Chapter 20

ECOSYSTEM CHANGES ASSOCIATED WITH *DREISSENA* INVASIONS: RECENT DEVELOPMENTS AND EMERGING ISSUES

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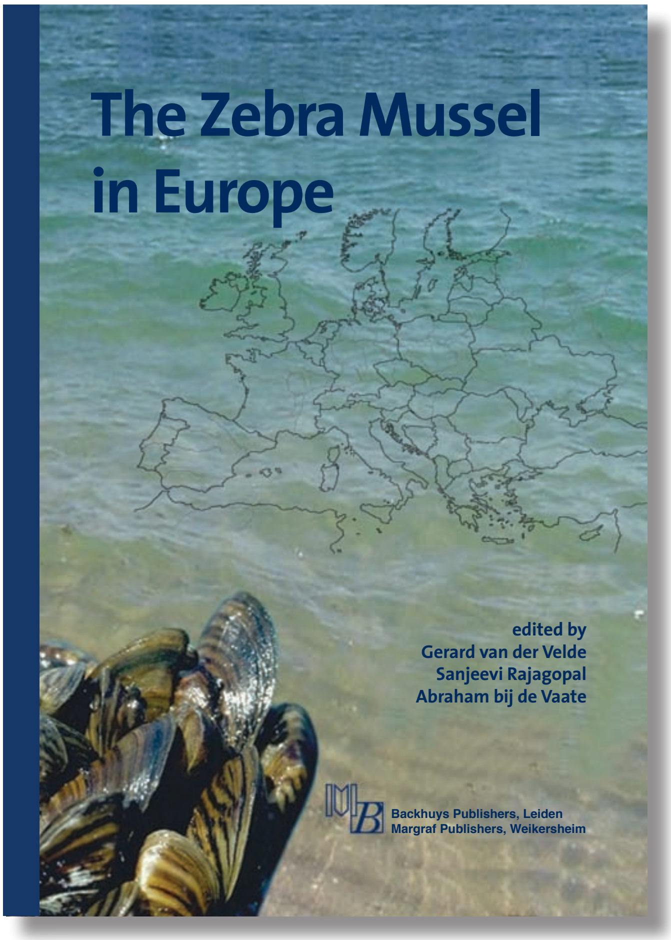

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20. Ecosystem changes associated with *Dreissena* invasions: recent developments and emerging issues

David W. Kelly, Leif-Matthias Herborg and Hugh J. MacIsaac

Abstract

Dreissena mussels are amongst the best-studied aquatic organisms. Here, we review the recent literature to explore biodiversity and ecosystem changes associated with invasions by dreissenid mussels. Physical changes are most pronounced in shallow lakes and rivers, though deeper systems may experience enhanced light penetration. Sediment resuspension in some rivers can limit this effect. Chemical changes vary, though generally mussels increase mineralization of phosphorus and nitrogen, particularly in benthic water directly above lake sediment. Some areas with large *Dreissena* populations experience hypoxia above and in mussel beds, though the effect can be moderated by physical factors. One of the strongest impacts *Dreissena* exert in nearshore systems is a 'shunt' of phytoplankton (and energy) from pelagic to benthic communities. While many benthic invertebrates benefit either directly from enhanced habitat availability (mussel shells) or indirectly via resource supplementation (mussel faeces and pseudofaeces), some taxa (e.g. unionids) may be suppressed or eliminated via *Dreissena* fouling. Zooplankton typically exhibit size-dependent community changes, with small-bodied species suppressed (ingested) by mussels, whereas larger species may experience food limitation associated with mussel grazing. Intense grazing by mussel populations may facilitate growth of small algal species with high growth rates or promote blooms of cyanobacteria, the mechanism underlying which is not clear. *Dreissena* invasion also may facilitate growth of macrophytes, increased seasonal abundances of molluscivorous waterfowl, and changes in organochlorine and metal contaminant accumulation patterns in foodwebs. Some of the recently reported changes to ecosystems attributed to *Dreissena* could not be predicted *a priori*. Thus, despite a long history of research on the species, many questions remain regarding *Dreissena*'s direct and indirect effects on aquatic ecosystems.

Introduction

Biological invasion by nonindigenous species is one of mankind's most profound ecological perturbations, and lakes are amongst the ecosystems most impacted by introduced species. As *Dreissena* mussels spread from their native Ponto-Caspian region to elsewhere in Europe and to North America, reports of their ecological impacts have grown. Because excellent reviews exist regarding the taxonomy, genetics, reproduction and ecology of *Dreissena* (e.g. Stanczykowska, 1977; Mackie et al., 1989; Ackerman et al., 1994; Rosenberg and Ludyanskiy, 1994; MacIsaac, 1996; Mills et al., 1996; Karatayev et al., 1997), the purpose of this paper is to explore recent findings with respect to direct and indirect effects of *Dreissena* on biodiversity and ecosystem functioning, and to identify areas where our understanding remains poor. As *Dreissena* is still spreading in North America, and, to a lesser extent, in Europe, we developed our review using studies from both continents. We began our search by utilizing the keywords '*Dreissena'* and 'zebra mussel' to search the ISI Web of Knowledge to identify papers published between 1998 and 2005; we added additional papers cited in the captured studies, as well as other recent papers of which we are aware. Our review synthesizes work published during this period to provide an account of recent trends in physical, chemical or biological changes in communities invaded by *Dreissena*. For a summary of these changes and the underlying mechanisms see Table 1.

Effects on water clarity

Forming dense colonies and with filtering rates that exceed that of displaced native unionids by over 10-fold, *Dreissena* can reduce turbidity and improve water clarity through top-down control of phytoplankton and particulate material (Strayer et al., 1999; Idrisi et al., 2001; Vanderploeg et al., 2002). Lake St. Clair, with a mean depth of 3 m, provides a striking example of an invaded shallow system where zebra mussel filtering has had a dramatic effect on water clarity. After mussel establishment, light penetration increased two-fold and now reaches much of the lake bottom (Vanderploeg et al., 2002). Similarly, in Oneida Lake, NY, a shallow and well mixed system, Idrisi et al. (2001) reported that Secchi depth increased up to 1 m concomitant following *Dreissena* invasion. However, this was tempered by enhanced phytoplankton production at greater depths. Thus, as lake depth increases more variable water clarity changes have been reported. In Lake Erie, water clarity initially improved coincident with mussel invasion. For example, Makarewicz et al. (1999) assessed trends in offshore phytoplankton and water clarity in Lake Erie from 1983-1993, a period spanning pre- and post-*Dreissena* invasion. In the well-mixed western basin, Secchi depth changed little, and even decreased at times owing to resuspension of mussel faeces and pseudofaeces and blooms of cyanobacteria (Makarewicz et al., 1999; Noonburg et al., 2003). Likewise, despite initial improvements, Secchi depth subsequently declined in Saginaw Bay, Lake Huron, and in western Lake Erie, owing to increasing phytoplankton biomass and cyanobacteria blooms (Conroy et al., 2005; Pillsbury et al., 2002; see also below).

