Potential Abiotic and Biotic Impacts of Zebra Mussels on the Inland Waters of North America[1]

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SYNOPSIS. The expansion of zebra mussel distribution into inland waterways of North America portends significant abiotic and biotic changes mediated either directly or indirectly by *Dreissena*. *Dreissena* fouls a wide array of submerged substrates including rock surfaces, macrophytes, native molluscs, canal and dock walls, and watercraft and motor outdrives. Fouling of water intake pipes and associated installations can severely impair water delivery to hydroelectric, municipal and industrial users, necessitating proactive or reactive control measures. Mussels increase water clarity by removing suspended clay, silt, bacteria, phytoplankton, and small zooplankton. Clear water phases associated with *Dreissena* grazing may exceed in magnitude and duration those generated by zooplankton grazing. Enhanced water clarity increases light transmittance and growth of benthic plants. Some benthic invertebrates (*e.g.,* unionid molluscs) are adversely affected by *Dreissena,* whereas others, including amphipod crustaceans, exploit structure associated with or wastes generated by zebra mussels. *Dreissena* is exploited by a host of predators, most notably waterfowl, fish and crayfish. Waterfowl predators that consume contaminated *Dreissena* have elevated concentrations of organic pesticides and polychlorinated biphenyl compounds. Invasion of shallow lakes and ponds by *Dreissena* may divert production and biomass from pelagic to benthic foodwebs, shifting ecosystems to an alternative state.

When new species arrive and spread, even if they do not have the appearance of the explosive invader, they may herald the onset of future changes in the balance of populations

—Charles Elton, 1958

INTRODUCTION

Charles Elton's (1958) classic work illustrated the extent to which human activities have deliberately or unwittingly facilitated the global movement and interchange of species. The introduction of species to new ecosystems often results in little conspicuous change in native species diversity, community composition or structure (Mills *et al.,* 1993). However, significant economic and ecological problems have been recorded in a diverse array of ecosystems invaded by exotic species (*e.g.,* see McCoid, 1991). In addition to affecting community composition and species diversity, exotic species may alter nutrient cycling and energy flow in ecosystems (*e.g.,* Walker and Vitousek, 1991).

At least 36 mollusc species have been introduced to Atlantic, Pacific and Gulf coasts of North America, including some that have caused significant economic and ecological problems (Carlton, 1992). For example, the Asian clam *Corbicula fluminea* has caused severe fouling of water works installations throughout the southern United States (McMahon, 1983). More recently, dramatic reductions in phytoplankton and zooplankton
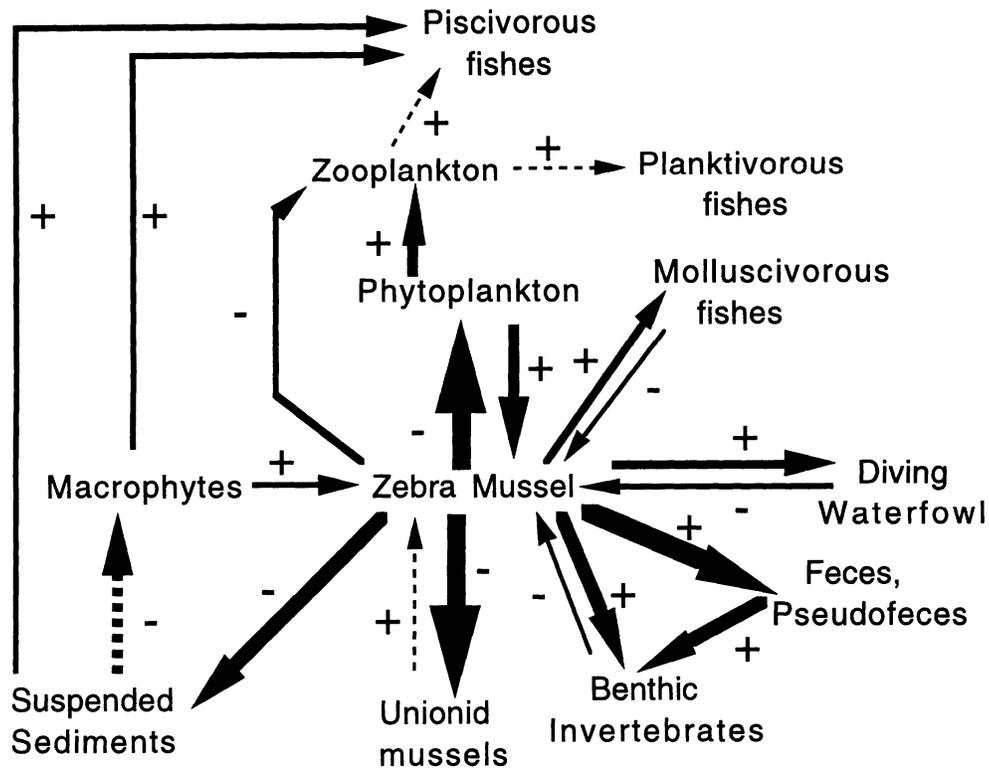
FIG. 1. Schematic of observed (solid line) and potential (dotted line) impacts of *Dreissena polymorpha* in freshwater communities based on European and North American studies. Taxa benefiting from *Dreissena* invasion are indicated with a (+) symbol on the arrowhead, those adversely affected by a (−) symbol. Strong interactions are denoted by thicker arrows. Only interactions in which *Dreissena* directly or indirectly affects other taxa are included. *Dreissena* may indirectly impact planktivorous and piscivorous fish by altering food supply or habitat quality. Refer to text for specific examples of each interaction.

