

Indirect effects of zebra mussels (*Dreissena polymorpha*) on the planktonic food web

Erik G. Noonburg, Brian J. Shuter, and Peter A. Abrams

Abstract: The exotic zebra mussel (*Dreissena polymorpha*) has caused dramatic reductions in phytoplankton density in lakes with dense mussel populations. However, the indirect effects of this invader on other trophic groups have been inconsistent and difficult to interpret. In some lakes, zebra mussels appear to have had little effect on zooplankton density, despite decreasing the abundance of their phytoplankton prey. We analyze food web models to test hypothesized mechanisms for the absence of a strong effect of dreissenids on zooplankton. Our results suggest that neither reduced inedible algal interference with zooplankton filtering nor reduced phytoplankton self-shading is sufficient to explain the insensitivity of zooplankton populations to dreissenid competition. Instead, we show how the impact of benthic filter feeders can be influenced by the rate of mixing within a basin, which limits phytoplankton delivery to the benthos. We explore the predictions of a simple spatially structured model and demonstrate that differences in abiotic factors that control mixing can result in large differences in direct and indirect effects of zebra mussel filtering.

Résumé : Les lacs qui possèdent de grandes densités de moules zébrées (*Dreissena polymorpha*), une espèce exotique, subissent de fortes réductions de la densité du phytoplancton. Cependant, les effets indirects de cette espèce envahissante sur les autres groupes trophiques sont variables et difficiles à interpréter. Dans certains lacs, les moules zébrées semblent avoir peu d'effet sur la densité du zooplancton, malgré le déclin de l'abondance du phytoplancton qui leur sert de nourriture. Des modèles de réseaux alimentaires nous permettent de vérifier les mécanismes suggérés pour expliquer l'absence d'effets significatifs des dreissenidés sur le zooplancton. Nos résultats montrent que ni la réduction de l'interférence des algues non comestibles sur la filtration du zooplancton, ni la diminution de l'auto-ombrage par le phytoplancton ne sont assez importantes pour expliquer que les populations de zooplancton ne soient pas affectées par la compétition des dreissenidés. Plutôt, l'impact des filtreurs benthiques est influencé par le degré de brassage dans le bassin, ce qui limite l'apport de phytoplancton au benthos. L'examen des prédictions d'un modèle simple à structure spatiale nous permet de démontrer que des différences dans les facteurs abiotiques qui contrôlent le brassage peuvent amener des différences importantes dans les effets directs et indirects de la filtration des moules zébrées.

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Introduction

Biological invasions pose a serious threat to native biodiversity as well as humans' ability to manage ecosystems for recreation and resource exploitation, yet managers are often unable to prevent the arrival of new species (Czech and Krausman 1997; Mack et al. 2000; Pimentel et al. 2000). Understanding and predicting the effects of exotic species are therefore crucial research goals (Parker et al. 1999). The direct effects of exotic species are often obvious, e.g., the replacement of competitors or the extirpation of prey. However, the indirect effects of exotics can be unexpected and the causal links may be difficult to demonstrate.

The introduction of dreissenid mussels to North America is an excellent example of an invasion with dramatic direct

effects and multiple hypothesized indirect effects (Nalepa and Schloesser 1993; Strayer et al. 1999). Zebra mussels (*Dreissena polymorpha*) were first reported in Lake St. Clair in 1989 (Hebert et al. 1989) and have since established populations in several drainages of eastern North America (Johnson and Carlton 1996). In shallow bays and lake basins with dense mussel populations, estimates of total filtering rate are extremely high. For instance, Bailey et al. (1999) estimated the time to filter the entire water column in part of the Bay of Quinte, Lake Ontario, to be as short as 0.05 days. Not surprisingly, in areas with sufficient suitable benthic habitat to support dense mussel populations, dreissenid filtering is generally associated with declines in phytoplankton abundance (e.g., Leach 1993; Nalepa et al. 1999; Idrisi et al. 2001). In contrast, despite potentially strong competition be-

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tween dreissenids and zooplankton for phytoplankton, impacts on zooplankton vary from site to site. In some lakes, sampling data show no significant change in zooplankton density after dreissenids invade, despite decreases in phytoplankton density over the same time period (Wu and Culver 1991; Idrisi et al. 2001). Indeed, Wu and Culver (1991) suggested that zooplankton continued to control phytoplankton dynamics in the western basin of Lake Erie even after the establishment of dense zebra mussel beds. This interpretation has been challenged (MacIsaac et al. 1992; Nicholls and Hopkins 1993), and other investigators have suggested that zooplankton declined in response to a dreissenid invasion in some systems (e.g., Bridgeman et al. 1995; Johannsson et al. 2000).

Two general types of mechanisms might explain the absence of a consistent negative effect of zebra mussel invasions on zooplankton abundance. The first type involves indirect positive effects on phytoplankton productivity that offset the increased consumption of phytoplankton by dreissenids. For instance, Padilla et al. (1996) constructed a food web model and predicted that zebra mussel filtering would disproportionately lower the density of phytoplankton taxa that are inedible to zooplankton, thereby relaxing nutrient competition and increasing zooplankton foraging efficiency, thus permitting a less abundant but more productive and edible phytoplankton community to support equal or even higher abundances of zooplankton. A second example of this sort of mechanism is provided by Idrisi et al. (2001), who suggested that the increases in water clarity that accompany mussel colonization could stimulate phytoplankton productivity, thus maintaining existing zooplankton abundances.

The second class of mechanism involves physical factors that potentially constrain the direct effects of mussel filtering on phytoplankton populations. In particular, zebra mussels attached to the benthos are isolated to some degree from their pelagic prey. Studies of vertical chlorophyll profiles and mussel ingestion rates in the field suggest that mussels re-filter the lower portion of the water column more rapidly than phytoplankton are delivered by mixing, and this might play a critical role in determining the impact of mussels on phytoplankton (MacIsaac et al. 1999; Yu and Culver 1999; Ackerman et al. 2001). Furthermore, dense dreissenid populations typically occur on hard substrates, and these can be patchily distributed across the bottom of a lake. Hence, mussel consumption of phytoplankton may be limited by vertical and horizontal mixing of the water column.

We evaluate these hypotheses using two food web models. First, we derive predictions for the effects of dreissenid invasions on the equilibrium abundances of zooplankton, phytoplankton, and phosphorus in a simple, well-mixed model of the pelagic food web. We then modify the model to incorporate inedible algal interference and phytoplankton self-shading and determine the effects of these mechanisms by comparison with results from the basic model. Using the western basin of Lake Erie as a case study, we show that primary production is insufficient to support the planktonic food web in the presence of a dense population of zebra mussels filtering a well-mixed water column. Next, we address the hypothesis that isolation of mussels from their pelagic prey limits the effect of dreissenids on zooplankton. We introduce simple spatial structure to the model and explore the effects

of water column mixing on the food web response to dreissenid filtering. We show that benthic–pelagic structure can explain why dreissenid invasions do not produce a strong, consistent response in the zooplankton community. We predict that the responses of phytoplankton and zooplankton to mussel filtering are sensitive to physical factors that determine the water column mixing rate.

Model 1: a single, well-mixed compartment

Structure

We model the dynamics of phytoplankton, zooplankton, and a limiting nutrient in a small lake basin or in a bay that is homogeneous but distinct from a larger lake. Water enters the system from rivers or runoff (inflow contains nutrients, but no organisms) and leaves at the same rate, resulting in constant volume. We assume that the limiting nutrient in the system is phosphorus and measure the abundance of all trophic groups in units of phosphorus concentration.

Throughout our analysis, we assume that dreissenid biomass is not dynamically linked to phytoplankton density. Instead, we treat mussel abundance as an independent variable and calculate its effect on the equilibrium concentrations of the other food web components. Our rationale is that dreissenids are limited by suitable hard benthic substrate. Dreissenid density has been observed to fluctuate within these habitats (Nalepa et al. 1995), and dreissenids have colonized some areas with soft sediment (Dermott and Munawar 1993; Coakley et al. 1997; Berkman et al. 1998); however, differences in suitable habitat appear to be the primary determinant of differences in mussel abundance among lake regions (Mellina and Rasmussen 1994).

We divide phytoplankton into two classes based on whether they are too large to be ingested by cladocerans. Characteristics of the two phytoplankton groups generate a trade-off between vulnerability to zooplankton filtering and competitive ability: small phytoplankton, which are edible to zooplankton, are superior to large phytoplankton in nutrient competition (reviewed in Andersen 1997).

We provide a brief description of the key model components here; the full equations appear in Table 1 and the parameters are defined in Table 2. The model describes the dynamics of available phosphorus (R), large (L) and small (S) phytoplankton, and zooplankton (Z) in terms of the concentration of phosphorus associated with each of these components. The rate of change in R is the sum of contributions from abiotic processes (inflow and outflow) and biotic processes (plankton growth and phosphorus recycling):

$$(1) \quad dR/dt = I_R + E_R - G_R - O_R$$

where I_R is inflow, O_R is outflow, E_R is the sum of excretion and other losses from all organisms, and G_R is phytoplankton population growth. Dynamics of small and large phytoplankton are determined by the difference between population growth (G_S, G_L) and losses to filtering (F_S, F_L), outflow (O_S, O_L), and sinking and other mortality (E_S, E_L):

$$(2) \quad dS/dt = G_S - F_S - E_S - O_S$$

$$(3) \quad dL/dt = G_L - F_L - E_L - O_L$$

Table 1. Dynamic equations for the four components of the food chain model: available phosphorus (*R*), edible phytoplankton (*S*), inedible phytoplankton (*L*), and zooplankton (*Z*).

