Nutrient Cycling by Dreissenid Mussels
Controlling Factors and Ecosystem Response

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CONTENTS

ABSTRACT

As a result of their high densities and filtration rates, dreissenid mussels are a major sink for particulate nutrients in lakes and rivers. These consumed nutrients are allocated to one of three fates: egestion as particulate feces and pseudofeces, assimilation into mussel biomass, and excretion in dissolved form. Of these three pathways, nutrient egestion and excretion are usually dominant, with the relative importance of egestion increasing when food supply is high and/or food quality is low. With the exception of several very high values, published mass-specific excretion rates generally range from 1 to 10 µmol gDW^{-1} h^{-1} for nitrogen and 0.1–2 µmol gDW^{-1} h^{-1} for phosphorus. Measured areal N excretion rates range from 155 to 624 µmol m^{-2} h^{-1}, while those for P range from 4.3 to 213 µmol m^{-2} h^{-1}. There is some evidence that P excretion rates for quagga mussels (*Dreissena rostriformis bugensis*) are lower than those for zebra mussels (*Dreissena polymorpha*). Major factors that regulate nutrient excretion include temperature, mussel size, and food quantity/quality, with reproductive stage, dissolved oxygen concentration, and substratum type also playing apparent roles. At the ecosystem scale, the effect of nutrient recycling by dreissenids is modulated by hydrodynamic processes, including vertical and horizontal mixing, which influence both the supply of phytoplankton to dreissenids and the distribution of excreted nutrients. Although the influence of dreissenids on ecosystem-scale nutrient dynamics varies among systems, common ecosystem responses include a decrease in phytoplankton abundance, a decrease in total nutrient concentrations, an increase in the dissolved nutrient to phytoplankton biomass ratio, and an increase in the biomass of benthic macroalgae. In large lakes, the alteration of nutrient dynamics by dreissenids has led to a management conundrum in which maintenance of productive pelagic fish populations and reduction of

nearshore nuisance algal blooms are apparently irreconcilable. Biogeochemical models that account for the influence of vertical and horizontal mixing processes on dreissenid grazing and nutrient excretion, as well as the long-term fate of dreissenid biomass and biodeposits, will help to define nutrient management strategies that produce an optimal balance between these two objectives.

INTRODUCTION

Within the Laurentian Great Lakes and many other North American aquatic ecosystems, there are a number of benthic organisms that obtain their food primarily through filter feeding, including clams, bryozoans, sponges, and some insect larvae. These organisms are occasionally present in locally dense aggregations, but their densities at the ecosystem scale are usually relatively low. As a result, prior to the establishment of dreissenid mussels (zebra mussel *Dreissena polymorpha*, quagga mussel *Dreissena rostriformis bugensis*), the trophic niche of benthic filter feeder was one that was largely unoccupied, and the flux of material from the water column to the lake bottom was controlled primarily by the physical processes of settling, resuspension, and advection. Benthic invertebrates were seen primarily as redistributors of material within the benthic region once sedimentation had occurred (Robbins et al. 1977).

After establishment of dreissenid populations in the Great Lakes in the late 1980s, it was almost immediately recognized that dense populations of these filter feeders had the potential to significantly influence plankton abundance and species composition. Initial studies quantified clearance and filtration rates of zebra mussels and used various approaches to extrapolate results to the ecosystem scale (MacIsaac et al. 1992, Bunt et al. 1993, Fanslow et al. 1995). Further studies refined filtration capacities by considering how the relationship between volumetric pumping rate and mass filtration rate is influenced by hydrodynamics and population density (Yu and Culver 1999, Ackerman et al. 2001, Boegman et al. 2008). While these studies led to more moderate estimates of feeding rates and ecosystem impacts, they supported the general contention that filter-feeding dreissenids have the capacity to remove significant quantities of plankton and other particulate material from lakes and rivers.

Measurements of high community filtration rates led to the realization that these organisms also had the potential to play an important role as nutrient cyclers. And so, following initial studies that focused on dreissenid filtering, there have been a number of studies that quantified nutrient excretion. The majority of these studies have measured excretion rates of dreissenids in controlled lab experiments, usually a short time after mussels were removed from their natural environment (Mellina et al. 1995, Arnott and Vanni 1996, Orlova et al. 2004, Conroy

et al. 2005, Turner 2010). Others studies have inferred quantitative or qualitative measurements of excretion rates by measuring spatial or temporal changes in natural systems (Johengen et al. 1995, Effler et al. 1997) and in mesocosms (Heath et al. 1995). Very few studies have measured excretion rates for undisturbed populations in the natural environment (Ozersky et al. 2009). In some cases, nutrient excretion rates of dreissenids have been incorporated into numerical ecosystem models, which use values obtained from empirical studies or infer values from mass balance calculations (Schneider 1992, Madenjian 1995, Mellina et al. 1995, Padilla et al. 1996, Canale and Chapra 2002).

A summary of published nitrogen (N) and phosphorus (P) excretion rates for dreissenids and other bivalves is presented in Table 35.1. The table includes recent measurements we have made for *D. r. bugensis* in Lake Michigan (Bootsma et al. unpublished). For dreissenids, the majority of studies included in Table 35.1 apply to *D. polymorpha*, as it was the dominant species in the Great Lakes until recently. However, since the displacement of zebra mussels by quagga mussels in most parts of the Great Lakes (Mills et al. 1999, Stoeckman 2003, Wilson et al. 2006, Nalepa et al. 2010), several studies have measured nutrient excretion of this more recent species. For the genus as a whole, excretion rates of dissolved P normalized to dry tissue weight (excluding shell) range from 0.08 to 3.4 µmol P gDW^{-1} h^{-1}, and excretion rates of dissolved nitrogen range from 1.4 to 26 µmol N gDW^{-1} h^{-1}. The highest P excretion rates were recorded for zebra mussels lying directly on sediment and likely represented both direct mussel excretion and sediment release (Turner 2010). If these measurements are omitted, the highest recorded P excretion rate is about 2 µmol P gDW^{-1} h^{-1}. Data presented in Table 35.1 were obtained under a large variety of experimental conditions and with a variety of measurement methods. Despite this variety, P excretion rates of quagga mussels appear to be lower than those of zebra mussels (mean quagga mussel rate = 0.33 ± 0.18 µmol gDW^{-1} h^{-1}; mean zebra mussel rate = 0.67 ± 0.56 µmol gDW^{-1} h^{-1}; $P < 0.06$). In one of the few studies to directly compare excretion rates of the two species, Conroy et al. (2005) reached this same conclusion. Lower specific excretion rates of the quagga mussel may reflect lower mass-specific clearance rates, lower respiration rates, and/or higher assimilation efficiencies of this species (Baldwin et al. 2002, Stoeckmann 2003). Zebra mussels appear to allocate a greater proportion of food intake to catabolic processes (and hence nutrient excretion), whereas quagga mussels allocate a greater proportion to tissue growth. Conroy et al. (2005) reported that N excretion rates for zebra mussels were greater than those for quagga mussels. This does not appear to be evident in our larger data set, but measurements of N excretion by quagga mussels are fewer in number than those of P excretion (Table 35.1).

Table 35.1 Nutrient Excretion Rates of Dreissenids (*D. polymorpha* and *D. r. bugensis*) and Other Bivalves

Species	Specific P Excretion	Areal P Excretion	Specific N Excretion	Areal N Excretion	Temperature (°C)	Length (mm)	Source	Notes
D. polymorpha	3.22	45.3	13.7	193	17	10–15	Turner 2010	On sediment
D. polymorpha	1.03	14.5	11.0	155	17	10–15		No sediment
D. polymorpha	0.8–2.2	43–121	3.5–7.5	222–624	18–25	<13.5	Arnott and Vanni (1996)	
	0.2–1.3		2.0–8.0			13.5–19		
	0.5–0.95		2.5–9.4			>19		
D. polymorpha		6.8–213					Orlova et al. (2004)	
D. polymorpha	0.14–0.17				17	20	Mellina et al. (1995)	
	0.32–0.37				22	20		
D. polymorpha	0.28	4.3	5.4	163	23	10–15	Conroy et al. (2005)	
D. polymorpha	0.72		26.1		23	20–25		
D. polymorpha	0.181	50.1	1.39	385	20–26		Effler et al. (1997, 2004)	Downstream vs. upstream
D. polymorpha	0.3–0.74	5.24	2.5–10.7		4–19	<14	Naddafi et al. (2008)	
	0.12–0.3		1.0–6.3		4–19	14–20		
	0.11–0.20		0.6–4.8		4–19	>20		
D. polymorpha	0.11	14.1	4.2	530	18	21	James et al. (1997)	
D. polymorpha			1.2		5.7		Quigley et al. (1993)	
			4.8		21			
D. r. bugensis	0.084	2.46			8		Ozersky et al. (2009)	
	0.361	4.15			9			
	0.265	8.11			14			
	0.195	5.47			16			
D. r. bugensis	0.55	41			7.5	17	Bootsma et al., unpublished	*In situ* measurements
	0.20	10.1			8.9	12.5		
	0.45	24.5			21	13		
	0.66	42.9			20	13.5		
D. r. bugensis	0.22		5.8		23	10–15	Conroy et al. (2005)	
D. r. bugensis	0.31		15.3		23	20–25		
L. radiata	0.042		1.16		10–23		Nalepa et al. (1991)	
L. siliquoidea	0.038–0.093		0.91–1.38		October		Davis et al. (2000)	
P. fasciolaris	0.043		1.16		July		Davis et al. (2000)	
P. fasciolaris	0.023–0.075		0.27–0.42		October		Davis et al. (2000)	
E. dilatata	0.017–0.022		0.36–0.55		October		Davis et al. (2000)	
C. fluminea	1.0				6		Lauritsen and Mozley (1989)	
	18.0				23			
A. wahlbergi	0.48		6.1		25		Kiibus and Kautsky (1996)	
M. edulis		850		320–5500	April–July		Asmus et al. (1990)	
M. edulis		50–429		1000–3700	April–September		Prins and Smaal (1994)	
M. senhousia	1.35		12.2		21	16.7	Magni et al. (2000)	
M. demissus	0.087				6–24		Kuenzler (1961)	
R. philippinarum	3.65		19.2		21	9.4	Magni et al. (2000)	
	1.05		8.6			15.5		
	0.80		4.4			18.9		
	1.45		13.3			23.5		
Various bivalves			~6.0				Table 5 of Magni et al. (2000)	

