Dam invaders: impoundments facilitate biological invasions into freshwaters

Pieter TJ Johnson[1*], Julian D Olden[2], and M Jake Vander Zanden[3]

Freshwater ecosystems are at the forefront of the global biodiversity crisis, with more declining and extinct species than in terrestrial or marine environments. Hydrologic alterations and biological invasions represent two of the greatest threats to freshwater biota, yet the importance of linkages between these drivers of environmental change remains uncertain. Here, we quantitatively test the hypothesis that impoundments facilitate the introduction and establishment of aquatic invasive species in lake ecosystems. By combining data on boating activity, water body physicochemistry, and geographical distribution of five nuisance invaders in the Laurentian Great Lakes region, we show that non-indigenous species are 2.4 to 300 times more likely to occur in impoundments than in natural lakes, and that impoundments frequently support multiple invaders. Furthermore, comparisons of the contemporary and historical landscapes revealed that impoundments enhance the invasion risk of natural lakes by increasing their proximity to invaded water bodies, highlighting the role of human-altered ecosystems as "stepping-stone" habitats for the continued spread of freshwater invaders.

Front Ecol Environ 2008; 6(7): 357–363, doi:10.1890/070156

An expanding global network of dams and impoundments has dramatically changed the distribution of freshwater across the landscape. Broad-scale physical impacts of such hydrological alterations include riverine fragmentation, sediment retention, enhanced evaporation, and increased greenhouse-gas production (Nilsson *et al.* 2005; Dudgeon *et al.* 2006; Poff *et al.* 2007). Less understood, however, is how dams or impoundments interact with other large-scale agents of global change, such as biological invasions. In the US alone, more than 80 000 large dams and 2.5 million smaller impoundments populate the landscape (Graf 1999; Smith *et al.* 2002), while close to 1000 introduced freshwater species contribute to the endangerment of native biodiversity (Rahel 2002; USGS 2007). Together, dam construction and biological invasions are major contributors to the current biodiversity crisis in freshwater ecosystems, which exhibit higher rates of extinction and a greater proportion of threatened and endangered species than in terrestrial or marine environments (Ricciardi and Rasmussen 1999; Dudgeon *et al.* 2006). Despite the increasing ubiquity of both impoundments and invasive species in freshwater ecosystems, a pressing, yet unanswered question remains: do impoundments enhance invasion risk by promoting the establishment and spread of non-indigenous species?

Creation of impoundments might be expected to promote invasions by increasing colonization opportunities for non-indigenous taxa and by enhancing their subsequent establishment success (Kolar and Lodge 2000; Shea and Chesson 2002; Havel *et al.* 2005). In addition to increasing the abundance of standing-water habitats, impoundments are frequently larger and more accessible to humans than are natural lakes; they are built on riverine systems with hydrologic connections to neighboring lakes, and are younger in age and experience greater disturbance than do natural systems (Thornton *et al.* 1990; Havel *et al.* 2005). All of these influences are hypothesized to enhance species colonization and establishment. If impoundments also provide greater opportunities for non-indigenous species to spread across the landscape, identification of these altered environments as invasion hubs could aid efforts aimed at predicting and preventing future invasions (Muirhead and MacIsaac 2005; Hulme 2006).

By coupling information on human behavior (ie boating), water body physicochemical characteristics, and the geographical distributions of five nuisance invaders, we quantitatively evaluated the hypothesis that impoundments facilitate biological invasions into freshwaters. Specifically, we addressed the following questions:

(1) Are impoundments more frequently invaded compared to natural lakes?
(2) What combination of factors related to colonization potential (ie propagule pressure) and establishment suitability (ie species' ecological niche) account for observed differences in invader occurrences between natural and impounded water bodies?
(3) Has the widespread creation of impoundments facilitated species invasions in freshwater ecosystems?

Our study examined five widespread nuisance invaders associated with substantial ecological or economic

[1]*Ecology and Evolutionary Biology, University of Colorado, Boulder, CO* [*]*(pieter.johnson@colorado.edu)*; [2]*School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA*; [3]*Center for Limnology, University of Wisconsin, Madison, WI*

