

## Temporal Pattern of Government Funding for Nonindigenous Species Research in the Great Lakes

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**ABSTRACT.** Establishment of nonindigenous species (NIS) has emerged as one of the leading environmental problems in the Great Lakes basin over the past quarter century. The purpose of this study was to assess responses by government agencies regarding allocation of funding to NIS projects between 2000 through 2005. NIS is considered a major and increasing problem by eight of ten major funding agencies in the basin. Despite this, total funding decreased from \$5.1 to \$3.2 million dollars per annum and the number of projects supported declined concomitantly from 145 to 98 during this period. Control or ecosystem effects received the greatest allotment of resources and represented the largest number of projects. Non-taxonomic specific topics, including risk assessment and ballast tank assessment and management, received more funding than any taxon-specific projects and comprised the majority of studies on prevention, spread, and socioeconomic impacts of NIS. Among the latter, fish and *Dreissena* mussels were the most popularly funded topics, and comprised the largest contribution to ecosystem effects and biology studies. Control studies principally addressed sea lamprey, round gobies and carp species. Prevention studies had the highest funding rate per capita (\$ per study). Surprisingly, no clear shifts occurred with respect to the relative importance of projects pertaining to prevention over the period studied despite the recognized importance of this aspect of research.

**INDEX WORDS:** Nonindigenous species, Great Lakes, research funding, invasive species.

### INTRODUCTION

The introduction of harmful nonindigenous species (NIS) has had profound and widespread detrimental effects on national economies (Claudi *et al.* 2002, Pimentel *et al.* 2005, Colautti *et al.* 2006). NIS are often associated with ecological changes including species composition and ecosystem goods or services (Chapin III *et al.* 2000). Extreme examples of non-market costs imposed by NIS include species extinctions and extirpations (see Wilcove *et al.* 1998, Lawler *et al.* 2006). Organizations world-wide have focused on the importance of prevention as a key step in addressing the growing NIS issue (see Lodge *et al.* 2006). Once NIS successfully establish, large sums of money may be required to control or eradicate nascent pop-

ulations. Pimentel *et al.* (2005) estimated that environmental damage, losses and control costs owing to NIS amount to \$120 billion per year in the United States. In a similar attempt to quantify NIS effects in Canada, Colautti *et al.* (2006) estimated that 18 NIS actually or potentially cause between \$13.3 and \$34.5 billion in damage, loss and control costs, and that this value likely represents only a small fraction of true costs. Pimentel *et al.* (2005) estimated that introduced zebra mussels *Dreissena polymorpha* and quagga mussels *Dreissena bugensis* cause \$1 billion/year in damages and associated control costs in the Great Lakes. It should be recognized that while these damage and control estimates are crude, market and non-market costs associated with NIS can be very steep.

The Great Lakes have been successfully invaded by at least 183 NIS, including 63 plants, 48 inverte-

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brates, 26 fish, 26 algae, and 20 parasites or pathogens (Ricciardi 2006). Many of the most commonly encountered taxa at each trophic level are non-native to the Great Lakes. In the late 18<sup>th</sup> century, the establishment of canal systems in the northeastern United States may have allowed the sea lamprey, one of the Great Lakes' most costly invaders, access to Lake Ontario (see Mills *et al.* 1993). Deliberate or unintentional release of fishes contributed to the growing NIS diversity observed in the Great Lakes beginning in the nineteenth century (Mills *et al.* 1994). In the 1840s, transoceanic vessels began using the lower Great Lakes, and by the 1880s, ballast water replaced solid ballast as a stability mechanism for transoceanic vessels (Mills *et al.* 1993). The opening of the enlarged St. Lawrence Seaway in 1959 permitted larger vessels with larger volumes of ballast water access to the lakes (Holeck *et al.* 2004). Since that time, transoceanic ships have been the strongest vector of NIS into the Great Lakes (Mills *et al.* 1993; Ricciardi 2001, 2006), contributing 65% of the newly-established NIS (Ricciardi 2006). It can be very difficult to gauge the efficacy of ballast water regulations implemented in 1993 using records of newly reported NIS in the lakes. On the one hand, new species have continued to be discovered in the lakes post-1993, while on the other hand, on-going experiments involving controlled, experimental flushing of ballast tanks on transoceanic vessels reveal a purging efficacy of at least 95% and often more than 99% (D. Gray, University of Windsor, pers. comm.). This paradox may be explained, in part, by the existence of time lags between the introduction and establishment of an NIS and its subsequent discovery and reporting.

