

The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes

R.E. Hecky, R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton, and T. Howell

Abstract: Dreissenid mussels have been exceptionally successful invaders in North American lakes and rivers, especially in the lower Laurentian Great Lakes. As benthic filter feeders capable of attaching to hard substrates, the magnitudes of their biomass and filtering activity in nearshore waters are without precedent. The dreissenid colonization has implications for the removal and fate of materials filtered from the water by the mussels and for the longer-term development of the nearshore benthic community and lake ecosystem. A conceptual model, the nearshore shunt, seeks to describe a fundamental redirection of nutrient and energy flow consequent to dreissenid establishment. The model explains some emergent problems in the Great Lakes, such as reemergence of *Cladophora* in some coastal zones while offshore P concentrations remain low, and highlights areas in need of more research. The source of particulate nutrient inputs to dreissenids and the fate of materials exported from the benthic community are critical to understanding the role of dreissenids in the lakes and assessing the applicability of current models for managing nutrients and fisheries. The nearshore shunt would require even more stringent P management for lakes strongly impacted by dreissenids to maintain nearshore water quality.

Résumé : Les moules dreissenidées ont envahi avec un succès exceptionnel les lacs et rivières d'Amérique du Nord, et en particulier les Grands Lacs inférieurs. Des animaux benthiques se nourrissant par filtration et capables de se fixer à des substrats durs, ils ont atteint des biomasses et des niveaux d'activité de filtration sans précédent dans les eaux côtières. La colonisation des dreissenidés a des conséquences sur le retrait et le sort des matériaux filtrés de l'eau par les moules, ainsi que sur le développement à plus long terme de la communauté benthique près du rivage et sur l'écosystème lacustre. Un modèle conceptuel, la « déviation côtière », cherche à décrire l'altération fondamentale du cheminement des nutriments et du flux d'énergie depuis l'établissement des dreissenidés. Le modèle explique certains des problèmes qui surgissent dans les Grands Lacs, comme la ré-émergence de *Cladophora* dans certaines zones côtières, bien que les concentrations de phosphore au large restent faibles et il identifie des domaines qui nécessitent des recherches supplémentaires. Une connaissance des sources des apports de particules nutritives pour les dreissenidés et du sort des matériaux exportés de la communauté benthique est essentielle pour comprendre le rôle des dreissenidés dans les lacs et pour évaluer l'applicabilité des modèles courants de gestion des nutriments et des pêches. La « déviation côtière » exigerait une gestion encore plus rigoureuse du phosphore dans les lacs fortement affectés par les dreissenidés afin de maintenir la qualité de l'eau près du rivage.

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Introduction

Emerging evidence portrays a seemingly contradictory situation in many parts of the Laurentian Great Lakes in recent years. Conditions in the offshore zones of Lake Erie, for example, were consistent in the late 1990s with attainment of the P concentration standards set by the International Joint Commission and international water quality agreements. As expected, and desired, the offshore zones appear to be mesotrophic (west basin) to oligotrophic (central and east basins) based on nutrient and plankton concentrations (Charlton et al. 1999; Makarewicz et al. 1999; Barbiero and Tuchman 2001). In contrast, the nearshore zones of the lake exhibit evidence of eutrophication, including some very negative symptoms previously associated with serious excess nutrient loading. Chief among these symptoms is the widespread abundance of the benthic filamentous alga *Cladophora*, manifested both in surveys of standing crops and in the fouling of shorelines (Howell 1998; Charlton et al. 2000; R. Hecky and T. Howell, unpublished data). Phosphorus concentrations in the Niagara River, at the outlet of Lake Erie, are anomalously high and have recently risen above concentrations observed in the 1980s (Williams et al. 2000; D.J. Williams, Environment Canada, P.O. Box 5050, Burlington, ON L7R 4A6, Canada, personal communication) even though concentrations offshore are low. The hypolimnetic O₂ regime of Lake Erie, which has remained problematic despite P loading controls, has raised concerns in recent years and moved the US Environmental Protection Agency to give it special attention. Elsewhere in the Great Lakes, algal fouling of shorelines is increasingly common even though the best assessments of P loading to Lake Erie do not suggest a consistent excess of loading over the International Joint Commission targets, nor is there evidence for recent P increases in monitored streams and rivers.

We suggest that these seemingly contradictory observations are caused by the reengineering of nutrient cycling in the nearshore zone after invasion by dreissenids. This reengineering has resulted in increased interception, retention, and recycling of nutrients by the littoral benthic community and has altered the composition of particulate material exported from the nearshore. We infer that dreissenids are very effective ecosystem engineers (Coleman and Williams 2002) and that they have created a new littoral material processing function that we call the nearshore shunt.

North American lakes have always contained benthic filter feeders that live on the bottom and remove particulate material from suspension. Soft substrates support filter feeders such as unionid clams and ephemeropterid mayflies (e.g., *Hexagenia* spp.). Hard substrates, in the more energetic littoral environments of very large lakes, supported attached filter feeders such as the larval stages of certain caddisfly (Trichoptera) species. Endemic populations of benthic filter feeders were characteristic and important parts of the aquatic food web (Shelford and Boesel 1942). Until recently, however, the filtering power of the benthic community has not been regarded by managers and modelers as large enough to exert a significant influence on particle and nutrient flux among different lake compartments, such as nearshore versus offshore retention, or water column and sediment exchange rates. Numerous investigators have emphasized the

great ability of dreissenids to divert energy and nutrients from the water column to the benthos (e.g., Griffiths 1993; Holland et al. 1995; Klerks et al. 1996) and to improve nearshore water transparency (Holland 1993; Howell et al. 1996). Less appreciated is the extent to which the attached mussels can physically alter the substratum roughness to enhance particle retention and increase surface area for attachment and growth of benthic algae and their probable effect on P partitioning between water and sediment. Dreissenids are both autogenic and allogenic engineers, as they alter the morphological and physical properties of the rocky areas and nearby areas accumulating shells, and their feeding behavior changes the nature of nearshore materials and thereby affects the availability of resources (Coleman and Williams 2002). Vanderploeg et al. (2002) delineated the physical and habitat changes that can follow dreissenid establishment; however, the implications for alteration of P cycling have not been specifically recognized. The full consequences of such P diversion to, and retention within, the nearshore are, we believe, still in the process of being fully manifested in the Great Lakes, and those consequences may well require new approaches to nutrient management in the Great Lakes.

