

Research Article

An empirical analysis of the consequences of zebra mussel invasions on fisheries in inland, freshwater lakes in Southern Ontario

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Received: 30 October 2013 / Accepted: 14 May 2014 / Published online: 21 July 2014

Handling editor: Calum MacNeil

Abstract

With increasing human use of North American inland lakes for recreational purposes, there is a greater probability of the incidental transfer and introduction of aquatic invasive species within them. This raises concern over the potential ecological and economic impacts that invasive species could have in these highly valued freshwater ecosystems. In this study, we focus our interests on 63 inland lakes distributed across the Southern Ontario landscape in order to evaluate whether concerns are warranted over potential adverse impacts of a well-known aquatic invasive species (the zebra mussel (*Dreissena polymorpha*)) on native fish assemblages and targeted game species (i.e., walleye (*Sander vitreus*), smallmouth bass (*Micropterus dolomieu*), lake trout (*Salvelinus namaycush*), and northern pike (*Esox lucius*)). Through the analysis of a comprehensive and multivariate dataset comprising lake morphometric, water chemistry, fish assemblage, fish metric, and zooplankton haul data, we examined the potential consequences of zebra mussel invasions in inland lakes. It was found that condition, growth, and relative abundance of some of the most highly valued game fish in inland lakes significantly varies among lakes with and without zebra mussel, though the nature of such effects differed for each of the fish species examined. In addition, it was shown that the species composition (i.e., identity and relative abundance) of active, large-bodied fish assemblages within a lake can indicate zebra mussel presence/absence with a high degree of certainty. Finally, while correlations between zebra mussel presence and the richness, abundance, growth, and condition of certain fish species were found, the results of this study indicate that the potential consequences of this well-known aquatic invader to fisheries in inland lakes may be less dramatic than those reported within the Great Lakes.

Key words: *Dreissena polymorpha*, aquatic invasive species, fish assemblage, growth, condition, relative abundance

Introduction

The rapidly increasing trend in species introductions has sparked a growing interest in the study of invasion ecology coincident with a growing awareness of the significant adverse ecological impacts that invasive species can cause (Simberloff 2004). For example, it is now well-documented that the introduction of invasive species can lead to losses in native species diversity, extinctions of native species, shifts in community structure and even whole-scale changes to ecosystem function (Elton 1958; Greenway 1967; Simberloff 1981; Drake et al. 1989; Ramakrishan and Vitousek 1989; Coblenz 1990). Furthermore, alterations to habitat conditions and food webs wrought by an invasive

species can facilitate further invasions and disturbances through a process termed ‘*invasional meltdown*’ (Simberloff and Von Holle 1999). Finally, beyond potentially significant impacts on ecosystem form and function, invasive species can also have significant socio-economic effects on human communities or industries dependent upon aquatic ecosystems (Pimentel et al. 2001; Reaser et al. 2007).

Whereas certain communities may be resilient to invasions, particularly in terrestrial ecosystems characterized by high native species diversity (Elton 1958; Case 1990), freshwater lakes appear to be particularly vulnerable to invasions by non-native species (Mills et al. 1993; Ricciardi and MacIsaac 2000). This is believed to be attributable

to their high degree of endemism and isolation (Richter et al. 1997; Dudgeon et al. 2006). The Great Lakes, for example, are among the most heavily impacted systems in the world, with more than 180 invasive species identified within their waters to date (Great Lakes Aquatic Nonindigenous Species Information System 2011). Not only are these lakes at the hub of major international shipping routes and surrounded by some of the highest density population centres in North America, but the connectivity among the lakes facilitates the spread of invasive species within them. While the extent of invasions within these lakes may seem unsurprising, the significant ecological and economic consequences resulting from the rapid and widespread establishment of several key invaders have been sobering (Ricciardi and MacIssac 2000).

