



An alternative hypothesis to invasional meltdown in the Laurentian Great Lakes region: General facilitation by *Dreissena*

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ABSTRACT

Invasional meltdown, where established non-indigenous species facilitate the establishment and spread of newly arriving non-indigenous species, may contribute to the increasing rate of biological invasions. The Laurentian Great Lakes have been used as an example of invasional meltdown, but our results suggest that this may not be the case. We propose that the increased numbers of facilitative interactions are not due to an invasion meltdown, but rather a strongly interacting species, such as *Dreissena*, promoting population level changes in both native and non-indigenous species. *Dreissena* are the facilitator in the majority of reported facilitations of non-indigenous species, and those non-indigenous species have not yet led to more invasions. Further, our results show that *Dreissena* facilitate non-indigenous and native species similarly. Literature reviews showed little evidence that *Dreissena* facilitate fish or are facilitated by phytoplankton. Consequently, the observed pattern of species interactions in the Great Lakes does not conform to the definition of invasional meltdown. We suggest that *Dreissena* cause strong interactions and change the benthos in a way that facilitates many organisms (native and non-indigenous), but that system-wide invasional meltdown is not occurring in the Great Lakes.

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Introduction

Invasive species have dramatically changed the structure and function of the Great Lakes ecosystem (e.g. Mills et al., 1993; Leung et al., 2002; Pimentel et al., 2005). Additionally, the pattern of invasion has been described as an “invasional meltdown” (Ricciardi, 2001). Despite the numerous impacts of invasive species in the Great Lakes, classifying the system as undergoing an invasional meltdown is a separate issue. Invasion meltdown is defined as a “community-level phenomenon in which the net effect of facilitations would lead to an increasing rate of establishment of introduced species and/or an accelerating impact” (Simberloff, 2006). An invasional meltdown should produce many mutualisms or commensalisms between

established and incoming non-indigenous species (Simberloff and Von Holle, 1999; Fig. 1(a)) because coevolved species are hypothesized to confer advantages to each other, creating a positive-feedback loop that accelerates the accumulation of non-indigenous species and replaces native communities (Ricciardi, 2001; Simberloff, 2006). Therefore, invasive species should be more likely to facilitate coevolved species compared to native species. Further, there should be a second tier of frequent facilitative interactions with additional non-indigenous species, and possibly additional levels of interactions (Gurevitch, 2006; Simberloff, 2006). Here, we evaluate an alternative pattern of species interactions in the Great Lakes; a single taxon (*Dreissena*) facilitates both native and non-indigenous species alike because it is an ecosystem engineer and has a disproportionately large effect on all species both native and non-indigenous; consequently, there is no second tier of interactions between resident and incoming non-indigenous species (Fig. 1(b)).

Ricciardi (2001) concluded that invasional meltdown (Simberloff and Von Holle, 1999) was better than the biotic resistance hypothesis (Moulton and Pimm, 1983; Case, 1990) in explaining the pattern of species introductions in the Great Lakes because facilitative interactions are more common than negative interactions, such as competition, among non-indigenous species. The original paper (Ricciardi, 2001) has been cited 167 times between its publication and June 2011 according to the Science Citation Index Expanded (ISI

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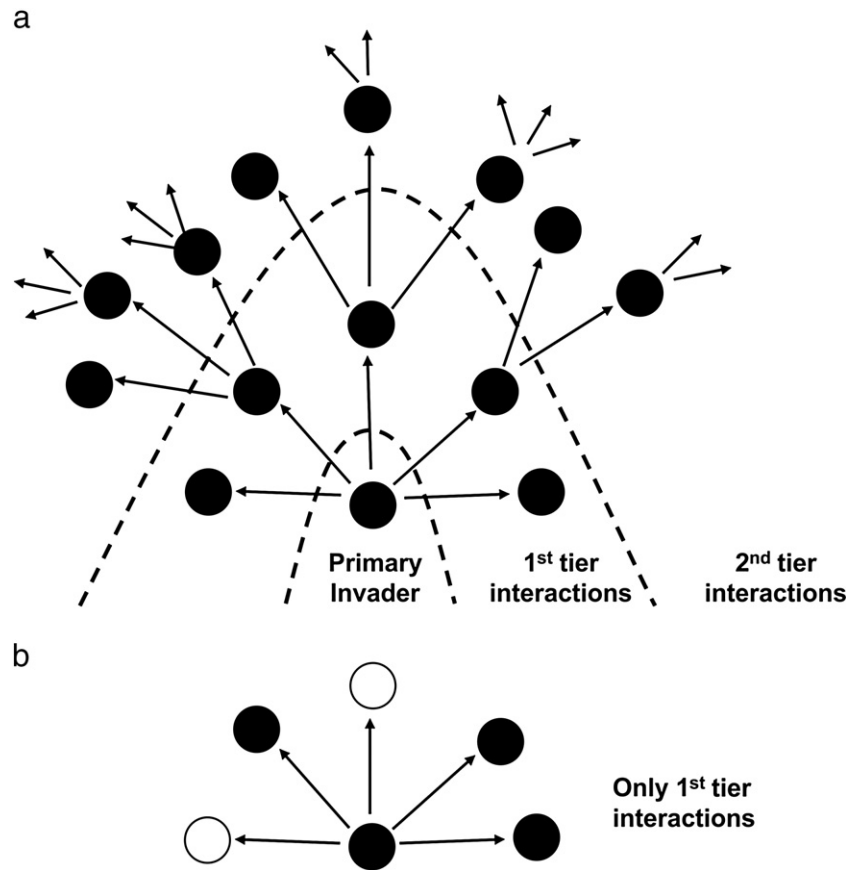


Fig. 1. Conceptual model of the expected interaction of species if invasional meltdown is occurring (a) compared to simple facilitation (b). Non-indigenous species are indicated by closed circles and native species by open circles. Invasional meltdown (a) results in non-indigenous species facilitating new invasions leading to an exponential increase in the rate of introductions, however not all non-indigenous species must facilitate new introductions. While general facilitation by *Dreissena* (b) results in *Dreissena* modifying the environment through ecosystem engineering, causing population level effects on many native and non-indigenous species without greater than one tier of interactions.

Web of Science), suggesting wide acceptance for the existence of an invasional meltdown by Great Lakes researchers. Likewise, invasion meltdown is also becoming commonly used in reports, such as the [Great Lakes Regional Collaboration \(2005\)](#) and the internationally produced State of the Great Lakes Report ([Environment Canada and U. S. Environmental Protection Agency, 2009](#)). Therefore, it is important to critically examine this prevailing paradigm and explore the invasion patterns and interactions between non-indigenous species in the Great Lakes more closely.