Short-term impacts of mussels on the nearshore

The arrival of dreissenid mussels has greatly increased the biomass of benthic animals in many parts of the Great Lakes (e.g., Griffiths 1993; Howell et al. 1996; Haynes et al. 1999). It has especially increased the filtering power of the attached community, particularly on hard substrates in nearshore areas. Mussels can also attain large biomass in deeper waters and on soft substrates (e.g., Coakely et al. 1997; Dermott and Kerec 1997; Bially and MacIssac 2000), but their contact with the water column is most favorable to rapid growth, and a high rate of particle removal, in the shallower and more energetic nearshore zone where strong currents can renew suspended particle concentrations to the dreissenids (Ackerman et al. 2001). Here, also, primary productivity and local contributions of allochthonous matter from local direct runoff and streams can maintain comparatively high supplies of particles.

Rocky nearshore habitats in the Great Lakes formerly supported high standing stocks of animals (Krecker and Lancaster 1933; Shelford and Boesel 1942; Barton and Hynes 1978), but the ability of dreissenids to attach via byssal threads has permitted a vast increase in community biomass in such areas (Stewart et al. 1998), creating a nearly continuous carpet of mussels on all hard surfaces below 1–2 m depth. The accumulation of shells after mussels have died is extending the area of hard substrate and increasing the area for settlement by dreissenids, thereby autogenically reengineering local environments.

Extrapolation from laboratory measurements is difficult, but potential filtration impacts by this extensive new community on suspended particles in shallow (<10 m) waters are large relative to the preexisting benthic community and, in some cases, to the planktonic community of grazers (e.g., Arnott and Vanni 1996; MacIsaac et al. 1999). Nearshore areas of Lakes Huron, Erie, and Ontario exhibited significant decreases in phytoplankton, P, chlorophyll, and chlorophyll

to P ratios coincident with establishment of dreissenids (e.g., Fahnenstiel et al. 1995; Nicholls et al. 1999, 2002), indicating that the filtering impact of the mussels has an appreciable effect on the nearshore water column. Further offshore, evidence for significant impact of mussels on concentrations of nutrients and plankton in the water column is generally weaker and less consistent in direction (Fahnenstiel et al. 1995; Charlton et al. 1999; Makarewicz et al. 1999). Unambiguous impacts of dreissenids on the offshore water column have been observed only where the offshore itself is shallow, as in western Lake Erie, and often mixed to the bottom (e.g., Charlton et al. 1999, Makarewicz et al. 1999, Ackerman et al. 2001).

These patterns imply a dreissenid-driven increase in rates of particle and nutrient removal from the water column in dreissenid-colonized nearshore versus offshore areas. This removal may be represented as a nearshore deposition rate that is large, on an areal basis, compared with that occurring offshore or in the predreissenid benthic community (Fig. 1). Such an increase in nearshore deposition through creation of dreissenid biomass and their biodeposits can, however, also increase the loss of particulate material at the outflow of the basin because of resuspension by storms and longshore transport providing these materials to the outflow (Fig. 1b).

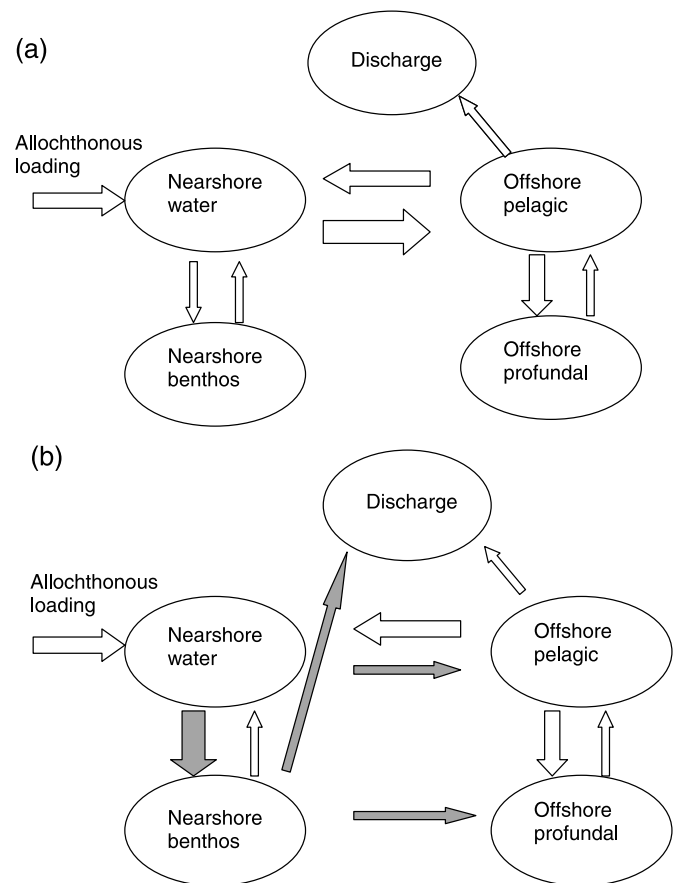
Fate of the filtered material and implications for the benthic community

Of the particulate nutrients contained in the inhalant current of mussels (approximately 0.7–1200 µm in diameter: Sprung and Rose 1988; Horgan and Mills 1997), a proportion is invested in new mussel biomass, but a large proportion is excreted in soluble form or released in particulate form as either feces or pseudofeces (see review by Schneider 1992) (Fig. 2). Much of this particulate material is then available to detritivores in the benthic community. The increase of some benthic animals, notably amphipods (Gonzalez and Downing 1999), contemporaneously with the dreissenids suggests such a benefit. In fact, a substantial community of detritivores and decomposers develops with the dreissenids (Stewart et al. 1998) and can further remineralize a significant proportion of the nutrients contained in the dreissenid wastes.

The remineralization of fecal and pseudofeces, together with direct excretion by the dreissenids, represents a potentially rich source of inorganic nutrients for benthic algae, especially attached algae preferring the same hard, rocky habitat (e.g., *Cladophora*). Dissolved nutrient release by mussels and associated benthic animals, which can be a significant component of P and N cycling (Mellina et al. 1995; Arnott and Vanni 1996; James et al. 1997) and cause increased nutrient concentrations nearshore (Holland et al. 1995), is then subject to efficient interception by the benthic algae. Enhancement of benthic plant growth by the activities of mussels (including exotic species) has been documented in coastal marine habitats (Reusch et al. 1994; Crooks 1998). We hypothesize that dreissenids have had a similar nutrient enrichment effect in the nearshore of the Great Lakes.