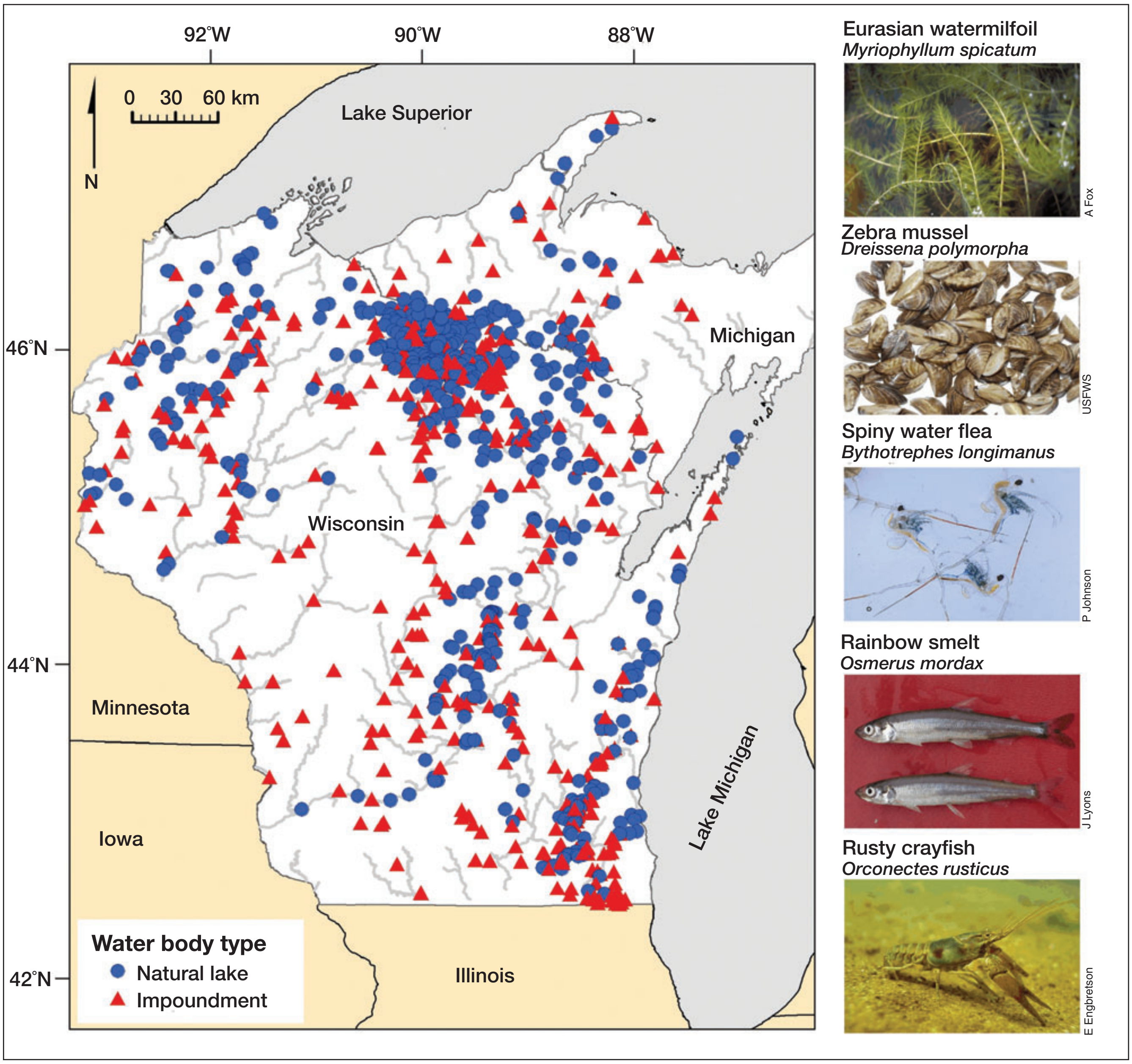

Figure 1. *Distribution of natural lakes (blue circles) and impoundments (red triangles) for which at least one non-indigenous species is established in Wisconsin and Upper Peninsula Michigan (n = 1080). Invasive species included: Eurasian watermilfoil, zebra mussels, spiny water fleas, rainbow smelt, and rusty crayfish.*

impacts: Eurasian watermilfoil (*Myriophyllum spicatum*), zebra mussels (*Dreissena polymorpha*), spiny water fleas (*Bythotrephes longimanus*), rainbow smelt (*Osmerus mordax*), and rusty crayfish (*Orconectes rusticus*; Figure 1). By including invasive species that vary widely in taxonomy, introduction pathway, life history, and physiological requirements, we provide a robust test of the aforementioned questions and reduce the likelihood that our results are idiosyncratic to a single species. The Laurentian Great Lakes region offers an ideal testing ground to evaluate interactions between biological invasions and hydrologic impoundments. Already rich in glacially-formed natural lakes, this region has undergone extensive damming in the 20th century, for agriculture, hydropower, paper mills, and recreation, creating a diverse mosaic of natural and artificial water bodies (Graf 1999). Moreover, by virtue of their close proximity to the highly invaded Great Lakes, inland lakes in this region have been colonized by a broad diversity of non-indigenous species (Holeck *et al.* 2004).