Despite the fact that NIS cause a great deal of economic and ecological disruption in the Great Lakes, to date there has been no systematic assessment of research funding related to this emergent threat. The objective of this study is to explore patterns in the allocation of research funding to different aquatic NIS "cost centres" in the Great Lakes from 2000 through 2005. We also consider deployment of funds by taxonomic grouping. A central question we are interested in is whether there has been a temporal shift of funding away from "ecosystem effects" studies toward prevention and control. We also explored whether funding priorities for ten of the largest agencies that fund NIS research had changed during this period.

## METHODS

To develop a list of target funding and research agencies which contribute to aquatic NIS studies in the Great Lakes basin, researchers previously known to be affiliated with NIS research were contacted and asked to identify any organizations that met the above-stated criteria. The data collected were compared to an existing research inventory furnished by the International Joint Commission (IJC). Agencies not already acknowledged by the database were then entered into it. To retrieve information on any additional organizations, help was enlisted from one NIS researcher in academia and one government official whose agency funded NIS research in each of the eight states and two Canadian provinces in the Great Lakes basin. We specifically asked these individuals to identify national and regionally-specific funding agencies that might not have been identified by the IJC database or by us. After records were received from each of these supplementary agencies, feedback was then entered into the database, producing the final full list of agencies to be contacted.

Initially, over 100 research and funding agencies were sent information request letters in April 2005. In September 2005, the focus of the questionnaire changed to target funding agencies only, and 50 letters were sent to these specific agencies. Participants were asked to provide information regarding any NIS research projects funded from 2000 through 2005. Agencies were encouraged to supply the title of the project, its principal investigators, the start date and end dates, annual (or total) projected funding, any additional funding agencies, and an abstract of the study, if available. Each organization was given the option to provide the information as a written response or via the internet through the research inventory database that was set up and maintained by the IJC's Council of Great Lakes Research Managers (see <http://ri.ijc.org>). When information was received identifying funding agencies that were not previously identified, those agencies were added to the list. Of the agencies contacted, one was approached repetitively and was ultimately unable to produce quantitative data. Five organizations provided insufficient data and were removed from the study. The final list consisted of 68 agencies that provided sufficient information to be utilized in our analyses.

Titles and abstracts of each project were reviewed to determine whether or not their content pertained to Great Lakes NIS research. Of these,

278 projects were accepted and assigned a project ID, and entered into the research inventory database. Based on these remaining projects, two sets of descriptive NIS study categories were developed. One set contained six categories that were based on the “cost centers” and included: control, ecosystem effects, prevention, socioeconomic impacts (e.g., impact on commercial fisheries), biology (e.g., life history, ecology), and dispersal patterns. The second set of categories was taxonomically-based: non-taxonomic specific species, plants, dreissenid molluscs, other invertebrates, parasites and pathogens, and fish. The non-taxonomic specific category included ballast water and tank studies, NIS modeling, or any project that did not address specific species. All studies were assessed on the basis of both cost center and taxonomy. Cost center and taxonomic categories were not mutually exclusive, as any one study could fit into more than one category. For example, a study that addressed effects of zebra mussels and round gobies on fisheries could have ecosystem effects and socioeconomic impacts as cost centers, and *Dreissena* and fish as taxonomic groupings.

All funding was converted to U.S. dollars based on the applicable exchange rate on the start date of the study. *In-kind* funding was not considered. If the research began in 2000 or later, the funds were divided by the number of years that the work spanned to determine a dollar amount per year. For projects that started prior to 2000, only post-1999 funding was considered. Likewise, if a project ended after 2005, only the portion calculated through 2005 was considered. Average funding was then allocated to each of the study years utilized by dividing total dollar amount by number of study years. The number of studies per year—categorized either by cost center or by taxonomy—consisted of all new and continuing projects for which funding was received. The average cost per study was calculated only for the cost center groupings by dividing the total number of dollars contributed to each cost center category from 2000 through 2005 by the total number of studies conducted over this period of time.