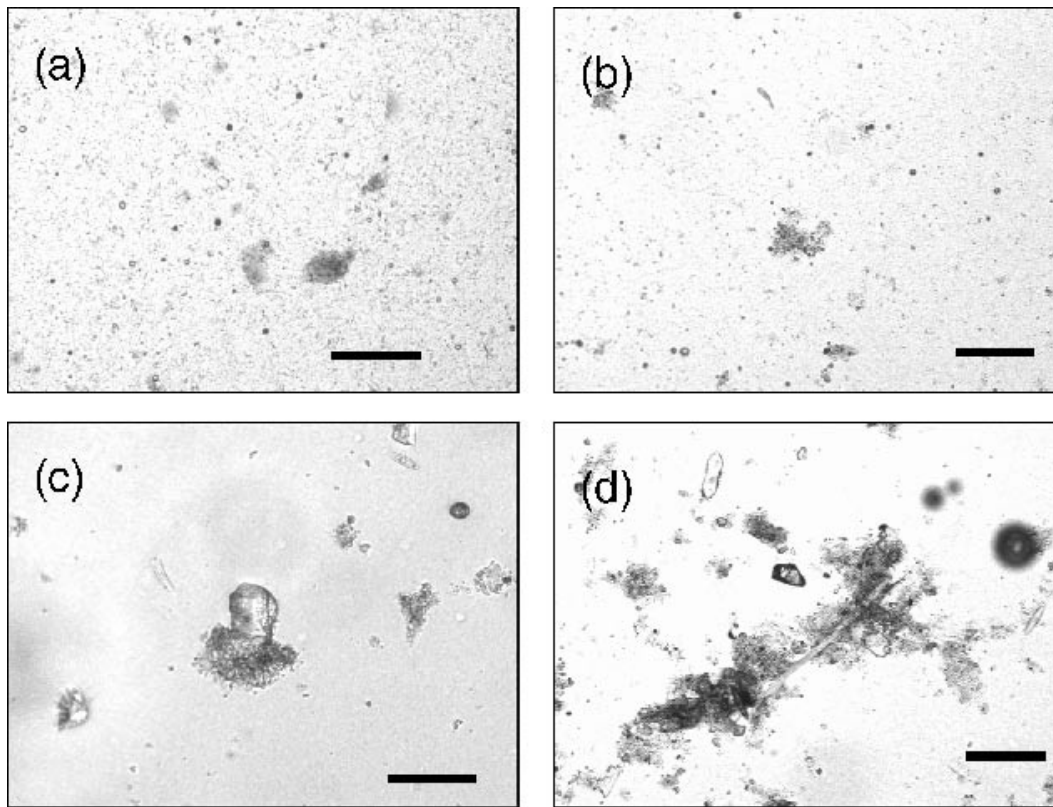
Dreissenids alter the nearshore environment in other ways that can encourage benthic algal growth. Filtration by mussels improves water clarity (Leach 1993; Fahnenstiel et al.

Fig. 1. Diagram of the nearshore shunt in which ovals represent major compartments for nutrients and arrows represent fluxes into and out of those compartments. Panels represent conditions pre- and post-dreissenid establishment. (a) Predreissenid: the nearshore retained P weakly and was a net source to the offshore pelagic, P loss was primarily by sedimentation into the offshore profundal, and concentrations in discharge were assumed to reflect those in the offshore. (b) Postdreissenid: the nearshore benthic community retains P from offshore and allochthonous sources strongly, at least during the growing season for benthic algae and mussels, and much of the P released is in larger particles that are likely to go to the outflow or directly to the profundal rather than return to the offshore pelagic. The shaded arrows highlight the fluxes that are most changed, creating the nearshore shunt, and the width of the arrow indicates the relative magnitude of the flux.



1995; Howell et al. 1996), increasing both the photosynthetic compensation depth (Lowe and Pillsbury 1995) and the illuminated area available for benthic algal growth. Dreissenids also increase the surface area available for benthic algal attachment by enhancing the roughness of the substratum and through extension of hard substrate area by accumulations of empty shells. Lastly, respiration by mussels and associated animals as well as decomposition of fecal and pseudofecal material are a new source of CO₂ in the nearshore. CO₂ can limit benthic algal and macrophyte photosynthetic rates because of boundary layer effects on the bottom and on plants (Stevenson 1988; Hecky and Hesslein 1995). Availability of CO₂ can limit benthic algal

Fig. 2. Photomicrographs of suspended matter from (a) the Grand River and (b) Lake Erie near Peacock Point (5 m depth) compared with sedimented material in chambers (c) without and (d) with dreissenids mussels feeding within the chambers. Note the increase in size and the aggregated nature of the particles in the material settling from the chamber in which mussels were feeding. Bar scale = 100 μm . Figures 2a and 2b are reproduced with permission from Brynn Upsdell and Figs. 2c and 2d from Paul Weidman, both at the Department of Biology, University of Waterloo, Waterloo, ON N2L 3G1, Canada.



photosynthesis in low-alkalinity lakes even when phytoplankton are P limited (Turner et al. 1994). In high-alkalinity situations such as the Great Lakes, CO_2 can limit macroalgal and macrophyte growth in dense stands unless the plants can produce carbonic anhydrase to allow them to access CO_2 from dissolved bicarbonate (Stevenson 1988). The increased supply of respiratory CO_2 from dense mussel beds may itself encourage increased benthic algal growth to take advantage of any increases in N and P availability from the nearshore shunt.

Through their effects on nutrient supply and physical environment, high densities of dreissenids therefore set the stage for enhanced benthic algal growth, especially the proliferation of a nuisance filamentous green alga like *Cladophora*. *Cladophora* is favored because its attachment keeps it in a nutrient-rich area, and its buoyant filaments create an upright architecture that can reduce C limitation relative to benthic microalgae. This "eutrophication" of the benthic algae can occur even if total P concentrations are relatively low in the pelagic or nearshore water columns. Observation of the rocky nearshore environment of eastern Lake Erie, for example, shows that mussels are often buried in dense *Cladophora* stands during early summer (Mitchell et al. 1996; R.E. Hecky, personal observation) that are much more luxuriant than during the mid-1970s (Howell 1998; D.R. Barton, personal observation). The roughness of

dreissenid beds and protection from bottom turbulence caused by dense *Cladophora* stands enhance sediment retention in the nearshore zone.