Available phosphorus, <i>R</i>	
$\frac{dR}{dt} = I_R + E_R - G_R - O_R$	
Inflow	$I_R = QR_{in}$
Total plankton losses	$E_R = l_S S + l_L L + l_Z Z + \frac{(1 - \epsilon)a_S S Z}{1 + a_S T_S S + a_L T_L L} + fbM(S + L)$
Total phytoplankton growth	$G_R = G_S + G_L$
Outflow	$O_R = QR$
Edible phytoplankton, <i>S</i>	
$\frac{dS}{dt} = G_S - F_S - E_S - O_S$	
Growth	$G_S = \frac{v_S SR}{k_S + R}$
Filtering loss	$F_S = \frac{a_S SZ}{1 + a_S T_S S + a_L T_L L} + bMS$
Other losses	$E_S = l_S S$
Outflow	$O_S = QS$
Inedible phytoplankton, <i>L</i>	
$\frac{dL}{dt} = G_L - F_L - E_L - O_L$	
Growth	$G_L = \frac{v_L LR}{k_L + R}$
Filtering loss	$F_L = bML$
Other losses	$E_L = l_L L$
Outflow	$O_L = QL$
Zooplankton, <i>Z</i>	
$\frac{dZ}{dt} = G_Z - E_Z - O_Z$	
Growth	$G_Z = \frac{\epsilon a_S SZ}{1 + a_S T_S S + a_L T_L L}$
Losses	$E_Z = l_Z Z$
Outflow	$O_Z = QZ$

Note: Each component is expressed in terms of the concentration of phosphorus associated with that component. Each process contributing to the overall dynamics of a component is separately defined. Reasonable values for the parameters that govern these processes are listed in Table 2.

Finally, zooplankton density increases with filtering (G_Z) and decreases due to outflow (O_Z) and excretion and other mortality (E_Z):

$$(4) \quad dZ/dt = G_Z - E_Z - O_Z$$

The functions in eqs. 1–4 are based on a set of assumptions regarding phosphorus transfer between trophic groups. First, we assume constant inflow phosphorus concentration (R_{in}) and inflow volume per day (q). If basin volume (V) is constant, inflow and outflow rates are identical. Hence, the outflow loss term for each model component is proportional to the concentration of that component in the lake (e.g., $O_S = QS$, where $Q = q/V$ is identical for all components in the model), and inflow of available phosphorus is $I_R = QR_{in}$.

Phytoplankton growth follows the Monod model; for small phytoplankton, with maximum growth rate v_S and half-saturation concentration k_S ,

$$(5) \quad G_S = \frac{v_S RS}{R + k_S}$$

The expression for G_L is equivalent, with subscripts changed appropriately.

We model zooplankton filtering with a type 2 functional response. We assume that large phytoplankton can interfere with zooplankton filtering, but that zooplankton can not ingest large phytoplankton. Hence, zooplankton spend time handling large phytoplankton but do not directly affect large phytoplankton dynamics. For attack rates a_S and a_L on small

Table 2. Parameter estimates for the western basin of Lake Erie.

Parameter	Description (units)	Value
l_S	Loss rate from edible phytoplankton (day^{-1})	0.01
l_L	Loss rate from inedible phytoplankton (day^{-1})	0.01
l_Z	Loss rate from zooplankton (day^{-1})	0.31
ϵ	Zooplankton assimilation efficiency (unitless)	0.54
a_S	Zooplankton attack rate on edible phytoplankton ($\text{L} \cdot (\mu\text{g P} \cdot \text{day})^{-1}$)	0.18
a_L	Zooplankton attack rate on inedible phytoplankton ($\text{L} \cdot (\mu\text{g P} \cdot \text{day})^{-1}$)	Variable
T_S	Zooplankton handling time for edible phytoplankton (days)	0.32
T_L	Zooplankton handling time for inedible phytoplankton (days)	0.32
v_S	Edible phytoplankton maximum phosphorus uptake rate (day^{-1})	1.8
k_S	Edible phytoplankton half-saturation phosphorus concentration ($\mu\text{g P} \cdot \text{L}^{-1}$)	0.7
v_L	Inedible phytoplankton maximum phosphorus uptake rate (day^{-1})	0.8
k_L	Inedible phytoplankton half-saturation phosphorus concentration ($\mu\text{g P} \cdot \text{L}^{-1}$)	0.7
f	Fraction of phosphorus consumed by mussels that is returned to the water column (unitless)	1
R_{in}	Inflow phosphorus concentration ($\mu\text{g P} \cdot \text{L}^{-1}$)	33
Q	Water outflow rate (day^{-1})	0.02
b	Mussel filtering rate ($\text{L} \cdot \text{day}^{-1}$)	Variable
M	Mussel density (L^{-1})	Variable

Note: See Appendix B for sources.

and large phytoplankton, respectively, handling times T_S and T_L , and assimilation efficiency ϵ ,

$$(6) \quad G_Z = \frac{\epsilon a_S S Z}{1 + a_S T_S S + a_L T_L L}$$

We do not explicitly model losses to higher trophic groups (e.g., fish predation on zooplankton) to keep the model simple. However, if the population dynamics of these groups are not tightly linked over the seasonal time scale of plankton dynamics, such consumption may be treated as part of the loss terms (e.g., E_Z).

We make two simplifying assumptions regarding dreissenid filtering. First, we model dreissenid filtering with a type I functional response, with attack rate b . Although dreissenid filtering rate decreases when phytoplankton density exceeds a threshold value (Walz 1978; Sprung and Rose 1988; Berg et al. 1996), this threshold is typically greater than the densities in systems considered here, and explicit consideration of the threshold does not affect our results. Second, we assume dreissenids filter small and large phytoplankton groups indiscriminately. Although there is evidence of selectivity among phytoplankton species, it generally occurs at the stage of rejection in pseudofeces (Ten Winkel and Davids 1982; Horgan and Mills 1997; Bastviken et al. 1998) after cells and colonies have been removed from the water. However, Vanderploeg et al. (2001) found that toxic *Microcystis* colonies rejected by zebra mussels could return to the water column and suggested that such filtering selectivity could facilitate *Microcystis* blooms. This situation involves a radical shift in the plankton food web not considered in this paper.

The final set of transfers involves phosphorus recycling. For simplicity, we assume that all phosphorus losses from planktonic groups (excretion, sinking, zooplankton egestion, etc.) return directly to the available phosphorus pool. In contrast, we allow a variable fraction (f) of mussel filtrate to be recycled, whereas the remainder ($1 - f$) is lost from the system via sedimentation and burial. Given these assumptions,

$$(7) \quad E_R = E_S + E_L + E_Z + \frac{1 - \epsilon}{\epsilon} F_Z + fbM(S + L)$$

where M is mussel density. A more realistic model structure would include a detritus compartment through which dead and egested material must pass before re-entering the available phosphorus pool. However, we have found through numerical simulations that the addition of a detritus compartment has little effect on our qualitative results, although the values of the equilibria depend on the rate at which detritus is recycled.

Qualitative behaviour

Here, we derive general qualitative predictions for the initial impact of the zebra mussel invasion on equilibrium plankton densities (Table 3). These predictions are simply the signs of the derivatives of the equilibria with respect to M , calculated at $M = 0$. In Appendix A, we derive conditions under which the initial impact of dreissenid invasion on the zooplankton equilibrium (Z^*) is positive ($dZ^*/dM|_{M=0} > 0$). If large phytoplankton do not interfere with zooplankton filtering ($a_L T_L = 0$), then this positive effect depends on two conditions. First, the parameter combination $(k_L - k_S)(Q + l_L)$ must be small relative to the product of large phytoplankton maximum growth rate and small phytoplankton half-saturation concentration ($v_L k_S$). The sum $Q + l_L$ will typically be small in systems such as the western basin of Lake Erie (inflow is small relative to total basin volume, large phytoplankton lose little phosphorus; see Appendix B), ensuring that this condition is met. The second condition is

$$(8) \quad \frac{v_S k_L}{v_L k_S} > 1$$

If small phytoplankton are better phosphorus competitors than large phytoplankton ($v_S > v_L$, $k_L \geq k_S$), the inequality in eq. 8 must be true. If large phytoplankton interfere with zooplankton filtering ($a_L T_L > 0$), dZ^*/dM at $M = 0$ can increase

Table 3. Equilibria for the basic model.