Methods

To determine how natural lakes and impoundments differ in attributes likely to affect invader introduction and establishment, we compiled physicochemical data for 5281 water bodies (4200 lakes and 1081 impoundments) distributed across Wisconsin and the upper peninsula of

Michigan. We focused on environmental characteristics potentially important for aquatic invader colonization and establishment, including surface area (km^2), upstream watershed area (km^2), maximum depth (m), mean summer water clarity (Secchi depth in m), specific conductance (μmhos cm^{-1}), hydrologic connectivity (seepage versus drainage), human accessibility (defined by the presence of a boat landing or navigable waterway), and straight-line distance to the nearest Great Lake (as a source population of non-indigenous species, particularly for spiny water fleas, zebra mussels, and rainbow smelt). Boater movement among water bodies is one of the dominant transport vectors for the spread of many freshwater non-indigenous species, so we followed Leung *et al*. (2006) in using the number of boat landings per water body as a proxy for invader propagule pressure. In support of this metric, we found a strong positive relationship between the number of boat landings and human visitations for 937 water bodies, according to boater movement data from a randomized survey of > 50 000 registered Wisconsin boaters (WebPanel 1).

We combined information on water body physicochemistry and boating behavior with the most recent distributional data for Eurasian watermilfoil (n = 682 sampled water bodies), zebra mussels (n = 353), rusty crayfish (n = 567), spiny water fleas (n = 341), and rainbow smelt (n = 83; Figure 1). Only data that met strict criteria were used; included data (1) pertained only to aquatic invaders reasonably classified as "nuisance" species; (2) contained presence and absence documentation; (3) were collected using standardized, validated sampling protocols; and (4) were recorded by trained biologists or from vouchered specimens, when they pertained to invader occurrences. Surveyed water bodies (n = 1080) were broadly distributed across the study region (Figure 1) and were similar to accessible water bodies in the comprehensive database. Sampling protocols, data sources, and an evaluation of potential systematic biases are presented in WebPanel 1.

We used two-tailed chi-squared tests of independence to compare the invasion likelihood of natural lakes and impoundments for each invader, and assessed the effect size of significant relationships using the odds ratio. The odds ratio estimates the increase in odds of being in one outcome category (eg invaded) when the value of a predictor changes (eg from natural lake to impoundment). We subsequently used logistic regression to develop species-specific models that predicted the probability of invader occurrence as a multivariate function of variables related to invader colonization and establishment, including impoundment status and the physicochemical variables described above (see WebPanel 1).

Finally, we estimated the potential for impoundments to increase the risk of invasion into natural lakes by comparing the straight-line distances between each uninvaded natural lake and that lake's nearest invaded neighbor under two scenarios: a landscape with impoundments (present-day environment) and one without impoundments ("historical" environment). We focused this analysis on zebra mussels and Eurasian watermilfoil, as these species are among the most likely to be transported by boating activity, and because they contrast a recent invasion (eg zebra mussels; first recorded in Wisconsin in 1994) with a well-established invasion (eg watermilfoil; first recorded in Wisconsin in 1965). For each uninvaded natural lake, we calculated the change in distance to the nearest invaded water body between the historical and contemporary scenarios. We compared observed changes in distance to the average distance traveled by 90% of registered boaters in Wisconsin using trailers (48 km; Buchan and Padilla 1999), and considered uninvaded lakes within 48 km of an invaded water body highly vulnerable to a potential introduction event. Importantly, because not all lakes and impoundments in Wisconsin were surveyed, calculated changes in distance between invaded and uninvaded water bodies are considered estimates. This analysis capitalizes on the observation that inter-lake distance is negatively correlated to invasion risk and assumes that, in the absence of impoundments, the number of invaded natural lakes would not have increased (eg due to increased visitation rates by boaters).

Results

Among the 1080 sampled water bodies, the invasion likelihood of impoundments exceeded that of natural lakes. For each of the five invaders, impoundments were significantly more likely than natural lakes to be invaded (two-tailed Pearson chi-squared analysis, df = 1, $P < 0.05$; Figure 2a). The association between impoundments and invader occurrences varied among the species: Eurasian watermilfoil (logistic regression odds ratio = 2.4), rusty crayfish (2.5), zebra mussel (2.7), rainbow smelt (3.0), and spiny water flea (7.8). Among the 189 water bodies surveyed for the three most common non-indigenous species (zebra mussels, Eurasian watermilfoil, and rusty crayfish), impoundments were also significantly more likely than natural lakes to support multiple invaders (Figure 2b).