Within basin variation in morphometry also influences spatial patterns of effects of *Dreissena*. Makarewicz et al. (1999, 2000) reported greater Secchi depths in offshore areas of the central and eastern basins of Lake Erie post-*Dreissena* invasion. However, by 2004, the central basin showed a decrease in clarity, while the western basin showed no evidence of improvement (Barbiero and Tuchman, 2004). The authors attributed this to the high suspended solids inputs to the western basin, and to resuspension of unassimilated non-algal particulates in the central basin. The only convincing improvement in clarity was in the deeper eastern basin where spring transparency increased, ostensibly through reduced sediment loads. However, Barbiero and Tuchman (2004) hypothesized that historical natural 'whiting' events from calcium super-saturation in the eastern basin may have been reduced by increased mussel assimilation. Mussel filtering effects on turbidity can also depend on sediment composition. For example, initial improvements in clarity in Saginaw Bay were attributed to the relatively large particle sizes and lower sediment resuspension rates (Vanderploeg et al., 2002).

In Lake Ontario, tangible improvements in water clarity followed implementation of a phosphorus abatement program. This effect was enhanced by introduced *Dreissena*, as both light penetration and euphotic depth increased, with the light extinction coefficient in the eastern end of the lake decreasing from 0.35 m^{-1} to 0.26 m^{-1} (Mills et al., 2003). However, other studies indicate that improvements to water clarity may be confined principally to the benthic boundary layer directly above (<2 m) mussel beds (MacIsaac et al., 1999; Yu and Culver, 1999; Ackerman et al., 2001; Edwards et al., 2005).

Water column mixing or the lack thereof plays an important role in determining mussel grazing and, indirectly, on improvements to water clarity (Vanderploeg et al., 2002; Noonburg et al., 2003). However, this effect depends on the concentration of inorganic particulates, turbulence, and the ability of mussel grazing to exceed downstream losses by advection (Strayer et al., 1999; Effler et al., 2004). Consistent clarity improvements have been documented in the Hudson, Seneca and Oswego Rivers of New York, where 50-250% increases in light penetration were reported post-*Dreissena* invasion (Strayer et al., 1999; Effler and Siegfried, 1998; Effler et al., 2004). Changes were mediated mainly by incorporation into pseudofaeces of light-regulating tripton. Descy et al. (2003) developed a model to predict effects of mussel grazing in the River Moselle, France. Their results, which were consistent with studies from North America, demonstrated increased water clarity and reduced turbidity when mussel densities were high, with effects most pronounced in summer. Although mussel filtering impacts were predicted to be highest under turbulent conditions (Bartsch et al., 2003), clarity improvements may be precluded by high turbidity and resuspension of pseudofaeces (Schneider et al., 1998b; Vanderploeg et al., 2002). Despite this, a general improvement in water clarity is typically reported from invaded rivers and shallow lakes.

Positive effects on water clarity may also lead to positive feedback on mussel recruitment by increasing the availability of suitable macrophyte settling substrate for larval *Dreissena* (Muskó and Bako, 2005).

Temperature changes

Studies on changes in thermal characteristics of systems invaded by *Dreissena* are limited, though evidence suggests that lentic systems may experience thermal shifts in conjunction with changes in the light environment. For example, Yu and Culver (2000) demonstrated that greater light penetration after *Dreissena* invasion of a small reservoir caused a dramatic increase in metalimnetic temperature (mean 1.7-2.7^{o}C). Lester et al. (2004) used a model to predict the interactive effects of water clarity, temperature and bathymetry on optimal habitat for walleye (*Stizostedion vitreum*) in the Great Lakes. Thermal-optical habitat area initially increased with clarity but then declined exponentially. *Dreissena* impacts on light and temperature may, in turn, affect dissolved oxygen, thereby adding to the indirect consequences of *Dreissena* invasion.

Table 1. Documented changes in physical, chemical and biological components after *Dreissena* invasions. Changes occur as a consequence of direct (D) interactions with *Dreissena*, indirectly (I) through *Dreissena* alteration of other processes or ecological levels, or as a consequence of unknown interactions (?) that appear associated with *Dreissena* invasion. The direction of change in each component is given where ↑ = increase; ↓ = decrease; **-** = no change.

Component	↑/↓	Direct (D) indirect (I)	Mechanism	Reference(s)
Water Clarity	↑	D/I	Mussel ingestion of phytoplankton, POM, Ca^{2+} and tripton.	Effler and Siegfried, 1998; Effler et al., 2004; Idrisi et al., 2001; Makarewicz et al., 1999, 2000; Mills et al., 2003; Strayer et al., 1999; Vanderploeg et al., 2002
	-			Barbiero and Tuchman, 2004
	↓	I	Pseudofaeces/ faeces & non-assimilated algal resuspension, increased cyanobacteria and phytoplankton growth	Conroy et al., 2005; Makarewicz et al., 1999; Noonberg et al., 2003; Pillsbury et al., 2002
Temperature	↑	I	Enhanced light penetration	Lester et al., 2004; Yu and Culver, 2000
Dissolved Oxygen	↓	D/I	Heterotrophic decomposition of mussel faeces/pseudofaeces, mussel respiration	Caraco et al., 2000; Conroy and Culver, 2004; Descy et al., 2003; Effler and Siegfried, 1998; Effler et al., 2004; Pelley, 2003
	↑	I	Increased photo-depth facilitates macrophyte growth and photosynthesis	Caraco et al., 2000; Matthews et al., 2001
Nutrient concentrations	↑	D/I	Heterotrophic decomposition of mussel faeces/ pseudofaeces, nutrients release from top down control by mussel grazing on phytoplankton, nutrient excretion	Conroy et al., 2005; Effler et al., 2004; Hecky et al., 2004; Makarewicz et al., 1999, 2000; Orlova et al., 2004a; Strayer et al., 1999; Strayer et al., 2004
	↓	D	P assimilation to maintain mussel tissue N:P ratio	Vanderploeg et al., 2002
Benthic Carbon supply	↑	D	Faeces/pseudofaeces deposition	Poepperl 2003; Marvin et al., 2000; Strayer et al., 1999
Contaminants				
Benthic food web	↑	D	Bioaccumulation, ingestion of contaminated *Dreissena* pseudofaeces	Berny et al., 2003; Cho et al., 2004
Avian predators	↑	D/I	Biomagnification	Berny et al., 2003; Fox et al., 2005; Holeck et al., 2004
Sediment	↑	D	POM egestion or in pseudofaeces	Marvin et al., 2000
Phytoplankton				
Phytoplankton	↓	D	Filter feeding	Ackerman et al., 2001; Barbiero and Tuchman, 2004; Idrisi et al., 2001; MacIsaac et al., 1999; Makarewicz et al., 1999; Nicholls, 2001; Strayer et al., 1999; Wilson, 2003
Diatoms	↑	I	Selective filter feeding/rejection	Baker et al., 1998; Bastviken et al., 1998
Cyanobacteria				
Single cells	↓	D	Filter feeding preference	Baker et al., 1998; Bastviken et al., 1998; Dionisio Pires et al., 2004
Cyanobacterial blooms	↑	D/I	*Dreissena* ingestion of zooplankton reduces phytoplankton grazing pressure, elevated nutrient and light conditions, altered N and P ratios	Conroy and Culver, 2004; Makarewicz et al., 1999; Matthews et al., 2001; Pillsbury et al., 2002; Raikow et al., 2004; Vanderploeg et al., 2001, 2002; Vincent et al., 2004
	↓	D	Selective ingestion of *Microcystis*	Baker et al., 1998; Dionisio Pires et al., 2004b
Zooplankton				
Zooplankton	↓	D/I	Mussel ingestion, reduction of phytoplankton and rotifers food supply	Horgan and Mills, 1999; Johannsson et al., 2000; Pace et al., 1998; Thorp and Casper, 2003; Wong et al., 2003
Cladocerans, copepods	-			Pace et al., 1998; Strayer et al., 1999