All present	$R^* = \frac{k_L(l_L + bM + Q)}{v_L - (l_L + bM + Q)}$ $S^* = \frac{(l_Z + Q)(1 + a_L T_L L^*)}{\epsilon a_S - a_S T_S (l_Z + Q)}$ $L^* = \left(R_{in} - \frac{(1-f)bMS^*}{Q} - (R^* + S^* + Z^*) \right) \left(1 + \frac{(1-f)bM}{Q} \right)^{-1}$ $Z^* = \left(\frac{v_S R^*}{R^* + k_S} - l_S - bM - Q \right) \left(\frac{1 + a_S T_S S^* + a_L T_L L^*}{a_S} \right)$
<i>L</i> extinct	$R^* = \left(QR_{in} + l_S S^* + l_Z Z^* + \frac{(1-\epsilon)a_S S^* Z^*}{1 + a_S T_S S^*} + fbMS^* \right) Q^{-1}$ $S^* = \frac{l_Z + Q}{\epsilon a_S - a_S T_S (l_Z + Q)}$ $Z^* = \left(\frac{v_S R^*}{R^* + k_S} - l_S - bM - Q \right) \left(\frac{1 + a_S T_S S^*}{a_S} \right)$
<i>L</i> and <i>Z</i> extinct	$R^* = \frac{k_S(bM + Q + l_S)}{v_S - (bM + Q + l_S)}$ $S^* = \frac{Q(R_{in} - R^*)}{\frac{v_S R^*}{k_S + R^*} - l_S - fbM}$

Note: As dreissenid filtering impact increases, the food chain undergoes successive simplifications as first the large phytoplankton and then zooplankton are driven to extinction (see Fig. 1). Equilibrium solutions for these simplified food chains follow the solution for the complete, native food chain. Explicit solutions can be found in each case, but extremely long solutions are left in implicit form.

or decrease with $a_L T_L$ and possibly become negative if interference is strong relative to handling time for small phytoplankton.

Direct inspection of the equation for R^* (Table 3) shows that the equilibrium concentration of available phosphorus always increases with mussel density. Furthermore, we demonstrate in Appendix A that if Z^* and R^* increase with dreissenids, then S^* and L^* must decrease.

We conclude that the initial increase in equilibrium zooplankton concentration with dreissenids does not require any of the mechanisms hypothesized to offset mussel consumption of phytoplankton. Instead, dreissenid filtering alters the competitive balance between the two phytoplankton groups. The additional mortality disproportionately affects the weaker competitor, L , and thereby increases the productivity of edible phytoplankton. The increased productivity is transferred to zooplankton biomass. This mechanism is independent of phosphorus recycling by dreissenids: the parameter f does not appear in the expression for Z^* if $a_L T_L = 0$. However, increasing f increases the filtering impact that can be withstood by the planktonic food web (see below).

Quantitative behaviour: western basin of Lake Erie

Parameterizing the model

The general qualitative predictions of the model offer a potential explanation for the apparent absence of a strong

negative effect of dreissenids on zooplankton in some systems. If mussel density (or filtering rate, b) is sufficiently low or the increase in Z^* is relatively small, the effect of dreissenids on zooplankton may be difficult to detect in survey data. We assess the plausibility of this explanation by first parameterizing the model. We then ask whether dreissenid density and filtering rate fall within the range over which equilibrium zooplankton density increases and whether the predicted increase is smaller than within-season fluctuations or measurement error.

We estimated parameter values for the western basin of Lake Erie from the literature (Table 2). Because this basin is shallow and does not stratify, its limnological features may more closely approximate a well-mixed compartment than most natural systems with zebra mussels. Furthermore, estimates of phosphorus loading, dreissenid abundance, and plankton density before and after the arrival of dreissenids are available in the literature.

We detail the parameterization in Appendix B. We use average phosphorus loading (R_{in}) for 1987–1990, i.e., 2 years before and 2 years after zebra mussels established dense populations in the western basin of Lake Erie. Lumping phytoplankton into two trophic groups necessitates some sacrifice of precision, and data for phosphorus uptake by phytoplankton species separated by edibility to zooplankton are difficult to obtain. Hence, we take the approach suggested by Andersen (1997): we use the upper and lower

quartiles of the distribution from his survey of measured species values for high and low maximum uptake rates (v_S and v_L). Wu and Culver (1991) found that two cladocerans, *Daphnia galeata* and *Daphnia retrocurva*, were the dominant zooplankton grazers during the dreissenid invasion of the western basin of Lake Erie. Our parameter values for zooplankton are based on *D. galeata*.

In our analysis, we focus on the occurrence of large and consistent deviations between observed and predicted behaviors and examine the sensitivity of these discrepancies to differences in the structure of our models. We do not present a detailed analysis of sensitivity to parameter variation for any one model structure because the effects produced, for reasonable parameter ranges, are small relative to the size of the deviations that we are interested in accounting for.

Responses of the food chain to increased mussel filtering impact

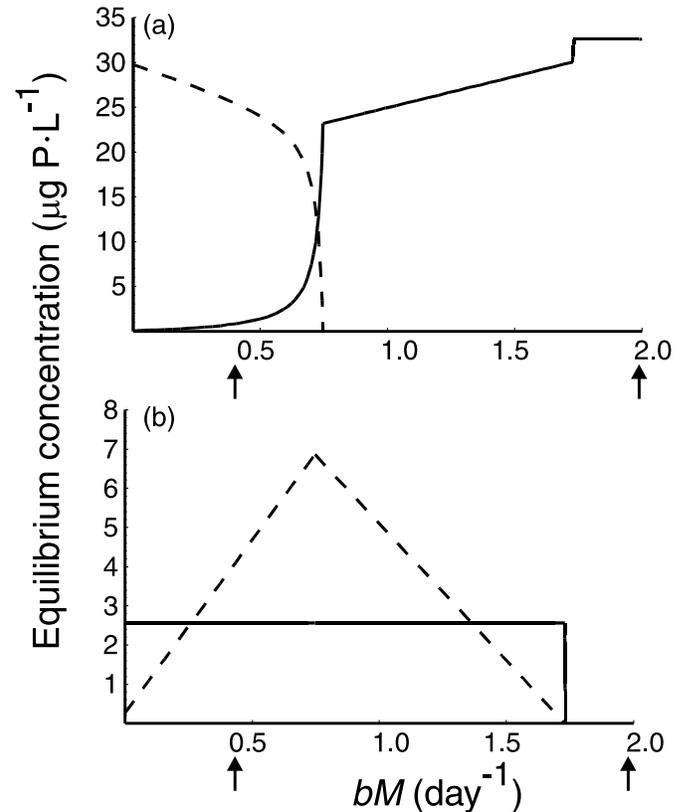
We show the predicted effects of dreissenid filtering on the equilibria for the western basin of Lake Erie (Fig. 1). Here, we use the product of mussel density and filtering rate (bM) as a measure of mussel "filtering impact". This parameter combination represents the total filtering rate of the mussel population and is equivalent to empirical measurements that incorporate effects of factors such as mussel size structure (e.g., MacIsaac et al. 1992). Filtering impact is equal to the inverse of the time required by the mussel population to filter the entire water column.

The predictions of the parameterized model are consistent with the general analysis in the previous section: as bM increases, zooplankton and available phosphorus initially increase and total phytoplankton decreases (L decreases, but S is independent of filtering impact if large phytoplankton do not interfere with zooplankton filtering). Further increases in bM drive large phytoplankton and then zooplankton extinct.

To generate Fig. 1, we let $f = 1.0$, which implies that all phosphorus consumed by dreissenids is returned to the water column via excretion or decomposition of feces, pseudofeces, and mussel biomass. Although complete recycling is unrealistic, decreasing f reduces the filtering impact that can be tolerated by the planktonic food web (all lines in Fig. 1 move to the left); hence, $f = 1.0$ gives the most conservative estimate of dreissenid effects. In simulations of the model, we found that loss of even a small fraction of phosphorus consumed by dreissenids has an extremely large negative effect on plankton productivity. We return to this issue below.

Given the density of mussels and their filtering rate, we can calculate the filtering impact for the western basin of Lake Erie, i.e., the appropriate point on the horizontal axis in Fig. 1. We can then use the model to predict the effect of the dreissenid invasion on phytoplankton and zooplankton populations. Zebra mussels primarily colonize hard substrate on reefs in the western basin of Lake Erie. This habitat is patchily distributed and makes up only approximately 15% of the total surface area of the basin (MacIsaac et al. 1992). Within these patches, mussel abundance varies widely, and surveys have found densities greater than 3×10^5 mussels·m⁻² (Leach 1993). We use population survey data from MacIsaac et al. (1992) because their density estimates are typical of samples taken during the first few years after the dreissenid invasion and they measured size structure, which has a large effect on the estimate of filtering

Fig. 1. Equilibria with parameters estimated for the western basin of Lake Erie and no inedible phytoplankton interference ($a_L = 0$): (a) solid line, available phosphorus, R^* ; broken line, large phytoplankton, L^* ; (b) solid line, small phytoplankton, S^* ; broken line, zooplankton, Z^* . For high filtering impact (bM), $S^* \rightarrow 0$ and $R^* \rightarrow R_{in}$ (not shown). Arrows indicate low and high estimates of whole-basin filtering impact. Estimates of local filtering impact are too large to be displayed in this plot.



rate (Kryger and Riisgård 1988). We calculate two estimates of filtering impact based on the local density of mussels on reefs or the average density assuming that the impact is distributed over the entire basin.

Estimates of zebra mussel filtering rate, measured in the laboratory and in the field, also vary considerably (Reeders et al. 1993). Padilla et al. (1996) used a value from Walz (1978), which is approximately in the middle of the range of 15 studies reviewed by Reeders et al. (1993, their table 1). MacIsaac et al. (1992) used the allometric scaling function for size-specific filtering rate from Kryger and Riisgård (1988). This function gives the highest value of filtering rate among the estimates compiled by Reeders et al. (1993). We compare the predictions of our model using low (Walz 1978) and high (Kryger and Riisgård 1988) estimates of filtering rate. These estimates ignore the effects of refiltration (Yu and Culver 1999); we consider the effects of incomplete mixing explicitly with the two-compartment model below.