biomass and displacement of the softshell clam *Mya arenaria* in San Francisco Bay have been ascribed to the clam *Potamocorbula amurensis*, a 1986 invader of the bay community (Nichols *et al.*, 1990; Kimmerer *et al.*, 1994).

While these introductions had pronounced effects on recipient communities, the 1986 invasion of the North American Great Lakes by the zebra mussel *Dreissena polymorpha* provides one of the most instructive examples to date of ecological modifications and economic damage associated with human-mediated species introductions (Hebert *et al.*, 1989). Despite its brief history in North America, the zebra mussel has already had dramatic effects on invaded systems. These impacts are both abiotic and biotic, direct and indirect. In the following sections, I review realized and

potential effects of *Dreissena* on inland lakes and rivers of North America based on European and Great Lakes' precedents. Forecasting specific impacts in a particular system is a tenuous practice, though evidence gleaned from previous *Dreissena* invasions permits some generalizations regarding anticipated impacts in newly invaded systems (Fig. 1).

IMPACTS ON WATER USERS

Perhaps the greatest abiotic effect expected of zebra mussels in newly invaded lakes, reservoirs, streams, navigation channels and locks will be problems associated with mussel biofouling. In the Great Lakes, *Dreissena* fouling is generally limited to structures submerged below 1.2-m depth (Claudi and Mackie, 1994). Permanent marine structures including pilings, bridges

and docks are particularly vulnerable to fouling. Temporary marine structures including buoys and other navigational aids, and fishing nets, may also be fouled depending on availability of competent larvae, resuspended postmetamorphic juveniles, and mobile adults (Martel, 1993). Fouling of recreational and commercial watercraft has contributed to the export of *Dreissena* from the Great Lakes (Carlton, 1993).

Water intake structures for municipal, industrial and hydroelectric plants are highly vulnerable to fouling if they draw from waterbodies contaminated with adult or larval *Dreissena*. Power plant components that may become fouled include crib structures, trash bars, screenhouses, steam condensers, heat exchangers, penstocks, service water systems and water level gauges (Kovalak *et al.*, 1993; Claudi and Mackie, 1994). Very long or narrow pipelines are particularly vulnerable to fouling and severely impeded flow (Claudi and Mackie, 1994). Kovalak *et al.* (1993) reported mussel densities as high as 750,000 ind.·m^{-2} at the Monroe power plant in western Lake Erie. These values far exceeded densities (<5000 ind.·m^{-2}) on adjacent lakebed at that time, and at a nearby (Fermi) nuclear power plant that utilized ~30 times less water than the Monroe facility (Kovalak *et al.*, 1993). Extraordinary mussel densities can be achieved in raw water intakes because of the enormous number of potential colonists entrained in the intake current, constant replenishment of food resources and removal of mussel wastes, and the absence of predators.

The intensity of mussel fouling depends critically on substrate type (Table 1). Kilgour and Mackie (1993) reported colonization differences greater than four orders of magnitude on substrates ranging from copper to stainless steel. Many materials used to construct dams, retaining walls, piers and pipelines (*e.g.*, concrete, galvanized iron, PVC) are suitable colonization substrates for *Dreissena* (Walz, 1975; Kilgour and Mackie, 1993). Mussel fouling also depends on current velocity. Flow velocities exceeding 1.5 m·sec^{-1} minimize mussel settlement in raw water intakes

TABLE 1. *Colonization of select substrates by D. polymorpha.*[1]

Settling substrate composition	Mussels· substrate^{-1}	Reference
Copper	0	Kilgour and Mackie,
Galvanized Iron	548	1993
Aluminum	2,324	
PVC	7,471	
Teflon	8,593	
Pressure-treated wood	15,255	
Polypropylene	17,554	
Stainless Steel	21,812	
Characeae	1,727	Lewandowski, 1982
D. polymorpha colonies	455	
Stones	61	
Sand	13	
Mud	13	
Polyvinylchloride	24	Walz, 1975[2]
Polypropylene	18	
Polyolefine	17	

[1] Methodological differences among studies limit comparisons to substrates within studies.