Physical and biological differences between lakes and impoundments contributed to the observed differences in invasion prevalence. In comparison with natural lakes, impoundments were 1.4 times lower in average water clarity, 2.1 times higher in conductivity, 4.3 times higher in number of boat landings, 8.7 times larger in surface area, and 44.6 times larger in watershed area (WebTable 1). Impoundments were also 68% more likely than natural lakes to be accessible by humans and 54% more likely to have hydrologic connections via stream networks (WebTable 1). Nevertheless, among the best-supported logistic regression models (based on Akaike's information criterion [AIC] values and associated diagnostics), impoundment status remained a significant explanatory variable for predicting the occurrence of four out of five invaders (odds ratio ranging from 2.1 to 300),

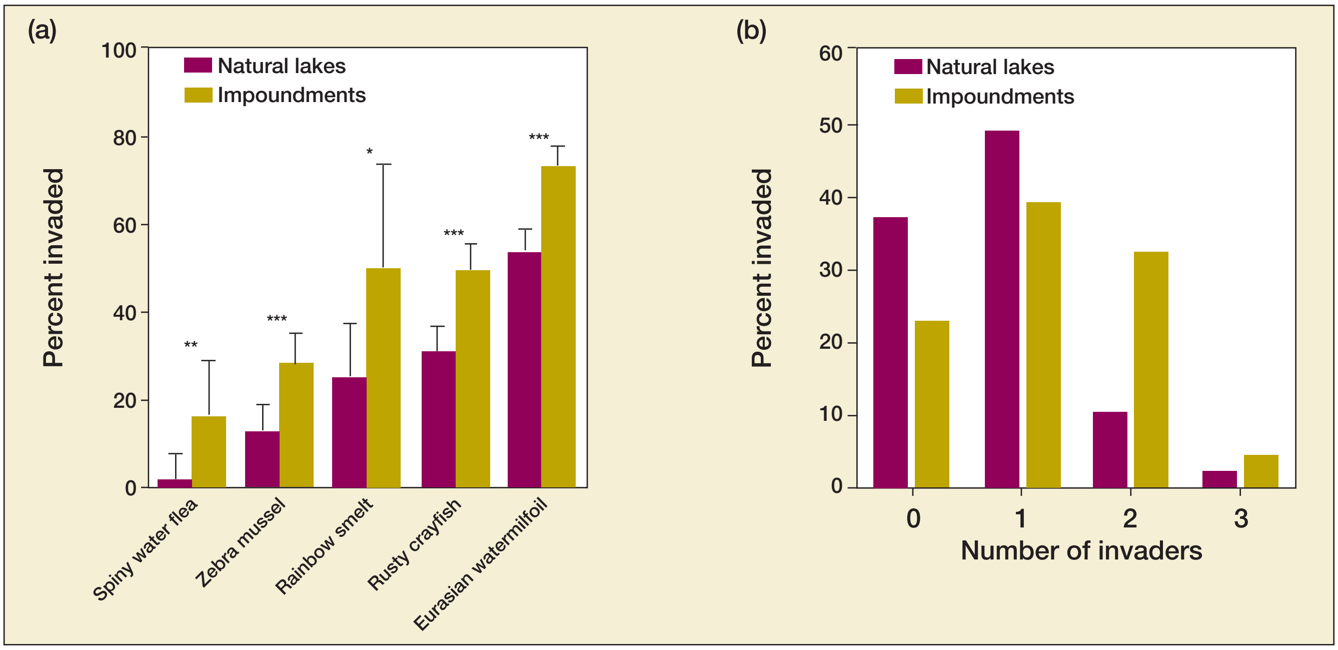

Figure 2. *(a) Percentage of surveyed lakes and impoundments that supported spiny water fleas (n = 341 sampled water bodies), zebra mussels (n = 353), rainbow smelt (n = 83), rusty crayfish (n = 567), and Eurasian watermilfoil (n = 682). Error bars represent 95% confidence intervals for a proportion. According to two-tailed Pearson chi-squared tests of independence, impoundments were significantly over-invaded relative to natural lakes for each invader (* = P < 0.05, ** = P < 0.005, *** = P < 0.0005). (b) Comparison of the number of invaders in lakes and impoundments for the 189 water bodies sampled for the three most common invaders (two-tailed Pearson $\chi^2[3] = 15.219$, P = 0.002).*