Dreissena were involved in 100% of mutualisms (+/+) and 57% of commensalisms (+/0) described by [Ricciardi \(2001\)](#). At that time, there were 162 known non-indigenous species in the Great Lakes, suggesting that *Dreissena* are disproportionately involved in facilitative interactions. *Dreissena polymorpha*, the zebra mussel, was first recorded in North America in 1986 ([Carlton, 2008](#)), followed by *Dreissena rostriformis bugensis*, quagga mussels, in 1988 ([Mills et al., 1993](#)). One explanation for the high percentage of interactions including *Dreissena* is because they are ecosystem engineers ([Karatayev et al., 2002; Zhu et al., 2006](#)), meaning that they alter the availability of resources to other species by causing physical state changes in biotic and abiotic resources ([Jones et al., 1994, 1997](#)). Ecosystem engineers may be more likely than other non-indigenous species to facilitate subsequent invasions ([Simberloff and Von Holle, 1999](#)). *Dreissena* modify habitats, including: 1) adding structural complexity to bottom habitats, which supports enhanced numbers of benthic invertebrates (e.g. [Botts et al., 1996; Ricciardi et al., 1997; Mayer et al., 2002](#)), 2) increasing water clarity leading to higher benthic algal production ([Lowe and Pillsbury, 1995; Cacula et al., 2008](#)) and larger populations of grazing benthic invertebrates ([Mayer et al., 2002](#)), and 3) altering the spatial distribution of

nutrients such as phosphorus ([Hecky et al., 2004](#)), resulting in high biomass accumulation of benthic algae ([Higgins et al., 2005](#)). Consequently, *Dreissena* may indiscriminately facilitate native and non-indigenous species alike.

Facilitation between non-indigenous species during an invasional meltdown can happen at different stages of invasion, with establishment being a distinct step from spread or impact. We assessed the temporal pattern of non-indigenous species introduction and establishment to determine how often facilitation of establishment was possible. A requirement for one species to facilitate establishment of an incoming species is that the facilitator must be present in the ecosystem before the incoming species. Positive interactions between non-indigenous species, and support for invasion meltdown, include the introduction of *Myrica faya*, a nitrogen-fixing tree in Hawaii, which has been implicated in facilitating the establishment and impact of several other non-indigenous species, such as earthworms and Japanese white eye (*Zosterops japonicus*) ([Vitousek and Walker, 1989; Simberloff and Von Holle, 1999](#)). Similarly, the presence of zebra mussels provided an immediate food source for the round goby (*Neogobius melanostomus*) in the Great Lakes ([Ray and Corkum, 1997; Barton et al., 2005](#)). We therefore pose the question: in what proportion of the facilitative interactions among invasive species in the Great Lakes was the facilitator present before the species benefitting from it? When the recipient of benefit was present before the assumed facilitator, the “establishment-facilitation” component between non-indigenous species during an invasional meltdown clearly did not occur.

The Laurentian Great Lakes are often used as an example of invasional meltdown; however, we hypothesize instead that *Dreissena* modify the environment, resulting in population level changes in both native and

non-indigenous species. The goal of this study is to quantitatively compare two competing hypotheses, 1) invasional meltdown or 2) indiscriminate facilitation by *Dreissena*. Our goal is not to provide a comprehensive survey of the impacts of *Dreissena* but rather to answer two specific questions: 1) What types of interactions (facilitative/neutral/negative) exist between *Dreissena* and both native and non-indigenous benthic invertebrates, macrophytes, phytoplankton, and fish? and 2) What was the timing of invasions where one species is thought to have facilitated another to determine whether facilitation of establishment was possible? We provide evidence that *Dreissena* have had a large impact on both native and non-indigenous species in the Great Lakes, and have not lead to a multi-tiered exponential increase in numbers of invaders, which is predicted by the theory of invasional meltdown.

Methods

In order to compare two hypotheses of species introduction pattern for the Great Lakes, Invasional Meltdown and General Facilitation by *Dreissena*, we examined 1) the types of interactions between *Dreissena* and native and non-native species and 2) the timing of introduction between non-indigenous species facilitating one another in the Great Lakes. To answer the first question we used published literature to closely examine the type of interaction (positive, negative, or neutral) between *Dreissena* and native and non-indigenous macrophytes, invertebrates, phytoplankton and fish. We statistically tested the proportion of each interaction type for macroinvertebrates and macrophytes using a Chi-square test for independence. We were unable to do the same test for fish and phytoplankton due to a lack of appropriate data. Therefore, we qualitatively assessed the facilitative interactions, similar to Simberloff and Von Holle (1999) and Ricciardi (2001), between *Dreissena* and non-indigenous fish and phytoplankton. The second question was addressed by analyzing the dates of first record as listed by the NOAA Great Lakes Aquatic Nonindigenous Species List (see below).

Interaction tables

We conducted a literature review to determine the nature of the responses of native and non-indigenous invertebrates and macrophytes in the presence of *Dreissena* in the Great Lakes basin. The literature review included experimental and observational studies where benthic invertebrate and/or macrophyte populations were quantified in both the presence and absence of live *Dreissena*, and the statistical significance of the population change was examined and reported. We only used manuscripts in which invertebrates and macrophytes were identified to the genus level or lower to ensure that the invertebrate or macrophyte was classified correctly as native or non-indigenous. If only genus was listed within the manuscript, but within that genus there are both native and non-indigenous species, the genus was not included. A species was determined to be non-indigenous if it was included on the Great Lakes Aquatic Nonindigenous Species List compiled by the National Oceanic and Atmospheric Administration (NOAA). All papers that met our above criteria cited in Ricciardi (2001) were used (4 total) as well as eleven additional studies found using Web of Science (search terms: Great Lakes, benthic invertebrate, benthos, macrophytes, *Dreissena*, zebra mussel, quagga mussel) (see Table 1).