[2] Based on exposure of colonization plates for 93 days.

(Claudi and Mackie, 1994). The raw water intake for the city of Windsor, Ontario, has a flow velocity ~2.5 m·sec^{-1} and has not been fouled internally by zebra mussels (P. McQuarrie, personal communication).

ABIOTIC EFFECTS

A prominent and important abiotic effect of *Dreissena* in invaded ecosystems is enhanced water clarity. In contrast to the generally negative attitude held of *Dreissena* by most North Americans, the species has been intentionally stocked in lakes in the Netherlands as a "biomanipulation" tool to remedy poor water quality (see Reeders and Bij de Vaate, 1990; Noordhuis *et al.*, 1992). Water clarity, measured as Secchi disk transparency, is inversely related to the concentration of suspended sediments, detritus and plankton (Preisendorfer, 1986). Zebra mussels possess unique attributes that render them suitable water quality management "tools." First, because zebra mussels are present year-round, filtering impacts are much less ephemeral than those of zooplankton (see MacIsaac *et al.*, 1992; Nicholls and Hopkins, 1993). Second, *Dreissena*

may achieve population biomasses far greater than those of herbivorous zooplankton. For example, dry mussel biomass values >150 mg·cm^{-2} rock surface area were observed in western Lake Erie (MacIsaac, 1996). Third, unlike most zooplankton that consume only a narrow size spectrum of foods, usually between 2 and 25 µm (Sterner, 1989), zebra mussels filter a much broader suite of particles. Ten Winkel and Davids (1982) described positive selection by *Dreissena* of particles between 15 and 40 µm, though particles up to 750 µm were ingested. *Dreissena* also appears capable of ingesting particles finer than those consumed by most zooplankton. Sprung and Rose (1988) observed that *Dreissena* ingested particles as small as 0.7 µm, though at low efficiency. More recent work has established that ~1-µm bacteria are efficiently cleared from suspension (see Silverman *et al.*, 1996). Roditi *et al.* (1995) reported that *Dreissena* removed particles between 0.4 and >40 µm with approximately equal efficiency. These findings support those of Cotner *et al.* (1995), who observed that *Dreissena* cleared 0.36 and 0.91 µm microspheres from suspension at nearly equivalent rates, and suggested that the lower limit for particle removal is in the range of 0.22–0.36 µm. Ingestion of submicron particles by *Dreissena* greatly expands the range and quantity of suitable resources.

Dreissena-induced improvements in water clarity need not result from ingestion of suspended particles. As with many marine bivalves, *Dreissena* selects particles for ingestion on the basis of size, and possibly taste (Morton, 1971; Ten Winkel and Davids, 1982; Sprung and Rose, 1988). Suspended clays, silts, and large phytoplankton cells (*e.g., Asterionella formosa*) entrained in the inhalant current are sorted on the labial palps, enveloped in mucus, and expelled as pseudofeces *via* the inhalant siphon (Walz, 1978; Ten Winkel and Davids, 1982). *Dreissena* increased feces and pseudofeces production when exposed to 25–250 mg·liter^{-1} suspensions of 1-µm illite-smectite clay (MacIsaac and Rocha, 1995). Field patterns generally support the view that biodeposition of feces and pseudofeces

associated with mussel filtering activities can improve water clarity. Griffiths (1993) reported that Secchi disk transparency in Lake St. Clair increased from 0.5 to 1.5 m prior to *Dreissena* invasion to between 1.8 and 2.8 m in 1990. Water transparency increased by 100% in the southern portion of the west basin of Lake Erie between 1990 and 1992 relative to 1984 and 1986 (Holland, 1993). Transparency also increased in the north section of the west basin, as well as in the west-central and eastern (Long Point Bay) basins of the lake following establishment of large *Dreissena* populations (Leach, 1993; R. Knapton, personal communication). This pattern has been repeated in inner Saginaw Bay, Lake Huron. Mean turbidity declined from 9.2 NTU in 1991, one year following initial observations of *Dreissena* in the bay, to 8.3 NTU in 1992 when maximum mussel density was almost five times higher; turbidity declined further in 1993 to 3.7 NTU (Skubinna *et al.*, 1995). A clear demonstration of *D. polymorpha*'s ability to clarify natural systems was provided following the introduction of mussels, at a density of 540 ind.·m^{-2}, into one of two adjacent, hypertrophic ponds in the Netherlands (Reeders *et al.*, 1993). Secchi disk transparency was consistently higher in the treated pond relative to the reference system.

