

Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion

ANTHONY RICCIARDI*, RICHARD J. NEVES† and
JOSEPH B. RASMUSSEN‡

*GIROQ, Département de biologie, Université Laval, Ste-Foy, Quebec G1K 7P4, Canada; †Virginia Cooperative Fish and Wildlife Research Unit, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0321, USA; and ‡Department of Biology, McGill University, Montréal, Quebec H3A 1B1, Canada

Summary

1. Freshwater mussels (Order Unionoida) are the most imperiled faunal group in North America; 60% of described species are considered endangered or threatened, and 12% are presumed extinct. Widespread habitat degradation (including pollution, siltation, river channelization and impoundment) has been the primary cause of extinction during this century, but a new stress was added in the last decade by the introduction of the Eurasian zebra mussel, *Dreissena polymorpha*, a biofouling organism that smothers the shells of other molluscs and competes with other suspension feeders for food. Since the early 1990s, it has been spreading throughout the Mississippi River basin, which contains the largest number of endemic freshwater mussels in the world. In this report, we use an exponential decay model based on data from other invaded habitats to predict the long-term impact of *D. polymorpha* on mussel species richness in the basin.

2. In North American lakes and rivers that support high densities ($> 3000 \text{ m}^{-2}$) of *D. polymorpha*, native mussel populations are extirpated within 4–8 years following invasion. Significant local declines in native mussel populations in the Illinois and Ohio rivers, concomitant with the establishment of dense populations of *D. polymorpha*, suggest that induced mortality is occurring in the Mississippi River basin.

3. A comparison of species loss at various sites before and after invasion indicates that *D. polymorpha* has accelerated regional extinction rates of North American freshwater mussels by 10-fold. If this trend persists, the regional extinction rate for Mississippi basin species will be 12% per decade. Over 60 endemic mussels in the Mississippi River basin are threatened with global extinction by the combined impacts of the *D. polymorpha* invasion and environmental degradation.

Key-words: biodiversity, biological invasion, exotic species, extinction rates, Unionoidae.

Journal of Animal Ecology (1998) **67**, 613–619

Introduction

Increasing numbers of introduced species and extensive alteration of natural habitat are occurring throughout many geographical regions, prompting predictions of an impending biodiversity crisis (Ehrlich & Ehrlich 1981; Lodge 1993; Pimm *et al.* 1995). These predictions have focused primarily on extinction trends in terrestrial ecosystems (e. g. Harvey & May 1997). By comparison, freshwater ecosystems have received little attention, even though they

encompass some of the most threatened species and habitats on the planet (Allan & Flecker 1993; Ambra-movitz 1996). The ecological consequences of the synergism between habitat degradation and biological invasion have been dramatically demonstrated in Lake Victoria (East Africa), where introduced species and organic pollution have driven hundreds of endemic fishes into rapid extinction (Kaufman 1992). Is Lake Victoria a unique environmental catastrophe or are similar mass extinction events occurring in other species-rich freshwater ecosystems?

North American lakes and rivers contain the world's highest diversity of freshwater mussels (Order Unionoida, 'unionid' mussels), comprising 297 species or one-third of the entire fauna (Bogan 1993; Williams *et al.* 1993). However, 12% (35 species) are presumed extinct and an additional $\approx 60\%$ are threatened by environmental degradation in the form of chemical pollution, siltation, stream channelization and impoundment, thus making this North America's most imperiled faunal group (Williams *et al.* 1993; Ambramovitz 1996; Turgeon *et al.* 1996). A significant new threat to this fauna is posed by the recent introduction of the Eurasian zebra mussel, *Dreissena polymorpha* Pallas, to North America. Since its initial colonization of the Great Lakes in the late 1980s, *D. polymorpha* has invaded several large river systems including the St Lawrence, Hudson, and Mississippi drainages (Ludyanskiy, McDonald & MacNeill 1993). There is concern that *D. polymorpha* will drastically reduce native mussel populations in these systems because it is a biofouling pest that overgrows and smothers other molluscs (Ricciardi, Whoriskey & Rasmussen 1995, 1996).