To assess the type of interactions that *Dreissena* have on macrophytes and benthic invertebrates, interaction tables were constructed that list whether populations were found to statistically increase (+), decrease (−) or remain unchanged (neutral; 0) in the presence of *Dreissena* and whether the interacting species was native or non-indigenous to the Great Lakes (Table 1). If contradictory results were found in the literature (e.g. *Dreissena* had positive impacts in one study and negative in another), the direction of each interaction (+/0/−) was determined by the number of times each interaction

was encountered (either within different studies in the same manuscript or in multiple manuscripts) divided by the total number of interactions found in the literature for that species. For example, in one study, *Potamogeton richardsonii* relative abundance decreased, but the depth of colonization increased after *Dreissena* introduction (Skubinna et al., 1995), resulting in two interactions, one negative and one positive. In a similar study, both the frequency of occurrence and colonization depth of *P. richardsonii* increased after *Dreissena* introduction (Zhu et al., 2006), resulting in 2 additional positive interactions. Therefore, *P. richardsonii* had a total of 4 interactions (1 negative and 3 positive) and were listed as being 0.25 negatively impacted (−) and 0.75 positively impacted (+). A Chi-square test of independence was conducted for *Dreissena* impacts on both macrophytes ($n = 13$ native and $n = 2$ non-indigenous species) and benthic invertebrates ($n = 101$ native and $n = 7$ non-indigenous species) testing the null hypothesis that the relative frequencies of interaction types are the same among native and non-indigenous species.

Qualitative evaluation of *Dreissena* interactions with phytoplankton and fish

Trophic interactions between *Dreissena* and non-indigenous phytoplankton and fish species were examined to determine the importance of *Dreissena* as both predator (facilitation by non-indigenous phytoplankton) and prey (facilitate non-indigenous fish). All papers cited in Ricciardi (2001) in which *Dreissena* were associated with phytoplankton or fish were reviewed, along with additional literature (Table 2) to determine the benefit of non-indigenous phytoplankton species to *Dreissena* and the dietary impact of *Dreissena* on five non-indigenous and one native fish species, with focus on percentage of *Dreissena* in diet, fish condition, and population abundance pre- and post-*Dreissena* invasion. Only strong facilitative interactions were considered as evidence for invasional meltdown.

Timing of invasions

In order for one non-indigenous species to facilitate the establishment of another non-indigenous species, the species facilitating the invasion must be present first. We examined how often this occurred in the Great Lakes by comparing the introduction year of the facilitating species with the introduction year of the species receiving benefit for each ecological interaction pair listed in Ricciardi (Table 1, 2001). Dates of first record were obtained from the NOAA Great Lakes Aquatic Nonindigenous Species List, and non-indigenous species maintained by governmental stocking programs were not included in this analysis. We also did not include *Gammarus fasciatus* in this analysis, as it was not listed as a non-indigenous species in the NOAA Great Lakes Aquatic Nonindigenous Species List. Facilitation pairs in which the species assisting the establishment were found prior to the species being facilitated are consistent with the occurrence of invasional meltdown in the Great Lakes, whereas situations in which the opposite occurs do not.

Results

Interaction tables

Our data support the hypothesis that *Dreissena* facilitate native and non-indigenous species at similar frequencies. Interactions between *Dreissena* and non-indigenous and native benthic macroinvertebrate populations were not significantly different (Chi-square, $\chi^2 = 1.989$, $p > 0.35$; Table 3(a)). *Dreissena* interactions with native macroinvertebrates were 32.86% positive, 52.94% neutral, and 14.20% negative, and interactions with non-indigenous macroinvertebrates were 57.86% positive, 27.86% neutral, and 14.28% negative. The relative frequencies of interaction types also did not differ among native and non-

Table 1

Interactions listed for all species of invertebrates and macrophytes used in this paper; including references, whether the interacting species was native or non-indigenous to the Great Lakes, and the proportion of citations where populations increased (+), decreased (–) or were neutral (0) in the presence of *Dreissena*. Asterisks (*) represent manuscripts in addition to ones cited in Ricciardi (2001, Table 1).

	Species being facilitated	Sources	Native or non-Indigenous	Proportion +	Proportion 0	Proportion –
Macroinvertebrates						
Annelida						
Hirudinea						
	<i>Alboglossiphonia heteroclita</i>	Stewart et al. (1998a)	Native	1.00	0.00	0.00
	<i>Desserobdella phalera</i>	Stewart and Haynes (1994)* and Stewart et al. (1998b)	Native	0.00	1.00	0.00
	<i>Piscicola punctata</i>	Stewart and Haynes (1994)*	Native	0.00	1.00	0.00
Oligochaeta						
	<i>Arcteonais lomondi</i>	Nalepa et al. (2003)*	Native	0.00	0.00	1.00
	<i>Aulodrilus limnobius</i>	Nalepa et al. (2003)*	Native	1.00	0.00	0.00
	<i>Aulodrilus pigueti</i>	Nalepa et al. (2003)*	Native	1.00	0.00	0.00
	<i>Chaetogaster</i> sp.	Stewart and Haynes (1994)*, Ricciardi et al. (1997), Stewart et al. (1998a), and Nalepa et al. (2003)*	Native	0.43	0.43	0.14
	<i>Limnodrilus cervix</i>	Nalepa et al. (2003)*	Native	0.00	0.00	1.00
	<i>Limnodrilus hoffmeisteri</i>	Nalepa et al. (2003)*	Native	0.00	0.00	1.00
	<i>Nais</i> sp.	Stewart and Haynes (1994)* and Stewart et al. (1998a)	Native	0.13	0.88	0.00
	<i>Piguetiella michiganensis</i>	Nalepa et al. (2003)*	Native	1.00	0.00	0.00
	<i>Potamothenis moldaviensis</i>	Stewart and Haynes (1994)* and Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Potamothenis vejovskyi</i>	Stewart and Haynes (1994)* and Stewart et al. (1998a)	Native	0.13	0.88	0.00
	<i>Pristina leidyi</i>	Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Pristinella osborni</i>	Stewart and Haynes (1994)* and Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Spirosperma ferox</i>	Stewart and Haynes (1994)*	Native	0.80	0.20	0.00
	<i>Stylaria lacustris</i>	Stewart and Haynes (1994)* and Stewart et al. (1998a)	Native	0.40	0.60	0.00
	<i>Tubifex tubifex</i>	Nalepa et al. (2003)*	Native	0.00	0.00	1.00
	<i>Vejovskyella</i> sp.	Stewart and Haynes (1994)* and Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Lumbriculus variegatus</i>	Stewart and Haynes (1994)*	Native	0.00	1.00	0.00
Polychaeta						
	<i>Manayunkia speciosa</i>	Stewart and Haynes (1994)*	Native	0.60	0.40	0.00
Arthropoda						
Arachnida						
	<i>Acarina</i> sp.	Stewart et al. (1998b)	Native	0.00	1.00	0.00
	<i>Lebertia</i> sp.	Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Limnesia</i> sp.	Stewart et al. (1998a)	Native	0.00	1.00	0.00
Insecta						
Coleoptera						
	<i>Dubiraphia</i> sp.	Beekey et al. (2004b)*	Native	0.50	0.50	0.00
Diptera						
	<i>Ablabesmyia</i> sp.	Beekey et al. (2004b)*	Native	0.00	0.75	0.25
	<i>Ceratopogonidae</i> sp.	Beekey et al. (2004b)*	Native	0.00	1.00	0.00
	<i>Chironomus anthracinus</i>	Nalepa et al. (2003)*	Native	1.00	0.00	0.00
	<i>Chironomus semireductus</i>	Nalepa et al. (2003)*	Native	0.00	0.00	1.00
	<i>Chironomus plumosus</i>	Nalepa et al. (2003)*	Native	0.00	0.00	1.00
	<i>Chironomus</i> sp.	Kuhns and Berg, (1999)* and Stewart and Haynes (1994)*	Native	0.57	0.29	0.14
	<i>Cladotanytarsus mancus</i>	Nalepa et al. (2003)*	Native	0.00	1.00	0.00
	<i>Clinotanytarsus</i> sp.	Stewart et al. (1998b)	Native	0.00	1.00	0.00
	<i>Cricotopus</i> sp.	Kuhns and Berg, (1999)*, Stewart and Haynes (1994)*, and Stewart et al. (1998a, b)	Native	0.17	0.67	0.17
	<i>Cryptochironomus</i> sp.	Kuhns and Berg, (1999)*, Stewart et al. (1998a,b), and Nalepa et al. (2003)*	Native	0.50	0.50	0.00
	<i>Dicrotendipes</i> sp.	Kuhns and Berg, (1999)*, and Stewart et al. (1998a,b)	Native	0.33	0.67	0.00
	<i>Endochironomus</i> sp.	Kuhns and Berg, (1999)* and Stewart and Haynes (1994)*	Native	0.33	0.67	0.00
	<i>Eukiefferiella</i> sp.	Stewart and Haynes (1994)*	Native	0.00	1.00	0.00
	<i>Eurylophella</i> sp.	Stewart and Haynes (1994)*	Native	0.00	1.00	0.00
	<i>Hemerodromia</i> sp.	Kuhns and Berg, (1999)*	Native	1.00	0.00	0.00
	<i>Heterotrissocladius</i> sp.	Stewart and Haynes (1994)*	Native	0.50	0.50	0.00

