laurentian Great Lakes region.

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Zebra mussel invasion can cause dramatic changes throughout the ecosystem (Karatayev et al. 1997). For example, zebra mussel populations have resulted in declines in phytoplankton biomass (Caraco et al. 1997), changes in the size structure of zooplankton populations (Pace et al. 1998), and increased growth rates in benthivorous fishes (Karatayev et al. 1997). In addition to the ecological effects, zebra mussels interfere with recreation and navigation by fouling boats, boat docks, buoys, and swimming beaches (Griffiths et al. 1991). In many lakes, chlorophyll concentrations have decreased following zebra mussel invasion (Karatayev et al. 1997). In Europe, managers have introduced zebra mussels into eutrophic ponds to improve water clarity (Reeders and Bij de Vaate 1990).

It is not universally true that lakes with large populations of zebra mussels have lower overall chlorophyll concentrations than would be expected given their phosphorus loads (Mellina et al. 1995). Chlorophyll reductions coincident with zebra mussel invasion may be attributable to other factors such as reduced non-point-source phosphorus emissions (Nicholls 1997). However, zebra mussel clearance rates are high (Sprung 1995) and populations tend to be dense (MacIsaac et al. 1992). Estimates of the potential for phytoplankton removal by zebra mussel populations include reductions of 36% of the primary productivity of Lake Erie (Madenjian 1995) and filtration of water volumes equivalent to Lake St. Clair twice a day (Hebert et al. 1991) or the freshwater estuary of the Hudson River every 2 days (Roditi et al. 1996).

The amount of phytoplankton actually removed from a water body by zebra mussels may be much less than maximum filtering rates would predict because removal rates are directly related to the amount of phytoplankton available (Sprung and Rose 1988). Also, because zebra mussels are stationary in the benthos, the entire phytoplankton population of a lake is not necessarily available for removal. Therefore, circulation patterns can control the amount of phytoplankton delivered to mussels. However, most analyses to date assume thoroughly mixed water bodies.

Lake Mendota has an extensive limnological database. For this study, we have compiled a 16-year time-series of summer temperatures and phytoplankton concentrations (Lathrop and Carpenter 1992; Wisconsin Department of Natural Resources, unpublished data accessible from the North Temperate Lakes Long-Term Ecological Research Project, Madison, Wis.). This database provides a stronger empirical basis for modeling than might otherwise be possible. In addition, Lake Mendota is typical of many lakes in the Laurentian Great Lakes region. Lake Mendota is a eutrophic lake receiving between 15 500 and 67 000 kg phosphorus-year⁻¹ from the surrounding agricultural basin (Lathrop et al. 1998). Ongoing non-point-source pollution reduction efforts are focused on reducing lake phosphorus concentrations, which leads to a reduction in summer blue-green algal densities and improves water clarity (Lathrop et al. 1998). The availability of long-term chlorophyll, temperature, and wind data with which to develop our model makes Lake Mendota an ideal system in which to investigate the potential effects of zebra mussel invasion on stratified, eutrophic lakes.

Lake Mendota is extremely vulnerable to invasion by zebra mussels. The water chemistry could support a dense ze-

bra mussel population (Koutnik and Padilla 1994), and frequent boat traffic between Lake Mendota and infected waters makes it likely that the mussels will invade in the relatively near future (Padilla et al. 1996a). Thus, Lake Mendota offers us an excellent opportunity to make predictions based on our current understanding of zebra mussel physiology and ecology that may later be tested against postinvasion data and may potentially be generalized to a number of similar lakes. By compiling what we know of zebra mussel physiology and ecology into a predictive model, the results of which can be tested postinvasion, we test the completeness of our current knowledge and add to our future predictive capabilities.

We coupled zebra mussel bioenergetics estimates of phytoplankton clearance rates with an empirical phytoplankton growth model to predict the impact of zebra mussels on water clarity, specifically the effects of zebra mussels on the frequency of cyanobacterial blooms. Previous models of zebra mussel impacts have assumed daily mixing of the epilimnion. Although the epilimnion of Lake Mendota is frequently subject to daily mixing, complete mixing may take several days at low wind speeds (Bryson and Ragotzkie 1955). Thus, we investigated the effects of mixing frequency on the phytoplankton removal potential of zebra mussel populations.

Methods and materials

We modeled the impact of zebra mussels on water clarity based on the quantity of phytoplankton that a mussel can remove from the water column, chlorophyll production rate, the number of mussels in the population, and the proportion of phytoplankton available to the mussels at any given time. In Lake Mendota, chlorophyll concentration and water clarity are related. As chlorophyll concentration decreases, light penetration increases (Lathrop and Carpenter 1992). Lake Mendota is relatively large and deep so that, in general, water clarity in the lake is not affected by resuspension of particles from wave action near the shoreline. Therefore, chlorophyll concentration may serve as a surrogate for other particulate matter that influences water clarity. Roditi et al. (1996) have shown that zebra mussels effectively clear all particulates, including phytoplankton and seston, from the water column.

Removal

The total quantity of phytoplankton removed by a zebra mussel population includes both the total amount consumed and the amount not consumed but deposited as pseudofeces. For consumption estimates, we used the consumption component of a zebra mussel bioenergetics model by Schneider (1992). Pseudofeces production was estimated after Madenjian (1995). This method allowed us to model phytoplankton removal by individual mussels within a population as a function of weight, temperature, and seston concentration. These individual estimates could then be summed to model the phytoplankton removal by a zebra mussel population of any given density and size distribution. Zebra mussels close their shells periodically, resulting in active filtration approximately two thirds of the time (Walz 1978). Therefore, consumption and pseudofeces production estimates were multiplied by 0.67 (after Padilla et al. 1996b).

Consumption

The zebra mussel bioenergetics model estimates growth from

consumption minus metabolic and reproductive costs (Schneider 1992). The consumption component of this model is

$$(1) \quad C = a_c W^{b_c} f(T)P$$

where C represents consumption (grams chlorophyll per mussel per day), a_c is the maximum consumption rate (grams chlorophyll per gram mussel per day), W^{b_c} factors in the weight dependence of consumption (with W as the wet weight (grams) of the mussel and b_c as the dimensionless exponent of maximum consumption). The temperature dependence of respiration is included in $f(T)$, and P ranges from 0 to 1 and reflects the proportion of maximum consumption realized (Schneider 1992).