We hypothesize that a benthic community dominated by *Dreissena* and (or) *Cladophora* efficiently retains P in the form of biomass and detritus so that the return of P to the water column is relatively minor (Fig. 1), especially during the growing season of May–September. When this community releases material during die-offs and storms, the particles mobilized are much larger and often denser than phytoplankton, so material tends to redeposit in the nearshore or is transported downslope along the bottom. Consequently, overlying waters remain relatively clear and pelagic sedimentation may be reduced compared with pre-dreissenid conditions (Fig. 1).

The close physical association of mussels and *Cladophora* may also play a role in shaping succession of the zoobenthic community. Quagga mussels (*Dreissena bugensis*) have been shown to grow more rapidly at low food concentrations than do zebra mussels (*Dreissena polymorpha*) (Baldwin et al. 2002). The displacement of zebra mussels by quagga mussels in eastern Lake Erie, even in very shallow water (Mitchell et al. 1996; Mills et al. 1999; Diggins 2001), may reflect a general decline in food availability as a result of the filtering of the water column and retention of P by benthic algal growth. This low-food condition may have been exacerbated

by the heavy overgrowth of algae, which reduces the contact between mussels and the water column, giving a further competitive advantage to quagga mussels.

Nearshore shunt: nutrient retention and altered export pathways

The particles and nutrients harvested from the water column by the mussels may originate partly in offshore water that is advected into the nearshore region. Nonpoint sources (e.g., direct runoff and tributaries) are also an important part of the total loading to the Great Lakes (Fraser 1987) and are likely to be important to many nearshore areas especially along urbanized coasts and intensive agricultural areas. The relative magnitudes of these two sources in providing P flux into the nearshore zone where they can be taken up by benthic processes are poorly known (Fig. 1). Most of the non-point-source loading of P from runoff is in the form of fine-grained particulates (<63 μm ; Stone and English 1993) (Fig. 2a) as opposed to the large soluble fraction characteristic of point sources such as sewage treatment plants. Prior to dreissenid colonization, the finer particles bearing the exchangeable and Fe-bound phosphate were retained only briefly in the well-oxygenated nearshore before being transported and deposited offshore as fine-grained sediments (Fig. 1). Dreissenids, however, will retain such allochthonous particles more effectively. Not only phytoplankton, but also non-living, micron-sized suspended particles can be effectively removed by dreissenids (Klerks et al. 1996). Material not ingested by the mussels is nonetheless packaged into larger and more cohesive organic–mineral aggregates (Fig. 2d), whether they be feces or pseudofeces, and such aggregates will not resuspend and travel as easily as the original, smaller particles (Figs. 2a–2c). Instead, they will be retained for a time in the nearshore benthic community, if only because the increased roughness of the bottom produced by the mussels themselves provides low-turbulence zones in the beds where detritivore and decomposer activity can regenerate P. During gut passage of normally oxygenated mineral material, P firmly bound to iron oxides could also be liberated to solution in the anoxic intestinal tracts of the mussels. These dreissenid-dependent transformations will, in effect, provide new sources of available P to the nearshore environment, and particularly for benthic algae, without requiring any increase in external P loading to Lake Erie.

The enhanced trapping and recycling of formerly unavailable allochthonous P (and other nutrients), as well as trapping of pelagic P, may help explain why we are now seeing postdreissenid symptoms of nearshore eutrophication despite apparently stable P loads from point sources. If non-point-source loads have increased over the last few decades, then the increased retention and processing by dreissenids may now be making this explicit as nearshore eutrophication. By intercepting and retaining particles introduced via tributaries and direct runoff, the nearshore shunt should not only increase benthic plant growth but also result in greater spatial heterogeneity in mussel distribution. As mussels become increasingly food limited by their own high densities, greater densities of mussels should be maintained in areas influenced by these external sources of particles and nutrients.

The nearshore shunt cannot accumulate nutrients indefinitely, as these rocky habitats are nondepositional environments under high wave energies. Some flux of soluble nutrients will leave the community, unless internal cycling is 100% efficient. High retention efficiency might be realized in the summer growing season when mussels and benthic algae are active, but winter will certainly reduce their activity and reduce trapping efficiency. More importantly, trapped particles (and their nutrients) will be exported periodically, e.g., during seasonal sloughing and die-off of *Cladophora*, which occurs in midsummer. Organisms and their remains, as well as detrital material (including dreissenid feces and pseudofeces), would be important components of the export flux, although the persistence of dreissenid-generated aggregates remains to be determined. In any case, the particles would be generally larger (Fig. 2d) and less prone to remain suspended for long periods than the smaller particles characteristic of lake seston or stream and non-point-source runoff. Larger particles will tend to travel mostly during episodes of high turbulence and resuspension in the wave zone and will be subject to longshore transport that follows shorelines and depth contours, as is typical of coarser sediments. This longshore movement would account for the increasing concentrations of P, primarily in particulate form and in late fall and winter, entering the Niagara River in recent years (Williams et al. 2000) and increased accumulation of organic material in nearshore sandy sediments (Howell et al. 1996).

According to our model (Fig. 1), low total P concentrations in the pelagic offshore zone can occur even while total P concentrations in the discharge (Niagara River) are increasing, especially in the suspended phase. There will also be an offshore component to the transport of particles from the nearshore. Relatively little of the coarser material resulting from dreissenid feeding (Fig. 2d) would be expected to reside for long in the deeper and less turbulent offshore water column, but episodic downslope transport would focus this material to the deeper offshore sediments (see major export arrows, Fig. 1). These coarser particles of nearshore origin are transported with less processing time than would be characteristic of smaller and more slowly sinking lake seston. One result could be enhanced rates of O_2 consumption in offshore hypolimnetic sediments without increased productivity in the overlying pelagic water column. The apparent disappearance of *Diporeia* from portions of the Great Lakes (Landrum et al. 2000; Dermott 2001) could be a reflection of greater O_2 demand from coarser organic debris originating from the nearshore.

