

PERSPECTIVE

Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes?

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Abstract: A widely cited hypothesis in ecology is that species-rich communities are less vulnerable to invasion than species-poor ones, owing to competition for limiting resources (the “biotic resistance” model). However, evidence for biotic resistance in aquatic ecosystems is equivocal. Contrary to the view that communities become more resistant to invasion as they accumulate species, the rate of invasion has increased over the past century in areas that have received frequent shipping traffic. Furthermore, introduced species may facilitate, rather than compete with, one another. A review of invasions in the Great Lakes indicates that direct positive (mutualistic and commensal) interactions among introduced species are more common than purely negative (competitive and amensal) interactions. In addition, many exploitative (e.g., predator–prey) interactions appear to be strongly asymmetric in benefiting one invading species at a negligible cost to another. These observations, combined with an increasing invasion rate in the Great Lakes, tentatively support the Simberloff – Von Holle “invasional meltdown” model. The model posits that ecosystems become more easily invaded as the cumulative number of species introductions increases, and that facilitative interactions can exacerbate the impact of invaders. It provides a theoretical argument for substantially reducing the rate of species introductions to the Great Lakes.

Résumé : Une hypothèse couramment citée en écologie veut que les communautés riches en espèces soient moins vulnérables aux invasions que les plus pauvres, à cause de la compétition pour les ressources limitantes (le modèle de la « résistance biotique »). Cependant, les preuves de l'existence d'une telle résistance biotiques dans les écosystèmes aquatiques sont équivoques. En contradiction avec l'opinion qui prétend que les communautés deviennent plus résistantes lorsqu'elles accumulent plus d'espèces, le taux d'invasion a augmenté au cours du siècle dernier dans les régions qui reçoivent un important trafic maritime. De plus, les espèces introduites peuvent même faciliter leur coexistence mutuelle plutôt qu'entrer en compétition. Une étude des invasions dans les Grands-Lacs révèle que les interactions directes positives (de mutualisme et de commensalisme) parmi les espèces introduites sont plus fréquentes que les interactions purement négatives (de compétition et d'amensalisme). De plus, plusieurs des interactions d'exploitation (e.g., de type prédateur-proie) semblent être fortement asymétriques en avantageant l'un des envahisseurs à un coût négligeable pour l'autre. Ces observations ainsi que le taux croissant des invasions dans les Grands-Lacs semblent vouloir appuyer le modèle d'« effondrement des communautés à la suite des invasions » de Simberloff – Von Holle. Le modèle prédit que les écosystèmes deviennent de plus en plus faciles à envahir à mesure que le nombre cumulatif d'espèces introduites y augmente et que des actions facilitantes viennent exacerber l'impact des envahisseurs. Il s'agit donc d'un argument théorique pour limiter de façon importante le taux d'introduction d'espèces dans les Grands-Lacs.

[Traduit par la Rédaction]

Introduction

Biological invasion studies often focus on interactions between introduced species and native species. When interactions involving introduced species are considered, competition is typically emphasized (Moulton and Pimm 1983; Case 1990; Case and Bolger 1991). A widely cited hypothesis in inva-

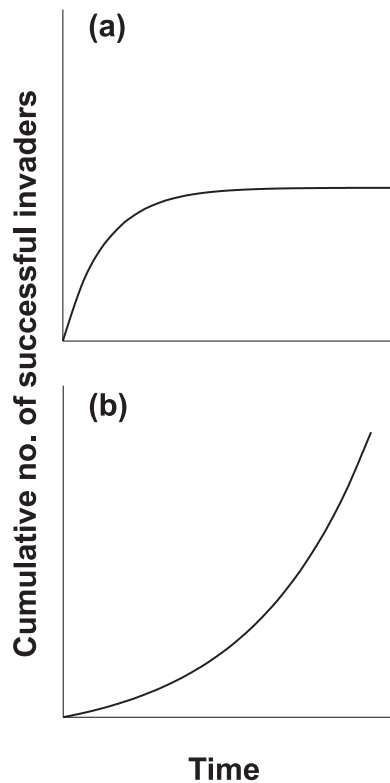
sion ecology is that species-rich communities are more resistant to invasion than species-poor ones because the former use limiting resources more completely and are also more likely to have competitors or predators that can exclude potential invaders (Elton 1958). This concept is the basis of the “biotic resistance model”, which predicts that successive invasions will cause a community to accumulate stronger com-

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Fig. 1. Temporal trend in the cumulative number of successful invasions as predicted by (a) the biotic resistance model and (b) the invasional meltdown model.



petitors, more efficient predators, and well-defended prey (Moulton and Pimm 1983; Case 1990). Thus, the rate of establishment of new species in a community should become increasingly limited over time.

Contrary to the idea that areas become less vulnerable to invasion as they accumulate species, the rate of invasion is increasing in several aquatic ecosystems (e.g., Ribera and Boudouresque 1995; Leppäkoski and Olenin 2000). Even the most speciose aquatic ecosystems on the planet have been invaded multiple times (Kaufman 1992; Dumont 1998; Hall and Mills 2000), whereas some species-poor ecosystems have shown remarkable resistance to invasion (e.g., Baltz and Moyle 1993). An alternative to the biotic resistance model has been proposed by Simberloff and Von Holle (1999), who suggested that if communities are the outcome of a nonrandom sorting and adjustment process, then frequent species introductions may generate an increasing threat to community integrity in two ways: (i) as the cumulative number of attempted (including unsuccessful) introductions increases, populations of resident species are disrupted and the community thus becomes more easily invaded; and (ii) once established, some invaders alter habitat conditions in favor of other invaders, thereby creating a positive feedback system that accelerates the accumulation of non-indigenous species and their synergistic impacts. This defines the “invasional meltdown” model, which emphasizes facilitative (rather than antagonistic) interactions among introduced species (Fig. 1). Simberloff and Von Holle (1999) reviewed several cases, primarily from terrestrial ecosystems, where one invading organism facilitated another

through mutualism, commensalism, or habitat modification (e.g., animals pollinating and dispersing plants). They cited European colonization of the New World as an example of a mutualistic process in which coevolved European animals, plants, and pathogens formed a “synergistic juggernaut” that facilitated their domination of native ecosystems. Furthermore, Simberloff and Von Holle (1999) suggested that such facilitation is a common phenomenon largely ignored by research that has focused on competitive interactions among invaders. Richardson et al. (2000) similarly concluded that facilitative interactions are widespread and important in accelerating the invasion of natural communities by plants. No such analysis has been done for aquatic invasions.

In this paper, I evaluate which of these models (biotic resistance or invasional meltdown) best explains the invasion history of the Great Lakes. First, I test two key components of the invasional meltdown model: (i) the premise that facilitative (positive) interactions are at least as common as negative interactions among introduced species; and (ii) the prediction of “an accelerating accumulation of introduced species” (Simberloff and Von Holle 1999), i.e., that the rate of invasion of the Great Lakes is increasing with time. Second, I examine evidence for biotic resistance in the aquatic ecology literature by reviewing studies that have explicitly tested the relationship between invasion success and the composition (diversity, trophic structure) of the resident community.