Source: Bayne, B.L. and Scullard, C. *J. Mar. Biol. Assoc. U.K.* 57, 355, 1977.
Units for specific excretion rates are μmol gDW^{-1} h^{-1}. Units for areal excretion rates are μmol m^{-2} h^{-1}. P excretion refers to the excretion of SRP, except for Mellina et al. (1995) who measured the change in total P after mussels were placed in filtered lake water. Most studies measured N excretion as $NH_3 + NH_4^+$ (see text for exceptions). This likely results in an underestimate of total N excretion because a significant amount of N may be excreted as amino acids.

FACTORS REGULATING NUTRIENT EXCRETION BY DREISSENIDS

Initial studies of dreissenid filtration rates were made with the primary objective of determining ecosystem-scale impacts that these filter feeders would have on the plankton community. Likewise, most studies of dreissenid nutrient excretion rates attempted to place rates into the context of ecosystem-scale nutrient dynamics. To do this, it is necessary to extrapolate rates over time and space, which requires knowledge of how mussel nutrient excretion responds to environmental conditions that are variable in time and space. This knowledge may also facilitate a more realistic inclusion of mussel-mediated nutrient dynamics in ecosystem-scale models. While some existing models account for nutrient excretion (Schneider 1992, Madenjian 1995, Padilla et al. 1996), few direct measurements of dreissenid nutrient excretion were available prior to development of these models, and they therefore relied on measurements made for other bivalves or on assumptions about the fraction of consumed food that is recycled as dissolved nutrients.

Recorded mass-specific N and P excretion rates vary more than an order of magnitude (Table 35.1). A full understanding of the role of dreissenids in ecosystem nutrient dynamics and how this role may be modulated by external drivers, including nutrient loading, weather conditions, and long-term climate change, must account for this variability and factors that control it. Several studies have examined factors that may potentially control dreissenid nutrient excretion rates, either by relating measured rates to environmental conditions (e.g., Arnott and Vanni 1996) or by testing the response of excretion rate to specific factors through direct experimentation. The factor that has received the greatest attention is mussel size, measured either as length or mass (Mellina et al. 1995, Arnott and Vanni 1996, Orlova et al. 2004, Conroy et al. 2005). Surprisingly, temperature effects have received relatively little attention, although its significance has been inferred in some studies (Arnott and Vanni 1996, Ozersky et al. 2009). The following is a summary of these factors and others that are most likely to play a dominant role as regulators of dreissenid nutrient excretion. In a number of cases, the relative importance of a factor is inferred from studies in which filtration rates were measured, because filtration rates and nutrient excretion rates are often correlated.

Food Quantity and Quality

Although several studies have examined the relationship between food supply and dreissenid filtration and clearance rates (Sprung and Rose 1988, Berg et al. 1996), there are virtually no studies that examine the quantitative relationship between food supply and the excretion rates of dissolved nutrients (but see Johengen et al. 2013). A positive correlation between food supply and nutrient excretion might be expected, and the range of recorded excretion rates for different water bodies appears to be explained in part by differences in phytoplankton concentrations (Arnott and Vanni 1996). However, the nature of this relationship will depend on how mussels allocate food resources to various pathways (pseudofeces, feces, tissue growth, dissolved excretion) as a function of food supply. For example, filtration rate may plateau or even decrease above a threshold food concentration (Fanslow et al. 1995), and production of pseudofeces generally increases when food concentration exceeds an incipient limiting threshold (Berg et al. 1996, Madon et al. 1998). Both of these processes will likely result in a nonlinear relationship between nutrient excretion and food supply. The nutrient excretion response to food supply will also differ from the feeding response because, while feeding rate may be dictated by food supply at very low food concentrations, excretion may be driven according to a basal metabolic rate. In fact, nutrient excretion rates may even increase at low food concentrations as a result of mussel emaciation (James et al. 2001). At this time, the paucity of data limits quantitative descriptions of the relationship between food supply and nutrient excretion. A better understanding of this relationship would be valuable to lake managers. Nutrient management strategies are guided by an understanding of the relationship between nutrient loading and algal growth, which is used to set nutrient loading and concentration targets. It now appears that, in many lakes, grazing and nutrient recycling by dreissenids have altered the way in which the algal community responds to nutrient loading, and mussels may be an important nutrient source supporting nuisance algal blooms (Hecky et al. 2004, Malkin et al. 2008, Auer et al. 2010). Any attempts to reduce the supply of nutrients from dreissenids will need to be informed by models that account for the relationship between phytoplankton biomass/composition and mussel nutrient excretion (see section on management implications in the following text).

Food quality can affect nutrient excretion rates by influencing both the amount and fate of ingested food. Various measures have been used to assess food quality. The most common measures are the inorganic–organic mass ratio, phytoplankton species composition, and seston C:N:P ratios. Madon et al. (1998) found that an increase in the inorganic–organic ratio resulted in lower clearance and ingestion rates, more pseudofeces production, and lower assimilation efficiency. Consequences of these responses for nutrient excretion are uncertain. While lower ingestion rates may result in lower nutrient excretion rates, lower assimilation efficiencies imply that a greater proportion of ingested material may be excreted, both in solid (feces) and dissolved forms. Ingestion of inorganic material is of little nutritive value to mussels, but if this inorganic material includes particulate P, this P may be released as dissolved phosphate after passing through the anoxic gut (Hecky et al. 2004).

To our knowledge, no studies have directly examined the potential effect of phytoplankton species on nutrient excretion by dreissenids. However, there is strong evidence that feeding rate is influenced by phytoplankton species composition, and therefore it is likely that there is also a nutrient excretion response. When mussels were fed monocultures of *Chlamydomonas reinhardtii* or *Pandorina morum*, Berg et al. (1996) found that clearance rates and proportions of ingested particles that were ejected as pseudofeces varied, depending on which algal species was being consumed. Both Lavrentyev et al. (1995) and Baker et al. (1998) found that the presence of *Microcystis* affected clearance rates of zebra mussels, although the former authors reported lower rates, while the latter authors reported higher rates. Combined, all these studies suggest that any relationships between food quantity and nutrient excretion rates will likely be moderated by food quality. Incorporation of these relationships into models is difficult given the limited data presently available, and it is unclear which taxonomic level of phytoplankton is mostly strongly linked to feeding selectivity. Results of the earlier studies suggest that at least some effect can be expected at the species level, but further experiments with multispecies phytoplankton assemblages are required to determine how well results of experiments with monocultures apply to natural phytoplankton communities. The contrasting findings of Lavrentyev et al. (1995) and Baker et al. (1998) suggest that dreissenid response to a given species or genus may even vary according to environmental conditions and the physiological status of the algae.

While several studies have measured the N:P ratio of nutrients excreted by dreissenids and other bivalves (Table 35.1), few studies have examined how excretion rates are affected by the nutrient stoichiometry of ingested foods. Yet ecological theory would suggest that nutrient ratios in food supplies will have an influence on nutrient excretion ratios of dreissenids (Elser and Hassett 1994). More specifically, dreissenid nutrient excretion should be regulated by the degree to which C:N:P stoichiometry of dreissenid tissue differs from that of the food source. In one of the few studies to measure the stoichiometry of both dreissenids and their food source, Arnott and Vanni (1996) reported N:P ratios of 7.0–22.3 for phytoplankton and N:P ratios of 16–33 for zebra mussels in Lake Erie, indicating that phytoplankton were N depleted relative to mussel requirements. Theory would predict that these mussels selectively retain N and recycle P. Indeed, the authors reported low N:P excretion ratios ranging from 4.9 to 17.5 and suggested these relatively low ratios could promote the dominance of cyanobacteria. In a similar study with zebra mussels from Lake Erken (Sweden), Naddafi et al. (2008) measured N:P ratios of 16.6–30.8 for seston and N:P ratios of 22.5–40.0 for mussels. Their reported N and P excretion rates (Table 35.1) indicate that N:P excretion ratios varied greatly (~5 to 30). However, N:P excretion ratios

were usually similar to or less than N:P ratios for the seston, suggesting selective retention of N and recycling* of P, as would be expected based on the relatively P-rich food supply. At a larger ecosystem scale, Effler et al. (2004) used upstream–downstream comparisons of dissolved N and P concentrations in the Seneca River to derive a N:P excretion ratio of 7.1:1. This is probably a minimum value, as they did not account for possible nitrification of ammonium (NH_4^+) between upstream and downstream sites. The authors did not measure seston nutrient concentrations, but phytoplankton in this river was derived from a hypereutrophic upstream lake and so was probably phosphorus replete. In this case eutrophic conditions appear to promote low N:P excretion ratios that are well below the Redfield ratio of 16:1, which may tend to favor cyanobacteria.