Table 1. Continued

Component	**↑/ ↓**	**Direct (D) indirect (I)**	**Mechanism**	**Reference(s)**
Benthic invertebrates				
Biomass/abundance	↑	D/I	Biomass of *Dreissena*, pseudofaeces release, shelter and particle accumulation	Beekey et al., 2004b; Bially and MacIsaac, 2000; Beekey et al., 2004a; Dieterich et al., 2004; Johannsson et al., 2000; Haynes et al., 1999; Kolar et al., 2002; Moertl and Rothhaupt, 2003; Stewart et al., 1998; Reed et al., 2004
Long term abundance	↓	I	Food competition	Lozano et al., 2001 Haynes et al., 2005
Biodiversity	↓	D/I	Food/ space competition, pseudofaeces blockage of interstitial spaces	Ratti and Barton, 2003
Native unionids	↓	D	Overgrowth and food competition	Schloesser et al., 1998; Thorp and Casper, 2002
Diporeia hoyi	↓	?	Unknown	Lozano et al., 2001; Mills et al., 2003; Nalepa et al., 2000
Fish				
Pelagic species	↓	I	Depletion of zooplankton forage species via *Dreissena* grazing	Strayer et al., 2004
Littoral species	↑	I	Energy shunt to benthos	Johannsson et al., 2000; Mills et al., 2003; Strayer et al., 2004
Lake whitefish *Coregonus clupeaformis*	↓	I	Decline in *D. hoyi* abundance	Lozano et al., 2001; Madenjian et al., 2002; Pothoven et al., 2004
Larval fish abundance	-	I	Food competition for small zooplankton	Bartsch et al., 2003; Raikow, 2004; Thorp and Casper, 2003
Invasive species				
Echinogammarus ischnus	↓	D	Pseudofaeces/particles as food, shelter	Nehring, 2002; Ratti and Barton, 2003; Van der Velde et al., 2002
Round goby *Neogobius melanostomus*	↓	D	*Dreissena* and *E. ischnus* as food source	Ricciardi, 2004

Changes in dissolved oxygen and nutrient cycling

Dreissena has a direct influence on biochemical oxygen demand, and an indirect effect through facilitation of heterotrophic decomposition of faeces and pseudofaeces (Effler and Siegfried, 1998). Caraco et al. (2000) ascribed significant oxygen declines in the Hudson River to an increase in net system respiration associated with zebra mussels. However, oxygen depleting effects of *Dreissena* can be moderated by physical factors, including increased light penetration and consequent enhanced macrophyte photosynthesis and growth (Caraco et al., 2000; Matthews et al., 2001). However, in the Seneca River drastic reductions in oxygen led to violations of water quality standards following establishment of large *Dreissena* populations, with phytoplankton supplied from eutrophic lakes upstream (Effler et al., 2004). These patterns closely resemble those observed in the Moselle River, France (Descy et al., 2003).

River flow and turbulence can moderate oxygen-depleting effects of mussels. For example, Caraco et al. (2000) calculated that despite higher mussel densities, per capita oxygen depletion rates were actually lower in the Seneca than Hudson River due to higher flows. Indeed, in the largely canalized Oswego River, low dissolved oxygen levels that were observed after *Dreissena* had invaded were likely exacerbated by limited water surface-atmospheric exchange and low turbulence (Effler and Siegfried, 1998). Thus, Caraco et al. (2000) suggested that oxygen depletion would be higher in lentic systems where advection is usually much lower.

In Lake Erie, the effects of cultural eutrophication (1950s-1970s) were largely mitigated by phosphorus abatement programs. However, from 1993-2003 total phosphorus concentration increased and could not be explained by point-source loadings (Makarewicz et al., 2000; Nicholls et al., 2001; Pelley, 2003; Marvin et al., 2004). The return of hypolimnetic hypoxic zones, particularly in the central basin, have been attributed, in part, to increased deposition and resuspension of organic material and excretion of nutrients by mussels (Pelley, 2003; Conroy and Culver, 2004).

Dreissena may alter nutrient concentrations through their cycling effects on organic and inorganic matter (Strayer et al., 1999; Vanni, 2002; Newell, 2004). Top-down control by filtering of particulate material causes a 'shunt' of energy from pelagic to benthic areas as *Dreissena* biomass, and to the sediments as deposited faeces and pseudofaeces (Mills et al., 2003; Hecky et al., 2004). This may increase resource availability to other benthic consumers but will depend on bottom retention and, for unassimilated nutrients in mussel faeces, bacterial decomposition and remineralization (Strayer et al., 1999; Vanni 2002). This shift is also mediated by indirect effects of *Dreissena* on benthic primary production through increased water clarity (see physical changes). Additionally, *Dreissena* can exert bottom-up control on nutrient fluxes by excreting phosphate and ammonia, and indirectly by grazing phytoplankton and reducing control of the latter over nutrients (Vanni, 2002; Conroy and Culver, 2004; Conroy et al., 2005). Effler et al. (2004) provided compelling evidence for this in the Seneca River where temporal decreases in chlorophyll, a 17-fold increase in soluble reactive phosphorus (SRP), and a 3-fold increase in ammonia occurred post- (1993-2002) *Dreissena* invasion. In the Gulf of Finland, Baltic Sea, mussels contributed 500 kg of dissolved inorganic phosphorus (DIP) per day along the shore of the Neva River estuary relative to the supply of 32 kg per day from the river and its tributaries (Orlova et al., 2004a). The magnitude of nutrient cycling effects appears to vary with *Dreissena* density, age class, water depth/mixing, and nutrient and phytoplankton supply (Makarewicz et al., 2000; Idrisi et al., 2001; Strayer et al., 2004; Conroy et al., 2005). For example, a much lower increase in SRP (only two-fold) was observed in the Hudson River than in the Seneca River, reflecting the latter's shallower depth, higher mussel densities and the influence of an upstream phytoplankton source (Strayer et al., 1999, 2004; Effler et al., 2004).