The resulting values of local and whole-basin average filtering impact for the two filtering rate measurements are listed in Table 4. Locating these points in Fig. 1 shows that for each estimate of filtering impact, the model predicts severe impacts on large phytoplankton and zooplankton. For both estimates of local impact, zebra mussel filtering drives

Table 4. Estimates of filtering impact (bM) for the western basin of Lake Erie.

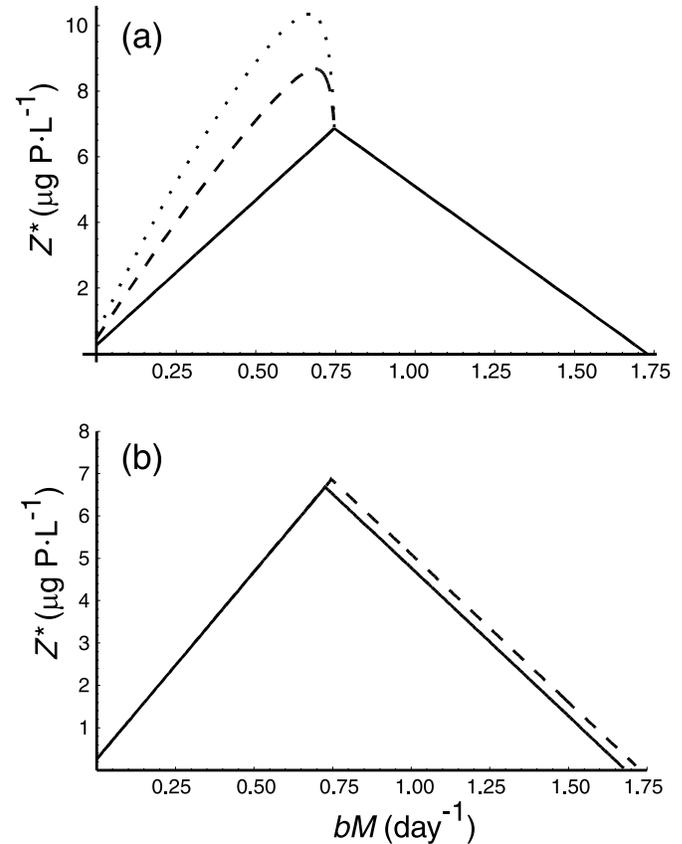
Filtering rate	Filtering impact (day^{-1})	
	Local	Whole basin
Low	2.93	0.44
High	13.3	2.0

Note: See Appendix B for sources.

zooplankton and large phytoplankton extinct. Using the larger of the averaged values gives the same result, whereas the smaller value results in zooplankton density increasing by an order of magnitude. These predictions are clearly inconsistent with survey data. Samples from the western basin of Lake Erie immediately following the dreissenid invasion show that zooplankton neither increased nor decreased significantly but generally remained within the bounds of pre-dreissenid seasonal variation (Wu and Culver 1991). Although inedible phytoplankton may have decreased relative to edible phytoplankton (Wu and Culver 1991), neither trophic group has been excluded from the community. Wu and Culver's (1991) data might have been collected before the system reached the predicted equilibrium values; however, more recent data (e.g., Johannsson et al. 2000) from the western basin of Lake Erie confirm that zooplankton have neither increased nor crashed.

Model behaviour before the mussel invasion also deviates significantly from observed behaviour. Predicted equilibrium phytoplankton densities in the absence of zebra mussels are roughly an order of magnitude higher than the densities observed just before the zebra mussel invasion: given $bM = 0$ and the parameter values in Table 2, predicted values for R^* , S^* , L^* , and Z^* are 0.027, 11, 21, and $0.67 \mu\text{g P}\cdot\text{L}^{-1}$, respectively; thus the value for $S^* + L^*$ is approximately eight times the value of $4 \mu\text{g P}\cdot\text{L}^{-1}$ that Leach (1993) observed in the western basin of Lake Erie in 1988 (conversion from $\mu\text{g chlorophyll (chl)}\cdot\text{L}^{-1}$ to $\mu\text{g P}\cdot\text{L}^{-1}$ assuming the 1:1 P-to-chl ratio given by Reynolds 1984) and is approximately three times the value of $12 \mu\text{g P}\cdot\text{L}^{-1}$ summer chlorophyll expected, given the input phosphorus concentration for our model ($R_{\text{in}} = 33 \mu\text{g P}\cdot\text{L}^{-1}$) and the Dillon–Rigler (Dillon and Rigler 1974) statistical relationship linking spring phosphorus concentrations to summer chlorophyll densities. This discrepancy can be easily explained. When $bM = 0$, our model is structured so that the total phosphorus concentration in the water ($R^* + S^* + L^* + Z^*$) must equal the inflow concentration (R_{in}). Although predicted R^* and Z^* values (0.027 and $0.67 \mu\text{g P}\cdot\text{L}^{-1}$, respectively) may be too small compared with pre-dreissenid data (e.g., zooplankton biomass on the order of $100 \mu\text{g}\cdot\text{L}^{-1}$ dry mass (Wu and Culver 1991) or approximately $1.8 \mu\text{g P}\cdot\text{L}^{-1}$, using the conversion factor from Peters and Rigler (1973)), altering parameter values to redistribute phosphorus such that S^* and L^* take on smaller, more reasonable values would clearly make the values for R^* and Z^* too large. Hence, the most likely explanation for the discrepancy between model predictions and data for pre-dreissenid invasion phytoplankton densities is that in the real system, phosphorus accumulates in components (e.g., detritus) that are not explicitly represented in our well-mixed model. However, if a phosphorus diversion of this sort is introduced into our model, we find that the sensitivity of both phyto-

Fig. 2. (a) Effect of large phytoplankton interference on equilibrium zooplankton concentration, Z^* : solid line, $a_L = 0$; broken line, $a_L = 0.5a_S$; dotted line, $a_L = a_S$. All three lines are identical for $bM > 0.75$ ($L^* = 0$). (b) Effect of self-shading on zooplankton equilibrium. Broken line indicates Z^* without self-shading. Predictions with and without self-shading are identical for $bM < 0.73$ ($L^* > 0$ in the model with self-shading).



plankton and zooplankton to mussel filtering is greatly increased, thus exacerbating the discrepancy between observed and predicted behaviour already noted above.

We now ask whether additional positive effects on either zooplankton feeding efficiency (i.e., reduction in feeding interference by inedible zooplankton) or phytoplankton productivity (i.e., reduction of phytoplankton self-shading) arising from declines in phytoplankton abundance could be sufficient to decrease the sensitivity of the zooplankton community to mussel filtering (i.e., expand the range of filtering impacts that zooplankton can withstand; Fig. 1).

Inedible phytoplankton interference is simply time spent by zooplankton handling inedible phytoplankton. In the basic model, this is represented by $a_L T_L > 0$. The effects of including interference in the model are displayed in Fig. 2a. We let $T_L = T_S$ and vary the attack rate, a_L . As $a_L T_L$ increases, the potential for dreissenid filtering to reduce interference increases and the initial positive effect of dreissenids on zooplankton increases. However, including interference in the model does not affect the value of filtering impact at which $Z^* = 0$.

Self-shading reduces the phytoplankton population growth terms, G_S and G_L . We apply the self-shading function used by Padilla et al. (1996), which was described by Carpenter

(1992). This function reduces G_S and G_L in proportion to the total phytoplankton density, $S + L$. For small phytoplankton,

$$(9) \quad G_S = \left(\frac{v_S SR}{k_S + R} \right) \left(1 - \frac{S + L}{z} \right)$$

where $z = 97 \mu\text{g P}\cdot\text{L}^{-1}$ for the western basin of Lake Erie (8 m average depth; see Carpenter 1992). The expression for G_L is also multiplied by the term $1 - (S + L)/z$.

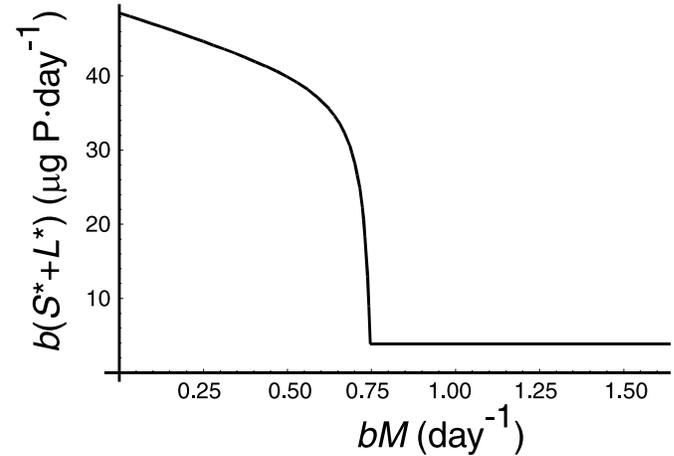
As mussel filtering impact increases, phytoplankton density decreases, and this reduces self-shading. However, this modification of the basic model has only minor quantitative effects on the predictions for Z^* (Fig. 2b). Over the range of filtering impact for which $L^* > 0$, the predictions for Z^* are identical. In this region, self-shading decreases large phytoplankton density, but small phytoplankton benefit from higher concentrations of available phosphorus. This compensation for the reduction of primary production by self-shading maintains zooplankton at the same density whether the self-shading effect is present or absent in the model. Once the filtering impact exceeds the level sufficient to drive the large phytoplankton to extinction, we see a relatively small reduction in the productivity of the small phytoplankton that remain. This is reflected in a small reduction in equilibrium zooplankton abundance and, consequently, reduction in the filtering impact sufficient to drive zooplankton to extinction.

