Impact of zebra mussel (*Dreissena polymorpha*) on phosphorus cycling and chlorophyll in lakes

**Eric Mellina, Joseph B. Rasmussen, and Edward L. Mills**

**Abstract:** We determined the effects of zebra mussel (*Dreissena polymorpha*) on water column phosphorus (P) and chlorophyll a levels and algal community size structure as well as rates of P excretion in laboratory experiments. Zebra mussel at a threshold density of 0.25/L were able to decouple the nutrient-chlorophyll relationship, to induce erratic patterns in P and chlorophyll a trends, and to decrease mean algal cell sizes. Using shell length we explained 75 and 71% of the variability in P excretion rates in trials held at 17 and 22°C. Using mass balance modeling, we examined the effects of zebra mussel growth and mortality on mean annual steady-state P levels as functions of hydraulic flushing and P loadings for the western basin of Lake Erie, for Lake St. Clair, and for Oneida Lake. Zebra mussel affected water column P levels only when the annual P accumulated into mussel biomass represented >20% of the lake's annual P loading. The mussel populations in all three lakes did not substantially affect water column P levels but decoupling of the nutrient-chlorophyll relationship was observed in lakes Erie and St. Clair. No evidence was found for increased decoupling of this relationship with increasing zebra mussel density in European lakes.

**Résumé:** Nous avons déterminé les effets de la moule zébrée (*Dreissena polymorpha*) sur les niveaux du phosphate (P) et de la chlorophylle a dans la colonne d'eau et la taille des communautés algales ainsi que sur les taux d'excrétion du P au cours d’expériences en laboratoire. A une densité seuil de 0.25/L, la moule zébrée a pu défaire la relation nutriments-chlorophylle, donner lieu à des variations erratiques des tendances du P et de la chlorophylle a et causer une diminution de la taille moyenne des communautés algales. En prenant la longueur moyenne des coquilles, nous sommes parvenus à expliquer 75 et 71% de la variabilité des taux d’excrétion du P au cours d’essais qui se sont déroulés à 17 et à 22°C. Grâce à la modélisation des bilans de masse, nous avons examiné les effets de la croissance et de la mortalité de la moule zébrée sur la concentration moyenne annuelle de P à l’état stable, en fonction de la chasse hydraulique et de la charge en P dans le bassin ouest du lac Érié et dans les lacs St. Clair et Oneida. La moule a exercé un effet sur la concentration du P trouvé dans la colonne d’eau seulement lorsque la quantité annuelle de P accumulée dans la biomasse de la moule était supérieure à 20% de la charge annuelle en P dans le lac. Dans les trois lacs, les populations de moules n’ont aucun effet substantiel sur la concentration du P dans la colonne d’eau; cependant, nous avons observé le biais de la relation nutriments-chlorophylle dans les lacs Érié et St. Clair. Nous n’avons trouvé aucune trace de ce phénomène dans les lacs d’Europe en fonction de la densité croissante de la moule zébrée.

[Traduit par la Rédaction]

**Introduction**

The recent introduction of the zebra mussel (*Dreissena polymorpha*) into North American waters (Hebert et al. 1989) has fueled much speculation concerning the mussel’s potential impact in rivers and lakes. Economically, industries that use raw water are known to incur staggering clean-up costs because of the mussel (Kovalak et al. 1993; Lepage 1993), but ecologically the mussel’s long-term impacts have only begun to be studied on this continent. Calcium and substrate suitability limit zebra mussel distribution and density (Ramcharan et al. 1992; Mellina and Rasmussen 1994), and the substantial cumulative filtration impact of large zebra mussel populations may be
responsible for local depletions of algal concentrations over densely populated reefs is Lake Erie (Mclsaac et al. 1992; Hunt et al. 1995; Mohamed et al. 1994). Increases in native unionid mortality (Hunter and Bailey 1992; Haag et al. 1993; Nalepa 1994; Schloesser and Nalepa 1994) as well as changes in the benthic fauna of Lake St. Clair (Griffiths 1993) have also been attributed to the arrival of the zebra mussel. However, the potential impact of the zebra mussel on nutri- ent cycles has been less well studied. Benthic invertebrates are important agents of nutrient cycling in lakes (Kuenzler 1961; Andersen et al. 1988; Lambers and Moeley 1988), and filter feeders in particular (when present in sufficient numbers) have the potential to remove large amounts of particulate matter from the water column and to deposit these in the form of feces and pseudofeces (Stanczykowska and Planter 1985; Nalepa et al. 1991). Some authors (Reeder and Bij de Vaate 1990; Hebert et al. ’96; Mackie 1991; Mclsaac et al. 1992; Griffiths 1993; Leach 1993) have proposed that a reduction in water column nutrient levels may occur as a result of the zebra mussel’s efficient filter feeding activities redirecting energy from the pelagic to benthic zones.

The goal of the present study was to examine the effects of zebra mussel on phosphorus (P) cycling and phytoplankton dynamics in lakes, and to examine the evidence supporting the generality of these effects. Because dense zebra mussel colonies have been reported to increase water clarity and decrease algal concentrations (Hebert et al. 1991; Reeder et al. 1989; Mclsaac et al. 1992; Griffiths 1993; Leach 1993), we advance two alternative hypotheses regarding possible mechanisms for any observed algal reactions and test these with data from experiments and from the literature. We examine whether such clearing effects, when they occur, are more likely to result from (i) a top-down mechanism or (ii) a bottom-up mechanism. With a top-down mechanism, zebra mussel would affect algal levels directly through grazing pressures that would exceed phytoplankton growth, leading to increased water clarity (without reducing nutrient levels) and ultimately resulting in a decoupling of the nutrient-phytoplankton relationship. To assess decoupling we compared P and chloro- phyll a (chl a) estimates with the Dillon and Riger (1974) P - chl a relationship, which predicts chl a levels for a given concentration of P. The P - chl a relationship assumes that P is the limiting nutrient, and departures from the relationship imply that P has been replaced by alternative limiting factors such as grazing pressure (Kaiser et al. 1994). By contrast, the bottom-up mechanism suggests that zebra mussel would affect nutrient levels directly through the incorporation of phytoplankton nutrients into mussel biomass. Thus, filtration would result in a reduction in steady-state water column P concentrations and indirectly lead to increased water clarity through a concomitant decrease in algal levels. The P - chl a relationship would therefore not be decoupled because a decrease in chl a would be consistent with any reduction in nutrients, as verified by the Dillon-Riger relationship.

Two experiments in laboratory microcosms were designed to determine (i) the effects of increasing zebra mussel densities on P and chl a levels and on algal community size structures and (ii) rates of zebra mussel P excretion. The first experiment allowed us to examine water clearance and nutrient-phytoplankton coupling (top-down mecha- nism) in tanks using zebra mussel at densities encountered in lakes on a volumetric basis, as well as helping to determine the threshold mussel density required for decoupling to take place. The second experiment allowed us to evaluate zebra mussel P excretion rates and to deter- mine the relative importance of excretion in comparison with other compartments of mussel population’s P budget (such as P accumulation into growth and gametes, and P biodeposition). Furthermore, we examined the effects of a growing zebra mussel population on mean annual steady-state P levels as a function of hydraulic flushing and P loadings for the western basin of Lake Erie, for Lake St. Clair, and for Oneida Lake, New York. The three lakes are well mixed (Nils et al. 1978; Scherrer et al. 1987; Leach 1991), but differ in their hydrology, morphology, and water chem- istry budgets: this allowed us to examine the effects of zebra mussel on P dynamics over a range of conditions. For each lake, we developed simple P mass balance mod- els to predict how much of a reduction in P levels would be expected because of zebra mussel growth, and compared our predictions with data from the literature. Using published filtration estimates, we also calculated the cumulative fil- tration impacts of local zebra mussel populations and com- pared these with algal growth rates to determine if mussel filtration could account for any observed depletions in chl a levels. Finally, we examined P and chl a estimates from European lakes (with zebra mussel densities span- ning three orders of magnitude) relative to the Dillon- Riger line, and determined whether or not chlorophyll reductions and decoupling increased with increasing mussel density.

Materials and methods
Tank experiment on phosphorus and chlorophyll a dynamics
To determine the effects of increasing zebra mussel density on P and chl a (whether top-down or bottom-up mecha- nisms were operating) and whether we could predict the densities required to induce decoupling of the P - chl a relationship using filtration and algal growth rates, we conducted an experiment (henceforth called the tank experi- ment) using 40-L aquaria as laboratory microcosms. Approximately 200 adult zebra mussels were collected from Lake St. Francis, Ontario (45°07’00”N, 74°26’49”W), along the St. Lawrence River in September 1992 and were kept in three 50-L stock tanks. They were fed daily on an algal culture dominated by Scenedesmus spp. and Chlamy- domonas spp., and the tanks were emptied and refilled every 4 days to ensure low levels of ammonia. Dead mus- sels were removed as soon as they were discovered. All zebra mussel were acclimated to aquarium conditions for 6 months prior to use in the experiment. At the start of the experiment, 40-L aquaria were filled with dechlorinated tap water containing the same algal culture used to feed the mussels. Total phosphorus (TP) levels were adjusted by adding NaH2PO4 to attain a
<table>
<thead>
<tr>
<th>Lake</th>
<th>Volume (km²)</th>
<th>Area (km²)</th>
<th>Mean depth (m)</th>
<th>p (yr⁻¹)</th>
<th>Water input (km³/yr)</th>
<th>Annual TP load (kg/yr)</th>
<th>TP input concentration (P₀, mg/m³)</th>
<th>TP input on area basis (mg m⁻² yr⁻¹)</th>
<th>K (m³/yr)</th>
<th>Loss of P to outflow (P₁P₀, %)</th>
<th>Loss of P to sedimentation (1− K P₀, %)</th>
<th>Preinvasion steady-state [TP] (mg/m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>St. Clair</td>
<td>3.4</td>
<td>11.2</td>
<td>3.3</td>
<td>4.0</td>
<td>140</td>
<td>3330 (117) (1975–1980)</td>
<td>25</td>
<td>3350</td>
<td>0</td>
<td>100</td>
<td>0</td>
<td>25 (9.3) (1973–1975)</td>
</tr>
</tbody>
</table>

Note: Values in parentheses beside estimates are standard errors. p, reciprocal of mean residence time; P₀ and P₁, phosphorus concentration in the water and the mean weighted average P-concentration in the drainage and atmospheric inputs, respectively; K, sedimentation coefficient.