We used values for a_c (0.027 g chlorophyll·g⁻¹ mussel·day⁻¹) and b_c (-0.39) from Madenjian (1995). Because zebra mussels have a linear response to increasing food concentrations up to 1250 µg chlorophyll·L⁻¹ (Sprung and Rose 1988), P was modeled as (chlorophyll concentration)·(maximum removable concentration)⁻¹ (Madenjian 1995). The temperature-dependence function was modeled after Thornton and Lessem (1978) with parameter values taken from Schneider (1992). The function is

$$f(T) = k_a k_b$$

where

$$k_a = \frac{k_1 l_1}{1 + k_1(l_1 - 1)}$$

$$l_1 = e^{g_1(T-Q)}$$

$$g_1 = \frac{1}{T_0 - Q} \ln \frac{0.98(1 - k_1)}{0.02k_1}$$

$$k_b = \frac{k_4 l_2}{1 + k_4(l_2 - 1)}$$

$$l_2 = e^{g_2(T_1 - T)}$$

$$g_2 = \frac{1}{T_1 - T_m} \ln \frac{0.98(1 - k_4)}{0.02k_4}$$

The temperature at each time step is given by T , T_0 (12°C) is the lowest and T_m (21°C) the highest temperature at which consumption is 98% of a_c , T_1 (32°C) is the highest temperature at which consumption is $k_4 a_c$, and Q (2°C) is the lowest temperature at which consumption is $k_1 a_c$. The empirical coefficients k_1 (0.1) and k_4 (0.02) are dimensionless. All parameter values except T are constant for this application.

To run the removal model, we relied on a database of biweekly chlorophyll samples and surface temperature measurements collected during the ice-free season on Mendota from 1977 to 1993 (Lathrop and Carpenter 1992; Wisconsin Department of Natural Resources, unpublished data, data accessible from the North Temperate Lakes Long-Term Ecological Research Project, Madison, Wis.). We set a lower bound on temperature (3°C), below which there was no removal of chlorophyll by zebra mussels. While zebra mussels survive below this temperature, filtering cilia are immobile (Reeders and Bij de Vaate 1990). For an upper thermal threshold, we chose 27°C, above which inhibition of activity has been reported (Karatayev et al. 1998). Temperatures in Lake Mendota during the ice-free season rarely exceed these boundaries. In our 16-year data set, the temperature fell below 3°C on five sampling occasions and above 27°C twice.

Pseudofeces production

By binding phytoplankton in pseudofeces, zebra mussels can remove as much or more chlorophyll than they consume (Walz 1978). We modeled pseudofeces using the proportion

$$Pf = 1.79(1 - e^{(1.346W^{-0.4}(0.247W^{0.4} - P)})}$$

where pseudofeces production is consumption \times Pf (grams per day) (Madenjian 1995). The values for W and P are the same as in the consumption component (see eq. 1).

Chlorophyll production

We used three measures of phytoplankton in Lake Mendota: (i) the amount of standing stock chlorophyll in the lake, (ii) a published estimate of daily summer primary production, and (iii) a phytoplankton growth model fit to Lake Mendota data. Most estimates of the effect of zebra mussel filtration of phytoplankton biomass have used some variant on the first (Hebert et al. 1991; Roditi et al. 1996) or second (Madenjian 1995) measure of phytoplankton abundance. By including the phytoplankton growth model in our analysis, we are able to evaluate zebra mussel impacts on phytoplankton biomass within a dynamic system.

Phytoplankton standing stock

To estimate the standing stock of chlorophyll, we multiplied its concentration by the average volume of lake water in the epilimnion. Chlorophyll concentration was estimated as the mean of samples collected biweekly during the ice-free seasons of 1977–1993 (Lathrop and Carpenter 1992; Wisconsin Department of Natural Resources, unpublished data, data accessible from the North Temperate Lakes Long-Term Ecological Research Project, Madison, Wis.). The average summer epilimnetic depth is 9 m (Soranno 1997) with a volume of 285.6×10^6 m³ (Brock 1985).

Lake Mendota primary productivity

Daily summer primary production in Lake Mendota was taken from Brock (1985) who estimated that production ranged from 0.5 to 6.0 g C fixed·m⁻²·day⁻¹ during the summers of 1979–1981. We converted these production estimates into chlorophyll concentrations using an average ratio of 0.04 g of chlorophyll for every gram of carbon fixed (Reynolds 1984).

Phytoplankton growth

An empirical model for predicting chlorophyll production was fit to the 16 years of ice-free season chlorophyll data from Lake Mendota. The data consisted of chlorophyll samples taken at intervals of 14 ± 2 days and ranged from 1 to 116 µg·L⁻¹ with a mean of 24.8 µg·L⁻¹ and a standard deviation of 19.4 µg·L⁻¹ (Lathrop and Carpenter 1992; Wisconsin Department of Natural Resources, unpublished data, data accessible from the North Temperate Lakes Long-Term Ecological Research Project, Madison, Wis.). Our goal was to find a simple empirical relationship that predicted chlorophyll concentration at each time step with minimal prediction error. To find the best model, we evaluated a family of regression models (Table 1). Because the relationship between chlorophyll sampled at time t and chlorophyll sampled 2 weeks later appeared to be roughly log-linear (Fig. 1), we constructed the models to predict log chlorophyll, denoted A (Table 1). We added a term, $\Delta t A_t$, for the effect of differences in the time between sampling. Density dependence was included as $\Delta t A_t^2$. Lake Mendota experiences a *Daphnia*-driven clearwater phase through the spring (Lathrop et al. 1999). To capture this, we added a dummy variable, D_t , valued at 1 during the clearwater phase and 0 thereafter (*Daphnia* data taken from Lathrop et al. 1999). The most appropriate day for the end of the clearwater phase was determined by fitting