In contrast to the earlier studies, Conroy et al. (2005) reported N and P excretion rates for zebra and quagga mussels in Lake Erie that equate to relatively high N:P excretion ratios (36–52). Conroy et al. (2005) did not report nutrient concentrations of seston, but at the time of sample collection NH_4^+ concentration was 52 μg N L^{-1} and soluble reactive phosphorus (SRP) was undetectable, suggesting that phytoplankton were likely P limited. These results were similar to the findings of Heath et al. (1995) who measured accumulation of dissolved N and P in Saginaw Bay (Lake Huron) mesocosms containing high densities of zebra mussels feeding on P-limited phytoplankton. They observed high dissolved N:P accumulation ratios, ranging from 40:1 to 101:1.

There remains a need for further research on effects of food stoichiometry on nutrient excretion by dreissenids. However, the earlier studies and stoichiometry theory suggest that when N:P ratios of seston are lower than N:P ratios of mussels, N:P ratios of excreted nutrients will be low. Conversely, high N:P ratios of seston will result in selective recycling of nitrogen by dreissenids. As a result, if phytoplankton within a system is N or P limited, nutrient recycling by dreissenids may exacerbate the current condition. Because phytoplankton communities in the Great Lakes tend to be P limited, nutrient recycling by dreissenids will likely reinforce this limitation. Exceptions may occur in more eutrophic systems, such as the western basin of Lake Erie where there is evidence for N limitation at times (Arnott and Vanni 1996).

Although stoichiometric theory and empirical observations suggest that dreissenid nutrient recycling will tend to reinforce the existing nutrient limitation, under certain conditions mussel nutrient recycling may result in a shift between N and P limitation. This is because the optimal N:P ratio for dreissenids may differ from that for phytoplankton. The potential of dreissenids to recycle nutrients and cause a shift between P and N limitation

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* In this chapter, the terms "excretion" and "recycling" are similar, but "excretion" refers to the release of a dissolved nutrient, whereas "recycling" refers specifically to the conversion of a nutrient from particulate to dissolved form.
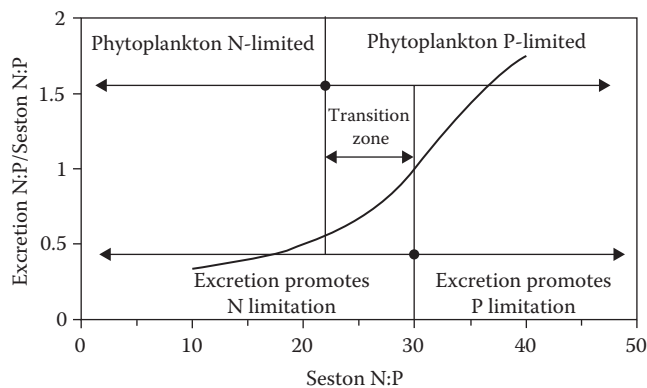
Figure 35.1 Conceptual model illustrating feedback between N:P ratios of seston and N:P ratios of mussel excretion. The model assumes that phytoplankton are P limited when seston N:P ratios are >22 (Healey and Hendzel 1980) and that mussels maintain a constant tissue N:P ratio of 30:1 (an approximate median of measurements made by Arnott and Vanni [1996] and Naddafi et al. [2009]). Excretion N:P was determined as a function of seston N:P, assuming that mussels excrete a constant 25% of ingested N as dissolved N when seston N:P is less than 30 and a constant 25% of ingested P as dissolved P when seston N:P is greater than 30. In the transition zone, where seston N:P ratio is less than that of mussel tissue but greater than the optimal N:P ratio of phytoplankton, recycling by mussels may result in a shift from P limitation to N limitation.

will be greatest when N:P ratios of seston are above the Redfield ratio of 16:1 but lower than N:P ratios of mussels. For example, if seston N:P is 22 and mussel N:P is 30, phytoplankton may be marginally P limited, but dreissenids may selectively retain N and recycle P to meet their stoichiometric requirements, resulting in a low N:P excretion ratio that could shift the phytoplankton community toward N limitation (Figure 35.1). The strength of this interaction will depend in part on the mussels' ability to adjust their tissue N:P ratios. If mussel tissue N:P fluctuates according to changes in food N:P (Naddafi et al. 2009), the ability of mussels to facilitate a switch between P and N limitation, or to reinforce limitation by either nutrient, will be limited. But mussel tissue N:P ratios can differ significantly from those of seston and may be as high as 40 in late summer (Arnott and Vanni 1996, Naddafi et al. 2009), and during these periods mussel excretion can be expected to have a strong influence on the balance between N and P limitation.
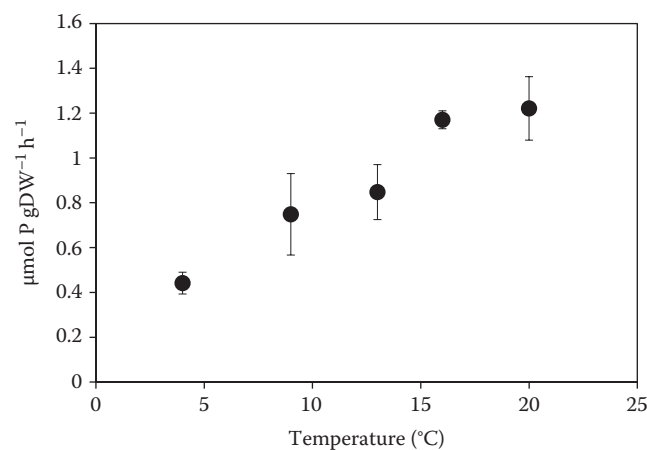
Dreissenid Size

Size is a primary determinant of biomass-specific metabolic rates in bivalves, and in general the relationship is inverse (Hamburger et al. 1983). This relationship appears to extend to nutrient excretion (Mellina et al. 1995, Young et al. 1996, Naddafi et al. 2008). In laboratory experiments, Mellina et al. (1995) found that dreissenid shell length

explained >70% of the variability in the biomass-specific P excretion rate at a given temperature. Whether this relationship between size and P excretion rate also applies to nitrogen is uncertain. Arnott and Vanni (1996) and Davis et al. (2000) both observed that mussel size explained a significant amount of variability in P excretion but not N excretion. This may reflect different metabolic pathways for the two elements. However, Quigley et al. (1993) provided indirect evidence suggesting that size may have some influence on mass-specific N excretion. They observed a strong inverse relationship between mass-specific oxygen consumption rate and tissue dry weight for zebra mussels collected from Lake St. Clair and, in a separate experiment, they observed a positive correlation between oxygen consumption and N excretion.

Differences in P excretion rates between small and large mussels are large enough that estimates of community excretion rates can include large errors if mussel size distribution is not accounted for. For example, Young et al. (1996) showed that rates of filtration and pseudofeces production in zebra mussels can be up to an order of magnitude greater in large (~25 mm) than in small (~5 mm) individuals. However, mass-specific excretion rates of SRP are much greater for small mussels than for large mussels (Arnott and Vanni 1996, Naddafi et al. 2008). Therefore, it is important to account for both mussel density and size distribution when areal filtration and nutrient excretion rates are calculated. A factor that may alter the observed relationship between size and excretion is the length of time mussels have been deprived of food before measurements are made, which in published studies spans from hours to days. To our knowledge, there are no direct measurements of gut passage time for dreissenids, but Wang and Fisher (1999) report a passage time of less than 3 for marine mussels, and Lauritsen and Mozley (1989) observed a decline in ammonium excretion rate after 2 of food deprivation for the clam, *Corbicula fluminea*. Because gut passage times are likely positively related to mussel size, a food deprivation period of more than a few hours may alter the size–excretion relationship, with excretion by small mussels declining more rapidly than that by large mussels. If mussel size does influence the temporal scales over which nutrient excretion responds to food supply, there will be implications for nutrient dynamics in natural communities. For example, the nearshore zone of large lakes can experience rapid fluctuations in temperature due to upwelling events, and these fluctuations are likely accompanied by large changes in food supply, which may explain lower dreissenid densities in regions of frequent upwelling (Wilson et al. 2006). In areas with populations dominated by small mussels, these fluctuations in food supply will likely lead to rapid changes in nutrient recycling, whereas the nutrient recycling response may be dampened in areas dominated by large mussels.