Data from Burns (1978).

Data from Nicholls and Hopkins (1993) and D.M. Dolan, International Joint Commission, 100 Ouellette Ave., Windsor, ON N9A 6T3, Canada (unpublished data).

Data from R. Holland, Department of Atmospheric, Oceanic, and Space Sciences, Ann Arbor, MI 48109-2143 (unpublished data), LeShi et al. (1991), J.H. Leach, Ontario Ministry of Natural Resources, Lake Erie Fisheries Station, Wheatley, ON N0P 2B0 (unpublished data), and Rockwell et al. (1989).

Data from Mills et al. (1978).

Value calculated using mean preinvasion steady-state TP concentrations for 1989–1991 (see text for explanation).

Data from Leach (1991).

Data from Lang et al. (1988).

Data from Herbold et al. (1986).
starting concentration of 50 μg/L, while NaN₃ was added at a N:P ratio of 15:1 by weight to prevent a shift to N limitation. Each aquarium was aerated with an air stone to provide oxygen and mixing, and each was lit by a single 100-W light bulb set on a 16-h light:8-h dark cycle to simulate summer conditions. Daily losses owing to evaporation were corrected by adding distilled water to the 40-L mark.

We began the experiment in March 1992 by placing different mussel densities (2, 5, 10, 20, and 40 mussels/tank) in five of the aquaria; a sixth tank with no mussels served as a control. These mussel densities were chosen to be well within the range of those encountered in the field on a volumetric basis (0.05–1 mussel/L). The mussels were all between 20 and 25 mm, and most individuals were observed actively filtering within 2–3 h of the start of the experiment. Each day for 21 days 1 L of water was siphoned from each tank and replaced with 1 L of dechlorinated tap water containing 50 μg P to simulate an inflow-outflow situation with a water residence time of 40 days. This P turnover and hydraulic regime was within the range of estimates for the western basin of Lake Erie and for Lake St. Clair (Table 1). From the litre of water we removed, duplicate subsamples were taken for TP and chl a analyses according to the methods of Griesbach and Peters (1991) and Bergman and Peters (1980), respectively. Water temperatures in each tank ranged from 21 to 22°C, and each tank was checked daily for mussel activity. Over the course of the experiment, only three mussels died and these were removed and replaced with fresh individuals from the stock tanks. Observed daily total P (TP) and chl a levels (both measured in milligrams per cubic metre) were plotted relative to the Dillon-Rigler (1974) relationship (log₂ chl a = 1.449 log₂ TP – 1.136) to examine if decoupling had occurred. We attempted to quantify decoupling of the nutrient–chlorophyll relationship by comparing mean observed chl a levels with mean predicted values within each tank. Predicted chl a values were calculated using observed TP data and the Dillon and Rigler (1974) relationship. Significant departures between observed and predicted values were interpreted as evidence that decoupling had taken place.

At the end of the experiment, an aliquot was removed from the center of each aquarium and run through a Coulter counter to generate size-class distributions of the algae present. The mean algal cell size of the control tank was compared with that of each of the remaining tanks using Bonferroni–corrected t-tests to determine whether mussel density (and therefore filtration) had an effect on the algal community size structure.

**Phosphorus excretion rates.**

To gain a more complete picture of the overall P flux through a zebra mussel population, P excretion rates were estimated in a series of laboratory experiments. Mussels were collected fresh before each experiment using self-contained underwater breathing apparatus (SCUBA) from Oneida Lake, a moderately eutrophic freshwater lake situated in upper New York state (Fig. 1), in late August 1993, and from Lake St. Francis, Ontario, in late September 1993. These two locations were chosen to determine whether P excretion rates differed between water bodies. A total of six P excretion experiments were conducted, four using mussels from Oneida Lake and two using mussels from the St. Lawrence River, with each experiment comprising two temperature trials: 17°C approximated the in situ water temperature, while 22°C was used to determine if temperature had an effect on P excretion.

Rocks were collected from a depth of approximately 8 m and taken to the laboratory in buckets containing lake or river water, and mussels were carefully detached and sorted into five size-classes: 0–5, 5–10, 10–15, 15–20, and 20+ mm. For each temperature trial, 13 zebra mussel (2 from each of the two smaller size-classes and 3 from each of the remaining classes) were randomly chosen and carefully scrubbed with a soft toothbrush and then rinsed to remove any attached algae on the shells. Each mussel was immersed in a sealed, 500-mL acid-washed flask (250 mL for the smaller size-classes) containing filtered (Whatman GF/C) lake or river water taken from the same site where the mussels were collected. Two control flasks containing filtered water without mussels were also used during each trial. Flasks were randomly immersed in a water bath to maintain constant temperature. The Cornell Biological Field Station borders Oneida Lake and provided quick access to laboratory facilities, while mussels collected from Lake St. Francis had to be returned to Montreal. The elapsed time between mussel collection and the start of each experiment was approximately 1 h for Oneida Lake and 3 h for Lake St. Francis.

After mussel immersion, 40 mL of water was extracted from each flask into an acid-washed 65-mL capacity Kimax® band culture tube (Fisher Scientific) and then refrigerated for later TP analysis. This was repeated 12 h later after each flask was swirled to ensure that the water was completely mixed. Mussels were checked periodically for extended siphons as a measure of activity, and those without extended siphons were removed from the experiment. The flasks were not aerated because we did not want to disturb the mussels; the short duration of each experiment (12 h) ensured that oxygen depletion would not be a problem. Water samples were analyzed for TP following the ascorbic acid method described by Griesbach and Peters (1991), and P excretion rates were expressed as the difference in TP concentrations over 12 h between flasks containing mussels and control flasks. At the termination of each experiment, the mean algal cell size of the control tank was compared with that of each of the remaining tanks using Bonferroni–corrected t-tests to determine whether mussel density (and therefore filtration) had an effect on the algal community size structure.
Phosphorus mass balance models
To examine the effects of a growing zebra mussel population on mean annual steady-state P concentrations, we examined three lakes differing in their water residence times and annual P loadings: the western basin of Lake Erie, Lake St. Clair, and Oneida Lake (Table 1). Wherever possible, P loading data and steady-state P concentrations were averaged across different studies to gain a more representative picture of P dynamics on a yearly basis. Data ranges for pre- and post-invasion periods were restricted to 3 yr each and were chosen to be as close as possible to the year marking the zebra mussel’s discovery. For Lake St. Clair, we were only able to find published presimulation P loading and water concentration data for the years 1975–1980 and 1973–1975, respectively (Table 1), and used the mDrange steady-state TP concentration for the postinvasion years 1992–1993 (D. MacLean, Lake St. Clair Fisheries Assessment Unit, Tilbury, ON N8P 2L0, unpublished data). P loading data were not separated into pre- and post-invasion periods because we were unable to find post-invasion data for Lake St. Clair and for Oneida Lake, and because the difference in Lake Erie’s P loadings for these two periods was less than 3% (6693 metric tons (1944–1966 versus 6852 t/year for 1990–1991; Nichols and Hopkins 1993; D. M. Dohn, International Joint Commission, 100 Ouettele Avenue, Windsor, ON N9A 6T3, personal communication) and would have had negligible effects on our predictions. Following Chapra and heck (1983), we used a first-order differential equation representing changes in the lake’s P concentration as a function of losses (o) and loadings (W):

\[ \frac{d[P]{tslash{h}}}{dt} = W{tslash{h}} - o{tslash{h}} \]

where W is the P loadings (milligrams per year), V is the lake volume (cubic meters), and P is the phosphorus concentration in the water (milligrams per cubic meter). o combines the loss of P through the outflow (QIV where Q is the total water load in cubic meters per year) and sedimentation (K{tslash{h}}; meters per year) so that

\[ \frac{d[P]V}{dt} = W{V} - K{P}V - QIV \]

where V is the lake mean depth (in meters). By substituting QIV = o (p is the reciprocal of mean residence time) and \( W{V} = p{P} \) (P is the mean weighted average P concentration in the drainage and atmospheric inputs) we arrived at

\[ \frac{d[P]}{dt} = p{P} - K{P}V = -o{P} \]