The zebra mussel, *Dreissena polymorpha* (Pallas, 1771) is native to the Ponto-Caspian region and was first detected in the Great Lakes (in Lake St. Clair) in 1988, believed to have been introduced through ballast water originating from the Baltic Sea (Griffiths et al. 1991). From the time it was first detected, zebra mussels spread rapidly throughout the Great Lakes and within commercially navigable waters (Johnson and Padilla 1996). Being filter feeders which consume plankton, zebra mussels have been shown to cause dramatic abiotic and biotic changes in lake ecosystems where they achieve high abundance (MacIsaac 1996). Specifically, zebra mussels modify the physical environment by increasing water clarity, which increases light penetration in the water column. As a further consequence of increased light penetration, zebra mussels can indirectly facilitate increased growth and depth distribution of aquatic macrophytes (MacIsaac 1996). In addition to changing water clarity, dense beds of zebra mussels can dramatically alter the bottom structure of a lake, as they are quick to colonize any submerged hard surface.

Beyond causing physical changes to their environments, zebra mussels can also disrupt aquatic food webs, primarily by shunting energy from pelagic to benthic pathways (Rennie et al. 2009). One of the more concerning ecological effects of zebra mussel invasions is that their establishment is often associated with a reduction in the abundance of small zooplankton (Pace et al. 1998; Higgins and Vander Zanden 2010) upon which the early life stages of many native fish species depend for food. In one of the better studied examples, zebra mussels in South Bay, Lake Huron have been implicated in the crash of

Diporeia (Bousfield, 1989) populations and the subsequent changes in growth and condition of lake whitefish (*Coregonus clupeaformis* (Mitchill, 1818)), which were historically dependent upon the native species of zooplankton as a major component of their diet (McNickle et al. 2006; Rennie et al. 2009). Not only do zebra mussels reduce phytoplankton biomass and thereby out compete and suppress small zooplankton species via food limitation, but they can also ingest certain small species directly (MacIssac 1996). Few invasive species in the Great Lakes have caused more significant changes in the physical environment and to aquatic food webs than the zebra mussel.

The threat of aquatic invasive species from the Great Lakes spreading throughout other freshwater systems in the region—or even throughout the continent—is a concern (Vander Zanden and Olden 2008). For a number of invasive species, this spread outside the Great Lakes and St. Lawrence Seaway has already begun, with detections documented not only in hydrologically connected waterbodies downstream of the source populations, but also in unconnected waterbodies inland. For example, by 1994 (six years after being introduced into the Great Lakes) adult zebra mussels had already been sighted in eight inland lakes, likely transported through transient recreational boating (Johnson and Padilla 1996). Given the widespread recreational boating and angling use of inland lakes in highly populated regions of Southern Ontario and the Midwest and Northeastern American states, the incidental movement of this species through lake to lake transfer of contaminated boats, gear or bait buckets is suspected to be the most likely vector for its continued spread in these systems (Johnson and Padilla 1996; Litvak and Mandrak 1999).

Given the documented adverse effects of zebra mussel in other systems where it has invaded, particularly within the Great Lakes, there is precedent to fear that the invasion of inland freshwater lakes by this aggressive, aquatic invasive species may cause similarly dramatic changes to the abiotic and biotic characteristics of inland lakes. More specifically, owing to the significant social and economic value of recreational fisheries within many potentially vulnerable inland freshwater lakes in North America, there is concern that zebra mussel invasions could reduce the diversity, abundance and condition of highly prized fish species.

In this study, we focus our interests on inland lakes distributed across the Southern Ontario