Predicted mussel ingestion rates and expected mussel food requirements

Our results suggest that the dreissenid population in the western basin of Lake Erie is capable of consuming primary production rapidly enough to drive zooplankton and even some phytoplankton taxa extinct, yet such extinctions have not been observed. A possible explanation for this discrepancy between model predictions and field observations is that gross overestimates of mussel ingestion rates are obtained when measured mussel filtering rates are simply multiplied by average water column phytoplankton densities. To examine this possibility, we compared mussel ingestion rates predicted using this approach with an estimate of the food requirements of a typical mussel, as derived from the dreissenid energy budget developed by Stoeckmann and Garton (1997). This energy budget is based on laboratory measurements of respiration plus field estimates of total growth and reproductive investment in the western basin of Lake Erie. It provides an estimated daily ration of $3.85 \text{ cal}\cdot\text{day}^{-1}$ for an individual mussel in the field and this converts to $0.15 \mu\text{g P}\cdot\text{day}^{-1}$, using the following conversion factors: $1000 \text{ cal}\cdot\text{g}^{-1}$ phytoplankton wet weight (Stoeckmann and Garton 1997), $0.1 \text{ g C}\cdot\text{g wet weight}^{-1}$ (Shuter 1978), and the C-P ratio of 48:1 in phytoplankton biomass (Reynolds 1984).

The ingestion rate estimate obtained by multiplying measured filtration rates (approximately $1.5 \text{ L}\cdot\text{day}^{-1}$ (Walz 1978)) and Leach's (1993) post-dreissenid invasion phytoplankton abundance measurements (monthly mean chlorophyll for 1989–1990 varies from 1 and $3 \mu\text{g}\cdot\text{L}^{-1}$) is $1.5\text{--}4.5 \mu\text{g P}\cdot\text{day}^{-1}$, an order of magnitude larger than the bioenergetics estimate of mussel food requirements. If we compare estimated consumption rates ($= b(S^* + L^*)$) from our mixed model over a range of mussel densities (Fig. 3), we obtain ingestion rates that are even higher. These unrealistically high ingestion

Fig. 3. Consumption rate per individual mussel at equilibrium phytoplankton density, using the lower estimate of filtering rate, $b = 1.5 \text{ L}\cdot\text{day}^{-1}$ (Walz 1978).



rates could stem from overestimating the mussel filtering rate (b). However, laboratory-based estimates of b are more likely to underestimate the true value, not overestimate it, because they are derived from mussels held in an unnatural environment. Furthermore, dreissenids are more likely to filter near their maximum rate (Walz 1978; Sprung and Rose 1988) when they are exposed to low food densities. Hence, we suspect the problem lies elsewhere.

Failures of the well-mixed model: a summary

The responses of our well-mixed model to a zebra mussel invasion failed to match many of the observed responses of the western basin of Lake Erie to the mussel invasion that began there in 1989. Some of the more instructive failures are listed here. (i) The model predicts that zooplankton abundance will increase significantly in the early stages of the invasion, when overall filtering rate is still relatively low; this was not observed. (ii) The model predicts that both zooplankton and larger species of phytoplankton will be driven to extinction by mussel filtering rates that are significantly less than those currently operating in the real system; this was not observed. (iii) Realistic phosphorus input rates produce equilibrium phytoplankton densities in the model that are an order of magnitude greater than observed; this discrepancy can be remedied by allowing some phosphorus to accumulate in a detritus pool; however, diverting phosphorus into detritus (e.g., $f < 1$) further reduces the maximum filtering impact that large phytoplankton and zooplankton can withstand. (iv) Mussel consumption rates derived from observed values for both mussel filtering rate and phytoplankton density are much larger than expected mussel food requirements.

Each of these discrepancies ultimately derives from the assumption that all of the phytoplankton in the water column are equally accessible to zebra mussel predation. This assumption denies a basic fact of zebra mussel biology, namely that they are bottom dwellers, whose access to surface water is dependent on high levels of turbulence and the absence of bottom boundary layers. In the section that follows, we extend our model to explicitly recognize the spatial separation between mussels and their prey, and we show that

Table 5. Equations for the two-compartment model.

$$\begin{aligned} \frac{dR_1}{dt} &= Q(R_{in} - R_1) + l_S S_1 + l_L L_1 + l_Z Z_1 + \frac{(1 - \epsilon)a_S S_1 Z_1}{1 + a_S T_S S_1 + a_L T_L L_1} + \mu_1(R_2 - R_1) - \frac{v_S S_1 R_1}{R_1 + k_S} - \frac{v_L L_1 R_1}{R_1 + k_L} \\ \frac{dR_2}{dt} &= Q(R_{in} - R_2) + l_S S_2 + l_L L_2 + l_Z Z_2 + \frac{(1 - \epsilon)a_S S_2 Z_2}{1 + a_S T_S S_2 + a_L T_L L_2} + \mu_2(R_1 - R_2) - \frac{v_S S_2 R_2}{R_2 + k_S} - \frac{v_L L_2 R_2}{R_2 + k_L} + fbM(S_2 + L_2) \\ \frac{dS_1}{dt} &= \frac{v_S S_1 R_1}{R_1 + k_S} - (Q + l_S) S_1 - \left(\frac{a_S S_1 Z_1}{1 + a_S T_S S_1 + a_L T_L L_1} \right) + \mu_1(S_2 - S_1) \\ \frac{dS_2}{dt} &= \frac{v_S S_2 R_2}{R_2 + k_S} - (bM + Q + l_S) S_2 - \left(\frac{a_S S_2 Z_2}{1 + a_S T_S S_2 + a_L T_L L_2} \right) + \mu_2(S_1 - S_2) \\ \frac{dL_1}{dt} &= \frac{v_L L_1 R_1}{R_1 + k_L} - (Q + l_L) + \mu_1(L_2 - L_1) \\ \frac{dL_2}{dt} &= \frac{v_L L_2 R_2}{R_2 + k_L} - (bM + Q + l_L) + \mu_2(L_1 - L_2) \\ \frac{dZ_1}{dt} &= \frac{\epsilon a_S S_1 Z_1}{1 + a_S T_S S_1 + a_L T_L L_1} - (l_Z + Q) Z_1 + \mu_1(Z_2 - Z_1) \\ \frac{dZ_2}{dt} &= \frac{\epsilon a_S S_2 Z_2}{1 + a_S T_S S_2 + a_L T_L L_2} - (l_Z + Q) Z_2 + \mu_2(Z_1 - Z_2) \end{aligned}$$

this extension permits a simple resolution of all of the discrepancies between predicted and observed behaviour that we identified in our well-mixed model.

Model II: partial mixing in a two-compartment model

Dreissenids are restricted to the bottom surface of the basin and potentially refilter the lowest portion of the water column more quickly than it mixes with water near the surface (Yu and Culver 1999; Ackerman et al. 2001). This hypothesis is supported by chlorophyll samples taken at multiple depths above mussel beds that show a gradient of increasing concentration with height for approximately 1–2 m above the benthos (MacIsaac et al. 1992, 1999; Ackerman et al. 2001). Although dreissenid filtering does not necessarily cause this gradient, low prey availability near the benthos implies that mussel filtering impact may be limited by the rate of vertical mixing. Furthermore, the patchy distribution of dreissenid populations within a basin suggests that mussel filtering impact may also be limited by horizontal mixing. These considerations suggest that there may be effective spatial separation between zebra mussels and their prey. We extend our well-mixed model to explicitly include such spatial separation in order to examine its role in moderating the impact of zebra mussel filtering on the pelagic food chain.

Structure

To analyze the effects of spatial structure on the predicted impact of mussels, we incorporate the simplest possible representation of spatial processes in our model. We divide the well-mixed compartment into two compartments, one occupied by dreissenids and the other unoccupied. Mussel filtering directly affects only the occupied compartment, but the two compartments are connected by mixing. In this struc-

ture, dreissenids are potentially limited by the rate of delivery of phytoplankton from the unoccupied to the occupied compartment. The two-compartment structure is not intended to represent true compartmentalization of lakes, such as thermal stratification, which severely restricts mixing. Rather, it is the simplest approximation to a continuously mixing basin in which localized mussel populations create differences in the effective filtering impact across space.