Finally, to determine whether the issue of NIS was perceived as an important and growing threat, we surveyed the top ten 10 agencies that funded the greatest number of invasion studies to determine the ranked priority of NIS as a funding issue, and whether the issue’s priority had increased, decreased, or stayed the same over the surveyed period. We also asked these 10 agencies to rank the

importance of different cost centers (above). We did not include funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) nor the U.S. National Science Foundation (NSF), because funding topics are not prioritized as with the agencies we did track. We are aware that NSF funded a \$2.9 million project on bioeconomic assessment of invasive species (Principal Investigator: David Lodge) during the years 2002–2007, whereas NSERC provided complementary funds (\$682,000) for this project for the years 2003–2007 (Principal Investigator: Mark Lewis).

## RESULTS

Overall \$25 million was spent on 278 NIS research projects from 2000 through 2005. Total funding of NIS projects declined during the 2000 through 2005 period and was approximately \$5.1, \$4.1, \$4.1, \$4.6, \$4.0, and \$3.2 million, respectively. The total number of studies likewise declined from 145, 115, 126, 138, 121, to 98. The single most costly study (\$1.8 million) assessed biological communities in, and threats posed by, vessels entering the Great Lakes carrying cargo and only residual ballast water and sediments in their ballast tanks (i.e., NOBOB ships). NOBOB ships enter the system with  $\sim 50 \text{ m}^{-3}$  of fresh, brackish or saline residual water, and carry a wide assortment of live NIS and their viable resting stages (Johengen *et al.* 2005). Because these vessels typically load and discharge Great Lakes ballast water (mixed with the ship’s residuals) during these inbound transits, they may constitute an invasion risk.

Funding patterns remained fairly consistent among the different cost centers. Projects addressing control or ecosystem effects were the most funded throughout the study period (Fig. 1a). Similarly, the number of studies did not vary widely across years, and those addressing ecosystem effects, control, and biology were the most numerous (collectively  $\sim 62\%$ ). Studies directed toward prevention and socioeconomic impact accounted for less than 25% of total studies (Fig. 1b).

More funding ( $\sim 46\%$ ) was devoted to studies of a non-taxonomic nature than those dealing with any particular group. Non-taxonomic studies consisted principally of ballast management research. The best funded taxonomic group were fishes, which garnered almost 29% of total funds (Fig. 2a). Parasites and pathogens were not funded by agencies at all over the time period, while funds for plants (both wetland and macrophytes) and dreissenids de-