(continued on next page)

Table 1 (continued)

	Species being facilitated	Sources	Native or non-Indigenous	Proportion +	Proportion 0	Proportion –
	<i>Krenopelopia</i> sp.	Kuhns and Berg, (1999)*	Native	0.00	1.00	0.00
	<i>Micropsectra</i> sp.	Stewart and Haynes (1994)*	Native	0.00	1.00	0.00
	<i>Microtendipes pedellus</i>	Stewart et al. (1998a,b)	Native	1.00	0.00	0.00
	<i>Nanocladius</i> sp.	Stewart et al. (1998b)	Native	0.00	1.00	0.00
	<i>Orthocladus</i> sp.	Stewart and Haynes (1994)* and Stewart et al. (1998b)	Native	0.17	0.67	0.17
	<i>Parachironomus</i> sp.	Kuhns and Berg, (1999)* and Stewart and Haynes (1994)*	Native	0.33	0.67	0.00
	<i>Paratanytarsus</i> sp.	Kuhns and Berg, (1999)* and Stewart and Haynes (1994)*	Native	0.50	0.50	0.00
	<i>Paratendipes</i> sp.	Beekey et al. (2004b)* and Stewart and Haynes (1994)*	Native	0.43	0.57	0.00
	<i>Phaenopsectra</i> sp.	Stewart and Haynes (1994)*	Native	0.00	1.00	0.00
	<i>Polypedilum</i> sp.	Kuhns and Berg, (1999)*, Stewart and Haynes (1994)*, and Stewart et al. (1998b)	Native	0.33	0.67	0.00
	<i>Procladius</i> sp.	Kuhns and Berg, (1999)*, Stewart et al. (1998a), and Nalepa et al. (2003)*	Native	0.14	0.71	0.14
	<i>Psectrocladius</i> sp.	Kuhns and Berg, (1999)* and Stewart and Haynes (1994)*	Native	0.40	0.60	0.00
	<i>Pseudochironomus</i> sp.	Stewart et al. (1998a,b)	Native	0.00	1.00	0.00
	<i>Rheotanytarsus</i> sp.	Kuhns and Berg, (1999)*, Stewart and Haynes (1994)*, and Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Tanytarsus</i> sp.	Kuhns and Berg, (1999)* and Stewart and Haynes (1994)*	Native	0.29	0.57	0.14
	<i>Thiennemanniella</i> sp.	Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Thiennemannimyia</i> sp.	Stewart and Haynes (1994)* and Stewart et al. (1998a,b)	Native	0.00	1.00	0.00
Ephemeroptera	<i>Ephemera</i> sp.	Beekey et al. (2004b)*	Native	0.50	0.50	0.00
	<i>Hexagenia</i> sp.	Beekey et al. (2004b)*	Native	0.00	0.50	0.50
	<i>Stenacron</i> sp.	Stewart and Haynes (1994)* and Stewart et al. (1998a)	Native	0.14	0.86	0.00
	<i>Stenonema</i> sp.	Stewart and Haynes (1994)* and Ricciardi et al. (1997)	Native	0.29	0.57	0.14
Lepidoptera	<i>Petrophila</i> sp.	Stewart et al. (1998a)	Native	0.00	1.00	0.00
Trichoptera	<i>Agraylea</i> sp.	Kuhns and Berg, (1999)* and Stewart and Haynes (1994)*	Native	0.60	0.40	0.00
	<i>Brachycentrus</i> sp.	Ricciardi et al. (1997)	Native	1.00	0.00	0.00
	<i>Ceraclea</i> sp.	Stewart and Haynes (1994)* and Haynes et al. (1999)*	Native	0.00	1.00	0.00
	<i>Cymellus</i> sp.	Ricciardi et al. (1997)	Native	0.50	0.00	0.50
	<i>Heliopsyche</i> sp.	Ricciardi et al. (1997)	Native	1.00	0.00	0.00
	<i>Hydroptila</i> sp.	Stewart et al. (1998a)	Native	1.00	0.00	0.00
	<i>Lepidostoma</i> sp.	Beekey et al. (2004b)*	Native	0.50	0.50	0.00
	<i>Molanna</i> sp.	Beekey et al. (2004b)*	Native	0.00	1.00	0.00
	<i>Nectopsyche</i> sp.	Ricciardi et al. (1997)	Native	1.00	0.00	0.00
	<i>Ochrotrichia</i> sp.	Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Oecetis</i> sp.	Kuhns and Berg, (1999)*, Beekey et al. (2004b)*, Stewart et al. (1998a), and Nalepa et al. (2003)*	Native	0.60	0.20	0.20
	<i>Polycentropus</i> sp.	Stewart and Haynes (1994)*, Stewart et al. (1998a,b), and Haynes et al. (1999)*	Native	0.21	0.79	0.00
Malacostraca						
Amphipoda	<i>Diporeia</i> sp.	Nalepa et al. (1998)*, Nalepa et al. (2003)*, and Nalepa et al. (2009)*	Native	0.00	0.00	1.00
	<i>Hyallela</i> sp.	Kuhns and Berg (1999)*	Native	1.00	0.00	0.00
Decapoda	<i>Orconectes propinquus</i>	Stewart and Haynes (1994)*	Native	0.50	0.50	0.00
Isopoda	<i>Asellidea</i> sp.	Beekey et al. (2004b)*	Native	1.00	0.00	0.00
	<i>Caecidotea</i> sp.	Kuhns and Berg, (1999)*, Stewart and Haynes (1994)*, Stewart et al. (1998a), and Nalepa et al. (2003)*	Native	0.25	0.50	0.25
Bryozoa	<i>Plumatella fungosa</i>	Ricciardi et al. (1997)	Native	0.00	0.00	1.00
Mollusca						
Bivalvia	<i>Musculium partumeium</i>	Stewart and Haynes (1994)* and Haynes et al. (1999)*	Native	0.00	0.91	0.09
	<i>Pisidium casertanum</i>	Lauer and McComish (2001)*	Native	0.00	0.00	1.00
	<i>Pisidium compressum</i>	Lauer and McComish (2001)*	Native	0.00	0.00	1.00
	<i>Sphaerium corneum</i>	Lauer and McComish (2001)*	Native	0.00	0.00	1.00
Gastropoda	<i>Amnicola limosa</i>	Stewart and Haynes (1994)*, Stewart et al. (1998a,b), and Haynes et al. (1999)*	Native	0.79	0.21	0.00
	<i>Birgella</i> sp.	Ricciardi et al. (1997)	Native	1.00	0.00	0.00
	<i>Elimia livescens</i>	Ricciardi et al. (1997), Stewart et al. (1998a,b), and Haynes et al. (1999)*	Native	0.17	0.50	0.33
	<i>Goniobasis livescens</i>	Stewart and Haynes (1994)*	Native	0.63	0.38	0.00
	<i>Valvata tricarinata</i>	Stewart and Haynes (1994)* and Haynes et al. (1999)*	Native	0.78	0.22	0.00