Ambient nutrient levels also appear important moderators of *Dreissena* effects on nutrients, and on the mussels themselves. In Oneida Lake, Idrisi et al. (2001) suggested that water column phosphorus levels were important in altering N:P excretion ratios of *Dreissena*. This contention is supported by the differing responses to *Dreissena* invasion of SRP levels in Saginaw Bay (dramatic decrease) and in western Lake Erie (increase). Saginaw Bay was phosphorus-poor relative to western Lake Erie and by maintaining homoestatic regulation of tissue N:P ratios, *Dreissena* decreased the level of seston phosphorus through higher assimilation rates, whereas increased phosphorus availability reduced assimilation in western Lake Erie (Vanderploeg et al., 2002). In addition, increased macrophyte growth in Saginaw Bay served as a phosphorus sink.

In oligohaline areas of the Baltic Sea, *Cladophora* growths have become a public bathing nuisance and appear linked to high DIP levels induced by *Dreissena* (Orlova et al., 2004a). In the Oswego River and its Lake Ontario outflow, increased SRP levels led Effler and Siegfried (1998) to predict symptoms of enrichment in nearshore areas of the Great Lakes. Studies of Lake Erie during the post-*Dreissena* period support this contention. The western basin has seen increases in a range of nutrients including SRP, nitrate and ammonia, and excessive *Cladophora* growth indicative of increasingly eutrophic conditions (Makarewicz et al., 1999, 2000; Hecky et al., 2004). These observations lead Hecky et al. (2004) to propose the 'nearshore shunt' model. The model proposes a fundamental distinction be made with respect to *Dreissena*-induced nutrient cycling processes between nearshore and offshore areas. In nearshore areas, mussel interception and retention of fine particulates advected from offshore areas and nearshore diffusive inputs facilitate the deposition of large, non-ingested material as organic-mineral complexes. Recently, offshore areas have received lower particulate loads since larger complexes are better retained in nearshore areas. In the pre-invasion scenario, nearshore particulates were smaller and more easily resuspended, transported and deposited offshore. Retention offered by *Dreissena* beds also facilitates decomposition and remineralization, enhancing phosphorus availability in nearshore areas (Hecky et al., 2004). Where sediment oxygen content is reduced, a decoupling of excretion rates by zebra and quagga mussels showed that mussels have increased nutrient fluxes in Lake Erie by reducing turnover times (Conroy et al., 2005). Higher excretion rates by zebra mussels as compared to quagga mussels, coupled with increasing dominance by quagga mussels, has implications for future nutrient cycling in this and other lakes invaded by these species (Conroy et al., 2005).

Evidence that *Dreissena* increase organic carbon supply to the benthos is consistent with an energy shunt model. In lowland rivers of Germany, filtering effects of *Dreissena* accounted for a high proportion of the system organic carbon budget (Poepperl, 2003). Although total organic carbon (TOC) is generally lower in pseudofaeces than in water column particulates, Marvin et al. (2000) reported two-fold greater TOC in *Dreissena* colonized versus non-colonised sediments in western Lake Erie. High retention of TOC in faeces and pseudofaeces was facilitated by sheltering effects associated bottom roughness of colonies, which reduced resuspension from wave action. In the Hudson River, peaks in *Dreissena* densities were associated with elevated carbon deposition, which may have facilitated consumer populations (Strayer et al., 1999). Thus, nutrient cycling and organic matter deposition by *Dreissena* may have significant ecosystem level effects.

Bioaccumulation of contaminants

Zebra mussels have been employed in 'mussel watch' programs to assess spatial and temporal patterns of contaminants. Roe and MacIsaac's (1998) study on Lake Erie illustrated that moderately hydrophobic organic contaminants with mid-K_{ow} (octanol-water partition coefficient) values exhibited higher accumulation rates than either low- or high-K_{ow} congeners, that correlations between high K_{ow} compounds and mussel lipid content was greatest for neutral lipids, and that reproduction indirectly affects contaminant levels. Binelli et al. (2001b) found that mussels collected from Lake Como, Italy, contained more than twice as much PCBs after the spawning period than before (lipid-adjusted values), although neutral lipid concentrations did not vary substantially between sampling intervals.

Researchers have used two general approaches to survey contamination patterns using *Dreissena*. First, they may conduct synoptic surveys across sites that are expected to vary in contaminant exposure, or they may conduct repeated surveys at a limited number of sites to assess temporal patterns in naturally occurring mussels (e.g. Robertson and Lauenstein, 1998; Cope et al., 1999; Binelli et al., 2001b, 2003b, 2004a, 2004b). Alternatively, researchers may utilize laboratory experiments or may experimentally transplant mussels whose contaminant levels have been ascertained prior to deployment such that accumulation and depuration kinetics can be determined (Berny et al., 2002). For example, Bervoets et al. (2005) found that *Dreissena* experimentally transplanted in 56 Flemish water bodies accumulated organic pollutants within a six-week interval. These workers also found that concentrations of only four PCB congeners (101, 153, 138, 180) surveyed were correlated with sediment concentrations. In contrast to some metals (see below), the absence of a relationship between sediment concentration and tissue concentration suggests mussels become contaminated from other sources, notably water (Binelli and Provini, 2003b) or food (Cho et al., 2004).

Much of the particulate organic matter processed by *Dreissena* may be egested as pseudofaeces, particularly when food concentration is high (Cho et al., 2004). Highly contaminated pseudofaeces may, in turn, be consumed by other benthic invertebrates, shunting contaminants to benthic taxa and their predators (Cho et al., 2004). While mussels appear not to become contaminated from sediments, the opposite does not hold true. Marvin et al. (2000) observed higher concentrations of dibenzo-p-dioxin and polychlorinated dibenzofuran congeners in sediment associated with *Dreissena* mussels in Lake Ontario than in otherwise similar sediments that had not been colonized by mussels. Thus, colonization of sediments by mussels may portend changes in contaminant exposure both for epibenthic and infauna.