Temperature

As for most invertebrates, ambient temperature is known to influence metabolic rates of dreissenids (Stoeckmann and Garton 1997) and other bivalves (Kuenzler 1961, Magni et al. 2000). Despite the potentially strong influence of temperature on nutrient excretion rates, few studies have directly quantified this relationship for dreissenids. While temperature is recognized as a factor that may explain observed differences in nutrient excretion rates over time or between systems (Arnott and Vanni 1996, Ozersky et al. 2009), most studies that have extrapolated measured rates to estimate ecosystem-scale or seasonal effects of dreissenid feeding and nutrient excretion have not accounted for temperature differences. Mellina et al. (1995) recorded SRP excretion rates of zebra mussels that were approximately two times greater at 22°C than at 17°C (Table 35.1). At higher temperatures, nutrient excretion may be decoupled from ingestion. For example, rates of ammonium excretion and oxygen consumption of zebra mussels were four times greater at 28°C and 32°C than at 20°C; however, filtration rates were lower at 28°C and 32°C than at 20°C (Aldridge et al. 1995). Over a temperature range that more closely matches that of many temperate lakes, we have observed strong temperature effects, with phosphorus excretion rates increasing more than threefold between 4°C and 20°C (Figure 35.2). Excretion rates measured in situ or measured with mussels that have been exposed to in-lake conditions do not always reveal a relationship to temperature that is predictable (Table 35.1) due to other confounding factors that may change over time and space. However, temperature effects are strong enough

that they can often be detected in studies that span one or more seasons (Arnott and Vanni 1996, Naddafi et al. 2008, Ozersky et al. 2009). This, along with the experimental observations cited earlier, indicates that these effects are critical enough such that temperature fluctuations must be accounted for in models of nutrient cycling by dreissenids or when seasonal or annual nutrient excretion rates are estimated from a small number of measurements.

While a number of studies have examined physiological responses of zebra mussels to temperature (Sprung 1995, Alexander et al. 1994), there are few studies that have examined responses of quagga mussels. Quagga mussels are often considered to be better adapted to cold-water conditions compared to zebra mussels. Yet, although quagga mussels appear to be able to reproduce at colder temperatures (Roe and MacIsaac 1997) and may have an upper thermal tolerance lower than that of zebra mussels (Domm et al. 1993, Spidle et al. 1995), the two species appear to exhibit similar clearance rates at both cold and warm temperatures (Baldwin et al. 2002). Therefore, while the recent increase in abundance of quagga mussels and decline of zebra mussels in the Great Lakes may affect nutrient cycling due to changes in absolute numbers of mussels and their spatial distribution, there is no evidence that a switch in dreissenid species will alter the temperature–nutrient excretion relationship.

Other Regulating Factors

Studies based on laboratory experiments and in situ measurements indicate that the factors discussed earlier—food quantity and quality, mussel size, and water temperature—are likely the dominant regulators of nutrient excretion by dreissenids. However, these same studies reveal that not all of the variability in nutrient excretion rates can be explained by these factors alone. In studies that have measured excretion rates of dreissenids at different times of the year, temporal differences in rates were not readily explainable by differences in temperature or food supply. Naddafi et al. (2008) suggested that the positive relationship between mussel size and mass-specific N excretion rate reported by Arnott and Vanni (1996), which is the opposite of findings in other studies, may have been due to nutrient loss during the release of gametes by large mussels. Supportive of this theory is that mussels may have lower P excretion rates and greater N excretion rates during gametogenesis, with a greater proportion of ingested P being allocated to gamete production and N being lost during protein catabolism (Davis et al. 2000). In Lake Erie, Stoeckmann and Garton (1997) found that, although temperature had a strong influence on mussel feeding and metabolism, temperature alone was a poor predictor of seasonal changes in metabolic rate and energy allocation, with other important drivers being reproductive state and food conditions. While they did not specifically address the relationship between these drivers and nutrient excretion, the dependence of excretion on feeding rate and metabolism means that excretion also likely responds to these multiple driving factors.

Figure 35.2 Excretion rates of soluble reactive P (μmol P gDW^{-1} h^{-1}) by quagga mussels at five different temperatures. Mussels were collected from Lake Michigan in March 2010. Mussels were fed a monoculture of *Scenedesmus quadricauda* (particulate carbon concentration = 25–33 μmol L^{-1}) and acclimated to experimental temperatures for 3 days prior to measurement of excretion rates. Mussel length was between 16 and 18 mm. Excretion rate was measured as SRP accumulation over 1.5 h after mussels were placed in filtered lake water.

To our knowledge, there have been no direct measurements of the effect of dissolved oxygen concentration on dreissenid nutrient excretion. However, several studies have documented the influence of dissolved oxygen on other metabolic processes. Sprung (1995) noted that filtration rate and ingestion capacity of zebra mussels were reduced at low oxygen concentrations. Similarly, Quigley et al. (1993) observed a significant decline in oxygen consumption rate of zebra mussels when dissolved oxygen concentration decreased. They fitted their data to a Michaelis–Menten model, which indicated that the oxygen consumption rate at 50% dissolved oxygen saturation was ∼57% of that at 100% saturation. They also observed a strong correlation between oxygen consumption rate and ammonium excretion rate ($r^2 = 0.76$, $P < 0.03$, using data in their Table 35.1). The implication is that ammonium excretion rate is positively correlated to dissolved oxygen concentration.

In addition to directly affecting mussel metabolism, dissolved oxygen concentrations may influence the fate of nutrients excreted or egested by mussels. There is little data to indicate the direct effect of dreissenids on dissolved oxygen in the benthic boundary layer or in sediment pore water, but it is reasonable to expect that both mussel respiration and bacterial decomposition of mussel biodeposits may lead to hypoxic or anoxic conditions in these environments (Turner 2010). Such conditions would tend to promote nitrogen loss through denitrification while enhancing the release of iron-bound phosphorus, resulting in low N:P recycling ratios. This is supported by experimental observations (Bruesewitz et al. 2006, Bykova et al. 2006, Turner 2010). As Bykova et al. (2006) point out, in lakes where dreissenid nutrient recycling rates are high relative to other internal recycling rates and to external loads, this effect may lead to a state of nitrogen limitation that promotes cyanobacteria dominance. Newell et al. (2005) have postulated a similar relationship between oyster egestion, sediment redox conditions, and N and P recycling in Chesapeake Bay. This link between oxygen dynamics and nutrient recycling will likely be influenced by substrate type, with fine-grained sediments in deep regions more likely to experience hypoxic or anoxic conditions than shallow or rocky substrata.

Most measurements of nutrient excretion by dreissenids have been made using mussels that have been removed from their natural environment and incubated in some sort of enclosure. The unstated assumption is that nutrient excretion in an artificial enclosure is similar to that on the natural bottom substrate, providing that temperature and food supply are similar. However, in the few studies in which dreissenid nutrient excretion has been measured on different substrata, there is evidence that substrate type may have a strong influence, either directly or indirectly. Turner (2010) found that P excretion by zebra mussels in cores with lake sediment was more than three times greater than that in cores without sediment. Because P excretion in the presence of sediment was greater than expected based on food consumption,

the elevated excretion rate was attributed to P release from sediment that had passed through mussel guts. Newell et al. (2005) also highlight the important role the substratum and its associated microbial community may play in modifying the effect of bivalves on nutrient recycling. In the study of Turner (2010), the presence of sediment did not appear to promote higher excretion rates of N, and so Turner (2010) suggested that recycling of sediment-bound P by dreissenids could promote low N:P recycling ratios and N limitation of phytoplankton. This raises the question of whether the recent displacement of zebra mussels by quagga mussels in the Great Lakes (Wilson et al. 2006, Nalepa et al. 2010) may further alter nutrient dynamics within these systems, as quagga mussels are more capable of colonizing soft sediments.

ECOSYSTEM IMPACTS OF DREISSENID NUTRIENT CYCLING

Influence of Dreissenids on Nutrient Pools and Fluxes

Dreissenids are major nutrient processors in systems where they are abundant. In Lake Michigan, this is evident by comparing dreissenid P excretion rates to P loads from rivers. Dreissenid dissolved P excretion rates in the lake range from 10.1 to 42.9 µmol P m^{-2} h^{-1} (Table 35.1). Areal imagery indicates that, in the Milwaukee region of the lake, most of the substrate is hard and dreissenids cover ∼80% of the bottom in waters shallower than 10 m (Janssen and Bootsma, unpublished). The average distance between the shore and the 10 m isobath in this region is approximately 2 km. Using these values and a median areal excretion rate of 27 µmol P m^{-2} h^{-1}, an approximate recycling rate in the nearshore (0–10 m) zone is 1 mole of P per meter of shoreline per day. In comparison, an approximate loading rate from the Milwaukee River (which receives input from the Menomonee and Kinnickinnic Rivers near its mouth) is 8000 moles of P per day.* Hence, the dreissenid P recycling rate in waters shallower than 10 m over an 8 km stretch of shoreline is similar to the average loading rate via the Milwaukee River. This suggests that for nearshore regions of Lake Michigan that are dominated by rocky substratum and are not in close proximity to a major tributary, mussels are the major source of dissolved P. Arnott and Vanni (1996) reached a similar conclusion for the western basin of Lake Erie, where they estimated that P excreted by zebra mussels exceeded that of all other sources and exceeded external loading by an order of magnitude. Likewise, Ozersky et al. (2009) determined that dissolved P excreted by dreissenids

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* Based on nutrient measurements made in these rivers by the Milwaukee Metropolitan Sewerage District and river discharge data collected by the U.S. Geological Survey

in an urbanized region of Lake Ontario was greater than external loading. The capacity of dreissenids to be major nutrient recyclers is not surprising considering their ability to ingest large fractions of the primary production in aquatic systems (Stoeckmann and Garton 1997, Naddafi et al. 2008).