Table 1 (continued)

	Species being facilitated	Sources	Native or non-Indigenous	Proportion +	Proportion 0	Proportion –
	<i>Ferrissia</i> sp.	Stewart and Haynes (1994)*, Ricciardi et al. (1997), and Stewart et al. (1998a,b)	Native	0.50	0.50	0.00
	<i>Fossaria</i> sp.	Stewart et al. (1998a)	Native	0.00	1.00	0.00
	<i>Gyraulus</i> sp.	Stewart and Haynes (1994)*, Ricciardi et al. 1997; Stewart et al. (1998a,b), and Haynes et al. 1999*	Native	0.15	0.85	0.00
	<i>Heliosoma</i> sp.	Stewart and Haynes (1994)* and Haynes et al. (1999)*	Native	0.36	0.64	0.00
	<i>Laevapex fuscus</i>	Stewart et al. (1998a)	Native	1.00	0.00	0.00
	<i>Physa heterostrophia</i>	Stewart and Haynes (1994)*	Native	0.75	0.25	0.00
	<i>Physella</i> sp.	Stewart et al. (1998a,b) and Haynes et al. (1999)*	Native	0.67	0.33	0.00
	<i>Stagnicola catascopium</i>	Stewart and Haynes (1994) and Haynes et al. (1999)*	Native	0.33	0.50	0.17
Platyhelminthes	<i>Dugesia tigrina</i>	Stewart et al. (1998a,b)	Native	1.00	0.00	0.00
Porifera	<i>Ephydatia muelleri</i>	Ricciardi et al. (1997)	Native	0.00	1.00	0.00
	<i>Eunapius fragilis</i>	Ricciardi et al. (1997)	Native	0.00	1.00	0.00
Arthropoda						
Malacostraca						
Amphipoda	<i>Echinogammarus ischnus</i>	Stewart et al. (1998a), Van Overdijk et al. (2003)*, and Bially and MacIsaac (2000)*	Non-Indigenous	1.00	0.00	0.00
	<i>Gammarus fasciatus</i>	Kuhns and Berg, (1999)*, Beekey et al. (2004b)*, Stewart and Haynes (1994)*, Ricciardi et al. (1997), Stewart et al. (1998b), Van Overdijk et al. (2003)*, Bially and MacIsaac (2000)*, Haynes et al. (1999)*, and Nalepa et al. (2003)*	Non-Indigenous	0.80	0.20	0.00
Mollusca						
Bivalvia	<i>Sphaerium corneum</i>	Lauer and McComish (2001)*	Non-Indigenous	0.00	0.00	1.00
Gastropoda	<i>Gillia altilis</i>	Beekey et al. (2004b)*	Non-Indigenous	0.25	0.75	0.00
	<i>Bithynia tentaculata</i>	Stewart and Haynes (1994)* and Haynes et al. (1999)*	Non-Indigenous	0.00	1.00	0.00
	<i>Valvata piscinalis</i>	Ricciardi et al. (1997)	Non-Indigenous	1.00	0.00	0.00
Platyhelminthes	<i>Dugesia polychroa</i>	Ricciardi et al. (1997)	Non-Indigenous	1.00	0.00	0.00
Macrophytes						
	<i>Ceratophyllum demersum</i>	Zhu et al. (2006)*	Native	0.50	0.50	0.00
	<i>Chara globularis</i>	Skubinna et al. (1995)	Native	1.00	0.00	0.00
	<i>Elodea canadensis</i>	Skubinna et al. (1995) and Zhu et al. 2006*	Native	0.50	0.50	0.00
	<i>Najas flexis</i>	Zhu et al. (2006)*	Native	1.00	0.00	0.00
	<i>Nitella flexilis</i>	Skubinna et al. (1995)	Native	1.00	0.00	0.00
	<i>Potamogeton illinoensis</i>	Skubinna et al. (1995)	Native	0.50	0.00	0.50
	<i>Potamogeton pectinatus</i>	Skubinna et al. (1995) and Zhu et al. (2006)*	Native	0.67	0.33	0.00
	<i>Potamogeton pusillus</i>	Zhu et al. (2006)*	Native	1.00	0.00	0.00
	<i>Potamogeton richardsonii</i>	Skubinna et al. (1995) and Zhu et al. (2006)*	Native	0.75	0.00	0.25
	<i>Potamogeton zosteriformis</i>	Zhu et al. (2006)*	Native	0.50	0.00	0.50
	<i>Ranunculus trichophyllus</i>	Zhu et al. (2006)*	Native	1.00	0.00	0.00
	<i>Vallisneria americana</i>	Skubinna et al. (1995) and Zhu et al. (2006)*	Native	1.00	0.00	0.00
	<i>Zosterella dubia</i>	Zhu et al. (2006)*	Native	1.00	0.00	0.00
	<i>Myriophyllum spicatum</i>	Skubinna et al. (1995) and Zhu et al. (2006)*	Non-Indigenous	0.33	0.33	0.33
	<i>Potamogeton crispus</i>	Zhu et al. (2006)*	Non-Indigenous	1.00	0.00	0.00