Several assumptions were made in deriving eq. 3. For the three lakes in our study the relatively short residence times (9–228 days) and well-mixed, oxygenated waters led us to assume that sedimentation of P would greatly exceed the return rate leached from the sediments, and we therefore treated P sedimentation as essentially a one-way downward process. This assumption is well supported by Burn (1976) for the western basin of Lake Erie and Lang et al. (1988) for Lake St. Clair, and the similarity of the hydrological processes to those in Lake Erie led us to extend the assumption of net sedimentation to Oneida Lake. Because we were looking at changes in the nutrient pool on a yearly basis, we also assumed that the volume of the lake over this period remained constant. We made the final assumption that the average P concentration in the water over the whole year remained constant, and that therefore \( d[P]{ht} = 0 \). This allowed for the removal of the differential term of eq. 3 and further simplification to

\[ P = \frac{operative P}{P} \]

Solving for K (the sedimentation coefficient; meters per year) we arrived at

\[ K = \frac{operative P}{P} \]

The fraction of the nutrient input that is lost through the outflow is

\[ \frac{P}{P} \]

while the fraction retained through sedimentation is

\[ 1 - \frac{P}{P} \]

The input concentration of phosphorus (\( P{I} \)) into the lake was calculated as

\[ P{I} = \frac{operative P}{water input (m3/yr)} \]

while the annual P input on an areal basis was calculated as

\[ P = \frac{mg\cdot m^{-2}·yr^{-1}}{P} = P{I} \times \frac{mg/m^3}{water input (m3/yr)} \times \frac{m}{z} \times \frac{m}{m} \]

Water input to the lake was calculated as

\[ water input (m3/yr) = \frac{volume (m3)}{\times \frac{m}{m} \times \frac{m}{z}} \]

While P loading data for the western basins of Lake Erie and Lake St. Clair were compiled from the literature, we were unable to find any recently published P loading data (which are needed to calculate \( P{I} \)) for Oneida Lake. Because zebra mussel were first discovered in Oneida Lake in 1991 (E.L. Mills, personal observation), we used the average yearly P concentration from 1987 to 1991 (data collected approximately once per week by staff at the Cornell Biological Field Station during the May–November growing season) as the steady-state P concentration (\( P \)) in eq. 6; to back calculate \( P{I} \) we assumed that losses of P owing to sedimentation had remained at the 1970s level of 62% of the input loadings (Greense 1971, cited in Mills et al. 1978).

To estimate the annual areal loss of P removed from the water column and incorporated into zebra mussel growth (soft tissue and shell), we first calculated a mean annual increase in zebra mussel density. This was done by averaging densities (for a given year) over the entire lake for each
of the three water bodies and averaging the differences in lake densities between successive years. For Omete Lake, mean lake-wide estimates were obtained from 9 sites in 1992 and 10 in 1993 over both hard and soft substrates (Fig. 1) using CSMRA and a randomly placed m- mesh quadrate. Rocks and boulders with zebra mussel from three replicate quadrats at each site were collected for sorting and counting. For Lake St. Clair, density estimates for 1988–1991 were gathered from the literature (Hebert et al. 1991; Hunter and Bailey 1992; Griffiths 1993; Nalepa et al. 1993) over a variety of hard and soft substrates and were assumed to be representative of lake-wide means. For the western basin of Lake Erie, density data over local reefs were compiled for 1989 and 1993. For Lake St. Clair and Haag 1993; Leach 1993) and converted to basin-wide densities by assuming that the reefs occupied 15% of the basin area (Harmantas 1973, cited in Maelseea et al. 1992). Next, the mean annual increase in zebra mussel density for each lake was converted to total biomass (dry weight of soft tissue) per unit area (milligrams dry weight per square meter per year) using the equation

\[ \text{total biomass} = \sum_{i} \left( \text{density} \times \text{weight} \right) \]

where \( i \) is the shell length, 1–4 mm, depending on the number of size-classes present in the frequency distribution used and published size-frequency distributions and length-weight regressions for Lake St. Clair (Hebert et al. 1991; Nalepa et al. 1993) and for Lake Erie (Butt et al. 1976; Clark and Lea 1976; Clark and Lea 1977; Nalepa and Riisgard 1988). Size-frequency distributions and length-weight regressions for Omede Lake were compiled using data from this study. For each lake the total biomass was then converted to an annual P accumulation into zebra mussel growth (\( \Omega \); milligrams P per square metre per year) by assuming a 15% P content by dry weight for soft tissue (Stanczykowska and Prayer 1985; Mills et al. 1993; Secor et al. 1993). The P content of shells was included by adding a P content of dry tissue (Stanczykowska and Prayer 1985). To predict the new steady-state P concentration (\( \text{P}_{\text{steady-state}} \)) taking into account the annual losses resulting from \( \Omega \), we included this loss term in eq. 3.

\[ \Delta P/\Delta t = p_{\text{P}} - K_{\text{P}}/\Delta t = p_{\text{P}} - \Delta \]

Applying the same assumption as above, we solved for \( \text{P}_{\text{steady-state}} \) as

\[ P_{\text{steady-state}} = \left( p_{\text{P}} + \Delta \right)/(p + K) \]

These predictions were then compared with observed P concentrations in the three lakes after zebra mussel invasion.

To contrast the effects of mussel growth on a lake's P levels, we also predicted the new steady-state P concentrations that would be expected in the event of a mass die-off (50 and 100%) of the zebra mussel population within a single year. Sudden reductions in excess of 30% of zebra mussel populations have been documented in Polish lakes, and in an extreme case between 1959 and 1960 zebra mussel virtually disappeared from Lake Mikolajskie after reaching densities of approximately 2200/m² (Stanczykowska and Lewandowski 1993). These new P concentrations were estimated by first calculating the total amount of P bound up in the mussel population (milligrams P per square metre) using a mean lakewide mussel density for a given year along with eq. 11 and the assumption of a 15% P content of soft tissue. Only dry tissue weights were used because it is not yet known how long P remains bound to the shell fraction after a zebra mussel die. This total annual P bound up in the lake-wide population was then substituted for \( \Omega \) in eq. 13 but was added to the term p_{P}, to simulate an input rather than a loss.

While most of our assumptions may not hold over short periods, we do consider them valid when applied on an annual basis and therefore limit our calculations and conclusions to a yearly time frame. We opted for a relatively crude mass balance model over more complicated, multi-compartment models because of its overall simplicity and ease of application to other lakes. We justify our use of mean annual increases in zebra mussel density versus local population densities in any given year by the reasoning that in a stable population with no net growth, P accumulates into mussel tissue would be balanced by losses resulting from mortality as long as no significant removal from the lake took place (e.g., through predation by diving ducks). Therefore, any observed net effects on the P budget would be due to a net increase in mussel biomasses (i.e., growth).

Effects of zebra mussel filtration on chlorophyll a

To determine if filtration rates could account for any observed algal depletion, we calculated the cumulative filtration impact of local zebra mussel populations and compared water turnover times (owing to mussel filtration) with algal growth rates. Local zebra mussel density and size frequency data were collated for Lake St. Clair (Hebert et al. 1991; Nalepa et al. 1993) and the western basin of Lake Erie (MacIsaac et al. 1992; Butt et al. 1993; Leach 1993). Because we did not collect chi a data at the exact sites where we sampled zebra mussels in Omea Lake, we used lakewide (rather than local) chi a and mussel density estimates. For the 1- to 12-mm mussel size-classes we calculated size-specific filtration rates using the equation of Bunt et al. (1993). For size-classes greater than 12 mm, two separate size-specific filtration rates were calculated using the equations from Kryger and Riisgard (1988) and Redding and Bij de Vaate (1998). Given the high variability in published zebra mussel filtration rates, these two equations (one exponential, the other sigmoidal) offered a range of rates with which to estimate filtration impacts. Because filtration rates calculated using the equation of Kryger and Riisgard (1988) required a conversion from body size to dry weight, we used the length-weight relationships of Nalepa et al. (1993) for Lake St. Clair and that of Kryger and Riisgard (1988) for Lake Erie. Length-weight data from this study were used for Omea Lake. The cumulative local zebra mussel filtration impact was calculated according to MacIsaac et al. (1992) as

\[ C_{\text{cumulative filtration impact}} = \frac{C_{\text{frequency distribution}}}{C_{\text{constant required to}}}
\]

where \( i \) is the shell length (1–4 mm, depending on the frequency distribution) and \( C \) is a constant required to
convert the units of filtration rate to cubic metres filtered per square metre per day. The cumulative filtration rates were converted to turnover rates (day^{-1}); the number of times per day the water was being filtered by dividing by the mean depth of the lake, and these were compared with mean and maximum algal growth rates.

Evidence for nutrient–chlorophyll decoupling in European lakes

From the literature we gathered data for spring TP levels, summer chl a levels, and zebra mussel density for European lakes. P and chl a data were plotted relative to the Dillon–Rigler line to determine if the nutrient–chlorophyll relationship in these lakes became more decoupled (as well as whether chl a levels decreased) as mussel density increased. Only lakes with N/P ratios greater than 12 were used, as specified by Dillon and Rigler (1974). In addition, least-squares regression analysis was attempted between TP and chl a concentrations to determine how much of the variability in chl a levels could be accounted for by TP, followed by multiple regression analysis to determine if mussel density (both on an areal and volumetric basis) was able to account for any residual variation.