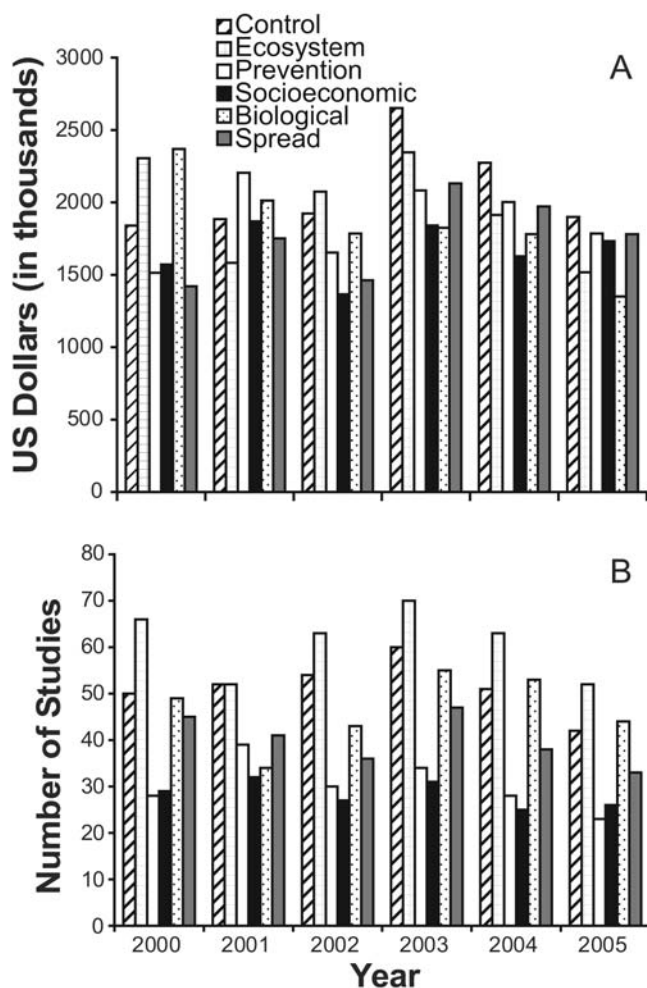


FIG. 1. Annual funding of nonindigenous species projects (a) and number of projects supported (b) between 2000 through 2005 in the Great Lakes by cost center.

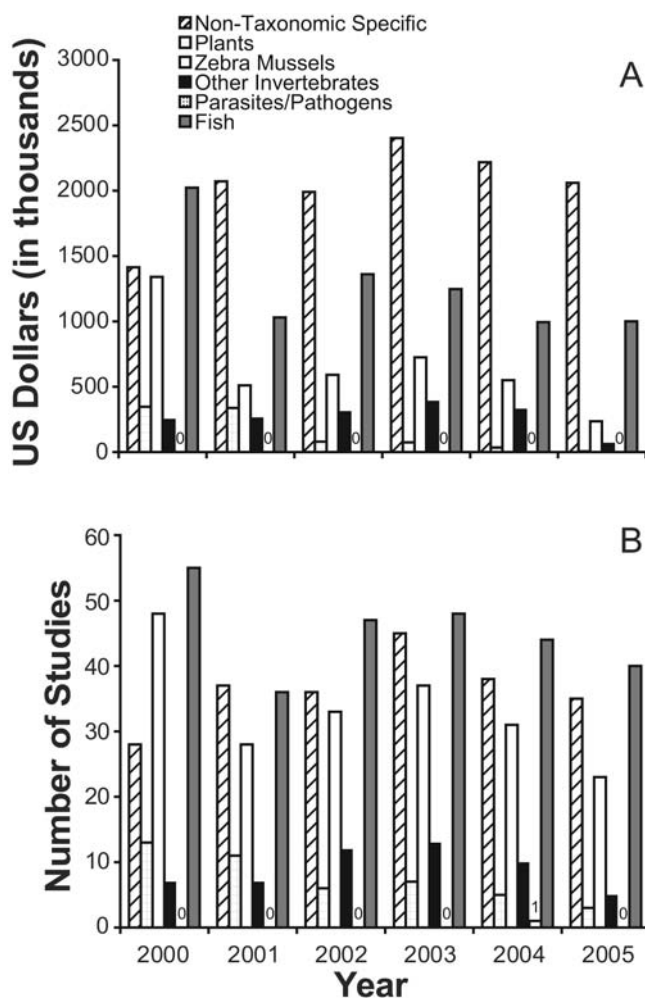


FIG. 2. Annual funding of nonindigenous species projects (a) and number of projects supported (b) between 2000 through 2005 in the Great Lakes by taxonomic grouping. Non-taxonomic specific grouping include studies on ballast water and risk assessment.

clined over the 6 years (Fig. 2a). Funding for other taxonomic groups was generally stable through time. More fish projects were funded than any other group (270 or ~34% of studies; Fig. 2b). Of these, 25% of studies addressed two invaders, the round goby and the sea lamprey. An additional 219 studies (28%) were of a non-taxonomic nature. There was only one *in-kind* study relating to parasites or pathogens, conducted during 2004.