Dreissena polymorpha attaches to solid surfaces using adhesive byssal fibers and possesses a planktonic larval (veliger) stage that can remain in the water column for several weeks before settlement; no native freshwater mollusc in North America has these attributes (Mackie 1991). Unionid mussels have a complex life cycle in which the larvae are obligate parasites of fish, with survivorship dependent on the availability of appropriate fish hosts and accessibility to favourable habitat (Neves & Widlak 1987). Adult unionids live partially buried in the sediments of lakes and rivers with their posterior shell exposed to the water column, providing a suitable surface for colonization by *D. polymorpha*. Having evolved without dominant fouling organisms, North American unionids have no adaptive mechanisms to deal with their effects. Infestation by *D. polymorpha* is believed to impair a unionid's metabolic activity (feeding, respiration, excretion) and locomotion in such a way as to deplete its energy reserves, effectively starving it to death (Haag *et al.* 1993; Baker & Hornbach 1997). Moreover, data from the Hudson River demonstrate that *D. polymorpha* can also harm other suspension-feeding bivalves by depleting food resources (phytoplankton) through massive filtration (Strayer & Smith 1996; Caraco *et al.* 1997). Thus, *D. polymorpha* is considered to be responsible for precipitous declines in the unionid populations of Lake Balaton, Hungary (Wagner 1936; Sebestyen 1937), the North American Great Lakes (Schloesser & Nalepa 1994; Nalepa *et al.* 1996), St Lawrence River (Ricciardi *et al.* 1996), the Detroit River (D. W. Schloesser, personal communication), and the Hudson River (Strayer & Smith 1996). Another exotic bivalve, the Asiatic clam *Corbicula fluminea*, has been spreading throughout rivers of the United States for the last 60 years, but while this spec-

ies has shown an impressive ability to thrive in environmental conditions deleterious to other bivalves, it does not appear to significantly affect the abundance or distribution of unionids (Kraemer 1979; Leff, Burch, & McArthur 1990). In fact, *C. fluminea* co-exists with dense and diverse unionid assemblages in the Mississippi River basin (Miller & Payne 1993).

Most North American river systems, including the bulk of native mussel habitat, will likely be colonized by *D. polymorpha* (Strayer 1991; Mellina & Rasmussen 1994). The recent invasion histories of the St Lawrence, Detroit and Hudson rivers suggest that *D. polymorpha* will substantially reduce the species richness of native North American mussels, but no attempt has been made to project the rate or magnitude of this species loss. In this report, we estimate the long-term impact of *D. polymorpha* on unionid mussels in the Mississippi River basin, a major centre of endemism for freshwater bivalves (van der Schalie & van der Schalie 1950). By comparing rates of species loss before and after *D. polymorpha* invasion into other habitats, we quantify the effects of *D. polymorpha* colonization and environmental degradation on the extinction rate of these unionids.

Methods

Using data obtained from the literature and personal communications with other researchers, we examined the time interval between initial colonization of unionids by *D. polymorpha* and subsequent extirpation or near extirpation ($>90\%$ decline in abundance) of unionid populations in invaded habitats to determine if such events follow a distinct temporal pattern.

We then assumed that the extinction rate of unionid mussel species would follow an exponential decay curve, and estimated the rate of proportional species loss per decade, r , using the equation $r = 1 - P^{1/n}$, where P is the proportion of the original fauna that is extant and n is the number of decades (or fraction of a decade) over which the extinctions took place. From the number of species present in a habitat immediately prior to *D. polymorpha* invasion and the number of subsequent local extinctions, we thus calculated the rate of species loss attributable to the combined impacts of *D. polymorpha* infestation and environmental degradation. The specific effect of environmental degradation was estimated by calculating species loss in the recent past (prior to *D. polymorpha* invasion). The proportional loss rate due to the combined effects of environment and *D. polymorpha* can also be expressed as $P_c = 1 - (1 - r_1)(1 - r_2)$, where r_1 is the rate of loss due to environmental degradation and r_2 is the rate of loss due to *D. polymorpha* infestation; therefore, the specific effect of *D. polymorpha* (r_2) was estimated from the other components by $1 - [(1 - P_c)/(1 - r_1)]$.

For Lake St Clair, historical data on unionid communities are scarce, so we conservatively estimated

the effect of environmental degradation on species loss that occurred in the 1980s prior to the formation of dense *D. polymorpha* populations throughout the lake (intense recruitment of the exotic mussel began in the summer of 1989; Nalepa *et al.* 1996). For all other sites, species data spanned several decades.

Results

A 4–8-year interval between initial colonization by *D. polymorpha* and the extirpation of unionid populations has occurred in a variety of habitats, ranging from small inland lakes to large rivers, that supported dense *D. polymorpha* populations (i.e. 10^3 – 10^5 mussels/m²; Table 1). Local extirpation tended to occur rapidly (\approx 4 years) at sites within water bodies, and cumulatively reduced unionid populations over larger areas as the range and abundance of *D. polymorpha* increased.