Results

Tank experiment on phosphorus and chlorophyll a dynamics

The control tank showed a gradual decline in P levels, asymptotically approaching a steady-state concentration.
at approximately day 10, while chl $a$ levels remained relatively stable after an initial increase (Fig. 2). The tanks with two and five zebra mussels also followed this basic pattern with only minor fluctuations in P and chl $a$ levels. The tank with 10 mussels, however, began to show some effect of zebra mussel density, with P levels falling and then rising again along with an increasingly erratic chl $a$ behavior. This pattern became more pronounced in the tank with 20 mussels and culminated in the tank with 40 mussels where the oscillations in P and chl $a$ concentrations were at their peak (Fig. 2). P and chl $a$ levels tended to change synchronously in tanks with 0, 2, and 5 mussels, but this synchrony became increasingly disrupted in tanks with more than 5 mussels, ending with inversely related P and chl $a$ trends in the 40-mussel tank (Fig. 2).

The erratic behavior of chl $a$ levels with increasing mussel density became apparent when plotted relative to the Dillon-Rigler line (Fig. 3). At densities up to 5 mussels/ tank, chl $a$ levels tended to rise steadily and then hover around the Dillon-Rigler line, while at higher densities
Fig. 4. Mean observed and predicted chl a concentrations plotted versus number of mussels per tank. Predicted values were calculated using the Dillon–Rigler TP – chl a relationship. Data were used only after day 10 of the experiment (after the control tank had reached steady state). Error bars represent standard errors. *, significant differences between observed and predicted mean values within each tank (ANOVA; $p < 0.05$).

![Graph showing mean observed and predicted chl a concentrations](image)

chl a concentrations displayed a more erratic behavior as shown by the increasingly irregular trajectories (Fig. 3). The increased erratic chl a behavior starting with the 10-mussel tank is further supported by departures of observed mean chl a levels from predicted levels in the tanks with 10, 20, and 40 mussels (ANOVA, $p < 0.05$), suggesting that the chl a-chlorophyll relationship had decoupled (Fig. 4).

Only the tank with the highest mussel density has mean P levels that were greater than those of the control tank, while tanks with more than 5 mussels had higher chl a levels than the control tank (ANOVA, $p < 0.0001$; Fig. 5A). There was also a shift to smaller algal cell sizes in the tanks with more than 5 mussels relative to the control tank (Bonferroni-corrected $t$ tests, $p < 0.0001$; Fig. 5B).

**Phosphorus excretion experiment**

Phosphorus excretion rates averaged over the 12-h experiments were fitted to power functions of mussel shell length in the following form: excretion = $a \cdot D W^{b}$, where DW is the dry weight (Fig. 6). Data from Oneida Lake and Lake St. Francis for each of the two temperatures were pooled across the two systems because slopes were similar within each temperature trial ($t$ tests for common slopes; $p > 0.30$). However, slopes between temperature trials differed ($t$ test for common slope; $p < 0.0001$), and using mussel shell length we were able to explain 75 and 71% of the variability in excretion rates for the 17 and 22°C trials, respectively (Fig. 6). Similarly, the relationships between zebra mussel dry tissue weight (milligrams) and weight-specific total phosphorus excretion rate (micrograms P per milligram dry weight per hour) for the 17 and 22°C temperature trials were excretion rate = (2.4 × $10^{-3}$)$D W^{-0.58}$ ($R^2 = 0.82$, $p < 0.0001$, $n = 60$) (Fig. 6) and (4.1 × $10^{-3}$)$D W^{-0.46}$ ($R^2 = 0.61$, $p < 0.0001$, $n = 68$), respectively.

Tissue dry weight (milligrams) were also fitted to power functions of mussel shell length (millimetres). For Oneida Lake this relationship was weight = (6.22 × $10^{-5}$)$D W^{0.61}$ ($R^2 = 0.95$, $n = 129$, $p < 0.0001$), while for Lake St. Francis the relationship was weight = (1.06 × $10^{-5}$)$D W^{0.96}$ ($R^2 = 0.96$, $n = 61$, $p < 0.0001$). The slopes of the two length-weight regressions were different ($t$ test for common slope; $p < 0.0001$). The length-weight relationship for Oneida Lake was used in subsequent calculations for the P mass balance models and for filtration and excretion estimates involving this lake’s mussel population.

**Mass balance modeling and phosphorus turnover in the water column**

**Oneida Lake**

Although there was considerable variation in zebra mussel densities at individual stations between 1992 and 1993, overall lakewide densities remained relatively stable (Table 2). Densities were >10,000/m² for most stations, and in areas where bottom sediments were composed of sand or mud, unitwix provided the only hard substrate available (Table 2). Mean lakewide length-frequency
Table 1. Depth, substrate composition, and zebra mussel densities (mean ± standard error) in Oneida Lake.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Substrate</th>
<th>1992 fall (no./m²)</th>
<th>1993 spring (no./m²)</th>
<th>1993 fall (no./m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Rock</td>
<td>2642 ± 8 694</td>
<td>54 161 ± 20 576</td>
<td>50 991 ± 8 730</td>
</tr>
<tr>
<td>2</td>
<td>sand-unionoid</td>
<td>41 379 ± 17 867</td>
<td>36 231 ± 9 222</td>
<td>61 317 ± 9 425</td>
</tr>
<tr>
<td>3</td>
<td>sand-cobble</td>
<td>27 464 ± 8 719</td>
<td>51 009 ± 3 485</td>
<td>109 675 ± 2 461</td>
</tr>
<tr>
<td>4</td>
<td>sand-unionoid</td>
<td>29 739 ± 11 694</td>
<td>18 272 ± 2 701</td>
<td>41 360 ± 8 172</td>
</tr>
<tr>
<td>5</td>
<td>sand-cobble</td>
<td>52 885 ± 10 016</td>
<td>19 030 ± 4 420</td>
<td>49 472 ± 15 374</td>
</tr>
<tr>
<td>6</td>
<td>mud-unionoid</td>
<td>1 804 ± 311</td>
<td>3 530 ± 1 057</td>
<td>2 812 ± 305</td>
</tr>
<tr>
<td>7</td>
<td>mud-unionoid</td>
<td>95 079 ± 35 807</td>
<td>61 750 ± 15 251</td>
<td>904 ± 415</td>
</tr>
<tr>
<td>8</td>
<td>Rock</td>
<td>40 808 ± 5 545</td>
<td>14 368 ± 3 009</td>
<td>40 592 ± 7 530</td>
</tr>
<tr>
<td>9</td>
<td>sand-unionoid</td>
<td>61 794 ± 20 576</td>
<td>38 992 ± 14 611</td>
<td>2 123 ± 138</td>
</tr>
<tr>
<td>10</td>
<td>sand-unionoid</td>
<td>na</td>
<td>na</td>
<td>9 231 ± 4 754</td>
</tr>
</tbody>
</table>

Mean: 44 137 ± 33 038

Note: Site numbers correspond to those in Fig. 1. na, not available.

Fig. 6. Relationship between zebra mussel shell size (mm) and total phosphorus concentration. The regression equations for (1) and (2) 22°C temperature trials are (i) concentration rate (μg P/l) = (2.6 × 10⁻⁶)shell⁻¹ (R² = 0.75, p < 0.0001, n = 50) and (ii) concentration rate (μg P/l) = (2.1 × 10⁻⁶)shell⁻¹ (R² = 0.71, p < 0.0001, n = 68).

Distributions also remained relatively unchanged, and while size-classes <5 mm were grouped together, these classes clearly dominated the population size structure for all three seasons (Fig. 7). In comparison, mussel populations in Lake Erie and Lake St. Clair were dominated by small size-classes (Brett et al. 1991; Bum et al. 1993; Leach 1993).

Between pre- and post-invasion periods, Secchi depths increased 22% from 2.7 ± 0.12 m (mean ± SE) in 1989-1991 to 3.3 ± 0.13 m during 1992-1993, the greatest difference occurring late in the fall (Fig. 8). There were also decreases in mean P (13%) and chlorophyll (34%) levels between pre- and post-invasion periods, with lower levels being recorded almost consistently in post-invasion years (Fig. 8).

Using density data and mass balance modeling, we calculated a mean annual increase in zebra mussel density of 19 900/m² corresponding to an annual P accumulation into growth of 246 mg P/m²-year⁻¹ (Table 3). The predicted steady-state P concentration was in general agreement with the observed mean for the post-invasion period (Table 3). In the event of a mass die-off of 50% and 61% increase in water column P levels, respectively, relative to pre-invasion levels (Table 3).

Depending on the filtration rates used, the mean lakewide zebra mussel population was estimated as having a filtration impact of between 3.5 and 9.7 m² filtered/day⁻¹, which translated into a water turnover rate of between 0.5 and 1.4 times/day (Table 4). The increase in P concentrations resulting from a 50% and 100% die-off would potentially result in a 19 and 61% increase in chl a levels, respectively, relative to pre-invasion levels (Table 4). Both pre- and post-invasion chl a levels were in agreement with those predicted by the Dillos and Rigler (1974) equation, indicating that the P - chl a relationship had not decoupled (Fig. 9).