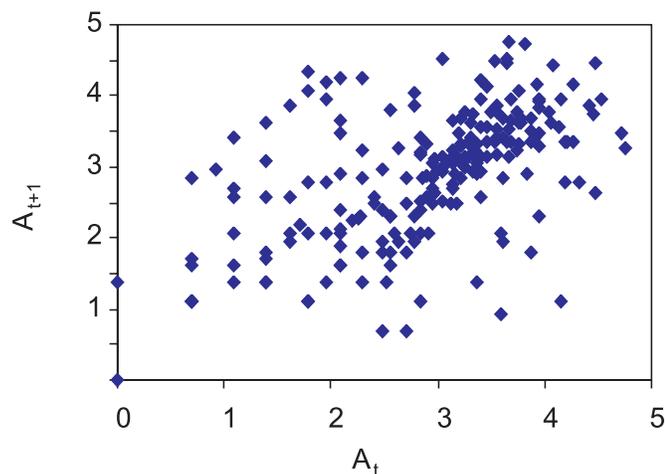
$$A_{t+1} = b_0 + b_1 D_{j,t} + \varepsilon_t$$

Table 1. Family of models evaluated to form the algal growth model.

Model No.	Formula	Negative log likelihood	Log likelihood ratio	AIC	r^2
1	$A_{t+1} = b_0 + \varepsilon_t$	290.96		293	0
2	$A_{t+1} = b_0 + b_1A_t + \varepsilon_t$	274.87	2:1 = 32.17	279	0.290
3	$A_{t+1} = b_0 + b_1A_t + b_2\Delta tA_t + \varepsilon_t$	274.04	3:2 = 1.66	280	0.291
4	$A_{t+1} = b_0 + b_1A_t + b_2\Delta tA_t^2 + \varepsilon_t$	273.09	4:2 = 3.57	279	0.291
5	$A_{t+1} = b_0 + b_1A_t + b_2D_t + \varepsilon_t$	270.92	5:2 = 7.91	277	0.334
6	$A_{t+1} = b_0 + b_1A_t + b_2\Delta tA_t + b_3\Delta tA_t^2 + \varepsilon_t$	273.26	6:3 = 1.56	281	0.291
7	$A_{t+1} = b_0 + b_1A_t + b_2\Delta tA_t + b_3D_t + \varepsilon_t$	270.1	7:3 = 7.88	278	0.334
8	$A_{t+1} = b_0 + b_1A_t + b_2\Delta tA_t^2 + b_3D_t + \varepsilon_t$	270.11	8:4 = 5.95	278	0.337
9	$A_{t+1} = b_0 + b_1A_t + b_2\Delta tA_t + b_3\Delta tA_t^2 + b_4D_t + \varepsilon_t$	269.02	9:6 = 8.48	279	0.339

Note: Models are nested so that each is grown from a "parent" by an additional term. A_t is the natural log of chlorophyll concentration at time t , ΔtA_t represents algal growth between sampling times, ΔtA_t^2 represents density dependence, D_t is a dummy variable for spring grazing by zooplankton, b_i are parameters estimated by maximum likelihood, and ε_t are independent and identically distributed, $N(0, \sigma^2)$. Parameter estimation was done using maximum likelihood. A likelihood ratio of >3.84 (given in bold) implies that the additional parameter is a significant improvement (Hilborn and Mangel 1997). The model that most closely fits the data is indicated by the lowest Akaike information criterion (AIC) value.

Fig. 1. Natural log of chlorophyll concentrations at time t (A_t) versus time $t + 1$ (A_{t+1}) in Lake Mendota during the ice-free seasons of 1977–1993. Data were collected approximately biweekly.

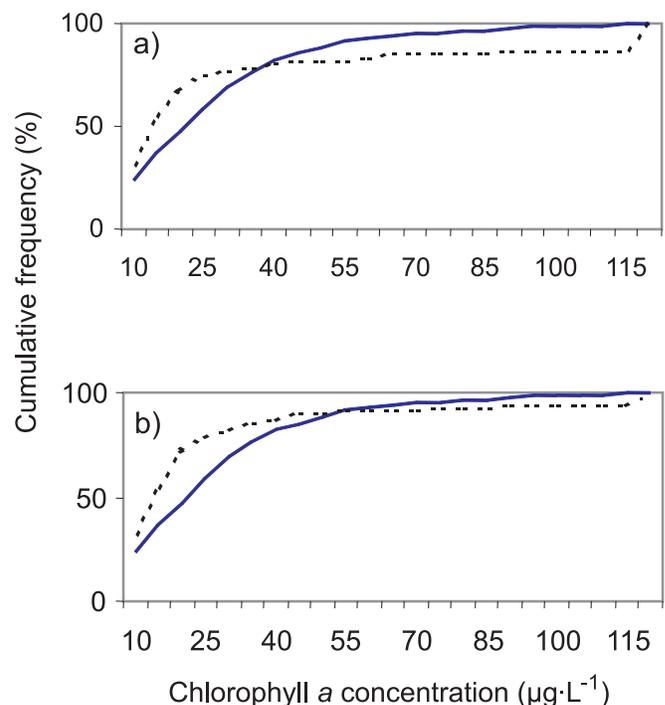


where $D_{j,t}$ is the value of D on day t when day j is the date of the end of the clearwater phase. Errors, ε_t , were normally distributed with mean 0 and homoscedastic variances. We used maximum likelihood for parameter estimation. The negative log likelihood, assuming a normal distribution, was minimized for $j = 143$.

For all models the residuals were approximately normally distributed. Model 1, that A_{t+1} was constant, was rejected on the basis of autocorrelation in the residuals. No other model showed evidence of autocorrelation as indicated by autocorrelation and partial autocorrelation function plots. Models were compared using the negative log likelihood ratio with the null hypothesis that the addition of a parameter did not significantly improve the fit of the model (Hilborn and Mangel 1997). Using this criterion, models 3, 4, and 6 were not significantly better than the next less complicated model (Table 1). As extensions of models 3, 4, and 6, models 7, 8, and 9 were also rejected. Model 5 produced the lowest Akaike information criterion value (Akaike 1973), indicating that it was the best fitting of the alternatives tested (Fig. 2). The distribution of predictions from model 5 fits observations more closely than predictions from model 2 (Kolmogorov–Smirnov statistic = 0.257 for model 5 and 0.281 for model 2).