It is interesting to note that *Dreissena*-mediated changes in water transparency have generally occurred in shallow, well-mixed lakes, ponds and embayments. The effects of *Dreissena* on water quality in lotic environments are less clear. A review of European studies revealed that mussels are confined largely to rivers >30 m wide (Strayer, 1991). Minimum nephelometric turbidity of Detroit River water declined significantly (33% overall) following *Dreissena* invasion of Lake St. Clair, the river's source (t = 3.96, df = 12, P = 0.0019) (Fig. 2). *Dreissena* colonized the Hudson River, New York, in 1991 and experienced a large population increase in 1992 (M. Pace, personal communication). The mussel is attributed with massive (~90%) reductions in algal and microzooplankton biomass but only a 7% increase in water transparency, perhaps owing to resuspension of
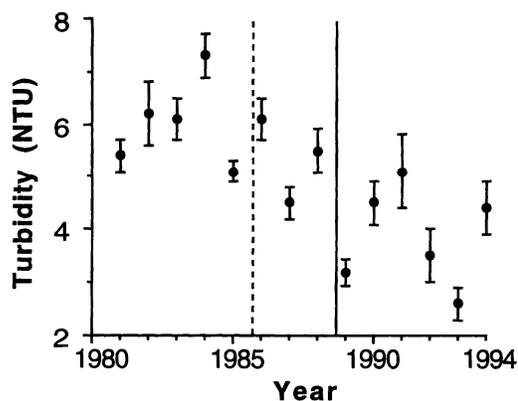
FIG. 2. Variation (mean ± 1 SE) in water turbidity in the Detroit River for the June 1–Sept. 30 period between 1981 and 1994. Means are based on 10-day minimum values for each month. The solid line separates years prior and subsequent to development of large *Dreissena* populations at upstream sites in Lake St. Clair (see Hebert et al., 1991); the dotted line indicates the putative invasion date (Hebert et al., 1989). Mean turbidity level declined significantly following *Dreissena* establishment in the lake (MacIsaac and Rocha, 1995).

feces and pseudofeces (M. Pace and N. Caraco, personal communications). Although empirical evidence is lacking, water transparency changes may be more apparent in slow-flowing rivers that mix less thoroughly than tide-influenced systems like the Hudson River. Thus, a continuum may exist from non-stratified lakes and rivers with poor to moderate mixing to stratified lakes and well mixed rivers, wherein respective *Dreissena* effects on turbidity and transparency decline from pronounced to almost nonapparent.

One factor that could reduce the impact of *Dreissena* on water quality is the presence of high concentrations of suspended inorganic particles. Alexander et al. (1994) observed significant but unexplained decreases in *Dreissena* respiration when animals were exposed to a moderate (31 mg·liter^{-1}) concentration of bentonite clay. *Dreissena* stopped filtering during sediment resuspension in Lake Druzno, Poland, and resumed only when small particles remained suspended (Wisniewski, 1990). Despite this sensitivity, overall ingestion rate (mg seston consumed·ind^{-1}·hr^{-1}) of mussels exposed to suspended sediment was equal to or greater than those of individuals in

treatments lacking sediment (Wisniewski, 1990). MacIsaac and Rocha (1995) observed that the proportion of time spent with valves closed was <3% even in the presence of high concentrations of illite-smectite clay. Mussels chronically exposed to high concentrations of suspended sediments may increase the palp to gill surface area ratio to effect efficient sorting of food and non-food particles (Payne et al., 1995). Thus, both behavioral and anatomical responses permit *Dreissena* to tolerate turbid water conditions characteristic of many river systems. It is unclear, however, whether *Dreissena* will demonstrably impact water quality in turbid systems like the southern Mississippi River, considering that additional stressors (e.g., temperature) may affect mussels at these localities.

One possible physical change yet to be explored in lakes and reservoirs invaded by *Dreissena* is alteration of mixing depth. Because Secchi disk depth is positively correlated with mixing depth (Mazumder et al., 1990), any *Dreissena*-induced reduction in concentrations of suspended inorganic or organic particles that results in greater incident solar radiation penetration could also increase epilimnion depth. Such a change could alter, among other things, the ratio between and respective volumes of the epilimnion and hypolimnion, as well as the hypolimnetic oxygen depletion rate. An increase in the latter parameter would be of particular importance in basins vulnerable to seasonal anoxia (e.g., central Lake Erie).

BIOTIC EFFECTS

Some European and North American freshwater communities have experienced profound ecological changes subsequent to invasion by *D. polymorpha*. Biota impacted by *Dreissena* encompass most categories of life in freshwater ecosystems.