Methods

To test the first prediction of the invasional meltdown model, I reviewed all available published data for interactions among sympatric nonindigenous species in the Great Lakes. Literature sources were obtained primarily from references cited in Mills et al. (1993) and MacIsaac (1999), as well as from the electronic Aquatic Sciences and Fisheries Abstracts (ASFA) database (<http://webspirs3.silverplatter.com>). Species interactions were categorized as follows: mutualism, in which the interaction is beneficial to the survival and (or) population growth of both species; commensalism, in which one species benefits from the presence of another species that is unaffected by the interaction; exploitation, in which one species benefits at the expense of another (e.g., predation, parasitism); amensalism, in which one species is inhibited while the other is unaffected; and antagonism, which is defined here as any mutually detrimental interaction (e.g., resource competition, interference, allelopathy). Only direct pairwise interactions were tabulated. In cases where one invader had various positive and negative effects on another’s abundance and survival, the net effect was estimated when information allowed at least a subjective ranking of the various effects; otherwise, the interaction was omitted. For less than 5% of the cases, when Great Lakes data were unavailable, an interaction was assumed to occur between sympatric species because it was observed between these species in another region.

The resulting dataset contained 101 pairwise interactions (Table 1). Obviously, this is a small sample of the actual set of interactions among Great Lakes invaders, because it includes only cases that are supported by empirical evidence, whereas the ecological interactions of most invaders are untested. Moreover, the dataset omits indirect interactions, such as indirect commensalisms in which one invader reduces the abundance or survival of another’s enemies. Examples of this in the Great Lakes include the indirect enhancement of both the alewife *Alosa pseudoharengus* and the rainbow smelt *Osmerus mordax* owing to the suppression of native

Table 1. Ecological interactions among nonindigenous species established in the Great Lakes – St. Lawrence River system.

Species pairs	Reference
Mutualism (+/+) (3 cases)	
<i>Bithynia tentaculata</i> / <i>Dreissena polymorpha</i>	Ricciardi et al. 1997
<i>Myriophyllum spicatum</i> / <i>Dreissena polymorpha</i>	MacIsaac 1996; Skubinna et al. 1995
<i>Potamogeton crispus</i> / <i>Dreissena polymorpha</i>	MacIsaac 1996; Skubinna et al. 1995
Commensalism (+/0) (14 cases)	
<i>Acineta nitocrae</i> + / <i>Nitocra hibernica</i> 0	Grigorovich et al. 2001
<i>Acineta nitocrae</i> + / <i>Nitocra incerta</i> 0	Grigorovich et al. 2001
<i>Bithynia tentaculata</i> + / <i>Myriophyllum spicatum</i> 0	Vincent et al. 1981
<i>Dugesia polychroa</i> + / <i>Dreissena polymorpha</i> 0	Ricciardi et al. 1997; Ricciardi unpublished data
<i>Dugesia polychroa</i> + / <i>Dreissena bugensis</i> 0	Ricciardi et al. 1997; Ricciardi unpublished data
<i>Echinogammarus ischnus</i> + / <i>Dreissena polymorpha</i> 0	Stewart et al. 1998a, 1998b, 1998c
<i>Echinogammarus ischnus</i> + / <i>Dreissena bugensis</i> 0	Stewart et al. 1998a, 1998b, 1998c
<i>Gammarus fasciatus</i> + / <i>Dreissena polymorpha</i> 0	Ricciardi et al. 1997
<i>Gammarus fasciatus</i> + / <i>Dreissena bugensis</i> 0	Ricciardi et al. 1997; Dermott and Kerec 1997
<i>Lophopodella carteri</i> + / <i>Myriophyllum spicatum</i> 0	Wood 1989
<i>Lophopodella carteri</i> + / <i>Potamogeton crispus</i> 0	Wood 1989
<i>Proterorhinus marmoratus</i> + / <i>Potamogeton crispus</i> 0	Jude et al. 1995
<i>Valvata piscinalis</i> + / <i>Dreissena polymorpha</i> 0	Ricciardi et al. 1997
<i>Valvata piscinalis</i> + / <i>Dreissena bugensis</i> 0	Ricciardi et al. 1997
Exploitation (+/-) (73 cases)	
Herbivory	
<i>Dreissena polymorpha</i> + / <i>Stephanodiscus binderanus</i> -	Holland 1993; MacIsaac 1999
<i>Dreissena polymorpha</i> + / <i>Stephanodiscus subtilis</i> -	Holland 1993; MacIsaac 1999
<i>Dreissena polymorpha</i> + / <i>Skeletonema subsalum</i> -	Holland 1993; MacIsaac 1999
<i>Dreissena polymorpha</i> + / <i>Cyclotella cryptica</i> -	Holland 1993; MacIsaac 1999
<i>Dreissena polymorpha</i> + / <i>Cyclotella pseudostelligera</i> -	Holland 1993; MacIsaac 1999
Predator-prey relationships	
<i>Alosa pseudoharengus</i> + / <i>Osmerus mordax</i> -	Smith 1970
<i>Alosa pseudoharengus</i> + / <i>Eubosmina coregoni</i> -	Mills et al. 1995
<i>Alosa pseudoharengus</i> + / <i>Bythotrephes longimanus</i> -	Grigorovich et al. 1998
<i>Alosa pseudoharengus</i> + / <i>Cercopagis pengoi</i> -	E. Mills, personal communication
<i>Alosa pseudoharengus</i> + / <i>Dreissena polymorpha</i> -	Mills et al. 1995
<i>Bythotrephes longimanus</i> + / <i>Eubosmina coregoni</i> -	Grigorovich et al. 1998
<i>Cordylophora caspia</i> + / <i>Dreissena polymorpha</i> -	Molloy et al. 1997; Olenin and Leppakoski 1999
<i>Cyprinus carpio</i> + / <i>Dreissena polymorpha</i> -	Tucker et al. 1996
<i>Cyprinus carpio</i> + / <i>Dreissena bugensis</i> -	Ricciardi, unpublished data
<i>Cyprinus carpio</i> + / <i>Sphaerium corneum</i> -	Ricciardi, unpublished data
<i>Cyprinus carpio</i> + / <i>Bithynia tentaculata</i> -	Ricciardi, unpublished data
<i>Gymnocephalus cernuus</i> + / <i>Gammarus fasciatus</i> -	Fullerton et al. 1998
<i>Gymnocephalus cernuus</i> + / <i>Megacyclops viridis</i> -	Ogle et al. 1995
<i>Morone americana</i> + / <i>Bythotrephes longimanus</i> -	Grigorovich et al. 1998
<i>Neogobius melanostomus</i> + / <i>Dreissena polymorpha</i> -	Ray and Corkum 1997; Molloy et al. 1997
<i>Neogobius melanostomus</i> + / <i>Dreissena bugensis</i> -	Molloy et al. 1997
<i>Neogobius melanostomus</i> + / <i>Gammarus fasciatus</i> -	Ray and Corkum 1997; Jude et al. 1995
<i>Neogobius melanostomus</i> + / <i>Echinogammarus ischnus</i> -	Shorygin 1952
<i>Oncorhynchus tshawytscha</i> + / <i>Alosa pseudoharengus</i> -	Jude et al. 1987
<i>Oncorhynchus tshawytscha</i> + / <i>Osmerus mordax</i> -	Conner et al. 1993; Jude et al. 1987
<i>Oncorhynchus tshawytscha</i> + / <i>Bythotrephes longimanus</i> -	Grigorovich et al. 1998
<i>Oncorhynchus gorbuscha</i> + / <i>Alosa pseudoharengus</i> -	Smith 1970
<i>Oncorhynchus gorbuscha</i> + / <i>Osmerus mordax</i> -	Conner et al. 1993
<i>Oncorhynchus gorbuscha</i> + / <i>Bythotrephes longimanus</i> -	Grigorovich et al. 1998
<i>Oncorhynchus kisutch</i> + / <i>Alosa pseudoharengus</i> -	Jude et al. 1987
<i>Oncorhynchus kisutch</i> + / <i>Osmerus mordax</i> -	Conner et al. 1993; Jude et al. 1987
<i>Oncorhynchus nerka</i> + / <i>Alosa pseudoharengus</i> -	Smith 1970
<i>Oncorhynchus nerka</i> + / <i>Osmerus mordax</i> -	Conner et al. 1993
<i>Oncorhynchus mykiss</i> + / <i>Alosa pseudoharengus</i> -	Jude et al. 1987
<i>Oncorhynchus mykiss</i> + / <i>Osmerus mordax</i> -	Conner et al. 1993; Jude et al. 1987
<i>Oncorhynchus mykiss</i> + / <i>Bythotrephes longimanus</i> -	Grigorovich et al. 1998
<i>Osmerus mordax</i> + / <i>Eubosmina coregoni</i> -	Mills et al. 1995
<i>Osmerus mordax</i> + / <i>Dreissena polymorpha</i> -	Mills et al. 1995