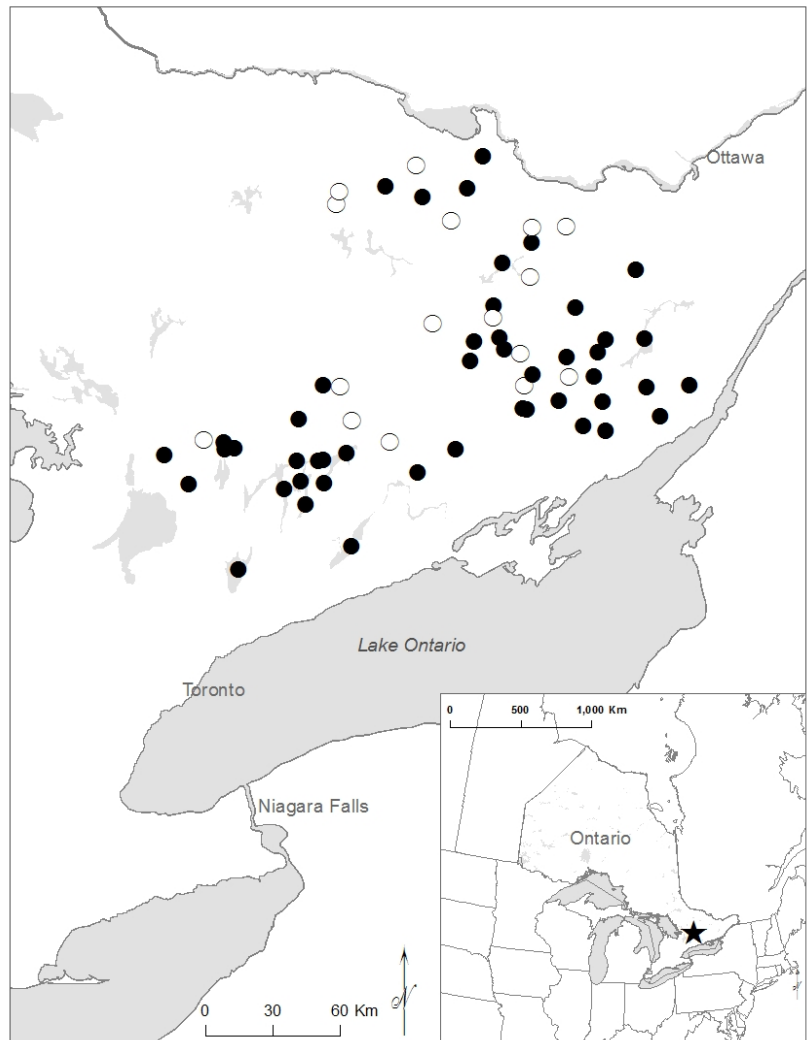


Figure 1. Location of 63 study lakes in Southern Ontario (with inset map of northeastern North America). Lakes in which zebra mussels were detected are labeled with black circles, and lakes without zebra mussels are labeled with open circles. For details see Supplementary material Table S1.

landscape in order to evaluate concerns over potential adverse impacts of this well-known aquatic invasive species on native fish assemblages and targeted game species in these systems. Specifically, we sought to evaluate whether there was a relationship between the presence of zebra mussel in inland lakes and (i) the richness, diversity, evenness, or dominance of existing fish assemblages; (ii) the condition, growth, relative abundance or depth selectivity of select game species including walleye (*Sander vitreus* (Mitchill, 1818)), smallmouth bass (*Micropterus dolomieu* (Lacépède, 1802)), lake trout (*Salvelinus namaycush* (Walbaum, 1792)), and northern pike (*Esox lucius* (Linnaeus, 1758)); and (iii) whether the identity and abundance of large-bodied fishes within a lake could identify

the presence of zebra mussel in lakes where otherwise unknown.

Methods

Lake selection

This study focused on 63 inland lakes within Southern Ontario (Figure 1, Table S1). All study lakes were sampled between 2008–2010 as part of the Ministry of Natural Resources’ (MNR’s) Broad-Scale Monitoring (BsM) Program, and as such had been randomly selected for monitoring from across Ontario (Sandstrom et al. 2011). BsM waterbodies for this study were selected on the basis of available fish attribute and ageing data,

and zooplankton haul analysis data. Lake characteristics (surface area, mean/max depth, volume) for the BsM lakes were derived from the Aquatic Habitat Inventory following the Manual of Instructions for Aquatic Habitat Inventory Surveys (Dodge et al. 1982), and from the Ontario Hydrographic Network spatial dataset using ArcGIS v9.3 (ESRI) to calculate surface area and volume.

To ensure that presence/absence groupings of lakes for zebra mussel were not biased by the inclusion of lakes in which they would not be expected to establish, we further excluded lakes that did not meet criteria to support them. Criteria were based on reported physiological tolerance limits of zebra mussel to critical water chemistry variables (i.e., pH and calcium concentration [Ca^{2+}]) as confirmed by zebra mussel presence/absence data for all lakes. Thus, lakes with pH values less than 6.9 (Claudi et al. 2012), that also had [Ca^{2+}] less than 10.0 mg/L (Claudi and Mackie 1993) were excluded from this study.