Prior to the introduction of *D. polymorpha*, the continental extinction rate for North American unionids was 1.4% per decade (i.e. 35 of 297 species lost since *c.* 1900). Previously, local extinction (extirpation) rates in habitats that historically supported diverse unionid assemblages ranged from 1.9% to 29.1% per decade. After dense *D. polymorpha* populations were established in these habitats, local extinction rates increased \approx 10-fold, on average (Table 2). For example, 50% of the fauna surveyed in Lake Oneida in 1917 had disappeared from the lake by 1967 (Harman & Forney 1970); the species loss rate per decade was thus $r_1 = 1 - (0.5)^{1/5} = 0.129$, i.e. 12.9%, prior to *D. polymorpha* invasion. Between 1991, when *D. polymorpha* was first discovered in the lake, and 1995, four of seven species were lost (W. Harman & C. Mayer, personal communication). This suggests that the combined impacts of environmental degradation and *D. polymorpha* in Lake Oneida have resulted in a local extinction rate of 87.9% per decade (i.e. $P_c = 1 - 0.429^{1/0.4}$), about 7-fold higher than the previous rate. Given $P_c = 0.879$ and $r_1 = 0.129$, the

specific effect (r_2) of *D. polymorpha* invasion on unionid species loss in Lake Oneida is estimated to be 86.1% per decade.

Given that 131 unionid species are extant in the Mississippi basin (van der Schalie & van der Schalie 1950; Williams *et al.* 1993; R. J. Neves, unpublished data), and 15 species endemic to the basin are presumed extinct (Turgeon *et al.* 1996), the regional extinction rate caused by environmental degradation is 1.2% per decade. Applying the 10-fold rate increase caused by *D. polymorpha* in other systems (Table 2), the predicted future extinction rate for unionids in the Mississippi basin is 12% per decade (Fig. 1).

Discussion

IMPACT OF *D. POLYMORPHA* INVASION ON NORTH AMERICAN UNIONID MUSSELS

Data from other North American habitats provide a basis for predicting the impact of *D. polymorpha* in the Mississippi basin. Within the decade following the introduction of *D. polymorpha*, enhanced mortality has reduced unionid mussel populations in the lower Great Lakes to perilously low levels of abundance and caused several species to disappear entirely (Schloesser & Nalepa 1994; Nalepa *et al.* 1996). Presque Isle Bay on Lake Erie formerly supported one of the most diverse and stable unionid assemblages in the Great Lakes (18 spp.; Masteller *et al.* 1993), but lost half of its species within 4 years of colonization by *D. polymorpha* (Maleski & Masteller 1994). In Lake St Clair, unionids were eliminated by a series of extirpations proceeding from the south-west basin to the north-east basin, tracking the establishment of dense *D. polymorpha* populations (Nalepa *et al.* 1996). Similar events are presently occurring in the St Lawrence and Hudson rivers. In the upper St Lawrence River, populations of unionids that had survived decades of environmental degradation were decimated within a few years of *D. polymorpha* invasion (Ricciardi *et al.*

Table 1. Number of years spanning initial colonization of *D. polymorpha* and >90% decline in abundance in North American unionid mussel populations. Peak *Dreissena* habitat densities during this time period are also shown

Location	Approximate no. of years before >90% decline	Peak <i>Dreissena</i> density (m ⁻²)	Reference
Lake St Clair	< 8	3200	Nalepa <i>et al.</i> (1996)
Lake Erie			
Western basin	4	342 000	Schloesser & Nalepa (1994)
Presque Isle Bay	4		Masteller <i>et al.</i> (1993); Maleski & Masteller (1994)
Lake Wawasee, Indiana	4	11 350	D. Garton, personal communication
Loon Lake, Indiana	< 5	48 400	D. Garton, personal communication
Lake Oneida, New York	4	30 000	W. N. Harman, personal communication
Detroit River	< 8	<i>c.</i> 5000	D. W. Schloesser, personal communication
Upper St Lawrence River various sites	< 5	4000–20 000	Ricciardi <i>et al.</i> (1996)

Table 2. Relative contribution of *D. polymorpha* and environmental degradation to the local extinction rate of unionid mussels (percentage of total number of species lost per decade)