We generated values for stochastic simulations as $\varepsilon_t = e^{z_t}$, where

Fig. 2. Comparisons of the 1977–1993 data (solid lines) with simulations (dashed lines) based on two chlorophyll growth models for Lake Mendota. (a) Model 2 predicts chlorophyll concentrations at time $t + 1$ from a constant plus chlorophyll concentrations at time t plus a stochastic error term. (b) Model 5 has an additional parameter for zooplankton grazing in the spring.



z_t is a series of independent normal pseudorandom numbers with mean 0 and variance v_t calculated as

$$v_t = \mathbf{x}_t' \mathbf{C} \mathbf{x}_t$$

where \mathbf{C} is the covariance matrix for the parameters of model 5 and \mathbf{x}_t is the predictor vector $[1, A_t, D_t]$ (Draper and Smith 1981). Technically, z_t should follow a Student's t distribution, but because of the large number of degrees of freedom for \mathbf{v} (167), the Student's t distribution is nearly identical with the more easily simulated normal distribution.

When we coupled the removal and production models, we used daily water temperatures interpolated from weekly samples taken in 1987, the year for which we had the most complete data.

Mussel population

The potential for zebra mussels to remove chlorophyll from Lake Mendota would depend on the number of mussels that the lake could support and the size distribution of mussels within that population (Young et al. 1996). We summarized the spatial distribution of substrates using a geographical information system (GIS) to estimate the area available for zebra mussel colonization (Fig. 3).

The size distribution of zebra mussel populations strongly influences the amount of phytoplankton that they remove. Populations dominated by smaller individuals remove substantially less phytoplankton from the water column (Young et al. 1996). We therefore identified two types of substrate in the lake likely to support different zebra mussel population size distributions. Type 1 substrates were sufficiently firm to support a mixed-age population of zebra mussels. Areas identified as type 1 consisted of rock, sand, gravel, and sandy mud (Karatayev et al. 1998). Zebra mussels also settle on macrophytes. However, because the macrophytes die back every year, the plants primarily support small mussels (Karatayev et al. 1998). We identified areas with silt bottoms and dense annual macrophyte growth as type 2 and assigned to them a zebra mussel population dominated by small (<5 mm) mussels. The total area (1100 ha) in these two substrate types was calculated using ARC/INFO (ESRI 1997).

The base coverage for the GIS was digitized from a hydrographic map of Lake Mendota (Eaton 1981). Two surveys were combined to form the sediment coverage used to estimate the area of type 1 substrate in the lake. The first, a sediment survey consisting of 50 cores taken in a 2000-m grid across Lake Mendota, was completed in 1954 (Murray 1956). We compared this with a second survey done in June 1996 to insure that the sediments had not changed substantially. For the 1996 survey, sediments were sampled along six transects around the lake at depths of 0.5, 1, 2, 4, 6, 8, 10, and 12 m. For samples taken from depths of ≤ 6 m, divers removed sediment from within 0.5-m² quadrats to a depth of approximately 10 cm. Ekman dredge samples were taken at water depths of >6 m.

A GIS coverage of macrophyte distribution was compiled from a survey completed in 1995 (Reed-Andersen 1999). Type 2 substrate was identified as the area where macrophytes were found but the substrate was not suitable for direct zebra mussel colonization. Areas where macrophytes were found with substrate that would support zebra mussels were classified as type 1 habitat.

Of the substrate available for zebra mussel colonization, 90% was composed of sand, rocks, and pebbles (type 1). The majority of this area consisted of sand and mud comparable with the substrate populated by zebra mussels in western Lake Erie reported by Berkman et al. (1998). The remaining 10% of available substrate was macrophytes (type 2). In the 1995 macrophyte survey, the most common plant found in these sites was Eurasian water milfoil (*Myriophyllum spicatum*), which was present at 64.5% of the sampling depths at which macrophytes were found (Reed-Andersen 1999). The next most common was coontail (*Ceratophyllum demersum*) at 47.3%. These tall plants could be expected to provide ample settling sites for zebra mussel veligers. The total available habitat including type 1 and 2 substrates was approximately 1 100 000 m², or 27.6% of the lake. Although Berkman et al. (1998) reported small zebra mussel populations on sediments with grain sizes <16 μm , Lake Mendota gyttja has much smaller particles (Brock 1985, p. 55); therefore, it is unlikely to support a mussel population (Karatayev et al. 1998). For each habitat type, mussel size distributions were modeled from mixed-age (type 1) and predominantly young (type 2) populations reported from Saginaw Bay (Nalepa et al. 1995). The predominance of type 1

habitat led to a simulated zebra mussel population of mixed age and a mean length of 13.3 mm.

Circulation

Physical modeling of water circulation in the lake is beyond the scope of this paper. A circulation model for Lake Mendota does not exist. Early studies of water movement in the lake suggest that the epilimnion may circulate completely about every 3 days (Bryson and Ragotzkie 1955). We used this as a crude estimate of the impact of imperfect mixing on the ability of zebra mussels to remove phytoplankton. We assumed that a third of the chlorophyll in the lake would come in contact with the nearshore areas and be available to zebra mussels on any given day. Because information about circulation patterns in Mendota is incomplete, we also evaluated the model at several lake circulation times ranging from 1 to 100 days.

Currents in Lake Mendota are primarily wind driven (Haines and Bryson 1961). In most summers, approximately 95% of the phytoplankton standing crop is cyanobacteria capable of buoyancy control (Lathrop and Carpenter 1992). Cyanobacteria floating on the surface of the water would be unavailable for zebra mussel removal. Soranno (1997) found that cyanobacterial blooms in Lake Mendota in the summer and fall of 1993 occurred on days when the average wind velocity for Madison was <2.68 m·s⁻¹. We modeled this pattern by assuming that only 5% of the chlorophyll was accessible on days when the average wind speed fell below 2.68 m·s⁻¹. The Wisconsin State Climatologist provided daily wind data collected at the Dane County Regional Airport, approximately 3 km from Lake Mendota. Average daily wind speed was calculated as the sum of daily hourly wind speeds divided by 24.