We hypothesize that the nearshore shunt should deprive the offshore pelagic zone of nutrients, both by intercepting allochthonous nutrient from nonpoint sources and by stripping nutrients from offshore water that may periodically be advected through the nearshore zone. Increased burial of P in coarse organic particles in nearshore sands and increased loss of particulate P at Niagara represent a net loss of P from the pelagic ecosystem. This is indicated by the imbalanced exchange of P between nearshore and offshore following dreissenid establishment (Fig. 1), especially during the prime (May–September) growing period of benthic algae and mussel feeding activity. As yet, evidence for systematic, dreissenid-associated decreases in plankton, nutrients, and

sedimentation rates in deeper offshore zones is limited, e.g., the eastern basin of Lake Erie (Charlton et al. 1999; Makarewicz et al. 1999, 2000). The enhanced export of coarser, nutrient-rich particles by downslope bed load transport to the offshore profundal zone may also lead to higher burial rates of this material and associated P than formerly. The net basin-wide effect of the repackaging of fine-grained materials into coarser feces and pseudofeces would be to accelerate P sedimentation, burial, and loss at the outflow that would result in lower dissolved P concentrations even if external loading rates are unchanged.

Current and future development of dreissenid-colonized lake ecosystems

The effects of the nearshore shunt that we describe are not the same as those of the initial colonization phase of the dreissenid community, when net mussel (and other zoobenthos) biomass accumulation was resulting in a substantial storage of P in the new littoral biomass and shell mass of mussels. What we suggest here is that the mussels have reengineered the biophysical environment in the littoral zone with profound and persistent effects on nutrient recycling, packaging, and transport. These will be permanent changes, although the strength of the shunt may vary in a complex way with mussel and benthic algal densities. This re-engineering may have critical consequences for the relative productivity of the littoral and pelagic zones and the routes and mechanisms of exchange between them. The effects would have been obscured by the profound increase in dreissenid biomass during the colonization phase of the invasion, when attention was directed to potential disruption of food webs through direct competitive effects on food resources and to the functioning of physical infrastructure such as water intakes. The effects that we hypothesize will not be fully manifested until the new, dreissenid-dominated benthic community has attained more of a steady state between nutrient accumulation and release in the reengineered littoral zone. For example, as the littoral environment retains organic material, O₂ conditions may suffer around mussel beds and beneath dense *Cladophora* stands. The development of hypoxic and anoxic zones in shallow water would further favor the release of P from fine sediments and also harbor an anoxic microflora including toxic species such as *Clostridium botulinum*, which has also recently caused alarm because of apparent increases in fish and bird kills on Lakes Ontario and Erie. This may explain why some of the hypothesized symptoms, such as nuisance growth of *Cladophora* or higher densities of fishes, including native species such as smallmouth bass (*Micropterus dolomieu*), exploiting the enhanced energy flow in the nearshore (P. Ryan, Ontario Ministry of Natural Resources, P.O. Box 429, Port Dover, ON N0A 1N0, Canada, personal communication), seem to have developed well after the initial dreissenid colonization phase.

The functioning of the nearshore shunt may also change again, of course, as additional organisms join the parade of exotic species into the Great Lakes. Prominent among these newer arrivals at present is the round goby (*Neogobius melanostomus*) that has achieved very high densities on rocky substrata (Charlebois et al. 2001; R.E. Hecky, personal observation). It might be anticipated that predation upon

dreissenids by gobies could only diminish the effectiveness of the nearshore shunt. In fact, the net effect is hard to predict, unless the gobies actually exterminate the dreissenids. For example, the in situ filtration efficiency of dreissenids in dense communities is less than that of individual specimens under less crowded conditions with better water circulation (Yu and Culver 1999). Diminished dreissenid abundance may, up to a point, be offset by increased filtering efficiency of the survivors. The gobies themselves, as exclusively bottom-dwelling fish with relatively low mobility, are part of the nearshore shunt and will contribute their own waste products to the recycling effort of the benthos. However, the gobies may be more amenable to consumption by predators, such as a variety of fish and birds, than are the dreissenids that they consume and so may facilitate alternative export pathways, especially if offshore piscivores make use of this new food resource (Schindler and Scheuerell 2002).

Research required to confirm the nearshore shunt

The nearshore shunt is still a hypothetical construct, and focused research will be necessary to verify the assumptions that we have had to make (summarized in Table 1). Several of these assumptions we consider to be well founded, particularly 1–5, although more study of nearshore conditions would strengthen our confidence and improve our ability to model these aspects. The altered cycling of nutrients and especially P (assumptions 6–9) requires specific research to establish quantitatively the link between dreissenid biodeposits and excretion and increased nutrient supply to benthic algae. The longer term (interseasonal) sedimentary fate of dreissenid biodeposits and of benthic algal material (assumptions 12 and 13) is an essential component of the nearshore shunt and the most poorly known. If biodeposits and benthic algal growth are fully regenerated annually into dissolved nutrients and mixed back into the pelagic water mass, then the net effect on offshore P concentrations and sedimentation may be negligible and the shunt only a seasonally ephemeral phenomenon. However, if the shunt leads to more rapid burial and more loss of particulate P at the outflow, then a new paradigm of P cycling will be required because lower offshore concentrations with unchanged external nutrient loading will result (assumption 13). Both laboratory and comparative field studies between lakes heavily impacted by dreissenids or with low impact, e.g., Lake Superior or northern Lake Huron, would provide tests of hypotheses formed from assumptions 5–11. Sediment transport studies, continued monitoring of the Niagara outflow, and paleolimnological studies would validate assumptions 12 and 13. The possibility of antagonistic interactions of *Cladophora* with dreissenids as they compete for space in the nearshore zone should also be examined to determine the stability of the nearshore shunt interannually. *Cladophora* and other benthic algae can benefit from the feeding activities of dreissenids, but dense growths of *Cladophora* would restrict the access of dreissenids to the overlying water column and might even asphyxiate mussels owing to low-O₂ conditions under *Cladophora* stands. The round gobies provide another negative feedback on dreissenid abundance; the temporal dynamics of these three species could result in dra-

Table 1. Assumptions necessary for the nearshore shunt to function or that can amplify its magnitude.