Table 1 (concluded).

Species pairs	Reference
<i>Osmerus mordax</i> + / <i>Bythotrephes longimanus</i> –	Grigorovich et al. 1998
<i>Proterorhinus marmoratus</i> + / <i>Dreissena polymorpha</i> –	Molloy et al. 1997
<i>Proterorhinus marmoratus</i> + / <i>Dreissena bugensis</i> –	Molloy et al. 1997
<i>Salmo trutta</i> + / <i>Alosa pseudoharengus</i> –	Jude et al. 1987; Smith 1970
<i>Salmo trutta</i> + / <i>Osmerus mordax</i> –	Conner et al. 1993; Jude et al. 1987
<i>Salmo trutta</i> + / <i>Bythotrephes longimanus</i> –	Grigorovich et al. 1998
Parasite–host relationships	
<i>Acanthostomum</i> sp. + / <i>Gymnocephalus cernuus</i> –	Pronin et al. 1997b
<i>Acentropus niveus</i> + / <i>Myriophyllum spicatum</i> –	Mills et al. 1993
<i>Acentropus niveus</i> + / <i>Potamogeton crispus</i> –	Mills et al. 1993
<i>Acentropus niveus</i> + / <i>Trapa natans</i> –	Mills et al. 1993
<i>Aeromonas salmonicida</i> + / <i>Salmo trutta</i> –	Mills et al. 1993
<i>Aeromonas salmonicida</i> + / <i>Carassius auratus</i> –	Mills et al. 1993
<i>Aeromonas salmonicida</i> + / <i>Cyprinus carpio</i> –	Mills et al. 1993
<i>Argulus japonicus</i> + / <i>Carassius auratus</i> –	Mills et al. 1993
<i>Dactylogyrus amphibothrium</i> + / <i>Gymnocephalus cernuus</i> –	Cone et al. 1994
<i>Dactylogyrus hemiamphibothrium</i> + / <i>Gymnocephalus cernuus</i> –	United States Department of the Interior 1993
<i>Glugea hertwigi</i> + / <i>Osmerus mordax</i> –	Mills et al. 1993
<i>Ichthyocotylurus pileatus</i> + / <i>Neogobius melanostomus</i> –	Pronin et al. 1997a
<i>Myxobolus cerebralis</i> + / <i>Oncorhynchus tshawytscha</i> –	Mills et al. 1993
<i>Myxobolus cerebralis</i> + / <i>Oncorhynchus gorbuscha</i> –	Mills et al. 1993
<i>Myxobolus cerebralis</i> + / <i>Oncorhynchus kisutch</i> –	Mills et al. 1993
<i>Myxobolus cerebralis</i> + / <i>Oncorhynchus nerka</i> –	Mills et al. 1993
<i>Myxobolus cerebralis</i> + / <i>Oncorhynchus mykiss</i> –	Mills et al. 1993
<i>Myxobolus cerebralis</i> + / <i>Salmo trutta</i> –	Mills et al. 1993
<i>Neascus brevicaudatus</i> + / <i>Gymnocephalus cernuus</i> –	United States Department of the Interior 1993
<i>Petromyzon marinus</i> + / <i>Oncorhynchus tshawytscha</i> –	Pearce et al. 1980
<i>Petromyzon marinus</i> + / <i>Oncorhynchus mykiss</i> –	Berst and Wainio 1967
<i>Petromyzon marinus</i> + / <i>Oncorhynchus gorbuscha</i> –	Noltie 1987
<i>Petromyzon marinus</i> + / <i>Oncorhynchus kisutch</i> –	Pearce et al. 1980
<i>Petromyzon marinus</i> + / <i>Oncorhynchus nerka</i> –	Pearce et al. 1980
<i>Petromyzon marinus</i> + / <i>Cyprinus carpio</i> –	Christie and Kolenosky 1980
<i>Sphaeromyxa sevastopoli</i> + / <i>Neogobius melanostomus</i> –	Pronin et al. 1997a
<i>Sphaeromyxa sevastopoli</i> + / <i>Proterorhinus marmoratus</i> –	Pronin et al. 1997a
<i>Trypanosoma acerinae</i> + / <i>Gymnocephalus cernuus</i> –	United States Department of the Interior 1993
Overgrowth	
<i>Lophopodella carteri</i> + / <i>Dreissena polymorpha</i> –	Lauer et al. 1999
Amensalism (–/0) (4 cases)	
Habitat alteration	
<i>Potamogeton crispus</i> – / <i>Cyprinus carpio</i> 0	Lundholm and Simser 1999
<i>Myriophyllum spicatum</i> – / <i>Cyprinus carpio</i> 0	Lundholm and Simser 1999
Interference	
<i>Elimia virginica</i> – / <i>Bithynia tentaculata</i> 0	Harman 1968
<i>Sphaerium corneum</i> – / <i>Dreissena polymorpha</i> 0	Lauer and McComish 2001
Antagonism (–/–) (7 cases)	
Predation vs. allelopathy	
<i>Oncorhynchus kisutch</i> / <i>Alosa pseudoharengus</i>	Fitzsimons et al. 1999
Interspecific predation of larvae	
<i>Proterorhinus marmoratus</i> / <i>Neogobius melanostomus</i>	Jude et al. 1995
Resource competition	
<i>Echinogammarus ischnus</i> / <i>Gammarus fasciatus</i>	Dermott et al. 1998
<i>Dreissena polymorpha</i> / <i>Dreissena bugensis</i>	Mills et al. 1999
<i>Sphaerium corneum</i> / <i>Dreissena bugensis</i>	Dermott and Kerec 1997
<i>Lythrum salicaria</i> / <i>Typha angustifolia</i>	Mal et al. 1997
<i>Oncorhynchus mykiss</i> / <i>Salmo trutta</i>	Landergren 1999