Location	Environmental effect	<i>D. polymorpha</i> effect	Combined effect	Reference
Lake Erie				
Western basin	29.1	100.0	100.0	Schloesser & Nalepa (1994)
Presque Isle Bay	1.9	88.7	88.9	Masteller <i>et al.</i> (1993); Maleski & Masteller (1994)
Lake St Clair, Ontario	12.0	96.0	96.5	Nalepa <i>et al.</i> (1996)
Lake Oneida, New York	12.9	86.1	87.9	Harman & Forney (1970); W. N. Harman, personal communication
Detroit River	4.1	64.1	65.6	D. W. Schloesser, personal communication
<i>Geometric mean</i>	<i>8.1</i>	<i>86.0</i>	<i>86.9</i>	

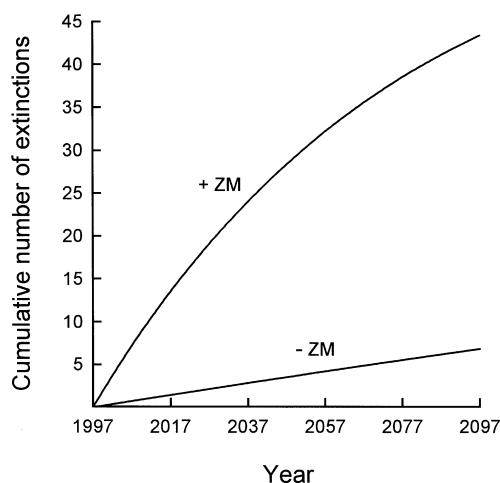


Fig. 1. Projected extinction curves for the mussel species restricted to the Mississippi River and Great Lakes basins. The lower curve (–ZM) denotes an extinction rate of 1.2% per decade, extrapolated from the number of extinctions that have occurred prior to the zebra mussel (*D. polymorpha*) invasion. The upper curve (+ZM) denotes extinction (12% per decade) due to the combined effects of environmental degradation and the zebra mussel, based on data from other invaded systems in North America.

1996). In the Hudson River, induced mortality has caused a net loss of ≈ 640 million native mussels since the *D. polymorpha* invasion began in the early 1990s; four of five species are on the verge of extirpation and will likely disappear within a decade (Strayer & Smith 1996; D. L. Strayer, personal communication).

Because none of the unionid species in the Great Lakes–St Lawrence River and Hudson River systems are endemic, these losses do not represent global extinctions. By contrast, the Mississippi River basin contains the richest endemic unionid fauna in the world (van der Schalie & van der Schalie 1950; Bogan 1993), and a similar reduction of unionid diversity would result in the extinction of ≈ 60 species that exist only in the Mississippi and Great Lakes drainages. Populations of 38 endemic species in the Mississippi

basin, including 18 endangered or threatened taxa (Williams *et al.* 1993; Turgeon *et al.* 1996), occur principally in large channels and mainstem rivers, where dense *D. polymorpha* populations will likely form. Most of these ‘large-river’ species will become extinct if the impacts observed in other North American lakes and rivers (Tables 1 and 2) are repeated in the Mississippi basin. For many other species, the spatial heterogeneity of the Mississippi River basin should provide refugia (e.g. streams that are too small to sustain dense *D. polymorpha* populations; Strayer 1991) and thus the system-wide extinction rate of unionids will not necessarily be as high as in the Great Lakes. Conversely, the impacts observed in the Great Lakes, St Lawrence River and Hudson River suggest that *D. polymorpha* invasion will reduce populations of a given species into small, fragmented assemblages that are more prone to extinction by other anthropogenic or stochastic causes (Harrison 1991; Lawton 1995). Because juvenile survivorship is low (Neves & Widlak 1987) and larval dispersal is impeded by dams (Williams *et al.* 1992), it is improbable that any unionid extinctions will be prevented by immigration or recolonization.

IMPACT OF ENVIRONMENTAL DEGRADATION ON NORTH AMERICAN UNIONIDS

Prior to the *D. polymorpha* invasion, North American unionids were profoundly affected by widespread river modification in the form of channelization, and the construction of locks and dams (Bogan 1993; Williams *et al.* 1993). By altering flow regimes, enhancing sedimentation, and obstructing the dispersal patterns of obligate host fish, dams have caused the extirpation of ≈ 30 –60% of mussel species in some US rivers (Williams, Fuller & Grace 1992; Layzer, Gordon & Anderson 1993). Moreover, dense populations of *D. polymorpha* have become established in all navigation locks on the mainstem Mississippi River (Cope, Bartsch & Hayden 1997); these areas have acted as

lentic incubation sites for veliger larvae, and thus facilitated rapid downstream colonization by *D. polymorpha*. In addition, pollution from industrial, agricultural and domestic sources have also played important roles in reducing unionid populations (Bogan 1993; Williams *et al.* 1993).