Evaluation of zebra mussel impact on water clarity

We used a three-step process to evaluate the possible impact of zebra mussels on the water clarity of Lake Mendota. We first compared daily estimates of chlorophyll removal with static assessments of the chlorophyll standing stock in Lake Mendota and the estimated primary productivity. We then combined the removal component and the phytoplankton growth component into a single dynamic model so that in each time step, chlorophyll was both removed and produced. Model runs extended from May 1 to October 31 (184 days). Average chlorophyll concentrations in Lake Mendota for this time period ranged from 9.28 to 37.25 $\mu\text{g}\cdot\text{L}^{-1}$. We began each model run with an initial chlorophyll concentration of 30 $\mu\text{g}\cdot\text{L}^{-1}$. Daily temperature values were based on interpolation of 1989 surface temperature values for Lake Mendota. Finally, we modified the dynamic model to account for intermittent circulation. At each postulated zebra mussel density, we ran the model five times for every circulation periodicity (including complete daily circulation).

For all three approaches, we ran the model assuming a range of zebra mussel densities. In North America, local zebra mussel densities can range from 100 to >10 000·m⁻² (Hebert et al. 1989; Mellina et al. 1995). For each density estimate, removal estimates were summed across both substrate types.

Results

A common method for estimating the impact of zebra mussels on a given water body has been to compare potential removal with the average phytoplankton standing stock (e.g., Hebert et al. 1991; Roditi et al. 1996). When we applied this method to Lake Mendota, we found that at densities of >2000 mussels·m⁻², a zebra mussel population could remove an amount of phytoplankton equivalent to the mean lake standing stock (Fig. 4). However, removal of phyto-

Fig. 3. Potential zebra mussel colonization sites within Lake Mendota. Firm substrate (type 1, maximum depth 8 m) could support a mixed-age population. Macrophyte substrate (type 2, maximum depth 4 m) could support a zebra mussel population dominated by small (<5 mm) mussels. Colonization of gyttja is unlikely. Maximum freezing depth rarely exceeds 0.75 m.

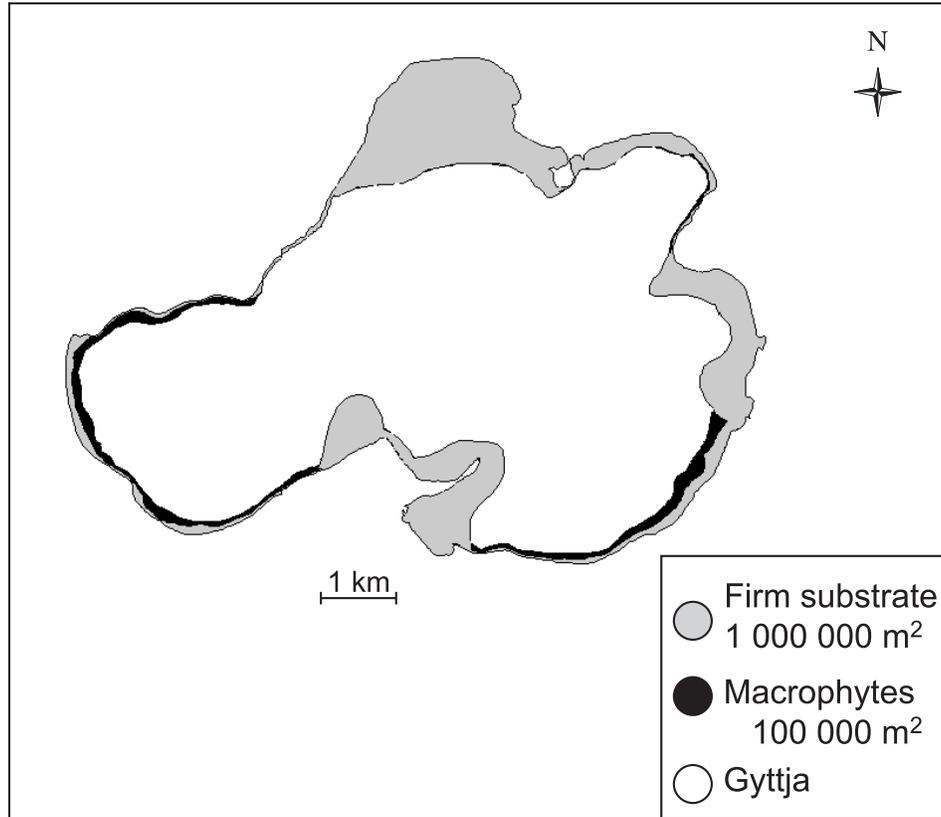
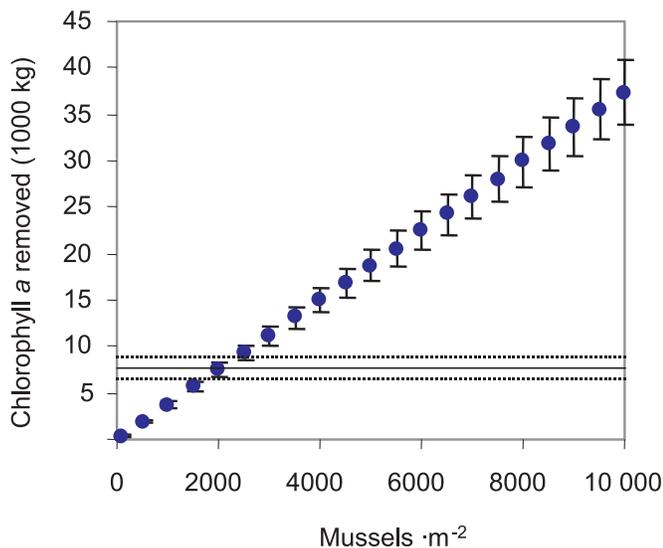


Fig. 4. Chlorophyll removal potential for zebra mussel populations across a range of densities. Points represent the modeled mean and standard error daily chlorophyll removal potential for each mussel density. The lines represent the mean and standard error of whole-lake chlorophyll in Lake Mendota during the ice-free seasons of 1977–1993.



plankton from the water column is only likely to impact water clarity when the amount removed exceeds production.