Note: +, Enhanced survival or population growth; –, survival or population growth negatively affected; 0, unaffected.

predatory salmonids by introduced sea lamprey *Petromyzon marinus* during the 1940s and 1950s (Smith 1970; Christie 1974). Similarly, by preying heavily upon planktivores, introduced salmonids

might have facilitated population expansion of large nonindigenous zooplankton such as *Bythotrephes longimanus* and *Cercopagis pengoi* (Jude et al. 1987; Conner et al. 1993). Indirect

commensalism also occurs when one invader augments the food resources of another invader; for example, the zebra mussel *Dreissena polymorpha* increases the diversity and abundance of invertebrate prey for benthivorous fishes like the ruffe *Gymnocephalus cernuus*, whose growth rate may increase as a result (Thayer et al. 1997). In the invasional meltdown model, both direct and indirect facilitation accelerate the establishment of non-indigenous species through positive feedback loops (Fig. 2).

I tested the second prediction of the invasional meltdown model using linear regression analysis of data on the number of Great Lakes invasions documented between 1810 and 2000. Only those species known to be established (i.e., having formed reproducing populations) were included; therefore, some introduced species such as skipjack herring *Alosa chrysochloris* (Fago 1993) and grass carp *Ctenopharyngodon idella* (Crossman et al. 1987) were omitted. My review yielded a total of 162 invaders (see Appendix A for species additional to those listed by Mills et al. 1993).

Finally, to assess evidence of biotic resistance in aquatic systems, I searched the ASFA database for published studies that contained the following combinations of key words: (INVAD* or INTRODUCED or NONINDIGENOUS or ALIEN or EXOTIC) and RESISTANCE. The ASFA database contained studies published from 1978 to 2000, inclusive. My intention was to determine whether negative relationships between invasion success and species diversity within a community have been demonstrated for freshwater, brackish-water, or marine communities.

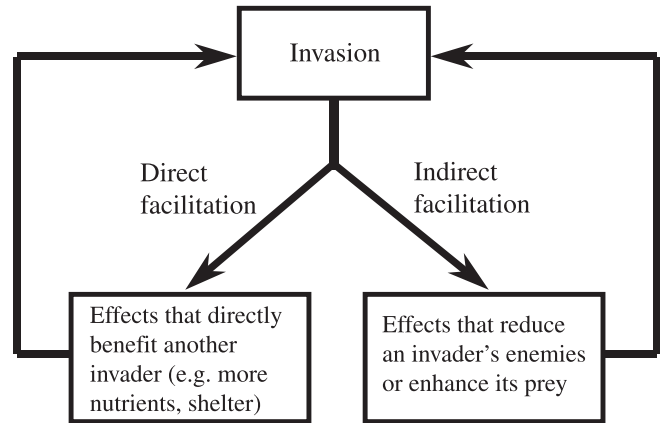
Results and discussion

Facilitative versus antagonistic interactions among invaders in the Great Lakes

Contrary to the biotic resistance model, which assumes the dominance of negative interactions among introduced species, the number of cases of direct positive interactions (3 mutualisms and 14 commensalisms) exceeds the number of cases of purely negative interactions (4 amensalisms and 7 antagonistic interactions) (Table 1). All mutualisms and commensalisms listed here are facultative. About 72% (73/101) of interactions in the dataset are exploitative, being mostly predator–prey and parasite–host relationships. These cannot be interpreted as purely negative interactions, because one invader clearly benefits from the other's presence. Moreover, in many cases, the interaction is probably strongly asymmetric such that the prey and (or) host population is only weakly affected because of its high recruitment rate or because of the relatively low abundance of the predator or parasite, i.e., prey abundance may control predator abundance, but not vice versa. These interactions appear to have such a negligible cost to the host or prey species that they could be considered commensal (examples include the moth *Acentropus niveus* and its plant hosts; some molluscivorous fishes and their zebra mussel prey; planktivorous fishes and zebra mussel larvae; Mills et al. 1993; Molloy et al. 1997).

In about one third (25/73) of the cases of exploitation, the newcomer benefited from the presence of a previously established invader. For example, the presence of abundant and widespread zebra mussel populations likely facilitated the establishment and spread of the round goby *Neogobius melanostomus*, one of the mussel's principal predators in the Ponto–Caspian (Black and Caspian Seas) region (Shorygin 1952; Ray and Corkum 1997). Similarly, the prior establishment of abundant zooplanktonic prey in the form of zebra

Fig. 2. Positive feedback mechanisms of the invasional meltdown model. An example of direct facilitation is the provision of biodeposits and shelter by an introduced mussel to an introduced detritivore. An example of indirect facilitation is the reduction of piscivores by an introduced parasite (e.g., sea lamprey), paving the way for invasion by a planktivore (e.g., alewife).



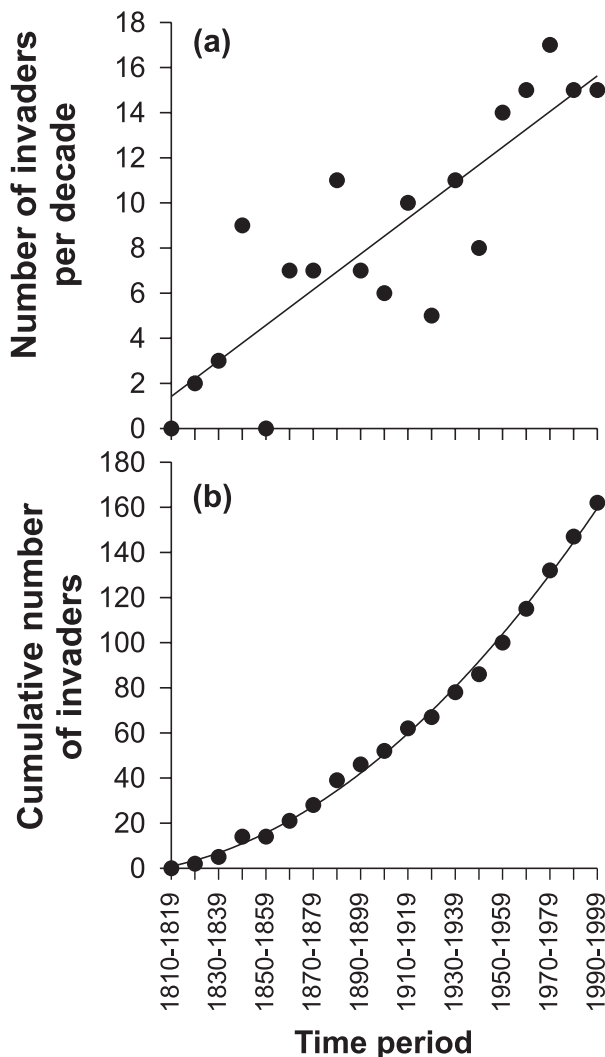
mussel larvae and the cladoceran *Eubosmina coregoni* may have aided the invasion of blueback herring, *Alosa aestivalis*, in Lake Ontario (Molloy et al. 1997; MacNeill 1998).