Western basin of Lake Erie

Between the years pre- and post-invasion of zebra mussel, mean annual P concentrations in the western basin of Lake Erie dropped 17% (Tables 1 and 3). With an estimated mean annual increase in zebra mussel density of 15 600/m², we calculated a P accumulation into growth of 370 mg/m²-year⁻¹ and a predicted steady-state P concentration that was in agreement with observed values (Table 3). A mass die-off of 50% of the mussel population within a single year would result in a 21% increase in P concentrations relative to pre-invasion levels, while a 100% mass die-off would lead to a 42% increase (Table 3).

A mean local mussel density of 2.2 × 10⁷/m² was calculated as having a cumulative filtration impact of between 17 and 75 m² filtered/m²-year⁻¹ (depending on the filtration rate used) and a water turnover rate of between 2.2 and 9.8 times/day (Table 4). Post-invasion years, chl a levels dropped 69% relative to pre-invasion levels over local reefs (Table 4). A 50 and 100% mass die-off would lead to potential increases in chl a levels, up to 66
and 109% from preinvasion levels (Table 4). While the mean preinvasion chl a level was in general agreement with that predicted by the Dillon and Rigler (1974) equation, the mean postinvasion chl a level was much below the predicted level (Fig. 9), suggesting that the P–chl a relationship had decoupled.

Lake St. Clair

For Lake St. Clair, we calculated a mean annual increase in zebra mussel density of 2239/m², which translated into an annual P accumulation into growth of 98 mg/m²-yr⁻¹ (Table 3). Although specific mean lakewide P data were unavailable for postinvasion years, there were no net changes in annual P concentrations between 1982 and 1990 (R. Griffiths, Ontario Ministry of Environment and Energy, 985 Adelaide Street South, London, ON N6E 1Y5, personal communication). The P lost to mussel growth resulted in a predicted P concentration that was in agreement with the observed postinvasion level (Table 3). Our mass balance models predict that in the event of either ≤50 or 100% mortality of the mussel population within a single year, between 88 and 177 mg P/m² would be released into the water (Table 3). However, the short water residence time in this lake would allow P concentrations to remain near preinvasion levels at approximately 26 mg/m² (Table 3).

With a local mussel abundance of 11 000/m², we calculated that between 2 and 8.5 m³ of m⁻²-day⁻¹ were being filtered by the mussel population, turning the water over between 0.6 and 2.6 times/day (Table 4). There was a 59% reduction in local chl a levels after the arrival of zebra mussel, and in the event of a 50 and 100% mussel die-off
Fig. 9. Mean annual water column TP and chl a concentrations before and after zebra mussel invasion for the western basin of Lake Erie, Lake St. Clair, and Onieda Lake plotted relative to the Díon–Rigler relationship (solid line). Sources for Lake Erie data were Rockwell et al. (1989), LeBolt et al. (1991), Nichols and Ippoliti (1993); J.H. Lasch, Ontario Ministry of Natural Resources, Lake Erie Fisheries Station, Wheatley, ON N0P 2P0, unpublished data; R. Holland, Department of Atmospheric, Oceanic, and Space Sciences, Ann Arbor, MI 48109-2143, unpublished data; Environment Canada, Inland Waters Directorate, Waier Quality Branch, Burlington, Ont.; U.S. Environmental Protection Agency, Great Lake National Program Office, Chicago, Ill. Sources for Lake St. Clair data were Herdendorf et al. (1986); Lang et al. (1988); Nalepa et al. (1993); D. MacLennan, Lake St. Clair Fisheries Assessment Unit, Tilbury, ON N0P 2L0, unpublished data. a, Lake Erie 1984–1986; c, Lake Erie 1990–1992; b, Onieda Lake 1989–1991; c, Onieda Lake 1992–1993; a, Lake St. Clair 1971–1975; c, Lake St. Clair 1990–1992.

of the mussel population, chl a levels would potentially increase by 3 times that of preinvasion mean concentration (Table 4). While the mean preinvasion chl a concentration was somewhat below that predicted by the Díon and Rigler (1974) equation, the further drop during postinvasion years suggests that a decoupling of the P = chl a relationship had also occurred in this lake (Fig. 9).

Evidence for nutrient–chlorophyll decoupling in European lakes

There was little evidence that Polish lakes with moderate zebra mussel densities (1000–5000 ml) had lower chl a levels (relative to P) than lakes with fewer or no mussels (Fig. 10). Spring TP (milligrams per cubic metre) and summer chl a (milligrams per cubic metre) were correlated for the European lakes (Zdanowicki 1983): Chl a = 0.0081TP0.84 (R2 = 0.66, n = 27, p < 0.001); however, using multiple regression, mussel density (both on an areal and volumetric basis) did not account for a significant proportion of the residual variability (p = 0.27 for density per square metre; p = 0.98 for density per cubic metre). There were no obvious patterns in either decoupling or reductions in chl a with increasing mussel density in the European lakes that paralleled the extreme P = chl a regimes seen in Lake Erie or Lake St. Clair in post-invasion years (Fig. 10). In general, the P = chl a regimes in the European lakes resembled more the situation that we described for Onieda Lake, which lies on the Díon–Rigler line despite mussel densities in excess of 10 000/ml (Fig. 10).

Discussion

Tank experiment on phosphorus and chlorophyll a dynamics

Results from our experiment in a laboratory microcosm suggest that, on a short time scale, the erratic behavior of P and chl a increase with increasing mussel densities (Fig. 2), contrary to the assumption that high zebra mussel densities significantly increase water clarity. When densities reached 10, 20, and 40 mussels/l tank there was some evidence to support the top-down hypothesis, with intermittent clearing of the water (wherein the water would clear and then become green again every 3–5 days), increasingly erratic P and chl a trends and deviations from the pattern shown by the control tank (Fig. 2), and increased deviations from the Díon–Rigler line (Figs. 3, 4). These results suggest that the filtration responses of zebra mussel to sediment concentration are more complex than the simple linear response described by Reeder and Bij de Vaate (1990). In particular, they imply a low algal density threshold below which filtration rates diminish or become highly variable as shown by Wata (1978a). Thus, we speculate that the erratic patterns observed may be due to the mussels’ initially clearing the tanks but then slowing down their filtration in response to lowered food levels. The reduction in filtration combined with the mussels’ cumulative P excretion rates (Table 5) that would continue to replenish the water column nutrient pool would then allow the algal population to rebound. This may also explain why the tanks with more than 10 mussels had higher mean chl a levels than the control tank (Fig. 5A). This hypothesis would require all mussels in a single tank to have their filtration and excretion rates roughly synchronized with each other, but as these densities and at this spatial scale this requirement is considered plausible. We would not expect to see a 3- to 5-day intermittent clearing pattern in lakes because of the larger spatiotemporal scale of lake hydrodynamics and the impossibility of synchronizing all the mussels in a larger population. In spite of this, we consider the experiment useful because it suggests, at least in a laboratory microcosm and at short time scales, that the mussels do not simply clear the water (although they are able to do so on a short-term basis) but may set up a cycle of clearing the water and then replenishing the food supply through excretion and reduced filtration in response to local food abundance.

The results of the experiment also suggest that the cumulative filtration rates of zebra mussel at densities >10000 mussels/L can affect chl a levels by matching or exceeding algal growth rates (µ). To test this, we calculated the cumulative filtration rates and water turnover times for each of the five tanks containing mussels by using the filtration equations from Kryger and Rintang (1988) and Reeder and Bij de Vaate (1990) (Table 5). With a mean µ of 0.33/day (Reeder and Bij de Vaate
Table 3. Zebra mussel density, P accumulated into tissue standing stock and growth, observed and predicted steady-state TP levels during postinvasion years, and predicted TP levels in the event of a 50% and 100% mass die-off of the lakewide mussel population for the western basin of Lake Erie, Oneida Lake, and Lake St. Clair.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Mean annual zebra mussel increase (no./m²)</th>
<th>Annual P accumulation into growth (mg m⁻³ yr⁻¹)</th>
<th>% of total annual P load incorporated into mussel growth</th>
<th>Mean postinvasion steady-state TP concentration (mg m⁻³)</th>
<th>Mean lakewide zebra mussel density (no./m²)</th>
<th>Amount of P accumulated in population soft tissue (mg P m⁻³)</th>
<th>Predicted [TP] with 50% die-off (mg m⁻³)</th>
<th>Predicted [TP] with 100% die-off (mg m⁻³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oneida</td>
<td>19 000</td>
<td>244</td>
<td>38</td>
<td>19 (0.74) (1990)</td>
<td>14</td>
<td>36 848 (10 111) (1993)</td>
<td>394</td>
<td>30</td>
</tr>
</tbody>
</table>

Note: Values in parentheses beside estimates are standard errors. The years corresponding to the lake-wide density estimates and observed TP concentrations are also listed.