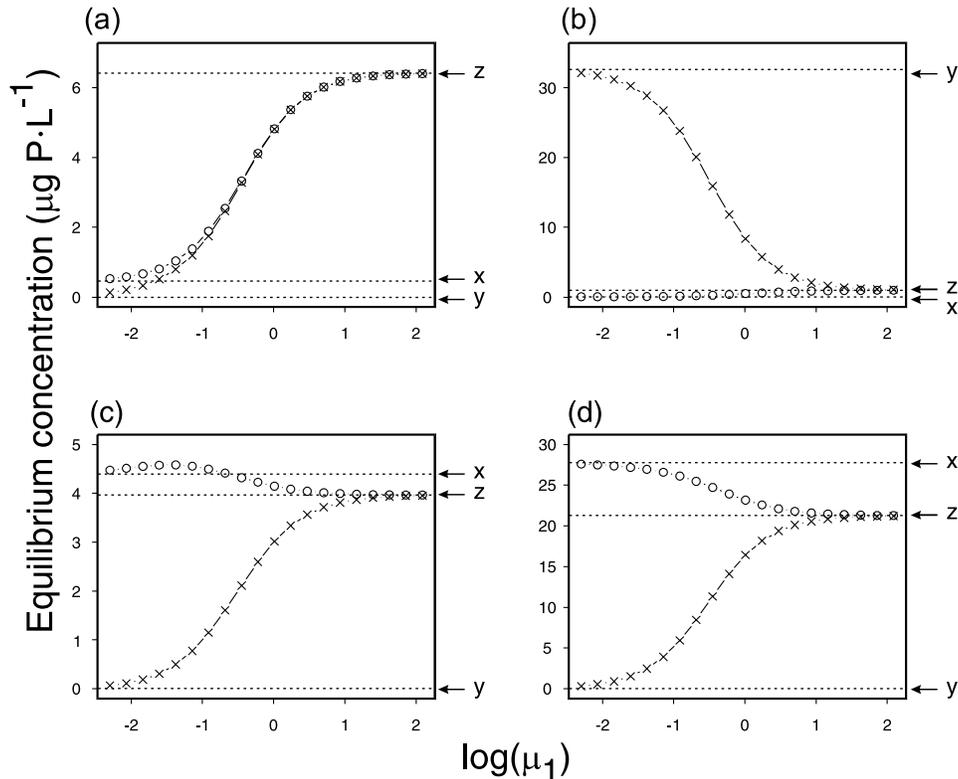
Equations for the two-compartment model are listed in Table 5. Modifications consist of splitting each food web component into populations in compartments occupied and unoccupied by zebra mussels and adding a mixing term to each equation. For simplicity, we assume that all four components have equal mixing rates between compartments and that basin inflow and outflow enter and leave the compartments in proportion to their relative volumes. The mixing rate for compartment i (μ_i) is proportional to the rate of water crossing the boundary surface shared by the two compartments, divided by the volume of the compartment:

$$(10) \quad \mu_i = \frac{\sigma A}{V_i}$$

where A is the shared surface area, V_i is the volume of compartment i , and σ is a rate coefficient (with units $\text{m}\cdot\text{day}^{-1}$).

The three parameters in eq. 10 are functions of physical characteristics of the basin that are difficult to quantify. Shared surface area and volume of each compartment depend on the fraction of the bottom of the basin that is occupied by dreissenids, the patchiness of the occupied habitat, and the fraction of the water column that is included in the occupied compartment. The mixing rate coefficient σ depends on turbulence in the water column generated by forces such as wind or currents.

Fig. 4. Equilibria for the two-compartment model as functions of water mixing rate: (a) zooplankton; (b) phosphorus; (c) small phytoplankton; and (d) large phytoplankton. We arbitrarily assume that the occupied compartment includes one-half of the water column. Relative size of the two compartments is held constant by increasing the mixing rates by the same factor, maintaining the ratio $\mu_2/\mu_1 = V_1/V_2 = (1 - (0.5)(0.15))/((0.5)(0.15)) = 12.3$ for 15% occupied surface. We set $bM = 5.86 \text{ day}^{-1}$, the lower value of the local filtering impact multiplied by 2 in order to maintain the same mussel abundance used in the original calculation of filtering impact. The whole-basin average filtering impact is therefore $bM = 5.86(V_2/(V_1 + V_2)) = 0.44 \text{ day}^{-1}$. \circ , compartment 1, mussels absent; \times , compartment 2, mussels present. Arrows and dotted lines indicate basic single-compartment model equilibria for (x) mussels absent, (y) $bM = 5.86 \text{ day}^{-1}$, and (z) $bM = 0.44 \text{ day}^{-1}$.



Qualitative behaviour

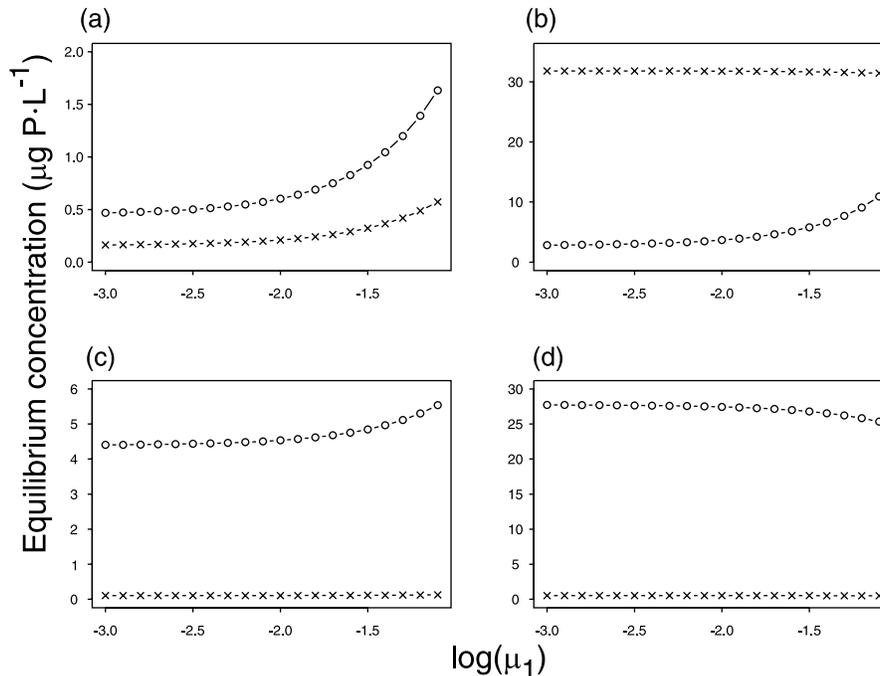
A thorough analysis of the effects of spatial structure on the model behavior is beyond the scope of this paper. Here, we present numerical solutions for the equilibria over a limited range of parameter values in order to show how mussel filtering can suppress phytoplankton populations, despite having a negligible effect on zooplankton abundance. In particular, we examine two abiotic features that are clearly linked to mussel filtering impact. First, increasing both μ_i s by the same factor increases the rate of mixing between the two compartments caused by, for example, increasing turbulence (higher σ) or more patchily distributed mussel beds (higher A). Second, increasing $\mu_1/\mu_2 = V_2/V_1$, where $i = 1$ for the unoccupied compartment and $i = 2$ for the occupied compartment, represents increasing the fraction of the bottom that is occupied or the fraction of the water column that is included in the occupied compartment, either of which increases the volume of the occupied compartment (V_2).

Equilibria calculated over a range of mixing rates with constant μ_1/μ_2 are displayed (Fig. 4). The equilibria vary between two extremes. First, with low mixing, the two compartments act approximately like isolated basins, either with or without dreissenids. Hence, the equilibria approach values calculated from the single-compartment model. In the occupied compartment, S^* , L^* , and Z^* approach zero because the

mussel filtering impact is sufficient to drive all three plankton groups extinct. In the unoccupied compartment, the equilibria approach values from the single-compartment model with $bM = 0$. As mixing increases, the two compartments act increasingly like a single well-mixed basin with mussel filtering impact diluted by the additional water volume of the unoccupied compartment.

We demonstrate the responses of the equilibria to increasing the area of the occupied compartment with filtering impact held constant (Fig. 5). Increasing the fraction of the benthos occupied by dreissenids implies that V_2 increases and V_1 decreases. If we assume that mixing increases with the proportion of benthic surface area occupied by dreissenids (i.e., vertical mixing), the ratio A/V_2 , and therefore μ_2 , are constant (eq. 10). Similarly, V_1 decreases and A increases, so μ_1 increases with occupied surface area. We fix μ_2 at a low value, where the equilibria approach values for isolated basins in Fig. 4, so spatial structure has a large effect. (For large μ_2 , the basin is approximately well mixed, and increasing the fraction of bottom surface occupied is effectively the same as increasing bM in Fig. 4.) The results in Fig. 5 demonstrate how increasing the fraction occupied by mussels enriches the unoccupied compartment with recycled phosphorus but simultaneously increases phytoplankton losses to mussel filtering in the occupied compartment. The

Fig. 5. Equilibria for the two-compartment model with increasing fraction of surface occupied (increasing μ_1/μ_2 , $\mu_2 = 0.1 \text{ day}^{-1}$): (a) zooplankton; (b) phosphorus; (c) small phytoplankton; and (d) large phytoplankton. In the occupied compartment, $bM = 5.86 \text{ day}^{-1}$ (see Fig. 4 legend). \circ , compartment 1, mussels absent; \times , compartment 2, mussels present. Equilibrium phosphorus concentration in compartment 1 multiplied by 100 for clarity.



changing balance between nutrient delivery and population losses favors the faster-growing small phytoplankton, which supports higher equilibrium zooplankton density.

We show that spatial isolation of mussels allows zooplankton and phytoplankton to persist, despite high mussel density and filtering rate, by reducing the effective filtering impact (Figs. 4, 5). However, spatial isolation reduces the positive effect of mussel filtering on zooplankton only slightly and only if mixing is low enough that the two compartments act as nearly separate basins. With such slow mixing, the effect of mussel filtering on both phytoplankton groups is weak (Fig. 4). Even at this low mixing rate, the zooplankton equilibrium increases with the fraction of benthic surface that is occupied by mussels, but the effect on phytoplankton abundance is minimal (Fig. 5). Indeed, the mechanism causing the increase in zooplankton in the single-compartment model operates in the identical fashion in the two-compartment model: mussel filtering decreases the competitive effect of large phytoplankton, which allows small phytoplankton to acquire a larger share of the available phosphorus and indirectly benefits zooplankton.