Evidence of an invasional meltdown in the Great Lakes

The invasional meltdown model is supported by the increasing rate of invasion in the Great Lakes over the past two centuries (Fig. 3). Among the 162 nonindigenous species in the system, 40 were recorded during the first half of the 20th century and 76 during the latter half of the 20th century. Since 1970, on average, there has been one invader recorded every eight months. The number of species established per decade has increased with time, and none has subsequently become extirpated. The trend in the cumulative number of successful invasions over the past two centuries is best described by a quadratic function (Fig. 3), which explains 4% more variance than a simple linear function. This trend might partially reflect recent awareness and monitoring efforts to locate invaders; however, much of the taxonomic and survey work on Great Lakes biota was carried out several decades ago. Undoubtedly, some invasions have gone unnoticed, and there are several species of cryptogenic invertebrates (species of uncertain origin but assumed to be holarctic or cosmopolitan) that may have been introduced in the distant past (Mills et al. 1993).

Another potential explanation for the increasing invasion rate is the strong positive relationship between the number of nonindigenous species established per decade and shipping activity (net tonnage of cargo ships) in the Great Lakes (Fig. 4). Shipping activity explains 62% of variation in the invasion rate, despite the fact that nearly half of all invasions that occurred over the past century are attributable to other vectors. Shipping still accounts for more invasions than any other single vector, and its influence has grown in recent decades: 77% (36 of 47) of invasions since 1970 were likely caused by transoceanic shipping (see Mills et al. 1993 and references in Appendix A). Surprisingly, the relationship obtained using data for all invaders is stronger than the one obtained using only species assumed to have been transported

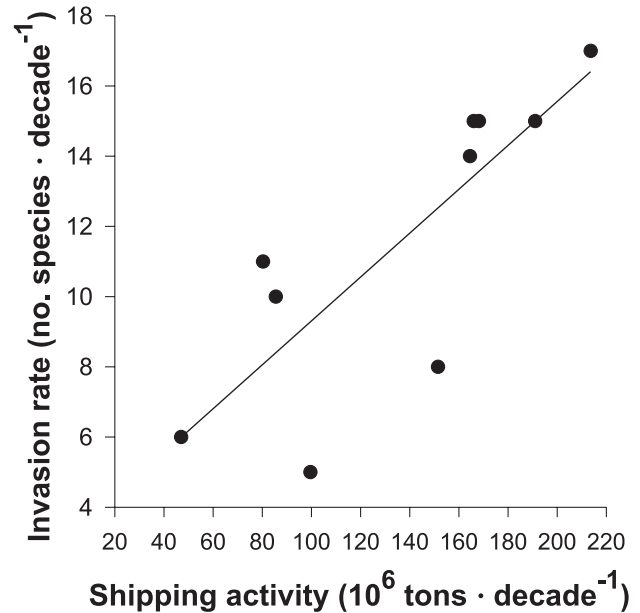
Fig. 3. Changes in the numbers of nonindigenous species established in the Great Lakes as a function of time (decades) in which the species was discovered or presumed introduced. (a) Number of invaders per decade ($y = 0.79x$, $r^2_{\text{adj}} = 0.71$, $P < 0.0001$). (b) Cumulative number of invaders over time ($y = 1.50x + 0.37x^2$, $r^2_{\text{adj}} = 0.997$, $P < 0.0001$). Least-squares regression lines are shown. Data are from Mills et al. (1993) and references are given in Appendix A.



with ships, either in ballast water or as fouling organisms on ship hulls ($r^2 = 0.43$, $P < 0.023$). The stronger correlation may be due, in part, to factors coincident with increasing shipping activity, such as changing trade patterns that have resulted in an increased diversity of donor regions linked to the Great Lakes. Alternatively, invasions may be succeeding more easily now than ever before because of facilitation among invaders. A positive feedback cycle of invasion should yield a stronger correlation involving all invaders rather than only a subset of species associated with a particular vector. Unfortunately, it is not possible to clearly separate the effects of facilitation and inoculation pressure (e.g., caused by increased ship traffic) on the rate of invasion.

Although shipping activity likely contributes to the increased accumulation of invaders in the Great Lakes, the number of invaders recorded in the 1990s (15 species) does

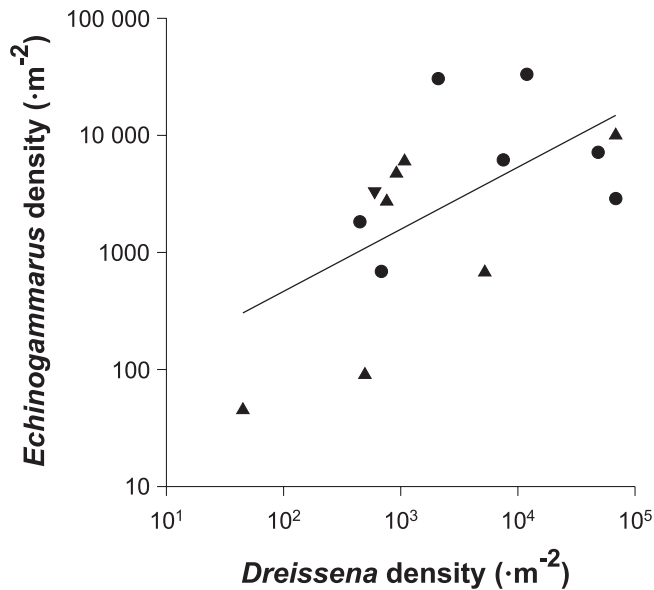
Fig. 4. Invasion rate versus shipping activity in the Great Lakes from 1900 to 1999 ($y = 0.062x$, $r^2_{\text{adj}} = 0.62$, $P < 0.004$). Shipping activity is measured in net tonnage (1 ton (Imperial) = 0.9842 t) of cargo ships (both foreign and domestic vessels) averaged over all years within each decade; data are from Lake Carriers' Association (1999).



not differ from previous decades (15 in the 1980s, 17 in the 1970s, 15 in the 1960s) despite regulations requiring inbound ships to exchange their freshwater-estuarine ballast with oceanic water. Voluntary ballast water exchange guidelines were initiated by the Canadian government in 1989, and approximately 90% of ships complied with the procedure even before it became mandatory by U.S. regulation in 1993 (Locke et al. 1993). In theory, mid-oceanic ballast water exchange should reduce the risk of invasion because freshwater organisms would be purged from the ballast tanks or killed by incoming seawater, and be replaced by marine organisms that could not survive if released into the Great Lakes. However, owing to the position of the pump intake, it is impossible to empty ballast tanks completely, so oceanic salinities are rarely achieved (Locke et al. 1993). Therefore, ballast water exchange may not prevent invasions by species with broad salinity tolerance and by species with resistant resting stages that are unlikely to be removed by exchange nor killed by contact with seawater.