Collection of fish assemblage and fish attribute data

All study lakes were sampled following the standardized protocols outlined in the BsM Manual of Instructions (Sandstrom et al. 2011) to assess fish abundance and community composition. The BsM protocol uses a combination of large mesh gillnet (mesh sizes 38, 51, 64, 76, 89, 102, 114, and 127 mm, 24.8 m long, 1.8 m high; North American gillnets (Bonar et al. 2009)) and small mesh gillnet (mesh sizes 13, 19, 25, 32, 38 mm, 12.5 m long, 1.8 m high) monofilament gillnets randomly set among different depth strata (1–3, 3–6, 6–12, 12–20, 20–35, 35–50, 50–75 and 75 + m) equally distributed throughout the waterbody. Small mesh nets were restricted to depths less than 20 m, and owing to frequent net saturation, were more qualitative in nature. The location, minimum number of nets set and the allocation of netting effort across depth strata were determined on the basis of lake surface area and maximum depth, as dictated by the BsM protocol. Surveys were conducted seasonally, and limited to the four to six week period when surface water temperatures exceeded 18°C. The period of sampling for both large and small mesh nets spanned the hours of 13:00–17:00 (set) and 8:00–11:00 (lift), such that set duration was between 16 and 22 hours.

All fish captured in both large and small mesh nets were identified, counted and measured for total length. In addition, sampling requirements

for large mesh efforts include mandatory detailed lethal sampling of the first 20 lake trout, walleye, and northern pike and the first 10 smallmouth bass caught in each lake survey. Detailed sampling for these sacrificed key game species included total length (nearest mm), round weight (nearest 10 g), and ageing structure (i.e., otolith for walleye and lake trout, spiny ray for smallmouth bass and cleithrum for northern pike). All fish were aged at MNR's ageing laboratory in Dryden and assigned a confidence level in interpretation (on a scale of 1–10). Fish age data for which the confidence level of age estimation was four or less were excluded from subsequent growth analyses.

Collection of zebra mussel presence/absence data

Zooplankton hauls were conducted on all study lakes using 250 μm mesh zooplankton nets, a target of five vertical hauls per lake—including two hauls in the middle of lake, one on the windward side along the fetch, and two access points. Zooplankton samples were preserved in 95% ethanol until laboratory analysis. The presence/absence of dreissenid veligers was assessed by examining 1 mL of the sample placed in a Sedgwick-rafter cell under polarized light (Hosler 2011). To verify veliger identification, specimens were measured and shapes assessed based on descriptions in Ackerman et al. (1994). If no veligers were found in the first 1 mL of sample, either a sugar separation was conducted (Schaner 1990), or the entire sample was scanned by filtering through a 50 μm plankton mesh, followed by examination under polarized light. For all subsequent analyses, zebra mussels were considered to be present within a lake if at least one veliger was detected, and absent if no veligers were observed or identified from the samples collected.

Collection and analysis of water quality data

Water samples were collected in polyethylene terephthalate (PET) bottles from all study lakes in the spring preceding summer index netting. Samples were analyzed for a suite of water quality and water chemistry variables (including pH, [Ca^{2+}] (mg/L), alkalinity (mg/L CaCO_3), conductivity ($\mu\text{S}/\text{cm}/\text{s}$)) at the Ministry of the Environment's Dorset Environmental Science Centre, following standardized protocols outlined in Ingram et al. (2006). Secchi depth (m) was also recorded at the time of sample collection.

Quantifying lake access and population density information

Aerial surveys of a number of BsM lakes were conducted to assess angler effort and recreational activity levels within the lakes for both weekdays and weekends in the summer months. Among the 63 lakes selected for this study, 54 had summer aerial effort count data. As an indicator of summer lake use, we combined the total boat count of all boat types for both weekday and weekend surveys and divided this value by the total number of aerial survey days to calculate the Mean Number of Boats Day⁻¹ for each surveyed lake.

Human population density estimates in the vicinity of each study lake was determined with Statistics Canada 2001 Census Data using ArcGIS v9.3 (ESRI). The sum of the total population within each census township boundary was determined within a 100 km radius of the centroid of each study lake. A 100 km buffer distance was chosen based on the distance many Ontario anglers are willing to travel in one day to use lakes within the study area.

To quantify an estimate of human accessibility to the study lakes, the sum of the distance (m) of primary road network within a 1 km buffer of the shoreline of each study lake was determined using ArcGIS.