indigenous macrophytes (Chi-square, $\chi^2 = 0.1814$, $p > 0.90$; Table 3 (b)). Overall, 80.2% of *Dreissena* interactions with native macrophytes were positive, 10.2% were neutral, and 9.6% were negative interactions. *Dreissena* interactions with non-indigenous macrophytes were 66.5% positive, 16.5% neutral, and 16.5% negative. Considering

there were only two non-indigenous species included in the macrophyte analysis, we hesitate to draw too many conclusions about the impact of *Dreissena* on non-indigenous macrophytes. However, our data show that *Dreissena* do have positive interactions with native macrophytes. All macrophyte and benthic invertebrate

Table 2

Literature sources for reviewing a) *Dreissena*/phytoplankton and b) *Dreissena*/fish interactions to determine strength of facilitative interactions.

(a) <i>Dreissena</i> /phytoplankton	
<i>Stephanodiscus binderanus</i>	Holland (1993) and MacIsaac (1999)
<i>Stephanodiscus subtilis</i>	Holland (1993) and MacIsaac (1999)
<i>Skeletonema subsalum</i>	Holland (1993) and MacIsaac (1999)
<i>Cyclotella cryptica</i>	Holland (1993) and MacIsaac (1999)
<i>Cyclotella pseudostelligera</i>	Holland (1993) and MacIsaac (1999)
Species non-specific	Winkel and Davids (1982), MacIsaac et al. (1991), Neumaun and Henk (1992), and Makarewicz et al. (1999)
(b) <i>Dreissena</i> /fish	
<i>Neogobius melanostomus</i>	Molloy et al. (1997), Ray and Corkum (1997), and Vanderploeg et al. (2002)
<i>Proterorhinus marmoratus</i>	Molloy et al. (1997), Vanderploeg et al. (2002), and Stepien and Tumeo (2005)
<i>Osmerus mordax</i>	Madenjian et al. (2002), Mills et al. (2003), and Riley et al. (2008)
<i>Alosa pseudoharengus</i>	Madenjian et al. (2002), Mills et al. (2003), and Riley et al. (2008)
<i>Cyprinus carpio</i>	Tucker et al. (1996) and Whillans (1996)
<i>Coregonus clupeaformis</i>	Madenjian et al. (2002), Pothoven et al. (2006), Pothoven and Madenjian (2008), Pothoven and Nalepa (2006), and Riley et al. (2008)

interactions with *Dreissena* used in this analysis and the proportion of each interaction type for each species are listed in Table 1.

Qualitative evaluation of *Dreissena* interactions with phytoplankton and fish

Although several species of Eurasian phytoplankton invaded the Great Lakes prior to the introduction of *Dreissena*, it is unlikely that these phytoplankton species facilitated the establishment or spread of *Dreissena*. Ricciardi (2001) lists five species of Eurasian phytoplankton that *Dreissena* feed on in the Great Lakes: *Stephanodiscus binderanus*, *Stephanodiscus subtilis*, *Skeletonema subsalum*, *Cyclotella cryptica*, and *Cyclotella pseudostelligera*. All of these species are from the phylum Bacillariophyta (diatoms). Based on phytoplankton population data pre- and post-*Dreissena* introduction, *Dreissena* feed on species from several different phyla, including: Bacillariophyta, Chlorophyta, Chrysophyta, Cyanobacteria, Pyrrophyta, and Cryptophyta (Makarewicz et al., 1999). Even within the phylum Bacillariophyta, there are many native species on which *Dreissena* feed, such as *Asterionella formosa* and *Dynobryon divergens* (Winkel and Davids, 1982). Moreover, food resources of *Dreissena* are not limited to phytoplankton; they also feed on zooplankton, fine detritus, and even their own veligers (MacIsaac et

Table 3

Chi-square summary table showing impacts of *Dreissena* on native and non-indigenous a) macroinvertebrate and b) macrophyte populations. Rows represent native vs. non-indigenous species and columns represent the summed proportion of citations where populations increased (+), decreased (−) or were neutral (0) in the presence of *Dreissena* across all genera.

	+	0	−	Total
(a) <i>Dreissena</i> -macroinvertebrate interactions				
Native species	33.19	53.47	14.34	101.00
Non-indigenous species	4.05	1.95	1.00	7.00
Total	37.24	55.42	15.34	108.00
(b) <i>Dreissena</i> -macrophyte interactions				
Native species	10.42	1.33	1.25	13.00
Non-indigenous species	1.33	0.33	0.33	2.00
Total	11.75	1.66	1.58	15.00

al., 1991; Neumaun and Henk, 1992). Thus, *Dreissena* are generalist feeders and are unlikely to have been strongly influenced by the presence of specific non-indigenous prey items.

Five species of non-indigenous fish are listed in Ricciardi (2001) as able to feed on *Dreissena*: the round goby, tubenose goby (*Proterorhinus marmoratus*), and common carp (*Cyprinus carpio*) can feed on adults, while alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) feed on veligers. Of these five, only the round goby has had a well-documented facilitative relationship with *Dreissena* (Ray and Corkum, 1997; Vanderploeg et al., 2002; Barton et al., 2005). It is difficult to relate changes in fish populations to the *Dreissena* invasion due to the lack of long-term data sets and controlled experimental data. We therefore discuss population trends in this section of the five non-indigenous fish species listed above, as well as native lake whitefish, with the understanding that many other changes in the Great Lakes have occurred during the same time period.