Dreissena accumulate other organic contaminants, including a variety of pesticides. A temporal survey on Lake Maggiore, Italy, demonstrated highly elevated concentrations of DDT and its breakdown products in *Dreissena* biomonitors following a large flood (Binelli et al., 2004b). *Dreissena* exhibited seasonal variation in tissue DDT concentrations, apparently owing to water column mixing during autumn and winter, which exposed them to more contaminated deeper waters. High levels of DDT during 2001 were associated with neuroendocrine interference of reproduction in *Dreissena* (Binelli et al., 2004a, 2004b). DDT in *Dreissena* collected from the Great Lakes was present primarily as DDD and DDE, except for eastern Lake Erie and Lakes Ontario where the parental chemical dominated (Robertson and Lauenstein, 1998).

Mussels also may accumulate other organochlorine pesticides to which they are exposed. A study of *Dreissena* on the Upper Mississippi River demonstrated contamination by α- chlordane and dieldrin at different sites (Cope et al., 1999). Berny et al. (2002) found that *Dreissena* could both accumulate and depurate lindane quickly, with an equilibrium achieved with four days. Accumulation of lindane in *Dreissena* in Lake Geneva varied both and spatially, and also was observed at high levels in tufted ducks (*Aythya fuligula*) that prey on *Dreissena* (Berny et al., 2003). Likewise, Fox et al. (2005) expressed concern about possible toxicological consequences of *Dreissena*-mediated transfer of selenium to lesser scaup (*Aythya affinis*) in North America.

Dreissena also may be used as a biomonitor of polybrominated diphenylethers (PBDEs), a class of flame retardant compounds (e.g. De Boer et al., 2003). Covaci et al. (2004) reported that *D. polymorpha* accumulated PBDEs, usually at concentrations lower than those observed in fish from the same sites (except congener 99). Tissue concentrations of PBDEs in *Dreissena* collected in the Netherlands tended to be similar to but slightly higher than those observed in *Mytilus edulis* collected in coastal areas of the country (De Boer et al., 2003).

Dreissena also bioaccumulate metal contaminants. For example, in their study of 56 Flemish water bodies, Bervoets et al. (2005) observed that some mussels were very heavily contaminated with cadmium, zinc, copper, nickel and lead. Tissue concentrations of the former two metals were well predicted by knowledge of dissolved and sediment-bound metal concentrations (51 and 75%, respectively). Mussel tissue concentrations of chromium and lead were predicted reasonably well (38 and 45%, respectively) by sediment-bound concentrations, when corrected for clay content and organic matter (Bervoets et al., 2005). This study also revealed that contaminated food was a significant source of metal uptake by mussels. Contamination by metals is predictive of *Dreissena* body condition within but not among sites (Bervoets et al., 2004c). Other studies have revealed contamination of *D. polymorpha* with lead, cadmium, mercury and other heavy metals in Lake Geneva, the Rhine and Meuse Rivers and the Oder River estuary (Hendriks et al., 1998; Wiesner et al., 2001; Berny et al., 2003).

In Lake Ontario, Johns and Timmerman (1998) determined that quagga (*D. bugensis*) and zebra mussels accumulated metal contaminants to differing extents. Quagga mussels accumulated greater amounts of cadmium, whereas zebra mussels had more copper and zinc and also exhibited greater interannual variation. As with organochlorine contaminants, metals in both species varied with reproductive cycle (Johns and Timmerman, 1998; Kwan et al., 2003). This pattern was not supported in another study on Lakes Ontario and Erie, which found that these mussel species tended to accumulate similar quantities of a broad spectrum of metals (Rutzke et al., 2000). Kwan et al. (2003) found that mussels could be used successfully for biomonitoring of metal availability in the St. Lawrence River if mussel size and seasonal effects were controlled. Conversely, Roditi et al. (2000) field tested a bioaccumulation model for metals in the Hudson and Niagara rivers, and found that predicted cadmium concentration was 2.6 fold higher than measured values. The model performed much better, however, for sites in Lakes Erie and Ontario, and for other metals (silver, chromium, mercury and selenium). The authors concluded that tissue concentrations could generally be predicted using their kinetic model that incorporated knowledge of dissolved and particulate metal concentrations (Roditi et al., 2000).

Phytoplankton

In many systems, *Dreissena* invasion is followed by a reduction in phytoplankton biomass and a shift in community composition but this appears dependent on physical factors and seasonality. In long-term studies of Lake Ontario and the upper Saint Lawrence River, major declines in chlorophyll-*a* were documented after *Dreissena* establishment (Nicholls, 2001). However, in the spatially heterogeneous Lake Erie effects were more variable. In the shallow western basin, where mussels had better access to the water column, Makarewicz et al. (1999) reported a general decline in diatoms and planktonic green algae, though little change was noted in the deeper and stratified central and eastern basins. However, a recent study of phytoplankton dynamics by Barbiero and Tuchman (2004) showed a decrease in chlorophyll-*a* in both the eastern and western basins during the spring isothermal and in all basins during summer stratification. Consistent with impacts on water clarity (see above), the vertical profile of phytoplankton may be moderated by lake depth and mixing (Noonburg et al., 2003). For example, in Lake Erie depletion rates of chlorophyll-*a* and organic seston were greatest immediately above mussel beds (MacIsaac et al., 1999; Ackerman et al., 2001). In contrast, chlorophyll-*a* declined by 46% in Oneida Lake, NY, after zebra mussel invasion, likely as a consequence of its shallow depth (Idrisi et al., 2001). Water flow rate influences delivery of food to *Dreissena*, as does the location of individual mussels within colonies (Tuchman et al., 2004). Because benthic waters above mussel beds may become depleted of food, individual ingestion rates and estimated colony consumption rates will be correspondingly lower than theoretically derived estimates.

Several studies have reported compositional changes in phytoplankton communities after invasion by *Dreissena*, suggesting selective ingestion. For example, although *Dreissena* caused large declines in phytoplankton in the Hudson River (Strayer, 1999), species of cyanobacteria declined while diatoms flourished (Baker et al., 1998). Baker et al. (1998) showed that this may be partly explained by preferential consumption of cyanobacteria and rejection of diatoms exhibited by *Dreissena*. Dionisio Pires et al. (2004b) also showed that adult *Dreissena* had higher clearance rates on cyanobacteria than on phytoplankton and detritus. Nevertheless, potential selection of cyanobacteria may be species-specific. However, these results are inconsistent with numerous other studies. For example, Wilson (2003) showed that zebra mussel filtering had little effect on colonial algae in mesocosm trials, despite a 53% reduction in phytoplankton biomass. Bastviken et al. (1998) demonstrated selective egestion of live phytoplankton in mussel pseudofaeces, and suggested that these cells could be resuspended and continue to grow in some systems. This finding supports the contention that other factors may have driven compositional changes in phytoplankton communities concomitant with invasion by *Dreissena*. For example, in a lake-wide comparison of phytoplankton community composition in Lake Ontario pre- and post-*Dreissena* invasion, Mills et al. (2003) suggested that a shift from diatoms and cyanobacteria to oligotrophic species was linked to decreasing phosphorus concentrations.