Fish and dreissenid mussels accounted for most of the studies of ecosystem impacts (68%), NIS biology (69%), and spread (51%). Control studies were dominated by a small number of species, notably the sea lamprey, carp species, and round gob-

ies. These studies included research on development and implementation of electric barriers to separate the Great Lakes and Mississippi River basins and the use of pheromone traps for gobies and lamprey. Non-taxonomic specific studies dominated three cost centers (i.e., prevention, dispersal patterns, and socioeconomic impact) and were also important to the control category. Plant studies were equally distributed across cost centers, while invertebrate studies focused primarily on ecosystem effects and biology.

The average per capita cost was highest for the

prevention (\$245,445 per study) cost center, followed by socioeconomic impacts and control (\$239,247 and \$215,965 per study, respectively). Ecosystem impact studies were the least costly, averaging \$128,688 per study.

## DISCUSSION

The Great Lakes continue to accumulate new NIS, even though management strategies for the principal recognized vector—shipping—have been in place for some time (Holeck *et al.* 2004, Ricciardi 2006). As some of these NIS have caused significant ecological and economic harm, interest by government and non-government agencies alike has spiked (e.g., International Joint Commission 2001, 2002). Despite this, our study—which provides a recent, comprehensive basin-wide assessment of funding of NIS research by both the USA and Canada—indicates that both funding and the number of projects given financial support appear to be in decline. The greatest differences we observed were with the bookend years 2000 and 2005. For example, funding dollars and projects supported were highest in 2000 and lowest during 2005 (Fig. 1a,b).

The most costly study lasted 4 years and received \$1.8 million. This project addressed an assessment of biological communities in the ballast tanks of transoceanic vessels with no ballast on board (NOBOB) and also tested the effects of open-ocean exchange in transoceanic vessels carrying fresh or low-salinity ballast water (e.g., Bailey *et al.* 2005, 2006). Almost 92% of inbound vessels between 1996 and 2000 declared NOBOB status, as compared to only < 52% between 1978 and 1982 (Colautti *et al.* 2003). However, these vessels carry much smaller populations of NIS than vessels fully laden with freshwater ballast, as may have occurred in the past when some vessels entered the Great Lakes without cargo.

The allocation of funds was very similar to the different cost centers in our study. For example, funding ranged from a high of 19% for control to a low of 15% for socioeconomic impacts. Much greater discrepancies existed with regard to the number of funded studies, with nearly twice as many ecosystem effects (136) studies as those pertaining to prevention or socioeconomic impacts (69 and 66, respectively).

Non-taxonomic specific projects, including the NOBOB ballast project, as well as risk assessments and general NIS control projects, received the most

funding (46%) yet comprised only 25% of funded studies. Clearly, funding agencies valued these projects. Non-taxonomic specific projects were spread across all cost centres, although larger numbers of studies fell under prevention, spread, control and socioeconomic impact than to biology or ecosystem effects.

Fish were the most intensively studied taxonomic group, accounting for 29% of funding and 35% of studies. Fish studied were skewed toward three areas: ecosystem effects, control, and biology. Ecosystem impact studies were dominated by projects addressing round gobies. Much of the funding for control was devoted to sea lampreys, including eradication via lampricides, interference in reproduction via pheromones or sterile male release, and creation of low-head dams to block migration to streams used for reproduction. Pheromone interference is also being explored as a means of control of round goby populations in the Great Lakes. In addition, an electrical field barrier was initially deployed in the Chicago Ship and Sanitary Canal to prevent downstream migration of round gobies into the Mississippi River drainage, though by the time it became operational, the species had already passed through (Stoksted 2003). Serendipitously, erection of this barrier may help prevent upstream dispersal of silver, bighead, and black carp species from the Mississippi basin to the Great Lakes (Stoksted 2003).

*Dreissena* mussels accounted for 26% of studies but only 15% of research funds allocated. These molluscs still receive considerable attention by Great Lakes funding agencies despite being well established in the lakes, in part because they exert strong and sometimes unpredictable effects (see Ricciardi 2001, 2005; Holeck *et al.* 2004; Pimentel *et al.* 2005; Colautti *et al.* 2006). Indeed, 52 of 78 *Dreissena* studies involved assessments of ecosystem impact. By comparison, however, there has been a relative dearth (17) of ecosystem impact studies for other invertebrate NIS, in part because they are perceived as having less impact on the lakes. It should be noted, however, that this view could be incorrect as some of these species (e.g., *Bythotrephes*, *Cercopagis*) are recognized as having strong ecosystem effects (e.g., Yan *et al.* 2002, Laxson *et al.* 2003).