even after accounting for the influence of other environmental and anthropogenic factors likely to affect introduction and establishment (Table 1). Overall rates of correct classification based on n-fold cross validation were 94% for spiny water fleas (Cohen's $\kappa = 0.6$, $P < 0.001$), 86% for rainbow smelt ($\kappa = 0.655$, $P < 0.001$), 86% for zebra mussels ($\kappa = 0.418$, $P < 0.05$), 81% for Eurasian watermilfoil ($\kappa = 0.603$, $P < 0.001$), and 65% for rusty crayfish ($\kappa = 0.302$, $P < 0.05$). Models for individual invaders included explanatory variables broadly consistent with previous research on these species or aquatic invaders generally (Table 1; WebPanel 1). For zebra mussels alone, inclusion of either conductivity or watershed area as predictor variables eliminated impoundment status from the best-fit model (Table 1). Conductivity, particularly as it predicts the concentration of calcium ions, can limit zebra mussel shell formation and, therefore population establishment. For water bodies with dissolved calcium concentrations and conductivity measurements, these variables were strongly positively correlated ($r = 0.80$; n = 168; $P < 0.001$).

Comparisons between present-day and historical landscape scenarios (ie with and without impoundments, respectively) revealed that, for zebra mussels, the presence of impoundments reduced mean distance to the nearest invaded water body by 45%, from 84.2 km to 46.4 km (mean change ± SE = 37.7 ± 3.1 km; $t_{114} = 12.1$, $P < 0.0001$; Figure 3a). Based on the distance traveled by 90% of registered Wisconsin boaters using trailers, this increased the number of uninvaded natural lakes considered vulnerable to boater movement from an invaded water body from 45 lakes to 67 lakes (~50% increase). For the more established Eurasian watermilfoil, impoundments reduced nearest invaded-neighbor distance by 23.9% from 17.6 km to 13.4 km (mean change ± SE = 4.2 ± 1.2 km; $t_{95} = 3.4$; $P = 0.001$; Figure 3b) and increased the number of vulnerable lakes from 87 to 95 (a 9.2% increase).

Discussion

A central challenge of invasion biology is to understand how invasive species interact with other large-scale agents of environmental change (Didham *et al.* 2007). Of paramount importance to this task is learning how these environmental drivers are likely to change and interact in shaping future rates and patterns of invasions. Our findings suggest that reservoir construction and the conversion of free-flowing rivers to standing waters may ultimately facilitate the spread of invasive species across the landscape. Although aquatic invasions have previously been linked to impoundments (eg Moyle and Light 1996; Kolar and Lodge 2000), the drivers of this association have remained ambiguous. Most studies of reservoirs and aquatic invaders have occurred in areas with few natural lakes, have focused on lotic (running water) environments, or have examined intentionally introduced game species, leaving open the possibility that any lentic (standing water) habitat – rather than impoundments per se – would have produced an identical increase in invasion risk. Here, we overcome previous limitations by

Table 1. Best-fit logistic regression models for each freshwater invasive species, as determined by AIC

Model variables	*Eurasian watermilfoil* $r^2_N = 0.58$ *n = 578*	*Zebra mussel* $r^2_N = 0.52$ *n = 306*	*Spiny water flea* $r^2_N = 0.78$ *n = 120*	*Rainbow smelt* $r^2_N = 0.16$ *n = 82*	*Rusty crayfish* $r^2_N = 0.19$ *n = 408*
Impoundment status	0.73 ± 0.29* (2.07)		5.70 ± 2.57* (298.9)	2.58 ± 0.96** (13.21)	0.74 ± 0.26** (2.1)
Number of boat landings	0.29 ± 0.09** (1.342)	0.20 ± 0.08* (1.218)	1.54 ± 0.55** (4.644)		–0.19 ± 0.06** (0.826)
Distance to Great Lakes		–1.37 ± 0.59* (0.255)	–4.39 ± 1.55** (0.012)	–5.23 ± 3.22 (0.005)	1.84 ± 0.57** (6.295)
Watershed area		0.84 ± 0.28** (2.307)			0.49 ± 0.22* (1.637)
Secchi depth		3.06 ± 1.27* (21.39)	12.73 ± 6.04* (336614)		1.73 ± 0.65* (5.617)
Maximum depth		2.23 ± 0.87* (9.314)	–6.52 ± 3.92 (0.001)	11.93 ± 3.03** (151669)	
Conductance	4.36 ± 0.40** (78.1)	5.50 ± 0.94** (244.92)			
Surface area	–1.07 ± 0.28** (0.345)			–2.76 ± 0.92** (0.003)	
Hydrology	–1.16 ± 0.34** (0.315)				0.49 ± 0.22* (1.637)
Constant	–6.45 ± 1.0** (0.002)	–15.81 ± 4.38** (0.00001)	6.44 ± 6.94 (624)	10.21 ± 16.0 (27121)	–11.75 ± 3.0** (0.0001)

Notes: Listed in the first row are each invader, the Nagelkerke r^2 value for the best model, and the total sample size of water bodies. In the first column are the independent variables included in each analysis; all continuous variables were $\log_{10}$-transformed. Provided in each subsequent column are the maximum likelihood parameter estimates ± 1 SE and the odds ratio (in parentheses) for each independent variable in the final model. A blank cell indicates that a given variable was not selected in the final model. * = Wald chi-squared $P < 0.05$; ** = Wald chi-squared $P < 0.005$.

quantitatively analyzing spatial patterns of invasions for a taxonomically diverse assemblage of species in a region rich with impoundments and natural lakes.