Nutrients ingested by dreissenids have one of three fates: assimilation into body mass, excretion in dissolved form, and egestion as feces or pseudofeces. The net ecosystem effect will depend on the relative magnitude of these pathways and how they vary in space and time. Heath et al. (1995) found that nutrient recycling by dreissenids resulted in increases in dissolved P concentrations in mesocosms. A number of other studies suggested that a similar effect occurs in large water bodies (Holland et al. 1995, Makarewicz et al. 2000, Orlova et al. 2004). However, Higgins and Vander Zanden (2010) found that this effect does not appear to apply to lakes in general but does appear to be a common response in rivers. They suggested that the difference in response of rivers versus lakes may be due to less P assimilation by benthic algae in rivers. Another possibility is that excreted P is more diluted in lakes due to greater water volumes relative to bottom areas.

During periods of rapid population growth, as occurred in the decade following the introduction of dreissenids to the Great Lakes, mussel biomass represented a significant nutrient sink. For example, shortly following the establishment of zebra mussels in Saginaw Bay (Lake Huron), the amount of P in mussel mass was equal to approximately one-half the annual P load to the bay, and total phosphorus concentrations decreased by approximately 50% (Johengen et al. 1995). Over the long term, the effect of nutrient assimilation by dreissenids on lake and river nutrient pools will depend in part on the fate of mussel tissue and shell following death. If most nutrients contained in tissues and shells are recycled following death, nutrient pools in the water column may increase once mussel populations have reached steady state. At this point, mussel growth no longer represents a net loss of nutrients from the system (although mussel grazing may still maintain water column total nutrient concentrations at levels lower than if there were no mussels). This dynamic can be seen in the temporal trend of dissolved calcium concentration (using alkalinity as a surrogate) in Lake Erie, which dramatically declined in the decade following the dreissenid invasion but since then has steadily increased toward the pre-dreissenid concentration (Barbiero et al. 2006). In Lake Ontario, calcium concentrations have continued to decline (Barbiero et al. 2006), indicating that calcium dynamics, and probably nutrient dynamics, may take much longer to reach steady state in this lake, perhaps due to its longer hydraulic residence time and continued expansion of its dreissenid population (Watkins et al. 2007).

For dreissenids, few studies have made direct comparisons of nutrients excreted, nutrients allocated to growth, and nutrients egested via feces and pseudofeces. Madenjian (1995) estimated that 22% of the phytoplankton removed by dreissenids from Lake Erie was deposited as pseudofeces. In eutrophic Lake Mikołajskie (Poland), feces/pseudofeces production rates by zebra mussels were several times greater than community assimilation rates (Stańczykowska and Lewandowski 1993). In Lake Erie, mass balance calculations made by Mellina et al. (1995) suggested that most P ingested by zebra mussels was allocated to excretion of dissolved forms, whereas in Lake Oneida biodeposition (feces and pseudofeces) was the dominant P pathway. In contrast, they estimated that P biodeposition in Lake St. Clair was negligible. They attributed these differences to differences in phytoplankton concentrations, arguing that high phytoplankton concentrations in Lake Oneida resulted in ingestion rates that were greater than the maximum assimilation rate, resulting in high rates of biodeposition. This is supported by other studies that have shown that pseudofeces production is related to phytoplankton concentration, phytoplankton species composition, and seston organic content (Berg et al. 1996, Lei et al. 1996, Madon et al. 1998, Schneider et al. 1998).

These observations suggest that, in more productive systems or in systems where a large portion of the seston is nonalgal, pseudofeces production may be a significant nutrient pathway. However, this does not appear to be the case in less productive water bodies. Several studies have reported that pseudofeces production by dreissenids is negligible at seston concentrations typical of those found in the Great Lakes (Lei et al. 1996, Madon et al. 1998). In these systems, nutrients egested via feces are likely a more important nutrient pathway than nutrients ejected via pseudofeces. However, the relative importance of nutrients egested via feces versus dissolved nutrients excreted is uncertain. When zebra mussels were fed algal cultures in the laboratory, Berg et al. (1996) found that absorption efficiencies (proportion of ingested food not egested as feces) were ~80% at low algal densities, indicating that ~20% of ingested food was egested as feces. Others have measured similar assimilation efficiencies when dreissenids were fed high-quality food (Stoeckmann and Garton 1997, Baldwin et al. 2002). In these estimates, "absorption" or "assimilation" generally represents the proportion of ingested food (excluding pseudofeces ejection) that is not egested as feces. This "assimilated" portion is partitioned between growth, reproduction, and metabolic processes, the latter of which produces excretory products. Stoeckmann and Garton (1997) determined that >90% of energy consumed by zebra mussels was allocated to metabolism. Unless the stoichiometry of ingested seston is greatly different from that of mussel tissue, assimilated nutrients will be partitioned in proportions similar to the nutrients ingested. High assimilation efficiencies along with a large fraction of assimilated nutrients being allocated to metabolism suggest that excretion of dissolved nutrients may be greater than fecal egestion of nutrients in systems with low concentrations of high-quality seston. Similar observations have been made for phosphorus excretion and egestion

by fish (Brabrand et al. 1990). Further measurements are needed to confirm this suggestion and to determine factors that determine how ingested nutrients are allocated between growth, excretion, and egestion in dreissenids.

The influence of pseudofeces and feces production on ecosystem nutrient dynamics will depend on the ultimate fate of this particulate material. Unlike excreted nutrients, which are readily available to autotrophs, nutrients tied up in pseudofeces and feces represent a loss from the water column. Even if nutrient egestion rates are low relative to excretion rates, feces and pseudofeces formation can significantly alter the total nutrient pool in the water column if this particulate material is retained in the benthos. If this is the case, then the benthic nutrient pool may support other benthic invertebrates (Limén et al. 2005) and fish (Thayer et al. 1997), may be recycled by bacteria and protozoans (Lohner et al. 2007), or may be permanently buried. In the absence of dreissenids, the internal loss of phosphorus in lakes is largely controlled by the passive settling of particulates and subsequent burial at depth. The fact that dreissenids accelerate the sedimentation process is evident since water clarity has increased and phytoplankton concentrations have decreased following dreissenid introductions in many systems (Descy et al. 2003, Hall et al. 2003, Zhu et al. 2007). In addition to accelerating sedimentation, dreissenids may alter the form of sedimented material, packaging it into larger aggregates that are less susceptible to resuspension. Resuspended sediment can make a significant contribution to water column nutrient concentrations (Eadie et al. 2002). If dreissenid production of feces and pseudofeces facilitates retention of particles and associated nutrients in the sediment, it will result in a net loss of nutrients from the water column (Hecky et al. 2004). The significance of this potential nutrient loss mechanism requires further testing and will likely be influenced by hydrodynamics and seston composition. For Lake Erie, Hecky et al. (2004) presented evidence for sediment aggregation by mussels and suggested that this promoted nutrient retention on the lake bottom. A similar mechanism may be acting in Saginaw Bay, where dreissenid filtration appears to have resulted in greater sedimentation rates and reduced inputs of P to Lake Huron (Cha et al. 2011). In contrast, Baker et al. (1998) found that zebra mussels in the Hudson River produced diffuse pseudofeces that were easily resuspended, and mussel filtration did not appear to significantly reduce turbidity. Similarly, Mellina et al. (1995) found that P loss from the water column in Lake Oneida could be accounted for by increased mussel biomass and therefore concluded that virtually all of the feces and pseudofeces were recycled.

Phytoplankton Response

There is some evidence that the excretion of nutrients by dreissenids may promote higher phytoplankton growth rates (Bierman et al. 2005, Higgins and Vander Zanden

2010). However, this effect is generally not strong enough to counter the loss of phytoplankton resulting from mussel filtration. As a result, total phytoplankton biomass either decreases following the establishment of dreissenids (Higgins and Vander Zanden 2010) or the phytoplankton become dominated by a small number of taxa, often cyanobacteria, that avoid grazing and benefit from the nutrients recycled by dreissenids (Bierman et al. 2005, Conroy et al. 2005, Zhang et al. 2008). A positive response in cyanobacteria is especially noticeable in shallower systems with moderate to high dissolved nutrient concentrations. For example, within the Laurentian Great Lakes, blooms of the cyanobacteria *Microcystis* spp. are common in the western basin of Lake Erie (Conroy et al. 2005), in Saginaw Bay (Lake Huron, Bierman et al. 2005), and in the Bay of Quinte (Lake Ontario, Nicholls et al. 2002). However, it appears that dreissenids can also promote cyanobacteria dominance in low-nutrient lakes (Raikow et al. 2004, Knoll et al. 2008). In Lake Michigan, total phytoplankton biomass has decreased following expansion of the dreissenid community, but cyanobacteria concentrations have actually increased (Fahnenstiel et al. 2010). In some cases, this transition to dominance by cyanobacteria has been attributed to a dreissenid-induced decrease in the dissolved N:P ratio (Arnott and Vanni 1996, Conroy et al. 2005). But other mechanisms, such as selective grazing (Vanderploeg et al. 2001, Vanderploeg et al. 2013), are likely also important and may play a larger role in Lake Michigan and other lakes where dissolved N:P ratios are high for most of the year.