Indeed, since the early 1990s, ships have continued to introduce species including the amphipod *Echinogammarus ischnus*, the copepod *Schizopera borutzkyi*, and the waterflea *Cercopagis pengoi* (Witt et al. 1997; MacIsaac et al. 1999; Horvath et al. 2001). A living specimen of another amphipod, *Corophium mucronatum*, was collected in Lake St. Clair in 1997, but the species has apparently not become established (Grigorovich and MacIsaac 1999). Other failed species introductions during the 1990s include non-reproducing European flounder (*Platichthys flesus*) and Chinese mitten crab (*Eriocheir sinensis*) (E.L. Mills, Cornell University, Biological Field Station, Bridgeport, N.Y., personal communication). Thus, during the 1990s there was a

Fig. 5. Density of the Ponto–Caspian amphipod *Echinogammarus ischnus* as a function of *Dreissena* mussel density in the Great Lakes (least-squares regression of log-transformed data, $y = 1.61 + 0.53x$, $r^2_{\text{adj}} = 0.32$, $P < 0.017$). Data are from Stewart et al. (1998a, 1998b, 1998c) and R. Dermott, Department of Fisheries and Oceans, Burlington, Ont. (personal communication). ●, Western Lake Erie; ▲, eastern Lake Erie; ▼, St. Clair River.



strong shift toward introductions of euryhaline animal species, most of which originate from Ponto–Caspian basins.

The recent influx of Ponto–Caspian invaders is attributable to strong invasion corridors (i.e., transportation vectors and dispersal pathways) linking the Great Lakes with Eurasia (Ricciardi and MacIsaac 2000). Invasion corridors shunt large numbers of propagules from particular donor pools into new regions, thereby assembling co-evolved alliances and foreign food webs in the recipient habitat like pieces of an ecological jigsaw puzzle. For example, sequential invasions by Ponto–Caspian species have completed the parasitic life cycle of the trematode *Bucephalus polymorphus* in Western Europe. The introductions of its first intermediate host (the zebra mussel) and its definitive host (the pikeperch *Stizostedion lucioperca*) allowed the trematode to spread into inland waters and cause high mortality in local populations of cyprinid fishes, which act as secondary intermediate hosts (Combes and Le Brun 1990). In the Great Lakes, facultative host–parasite complexes of nonindigenous species have become established, including parasites of introduced gobies (*N. melanostomus* and *Proterorhinus marmoratus*) and of the ruffe *Gymnocephalus cernuus* (Pronin et al. 1997a, 1997b; Cone et al. 1994). These parasites were probably introduced simultaneously with their hosts.

Ponto–Caspian invaders have also been facilitated by habitat alterations caused by dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*). *Dreissena* spp. are involved in all three cases of mutualism and 8 of the 14 cases of commensalism (e.g., Fig. 5). Food (in the form of fecal deposits) and habitat complexity produced by mussel beds have stimulated a 20-fold increase in the biomass of the amphipod *E. ischnus* in Lake Erie (Stewart et al. 1998a). Mus-

sel beds might also offer amphipods a refuge from fish predation (Gonzalez and Downing 1999). In addition, by colonizing fine sediments in western Lake Erie, *Dreissena* has facilitated the expansion of *Echinogammarus* into habitats that were previously unsuitable (Bially and MacIsaac 2000). Thus, the introduced mussels stimulate a prey resource for juvenile round gobies, which feed predominantly on gammarid amphipods in their native range, whereas adult gobies feed preferentially on the mussels themselves (Shorygin 1952; Ray and Corkum 1997). Another beneficiary is the Ponto–Caspian hydroid *Cordylophora caspia*, which consumes zebra mussel larvae and uses mussel shells as substrate (Olenin and Leppäkoski 1999). After having been relatively inconspicuous in the Great Lakes for decades, *Cordylophora* has been observed growing luxuriantly on mussel beds in Lake Michigan in recent years (T. Lauer, Ball State University, Muncie, Ind., personal communication). In Lake St. Clair and Saginaw Bay, Lake Huron, zebra mussel filtration has substantially increased water transparency, thereby stimulating the growth of exotic and native macrophytes (Skubinna et al. 1995; MacIsaac 1996), which in turn provide substrate for settling juvenile mussels and facilitate their dispersal (Horvath and Lamberti 1997). In the St. Lawrence River, the European faucet snail, *Bithynia tentaculata*, has tripled its abundance in association with the growth of dense mussel populations, whose shells support rich microflora and provide the small snail with increased grazing area (Ricciardi et al. 1997) as well as potential refuge from large predators (Stewart et al. 1999). In return, the grazing activities of the snail reduce fouling sponge colonies that can overgrow and smother mussels (Ricciardi et al. 1995; A. Ricciardi, unpublished data).

If co-evolution reduces the intensity of interspecific interactions (Case and Bolger 1991), then successive introductions of species originating from the same endemic region may not be limited by competition, contrary to predictions of community assembly models. In addition to the Great Lakes, facilitation among invaders and reassembly of co-evolved food webs have also been observed in the Baltic Sea, where most of the invaders discovered since 1990 are of Ponto–Caspian origin (Leppäkoski and Olenin 2000). However, positive interactions in the Great Lakes and the Baltic Sea often involve species that share no evolutionary history. In the Great Lakes, for example, the Asian bryozoan *Lophopodella carteri* commonly uses Eurasian macrophytes as substrate (Wood 1989). The amphipod *Gammarus fasciatus*, native to the Atlantic region of North America, thrives in Ponto–Caspian mussel beds (Ricciardi et al. 1997). In the Baltic Sea, shells of the American barnacle *Balanus improvisus* provide shelter for Ponto–Caspian amphipods (Olenin and Leppäkoski 1999). *Balanus* itself uses zebra mussels as substrate (Olenin and Leppäkoski 1999), and may benefit from direct exposure to mussel filtration currents as it does in its commensal relationship with *Mytilus* (Laihonen and Furman 1986).

Is the biotic resistance hypothesis generally valid for aquatic communities?

Elton's (1958) proposition that species-rich communities are more resistant to invaders is supported by mathematical models and some field studies (e.g., Moulton and Pimm

1983; Case 1990; Reusch 1998). The evidence is equivocal, however. As noted by Levine and D'Antonio (1999), mathematical models are based on communities that are at equilibrium prior to invasion, whereas many natural communities appear to be unsaturated or successional (Cornell 1999). Various studies have found the relationship between invasion success and community diversity to be negative, positive, or insignificant (reviewed by Levine and D'Antonio 1999). Negative relationships, when observed, occur at small spatial scales (e.g., $\sim 1 \text{ m}^2$ or less). Positive relationships tend to occur at regional scales (thousands of square metres) and suggest that the same environmental properties that support a rich diversity of native species may also support a rich diversity of introduced species (Levine and D'Antonio 1999).