1	Dreissenid feeding clears a significant proportion of particulate material from pelagic, riverine, and local runoff sources
2	Dreissenid shell production increases the area available for dreissenid settlement and benthic algal attachment
3	Dreissenid feeding results in more transparent waters on average in the nearshore
4	Depth of euphotic zone increases in the presence of abundant dreissenids, as does the areal extent of well-illuminated benthic algal habitat
5	Particulate products of dreissenid feeding are larger and often denser than filtered material
6	Feces and pseudofeces of dreissenids and associated invertebrates will regenerate nutrients primarily in the nearshore
7	During the growing season, benthic algae and especially <i>Cladophora</i> will have an advantage over phytoplankton in taking up nutrients regenerated benthically by dreissenids in excretion or benthic detritivores and bacteria degrading feces and pseudofeces
8	CO ₂ regenerated from dreissenids and from benthic detritivores and bacteria can stimulate benthic algal production in the benthic boundary layer
9	Dreissenid feeding can release iron oxide bound P to solution during gut passage
10	As a result of increased transparency, increased nutrient availability, and more hard substrate (from shells), benthic algal biomass, growth, and nutrient demand become a substantial proportion of P loading
11	Increased biomass of <i>Cladophora</i> and its decomposition in the nearshore can cause local, shallow anoxia that can further release P from iron oxides in allochthonous particulate matter
12	Coarse residual feces and pseudofeces as well as detrital material from <i>Cladophora</i> will move laterally in longshore currents or downslope to deeper waters rather than be returned to the pelagic
13	An increased proportion of P loading will reside in the nearshore and be lost at the Niagara outflow and offshore P sedimentation and offshore P concentrations will decline

matic year-to-year changes in nearshore water quality conditions and the strength of the nearshore shunt.

A very important question concerns the magnitude and fate of benthic algal production, including *Cladophora*. *Cladophora* that accumulates on shorelines is obvious and obnoxious, but what eventually happens to it and other benthic algal production, how much is exported elsewhere, and its overall role in the food web of the lakes are just some of the questions requiring answers. Benthic algae, even the notoriously inedible *Cladophora*, may help explain the apparent substantial imbalance between primary production and community consumption that has been suggested to exist in Lake Erie (Johansson et al. 2000; O. Johansson, Fisheries and Oceans Canada, P.O. Box 5050 Burlington, ON L7R 4A6, Canada, personal communication; G. Sprules, Department of Zoology, University of Toronto at Mississauga, Mississauga, ON L5L 1C6, Canada, personal communication). This would imply a fundamental redirection of energy flow in the lake compared with previous, pelagic-oriented models, but we still lack good quantitative data to assess this possibility.

Implications for Great Lakes nutrient modeling

Mass balance models of nutrients in the Great Lakes, particularly for P, have been successful in describing nutrient distributions on the broad scale without reference to benthic activity or any distinctive cycling pathways in the nearshore. The nine-box model for Lake Erie is a good example (Lam et al. 1987). In the horizontal, the lake's basins are assumed to be well mixed. Particle and nutrient removal from the water column is modeled by average sedimentation coefficients that are uniform across the area of each lake basin. No differentiation is made in the model between nearshore and offshore regions, implying that concentrations are uniform across the basin and that offshore concentrations can be used to estimate loss at the outflow. External loading, although

delivered mainly to the nearshore, is assumed to be mixed uniformly across the basin. While never intended as a realistic ecological model, the success of the nine-box model in predreissenid times is demonstrable (Lam et al. 1987) and is an example of the type of model that we must have to estimate loading targets and other management criteria. Whether such well-mixed reactor models are still acceptable, despite the development of the nearshore shunt, is an important management question in the Great Lakes, as is the structure of current monitoring programs on the Great Lakes that focus almost entirely on pelagic conditions. Throughout the invasion and establishment of dreissenids and the reemergence of *Cladophora* as a concern, the offshore chlorophyll and total P concentrations have met or exceeded target concentrations set by international agreement. Consequently, the deterioration of nearshore conditions has been largely unobserved, leading to confusion and consternation in the face of public concern about these changes (e.g., McGuinness 2002; Mittelstaedt 2002).

How to manage the nearshore shunt?

The phenomenon of high-productivity communities on hard substrata in the midst of ultraoligotrophic waters is well known from coral reefs. This high production is in part maintained by effective suspension-feeding by corals from low particle concentrations and tight recycling of materials within the coral community. The dreissenids have provided the mechanism for the establishment of similar productive benthic communities even in meso- and oligotrophic lakes. Unfortunately, the relatively low biodiversity of the Laurentian Great Lakes compared with healthy coral reefs allows energy to accumulate as high standing crops in often undesirable species such as *Cladophora* and round gobies. Similarly, the role of benthic suspension-feeding mollusks in retaining and recycling nutrients from river runoff and maintaining nearshore nutrient concentrations and algal growth

has recently been shown for the nutrient Si and diatoms in a coastal marine bay (Ragueneau et al. 2002). The potential for dreissenids to perform a similar function with regard to P and *Cladophora* in the Great Lakes is clear, but the near-shore water quality implications are undesirable and the management actions required to mitigate such changes are as yet undefined but likely significant. Contaminants as well as P may be subject to retention by the nearshore shunt, which would also have implications for utilization of the burgeoning nearshore food web (Bruner et al. 1994).

We conclude that dreissenids are ecosystem engineers (sensu Coleman and Williams 2002) that substantially modify the physical habitat and whose ecological activities also change the availability of resources to other species at the ecosystem scale. Their long-term impacts will extend beyond direct competition for planktonic food resources or nuisance growths on infrastructure. Concerns about food competition have led to calls for relaxing P control in the Great Lakes to ensure adequate primary production to support fish populations. This would likely be a mistake; the nearshore shunt might effectively redirect any increase in nutrient loading into excess benthic algal growth and degradation of ecological and aesthetic conditions along Great Lakes coastlines. The long-term consequences of reengineered nutrient flows in the Great Lakes are uncertain and require focused research before any modification is made to current P control strategies. Rather than relaxing P control to offset some of the consequences of dreissenid invasion, the dreissenid-driven nearshore shunt may require increased regulation of nonpoint sources of P, which are not addressed by existing international conventions, as well as more stringent controls on point sources to maintain beneficial uses of the nearshore where most people interact with the lakes.