One of the most predictable effects of *Dreissena* invasions of lakes and rivers is greatly diminished phytoplankton biomass. By ingesting or enveloping phytoplankton cells in negatively buoyant pseudofecal pellets, mussels can greatly reduce phytoplankton standing biomass, particularly in well mixed systems in which refiltration of water is reduced. For example, Reeders et

al. (1993) reported a pronounced decline (~46%) in phytoplankton biovolume in a pond stocked with *Dreissena* relative to a reference pond lacking mussels. Phytoplankton biomass, as estimated by chlorophyll *a* concentration, also declined dramatically (~60%) in the western and west-central basins of Lake Erie between 1988 and 1991, and in Saginaw Bay (59%) subsequent to establishment of large *Dreissena* populations (Leach, 1993; Fahnenstiel *et al.*, 1995). Depletion of phytoplankton in western Lake Erie was most severe directly over mussel beds (MacIsaac *et al.*, 1992), and in the southeastern section of the basin (82–91% reduction) (Holland, 1993). Phytoplankton depletion has also been observed in inland lakes and rivers. Chlorophyll *a* concentration declined sharply between 1990 and 1993 in Oneida Lake, and between 1991 and 1992 in the Hudson River (90% decline) commensurate with dramatic growth of *Dreissena* populations (E. L. Mills, M. Pace, personal communications). Nicholls and Hopkins (1993) stated that the decline in phytoplankton density in Lake Erie was incompatible with predictions based on phosphorus concentration, but was consistent with that expected by *Dreissena* feeding.

It is not clear whether vulnerability to mussel ingestion varies among phytoplankton taxa, nor whether *Dreissena* filtering activities promote changes in phytoplankton community composition. In western Lake Erie, all major phytoplankton taxa (*e.g.*, Bacillariophyceae, Cyanophyceae, Cryptophyceae), including large colonial forms, experienced abundance declines following invasion of the basin by *Dreissena* (Nicholls and Hopkins, 1993). Similarly, *Dreissena* ingested spherical algal colonies (>1-mm) and filaments (>3-mm length) from Oneida Lake (E. L. Mills, personal communication). These studies corroborate earlier work that established broad feeding capabilities of *Dreissena* (Ten Winkel and Davids, 1982), but contradict results from a mesocosm grazing experiment in Saginaw Bay in which the standing crops of diatoms and chlorophytes were differentially suppressed relative to those of colonial cyanobacteria (*Microcystis*) and large chryso-

phytes (*Synura*) when exposed to *Dreissena* (Heath *et al.*, 1995). Thus, despite the *ability* to consume a wide size range of phytoplankton cells, *Dreissena* may feed *preferentially* on particles between <1- and <50-μm (Ten Winkel and Davids, 1982; Cotner *et al.*, 1995; Roditi *et al.*, 1996; Silverman *et al.*, 1996). Results from different studies may be reconciled if feeding selectivity is hunger-dependent; Ten Winkel and Davids (1982) observed that mussels temporarily deprived of food fed indiscriminately on natural seston that included cells as large as 750-μm, whereas well-nourished individuals fed selectively on a much narrower range of particles. Non-selective feeding could be important in systems supporting high mussel densities but low phytoplankton biomass.

Cyanobacteria blooms have been reported in basins supporting large mussel populations, including western Lake Erie (J. H. Leach, unpublished data), Saginaw Bay (Heath *et al.*, 1995) and Oneida Lake (E. L. Mills, personal communication). Conversely, cyanobacteria (*Anabaena, Oscillatoria* and *Aphanizomenon*) blooms developed in a reference pond lacking *Dreissena*, but not in a pond stocked with mussels (Reeders *et al.*, 1993). Possible factors that may account for enhanced cyanobacteria abundance in systems with *Dreissena* include a reduction in the N:P ratio, enhanced light penetration, greater buoyancy of cyanobacteria filaments, or chemical or mechanical inhibition of mussel filtering by cyanobacteria. *D. polymorpha* and *D. bugensis* (quagga mussel) did not open their valves or feed, and experienced between 30 and 100% mortality, when exposed to 10–25 g·liter^{-1} *Mycrocystis aeruginosa* (Birger *et al.*, 1978). Mussel filtering activity was also diminished in Saginaw Bay during a cyanobacteria bloom (Heath *et al.* 1995). Mechanical interference by large, armored *Ceratium* cells was attributed with seasonal declines in *Dreissena* filtering rate in Lake Mikolajskie, Poland (Stańczykowska *et al.*, 1976).

Three important factors that can influence *Dreissena* filtering impact in lakes and rivers are ambient temperature, seston concentration and mussel size frequency distri-

bution. Reeders and Bij de Vaate (1990) proposed that filtering rate (ml filtered·mussel^{-1}·hr^{-1}) was maximal between 5 and 20°C, but declined sharply at either lower or higher temperatures. By contrast, Morton (1971) reported progressive increases in filtering rate up to a maximal value at 30°C; beyond this temperature, two of three mussels died. Walz (1978) observed that *Dreissena* ingestion rate (μg ingested·mussel^{-1}·hr^{-1}) could be modeled by a bell curve, with an optimal value at 12.5°C. Despite these divergent results, temperature could be a very important factor limiting activity or distribution of mussels in southern U.S.A. rivers, lakes and reservoirs if the mussels' thermal preference or tolerance limits are exceeded.