Mussels and cyanobacteria blooms

One of the most complex and controversial aspects of *Dreissena* ecology is whether the mussels facilitate the growth and dominance of cyanobacteria in lakes (Sarnelle et al., 2005). While the Great Lakes, and especially Lake Erie, have sustained cyanobacterial blooms prior to *Dreissena* invasions, the species involved and their relative abundance have changed following mussel invasion. For example, large ‘blooms’ of *Microcystis aeruginosa* were observed in the western Lake Erie and in Saginaw Bay, Lake Huron, following invasion by *Dreissena* (Makarewicz et al., 1999; Pillsbury et al., 2002; Vanderploeg et al., 2001; Conroy et al., 2005; Vincent et al., 2004). Makarewicz et al. (1999) also reported cyanobacteria biomass increased during spring following *Dreissena* invasion in all three basins of the lake, but noted that biomass declined in the western basin during summer owing to a loss of *Aphanizomenon flos-aquae*. Indeed, historic blooms of cyanobacteria in Lake Erie involved nitrogen-fixing taxa (e.g. *Aphanizomenon flos-aquae*, *Anabaena spiroides*) - rather than *Microcystis* - which flourished under low N:P ratios associated with cultural eutrophication (see Vanderploeg et al., 2001). Recent blooms of *Microcystis* have occurred despite successful reductions in phosphorus loading and a general improvement in water quality (Vanderploeg et al., 2001). These blooms all followed invasion by dreissenid mussels. Likewise, *Microcystis* was not abundant in Saginaw Bay for the two years prior to *Dreissena* invasion, but was abundant in three of five years immediately following mussel establishment (Vanderploeg et al., 2001). Additional evidence for enhanced growth of *Microcystis* in the presence of introduced *Dreissena* is derived from inland lakes (e.g. Raikow, 2004; Raikow et al., 2004). Matthews et al. (2001) suggested that a severe *Microcystis* bloom in Onondaga Lake, NY, was likely caused by explosive population growth of introduced *D. polymorpha*. Likewise, a survey of 61 inland lakes in Michigan revealed a positive relationship between *Dreissena* presence and *Microcystis* dominance, although the effect was limited to lakes in which total phosphorus concentration was $< 25\ \mu g\ l^{-1}$ (Raikow et al., 2004). Because phosphorus levels in many European lakes exceed $25\ \mu g\ l^{-1}$, any relationship between *Dreissena* and *Microcystis* would be difficult to discern. Moreover, these species have co-occurred in many European lakes for long periods, rendering it difficult to link invasion by the former to dominance by the latter. Facilitation of cyanobacteria by *Dreissena* may be confined to standing waters, as in the well-studied Hudson River pronounced declines of phytoplankton included cyanobacteria, particularly *Microcystis* (Strayer et al., 1999; Baker and Levinton, 2003).

A debate has developed regarding the mechanism(s) responsible for elevated cyanobacteria abundance in lakes invaded by *Dreissena*. Alternative hypotheses propose that either population growth rates of *Microcystis* are elevated in invaded systems, and/or that grazing rate on the species is reduced. Elevated growth rates by cyanobacteria in *Dreissena*-altered environments could be caused by elevated nutrient or light conditions, while dominance could be fostered by selective grazing on more palatable species by mussels. Evidence to separate these hypotheses is very difficult to obtain because of confounding and the lack of opportunity for replicated field studies (Conroy and Culver 2004). It is possible, and indeed likely, that more than one of the mechanisms may function simultaneously to enhance growth and dominance of cyanobacteria, particularly *Microcystis*, in *Dreissena*-invaded lakes. Conroy and Culver (2004) and Conroy et al. (2005) determined that introduced dreissenids increased nitrogen and phosphorus mineralization in western Lake Erie, shortened turnover times, and reduced the N:P ratio in a manner that promoted growth of *Microcystis*. However, Raikow et al. (2004) found that the N:P ratio was related to cyanobacteria dominance only in lakes lacking *Dreissena*. Pillsbury et al. (2002) also implicated favourable resource conditions for growth of cyanobacteria, noting that mid-summer blooms of *Microcystis* in Saginaw Bay were not associated with eutrophic conditions, but rather seemed consistent with reduced competition with phytoplankton, a condition created by selective grazing of the latter by *Dreissena*. This view implicitly incorporates the corollary that once present, *Microcystis* cells are differentially rejected or otherwise not ingested by *Dreissena*, resulting in its eventual dominance.

An alternative paradigm suggests that *Microcystis* may dominate phytoplankton because of differential ingestion of more palatable species by *Dreissena*. Vanderploeg et al. (2002) conducted a series of laboratory feeding trials with toxic strains of *M. aeruginosa* and found that *Dreissena* filtered at normal or reduced rates in the presence of the cyanobacterium. Filtered cells were rejected in pseudofaeces, whereas palatable *Cryptomonas* was ingested. In this way, *Dreissena* could induce a shift in phytoplankton community composition by differentially ingesting palatable species and rejecting *Microcystis*. However, available evidence in North America and Europe do not support this hypothesis. For example, Baker et al. (1998) observed that both colonial and single-celled forms of a toxic *M. aeruginosa* strain (LB 3835) were preferentially ingested over most other food sources by *D. polymorpha* from the Hudson River, a finding consistent with the observed decline of *Microcystis* in the river since its invasion by *Dreissena*. Dionisio Pires et al. (2004b) used flow cytometry to assess grazing by adult and larval *Dreissena* from Lake IJsselmeer, Netherlands, and noted that toxic *Microcystis* cells were apparently preferentially ingested over other foods and that mussel clearance rates on a mixture of the green alga *Scenedesmus* and *Microcystis* was higher than that with only the former species. Even if *Microcystis* were differentially rejected by filtering *Dreissena*, many of the cells contained in the rejected pseudofaeces are dead and thus incapable of contributing to future growth of and dominance by *Microcystis* in lakes (Dionisio Pires and Van Donk, 2002). Sarnelle et al. (2005) argued that even though *Dreissena* may feed on *Microcystis* cells, its stimulative effects on the species more than offset consumptive losses and thereby facilitates growth and dominance of the cyanobacterium.