¹Data from Leach (1993) and Garton and Haag (1993).
²Data from R. Holland, Department of Atmospheric, Oceanic, and Space Sciences, Ann Arbor, MI 48109-2143 (unpublished data), and Environment Canada, Inland Waters Directorate, Water Quality Branch, Burlington, ON L7R 4A6, and U.S. Environmental Protection Agency, Great Lakes National Program Office, Chicago, IL 60604.
³Data from Zieske and Hower (1993); Hunter and Bailey (1992); Hebert et al. (1991), and Nuliak et al. (1939).
⁴Data from D. MacLennan, Dir. St. Clair Fisheries Assessment Unit, Tilbury, ON N0P 2L0, unpublished data.
⁵Data from Griffiths (1993) and Hunter and Bailey (1992).
Table 4: Local zebra mussel density, cumulative filtration impacts, water turnover rates owing to filtration, and observed chl a levels during pre- and post-invasion years for the western basin of Lake Erie, Oneida Lake, and Lake St. Clair.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Local zebra mussel abundance (no./m²)</th>
<th>Cumulative local filtration impact (m³/m² day⁻¹)</th>
<th>Turnover (day⁻¹)</th>
<th>Mean preinvasion chl a level (mg/m³)</th>
<th>Mean postinvasion chl a level (mg/m³)</th>
<th>Expected postinvasion chl a level with 50% die off (mg/m³)</th>
<th>Predicted chl a level with 100% die off (mg/m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erie (western basin)</td>
<td>222,500 (49,976) (1990)</td>
<td>74.8 16.6 9.8 2.2</td>
<td>5.5 (0.09) (1984–1986)</td>
<td>5.8 (0.58) (1989–1991)</td>
<td>5.6 (0.62) (1992–1993)</td>
<td>5.6</td>
<td>9.6</td>
</tr>
<tr>
<td>Oneida</td>
<td>38,843 (10,911) (1993)</td>
<td>9.7 3.3 1.4 0.5</td>
<td>8.5 (0.58) (1989–1991)</td>
<td>5.6 (0.62) (1992–1993)</td>
<td>5.2</td>
<td>10.1</td>
<td>13.7</td>
</tr>
<tr>
<td>St. Clair</td>
<td>11,000 (1990)</td>
<td>8.5 2.0 2.6 0.6</td>
<td>2.7 (0.42) (1971–1975)</td>
<td>1.1 (0.34) (1992–1993)</td>
<td>6.7</td>
<td>8.2</td>
<td>8.3</td>
</tr>
</tbody>
</table>

Note: Values in parentheses beside estimates are standard errors. Expected postinvasion chl a levels were calculated using observed postinvasion TP values and the Dillon and Rigler (1974) relationship. Predicted chl a levels were calculated using pre-invasion TP values and the Dill on and Rigler (1974) relationship. Predicted chl a levels in the event of a 50 and 100% mass die-off were calculated using the predicted TP levels in Table 3. The years corresponding to observed chl a values are also bolded. FR is FR, and FR denotes calculations using filtration rates from burnt et al. (1993) and Kuyper and Rutgers (1988) for FR, and burnt et al. (1993) and Kuyper and Rutgers (1988) for FR.

1Data from Leach (1993).
2Data from J.H. Leach, Ontario Ministry of Natural Resources, Lake Erie Fisheries Station, Wheatley, ON, N0P 2P0 (unpublished data), Nicholls and Hopkins (1993), and Rockwell et al. (1989).
3Data from J.H. Leach, Ontario Ministry of Natural Resources, Lake Erie Fisheries Station, Wheatley, ON, N0P 2P0 (unpublished data).
4Lakeside mean.
5Data from Nalepa et al. (1993). Their did not report a standard error.
6Data from D. MacLennan, Lake St. Clair Fisheries Assessment Unit, Tilbury, ON, N0P 2L0 (unpublished data) and Hudesendorf et al. (1986).
7Data from Nalepa et al. (1993) and D. MacLennan, Lake St. Clair Fisheries Assessment Unit, Tilbury, ON, N0P 2L0 (unpublished data).
Table 5. Zebra mussel densities and P excretion and water turnover rates for the tank experiment.

<table>
<thead>
<tr>
<th>No. of mussels per tank</th>
<th>Cumulative excretion rate (µg P/day)</th>
<th>Cumulative filtration rate (L/day)</th>
<th>Turnover (day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>FR₁ (mussel/L)</td>
<td>FR₂ (mussel/L)</td>
<td>FR₁ (mussel/L)</td>
</tr>
<tr>
<td>40</td>
<td>215</td>
<td>1.0</td>
<td>276</td>
</tr>
<tr>
<td>20</td>
<td>108</td>
<td>0.5</td>
<td>138</td>
</tr>
<tr>
<td>10</td>
<td>54</td>
<td>0.25</td>
<td>69</td>
</tr>
<tr>
<td>5</td>
<td>27</td>
<td>0.125</td>
<td>35</td>
</tr>
<tr>
<td>2</td>
<td>11</td>
<td>0.05</td>
<td>14</td>
</tr>
</tbody>
</table>

Note: Cumulative P excretion was determined using the relationship between mussel shell size and excretion rate for 22°C. Aquatic density was calculated by dividing the number of mussels by the 40 L volume in each aquarium. Filtration rates (FR₁ and FR₂) were calculated according to Kriger and Bristig (1988) and Reenders and Bij de Vaate (1990), respectively. Turnover was calculated by dividing filtration rate by aquarium volume (40 L).

1990) and a maximum µ of 1.4/day (Droop 1974), we see that at 10 mussels/tank the range in turnover times begins to exceed the maximum algal growth rate (Table 5). The observed threshold density of 0.25 mussel/L, where effects on chl a concentrations begin to be seen in the experiment, is therefore consistent with what we would expect on the basis of phytoplankton growth potentials.

Phosphorus excretion rates and zebra mussel phosphorus budgets

Size-specific P excretion rates for zebra mussel were generally lower than those reported for other freshwater bivalves. Using our estimates, a 20-µg DW zebra mussel would excrete 0.11 µg P·mg⁻¹·day⁻¹ at 17°C and 0.25 µg P·mg⁻¹·day⁻¹ at 22°C. By contrast, Lauritsen and Mosley (1989) determined P excretion rates for a 200-µg DW Corbicula fluminea to be around 1.4 µg P·mg⁻¹·day⁻¹ in the summer and 0.084 µg P·mg⁻¹·day⁻¹ in the winter, while Nalepa et al. (1991) determined that a 1-g DW Lampsilis silicicola would excrete approximately 1 µg P·mg⁻¹·day⁻¹ during the period from May to October. Temperature, which had a significant effect on P excretion rates for the zebra mussel (Fig. 6), also affects nutrient excretion rates in the marine mussel Mytilus edulis (Bayne and Scullard 1977) as well as in certain benthic invertebrates (Gardner et al. 1981; Ejmont-Karabin 1984; Fukuhara and Yasuda 1985).

While our experiments were carried out as soon as possible after collection to better assess excretion rates reflective of in situ conditions, our rates may not be representative of year-round mean values. For example, we did not take into account any effects of seasonality or spawning condition, both of which affect P excretion rates in bivalves (Kuenzel 1961; Lauritsen and Mosley 1989; Nalepa et al. 1991). Spawning condition affects P excretion because more P is used up during gametogenesis (thereby lowering the availability of P for metabolism and excretion), leading to lower excretion rates in individuals that are not spent (Koenzler 1961). Because zebra mussel spawn in mid to late August in Lake Erie (Garton and Haag 1993), our mussels collected in late August to late September may have already been spent and our excretion estimates may therefore overestimate mean values. As for seasonal effects, using the summer and winter excretion rates of Lauritsen and Mosley (1989), we calculated a mean P excretion rate for Corbicula fluminea that was half their summer rate. Therefore, if we assume our zebra mussel excretion estimates at 17°C to represent maximum rates, then using mean lakewide density estimates (Table 3) and their respective size-frequency distributions, we calculated that in Lake Erie the mussel population would excrete a maximum of 1.2 mg P·m⁻²·day⁻¹, compared with 3.0 mg P·m⁻²·day⁻¹ for Lake St. Clair and 19.4 mg P·m⁻²·day⁻¹ for

![Fig. 10. Mean spring TP and summer chl a concentrations for Polish lakes plotted relative to the Döllmeyer-Boehl relationship (solid line). Only lakes with N/P ratios greater than 12 were used. Mussel densities are per square metre. Pre- and post-inversion mussel means for Lake Erie, Oneida Lake, and Lake St. Clair are also shown. Data sources for the Polish lakes were Zdanowski (1983) and Staniszewska and Lewandowski (1993). *: 0 mussels; #: 1–100 mussels; #: 100–1000 mussels; ¥: 1000–5000 mussels; a: Lake Erie; b: Lake St. Clair; c: Oneida Lake.](image-url)
Table 6. Phytoplankton biomass and P content means cumulative filtration rates and the components of daily P budgets for zebra mussel populations in Lake Erie, Onedia Lake, and Lake St. Clair.

<table>
<thead>
<tr>
<th>Location</th>
<th>Mean cumulative filtration rate (mg P/m²/day)</th>
<th>P content of phytoplankton biomass (mg P/m²)</th>
<th>P content of stock tissue (mg P/m²)</th>
<th>P content of excretion (mg P/m²)</th>
<th>P content of biodeposition (mg P/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lake Erie</td>
<td>1.0</td>
<td>0.51</td>
<td>0.36</td>
<td>0.12</td>
<td>0.01</td>
</tr>
<tr>
<td>Onedia Lake</td>
<td>1.0</td>
<td>0.51</td>
<td>0.36</td>
<td>0.12</td>
<td>0.01</td>
</tr>
<tr>
<td>Lake St. Clair</td>
<td>1.0</td>
<td>0.51</td>
<td>0.36</td>
<td>0.12</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Note: Percentages of the total amount of P filtered daily are included in parentheses for the different budget components.

Oseida Lake. Mean, year-round excretion rates would probably be closer to half the above values.