Seston concentration has a profound effect on assimilation efficiency of *Dreissena*. Ingestion rate increases linearly with food concentration until an asymptote is reached at the incipient limiting level (Walz, 1978; Sprung and Rose, 1988). Filtering rate, which is constant and maximal below the incipient limiting level, declines exponentially above it (Sprung and Rose, 1988). Walz (1978) estimated the incipient limiting level at ~2 μg C·ml^{-1}, and the onset of pseudofeces production at approximately one tenth this value. The proportion of food expelled as pseudofeces increased rapidly at food levels above 0.2 μg C·ml^{-1} (Walz, 1978).

Zooplankton populations may be adversely impacted either indirectly or directly by *Dreissena*. Populations of small zooplankton, particularly rotifers and *Dreissena* veligers, were suppressed when incubated with *Dreissena* ≥10-mm (MacIsaac *et al.,* 1991, 1995). Small zooplankton (*e.g., Keratella, Polyarthra*) entrained in the inhalant stream of feeding mussels fail to elicit a rejection response by *Dreissena,* are incapable of escaping from the current, and are ingested (MacIsaac *et al.,* 1991). Large zooplankton can either evade mussel feeding currents or are expelled from the inhalant siphon area following contact with, and irritation of, siphonal tentacles. In western Lake Erie, rotifer abundance declined by 74% between 1988 and the 1989–1993 period; this change occurred coincident with

establishment of enormous *Dreissena* populations (up to 342,000 ind.·m^{-2}) beginning in 1989 (Leach, 1993; MacIsaac *et al.,* 1995). Cladoceran density has not changed appreciably, though total copepod abundance (mainly nauplii) declined between 39% and 69% between 1988 and 1993. It is difficult to discriminate between suppression of zooplankton resulting from direct ingestion by *Dreissena* and that caused food limitation. However, the direct suppression hypothesis is supported by results from San Francisco Bay, where the exotic clam *Potamocorbula* is attributed with ingestion and strong suppression of copepod nauplii (Kimmerer *et al.,* 1994). Moreover, recruitment of settling *Dreissena* on tiles in Saginaw Bay was inversely related to adult density, indicating possible direct ingestion of larvae (Nalepa *et al.,* 1995). Rotifers and protozoans were strongly suppressed in the Hudson River subsequent to development of a large *Dreissena* population in 1992, possibly owing to food limitation (M. Pace, personal communication).

Suppression of small zooplankton may reduce food availability to fishes that are planktivorous at some developmental stage. Yellow perch (*Perca flavescens*) recruitment and commercial harvest declined dramatically in western Lake Erie concomitant with the zebra mussel invasion, though other factors, notably an expanding white perch (*Morone americana*) population, may partially account for observed changes (OMNR, 1994). Spawning success of walleye (*Stizostedion vitreum*) in western Lake Erie was poor between 1987 and 1989, increased in 1990 and 1991, but declined again in 1992 (OMNR, 1994). Commercial walleye quotas have been met in the basin despite the presence of *Dreissena* (OMNR, 1994). A factor of greater concern with respect to walleye is alteration of habitat associated with increased light transmittance. Rod-hour sport landings and net-based fisheries assessment catches declined by ~50% in Lake St. Clair subsequent to establishment of *Dreissena* (OMNR, 1995). In addition, adult walleye are now found primarily in the shipping channel, the deepest and most turbid portion of the lake (D. MacLennan, personal communication).

Changes in fish abundance do not appear related to recruitment as both spawning and hatching success were good in the Thames River, a major contributor to fish populations in the lake (OMNR, 1995). It is quite likely that young walleye were consumed by smallmouth bass (*Micropterus dolomieu*), largemouth bass (*M. salmoides*), northern pike (*Esox lucius*), and muskellunge (*E. masquinongy*), all of which have increased in abundance in recent years (OMNR, 1995).

In contrast to hypothesized, adverse indirect effects on walleye, zebra mussels represent an abundant food source for many fish species (Fig. 1). French (1993) reported that fishes with upper and lower pharyngeal teeth or lower pharyngeal teeth and chewing pads were likely consumers of zebra mussels in North America. Fishes known or expected to exploit *Dreissena* include freshwater drum (*Aplodinotus grunniens*), redear sunfish (*Lepomis microlophus*), pumpkinseed (*L. gibbosus*), copper (*Moxostoma hubbsi*) and river (*M. carinatum*) redhorse and common carp (*Cyprinus carpio*) (French, 1993). Zebra mussels have been reported in digestive tracts of other fishes in the Great Lakes including yellow perch, white perch, walleye, white bass (*Morone chrysops*), lake whitefish (*Coregonus clupeaformis*), lake sturgeon (*Acipenser fulvescens*) and the round goby (*Neogobius melanostomus*) (French, 1993).