MODEL ASSUMPTIONS AND PREDICTIONS

The predicted future extinction rate of 12% per decade for Mississippi unionids is based, in part, on an extrapolation of the historical effect of environmental degradation (1.2% per decade). However, 46 of the 131 unionid species that presently occur in the Mississippi basin are considered as endangered or threatened (Turgeon *et al.* 1996), including several species that are functionally extinct, i.e. their populations are not reproducing and will diminish as adults age and die (Bogan 1993; R. J. Neves, unpublished data). If this group of species is destined to become extinct within the next century (which seems plausible, barring major watershed restoration), then the future rate of extinction, independent of *D. polymorpha*, would be 4.2% per decade; when the exacerbating effect of *D. polymorpha* is taken into account, the projected rate becomes 10-fold higher. Thus, our estimate of 12% per decade is probably conservative.

Our predictions assume that the dynamics of infestation, unionid mortality and species loss in the Mississippi basin will be similar to those of other invaded systems. Mainstem rivers in the basin, which contain diverse unionid beds (van der Schalie & van der Schalie 1950; Miller & Payne 1993), are being extensively colonized by *D. polymorpha*; all species sympatric with *D. polymorpha* are becoming infested. Infestation levels of *D. polymorpha* on unionids in the upper Mississippi River have increased several-fold since the early 1990s and, in several areas, are comparable to those recorded in the Great Lakes–St Lawrence River system (Tucker 1994; Welke 1995; Whitney, Blodgett & Sparks 1995). The linear relationship between *D. polymorpha* field density and infestation on unionid populations (Fig. 2) is similar to that of other invaded systems (Ricciardi *et al.* 1995), and suggests that infestation levels will continue to grow as *D. polymorpha* increases in abundance. Increased infestation levels will reduce unionid condition and survivorship (Haag *et al.* 1993; Ricciardi *et al.* 1995, 1996; Nalepa *et al.* 1996), particularly in mussels that are already stressed by other environmental factors (Baker & Hornbach 1997). Rates of decline may vary slightly among taxa (Haag *et al.* 1993; Ricciardi *et al.* 1996), but no North American unionid species has shown an ability to resist the effects of fouling; thus, even diverse communities diminish rapidly following intense infestation (Table 1). To date, heavily infested unionids in the Ohio River have significantly low glycogen levels (M. A. Patterson, B. C. Parker & R. J. Neves, in preparation), and increased mortality of recently infested

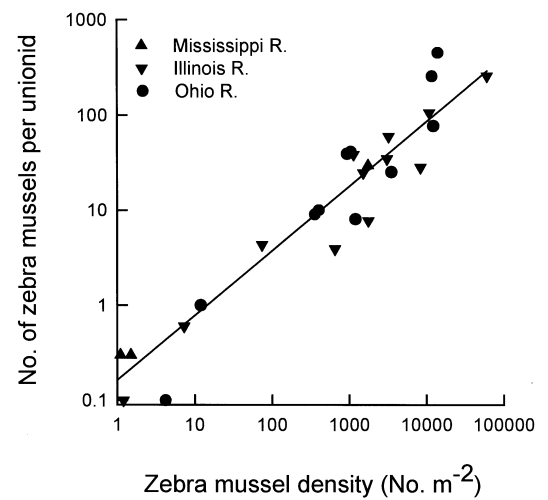


Fig. 2. Relationship between zebra mussel (*D. polymorpha*) field density and mean infestation on native unionid mussels for various unionid populations in the Mississippi River basin (line fitted by least-squares regression: $y = 0.678x - 0.785$, $r^2 = 0.91$, $P < 0.0001$). Data from Tucker *et al.* (1993); Tucker (1994); R. Hart, personal communication (Mississippi River); Whitney *et al.* 1995 (Illinois River); P. Morrison, personal communication (Ohio River).

populations has been observed in both the Ohio and Illinois rivers (Whitney *et al.* 1995; P. Morrison, personal communication). The temporal trend inferred from Table 1 predicts high unionid mortality resulting in a series of extirpations in the Mississippi, Illinois, and Ohio rivers within the next 2–3 years, assuming that *D. polymorpha* densities remain at sufficiently high levels.