Dreissena health is obviously affected by the food it ingests. Assessments of the biochemical composition of foods ingested by *Dreissena* may provide a more meaningful view of diet than its simple taxonomic composition. For example, foods rich in polyunsaturated fatty acids are highly nutritious and strongly affect mussel reproductive investment (Wacker and Von Elert, 2003a). Thus, a feedback system may exist in lakes colonized by *Dreissena* in which mussel grazing activities either directly or indirectly alter phytoplankton composition, and phytoplankton composition in turn affects mussel health, reproduction and population size.

Zooplankton

Dreissena feeding can have important consequences for zooplankton communities, mediated via two main mechanisms. First, mussel feeding can negatively affect zooplankton through direct predation on the small and weak-swimming species, including tintinnids, rotifers, and copepod nauplii. Secondly, mussels may indirectly suppress zooplankton by depleting food resources. For example, in the Hudson River, rotifers constituted 25 % of the daily energy requirement of *Dreissena* (Wong et al., 2003). In the same system, small zooplankton declined to 10-20 % of pre-*Dreissena* invasion levels, whereas adult copepod and cladoceran densities did not change (Pace et al., 1998; Strayer et al., 1999). In contrast, *in situ* mesocosm experiments conducted on the Mississippi River found that zebra mussels reduced the abundance of both small and large zooplankton that encompassed eight out of ten groups of rotifers, copepods, and cladocerans (Thorp and Casper, 2003). In Lake Erie, a reduction in zooplankton was attributed both to predation on small-bodied zooplankton and to depression of primary production (Johannsson et al., 2000). This suppression was particularly acute in unstratified bays due to water column mixing. Similar indirect effects were found in Lake Oneida where *Daphnia* biomass declined post-*Dreissena* invasion owing to food limitation (Horgan and Mills, 1999).

The presence of dreissenid veligers may also have a direct influence on the structure of the zooplankton community or, if occurring in sufficient density, alter such communities through competitive interactions. *Dreissena* veligers contribute between 10% and 25% to overall zooplankton production in Lake Erie (Johannsson et al., 2000). Despite the dominance of zebra mussel veligers (up to 80% abundance) in the tidal freshwater zooplankton assemblage of the highly productive St. Lawrence River estuary, the abundance of potential planktonic competitors did not decrease (Winkler et al., 2005). Declines in small-bodied zooplankton species were consistent with studies that reported direct ingestion by mussels.

Benthic invertebrates

The colonization of the benthos by *Dreissena* alters habitats in several ways, the most pronounced of which is the energy ‘shunt’ (Mills et al., 2003). Johannsson et al. (2000) reported a marked increase in biomass of most benthic invertebrates after *Dreissena* invasion, but noted that mussels accounted for >90% of biomass at five of six study sites in Lake Erie. Dense *Dreissena* colonies also increase habitat complexity, transforming soft sediment or bare cobble into a three dimensional substrate. In Lake Ontario, this resulted in a shift in community structure with an increase in snail abundance, a decrease in insect (e.g. chironomids, trichopterans), sphaeriid and oligochaete abundances, and continued dominance by amphipods (Lozano et al., 2001; Haynes et al., 2005). This pattern was corroborated in Lake Michigan, where *Dreissena* colonies teemed with amphipods, while adjacent soft sediments harboured mainly oligochaetes and chironomids (Reed et al., 2004). Although studies typically find a two- to five-fold increase in benthic invertebrates density in association with *Dreissena*, this may occur with or without a shift in community composition (Stewart et al., 1998; Bially and MacIsaac, 2000; Mörtl and Rothhaupt, 2003; Beekey et al., 2004a). Some invertebrates benefit directly from the abundance of hard mussel substrate. For example, sponges settle on mussel shells and benefit from enhanced water flow (Lauer and Spacie, 2004) or reduction in turbidity.

Despite local increases in density, long-term declines in invertebrate biodiversity have been observed in *Dreissena*-associated communities relative to pre-invasion assemblages (Lozano et al., 2001; Ratti and Barton, 2003). In Lake Ontario, oligochaetes and gastropods increased in abundance after *Dreissena* invasion, though most such increases were not sustained (e.g. turbellarians, bivalves and gastropods) (Haynes et al., 1999). Follow-up studies 8-9 years after the *Dreissena* invasion found that a native bivalve, trichopterans and chironomids decreased, while results were mixed for 4 species of gastropods (Haynes et al., 2005). Similarly, in eastern Lake Erie, formerly abundant ephemeropterans, trichopterans and other insect species disappeared, while gastropods and the invasive amphipod *Echinogammarus ischnus* increased (Ratti and Barton, 2003). Interestingly, field experiments have found no difference in macroinvertebrate abundance associated with empty mussel shells as compared to live mussels, suggesting that physical habitat was the factor responsible for reported changes (Stewart et al., 1998; Mörtl and Rothhaupt, 2003).

In addition to increasing the availability of habitat for fouling species like *Cladophora*, *Dreissena* beds provide other species with shelter from predators. Numerous studies have demonstrated enhanced amphipod abundance and survival in the presence of *Dreissena* when exposed to fish and crayfish predators (Bially and MacIsaac, 2000; Kolar et al., 2002; Beekey et al., 2004b; Dieterich et al., 2004; Reed et al., 2004). However, these studies also showed performance differences between fish species when feeding near *Dreissena* substrates. Indeed, invasive Eurasian ruffe (*Gymno-*

cephalus cernuus) were better able than native yellow perch (*Perca flavescens*) to forage on amphipods in the presence of *Dreissena* (Kolar et al., 2002).

Dreissena colonization of lakes has a profound, negative effect on native unionid molluscs (Burlakova et al., 2000). *Dreissena* compete with unionids both exploitatively for food and via interference fouling of their shells. Though *Dreissena* has not caused unionid species extinctions, it does cause local extirpations (Ricciardi, 2004). For example, in the Detroit River unionid populations have declined sharply with eight species extirpated within six years of *Dreissena* colonization (Schloesser et al., 1998). The number of live unionids has declined from >84% pre-*Dreissena* to <10% post-*Dreissena* (Schloesser et al., 1998). A number of traits may favour *Dreissena* over native unionids. Firstly, unionids infested with *Dreissena* experience a sharp reduction of algal cells in the gut almost certainly because the invaders have first access to the water containing food (Parker et al., 1998). Secondly, while unionids and *Dreissena* compete directly for bacterioplankton and phytoplankton, zooplankton can only be effectively exploited by *Dreissena* (Thorp and Casper, 2002), thereby providing it with an exclusive food resource. Despite inherent competitive disadvantages, native unionids may persist in certain settings, including marsh lands and wave-swept shorelines, where *Dreissena* perform poorly (Strayer, 1999). Dreissenids also appear to have contributed to the demise of the once dominant deepwater amphipod *Diporeia hoyi* in Lakes Ontario, Erie and Michigan. This is of particular concern since *Diporeia* was a key consumer within the benthic food web and dominated the diet of many fishes at some point in their life cycle (Lozano et al., 2001). Although the precise mechanism for the decline of *Diporeia* has not been ascertained, strong evidence exists for a link to *Dreissena* invasion. *Diporeia* declined in 40% of soft substrates in Lake Ontario coincident with the increase of dreissenids on soft and hard substrates (Lozano et al., 2001; Mills et al., 2003). Further, lipid content of *Diporeia* was at a level that compromised reproductive success in *Dreissena*-infested areas of Lake Michigan, suggesting poor food quality (Nalepa et al., 2000). This was supported by laboratory experiments in which exposure to *Dreissena* pseudofaeces caused a 30% decrease in *Diporeia* survival (Dermott et al., 2005).