Biotic resistance is hypothesized to occur at two stages of invasion: at the establishment stage and, if establishment is successful, during subsequent population growth, when the abundance of the invader (and thus its community-wide impact) is limited by resident species richness (Elton 1958; Case 1990; Shurin 2000). I have found only four documented studies (published before 2001) that have explicitly tested biotic resistance to establishment in aquatic communities; two of these support the biotic resistance model. After inoculating fishless ponds with nonindigenous zooplankton, Shurin (2000) found that both the proportion of successful introductions and the biomass of introduced species was negatively correlated with native species richness. In the second study, using experimental communities of sessile marine invertebrates, Stachowicz et al. (1999) reported that survivorship among introduced species declined with increasing community richness, apparently because of competition for space. However, they tested communities composed of only 0 to 4 epifaunal species. Experiments with small communities may have little predictive power if the relationship between invasibility and species richness is asymptotic over the range of community sizes commonly found in nature.

The two remaining studies do not support the biotic resistance model. In an analysis of 125 North American drainages, Gido and Brown (1999) found a weak negative correlation between the number of introduced fish species and the number of native fish species historically present in a drainage. However, their random simulations showed that this pattern was due to a statistical artifact: drainages with low native diversity may receive introductions from a greater pool of potential invaders in neighboring drainages. Furthermore, not all drainages with low native diversity were colonized by large numbers of introduced fishes; relatively fewer invasions occurred in drainages situated in extreme northern environments and in drainages whose river flow was less regulated.

Contrary to the notion that species-poor communities are highly vulnerable to invasion, Baltz and Moyle (1993) observed that a depauperate fish assemblage in an unregulated stream resisted invasion, despite inoculation pressure from several nonindigenous fishes inhabiting other parts of the drainage basin. Their analysis suggested that abiotic factors and the presence of native predators were more important than interspecific competition in maintaining community integrity. Similarly, an abundance of large piscivores may have

been responsible for preventing the expansion of the alewife from the St. Lawrence River into the Great Lakes, prior to the construction of the Erie Canal (Smith 1970). However, predator diversity does not appear to be a good predictor of invasibility. Although European studies suggest that fish predation may exclude the waterflea *Bythotrephes longimanus* (= *cederstroemi*) from lakes within its natural range (Grigorovich et al. 1998), selective predation by planktivorous fishes did not prevent *Bythotrephes* or another waterflea, *Cercopagis pengoi*, from becoming established in Lake Ontario (MacIsaac et al. 1999), which has the highest degree of planktivory among the Great Lakes (Rand et al. 1995). Both species were established in Lake Ontario prior to invading other Great Lakes. *Bythotrephes* also became established in Harp Lake, Ontario, despite the presence of (i) a rich, stable zooplankton community, and (ii) intense planktivory from lake herring *Coregonus artedii* and from a diverse assemblage of macroinvertebrate predators including *Leptodora kindtii*, opossum shrimp *Mysis relicta*, phantom midge *Chaoborus punctipennis*, and the jellyfish *Craspedacusta sowerbyi* (Yan and Pawson 1997; Coulas et al. 1998). Similarly, rainbow smelt have colonized a wide variety of inland lakes possessing sparse to rich communities of predators (Evans and Loftus 1987). There are also several examples of marine algae that have become established in the presence of a diverse assemblage of invertebrate grazers (Trowbridge 1995). In fact, there are theoretical reasons for predicting a positive relationship between invasibility and predator diversity. Pimm (1989) hypothesized that communities having a large variety of predators might be more vulnerable to invasion because predators reduce interspecific competition at lower trophic levels. Interference competition among predator species may also reduce pressure on introduced prey organisms (Soluk 1993).

Evolved versus contrived community diversity

Are rich communities of co-evolved fauna more resistant to invasion? Perhaps so, but numerous examples demonstrate the vulnerability of such communities. Lake Victoria had one of the richest endemic fish communities on the planet, but was devastated by a single invader, Nile perch *Lates niloticus*, which encountered neither predation nor competition from native fishes (Kaufman 1992). Rich, co-evolved communities in the Caspian Sea, Lake Baikal, Lake Biwa, and Lake Titicaca have also been invaded multiple times (Dumont 1998; Hall and Mills 2000). Mississippi River fish communities are among the most speciose of all temperate rivers, but have been invaded by several nonindigenous fishes including common carp *Cyprinus carpio*, goldfish *Carassius auratus*, grass carp *Ctenopharyngodon idella*, striped bass *Morone saxatilis*, rainbow smelt *Osmerus mordax*, rainbow trout *Oncorhynchus mykiss*, and white catfish *Ictalurus catus* (Burr and Page 1986). The zebra mussel has become established at high densities throughout the Mississippi River basin, which contains the world's richest endemic assemblage of freshwater mussels (Ricciardi et al. 1998). However, Lake Victoria cichlids and Mississippi River mussels are rapidly evolving species flocks that developed in the absence of predators like the Nile perch and biofoulers like the zebra mussel, and thus were ecologically naïve to their effects.

The hypothesis that a community is less likely to be invaded when introduced species encounter diverse competitors is suggested by terrestrial field studies (Moulton and Pimm 1983; Case and Bolger 1991), but is difficult to test rigorously because of the scarcity of data on failed introductions. Nevertheless, numerous counterexamples suggest that this hypothesis is not broadly valid in aquatic systems. The presence of ecologically or taxonomically similar native species has not prevented the establishment of several non-indigenous algae in coastal marine communities worldwide (Trowbridge 1995; Ribera and Boudouresque 1995). Following the opening of a major shipping canal between the Don and Volga rivers, the Caspian Sea was invaded by several Mediterranean invertebrates, including a mussel *Mytilaster lineatus* that caused the extinction of a confamilial endemic mussel *Dreissena caspia* (Dumont 1998). *Echinogammarus ischnus*, a deposit-feeding amphipod that inhabits zebra mussel beds in Europe (Köhn and Waterstraat 1990), is replacing the previously dominant amphipod *G. fasciatus* from mussel-covered substrate in Lake Erie, Lake Ontario, and the upper St. Lawrence River (Dermott et al. 1998; A. Ricciardi, unpublished data). Moyle (1986) noted that North American cold-water lakes and streams often contain several species of salmonids not co-evolved; brook trout *Salvelinus fontinalis*, rainbow trout *O. mykiss*, and brown trout *Salmo trutta* coexist in many streams because of their differing temperature preferences and spawning times. Similarly, numerous cyprinid minnows have become established in North American lakes and rivers where rich communities of native cyprinids were already present (Moyle 1986).

Unsuccessful introductions are less likely to be reported, or even noticed, than successful ones; this bias could obscure evidence of communities that have resisted invasion. However, where failed introductions are documented, they are often attributable to an invader's inability to adapt to abiotic conditions. For example, the Chinese mitten crab *E. sinensis* and the European flounder *P. flesus* have been frequently introduced to the Great Lakes in ship ballast water over the past few decades (Emery and Teleki 1978; MacIsaac 1999), but the environment is not saline enough for their successful reproduction. Reproducing populations of the Asiatic clam *Corbicula fluminea* in western Lake Erie, southern Lake Michigan, and the St. Clair River are restricted to waters artificially heated by discharge from power plants (Mills et al. 1993); *Corbicula*'s absence from most of the Great Lakes is better explained by its narrow thermal tolerance rather than biotic factors. Other examples are provided by introduced fishes, which often fail to invade rivers with extreme natural flow regimes (Meffe 1991; Baltz and Moyle 1993), but may do so when river flow is stabilized by impoundment (Moyle 1986; Gido and Brown 1999).