Although *D. polymorpha* has been spreading across Europe during the last two centuries (Ludyanskiy *et al.* 1993), its severe impact on native bivalves in North America could not have been predicted from the European experience for three reasons. First, very few European studies have examined changes in native mussel communities following invasion by *D. polymorpha*. Secondly, densities and infestation levels of *D. polymorpha* in European habitats are generally 10–100 times lower than those in North American habitats (reviewed by Ricciardi *et al.* 1995). After more than a decade following its introduction, *Dreissena* densities remain high (10^3 – 10^5 individuals m^{-2}) at sites throughout the Great Lakes–St Lawrence River system (Ricciardi *et al.* 1995, 1996; Nalepa *et al.* 1996). Finally, the European fauna is depauperate (only 10 species are known in Europe and the former Soviet Union, Bogan 1993) and has had evolutionary experience with *D. polymorpha*, which occurred throughout northern and central Europe prior to the last glacial epoch before being confined to the Caspian Sea region (Ludyanskiy *et al.* 1993). European species, therefore, may have already had selection pressure to adapt to fouling by *D. polymorpha*, and may not have retained the same ecological sensitivity to fouling as their North American relatives. Nevertheless, both

environmental degradation and dense *D. polymorpha* colonization may have contributed to unionid declines in Lake Balaton (Sebestyen 1937; Ponyi 1992), Lake Bourget in France (Favre 1940), Lake Mikolajskie in Poland (Lewandowski 1991) and Lake Hallwil in Switzerland (Arter 1989).

Conclusions

Given the important role that unionids play in particle dynamics (Strayer *et al.* 1994), nutrient cycling (Nalepa, Gardner & Malczyk 1991) and sediment mixing (McCall *et al.* 1979), we expect that the replacement of unionid mussels by *D. polymorpha* will alter the functional ecology of river ecosystems in North America (e.g. Caraco *et al.* 1997). Furthermore, a substantial economic loss will be felt by the commercial shellfishery in the United States, which harvests and exports thousands of metric tons of mussel shell to the Japanese pearl industry at an annual value exceeding \$40 million US (Williams *et al.* 1993; Bowen *et al.* 1994). *Dreissena* shells are thin and lack nacre, and therefore are not a suitable replacement for commercial exploitation.

Our results suggest an impending mass extinction of freshwater mussels in the Mississippi River basin. Therefore, we advocate immediate conservation action, including the collection of endemic unionid species for captive propagation and transplantation (Cope & Waller 1995). Efforts should be made to identify habitats where *D. polymorpha* recruitment is insufficient to maintain high population densities deleterious to unionid survival (Ricciardi *et al.* 1995). In some areas of the Mississippi basin, *D. polymorpha* population densities may remain low for several years (e.g. Tucker & Atwood 1995), or may be limited by high water temperatures (McMahon 1996); these types of areas may serve, at least temporarily, as refugia for rare unionids and facilitate management strategies to conserve these species. However, because regional (rather than local) factors appear to determine mussel community structure (Vaughn 1997), conservation and restoration efforts must be focused ultimately on watersheds rather than on individual species.

Acknowledgements

We thank D. Garton, W. Harman, R. Hart, C. Mayer, P. Morrison and D. Schloesser for providing information for this study, and J. Vander Zanden and D. Strayer for commenting on earlier drafts of the manuscript. We are also grateful for the comments and encouragement provided by S. Pimm.

References

Allan, J.D. & Flecker, A.S. (1993) Biodiversity conservation in running waters. *BioScience*, **43**, 32–43.