References

- Ackerman, J.D., Loewen, M.R., and Hamblin, P.F. 2001. Benthic–pelagic coupling over a zebra mussel reef in western Lake Erie. *Limnol. Oceanogr.* **46**: 892–904.
- Arnott, D.L., and Vanni, M.J. 1996. Nitrogen and phosphorus recycling by the zebra mussel (*Dreissena polymorpha*) in the western basin of Lake Erie. *Can. J. Fish. Aquat. Sci.* **53**: 646–659.
- Baldwin, B.S., Mayer, M.S., Dayton, J., Pau, N., Mendilla, J., Sullivan, M., Moore, A., Ma, A., and Mills, E.L. 2002. Comparative growth and feeding in zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for North American lakes. *Can. J. Fish. Aquat. Sci.* **59**: 680–694.
- Barbiero, R.P., and Tuchman, M.L. 2001. Results from the U.S. EPA's biological open water surveillance program of the Laurentian Great Lakes: I. Introduction and phytoplankton results. *J. Gt. Lakes Res.* **27**: 134–154.
- Barton, D.R., and Hynes, H.B.N. 1978. Seasonal study of the fauna of bedrock substrates in the wave-zone of Lakes Huron and Erie. *Can. J. Zool.* **56**: 48–54.
- Bially, A., and MacIsaac, H.J. 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshw. Biol.* **43**: 85–97.
- Bruner, K.A., Fisher, S.W., and Landrum, P.F. 1994. The role of zebra mussel, *Dreissena polymorpha* in contaminant cycling. II. Zebra mussel contaminant accumulation from algae and suspended particles and transfers to the benthic invertebrate *Gammarus fasciatus*. *J. Gt. Lakes Res.* **20**: 735–750.
- Charlebois, P.M., Corkum, L.D., Jude, J.D., and Knight, C. 2001. The round goby (*Neogobius melanostomus*) invasion: current research and future needs. *J. Gt. Lakes Res.* **27**: 263–266.
- Charlton, M.N., LeSage, M.N., and Milne, J.E. 1999. Lake Erie in transition: the 1990's. In *State of Lake Erie: past, present and future*. Edited by M. Munawar, T. Edsall, and I.F. Munawar. Backhuys Publishers, Leiden, Netherlands. pp. 97–124.
- Charlton, M.N., L'Italien, S., Howell, T., Bertram, P., Zarull, M., Thoma, R., and Culver, D. 2000. Review of eutrophication and undesirable algae: preliminary beneficial use impairment assessment (Lake Erie). Tech. Rep. No. 10, Lake Erie Lakewide Management Plan, Environment Canada, Burlington, Ontario, and US Environmental Protection Agency, Chicago, Ill.
- Coakely, J.P., Brown, G.R., Ioannou, S., and Charlton, M. 1997. Colonization patterns and densities of zebra mussel *Dreissena* in muddy offshore sediments of western Lake Erie, Canada. *Water Air Soil Pollut.* **99**: 623–632.
- Coleman, F.C., and Williams, S.L. 2002. Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends Ecol. Evol.* **17**: 40–44.
- Crooks, J.A. 1998. Habitat alterations and community-level effects of an exotic mussel, *Musculista senhousia*. *Mar. Ecol. Prog. Ser.* **162**: 137–152.
- Dermott, R. 2001. Sudden disappearance of the amphipod *Diporeia* from eastern Lake Ontario, 1993–1995. *J. Gt. Lakes Res.* **27**: 423–433.
- Dermott, R., and Kerec, D. 1997. Changes to the deepwater benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. *Can. J. Fish. Aquat. Sci.* **54**: 922–930.
- Diggins, T.P. 2001. A seasonal comparison of suspended sediment filtration by quagga (*Dreissena bugensis*) and zebra (*D. polymorpha*) mussels. *J. Gt. Lakes Res.* **27**: 457–466.
- Fahrenstiel, G.L., Lang, G.A., Nalepa, R.F., and Johengen, T.H. 1995. Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. *J. Gt. Lakes Res.* **21**: 435–448.
- Fraser, A.S. 1987. Tributary and point source total phosphorus loading to Lake Erie. *J. Gt. Lakes Res.* **13**: 659–666.
- Gonzalez, M.J., and Downing, A. 1999. Mechanisms underlying amphipod responses to zebra mussel (*Dreissena polymorpha*) invasion and implications for fish–amphipod interactions. *Can. J. Fish. Aquat. Sci.* **56**: 679–685.
- Griffiths, R.W. 1993. Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair. In *Zebra mussels. Biology, impacts and control* Edited by T.F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 415–437.
- Haynes, J.M., Stewart, T.W., and Cook, G.E. 1999. Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena*: continuing change. *J. Gt. Lakes Res.* **25**: 828–838.
- Hecky, R.E., and Hesslein, R.A. 1995. The importance of benthic algal carbon to food webs in tropical, temperate and Arctic lakes. *J. North Am. Benthol. Soc.* **14**: 631–653.
- Holland, R.E. 1993. Changes in planktonic diatoms and water transparency in Hatchery Bay, Bass Island area, western Lake Erie, since the establishment of zebra mussel. *J. Gt. Lakes Res.* **19**: 617–624.
- Holland, R.E., Johengen, T.H., and Beeton, A.M. 1995. Trends in nutrient concentrations in Hatchery Bay, western Lake Erie, before and after *Dreissena polymorpha*. *Can. J. Fish. Aquat. Sci.* **52**: 1202–1209.
- Horgan, M.J., and Mills, E.L. 1997. Clearance rates and filtering activity of zebra mussel (*Dreissena polymorpha*): implications for freshwater lakes. *Can. J. Fish. Aquat. Sci.* **54**: 249–255.