Consistent with the hypothesis that impoundments facilitate freshwater invasions, impoundment status was a strong predictor of non-indigenous species' occurrences. For each of the five invaders, impoundments were 2.5 to 7.8 times more likely than natural lakes to have established populations, and these patterns were robust to variation in the definition of impoundment (see WebPanel 1). Among the subset of water bodies surveyed for the three most common invaders (zebra mussels, Eurasian watermilfoil, and rusty crayfish), impoundments were also significantly more likely than natural lakes to support multiple invaders. Considering that current sampling efforts were weighted toward accessible water bodies, notably underrepresenting the thousands of less accessible natural lakes in this region, we expect that the reported invasion bias in favor of impoundments is a considerable underestimate; inaccessible lakes are less likely to be visited by humans and, therefore, to be invaded.

Despite inclusion of numerous anthropogenic and environmental variables hypothesized to affect the probability of invader introduction and establishment, impoundment status remained a significant predictor of occurrence for four of the five invaders (Table 1). In several cases, inclusion of additional explanatory variables enhanced the strength of the impoundment effect, as estimated by the odds ratio (up to 300 times over natural lakes). Models for individual invaders included a variety

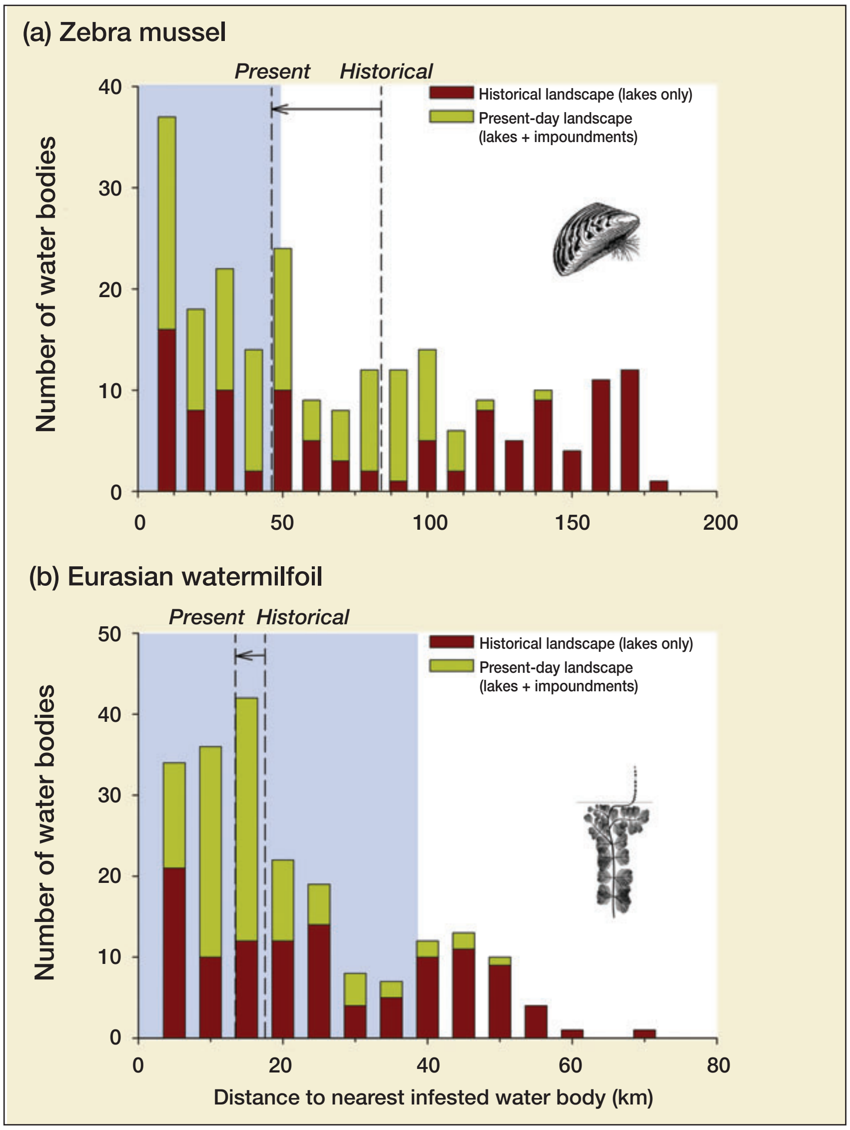

Figure 3. *Comparison of the distance between uninvaded natural lakes and the nearest water body invaded by (a) zebra mussels and (b) Eurasian watermilfoil under two scenarios: present-day landscape with lakes and impoundments (top stacked bars) and historical landscape with lakes and no impoundments (bottom stacked bars). Dashed lines indicate the mean distance between uninvaded natural lakes and the nearest invaded water body under the two scenarios; shaded region reflects the average inter-lake distance traveled by boaters in the study region.*

of predictors broadly consistent with previous research on these species. The number of boat landings and/or the proximity of a water body to the nearest Great Lake positively predicted the occurrence of spiny water fleas, Eurasian watermilfoil, rainbow smelt, and zebra mussels, highlighting the importance of human boating activity and distance to invader source population (eg MacIsaac *et al.* 2004; Leung *et al.* 2006). The importance of watershed area for both zebra mussels and rusty crayfish probably reflected increased colonization opportunities through upstream lake or river connections (eg Puth and Allen 2005; Havel and Medley 2006).

We suggest that the strong association between impoundments and non-indigenous species results from the young age, increased niche availability, and high disturbance regime characteristic of most impoundments. Natural lakes in the Great Lakes region are at least 10 000 years old and formed during glacial retreat in the Pleistocene, whereas the oldest impoundment in our dataset was 161 years old (median = 68 years), indicating that these communities have had substantially less time to assemble. Newly assembled native communities in impoundments may exhibit correspondingly lower biotic resistance, thereby making them particularly vulnerable to species invasions (Levine and D'Antonio 1999; Kolar and Lodge 2000; Shea and Chesson 2002; Havel *et al.