As an example, *D. polymorpha* colonized primarily nearshore areas of Lake Michigan in 1989; since 1997, *D. rostriformis bugensis* has been replacing *D. polymorpha* (Nalepa et al., 2009). Since *Dreissena* colonization, many changes have occurred in the Lake Michigan fish community, including a 71% decline in fish biomass density (mainly planktivores) from 2004 to 2007 (Bunnell et al., 2009). Native lake whitefish (*Coregonus clupeaformis*) size-at-age and condition factors have decreased since the 1990's, and have been attributed to a switch in diet from *Diporeia* to mainly dreissenids and gastropods (Madenjian et al., 2002; Pothoven and Madenjian, 2008). *Dreissena* consist of 50% indigestible shell material and are hence considered energetically unprofitable (Magoulick and Lewis, 2002). Therefore, despite maintaining consumption levels, native fish that undergo diet shifts toward dreissenid species often experience decreased growth (Pothoven et al., 2006; Pothoven and Nalepa, 2006; Pothoven and Madenjian, 2008). However, non-indigenous alewife condition and rainbow smelt biomass have also decreased since the mid-1990's (Madenjian et al., 2002). Similar trends in *Dreissena*, lake whitefish, alewife, and rainbow smelt populations have been observed in Lakes Huron and Ontario (see Mills et al., 2003; Pothoven et al., 2006; Nalepa et al., 2007; Riley et al., 2008). This suggests that although some native and non-indigenous fish have begun to feed extensively on *Dreissena*, dreissenids are not in general facilitating population level increases of non-indigenous fish in Lakes Michigan, Huron, and Ontario, and may even indirectly, through the decrease in *Diporeia*, have negative effects on the biomass and condition of both native and introduced fish.

The consumption of *Dreissena* by tubenose gobies seems debatable (see Molloy et al., 1997 and Vanderploeg et al., 2002). Regardless, the population of tubenose gobies in the Great Lakes has remained small (Stepien and Tumeo, 2005). Additionally, some predation of *Dreissena* by common carp has been observed, but the population level of common carp in the Great Lakes has been steady since the late 1800's and was not altered by the introduction of *Dreissena* in the late 1980's (Whillans, 1996; Molloy et al., 1997). Many changes have occurred in the Great Lakes since the introduction of the zebra mussel. These population level changes are most certainly confounded by other environmental and ecological factors. Regardless, the literature suggests that *Dreissena* are not triggering population level increases of non-indigenous fish populations (with the single exception of round gobies) and therefore should not be used as evidence for invasion meltdown in the Great Lakes.

Timing of invasions

There was no relationship between the date of first introduction of facilitating and facilitated non-indigenous species (Fig. 2). There were 36 of 68 incidences where the facilitating species was discovered before the species being facilitated, whereas in 32 of 68 incidences the facilitated species was discovered before the species facilitating it.

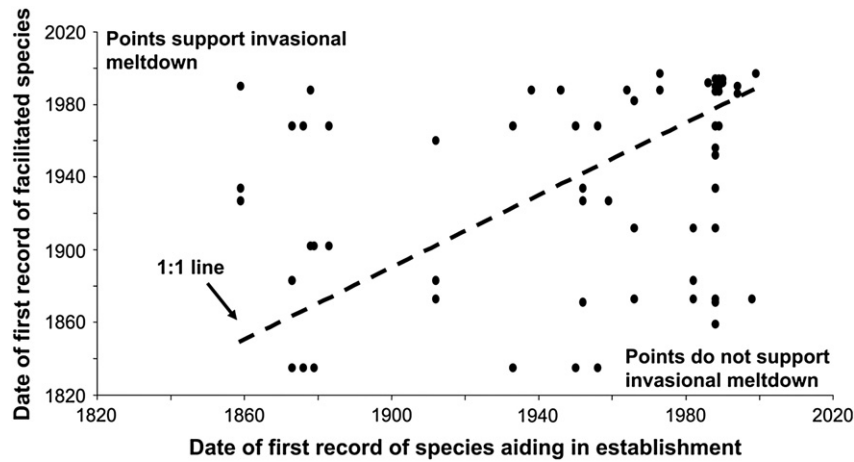


Fig. 2. Comparison of the date of first record of the species aiding (i.e. facilitating) in the establishment of a non-indigenous species with the date of first record of the species being facilitated for each ecological interaction pair listed in Ricciardi (2001, Table 1). For timing reference, *Dreissena polymorpha* was first recorded in the Great Lakes in 1886 (Carlton, 2008), followed by *Dreissena rostriformis bugensis* in 1988 (Mills et al. 1993).

Therefore, only half of the interactions listed in Ricciardi (2001) are consistent with invasional meltdown theory based solely on the timing of introductions.

Discussion

Our analysis does not support the occurrence of an invasional meltdown in the Great Lakes. The definition of invasional meltdown is “the process by which non-indigenous species facilitate one another's invasion in various ways, increasing the likelihood of survival and/or magnitude of impact and potentially leading to an accelerating increase in number of introduced species and their impact” (Simberloff, 2006). Rather, a single taxon, *Dreissena*, is responsible for the majority of reported facilitations of non-indigenous species, and those non-indigenous species have not yet facilitated more invasions. Further, our results show that *Dreissena* facilitate an equal number of non-indigenous and native species (Table 3). *Dreissena* are ecosystem engineers and tend to have strong interspecies interactions (Karatayev et al., 2002) and it is likely their alteration of both benthic and water column habitat is responsible for the number and strength of these interactions. Consequently, the observed pattern of species interactions in the Great Lakes does not conform to the definition of invasional meltdown.

Dreissena appear to be good facilitators of macrophytes and benthic invertebrates in general, unlike examples of invading terrestrial plants that change fire regimes or soil nutrients, thereby inhibiting native species and accelerating the rate of established non-indigenous species (see Simberloff and Von Holle, 1999 for a full discussion). *Dreissena* are associated with declines of some native deep-water and filter-feeding organisms such as *Diporeia* (Nalepa et al., 1998, 2003, 2009); however, this negative ecological impact is distinct from an invasional meltdown. *Diporeia* are not yet being replaced by an invasive species facilitated by *Dreissena*, although *Dreissena* biomass now dominates their habitat (Nalepa et al., 2009). *Dreissena* are well recognized as having serious impacts on the Great Lakes ecosystem; however, the pervasive effect of a single species is not the same thing as an invasional meltdown.