- Howell, T. 1998. Occurrence of the alga *Cladophora* along the north shore of eastern Lake Erie in 1995. Ontario Ministry of the Environment, Queen's Printers for Ontario, Toronto, Ont. ISBN 0-7778-8172-1.
- Howell, E.T., Marvin, C.H., Bilyea, R.W., Kauss, P.B., and Somers, K. 1996. Changes in environmental conditions during *Dreissena* colonization of a monitoring station in eastern Lake Erie. *J. Gt. Lakes Res.* **22**: 744–756.
- James, W.F., Barko, J.W., and Eaking, H.L. 1997. Nutrient regeneration by the zebra mussel (*Dreissena polymorpha*). *J. Freshw. Ecol.* **12**: 209–216.
- Johansson, O.E., Dermott, R., Graham, D.M., Dahl, J.A., and Millard, E.S. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. *J. Gt. Lakes Res.* **26**: 31–54.
- Klerks, P.L., Fraleigh, P.C., and Lawniczak, J.E. 1996. Effects of zebra mussels (*Dreissena polymorpha*) on seston levels and sediment deposition in western Lake Erie. *Can. J. Fish. Aquat. Sci.* **53**: 2284–2291.
- Krecker, F.H., and Lancaster, L.Y. 1933. Bottom shore fauna of western Lakes Erie: a population study to a depth of six feet. *Ecology*, **14**: 79–93.
- Lam, D.C.L., Schertzer, W.M., and Fraser, A.S. 1987. A post-audit analysis of the NWRI nine-box water quality model for Lake Erie. *J. Gt. Lakes Res.* **13**: 782–800.
- Landrum, P.F., Gossiaux, D.C., Nalepa, T.F., and Fanslow, D.L. 2000. Evaluation of Lake Michigan sediment for causes of the disappearance of *Diporeia* spp. in southern Lake Michigan. *J. Gt. Lakes Res.* **26**: 402–407.
- Leach, J.H. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. In *Zebra mussels, biology, impacts and control*. Edited by F. Nalepa and D.W. Schloesser. Lewis Publishers, Boca Raton, Fla. pp. 381–397.
- Lowe, R.H., and Pillsbury, R.W. 1995. Shifts in benthic algal community structure and function following the appearance of zebra mussels (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron. *J. Gt. Lakes Res.* **21**: 558–566.
- MacIsaac, H.J., Johannsson, O.E., Ye, J., Sprules, W.G., Leach, J.H., McCorquada, J.A., and Grigorovich, I.A. 1999. Filtering impacts of an introduced bivalve (*Dreissena polymorpha*) in a shallow lake: application of a hydrodynamic model. *Ecosystems*, **2**: 338–350.
- Makarewicz, J.C., Lewis, T.W., and Bertram, P. 1999. Phytoplankton composition and biomass in the offshore waters of Lake Erie: pre- and post-*Dreissena* introduction (1983–1993). *J. Gt. Lakes Res.* **25**: 135–148.
- Makarewicz, J.C., Bertram, P., and Lewis, T.W. 2000. Chemistry of the offshore waters of Lake Erie: pre- and post- *Dreissena* introduction (1983–1993). *J. Gt. Lakes Res.* **26**: 82–93.
- McGuinness, E. 2002. Stalking the critters of the deep. *Hamilton Spectator*, August 15, 2002. p. A4.
- Mellina, E., Rasmussen, J.B., and Mills, E.L. 1995. Impact of zebra mussel (*Dreissena polymorpha*) on phosphorus cycling and chlorophyll in lakes. *Can. J. Fish. Aquat. Sci.* **52**: 2553–2573.
- Mills, E.L., Chrisman, J.R., Baldwin, B.S., Owens, R.W., O'Gorman, R., Howell, T., Rosemand, E.F., and Raths, M.K. 1999. Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. *J. Gt. Lakes Res.* **25**: 187–197.
- Mitchell, J.S., Bailey, R.C., and Knapton, R.W. 1996. Abundance of *Dreissena polymorpha* and *Dreissena bugensis* in a warm water plume: effects of depth and temperature. *Can. J. Fish. Aquat. Sci.* **53**: 1705–1712.
- Mittelstaedt, M. 2002. Dead in the water. *Toronto Globe and Mail*, October 5, 2002. p. F1.
- Nicholls, K.H., Hopkins, G.J., and Standke, S.J. 1999. Reduced chlorophyll to phosphorus ratios in nearshore Great Lakes waters coincide with the establishment of dreissenid mussels. *Can. J. Fish. Aquat. Sci.* **56**: 153–161.
- Nicholls, K.H., Heintsch, L., and Carney, E. 2002. Univariate step-trend and multivariate assessments of the apparent effects of P reductions and zebra mussels on the phytoplankton of the Bay of Quinte, Lake Ontario. *J. Gt. Lakes Res.* **28**: 15–32.
- Ragueneau, O., Chayvayd, K., Leynaert, A., Thouzeau, G., Paulet, Y.-M., Bonnet, S., Lorrain, A., Grall, J., Corvaisier, R., Le Hir, M., Jean, F., and Clavier, J. 2002. Direct evidence of a biologically active coastal silicate pump: ecological implications. *Limnol. Oceanogr.* **47**: 1849–1854.
- Reusch, T.B.H., Chapman, A.R.O., and Groger, J.P. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. *Mar. Ecol. Prog. Ser.* **108**: 265–282.
- Schindler, D.M., and Scheuerell, M. 2002. Habitat coupling in lake ecosystems. *Oikos*, **98**: 177–189.
- Schneider, D.W. 1992. A bioenergetics model of zebra mussel, *Dreissena polymorpha*, growth in the Great Lakes. *Can. J. Fish. Aquat. Sci.* **49**: 1406–1416.
- Shelford, V.E., and Boesel, M.W. 1942. Bottom animal communities of the island area of western Lake Erie in the summer of 1937. *Ohio J. Sci.* **42**: 179–190.
- Sprung, M., and Rose, U. 1988. Influence of food size and food quantity on the feeding of the mussel *Dreissena polymorpha*. *Oecologia*, **77**: 526–532.
- Stevenson, J.C. 1988. Comparative ecology of submersed grass beds in freshwater, estuarine and marine environments. *Limnol. Oceanogr.* **33**: 867–893.
- Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. *J. North Am. Benthol. Soc.* **17**: 81–94.
- Stone, M., and English, M.C. 1993. Geochemical composition, phosphorus speciation and mass transport characteristics of fine-grained sediment in two Lake Erie tributaries. *Hydrobiologia*, **253**: 17–29.
- Turner, M.A., Howell, E.T., Robinson, G.G.C., Campbell, P., Hecky, R.E., and Schindler, E.U. 1994. Roles of nutrients in controlling growth of epilithon in oligotrophic lakes of low alkalinity. *Can. J. Fish. Aquat. Sci.* **51**: 2784–2794.
- Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., and Ojaveer, H. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* **59**: 1209–1228.
- Williams, D.J. Neilson, M.A.T., Merriman, J., L'Italien, S., Painter, S., Kuntz, K., and El-Shaarawi, A.H. 2000. The Niagara Rivers upstream–downstream program, 1986/87–1996/97. Report No. EHD/ECB-OR/00-01. Ecosystem Health Division, Environment Canada, Burlington, Ont.
- Yu, N., and Culver, D.A. 1999. Estimating the effective clearance rate and refiltration by zebra mussels, *Dreissena polymorpha*, in a stratified reservoir. *Freshw. Biol.* **41**: 481–492.