Some studies support the hypothesis that the abundance of an invading species is limited by resident species richness. Shurin (2000) found that introduced zooplankton achieved higher biomasses in enclosures where the resident species biomass was artificially reduced; therefore, he concluded that invaders were suppressed by strong interactions with resident species. Using fish exclusion cages, Robinson and Wellborn (1988) found a 29-fold reduction in the density of *C. fluminea* in the presence of a diverse assemblage of molluscivores within a Texas reservoir. Conversely, only a

small number of native molluscivores were necessary to limit the abundance of the introduced marine mussel *Musculista senhousia* in a southern California bay; 65% of mussel mortality was caused by one species of muricid snail (Reusch 1998). Thus, a single predator or parasite species might be sufficient to prevent an introduced species from becoming dominant. Conversely, even when an introduced species encounters predation pressure from a diverse assemblage of consumers it may not necessarily be prevented from becoming dominant, as demonstrated by both the *Bythotrephes longimanus* and the round goby, *N. melanostomus*, invasions in the Great Lakes (Jude et al. 1995; Yan and Pawson 1997). Clearly, statistical syntheses are needed to test the generality of biotic resistance in aquatic communities.

Conclusion

The invasion history of the Great Lakes is explained better by the invasional meltdown model than by the biotic resistance model. Mutualistic, commensal, and asymmetric exploitative interactions facilitate the survival and population growth of many Great Lakes invaders. Direct positive interactions are more common than negative ones, and often involve species that have no co-evolutionary history. The recent influx of Ponto-Caspian animals suggests that Great Lakes communities remain highly susceptible to invasion. Further colonization by Ponto-Caspian species is likely because current ballast water controls apparently cannot prevent the delivery of euryhaline organisms; Ricciardi and Rasmussen (1998) identified 17 additional Ponto-Caspian species that are probable future invaders of the Great Lakes based on their invasion histories in Europe and their likelihood of surviving overseas transport in ship ballast tanks.

There is no compelling evidence that rich aquatic assemblages resist invasion when organisms are introduced repeatedly. If abiotic conditions are suitable and dispersal opportunities exist, aquatic species will likely invade regardless of the composition of the resident community. If biotic resistance to establishment exists only at a low frequency of attempted introductions, then invasional meltdown might be a threshold effect of inoculation pressure, which is high in aquatic systems subject to frequent ballast water discharge. Moreover, biotic resistance appears more likely to operate only at small scales (Levine and D'Antonio 1999), while invasional meltdown is hypothesized to operate at multiple scales—from communities to ecosystems (Simberloff and Von Holle 1999).

The invasional meltdown model has important implications for ecosystem management and biodiversity. If an increased frequency of introduction causes an ecosystem to be more susceptible to invasion, then efforts to severely reduce the rate of invasion are warranted. This refutes the criticism that resources allocated toward prevention are wasted if some future invasions are inevitable. Furthermore, because the impact of an invader is a function of its abundance, and because its abundance may be enhanced by facilitative interactions with other invaders, frequent introductions may result in synergistic impacts (Simberloff and Von Holle 1999). Complex combinations of interactions may render these impacts unpredictable. Finally, although invasional meltdown may increase local diversity through the accumulation of introduced species, the continuing replacement of endemic

species by widespread invaders will inevitably reduce diversity among habitats and among regions (e.g., Rahel 2000). Invasional meltdown may accelerate the homogenization of ecosystems.

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Appendix A. Nonindigenous species in the Great Lakes basin not listed by Mills et al. (1993).

Species	Common name	Endemic region	Date	Reference
Algae				
<i>Thalassiosira baltica</i>	Diatom	Europe	1988*	Edlund et al. 2000
Myxozoans				
<i>Sphaeromyxa sevastopoli</i>	Mixosporidian	Black Sea	1994	Pronin et al. 1997a
Protozoans				
<i>Acineta nitocrae</i>	Suctorian	Eurasia	1970s*	Grigorovich et al. 2001
<i>Trypanosoma acerinae</i>	Flagellate	Black Sea	1980s*	United States Department of the Interior 1993
Monogeneans				
<i>Dactylogyrus amphibothrium</i>	Monogenetic fluke	Eurasia	1980s*	Cone et al. 1994

Appendix A (concluded).

Species	Common name	Endemic region	Date	Reference
<i>Dactylogyrus hemiamphibothrium</i>	Monogenetic fluke	Eurasia	1980s*	United States Department of the Interior 1993
Trematodes				
<i>Neascus brevicaudatus</i>	Digenean fluke	Eurasia	1980s*	United States Department of the Interior 1993
<i>Acanthostomum</i> sp.	Digenean fluke	Unknown	1992	Pronin et al. 1997b
<i>Ichthyocotylurus pileatus</i>	Digenean fluke	Black Sea	1994	Pronin et al. 1997a
Mollusks				
<i>Pisidium supinum</i>	Humpback pea clam	Europe	1959	MacIsaac 1999
<i>Pisidium henslowanum</i>	Henslow's pea clam	Eurasia	<1916	MacIsaac 1999
<i>Potamopyrgus antipodarum</i>	Mud snail	New Zealand	1991	Zaranko et al. 1997
Crustaceans				
<i>Nitocra hibernica</i>	Harpacticoid copepod	Eurasia	1973	Hudson et al. 1998
<i>Nitocra incerta</i>	Harpacticoid copepod	Black Sea	1999	Grigorovich et al. 2001
<i>Megacyclops viridis</i>	Cyclopoid copepod	Europe	1994	Hudson et al. 1998; Ogle et al. 1995
<i>Echinogammarus ischnus</i>	Amphipod	Black Sea	1995	Witt et al. 1997
<i>Bosmina maritima</i>	Cladoceran	Eurasia	<1980s*	De Melo and Hebert 1994
<i>Heteropsyllus</i> cf. <i>nunni</i> .	Harpacticoid copepod	unknown	1990s*	Horvath et al. 2001
<i>Schizopera borutzkyi</i>	Harpacticoid copepod	Black Sea	1998	Horvath et al. 2001
<i>Cercopagis pengoi</i>	Fish-hook waterflea	Black Sea	1998	MacIsaac et al. 1999
<i>Daphnia lumholtzi</i>	Waterflea	Africa, Asia	1999	Muzinic 2000
Ectoproct bryozoans				
<i>Lophopodella carteri</i>	Bryozoan	Asia	1934	Ricciardi and Reising 1994
Fishes				
<i>Alosa aestivalis</i>	Blueback herring	Atlantic North America	1995	MacNeill 1998

Note: Date refers to year of first collection. Assumed date of introduction is indicated by an asterisk.