The dual effect of filtration and nutrient excretion by dreissenids has altered the relationship between dissolved nutrient concentration and phytoplankton abundance in many lakes, which is frequently reflected in lower chlorophyll–total phosphorus ratios (Mellina et al. 1995, Hall et al. 2003). This "biological oligotrophication" (Holland et al. 1995, Evans et al. 2011) appears to have altered long-standing paradigms describing nutrient and plankton dynamics. Indeed, the ability of dreissenids to so dramatically reduce phytoplankton abundance and increase water clarity in many lakes gives validity to the concept of top-down control (Carpenter et al. 1995). In the Great Lakes, some earlier models of nutrient and plankton dynamics do not account for the effects of dreissenids (Chen et al. 2002, Pauer et al. 2008), but more recent models do account for dreissenids and highlight their potential impact both as a sink for some forms of phytoplankton and as a source of dissolved nutrients (Bierman et al. 2005, Zhang et al. 2008).

Role of Hydrodynamics and Lake Morphometry

As discussed earlier, there are a number of factors that influence filtration and nutrient excretion rates of dreissenids. If relationships between these factors and rates are well

quantified and population densities are known, the potential effect of dreissenids on phytoplankton loss rates and nutrient recycling rates can be estimated. However, potential effects will be modulated by hydrodynamics, which influence both the delivery of particulate material to benthic dreissenids and the distribution of dissolved nutrients released by this community. The extent of vertical mixing in the water column will determine the relationship between filtration rate (the volume of water that passes through a mussel per unit time) and clearance rate (the volume of water that a mussel effectively clears of particulate material per unit time). In natural settings, a vertical gradient of particulate material is often observed above mussel beds (Ackerman et al. 2001, Boegman et al. 2008), which indicates that grazing by the mussel community can deplete particulates on time scales that are shorter than time scales over which particulates are replenished by vertical mixing. Under these conditions, clearance rates are lower than filtration rates, and as a result grazing rate is significantly lower than the maximum potential. For example, in situ measurements in Lake Erie indicated that dreissenid clearance rates were as low as 0.14 times filtration rates due to re-filtration (Yu and Culver 1999). Similar results were reported by Edwards et al. (2005) and Boegman et al. (2008).

In deep lakes, three physical properties may limit the effect of dreissenids on phytoplankton populations and nutrient recycling: (1) minimal wind-induced, near-bottom turbulence, which may decrease the rate of phytoplankton being supplied to bottom-dwelling dreissenids; (2) high lake volumes relative to mussel populations, resulting in a small fraction of the lake being filtered per unit time; (3) the presence of a thermocline, which hinders phytoplankton produced in the epilimnion from reaching the dreissenid population for at least part of the year. This third factor also applies to smaller lakes that are deep enough and sheltered enough from wind to establish a thermocline. While these physical properties of large lakes may help minimize the role of mussels in nutrient cycling, in fact a significant portion of total annual phytoplankton growth may occur during the spring bloom before these lakes stratify and the water column is well mixed. Dreissenids can reduce this spring bloom because they have access to the entire water column during this period. In addition, quagga mussels, which are able to maintain relatively high filtration rates at low temperatures (Baldwin et al. 2002), may be able to effectively graze phytoplankton throughout the winter, resulting in lower "seed" populations of phytoplankton during the spring bloom period. The capacity of dreissenids to impact the spring bloom appears to be significant even in deep regions of Lake Michigan, where photosynthesis and phytoplankton abundances are now one-third to one-fifth lower than what they were prior to establishment of dreissenids in these regions (Fahnenstiel et al. 2010). Over this same time span, phytoplankton biomass in summer did not change. Implications of the lost spring bloom

for nutrient dynamics are uncertain. Brooks and Edgington (1994) have argued that most recycling of phosphorus from the sediment to the water column occurs during the spring in Lake Michigan, which is the time when uptake of dissolved P by phytoplankton displaces the sediment–water equilibrium with regard to apatite, promoting dissolution of P from the sediment. By depleting the spring phytoplankton population, dreissenids may have effectively turned this mechanism off. This diminished benthic recycling, along with additional nutrients being bound in mussel biomass and biodeposits, may explain the rapid decrease in concentrations of total P found in the water column in the late 1990s (Mida et al. 2010).

Although dreissenid populations in deep regions are isolated from phytoplankton in the epilimnion during the stratified period, populations in shallow, nearshore regions are not. In shallow lakes where a significant proportion of the lake bottom is within the epilimnion, dreissenids can be expected to have a strong influence on phytoplankton and nutrient dynamics throughout the summer-stratified period. In large lakes, the effect of nearshore dreissenid populations on whole-lake plankton and nutrient dynamics will depend on horizontal exchange rates between nearshore and offshore waters. These exchange rates will also determine the degree to which the nearshore dreissenid populations can process particles and nutrients entering directly from rivers, as they will affect the residence time of river plumes in the nearshore zone. Longer nearshore residence times may result in more efficient nutrient retention and a significant reduction of the effective nutrient load to offshore regions, as appears to occur as river water passes through Saginaw Bay into Lake Huron (Cha et al. 2011).

During the stratified period in large lakes, the direction of nearshore currents tends to be parallel to shore within several km of shore, minimizing nearshore–offshore exchange and trapping river effluent close to shore (Rao and Schwab 2007). However, nearshore–offshore exchange can occur as the result of internal seiches, wind-induced upwelling and downwelling, advection by coastal jets, and horizontal mixing resulting from current shear (Rao and Schwab 2007). Because these processes tend to be transient in space and time, they can be difficult to quantify. They are best characterized through combination of approaches including in situ current measurements, satellite imagery, and hydrodynamic modeling (e.g., Rao et al. 2002). Although several studies have considered the role of nearshore–offshore exchange in the transport of pollutants and sediment in the Great Lakes (Shen et al. 1995, Lou et al. 2000), interactions between nearshore dreissenid populations and the offshore plankton community have received little attention. While the expansion of dreissenids into offshore regions has affected plankton abundances in the pelagic waters of even the largest lakes (Fahnenstiel et al. 2010), there remains a need for quantitative data to demonstrate whether nearshore filtration
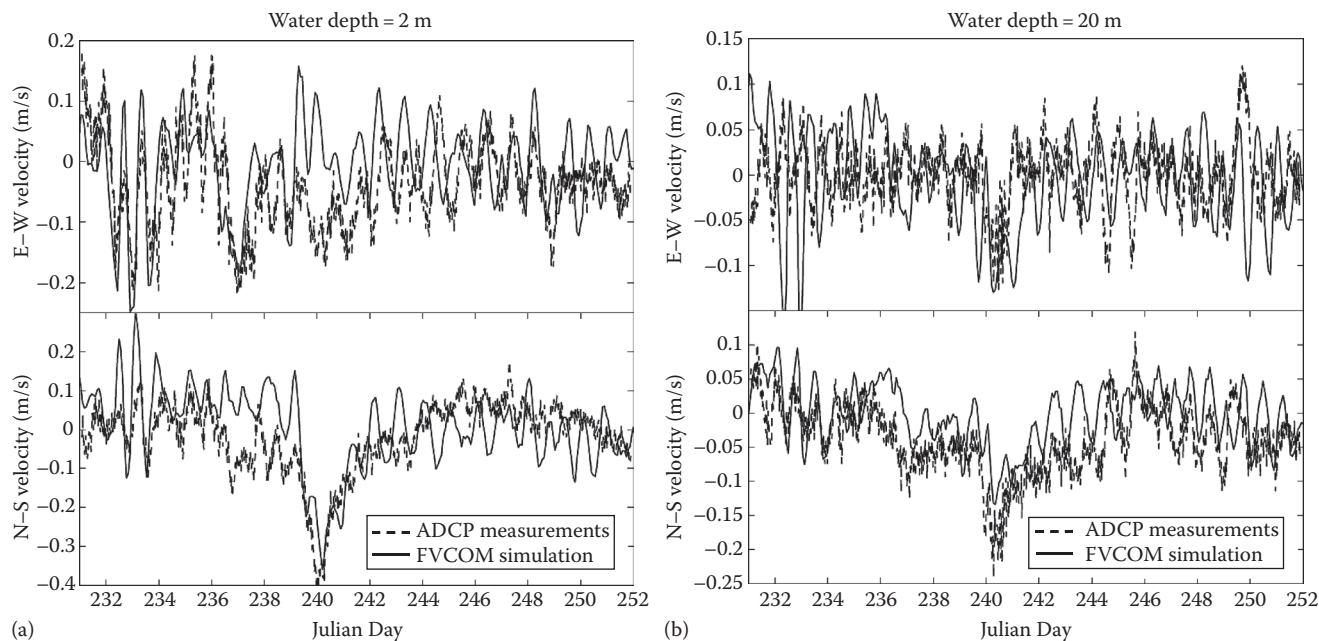
Figure 35.3 Comparison of current velocities (m/s) simulated with the 3-D hydrodynamic model (FVCOM) to current velocities measured with an ADCP at water depths of 2 m (a) and 20 m (b) near the harbor of Milwaukee in summer 2009. Upper panels: east–west current velocity; lower panels: north–south current velocity.

rates and nearshore–offshore exchange rates are sufficient to affect pelagic offshore waters (Barbiero et al. 2011).