Nonindigenous parasites and pathogens contribute 10% of the total NIS in the Great Lakes region (A. Ricciardi, pers. comm.), yet only one (unfunded) study was identified that addressed these groups. Certain non-native, fish pathogens,

including salmon whirling disease and furunculosis, have impacted fish communities in the Great Lakes (Mills *et al.* 1994). Troublingly, the pathogenic Viral Hemorrhagic Septicemia virus was first observed in Lake St. Clair and in the Bay of Quinte, Lake Ontario, during 2005 and caused mortality of susceptible fish including round gobies, muskellunge (*Esox masquinongy*), and the freshwater drum (*Aplodinotus grunniens*) (P.R. Bowser, Cornell University, pers. comm.). Problems associated with this virus reoccurred during 2006. The scale of the problem might also be expected to grow, if the species spreads to other Great Lakes and to inland lakes. Clearly, understanding the full effects of this virus will require further investigation and resources.

Plants account for more established NIS (63 species; 35%) in the Great Lakes than any other taxonomic group, yet they received only 3% of funding and accounted for 7% of funded studies. Some established plant NIS dominate wetland areas in the Great Lakes (e.g., purple loosestrife *Lythrum salicaria*), forming virtual monocultures (Leach 1995). Use of biological control agents has proven successful in reducing the size of some of these populations in the lower Great Lakes. However, other very troublesome NIS including water chestnut (*Trapa natans*), fanwort (*Cabomba caroliniana*), and hydrilla (*Hydrilla verticillata*) are either present in the Great Lakes or poised to enter. Thus, for both plants and parasites/pathogens, pressing research needs exist with respect to vectors and pathways of entry, control and prevention mechanisms, and possible ecological and socioeconomic impacts.

NIS was the 1<sup>st</sup> or 2<sup>nd</sup> priority for eight the ten most prominent funding agencies (Great Lakes Fishery Commission, United States Geological Survey, Illinois/Indiana, New York, and Ohio Sea Grants, Great Lakes Protection Fund, National Oceanic and Atmospheric Administration, Department of Fisheries and Oceans). It was a much lower research priority for the United States Environmental Protection Agency and Environment Canada, both of whom focus more on chemical contamination of the lakes. Among the top ten agencies, priority given to NIS had either stayed the same (4) or increased (6) during the period covered. Agencies for which NIS was a top research priority were not wedded to a single focal topic. For example, within this group, three agencies were most concerned with prevention of new invasions, while one each was concerned with biology, ecosystem effects, and control.

Our paper utilized solicited and publicly available information on funding of NIS research between 2000 through 2005. While we are confident that the vast majority of funding sources and funded NIS projects were included in our analyses, the apparent decline of funded projects during 2005 could be due, in part, to incomplete reporting for that year. However, at present we lack the ability to discern the scale of this effect. As the same funding agencies that provided data for earlier years also furnished data for 2005, the overall effect is likely to be small and inconsequential to overall patterns. Nevertheless, a complete picture of research funding will require information from all agencies that sponsor Great Lakes NIS research.

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### REFERENCES

- Bailey, S.A., Nandakumar, K., Duggan, I.C., van Overdijk, C.D.A., Johengen, T.H., Reid, D.F., and MacIsaac, H.J. 2005. *In situ* hatching of invertebrate diapausing eggs from ships' ballast sediment. *Diver. Distrib.* 11:453–460.
- , Nandakumar, K., and MacIsaac, H.J. 2006. Does saltwater flushing reduce viability of diapausing eggs in ship ballast sediment? *Diver. Distrib.* 12:328–335.
- Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., and Diaz, S. 2000. Consequences of changing biodiversity. *Nature* 405:234–242.
- Claudi, R., Nantel, P., and Muckle-Jeffs, E. (eds.) 2002. *Alien Invaders in Canada's waters, wetlands, and forests*. Natural Resources Canada, Ottawa.
- Colautti, R.I., Niimi, A.J., van Overdijk, C.D.A., Mills, E.L., Holeck, K., and MacIsaac, H.J. 2003. Spatial and temporal analysis of transoceanic shipping vectors to the Great Lakes. In *NIS: Vectors and Management Strategies*. G. Ruiz and J.T. Carlton, eds., pp. 227–246. Island Press.
- , Bailey, S.A., van Overdijk, C.D.A., Amundsen,