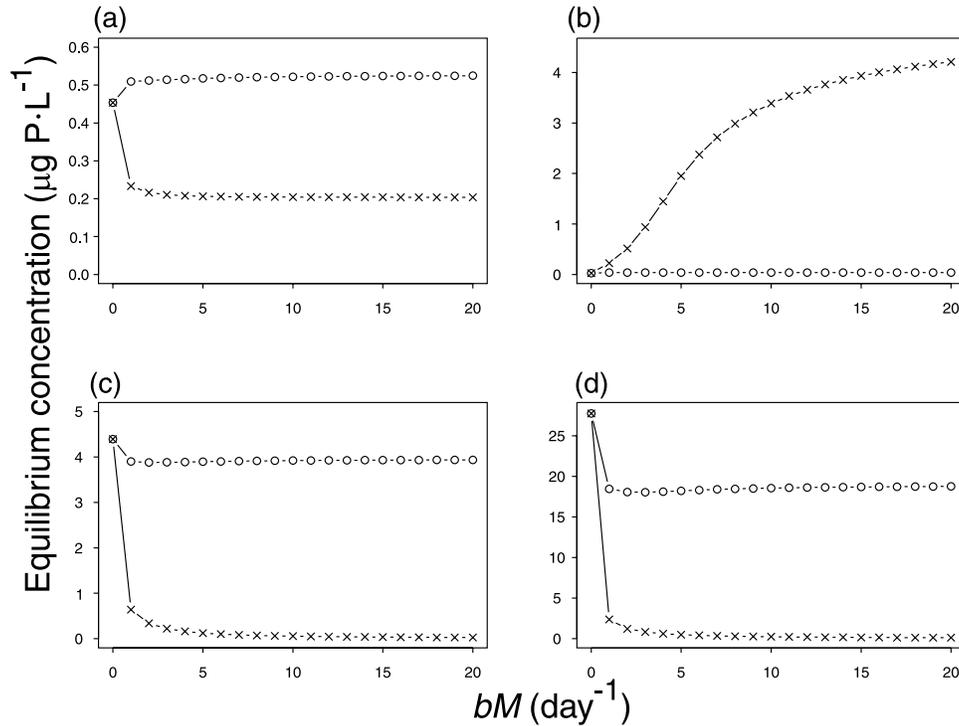
The importance of nutrient competition to predicting the effect of dreissenid filtering on zooplankton suggests that sequestration and burial of phosphorus by mussels provides a key to understanding the insensitivity of zooplankton populations to the dreissenid invasion in the western basin of Lake Erie. Although reducing the fraction of phosphorus returned to the water column by mussels quickly reduces productivity such that the planktonic food web cannot persist in the single-compartment model, spatial isolation can minimize this effect of dreissenids. We demonstrate the effect of dreissenid filtering on the equilibria for low mixing and low

fraction of phosphorus returned to the water column ($f = 0.01$; Fig. 6). Under these conditions, zooplankton density in the unoccupied compartment is insensitive to mussel filtering impact, whereas both phytoplankton groups decrease but persist for a broad range of plausible values. Most phosphorus consumed by mussels is lost from the system, and the competitive advantage of small phytoplankton over large phytoplankton is offset by reduced nutrient supply.

Discussion

We used a simple model to show that basic assumptions about plankton dynamics result in unrealistically extreme effects of dreissenid filtering. However, consideration of the spatial structure created when sessile benthic filter feeders invade a pelagic food web leads to radically different results, which are consistent with empirical data from the western basin of Lake Erie. Previous studies have suggested that dreissenid filtering impact is not simply related to mussel density, as in the well-mixed case, but also depends on local effects. For instance, Yu and Culver (1999) demonstrated that mussels refilter water more rapidly than seston is replenished by mixing and that refiltering increases with mussel clumping. MacIsaac et al. (1999) reproduced the observed vertical gradient in chlorophyll concentration over a mussel bed with a simulation model of mussel grazing and phytoplankton distribution in a continuous vertical cross section of the water column. Here, we simplified the spatial structure into distinct compartments occupied and unoccupied by dreissenids to analyze the indirect effects of mussel filtering on zooplankton and phytoplankton.

Fig. 6. Equilibria for the two-compartment model with increasing filtering impact, low phosphorus recycling by mussels ($f = 0.01$), and low mixing ($\mu_1 = 0.01 \text{ day}^{-1}$, $\mu_2 = 0.123 \text{ day}^{-1}$): (a) zooplankton; (b) phosphorus; (c) small phytoplankton; and (d) large phytoplankton. O, compartment 1, mussels absent; X, compartment 2, mussels present.



Our analysis of the single-compartment model, in which we assumed the entire water column is well mixed, demonstrated that the initial positive effect of dreissenids on zooplankton density is predicted for a broad range of conditions. This response is driven by the difference in competitive abilities of the two phytoplankton groups. Such differences have been documented in diverse taxa (reviewed in Andersen 1997). By excluding terms describing phytoplankton self-shading and inedible phytoplankton interference with zooplankton filtering, we showed that these mechanisms can contribute to the positive effect, but they are not necessary to explain it. However, the initial increase in zooplankton is not sufficient to offset high mussel filtering impact and the model predicts that zooplankton disappear from the system at filtering rates that are much lower than those that have been observed. Indeed, with a well-mixed water column, the food web cannot withstand a mussel filtering impact greater than the maximum growth rate of edible phytoplankton, and the value of this parameter (v_3) is bounded by a large body of empirical data (e.g., Andersen 1997). We conclude that even with more careful parameterization, our well-mixed, single-compartment model can not account for the observed insensitivity of zooplankton abundance to mussel filtering.

The well-mixed model developed in this paper differs from earlier work by Padilla et al. (1996) in several ways. The most important difference is in our treatment of water flow through the system and its effect on nutrients and plankton groups. We assumed that water movement through the system imposes a density-independent loss term on each component of the food web such that nutrients and all three planktonic groups flow out of the system at a rate that is

proportional to their density in the basin. This assumption is based on the expectation that the biotic and abiotic components of the model will exhibit largely passive movement with respect to water outflow from the system. In contrast, Padilla et al. (1996) assumed that biotic components remain in the system, whereas available phosphorus is flushed out at a constant rate, independent of its concentration. If the flushing rate is less than the inflow rate, the system accumulates phosphorus with time. It is difficult to see how this structure could be realized in the field; however, it is this buildup of phosphorus over the growing season that offsets phytoplankton production lost to zebra mussel filtering and thus is fundamental to the prediction of the Padilla et al. (1996) model that zooplankton will be relatively insensitive to zebra mussel filtering. In our model, the same prediction derives from the well-founded assumption that the phytoplankton community consists of edible and inedible forms of algae that compete for the same limiting nutrient. In our well-mixed model, careful accounting for phosphorus inflow and outflow leads to the prediction that the zooplankton population increases for low mussel abundance but can not withstand realistically high mussel filtering impact.

However, our model is still a highly simplified representation of the plankton community. For instance, in experiments with two zooplankton taxa with different feeding modes, Sommer et al. (2001) demonstrated an interactive effect on total phytoplankton density. Similarly, the phytoplankton community and its responses to herbivory and nutrient supply can be complex and vary spatially and temporally. Evidence from the western basin of Lake Erie suggests that, in offshore waters, the density of some phytoplankton taxa in-

creased after dreissenid invasion, whereas others decreased (Makarewicz et al. 1999; Munawar and Munawar 1999). On the other hand, Nicholls and Hopkins (1993) found that all species decreased in nearshore samples.

Nevertheless, we suggest that the mechanisms underlying the indirect effects of mussel filtering on plankton populations, revealed by our analysis of the basic model, operate in natural systems. Indeed, the predicted increase in relative abundance of edible phytoplankton in response to mussel filtering is consistent with data from the western basin of Lake Erie (Wu and Culver 1991). Furthermore, the processes that drive the counterintuitive effect of dreissenid filtering on zooplankton in the basic model are crucial to explaining our results from the spatially structured model. The ability of zooplankton to persist despite strong mussel filtering impact depends on limited delivery of phytoplankton to the benthos and phosphorus burial by dreissenids, in addition to differences in edibility and competitive ability between phytoplankton groups. Low mixing between compartments reduces the capture rate of mussels, similar to low filtering impact in the well-mixed model; however, the positive effect of low filtering impact on zooplankton is offset by phosphorus burial in the two-compartment model. These mechanisms are not specific to the two-compartment spatial structure that we have used in our model but are applicable to a continuously mixing water column.

Results from the two-compartment model support the conclusion that water column turnover time, a frequently reported measure of filtering impact (e.g., MacIsaac et al. 1992; Bunt et al. 1993; Bailey et al. 1999) that is based on the assumption that the water column is well-mixed, generally overestimates the direct effect of mussels on plankton dynamics (Yu and Culver 1999; Ackerman et al. 2001). Instead, we suggest that the realized dreissenid filtering impact is modified by abiotic features of the basin, such as turbulent mixing, depth, and spatial arrangement of suitable benthic substrate. These characteristics determine the rate of phytoplankton delivery to mussels.