To examine the potential impact of dreissenids on the nearshore plankton community and how this impact may be regulated by nearshore–offshore exchange, we adapted and calibrated an unstructured-grid Finite-Volume Coastal Ocean Model (FVCOM; Chen et al. 2003) to simulate the hydrodynamic circulation of Lake Michigan with an average horizontal resolution of 3 km and nearshore resolution of 1.5 km. Good agreement was found between the simulation and nearshore (20 m) ADCP data acquired near Milwaukee Harbor (Figure 35.3). Using simulation results, the horizontal and vertical mixing coefficients were obtained through a large eddy simulation approach (Smagorinsky 1963). Extracted horizontal and vertical mixing coefficients distributed over a cross-lake transect in August are shown in Figure 35.4. Extracted results were used to evaluate the relative importance of mussel filtration and horizontal exchange between nearshore and offshore as factors affecting plankton abundance in the nearshore. A vertical 2-D plane representing a transect starting from Milwaukee Harbor and extending eastward to a water depth of 70 m was selected as being representative of the Lake Michigan nearshore–offshore system. A 2-D turbulent diffusion-driven mass exchange model was then built on this transect. Mussels were assumed to cover the lake bottom with a density of 10,000 m^{-2} at depths of <40 m, and the clearance rate was set constant at 2.7 L $mussel^{-1}$ day^{-1} (based on in situ measurements of particle concentration and particle filtration rate

[Liao et al. 2009]). Particle (plankton) concentration (C) was set at 1.0 (C_0) everywhere as the initial condition and was kept constant at the eastern (offshore) boundary. A 30 day simulation was conducted for the month of August when the lake was stratified. Particle concentrations normalized to C_0 after 30 days are shown in Figure 35.5. It is evident that a strong gradient in particle concentration developed between the nearshore and offshore regions at about 6 km eastward of the shoreline (about 30 m water depth). A near-bottom gradient was also noticeable in the nearshore region. This indicates that the filtration capacity of the dreissenid population was significant and the time scale of particulate removal through filtration in the nearshore was shorter than the time scales of nearshore–offshore exchange. From these results, it is reasonable to infer that the impact of nearshore dreissenids on whole-lake nutrient dynamics and energy flow is also regulated by the strength of horizontal exchange.
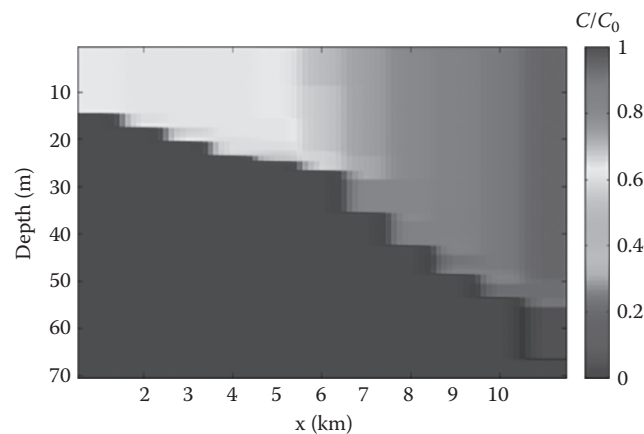
Benthic Algal Response

While dreissenids have caused declines in phytoplankton abundance in many lakes, they have had the opposite effect on the benthic algal community in the nearshore. In smaller lakes and rivers, dreissenids appear to be responsible for increases in the abundance of macrophytes (Effler et al. 1997, Zhu et al. 2007). In the larger Laurentian Great Lakes, there has been an increase in the abundance of both macrophytes and benthic algae, primarily *Cladophora* sp., coincident with the increase in mussel populations in the nearshore (Skubinna
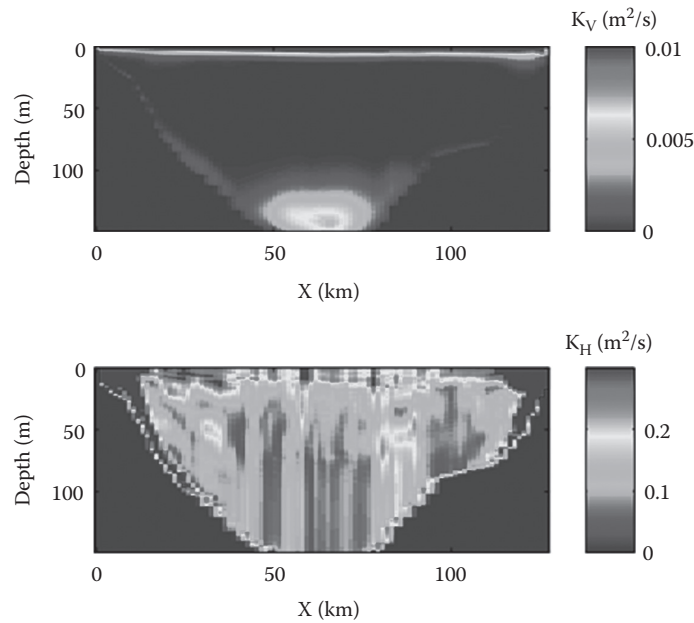
Figure 35.4 (See color insert.) Average monthly vertical (K_V, m²/s, top panel) and horizontal (K_H, m²/s, bottom panel) diffusivity in Lake Michigan as derived from the 3-D hydrodynamic simulation during strongly stratified conditions (August, 2009). The cross section is along a line that extends (in km) between Milwaukee, Wisconsin (left: west shoreline), and Muskegon, Michigan (right: east shoreline).

et al. 1995, Higgins et al. 2008, Auer et al. 2010). During the past decade, *Cladophora* biomass has increased to the nuisance levels observed in the 1960s and 1970s. However, while earlier *Cladophora* problems were generally associated with localized P sources such as river mouths and waste water treatment plants (Canale and Auer 1982), the recent problem

Figure 35.5 (See color insert.) Cross-section distribution of particle concentrations (*C*) normalized to a constant offshore concentration (C_0) after a 30 day simulation period as derived from a 2-D turbulent diffusion-driven mass exchange model. The area was located in Lake Michigan along the western shoreline near Milwaukee, Wisconsin, and extended from the shoreline eastward to a water depth of 70 m, a distance of about 11 km. See text for further details.

appears to be more widespread (Auer et al. 2010). Analysis of historical data suggests that increased water clarity is a primary cause of this resurgence (Malkin et al. 2008, Auer et al. 2010). Increased light flux to the nearshore benthic community as a result of particulate removal by dreissenid filtration has increased the growth rate of *Cladophora* and expanded its depth range. This resurgence of *Cladophora* has occurred despite declines in the concentration of total and dissolved P in most parts of the Great Lakes (Dove 2009, Mida et al. 2010). However, without sufficient nutrients, *Cladophora* would not be able to take advantage of the improved light environment. Hecky et al. (2004) suggested that dreissenids may be a significant nutrient source for *Cladophora*, and measurements made in Lake Ontario indicate that P excretion by dreissenids is more than sufficient to meet the P demand of *Cladophora* in the nearshore region (Ozersky et al. 2009). Studies of other systems have shown that nutrient excretion by bivalves can indeed promote the growth of macroalgae and macrophytes (Peterson and Heck 2001, Pfister 2007, Vaughn et al. 2007). However, while dreissenids have the potential to be a significant nutrient source for *Cladophora* and other benthic algae, there has been no direct quantification of this nutrient pathway.

Just as vertical mixing regulates the supply of seston from the water column to bottom-dwelling dreissenids and hence the extent by which dreissenid filtration affects phytoplankton abundance, vertical mixing also regulates the fate of dissolved P excreted by dreissenids and the

extent *Cladophora* may access this P. The proportion of excreted P that is assimilated by benthic algae will depend on the relative time scales of vertical mixing and P uptake kinetics. Under well-mixed conditions, mussel-derived P will dilute rapidly into the overlying water column, maintaining low concentrations in the benthic boundary layer and minimizing uptake by *Cladophora*. By contrast, under low mixing conditions, dissolved P will accumulate in the benthic boundary layer, allowing for greater uptake by *Cladophora*. The influence of mixing rate can be explored by constructing a simple mass balance model that simulates phosphorus dynamics within the near-bottom layer inhabited by mussels and *Cladophora*. Within this layer, mussel excretion serves as a SRP source, while uptake by *Cladophora* represents a loss. Vertical mixing with the overlying water column represents an input or output, depending on the SRP gradient (positive or negative) between the near-bottom layer and the overlying water column:

$$\frac{dC_1}{dt} = \frac{R - F - U}{z} \qquad (37.1)$$

where

C_1 is the SRP concentration in the near-bottom layer

t is the time

R is the areal SRP excretion rate

F is the areal vertical SRP flux rate from the near-bottom layer to the overlying water

U is the areal SRP uptake rate by *Cladophora*

z is the thickness of the near-bottom layer

For the simulations presented here, R was set at 0.17 μg P m^{-2} s^{-1} (an approximate median of the Lake Michigan rates in Table 35.1). F was determined as

$$F = D(C_1 - C_0) \qquad (37.2)$$

where

D is the vertical exchange coefficient at the top of the near-bottom layer

C_0 is the SRP concentration in the overlying water, which was set constant at 0.5 μg L^{-1}

Kinetics of SRP uptake by *Cladophora* were determined following the approach of Auer and Canale (1982):

$$U = \hat{U} \frac{P}{K_m + P} \qquad (37.3)$$

where

$\hat{U}$ is the maximum phosphorus uptake rate

P is the SRP concentration in the near-bottom layer

K_m is the half-saturation constant for SRP uptake

Auer and Canale (1982) reported $\hat{U}$ values ranging from 0.2 to 1.64 μg P mgDW^{-1} h^{-1}, depending on the P content of *Cladophora*. Here we use an intermediate value of 0.6 μg P mgDW^{-1} h^{-1}. *Cladophora* biomass was set at 100 gDW m^{-2}, which is the approximate median of our measurements over the growing season in Lake Michigan. Like Auer and Canale (1982), we set K_m constant at 125 μg P L^{-1}. The value of z was set at 10 cm, which is the approximate thickness of *Cladophora* beds in Lake Michigan in midsummer.