Positive feedback may exist between production of macrophytes and *Dreissena* in shallow, light-limited systems (Figs. 1, 2). Mussel production may promote enhanced water clarity, which in turn facilitates increased macrophyte production and increased settling substrate for *Dreissena*. European workers described high settlement rates of competent *Dreissena* on macrophytes (Table 1; Lewandowski, 1982).

The increase in abundance of northern pike, muskellunge and bass in Lake St. Clair may relate to increased production of macrophytes in conjunction with enhanced water clarity and increased euphotic depth. The euphotic zone in Lake St. Clair has expanded to encompass most of the benthic surface area. Large regions of the lake now support macrophyte growth (Griffiths,

1993). During spring and summer 1994, enormous volumes of decaying *Elodea canadensis* and, to a lesser extent, *Myriophyllum spicatum, Vallisneria americana, Najas flexilis* and *Potamogeton* spp., washed ashore on both Canadian and American shorelines causing severe water quality problems and beach fouling. Metropolitan Beach, southwest of the Clinton River, MI, was closed owing to high bacterial counts and macrophyte stranding. Front-end loaders were employed to remove macrophytes fouling the beach. Stranding resulted from unusual wind patterns that trapped macrophytes along shorelines rather than flushing the material into the Detroit River. Nevertheless, the current nutrient status of Lake St. Clair coupled with enhanced solar radiation penetration indicates that prolific growth of macrophytes may become the norm. Production of shade-sensitive water celery (*Vallisneria*) also increased in Long Point Bay in eastern Lake Erie concomitant with establishment of *Dreissena* (R. Knapton, personal communication).

Dreissena invasion and the attendant shift in energy from planktonic to benthic foodwebs may profoundly affect benthic invertebrate communities (Fig. 1). Unionid molluscs are among the taxa most affected, and may be extirpated from systems supporting large *Dreissena* populations (see Schloesser *et al.,* this volume). By contrast, many other invertebrates may benefit from structure associated with *Dreissena* colonies or from enhanced food supply. Stewart and Haynes (1994) assessed macroinvertebrate communities in southwestern Lake Ontario before (1983) and after (1991–1992) invasion of *D. polymorpha* and *D. bugensis. Dreissena* dominated invertebrate communities numerically (79–93%) in 1991 and 1992, though all taxa increased in abundance following *Dreissena* establishment. Total non-*Dreissena* invertebrate abundance increased between 1,316 and 4,595 ind.·m^{-2} following establishment of *Dreissena*. Taxa showing the greatest increases included annelids (*Manayunkia speciosa, Spirosperma ferox* and unidentified tubificids), gastropods (*Helisoma anceps, Physa heterostropha, Stagnicola catascopium, Valvata tricarinata, Goniobasis liv-*

escens and *Amnicola limosa*), amphipods (*Gammarus fasciatus*), and crayfish (*Orconectes propinquus*) (Stewart and Haynes, 1994). These patterns strongly parallel results for eastern Lake Erie (Dermott *et al.*, 1993) and Lake St. Clair (Griffiths, 1993). Increased abundances of amphipods, leeches, triclads, snails, mayflies, caddis flies and true flies were attributed to enhanced habitat structure, whereas annelid worms and crayfish may have increased owing to enhanced food supply (Dermott *et al.*, 1993; Griffiths, 1993; Stewart and Haynes, 1994; MacIsaac, 1994; Martin and Corkum, 1994). Griffiths (1993) argued that benthic invertebrate communities in southeastern Lake St. Clair shifted toward those characteristic of more oligotrophic systems.

Benthic invertebrate diversity may also benefit from *Dreissena* invasion. Total invertebrate diversity increased from ≤22 species to between 27 and 32 taxa at a cobble site, and from ≤15 species to between 19 and 26 taxa at an artificial reef site in Lake Ontario following *Dreissena* invasion (Stewart and Haynes, 1994). This result should be interpreted with caution, however, because Griffiths (1993) observed increased macroinvertebrate diversity between 1980 and 1990 at sites in Lake St. Clair both with and without *Dreissena*.

Diving waterfowl are important predators of *Dreissena* in Europe (Stempniewicz, 1974; Stańczykowska *et al.*, 1990; Bij de Vaate, 1991; Cleven and Frenzel, 1993) and North America (Wormington and Leach, 1992; Hamilton *et al.*, 1994; Mazak, 1995). Wormington and Leach (1992) reported greater waterfowl flock size and staging duration in the Point Pelee, Ontario area subsequent to development of *Dreissena* populations in Lake Erie. Numerical responses were greatest for greater scaup (*Aythya marila*), lesser scaup (*A. affinis*) and common goldeneye (*Bucephala clangula*). Each of these species, as well as bufflehead (*B. albeola*), feed extensively on zebra mussels in western Lake Erie (Wormington and Leach, 1992; Hamilton *et al.*, 1994; Mazak, 1995). Ducks consumed 57% of autumn mussel biomass in western Lake Erie, but had little impact on mussel biomass the following spring because of growth of small

individuals (Hamilton *et al.*, 1994). Ducks likewise consumed 90% of standing biomass in River Seerhein (Lake Constance) during winter months, but had little impact on the population owing to recruitment and immigration of new individuals (Cleven and Frenzel, 1993). Regulation of *Dreissena* biomass and abundance by waterfowl is unlikely in central North America because predation is limited to ice-off periods (Hamilton *et al.*, 1994). Regulation of mussel populations is more likely at southern localities in the U.S.A. where waterfowl could prey on mussels for protracted periods of time.