* 2005). Impoundments are also more disturbed than natural lakes, often exhibiting marked fluctuations in water levels, temperature, fish stocking, and nutrient content (Thornton *et al.* 1990) – conditions that should increase invasibility (eg Davis *et al.* 2000). Broadly distributed invasive species may also have become adapted to impoundments in other parts of their native or non-native ranges, further facilitating their success in North American impoundments. However, we cannot exclude the possibility that lakes and impoundments differ in invader propagule pressure beyond what we showed in our analysis. Despite the combined strength of water body area and number of boat landings in predicting water body popularity (see WebPanel 1), additional differences in boat landing quality, visitation rates, or type of boater could generate differences in invasion risk.

An additional challenge beyond understanding the factors driving the impoundment–invasion linkage is identifying its consequences for natural lake ecosystems. We estimated the potential for impoundments to increase the invasion risk of natural lakes by comparing the distances between each uninvaded natural lake and its nearest invaded neighbor under two scenarios: a contemporary landscape with impoundments and a historical landscape devoid of impoundments. We found that impoundments reduced the mean distance between an uninvaded lake and its nearest zebra mussel-invaded neighbor by half, increasing the number of natural lakes considered highly vulnerable to invasion by almost 50%. For the more established Eurasian watermilfoil, impoundments increased the number of highly vulnerable lakes by about 10%. This finding suggests that the facilitative role of impoundments in invasion may attenuate as the landscape becomes saturated with invaded water bodies. These results also suggest that impoundments increase the risk of invasion into natural lakes by both decreasing inter-lake distance and by increasing the total number of invaded water bodies on the landscape.

Predicting which ecosystems are vulnerable to invasions is an important goal of invasion biology, and identification of environments that will not only become invaded but will contribute disproportionately to secondary spread of invasive species offers the promise of targeted and cost-effective management (Hulme 2006). We argue that impoundments may function as invasion "hubs" for freshwater invaders (Muirhead and MacIsaac 2005), facilitating their subsequent spread and establishment into natural water bodies. Impoundments are now a ubiquitous feature of the global hydrologic system (Smith *et al.* 2002; Downing *et al.* 2006), and vast regions where lakes were formerly rare are now home to hundreds of impoundments, while other regions historically dominated by natural lakes now also include numerous impoundments. Furthermore, climate-induced changes to water availability and increasing human demand for water are likely to prompt the construction of new reservoirs to increase water supplies in many regions (Palmer *et al.* 2008). The widespread distribution of contemporary impoundments and the ongoing creation of new impoundments could provide enhanced opportunities for invasive species to establish in natural lakes and spread across the landscape.