- Ambramovitz, J.N. (1996) *Imperiled waters, impoverished future: the decline of freshwater ecosystems*. Worldwatch Institute Paper No. 128, Washington, D.C.
- Arter, H.E. (1989) Effect of eutrophication on species composition and growth of freshwater mussels (Mollusca, Unionidae) in Lake Hallwil (Aargau, Switzerland). *Aquatic Science*, **51**, 87–99.
- Baker, S.M. & Hornbach, D.J. (1997) Acute physiological effects of zebra mussel (*Dreissena polymorpha*) infestation on two unionid mussels, *Actinonaias ligamentina* and *Ambelma plicata*. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 512–519.
- Bogan, A.E. (1993) Freshwater bivalve extinctions (Mollusca: Unionoida): a search for causes. *American Zoologist*, **33**, 599–609.
- Bowen, Z.H., Malvestuto, S.P., Davies, W.D. & Crance, J.H. (1994) Evaluation of the mussel fishery in Wheeler Reservoir, Tennessee River. *Journal of Freshwater Ecology*, **9**, 313–319.
- Caraco, N.F., Cole, J.J., Raymond, P.A., Strayer, D.L., Pace, M.L., Findlay, S.E.G. & Fischer, D.T. (1997) Zebra mussel invasion in a large, turbid river: phytoplankton response to increased grazing. *Ecology*, **78**, 588–602.
- Cope, W.G., Bartsch, M.R. & Hayden, R.R. (1997) Longitudinal patterns in abundance of the zebra mussel (*Dreissena polymorpha*) in the upper Mississippi River. *Journal of Freshwater Ecology*, **16**, 235–238.
- Cope, W.G. & Waller, D.L. (1995) Evaluation of freshwater mussel relocation as a conservation and management strategy. *Regulated Rivers: Research and Management*, **11**, 147–155.
- Ehrlich, P.R. & Ehrlich, A.H. (1981) *Extinction*. Random House, New York.
- Favre, J. (1940) La faune malacologique post-glaciare et actuelle du lac du Bourget. *Annales de l'École Nationale des Eaux et Forêts*, **7**, 295–444.
- Haag, W.R., Berg, D.J., Garton, D.W. & Farris, J.L. (1993) Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 13–19.
- Harman, W.N. & Forney, J.L. (1970) Fifty years of change in the molluscan fauna of Oneida Lake, New York. *Limnology and Oceanography*, **15**, 454–460.
- Harrison, S. (1991) Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, **42**, 73–88.
- Harvey, P.H. & May, R.M. (1997) Case studies of extinction. *Nature*, **385**, 776–777.
- Kaufman, L. (1992) Catastrophic change in species-rich freshwater ecosystems. *BioScience*, **42**, 846–858.
- Kraemer, L.R. (1979) *Corbicula* (Bivalvia: Sphaeriacea) vs. indigenous mussels (Bivalvia: Unionacea) in U.S. rivers: a hard case for interspecific competition? *American Zoologist*, **19**, 1085–1096.
- Lawton, J.H. (1995) Population dynamic principles. *Extinction Rates* (eds J.H. Lawton & R.M. May), pp. 147–163. Oxford University Press, New York.
- Layzer, J.B., Gordon, M.E. & Anderson, R.M. (1993) Mussels: the forgotten fauna of regulated rivers—a case study of the Caney Fork River. *Regulated Rivers: Research and Management*, **8**, 63–71.
- Leff, L.G., Burch, J.L. & McArthur, J.V. (1990) Spatial distribution, seston removal, and potential competitive interactions of the bivalves *Corbicula fluminea* and *Elliptio complanata*, in a coastal plain stream. *Freshwater Biology*, **24**, 409–416.
- Lewandowski, K. (1991) Long-term changes in the fauna of Family Unionidae bivalves in the Mikolajskie Lake. *Ekologia Polska*, **39**, 265–272.