With these estimates we can begin to formulate a tentative picture of the daily P budget (with growth, gametogethesis, excretion, mortality, and biodeposition components) cycling through a zebra mussel population for Lake Erie, Lake St. Clair, and Oseida Lake (Table 6). P accumulated into standing stock biomass (tissue and shell) was calculated using the mean lake wide density estimates from Table 3. To determine the total P filtered daily, we first converted postinvasion P at levels (milligrams per litre) in the three lakes to phytoplankton biomass (milligrams per litre) using a relationship derived from biomass and chlorophyll a data from the Great Lakes (Vollenweider et al. 1974); phytoplankton biomass = 0.541chl a^0.82 (R^2 = 0.66, n = 37, p < 0.001). We then assumed that all of the P is bound to the phytoplankton and that the P content of phytoplankton is 0.28% (Stanczykowska and Planter 1985). Daily population filtration rates were estimated by applying the methods used in calculating the cumulative filtration impact of local populations (Table 4) to the mean lake wide densities listed in Table 3. A mean population filtration rate was calculated by averaging the two cumulative filtration estimates derived from Kryger and Rinserg (1988) and Reenders and Bij de Vaate (1990), and this mean rate was multiplied by the P content of phytoplankton biomass to generate an estimate of the total P filtered daily on an areal basis. To estimate the daily growth component of the P budget we divided the annual P accumulated into E (Table 3) by 365. We assumed mean daily losses owing to gametogethesis to be approximately equal to growth (Nalepa et al. 1991), and losses owing to excretion to be one half of the presumed maximum values listed above. Losses owing to mortality were calculated by first multiplying the amount of P accumulated into the mussel population’s biomass (standing stock tissue and shell; Table 6) by a P:B ratio of 6.83 (Walz 1978b) to estimate annual production. We then divided this production value by 365 and subtracted from it the daily growth component of the P budget to generate an estimate of daily P losses owing to mortality. Finally, we subtracted these four components (growth, gametogethesis, excretion, and mortality) from the total P filtered to estimate daily biodeposition (feces and pseudofeces).

The total P filtered daily by the zebra mussel populations ranged from 4 mg P/m²-day^-1 for Lake St. Clair to 40 mg P/m²-day^-1 for Oseida Lake, and the portions of this total P filtered daily that could be accounted for by the growth, gametogethesis, and excretion components of the P budget remained relatively stable, the proportions accounted for by mortality and biodeposition varied considerably (Table 6). For Lake St. Clair, the sum of the proportions of the different P budget components was greater than 100% (Table 6), and this is most likely due to the error associated with each estimate.

The proportion of the total P filtered daily that could be accounted for by a combination of growth and gametogethesis production is in general agreement with the value reported for zebra mussel by Stanczykowska and Planter (1985) (12%) and for L. silicula by Nalepa et al. (1991) (17%), but our estimate of the relative proportion of game
production is approximately 10 times that reported by Kieweler et al. (1961) for a population of the mussel *Modiolus demissus* (0.2%). Our daily excretion proportions are also somewhat higher than those of Kuenzler (1961) and Nalepa et al. (1991), who estimated that approximately 5 and 15%, respectively, of the total P filtered was returned to the water column via excretion, albeit for different bivalve families. Our estimates of the proportion of P lost to mortality, however, are considerably higher than those of Kuenzler (1961) (0.4%) and Nalepa et al. (1991) (45%); this is a direct consequence of our assumption that a large P:B ratio of 6.83 (Walz 1978b). Although this ratio is approximately 10 times higher than the P:B ratios reported by Stanczykowska (1976), we felt it was the more appropriate ratio for our calculations because the zebra mussel population size structure used by Walz (1978b) was dominated by small-size classes (similar to the size structures seen in our three lakes) and because mortality in zebra mussel populations is highest for postveligers and 1-yr-old individuals (Stanczykowska 1977; Lewandowski 1982).

Our biodioposition proportions also differ from those of Kuenzler (1961), Stanczykowska and Planter (1985), and Nalepa et al. (1991), who reported proportions of 95, 50, and 64%, respectively, for different bivalve populations. Zebra mussel filter more seston than they assimilate (Stanczykowska and Planter 1985), but biodioposition would only be expected when excess food is available that is not required for the mussels' biological processes. In Oenida Lake, with a phytoplankton biomass of 2 mg/L (Table 6), food does not appear to be limiting to the zebra mussel population. Filtration may therefore be able to provide P in excess of the mussels' biological demands and this excess P can then be biodioposed in the form of feces and pseudofeces. In contrast, the mussel population in Lake St. Clair (with a phytoplankton biomass of only 0.6 mg/L) may be limited by food, thereby using all of the filtered P for biological processes and leaving none for biodioposition (Table 6). Because the western basin of Lake Erie has an intermediate phytoplankton biomass concentration, the proportional biodioposition estimate of its mussel population would be expected to lie between those of Oenida Lake and Lake St. Clair (Table 6). Furthermore, Haven and Morales-Alamo (1966) found a linear relationship between feces and pseudofeces production and the total seston content of the water for the oyster *Crassostrea virginica*, and if this relationship holds for zebra mussel it may explain some of the high variability surrounding our biodioposition estimates. Machaesa et al. (1992) have already speculated that intensive food limitation may become apparent in the western basin of Lake Erie because of high densities of settled mussels.

The substantial filtration impacts and water column turnover rates associated with zebra mussel filtration (Table 4) imply that the potential exists to cycle each day a large proportion of the annual P load entering a lake. We estimated that between 0.1 and 6% of the annual P load was being recycled daily by the mussel populations in Lake Erie, Lake St. Clair, and Oenida Lake (Table 6), and this very rapid daily cycling underlies the potential importance of a mussel population to a lake’s P dynamics.

**Mass balance modeling and phosphorus turnover in the water column**

Densities of zebra mussel in Oenida Lake increased 30-fold from the summer and fall of 1992 (Medina and Rasmussen 1994), remained relatively stable to the fall of 1993 (Table 2), and may be reaching equilibrium densities as competition for suitable substrate or other factors increases. In Lake St. Clair, mean densities increased 86-fold between 1988 and 1989 (Hebert et al. 1991), and in the western basin of Lake Erie the zebra mussel populations also increased rapidly in the early years of colonization between 1988 and 1990 (Leach 1993). By 1992 both populations may have approached maximum numbers. In comparing the mass balance results for the three lakes, we found that the zebra mussel population in Lake St. Clair had a negligible effect on mean annual P levels, while for the western basin of Lake Erie and for Oenida Lake the effects were more pronounced and resulted in a 17% decrease between pre- and post-invasion years (Table 3). This is consistent with the proportion of the P loads that accumulated as zebra mussel biomass (Table 3), which is much lower in Lake St. Clair (3%) than in either Lake Erie (28%) or Oenida Lake (38%). This proportion is probably a reflection of the mean water residence time because Lake St. Clair, with the highest water and P throughput, had the most stable steady-state P levels with only a slight impact from either mussel growth or die-off (Table 3). By contrast, the western basin of Lake Erie and Oenida Lake, with slower water and P turnover rates, exhibited more pronounced fluctuations in P levels in response to growth and mortality in the mussel population. Thus, hydrologic flushing may impart a buffering effect to a lake’s P regime, minimizing the impact of within-lake processes. Meisner et al. (1993) also proposed that while zebra mussel may initially reduce water column P levels in the Bay of Quinte, Lake Ontario, the long-term effects would be a return to preinvasion concentrations.

**Why do we overestimate the reduction in postinvasion steady-state phosphorus concentrations?**

We overestimated the reduction in P for the western basin of Lake Erie and for Oenida Lake (Table 3), and in addition to possible inherent errors in our calculation of Ω we advance two further hypotheses that may have influenced our predictions. The first involves P being released to the water column from dead and dying unionid bivalves (because of epizootic colonization by zebra mussel; Nalepa 1994; Schloesser and Nalepa 1994; Ricciardi et al. 1995). To test this we gathered unionid biomass data for preinvasion years and added the P content on an aerial basis (assumed to represent 2.75% of dry weight; Nalepa et al. 1991) to the numerator of eq. 13 to simulate an additional input. We used various mortality rates (25, 30, 50, 100%) of the unionid population per year to determine what effect this had on our predictions. For Lake Erie we used a unionid abundance of 29/m² (14 g DW/m², or 385 mg P/m²) for the year 1989 (Schloesser and Nalepa 1994). For Oenida Lake, only abundance and shift in length data (for both live and dead unionids) were available for 1993, and we assumed that 50% of those unionids were alive during preinvasion years (see Fig. 3 in Schloesser and...
Nalepa 1994). Using a length-DW regression derived from Lampaulia radiata silica flux data (Nalepa and Guerin 1988), we estimated that in 1990 in Oneida Lake there were 13 unionidum, representing 26 g DW/m² or 715 mg P/m². By adding the previous parameters to eq. 13, we found that 25% of the unionid population died each year; our predicted steady-state P values would match the observed levels for both lakes. This estimate is in agreement with Ricciardi et al. (1995), who found that zebra mussel were capable of decimating a population of unionids in 3 years (Fig. 2).