Calculation of fish biodiversity metrics

All biodiversity metrics were calculated based on catch data from both large and small mesh net sets from each lake. Species richness was calculated as the total number of fish species caught each lake. Shannon's Diversity Index (H) was calculated for each lake as follows:

$$H = -\sum_{i=1}^s p_i \ln p_i$$

Where s is the number of species in the lake and p_i is the proportion of total sample represented by the i^{th} species. Simpson's Diversity Index (DI) was similarly calculated for each lake according to the equation:

$$DI = 1 - \sum_{i=1}^s (p_i)^2$$

Evenness (J) was calculated for each lake based upon Shannon's Diversity Index (H) according to the following:

$$J = H / \ln(s)$$

Finally, dominance (D_3), representing the total proportion of individual fish represented by the three most dominant species in the lake was calculated as:

$$D_3 = p_1 + p_2 + p_3$$

where p_1 , p_2 and p_3 are the relative proportions of the total number of fish in the lake make up by the first, second and third-most abundant species, respectively.

Statistical analyses

Since the study lakes were, by design, all randomly selected and distributed across the landscape within a geographically constrained area, we were able to group lakes according to the presence or absence of zebra mussel and assess differences in various endpoints within and between these groups, thereby increasing our statistical power to detect differences.

To test for differences in lakes beyond zebra mussel presence/absence that could potentially confound analyses of fish condition, growth, and relative abundance, we compared various lake attributes including lake morphometry and water chemistry between lakes with and without zebra mussels. To do this, we first ran a principal component analysis (PCA) on the following normalized and standardized variables: lake surface area, mean and maximum depth, volume, pH, alkalinity, conductivity, $[Ca^{2+}]$ and Secchi depth. We then tested for differences between lakes with and without zebra mussels by performing student's t -tests on the first and second principle component scores for each lake. We used the same approach to test for differences in indicators of lake access (i.e., summer lake use, local human population density estimates, and lake accessibility) between lakes with or without zebra mussels. Finally, to test for potential spatial differences between lakes with or without zebra mussels, principal coordinate analysis was run on the latitudinal and longitudinal coordinates of each lake, to yield distance coordinates along two dimensions for each lake. These were then compared between lakes with and without zebra mussels by conducting t -tests.

To assess the effect of zebra mussel presence/absence within a lake on fish biodiversity metrics, we conducted t -tests to compare the mean values of species richness, H , DI , J and D_3 between lakes with and without this invasive species. To control for possible type I errors with multiple tests, we adjusted significance levels

using the Bonferroni correction (i.e., $\alpha = (0.05/5 \text{ tests}) = 0.01$; Quinn and Keough 2002).

Analysis of Covariance (ANCOVA) was used to test for differences in the condition of each of the four select species (walleye, smallmouth bass, lake trout and northern pike) between lakes with and without zebra mussels. Total length was used as the covariate and round weight as the dependent variable. The interaction between zebra mussel presence/absence and total length was incorporated into the model to test for differences in slope (Pope and Kruse 2007). Fish growth was similarly assessed for each species using an ANCOVA, with total length as the dependent variable and age as a covariate. Tests were run to assess differences in growth between lakes with and without zebra mussel for each fish species.

As a measure of relative abundance, catch per unit effort (CUE) was calculated as the total number of individual fish caught within a given net set (effort). For the purposes of this study, catch per unit effort data was used from only the large mesh nets as an index of relative abundance. Furthermore, for each of the four game fish species of interest, CUE data was assessed only for lakes where at least one individual of that species was caught. An ANOVA was conducted to assess difference in relative abundance grouped by presence or absence of zebra mussel within a waterbody. However, because catch count data can often include many zeros and are not normally distributed, the assumptions of an ANOVA were not met therefore a Poisson regression was conducted. Violations to the assumption of a Poisson regression (i.e., variance was over dispersed) resulted in the use of a negative binomial regression. Consequently, to test for differences in the abundance (CUE) of each game fish in the presence and absence of zebra mussels, we used a generalized linear model with a negative binomial function to fit the data. Similarly, to assess whether the depth selectivity of the four fish species of interest differed among lakes with or without the presence of zebra mussels, we examined differences in the CUE of each species within discrete depth strata using a negative binomial generalized linear model.