Acknowledgements

The authors gratefully acknowledge the data contributions of J Maxted, K Webster, P Soranno, L Herman, R Martin, T Mojo, D Balsiger, K Grande, T Asplund, D Olson, J Filbert, L Joppa, and S Knight. The following agencies generously shared information: Wisconsin Department of Natural Resources (WDNR), Michigan Department of Environmental Quality, the North Temperate Lakes LTER and Biocomplexity programs, and the Great Lakes Indian Fish and Wildlife Commission. S Carpenter, J Havel, D Strayer, H MacIsaac, and E Stanley provided feedback helpful in shaping the manuscript. This project was funded by grants from the WDNR, the Wisconsin Coastal Management Program, and the National Science Foundation (DEB-0411760, DEB-0217533, and DEB-0083545).

References

Buchan LAJ and Padilla DK. 1999. Estimating the probability of long-distance overland dispersal of invading aquatic species. *Ecol Appl* **9**: 254–65.

Davis MA, Grime JP, and Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* **88**: 528–34.

Didham RK, Tylianakis JM, Gemmell NJ, *et al.* 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol Evol* **22**: 489–96.

Downing JA, Prairie YT, Cole JJ, *et al.* 2006 The global abundance and size distribution of lakes, ponds, and impoundments. *Limnol Oceanogr* **51**: 2388–97.

Dudgeon D, Arthington AH, Gessner MO, *et al.* 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol Rev* **81**: 163–82.

Graf WL. 1999. Dam nation: a geographic census of American dams and their large-scale hydrologic impacts. *Water Resour Res* **35**: 1305–11.

Havel JE, Lee CE, and Vander Zanden MJ. 2005. Do reservoirs facilitate invasions into landscapes? *BioScience* **55**: 518–25.

Havel JE and Medley KA. 2006. Biological invasions across spatial scales: intercontinental, regional and local dispersal of cladoceran zooplankton. *Biol Invasions* **8**: 459–73.

Holeck KT, Mills EL, MacIsaac HJ, *et al.* 2004. Bridging troubled waters: understanding links between biological invasions, transoceanic shipping, and other entry vectors in the Laurentian Great Lakes. *BioScience* **54**: 919–29.

Hulme PE. 2006. Beyond control: wider implications for the management of biological invasions. *J Appl Ecol* **43**: 835–47.

Kolar CS and Lodge DM. 2000. Freshwater nonindigenous species: interactions with other global changes. In: Mooney HA and Hobbs RJ (Eds). Invasive species in a changing world. Washington, DC: Island Press.

Leung B, Bossenbroek JM, and Lodge DM. 2006. Boats, pathways, and aquatic biological invasions: estimating dispersal potential with gravity models. *Biol Invasions* **8**: 241–54.

Levine JM and D'Antonio CM. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**: 15–26.

MacIsaac HJ, Borberly JVM, Muirhead JR, and Graniero PA. 2004. Backcasting and forecasting biological invasions of inland lakes. *Ecol Appl* **14**: 773–83.

Moyle PB and Light T. 1996. Biological invasions of freshwater: empirical rules and assembly theory. *Biol Conserv* **78**: 149–61.

Muirhead JR and MacIsaac HJ. 2005. Development of inland lakes as hubs in an invasion network. *J Appl Ecol* **42**: 80–90.

Nilsson C, Reidy CA, Dynesius M, and Revenga C. 2005. Fragmentation and flow regulation of the world's large river systems. *Science* **308**: 405–08.

Palmer MA, Reidy Liermann CA, Nilsson C, *et al.* 2008. Climate change and the world's river basins: anticipating management options. *Front Ecol Environ* **6**: 81–89.

Poff NL, Olden JD, Merritt DM, and Pepin DM. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. *P Natl Acad Sci USA* **104**: 5732–37.

Puth LM and Allen TFH. 2005. Potential corridors for the rusty crayfish, *Orconectes rusticus*, in northern Wisconsin USA lakes: lessons for exotic invasions. *Landscape Ecol* **20**: 567–77.

Rahel FJ. 2002. Homogenization of freshwater faunas. *Ann Rev Ecol Syst* **33**: 291–315.

Ricciardi A and Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Conserv Biol* **13**: 1220–22.

Shea K and Chesson P. 2002. Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* **17**: 170–76.

Smith SV, Renwick WH, Bartley JD, and Buddemeir RD. 2002. Distribution and significance of small, artificial water bodies across the United States landscape. *Sci Tot Environ* **299**: 21–36.

Thornton KW, Kimmel BL, and Payne FE. 1990. Reservoir limnology: ecological perspectives. New York, NY: John Wiley and Sons.

USGS (US Geological Survey). 2007. Nonindigenous Aquatic Species Database. Gainesville, FL: US Geological Survey. http://nas.er.usgs.gov. Viewed 18 Dec 2007.