The second hypothesis involves altering the sedimentation coefficient (K) in eq. 13. The sinking speed of a particle is proportional to its diameter (Hutchinson 1967), and assuming that under heavy grazing pressure the mean cell size of algal populations becomes smaller (Williams 1971; Sterner 1989), we calculated that for both lakes a 25–30% decrease in algal cell diameter was required to alter K sufficiently to bring our predictions in line with observed values. This agrees with the results of the tank experiment, where a 35% reduction in mean algal cell size was observed in our high density tanks relative to the control (Fig. 5B). While not exhaustive, these two hypotheses serve to point out additional potential effects of zebra mussel on a lake ecosystem.

Why does biodeposition not contribute to reduced water column phosphorus levels?

In our mass balance models (eq. 13), we considered only the P losses derived from net increases in mussel biomass and ignored biodeposition because we had no direct estimates of it, and because we had little reason to believe that feces and pseudofeces permanently removed P from the water column. Our calculations for Oneida Lake show that if an abundant supply of phytoplankton exists, the biodeposition rates have the potential to exceed mussel growth rates by over an order of magnitude (Table 6). Thus, if biodeposition did represent permanent removal from the water column, the term represented by Ω in eq. 13 would be more appropriately estimated as (growth + biodeposition). The reductions in steady-state P values predicted using this model are greater than those predicted by equation 11, yet the close correspondence between the observed values and the predictions based on growth alone (Table 3) implies that biodeposition does not represent permanent removal from the water column, and that alternatively this material may be respired (Haven and Morales-Alamo 1966). To date, we found no studies that examine the fate of biodeposited material; however, several studies have speculated on its importance to amphipods, cladocerans, and other benthic deposit feeders (Izvekova and Lyova-Katchkova 1972; Stanczykowska 1977; Walz 1978b; Nalepa et al. 1991; Griffiths 1993).

Turnover of seston by zebra mussel filtration

In comparisons using cumulative local filtration impacts with mean and maximum algal growth rates, the local zebra mussel population in Lake Erie had the potential to produce the highest water turnover rates (Table 4) and was probably responsible for the clearly decoupled Dillon–Rigler P–chla relationship (Fig. 9). Because of our combination of juvenile and adult filtration rates, our estimated filtration impacts are intermediate between those reported by Bunt et al. (1993) and MacIsaac et al. (1992) for western Lake Erie.

Relative to the Dillon–Rigler line, the biggest drop in chla occurred in Lake St. Clair, which, despite having relatively low local zebra mussel densities, also seems to have undergone decoupling of the P–chla relationship (Fig. 9). Lake St. Clair’s low preinvasion chla level (relative to P) may have been due to light limitation induced by the lake’s natural turbidity, and why we might have expected zebra mussel filtration to decrease turbidity levels (thereby allowing chla to rise), the further drop in chla during postinvasion years underlines the dramatic impact of zebra mussel on this lake’s phytoplankton population. Hebert et al. (1991) proposed that mean lakewide zebra mussel densities of 6000/m² in Lake St. Clair would be sufficient to filter the entire lake twice a week.

From our findings, it seems likely that the top-down mechanism appropriately describes the nutrient–phytoplankton interplay for lakes Erie and St. Clair. Similarly, Maasz (1994) found that for a given level of TP, lakes containing large Daphnia had four times less chlorophyll than lakes in which large Daphnia were absent, suggesting that grazing pressure from these large grazers (like zebra mussel) may have the potential to override nutrient as limiting primary productivity. A corollary to the top-down hypothesis is that soluble reactive P should increase with diminishing phytoplankton populations, because of insufficient numbers taking up this nutrient. Evidence for this can be found in Hatchery Bay of western Lake Erie, where soluble reactive P levels during postinvasion years were similar to or higher than preinvasion levels (Holland 1993).

By contrast, the e-idence for Oneida Lake seems to point to the bottom-up mechanism as being responsible for the congruent decreases in P and chla levels but with-out a decoupling of the P–chla relationship, despite den-sities in excess of 10 000 mussels/m² (Table 2) and mod-erate filtration impacts and water turnover times (Table 4). One possible explanation for this lack of decoupling is that while the range of filtration-induced water turnover times exceeds the mean algal growth rate of 0.33/day, it does not exceed the maximum growth rate of 1.4/day (con-trary to the range in turnover times for lakes Erie and St. Clair; Table 4). In the presence of heavy predation, algal populations may switch to smaller cells and faster growth rates (Williams 1971; Sterner 1989), and it is of interest that in 1993 in Oneida Lake there was an increase in both in the number of small algal cells (<10 μm) and in the primary productivity of those cells relative to preinvasion years (N. Idriss, Cornell University Biological Field Station, 900 Shackett Point Road, Bridgeport, NY 13039, unpublished data). Thus, it is possible that the shift in algal size seen not only in Oneida Lake but also in our tanks above the threshold density of 0.25 mussels/l (Fig. 5B) may be in response to zebra mussel grazing pressure, with smaller cells reproducing more quickly to counteract the effects of filtration. Similarly, there may have been a shift in the species composition of the algal population, with algae resistant to mussel filtration, for example, too large or
inedible taking advantage of the available nutrient pool (Gilow; 1990; Sterner 1989). In Oneida Lake, blue-green algal blooms occurred in late summer in 1992 and 1993, and since filamentous blue-green algae may be too large for zebra mussel (Stanczykowski 1977; Ten Winde and Davids 1982) as well as possessing flotation mechanisms to keep them suspended in the water column beyond the reach of the benthic layer (Lee 1989), their presence may explain why chl a levels in this lake remain coupled to nutrient levels. Similarly, blue-green algal blooms were observed in Saginaw Bay, Lake Huron, after the arrival of zebra mussel (W.S. Gardner, Great Lakes Environmental Research Laboratory, National Oceanic and Atmospheric Administration, 2205 Commonwealth Boulevard, Ann Arbor, MI 48105, personal communication). By contrast, we found no published reports of blue-green algal blooms in lakes Erie or St. Clair during postinvasion years. Further support for decoupling of the P – chl a relationship in lakes Erie and St. Clair (but not in Oneida Lake) may be found in comparing predicted (calculated using observed post–post invasion TP levels) and observed post–invasion chl a levels in the same manner as was used in Fig. 4. Only lakes Erie and St. Clair showed departures between observed and predicted values (ANOVA; p < 0.05), which we interpret as quantitative evidence for decoupling. The relative synchrony of P and chl a in Oneida Lake in 1993 (Fig. 11), where both trends track each other closely, also supports a lack of decoupling in this lake. We would expect such a plot to be unsynchronized if decoupling had occurred, as we observed in the tank experiment with 40 mussels (Fig. 3).

While we attempted to account for some of the variability in published zebra mussel filtration rates by using two filtration equations, the equation of Kryger and Risgård (1988) resulted in water turnover rates that are well in excess of the maximum μ (Table 4), and we suggest that their equation may lead to filtration rates that are somewhat high. Clearly, if algal growth rates cannot match water clearance rates, then the algal population should be decimated. Because both lakes Erie and St. Clair retain chl a (despite being heavily affected), we propose that the equation of Reeder and Bij de Vaate (1990) is more appropriate because it results in water turnover rates that are below the maximum μ, thereby allowing persistence of the algal population. The calculations for our tank experiment also suggest that the equation of Reeder and Bij de Vaate (1990) is the more reasonable one (Table 5).

Generalities of decoupling of the nutrient–chlorophyll relationship in lakes Although both lakes Erie and St. Clair showed evidence for decoupling of the P–chl a relationship (Fig. 9), we are not convinced that this is a general trend; rather, we propose that these two lakes represent extreme cases. We would have expected European lakes with 1800–5000 mussels/m² to deviate further from the Dillon-Ziegler line relative to lakes with fewer mussels, but there is no evidence for this (Fig. 10) and mussel density did not account for any of the variability in chl a not explained by TP. Mussel densities in European lakes may not have been quite high enough (relative to lakes Erie and St. Clair) over the entire lake to provide the rapid turnover required to induce decoupling. It is likely that the extreme water column turnover rates calculated for lakes Erie and St. Clair only occur either where mussel densities are extraordinarily high (as in Lake Erie) or in extraordinarily shallow lakes (as in Lake St. Clair). None of the European lakes studied even remotely approach Lake Erie mussel densities, and few are as shallow as Lake St. Clair. Thus, it would appear that most lakes containing zebra mussel have populations that are too small to deplete their water columns of chl a and (or) decouple nutrient–chlorophyll relationships.

Summary In a laboratory setting, zebra mussel are able to intermittently deplete water of chl a, and by comparing water turnover times induced by mussel filtration with mean and maximum algal growth rates, we support the conclusions of previous authors that high densities of zebra mussel are capable of depleting local algal concentrations in lakes Erie and St. Clair. We also predict that zebra mussel will only begin to affect a lake’s water column P levels when the P accumulated annually into mussel biomass reaches a substantial proportion of the lake’s annual P loadings (which in turn are affected by such factors as water residence time and mean depth). We limit our conclusions to the annual time scale over which the assumptions of our mass balance modeling are based, and to lakes where the natural sedimentation of P exceeds internal loading. We also suggest that zebra mussel should only begin to affect the nutrient–chlorophyll relationship when densities become extremely high or when lakes are extremely shallow. Further research concerning the effects of filtration on algal communities, the fates of benthic deposited materials, and the effects of zebra mussel on P dynamics in lakes that differ in hydrology and limnometry from the three lakes in our study should be addressed in future studies.

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