Therefore, Brock's (1985) estimates of daily production during 1979–1981 were compared with removal estimates generated from the removal component of our model and based on chlorophyll and temperature data from that same period. We found that, within a 2-week period, even at a zebra mussel density of 500 mussels·m⁻², removal potential often exceeded production (Fig. 5). This was particularly true at midsummer temperatures.

We developed the phytoplankton production model to allow us to estimate the relationship between daily removal and production. Model runs with mussel densities of 0 should produce similar frequencies as were found in the data. The production model predicted fewer intermediate values (25–40 µg·L⁻¹) than exist in the data ($r^2 = 0.33$) but fairly accurately predicted the number of days when chlorophyll concentrations exceed 50 µg·L⁻¹ (Fig. 6). Potential bloom conditions exist in Lake Mendota at concentrations exceeding 50 µg·L⁻¹. Therefore, we chose this as the currency for the coupled production and removal model.

When we coupled removal and production, low densities of zebra mussels (100 mussels·m⁻²) did not appear to impact chlorophyll concentrations (Fig. 6). However, moderate densities of zebra mussels (500–1000 mussels·m⁻²) removed enough phytoplankton to reduce the occurrence of chlorophyll concentrations exceeding 50 µg·L⁻¹. At densities of >2000 mussels·m⁻², chlorophyll concentrations rose above 50 µg·L⁻¹ <1% of the time.

When we assumed mixing of the epilimnion every 3 days,

Fig. 5. Comparison of chlorophyll removal and production estimates for Lake Mendota. (a) Brock's (1985) production estimates for the ice-free season in 1979 (circles), 1980 (triangles), and 1981 (squares); (b) removal estimates modeled using temperature and chlorophyll data from the same years.

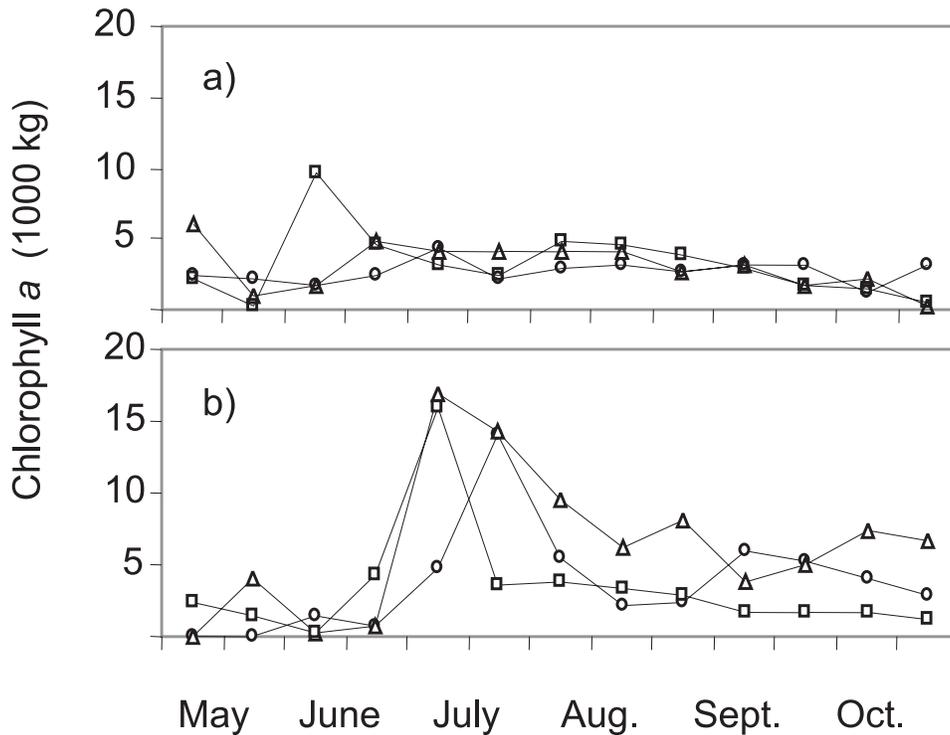
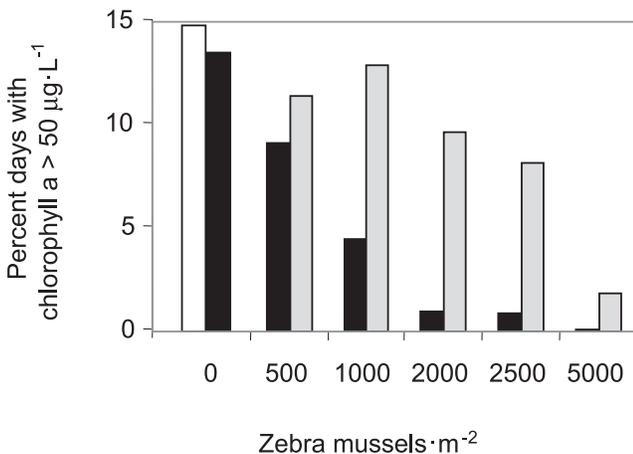


Fig. 6. Results of the coupled removal and production models summarized as the percentage of days when chlorophyll concentrations exceeded $50 \mu\text{g}\cdot\text{L}^{-1}$, indicating a potential cyanobacterial bloom. Solid bars represent model runs assuming daily epilimnetic circulation. Hatched bars represent model runs for which we assumed that each day, 33% of the chlorophyll was available for removal by zebra mussels (circulation time 3 days). For reference, an open bar is presented that summarizes the percentage of days when Lake Mendota chlorophyll concentrations exceeded $50 \mu\text{g}\cdot\text{L}^{-1}$ during the ice-free seasons of 1977–1993.



the mussel density sufficient to impact water clarity substantially increased (Fig. 6). The model assuming complete circulation predicted that a zebra mussel population of $2000\cdot\text{m}^{-2}$ would reduce the number of days when chlorophyll concen-

trations exceeded $50 \mu\text{g}\cdot\text{L}^{-1}$ to $<1\%$. With an epilimnetic circulation period of 3 days, the mussel density required to achieve this reduction was more than twice that required when we assumed complete circulation.