The model was run for D values ranging between 1 and 50 cm^2 s^{-1}, which encompasses the vertical mixing rates that have been measured over dreissenid beds (Boegman et al. 2008, Liao et al. 2009). For each D value the model was run until steady state was reached, which occurred between ~2 and ~30 min, depending on mixing rate. Model results indicate that, at low mixing rates, P uptake by *Cladophora* may be several times greater than P flux to the water column (Figure 35.6). By contrast, at higher mixing rates, more P was lost to vertical flux than to *Cladophora* uptake. SRP uptake by *Cladophora* was never zero, because even at high mixing rates, when SRP concentration in the near-bottom layer approached the ambient value of 0.5 μg L^{-1}, *Cladophora* was able to assimilate SRP. However, model results indicated that *Cladophora* benefits much more from SRP excretion by dreissenids under slow mixing conditions than under rapid mixing conditions.

These results highlight the potential influence of near-bottom hydrodynamics on the relationship between nutrient excretion by dreissenids and nutrient uptake by *Cladophora*. While dreissenids may provide a large portion of *Cladophora* P demand, there remains a need for quantitative measurements of the nutrient flux between
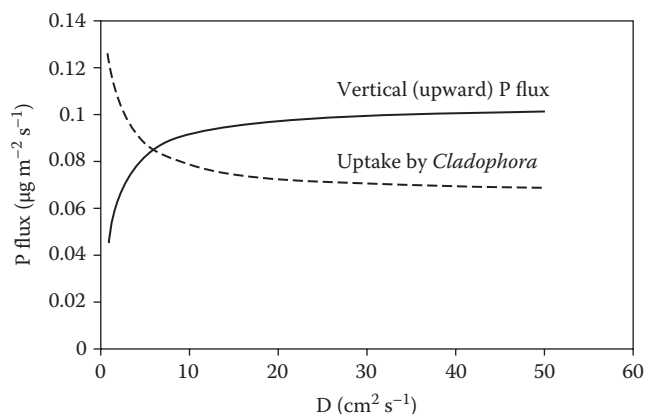
Figure 35.6 Simulated relationship between near-bottom, vertical mixing rates (D, cm^{2}s^{-1}) and the relative fate of dissolved P excreted by dreissenid mussels. The areal flux rate of excreted P (μg m^{-2} s^{-1}) was determined, and the vertical flux rate of P to the water column (solid line) was compared to P uptake by *Cladophora* (dashed line) at different vertical mixing rates. See text for further details.

dreissenids and *Cladophora* and how this flux is modulated by physical processes. Low mixing rates may enhance the ability of *Cladophora* to directly utilize dreissenid-derived nutrients, but such conditions also tend to result in reduced food supply to dreissenids due to increased water column stratification and greater re-filtration of near-bottom water (Boegman et al. 2008). This reduced food supply would likely lead to lower P excretion rates that may offset greater retention of P within *Cladophora* beds. Hence, the net effect of near-bottom mixing on the nutrient relationship between dreissenid and *Cladophora* remains unclear.

MANAGEMENT IMPLICATIONS

Since the arrival of dreissenids in North America over 20 years ago, a large amount of experimental work has greatly improved our understanding of dreissenid physiology and ecology and of the role these bivalves play in the functioning of whole ecosystems. As a result of their high densities, rapid reproduction, high metabolic rates (and hence, filtration rates), and relative resistance to predation, these organisms play a major role in the nutrient dynamics and trophic structure of many rivers and lakes. This role appears to have become even more significant in systems where zebra mussels have been replaced by quagga mussels. The latter species is more widely distributed due to its ability to colonize both hard and soft substrates and to reproduce and grow in cold, hypolimnetic waters (Claxton and Mackie 1998). However, there remains some uncertainty about long-term impacts of dreissenids, especially in large lakes where relatively long residence times of water and nutrients result in long times for these lakes to approach steady state following a major disturbance. In Lake Erie, with a hydraulic residence time of just over two years, it took more than 15 years for alkalinity to approach a return to steady state following the establishment of dreissenids (Barbiero et al. 2006). Depending on the turnover time of the dreissenid nutrient pool, it may take a similar amount of time for nutrient dynamics to return to a steady state. This response time will be even greater in larger lakes (i.e., Lakes Michigan, Huron, and Ontario) where nutrient residence times are longer and where dreissenid populations have continued to expand over the past decade (Wilson et al. 2006, Nalepa et al. 2007, 2009). The immediate effects of dreissenids on plankton abundance and nutrient recycling have been measured in many lakes and rivers, but in large lakes the short-term effects may differ in magnitude or nature from the long-term, ecosystem-scale effects, due to long residence times and lags in biological and biogeochemical feedbacks.

A critical question is whether the decrease in total nutrient concentration that has been observed in many lakes following establishment of dreissenids (Higgins and Vander Zanden 2010) is due to temporary sequestration in shells and tissues of living mussels or to increased burial in sediments as feces, pseudofeces, and dead mussel material. If the former mechanism is dominant, then total nutrient concentrations may partially rebound once populations reach steady state and the decomposition rate of dead mussels equals the production rate of new mussels. But if mussels promote more efficient burial of nutrients, then total nutrient concentrations will remain low, even after populations and nutrient dynamics approach new steady states. Data from European systems, where dreissenids have been established for a much longer period of time, may provide some insight into long-term effects. For example, many North American studies have observed an upward shift in SRP–chlorophyll *a* ratios due to dreissenid filtration, but Mellina et al. (1995) point out that this observation is not as common in European lakes. If this difference is indeed real, there are several mechanisms that may explain it, including higher overall densities of dreissenids in North American lakes (Ramcharan et al. 1992) and higher production–biomass ratios in North American populations (at least those that are still growing exponentially; Mackie and Schloesser 1996).

The ability of dreissenids to reallocate nutrients in aquatic ecosystems has fundamentally changed the structure and function of these systems. This presents a major challenge for researchers and managers. For over half a century, nutrient control has been a focal point for lake management efforts. These efforts have been underpinned by a basic understanding of how critical lake properties, including algal abundance and species composition, dissolved oxygen concentration, and fish production, are linked to nutrient loads and internal nutrient cycles. While the full impact of dreissenids on these relationships continues to be explored, it is obvious that conventional paradigms of nutrient dynamics are being challenged. In the Great Lakes, a particularly challenging conundrum is the simultaneous decrease in pelagic phytoplankton in nearshore and offshore regions and resurgence of nuisance benthic algae, primarily *Cladophora* sp., in the nearshore region. In the 1960s and 1970s, excessive algal growth was a problem in both the benthic and pelagic zones of the nearshore region in the Great Lakes, and both of these zones benefited from phosphorus abatement. This is no longer the case, and it has become more difficult to define a phosphorus loading target that supports pelagic plankton and fish populations while minimizing nuisance algal growth in the nearshore region. Dreissenid filtration has likely altered the relationship between P loading and pelagic phytoplankton concentration, and biogeochemical models will need to be revised to account for this shift. In the nearshore region, increased water clarity resulting from dreissenid filtration has led to increased growth rates of benthic algae, despite the fact that total P concentrations in the water column are at or below target levels

(Auer et al. 2010). This raises the question: is it possible to obtain P loading rates and P concentrations in the water column that will result in acceptably low *Cladophora* biomass? To answer this question, it will be necessary to identify and quantify pathways that link P loading to *Cladophora* growth. In particular, a better understanding of factors that regulate near-bottom dissolved P concentrations in the nearshore zone is required. In addition, models of *Cladophora* dynamics (Higgins et al. 2005, Malkin et al. 2008, Tomlinson et al. 2010) must account for these near-bottom P dynamics. If mussels are able to maintain relatively high concentrations of dissolved P in near-bottom waters where *Cladophora* grows, even when P concentrations in the rest of the water column are low, then high *Cladophora* biomass may be the new "normal" for at least some areas of the Great Lakes (Ozersky et al. 2009). However, large-scale gradients of nutrient concentrations and *Cladophora* biomass in nearshore Lake Michigan (Greb et al. 2005) and apparent localized effects of external P loading on *Cladophora* biomass (Higgins et al. 2012) suggest that acceptable levels of *Cladophora* biomass might be attainable with moderate reductions in P loading. As discussed earlier, such reductions may exacerbate the decline of pelagic plankton populations. Revised biogeochemical models will allow managers to better determine optimal nutrient loads and the time scales over which lakes will respond to changes in nutrient loads and internal cycling by dreissenid mussels.

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