Fish

Dreissena could impact fish directly through changes in habitat quality, particularly with respect to the light intensity or quality (see previously), by consumption of zooplankton suitable as fish food, or indirectly through suppression of foods required by larval or adult fishes and as fish food. The energy 'shunt' from the pelagic to the benthic habitats is a central factor determining the effects of *Dreissena* on fishes. In the Hudson River, for example, a marked shift in fish community was observed after the *Dreissena* invasion as open water fish species abundance decreased by 28% while littoral species increased by 97% (Strayer et al., 2004). Open water fish species and their larval stages suffered from suppression of phytoplankton and zooplankton, while littoral fish species benefited from increased benthic productivity (Strayer et al., 2004). Likewise, in Lake Erie, the benthic food chain supported 75% to 95% of fish production after *Dreissena* invasion (Johannsson et al., 2000). These shifts obviously benefit some species, including the deepwater sculpin (*Myoxocephalus thompsoni*) in Lake Ontario (Mills et al., 2003).

For other recreationally and commercially important fish species, *Dreissena* appears to have more negative than positive effects. In Lake Erie, eight fish species have declined in abundance, though mussel-induced effects are difficult to separate from oligotrophication associated with phosphorus abatement (Ryan et al., 1999). Following *Dreissena* invasion, the decline of the amphipod *D. hoyi* caused a shift in the diet of lake whitefish (*Coregonus clupeaformis*) to one dominated by lower quality foods, as well as reduced fish body weight and growth rates (Lozano et al., 2001; Madenjian et al., 2002; Pothoven et al., 2004).

Several studies have explored exploitative competition between *Dreissena* and larval fish for zooplankton prey, but results are inconclusive. Juvenile yellow perch (*Perca flavescens*) and fathead minnows (*Pimephales promelas*) may or may not compete with *Dreissena* for rotifers (Thorp and Casper, 2003; Bartsch et al., 2003). This may be attributed to differences in prey preferences, with larval white perch (*Morone americana*) and striped bass (*Morone saxatilis*) selective for copepods and cladocerans, while *Dreissena* tend to feed on smaller zooplankton (Pace et al., 1998). Indeed, fish may experience higher growth rates in some systems following mussel invasion. Raikow (2004) reported increased growth rates of juvenile bluegill (*Lepomis macrochirus*) in mesocosms with *Dreissena*, though larval fishes were adversely affected.

Invasional meltdown

Dreissena provides habitat for or is consumed by an array of species, including some that also are nonindigenous (Thorp et al., 1998; Petrie and Knapton, 1999; Reynolds and Donohoe, 2001; Sietman et al., 2003; Werner et al., 2005). The 'invasional meltdown' hypothesis states that nonindigenous species facilitate one another's establishment in new habitats (Ricciardi, 2001). Indeed, facilitative interactions involving introduced species have increased exponentially in the Great Lakes over the last 120 years (Ricciardi, 2005).

A study of the Great Lakes revealed 101 interactions between pairs of introduced species, including 17 cases of positive interactions (mutualism and commensalism) and 11 cases of negative interactions (antagonism and amensalism). In fact, there are some indications that a Black Sea foodweb is being reconstructed in the Great Lakes (as well as in the lower Rhine River). *Dreissena* seemingly facilitated subsequent invasion by the round goby (*Neogobius melanostomus*), which feeds on it in its native range. *Dreissena* also may have facilitated establishment and spread of the amphipod *Echinogammarus ischnus*, which exploits mussel shell habitats in the native range. *Echinogammarus* is also an important food item for juvenile round gobies. A somewhat similar sequence has transpired on the lower Rhine River following the opening of the Main-Danube Canal in 1992, which dramatically increased connectivity between the Black and North Sea basins allowed an influx of Ponto-Caspian species (Nehring, 2002; Van der Velde et al., 2002). Many of the late arriving invasive species (e.g. *Chelicorophium curvispinum* and *Dikerogammarus villosus* amphipods) consumed or otherwise adversely affected invaders that established in the system at an earlier date (e.g. see Devin et al., 2003).

Not all of the effects involving introduced *Dreissena* populations can be predicted based upon knowledge of populations elsewhere. Two primary examples of this include massive ‘blooms’ of cyanobacteria in North American systems invaded by *Dreissena* (see above), as well as possible links between *Dreissena* and mortality of piscivorous waterfowl principally red-breasted mergansers (*Mergus serrator*) and common loon (*Gavia immer*) – on eastern Lake Erie. In the latter case, *Dreissena* appears to facilitate growth of the bacterium *Clostridium botulinum*, which, in turn, is consumed by a food chain of *Dreissena*, round gobies (*Neogobius melanostomus*) and waterfowl, which may be killed by exposure to the bacterial toxin (Holeck et al., 2004). Clear precedents for cyanobacteria blooms and waterfowl mortality associated with *Dreissena* invasion are lacking in the European literature. These intercontinental differences highlight the fact that despite the tremendous amount of study devoted to this species, much remains to be learned regarding its direct and indirect impacts in invaded foodwebs.

Emerging and unresolved issues

1. How does basin morphometry, stratification, and water flow patterns affect mussel populations (e.g. biomass, recruitment), and how is this translated into ecological impacts?
2. In recently invaded systems such as the North American Great Lakes, how will mussel populations change over time?
3. What factors determine the intensity of the near-shore ‘shunt’ attributed to *Dreissena*?
4. How does invasion by *Dreissena* mussels affect local and regional biodiversity, and what taxa exhibit the greatest response (+/-) to the presence of *Dreissena*?
5. Does *Dreissena* facilitate establishment and proliferation of other ‘invasive’ species, including cyanobacteria and other nonindigenous species?
6. What role, if any, does *Dreissena* have on transmission of pathogens or toxins to higher trophic levels?

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