- K., and MacIsaac, H.J. 2006. Characterised and projected costs of nonindigenous species in Canada. *Biol. Invas.* 8:45–59.
- Holeck, K., Mills, E.L., MacIsaac, H.J., Dochoda, M., Colautti, R.I., and Ricciardi, A. 2004. Bridging troubled waters: understanding links between biological invasions, transoceanic shipping, and other entry vectors in the Laurentian Great Lakes. *Bioscience* 10:919–929.
- International Joint Commission. 2001. *The Alien Invasive Species and Biological Pollution of the Great Lakes Basin Ecosystem*. IJC Great Lakes Water Quality Board.
- . 2002. *11<sup>th</sup> Biennial Report*.
- Johengen, T., Reid, D.F., Fahnenstiel, G., MacIsaac, H.J., Dobbs, F., Doblin, M., Ruiz, G. and Jenkins, P. 2005. *Assessment of transoceanic NOBOB vessels and low-salinity ballast water as vectors for nonindigenous species introductions to the Great Lakes*. Final Report. Great Lakes Protection Fund.
- Lawler, J.J., Aukema, J.E., Grant, J.B., Halpern, B.S., Karieva, P., Nelson, C.R., Ohleth, K., Olden, J.D., Schlaepfer, M.A., Silliman, B.R. and Zaradic, P. 2006. Conservation science: a 20-year report card. *Front. Ecol. Env.* 4:473–480.
- Laxson, C.L., McPhedran, K.N., Makarewicz, J.C., Telesh, I.V., and MacIsaac, H.J. 2003. Effects of the invasive cladoceran *Cercopagis* on the lower food web of Lake Ontario. *Freshwat. Biol.* 48:2094–2106.
- Leach, J.H. 1995. Non-indigenous species in the Great Lakes: were colonization and damage to ecosystem health predictable? *J. Aquat. Ecosyst. Health* 4:117–128.
- Lodge, D.M., Williams, S., MacIsaac, H.J., Hayes, K., Leung, B., Reichard, S., Mack, R.N., Moyle, P.B., Smith, M., Andow, D.A., Carlton, J.T., and McMichael, A. 2006. Biological invasions: recommendations for U.S. policy and management. *Ecol. Applic.* 16:2035–2054.
- Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *J. Great Lakes Res.* 19:1–54.
- , Leach, J.H., Carlton, J.T., and Secor, C.L. 1994. Exotic species and the integrity of the Great Lakes: lessons from the past. *Bioscience* 44:666–676.
- Pimentel, D., Zuniga, R., and Morrison, D. 2005. Update on the environmental and economic costs associated with alien-NIS in the United States. *Ecol. Econ.* 52:273–288.
- Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes? *Can. J. Fish. Aquat. Sci.* 58:2513–2525.
- . 2005. Facilitation and synergistic interactions among introduced aquatic species. In *Invasive Alien Species: A New Synthesis*, H.A. Mooney, R.N. Mack, J. McNeely, L.E. Neville, P.J. Schei and J.K. Waage, eds., pp. 162–178. Washington, D.C.: Island Press.
- . 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. *Divers. Distrib.* 12:425–433.
- Stocksted, E. 2003. Can well-timed jolts keep out unwanted exotic fish? *Science* 301:157–159.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., and Losos, E. 1998. Quantifying threats to imperilled species in the United States. *Bioscience* 48:607–615.
- Yan, N.D., Girard, R. & Boudreau, S. 2002. An introduced predator (*Bythotrephes*) reduces zooplankton species richness. *Ecol. Lett.* 5: 481–485.

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