At densities of $<5000 \text{ mussels}\cdot\text{m}^{-2}$, increasing the circulation period to once every 7 days produced results similar to those of the 3-day circulation model (Fig. 7). At higher zebra mussel densities, the percentage of days with chlorophyll concentrations above $50 \mu\text{g}\cdot\text{L}^{-1}$ was greater with circulation every 7 days than with circulation every 3 days. At circulation periods >30 days, even mussel densities of $10\,000\cdot\text{m}^{-2}$ had minimal impact on the frequency of chlorophyll concentrations exceeding $50 \mu\text{g}\cdot\text{L}^{-1}$.

Assuming daily epilimnetic circulation, temporal variability in chlorophyll concentration declined substantially with increased mussel density (Fig. 8). With no zebra mussel predation, the coefficient of variation (CV) was 1.26 ± 0.05 . For the model assuming complete circulation, the mean CV for 5 simulated years decreased from 1.21 at a density of $500 \text{ mussels}\cdot\text{m}^{-2}$ to 0.53 at $5000 \text{ mussels}\cdot\text{m}^{-2}$.

Population density also determined how increasing the circulation period affected the variability of chlorophyll concentration. For a zebra mussel population of $2000 \text{ mussels}\cdot\text{m}^{-2}$, the circulation period had no impact on the variability of chlorophyll concentrations (Fig. 9a). However, with a dense zebra mussel population ($10\,000 \text{ mussels}\cdot\text{m}^{-2}$), variability increased with circulation period, approaching the variability observed with no mussels (Fig. 9b).

Discussion

Most estimates of phytoplankton removal potential have

Fig. 7. Percentage of potential bloom days (chlorophyll $>50 \mu\text{g}\cdot\text{L}^{-1}$) across a range of zebra mussel densities modeled given various circulation periodicities. A circulation time of 100 days indicates that 1% of the chlorophyll was available to the mussels in each time step.

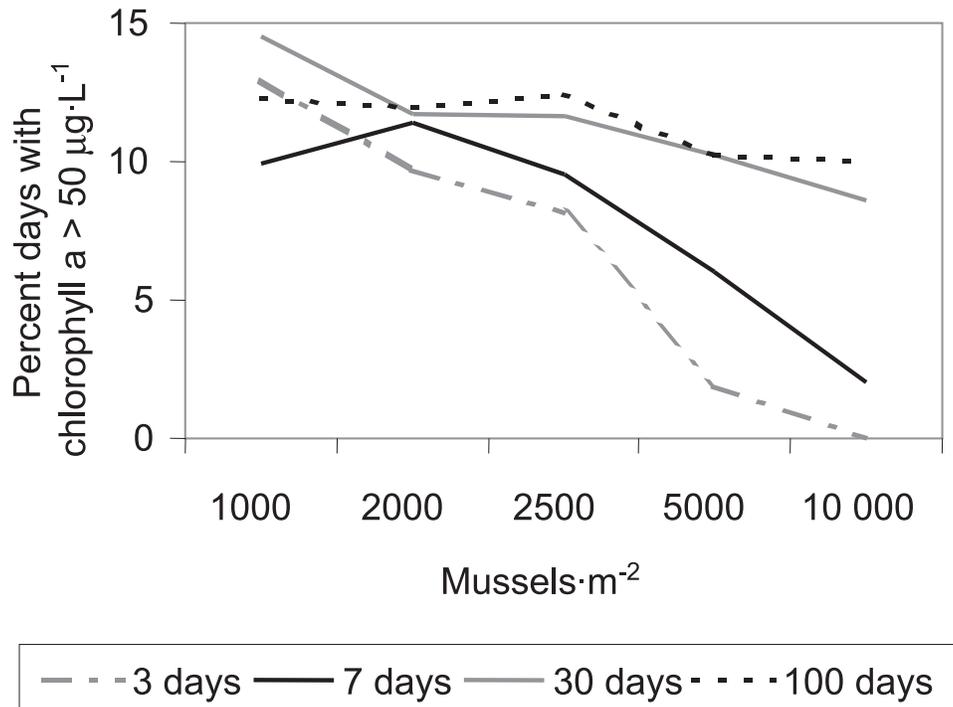
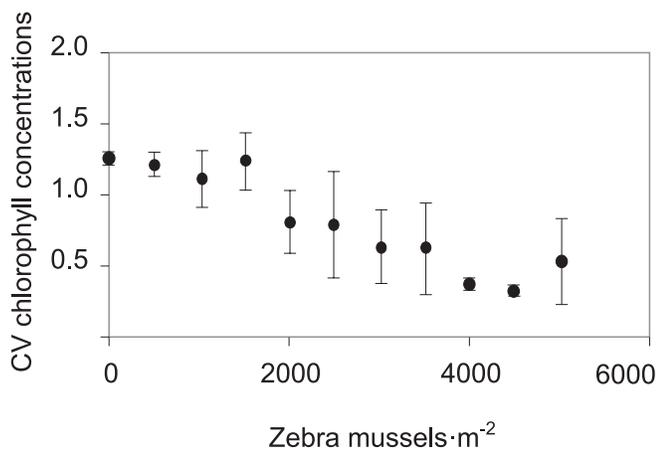


Fig. 8. CV in modeled chlorophyll concentrations at zebra mussel densities of 0–5000 mussels·m⁻², assuming daily circulation of the epilimnion. Data points represent mean CV; error bars are the standard deviation in five simulated years.