Dreissena can facilitate benthic invertebrates and macrophytes in various ways that are different from any other organisms native to the Great Lakes. *Dreissena* create a new level of structural complexity on the bottom of the Great Lakes, which leads to increased habitat (e.g. Botts et al., 1996; Ricciardi et al., 1997; Stewart et al., 1998a,b) and protection from predation (e.g. González and Downing, 1999; Mayer et al., 2001; Beekey et al., 2004a). *Dreissena* also filter large amounts of

sediment out of the water column into a layer of rich organic matter that can be used as a resource by deposit-feeding invertebrates (Roditi et al., 1997; Stewart et al., 1998a) and facilitates growth and spread of macrophytes due to increased water clarity (Skubinna et al., 1995; Zhu et al., 2006). Therefore, the results we have shown support that *Dreissena* are good facilitators of species in general, and ways in which *Dreissena* facilitate other organisms do not preferentially favor non-indigenous species.

We did not include unionids (Bivalvia: Unionidae) in our formal analysis because we found no papers that met our criteria for inclusion in the analysis, specifically: populations must be quantified in the presence and absence of live *Dreissena* and any reported population level change in response to *Dreissena* must be statistically tested. For example, Nalepa et al. (1996) and Schloesser et al. (1997) have unionid densities pre and post-*Dreissena* introduction, but the significance of those changes were not assessed and therefore it is difficult to attribute observed changes to *Dreissena*. *Dreissena* have had documented negative effects on unionids in the Great Lakes (e.g. Schloesser and Nalepa, 1994; Nalepa et al., 1996; Schloesser et al., 1996), but populations were shown to be declining prior to *Dreissena* introduction (Nalepa et al., 1991). Also, more recent studies have found nearshore refuges for unionids in the Great Lakes where unionid populations are abundant and are able to coexist with *Dreissena* by altering habitat selection and burrowing behavior (Nichols and Wilcox, 1997; Nichols and Amberg, 1999; Zanatta et al., 2002). Regardless, we recalculated the Chi-square analysis for benthic species adding each species of native unionid found in the lower Great Lakes between 1860 and 1996 (40 species, Metcalfe-Smith et al., 1998) as a native/negative interaction, and this did not change the overall results of our analysis.

Our study found only one possible example of a multi-tiered invasion supporting the invasion meltdown hypothesis. Round gobies were likely facilitated by *Dreissena* and may have facilitated a second tier of species – parasites *Ichthyocotylurus pileatus* and *Sphaeromyxa sebastopoli* (Pronin et al., 1997). A more recent study (Kvach and Stepien, 2008) did not find *S. sebastopoli* on round gobies in the Great Lakes, suggesting that though non-indigenous parasites may have traveled to the Great Lakes with round gobies, they have not become established. A single event in which an invasion with possible second tier invasions was facilitated is not sufficient evidence for invasional meltdown in the Great Lakes. However, this study is current to the time of publication, and the next suite of non-indigenous species may be facilitated by species interacting with *Dreissena*. Currently, there is no pattern of species facilitating the establishment of a second tier of non-indigenous species.

Trophic interactions of *Dreissena* with non-indigenous phytoplankton and fish species do not provide strong support for the occurrence of facilitation for or by *Dreissena* in the Great Lakes. *Dreissena* are generalist feeders, not exclusively dependent on phytoplankton from their native environment, and therefore unlikely dependent on such food for their introduction and establishment. Also, with the exception of round gobies (Ray and Corkum, 1997; Vanderploeg et al., 2002; Barton et al., 2005), *Dreissena* do not facilitate population level growth of native or non-indigenous fish species (Table 4), although some fish have been shown to feed heavily on adult *Dreissena* or veligers (Pothoven et al., 2006; Pothoven and Madenjian, 2008; Riley et al., 2008). Overall, *Dreissena* are low-quality prey items for fish and non-selective filter feeders, which leads to weak evidence for *Dreissena* facilitation of non-indigenous fish and facilitation by non-indigenous phytoplankton in the Great Lakes.

The order of introduction for interacting species pairs (Ricciardi, 2001) appears to be random. The facilitating species is only present during the introduction of the recipient species in 36 of the 68 cases (Fig. 2). This shows that true facilitative interactions, leading to the establishment of a non-indigenous species, were possible in only 53% of the cases analyzed. There does appear to be a break in pattern in the 1980's, with points from prior to 1980 equally distributed above and below the line and many of the points after 1980 below or on the line. This further highlights the pervasiveness of facilitation by *Dreissena*, which became established in the 1980's. However our analysis suggests that *Dreissena*'s ability to facilitate benthic and macrophyte species extends equally to native and non-indigenous species. Although there are multiple stages of invasion where facilitation can occur, we have shown that of all of the facilitated non-indigenous species listed in Ricciardi (2001), facilitation of establishment was only possible for about half of the cases.

Non-indigenous species are causing major changes to the world's ecosystems (Sala et al., 2000), including the Great Lakes (Mills et al., 1993), and *Dreissena* have likely caused large-scale changes in ecosystem function in the Great Lakes region. However, this change does not appear to be due to an invasional meltdown in the Great Lakes, rather it is the strong ecological interactions that *Dreissena* exert as ecosystem engineers. The number of non-indigenous species in the Great Lakes is increasing (Mills et al., 1993), which has been used as evidence of invasional meltdown (Holeck et al., 2004; but see Drake et al., 2005), but this increase is more likely due to increased

propagule introduction or simply better monitoring and detection of species that become invasive (Costello and Solow, 2003). Consequently, this and other critical assessments of the validity of large-scale trends such as an invasional meltdown are essential to maintaining ecosystem integrity in the Great Lakes and other anthropogenically-impacted systems.

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Table 4

Population trends of five non-indigenous fish (as listed in Ricciardi (2001)) and one native fish after *Dreissena* invasion.

Fish species	Non-indigenous or native	Population trends after <i>Dreissena</i> invasion	Sources
<i>Neogobius melanostomus</i> , round goby	Non-indigenous	Increasing	Ray and Corkum (1997), Vanderploeg et al. (2002), and Barton et al. (2005)
<i>Proterorhinus marmoratus</i> , tubenose goby	Non-indigenous	Steady and population remains small	Stepien and Tumeo (2005)
<i>Osmerus mordax</i> , rainbow smelt	Non-indigenous	Declining	Madenjian et al. (2002), Mills et al. (2003), and Riley et al. (2008)
<i>Alosa pseudoharengus</i> , alewife	Non-indigenous	Declining	Madenjian et al. (2002), Mills et al. (2003), and Riley et al. (2008)
<i>Cyprinus carpio</i> , common carp	Non-indigenous	Steady	Whillans (1996) and Molloy et al. (1997)
<i>Coregonus clupeaformis</i> , lake whitefish	Native	Steady, but decreased growth and condition	Madenjian et al. (2002), Pothoven et al. (2006), Pothoven and Madenjian (2008), and Riley et al. (2008)

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