- Lodge, D.M. (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution*, **8**, 133–177.
- Ludyanskiy, M.L., McDonald, D. & MacNeill, D. (1993) Impact of the zebra mussel, a bivalve invader. *BioScience*, **43**, 533–544.
- Mackie, G.L. (1991) Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia*, **219**, 251–268.
- Maleski, K.R. & Masteller, E.C. (1994) The current status of the Unionidae of Presque Isle Bay, Erie, PA. *Bulletin of the North American Benthological Society*, **11**, 109.
- Masteller, E.C., Maleski, K.R. & Schloesser, D.W. (1993) Unionid bivalves (Mollusca: Bivalvia: Unionidae) of Presque Isle Bay, Erie, Pennsylvania. *Journal of Pennsylvania Academy of Science*, **67**, 120–126.
- McCall, P.I., Tevesz, M.J.S. & Schwelgien, S.F. (1979) Sediment mixing by *Lampsilis radiata siliquoidea* (Mollusca) from western Lake Erie. *Journal of Great Lakes Research*, **5**, 105–111.
- McMahon, R.F. (1996) The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American Zoologist*, **36**, 339–363.
- Mellina, E. & Rasmussen, J.B. (1994) Patterns in the distribution and abundance of zebra mussels (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and other physico-chemical factors. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1024–1036.
- Miller, A.C. & Payne, B.S. (1993) Qualitative vs. quantitative sampling to evaluate population and community characteristics at a large-river mussel bed. *American Midland Naturalist*, **130**, 133–145.
- Nalepa, T.F., Gardner, W.S. & Malczyk, J.M. (1991) Phosphorus cycling by mussels (Unionidae: Bivalvia) in Lake St. Clair. *Hydrobiologia*, **219**, 239–250.
- Nalepa, T.F., Hartson, D.J., Gostenik, G.W., Fanslow, D.L. & Lang, G.A. (1996) Changes in the freshwater mussel community of Lake St. Clair: from Unionidae to *Dreissena polymorpha* in eight years. *Journal of Great Lakes Research*, **22**, 354–369.
- Neves, R.J. & Widlak, J.C. (1987) Habitat ecology of juvenile freshwater mussels (Bivalvia: Unionidae) in a headwater stream in Virginia. *American Malacological Bulletin*, **5**, 1–7.
- Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347–350.
- Ponyi, J.E. (1992) The distribution and biomass of Unionidae (Mollusca, Bivalvia), and the production of *Unio tumidus* Retzius in Lake Balaton (Hungary). *Archiv für Hydrobiologie*, **125**, 245–251.
- Ricciardi, A., Whoriskey, F.G. & Rasmussen, J.B. (1995) Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1449–1461.
- Ricciardi, A., Whoriskey, F.G. & Rasmussen, J.B. (1996) Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1434–1444.
- van der Schalie, H. & van der Schalie, A. (1950) The mussels of the Mississippi River. *American Midland Naturalist*, **44**, 448–466.
- Schloesser, D.W. & Nalepa, T.F. (1994) Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussel, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 2234–2242.
- Sebestyen, O. (1937) Colonization of two new faunal elements of Pontus-origin (*Dreissena polymorpha* Pall. & *Corophium curvispinum* G.O. Sars forma *devium* Wundsch) in Lake Balaton. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, **8**, 169–182.
- Strayer, D.L. (1991) Projected distribution of the zebra mussel, *Dreissena polymorpha*, in North America. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1389–1395.
- Strayer, D.L., Hunter, D.C., Smith, L.C. & Borg, C.K. (1994) Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River. *Freshwater Biology*, **31**, 239–248.
- Strayer, D.L. & Smith, L.C. (1996) Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of the zebra mussel invasion of the Hudson River. *Freshwater Biology*, **36**, 771–779.
- Tucker, J.K. (1994) Colonization of unionid bivalves by the zebra mussel, *Dreissena polymorpha*, in pool 26 of the Mississippi River. *Journal of Freshwater Ecology*, **8**, 129–134.
- Tucker, J.K. & Atwood, E.R. (1995) Contiguous backwater lakes as possible refugia for unionid mussels in areas of heavy zebra mussel (*Dreissena polymorpha*) colonization. *Journal of Freshwater Ecology*, **10**, 43–47.
- Tucker, J.K., Theiling, C.H., Blodgett, K.D. & Theil, P.A. (1993) Initial occurrences of zebra mussels (*Dreissena polymorpha*) on freshwater mussels (Family Unionidae) in the Upper Mississippi River system. *Journal of Freshwater Ecology*, **8**, 245–251.
- Turgeon, D.D., Bogan, A.E., Coan, E.V., Emerson, W.K., Lyons, W.G., Mikkelsen, P.M., Quinn, J.F., Roper, C.F.E., Rosenberg, G., Roth, B., Sweeney, M.J., Scheltema, A.H., Thompson, F., Vecchione, M. & Williams, J.D. (1996) *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks*, 2nd edn. American Fisheries Society Special Publication, Bethesda, Maryland.
- Vaughn, C.C. (1997) Regional patterns of mussel species distributions in North American rivers. *Ecography*, **20**, 107–115.
- Wagner, H. (1936) Die Wandermuschel (*Dreissensia*) erobert den Platten-See. *Natur und Volk*, **66**, 37–41.
- Welke, K. (1995) *Current Status of the Zebra Mussel in the Upper Mississippi River (UMR)*. Technical report, Wisconsin Department of Natural Resources, USA.
- Whitney, S.D., Blodgett, K.D. & Sparks, R.E. (1995) *Zebra Mussels and Native Unionids in the Illinois River*. Technical report, Illinois Natural History Survey, USA.
- Williams, J.D., Fuller, S.L.H. & Grace, R. (1992) Effects of impoundment on freshwater mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black Warrior and Tombigbee rivers in western Alabama. *Bulletin of the Alabama Museum of Natural History*, **13**, 1–10.
- Williams, J.D., Warren, M.L. Jr, Cummings, K.S., Harris, J.L. & Neves, R.J. (1993) Conservation status of freshwater mussels of the United States and Canada. *Fisheries*, **18** (9), 6–22.

Received 16 July 1997; revision received 27 October 1997