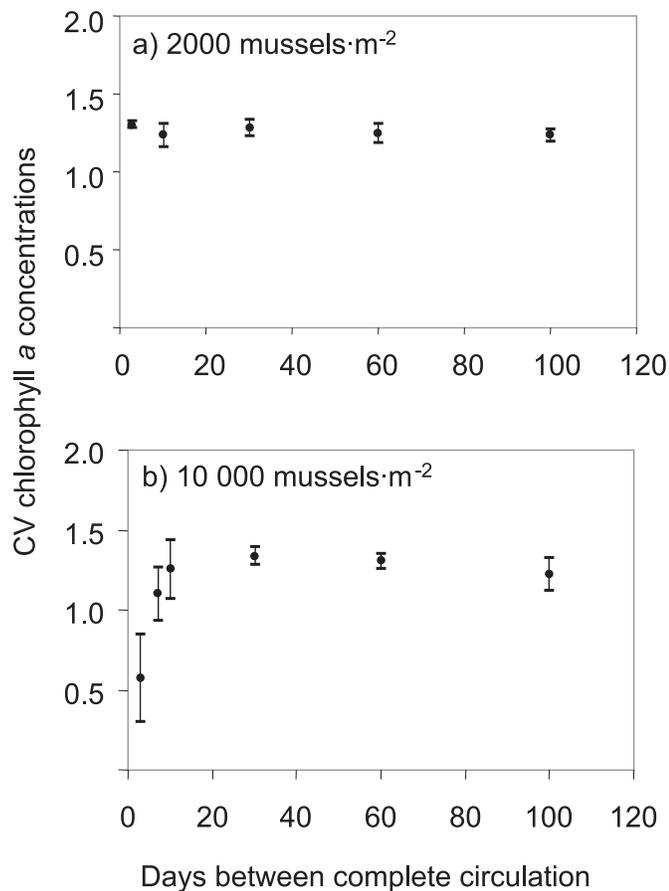
compared removal estimates based on field or laboratory experiments with independent estimates of phytoplankton biomass or primary productivity (Madenjian 1995). These studies indicate that mussel populations are capable of removing a substantial proportion of the chlorophyll. When we use these same techniques to predict zebra mussel impact on Lake Mendota, our results agree. However, when we incorporate daily phytoplankton production in the analysis, we find that while relatively small zebra mussel populations may increase overall water clarity, even dense zebra mussel populations do not remove the possibility of occasional

chlorophyll concentrations high enough to presage cyanobacterial blooms.

By coupling the phytoplankton growth and removal estimates dynamically, we were able to evaluate the potential chlorophyll removal given changes in the chlorophyll concentration at each time step. This calculation approximates natural conditions where, if the mussels remove enough phytoplankton to impact the standing stock on one day, less is available to them the next. This feedback decreased our estimates of the total amount removed. However, because the reductions in chlorophyll concentration were carried over from one day to the next, an impact on phytoplankton production was predicted at lower zebra mussel densities than when we assumed that chlorophyll concentrations remained static. Our simulations indicate that, for a homogeneously mixed lake, substantial reductions in chlorophyll concentrations could occur at densities of around 500 mussels·m⁻². These findings agree with the results of a biomanipulation project involving zebra mussels (Reeders and Bij de Vaate 1990). In three eutrophic lakes, Reeders and Bij de Vaate (1990) found that the density of zebra mussels required to reduce local phytoplankton biomass ranged from 540 to 675 mussels·m⁻².

The removal potential of a zebra mussel population is a function of the prodigious filtering capabilities of zebra mussels. However, this is mediated by the availability of phytoplankton for removal. Therefore, actual removal also depends on wind patterns, currents, and mixing. Because of soft midlake sediments in Lake Mendota, mussels would be restricted to nearshore areas. The impact of intermittent mixing would be to reduce the amount of phytoplankton available for removal. This could create a refuge for cyanobacteria in the deep waters, especially on calm days when improved water clarity inshore could be coupled with

Fig. 9. CV in modeled chlorophyll concentrations across a range of circulation periods for zebra mussel densities of (a) 2000 and (b) 10 000 mussels·m⁻². Data points represent mean CV; error bars are the standard deviation in five simulated years.



midlake cyanobacterial blooms. *Aphanizomenon* bloom periodically in Oneida Lake (Horgan and Mills 1997) despite reduced lake-wide chlorophyll concentrations following zebra mussel invasion (Mellina et al. 1995). Once cyanobacterial blooms occur, mussel populations could be expected to have little impact on water clarity.

In the absence of bloom conditions, zebra mussels could be expected to remove substantial quantities of cyanobacteria. Reeders and Bij de Vaate (1990) found that the filtration rate of the zebra mussels was unaffected by cyanobacterial concentrations. In fact, recent studies indicate that zebra mussels may preferentially remove cyanobacteria (Lavrentyev et al. 1995; Baker et al. 1998; Bastviken et al. 1998). However, zebra mussels are unlikely to entirely remove cyanobacteria from the water column.

The periodicity of epilimnetic mixing has a strong influence on the availability of phytoplankton to mussels, and therefore on water clarity. During extended calm periods, even a dense population of mussels would be unlikely to improve water clarity. In a 3-year study of water circulation in a large bay of Lake Mendota, Bryson and Ragotzkie (1955) found that water replacement frequently required less than a day. However, they also reported replacement times of 5 and 28 days. We expect therefore that invasion of zebra mussels into Lake Mendota could lead to periods of both increased

water clarity and severe midlake blooms. For lakes, studies that assume complete daily mixing of the water body may overestimate the actual potential of zebra mussel populations to remove phytoplankton. It is important to note that chlorophyll concentrations consistent with bloom conditions were not entirely absent in any simulations.

Following zebra mussel invasion, other impacts on the lake could easily outweigh any benefits to water clarity. Because buoyancy gives cyanobacteria a refuge from zebra mussel predation, these undesirable phytoplankton would be least impacted. During blooms, selective predation by mussels could lead to an even greater dominance of cyanobacteria in Lake Mendota. In addition, lower chlorophyll concentrations in the pelagic zone could have unexpected consequences for the food web.

In other systems, both available phosphorus and light penetration have increased following zebra mussel invasion (Caraco et al. 1997). Increased light and nutrient availability would lead to greater phytoplankton production and could increase the probability of cyanobacterial blooms. It is interesting to note that zebra mussels thrive in oligotrophic and mesotrophic lakes but are less abundant in extremely eutrophic systems (Karatayev et al. 1998). One of the ironies of zebra mussel invasion could be that increases in water clarity would undermine popular support for reduction of non-point-source pollution. Yet, in the long term, the ongoing management efforts aimed at reducing non-point-source phosphorus pollution are likely to provide a more sustainable solution for reducing nuisance blooms in eutrophied lakes.

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