Mixing rate and phosphorus recycling are probably correlated and typically low in the western basin of Lake Erie. Turbulent mixing of the water column resuspends mussel feces and pseudofeces, in which much of the captured food is deposited (e.g., Walz (1978) found that over 60% of captured phytoplankton was rejected as pseudofeces at high food concentration). Although wind at the water surface can mix the entire water column in such a shallow basin, current velocity near the benthos is often low (MacIsaac et al. 1999; Ackerman et al. 2001). The chlorophyll gradient above mussel beds observed by MacIsaac et al. (1992, 1999) and Ackerman et al. (2001) suggests a combination of filtering at the bottom surface and relatively slow turbulent mixing with upper portions of the water column.

The two-compartment model predicts that if mixing and dreissenid recycling are low, changes in mussel abundance above a relatively low density will have little effect on phytoplankton or zooplankton populations. After the invasion has surpassed this threshold, mussels capture nearly all phytoplankton that enter the occupied compartment. This prediction implies that dreissenids can be food-limited while their food is still abundant in the upper portion of the water

column, even in a shallow, unstratified basin. Alternatively, zebra mussels may obtain a substantial portion of their food from dead or sinking phytoplankton (Yu and Culver 1999) and even dissolved organic carbon (Roditi et al. 2000), which could weaken the link between mussel and phytoplankton dynamics. Knowledge of the rate at which phytoplankton are delivered to the benthos by turbulent mixing would allow estimation of the relative importance of food and suitable benthic habitat to dreissenid population regulation.

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Appendix A: response of equilibria to dreissenid invasion

First, we differentiate R^* with respect to M :

$$(A1) \quad \frac{dR^*}{dM} = \frac{k_L b v_L}{(v_L - (l_L + bM + Q))^2}$$

This expression is positive for all $M \geq 0$, so mussel invasion increases the equilibrium concentration of available phosphorus. Similarly,

$$(A2) \quad \frac{dS^*}{dM} = \frac{(l_Z + Q)a_L T_L}{a_S(\epsilon - T_S(l_Z + Q))} \frac{dL^*}{dM}$$

Because $\epsilon - T_S(l_Z + Q) > 0$ for $S^* > 0$ (Table 3), the change in the two phytoplankton groups must have the same sign.

Differentiating Z^* with respect to M and setting $M = 0$ gives

$$(A3) \quad \left. \frac{dZ^*}{dM} \right|_{M=0} = \left(\frac{v_S k_S}{(k_S + R^*)^2} \frac{dR^*}{dM} - b \right) \left(\frac{1 + a_S T_S L^* + a_L T_L L^*}{a_S} \right) + \left(\frac{v_S R^*}{k_S + R^*} - (l_S + Q) \right) \left(\frac{a_S T_S}{a_S} \frac{dS^*}{dM} + \frac{a_L T_L}{a_S} \frac{dL^*}{dM} \right)$$

where the derivatives on the right-hand side are evaluated at $M = 0$. For the case in which large phytoplankton do not interfere with zooplankton filtering ($a_L T_L = 0$), $dS^*/dM = 0$ (eq. A2) and the second term in eq. A3 disappears. With $a_L T_L = 0$, we can insert eq. A1 into eq. A3 and simplify to obtain

$$(A4) \quad \left. \frac{dZ^*}{dM} \right|_{M=0} = \left(\frac{v_S k_S v_L k_L}{((k_L - k_S)(l_L + Q) + v_L k_S)^2} - 1 \right) \times \left(\frac{1 + a_S T_S S^*}{a_S} \right) b$$

The second term in parentheses is positive if $S^* \geq 0$. If $(k_L - k_S)(l_L + Q)$ is small relative to $v_L k_S$, the first term is positive if

$$(A5) \quad \frac{v_S k_L}{v_L k_S} > 1$$

This condition is eq. 8 in the text.

Phytoplankton density ($S^* + L^*$) must decrease with M during the initial invasion because R^* and Z^* increase, and

total phosphorus in the system remains the same or decreases (if $f < 1$) with M .

Appendix B: parameterization

Water inflow and phosphorus concentration

Mellina et al. (1995, their table 1) summarize hydrological parameters for the western basin of Lake Erie. To calculate the water inflow rate, we divide average daily water inflow ($0.518 \text{ km}^3 \cdot \text{day}^{-1}$) by basin volume (28 km^3) to obtain $Q = 0.02 \text{ day}^{-1}$. For the phosphorus concentration of water inflow, we divide the average phosphorus load for 1987–1990 (Nicholls and Hopkins 1993, their table 1) by the average annual water inflow from Mellina et al. (1995). The result is $R_{in} = 33 \text{ } \mu\text{g P} \cdot \text{L}^{-1}$.

Phytoplankton

The Monod model of phosphorus uptake by phytoplankton depends on two parameters: the maximum uptake rate (v_S, v_L) and the half-saturation concentration (k_S, k_L). Based on a literature survey of parameter estimates for individual phytoplankton species, Andersen (1997) suggested that the upper and lower quartiles of the distribution are reasonable approximations for two species groups with a trade-off between competitive ability and grazer resistance. Scavia et al. (1988) and Padilla et al. (1996) present values for phytoplankton groups distinguished by their edibility to zooplankton in Saginaw Bay (Lake Huron) and Green Bay (Lake Michigan), respectively. Estimates of maximum uptake rates for edible and inedible phytoplankton in both bays are roughly equal to the upper and lower quartiles in Andersen's (1997) survey distribution. We use the upper quartile for small phytoplankton ($v_S = 1.8 \text{ day}^{-1}$) and the lower quartile for large phytoplankton ($v_L = 0.8 \text{ day}^{-1}$).

The difference between the two phytoplankton groups in their half-saturation constants reported by Scavia et al. (1988) and Padilla et al. (1996) was small relative to the difference between quartiles in Andersen (1997), which suggests that the primary competitive difference between small and large phytoplankton is in their maximum uptake rates. Although estimates of the half-saturation concentrations from Scavia et al. (1988) are consistent with Andersen's (1997) survey, the values used by Padilla et al. (1996) are an order of magnitude larger than the upper quartile of the survey distribution. This seems surprising, because the parameter represents a composite of several species and should take a typical value. Hence, we let $k_S = k_L = 0.7 \text{ } \mu\text{g P} \cdot \text{L}^{-1}$, the median of the distribution from Andersen (1997).

Phytoplankton loss to sinking and other density-independent mortality is difficult to measure. Values listed by Scavia et al. (1988) and Padilla et al. (1996) suggest the range $0-0.05 \text{ day}^{-1}$. Because the western basin of Lake Erie does not stratify, phytoplankton cannot be trapped beneath the thermocline and may be resuspended by turbulence. Hence, we use a value at the low end of the range and let $l_S = l_L = 0.01 \text{ day}^{-1}$.

Zooplankton

Zooplankton require six parameters: capture rates (a_S, a_L) and handling times (T_S, T_L) for the two phytoplankton groups, excretion rate (l_Z), and assimilation efficiency (ϵ). Our esti-

mates for these parameters are based on measurements of adult *D. galeata*. We use data from McCauley et al. (1996), who report carbon ingestion and loss rates. We convert their estimates to units of phosphorus.

We assume that the ratio of phosphorus and carbon in *Daphnia* tissue is approximately constant. Hence, we use the mass-specific maintenance rate, 0.176 day^{-1} , reported by McCauley et al. (1996) for the loss parameter l_z . This value falls within the range of phosphorus excretion rates measured directly in *D. pulex* by Olsen and Østgaard (1985).

Zooplankton capture rate and handling time for edible phytoplankton can be calculated from maximum ingestion rate (I_{\max}) and half-saturation food concentration (F_H) as $a_S = I_{\max}/F_H$ and $T_S = 1/I_{\max}$. Using the ratio P:C = 0.02 for phytoplankton (Reynolds 1984), P:C = 0.038 for *Daphnia* (Peters and Rigler 1973), and $I_{\max} = 0.025 \text{ mg C}\cdot\text{day}^{-1}$ and $F_H = 0.98 \text{ mg C}\cdot\text{L}^{-1}$ for *D. galeata* (McCauley et al. 1996), we obtain $a_S = 0.16 \text{ L}\cdot(\mu\text{g P}\cdot\text{day})^{-1}$ and $T_S = 0.32 \text{ days}$. We assume $T_L = T_S$ and $a_L = a_S$ to study the effects of inedible phytoplankton interference.

We let $\varepsilon = 0.54$, based on measurements of phosphorus assimilation efficiency by Peters and Rigler (1973).

Dreissenid filtering impact

MacIsaac et al. (1992) estimate the whole basin filtering impact per unit benthic area to be $bM = 13.9 \text{ m}^3\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. This value is based on their measurements of mussel density and size structure and on size-specific filtering rate measurements from Kryger and Riisgård (1988). We divide the estimate from MacIsaac et al. (1992) by the average depth of the western basin of Lake Erie (7 m) to obtain the volume-specific filtering impact, 2.0 day^{-1} . If 15% of the benthic surface is occupied by mussels, the local impact is 13.3 day^{-1} .

We take our lower estimate of dreissenid filtering rate from Walz (1978). Walz's estimate of b is 0.22 times Kryger and Riisgård's (1988) value. Hence, the local and whole-basin filtering impacts are 2.93 day^{-1} and 0.44 day^{-1} , respectively.