Zebra mussels, by virtue of their ability to biomagnify metal and organochlorine contaminants, may serve as an effective conduit for transfer of contaminants to high trophic levels (*e.g.*, see Mersch and Pihan, 1993; Bruner *et al.*, 1994). For example, lesser and greater scaup in western Lake Erie that consumed *Dreissena* contained elevated concentrations of a broad spectrum of organic contaminants relative to conspecifics from the lower Detroit River that consumed mainly macrophytes (Mazak, 1995). Biomagnification of organochlorine contaminants in ducks that consumed mussels depended on the chemicals' octanol-water partition coefficient (K_{ow}) (Fig. 3). Biomagnification factors are higher for highly hydrophobic chemicals (high K_{ow}) than for less hydrophobic ones (Fig. 3). Previous work demonstrated that tufted ducks (*A. fuligula*) fed a diet of highly contaminated *Dreissena* experienced a host of reproductive problems ranging from smaller clutch and egg size, to higher embryo mortality and higher incidence of nest abandonment (de Kock and Bowmer, 1993). To date, however, reproductive problems associated with organic contaminants have not been identified for Lake Erie waterfowl that utilize *Dreissena*.

Alternate ecosystem states?

Scheffer *et al.* (1993) proposed that shallow lakes may have two alternative equilibria: a clear state dominated by macrophytes, and a turbid state supporting high algal biomass. The transition between clear and turbid states is believed to be governed by
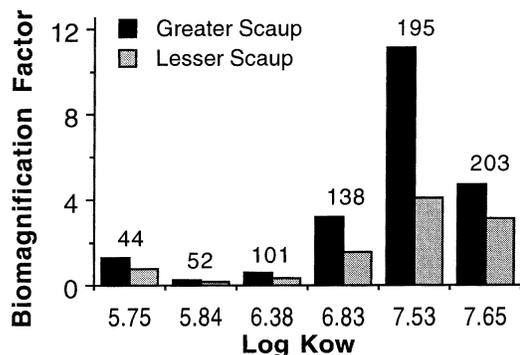
FIG. 3. Biomagnification factors ([duck]/[*Dreissena* prey]) of greater and lesser scaup from western Lake Erie in relation to octanol–water partition coefficients (K_{ow}) of six polychlorinated biphenyls (PCBs). IUPAC congener number is provided above each bar for each PCB. Duck diets consisted of >95% *Dreissena* by mass. Data courtesy of Ed Mazak.

feedback relationships between macrophytes and turbidity. Because the lower depth limit of macrophytes is positively correlated with Secchi disk transparency (Scheffer et al., 1993), turbid systems have a limited ability to support benthic vegetation. By stripping suspended sediments and algae from the water column, *Dreissena*-induced increases in transparency may facilitate the growth of macrophytes in shallow lakes. The presence of macrophytes and *Dreissena* feces and pseudofeces provide habitat and food to many benthic invertebrates and fishes. Thus, it is possible that shallow systems invaded by *Dreissena* may experience dramatic shifts in energy and biomass from pelagic to benthic foodwebs. In this regard, water quality effects exerted by *Dreissena* resemble, but may be stronger than, those associated with "biomanipulation" programs in which piscivorous fishes are stocked to reduce algal biomass and enhance water transparency.

SUMMARY

Invasion of inland waterways by *Dreissena* may result in dramatic physical and biological changes, particularly in shallow or well-mixed systems. Based on European and Great Lakes precedents, users of raw water from invaded systems may incur significant biofouling mitigation expenses. Mussel filtering activities often result in re-

duced concentrations of suspended solids and phytoplankton, with attendant increases in light transmittance and macrophyte production. Zooplankton may be suppressed owing to food limitation or, for small taxa, direct ingestion by *Dreissena*. Habitat structure associated with, and waste products generated by, colonies of *Dreissena* enhance production of many benthic invertebrates. Invertebrate (e.g., crayfish) and vertebrate (fishes, waterfowl) predators may experience numerical responses in habitats supporting high *Dreissena* densities. Predators of contaminated *Dreissena* biomagnify organochlorine compounds, thereby altering contaminant cycling.

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