Finally, we used discriminant function analysis (DFA) to assess if fish catch data (i.e., species composition and relative abundance) could be used to predict the presence or absence of zebra mussel in inland lakes in Ontario, if previously undetected. For this analysis, we included the CUE of all fish species caught in large mesh nets in each of the study lakes as predictor variables,

and classified lakes based on zebra mussel presence or absence (i.e., grouping variable). We excluded any fish species for which total catch in all lakes was less than 10 individuals.

Where dictated by the assumptions of the specific test, all data (or residuals) were tested for normality using the Shapiro Wilk test ($\alpha = 0.05$) and for heteroskedasticity using the Cook-Weisberg test ($\alpha = 0.05$). Where data failed to meet these assumptions, they were log or square-root transformed. In addition, all normalized data were standardized prior to running PCA. No data transformations were conducted for the DFA or negative binomial regressions. All analyses were run using STATA 12.0 (StataCorp 2011; College Station, TX).

Results

Of the 63 lakes examined in this study, zebra mussels were detected in 47 lakes while none were detected in the remaining 16 lakes (Figure 1). A total of 1032 walleye, 1438 smallmouth bass, 192 lake trout, and 527 northern pike were caught in large mesh nets in the study lakes, and fish metric data was available for 716, 796, 205, and 332 individuals of these species, respectively.

Lake attributes

Principal component analysis of lake morphometry and lake chemistry variables resulted in three principal components with eigenvalues greater than one, explaining 88% of the variation in the data. The first principal component explained 47% of the variation, and was strongly correlated with $[Ca^{2+}]$, conductivity, alkalinity, and pH. The second principal component explained 28% of the variation and was highly correlated with lake volume, surface area, maximum depth and mean depth. There was a significant difference in the first principal component scores (i.e., lake water chemistry parameters; means presented in Table 1a) between lakes with and without zebra mussels ($F_{1,46} = 6.73$; $p = 0.013$), but no difference in the scores for the second principal component (i.e., lake morphometry metrics; means presented in Table 1a) ($F_{1,46} = 0.00$; $p = 0.998$).

Principal component analysis of lake access and human population density estimates resulted in one principal component with an eigenvalue greater than one, which explained 62% of the variation in the data, and was strongly correlated with all three indicators of lake access. There was a significant difference in the first principal component scores between lakes with and without

Table 1a. Means (with standard deviation in brackets) of raw lake morphometry and water chemistry data for study lakes with (Y) and without (N) zebra mussels.

Zebra Mussel	Surface Area (ha)	Mean Depth (m)	Max Depth (m)	Volume ($\times 10^8$ L)	pH	Ca ²⁺ (mg/L)	Alkalinity (mg/L CaCO ₃)	Conductivity (μ S/cm/s)	Secchi depth (m)
N	911.4 (888.8)	8.74 (5.83)	29.8 (17.3)	1.36 (1.93)	7.48 (0.41)	18.38 (11.73)	55.42 (36.36)	130.4 (71.7)	4.58 (1.46)
Y	1519.6 (2181.4)	7.26 (7.15)	26.7 (27.3)	1.29 (2.10)	7.76 (0.35)	26.87 (12.94)	73.75 (39.41)	184.7 (93.3)	4.34 (2.09)

Table 1b. Means (with standard deviation in brackets) of derived lake access metrics for study lakes with (Y) and without (N) zebra mussels.

Zebra Mussel	Summer Lake Use (mean # boats day ⁻¹)	Local Population Density (population estimate within 100 km radius of lake centroid)	Lake Accessibility (total distance (m) of primary road network within 1 km of shoreline)
N	6.03 (5.16)	560,858 (493,792)	3,454 (5,410)
Y	13.98 (20.36)	1,167,868 (1,216,630)	13,863 (14,052)

Table 2. Summary statistics of t-tests comparing mean biodiversity metrics for fish assemblages between lakes with (Y) and without (N) zebra mussels. Significant results (Bonferroni-adjusted p value; $p < 0.01$) are in bold.

Biodiversity Metric	Zebra Mussel	Mean (SD)	F statistic _{d.f.}	p value
<i>Species Richness</i>	N	11.94 (2.77)	$F_{1,61} = 7.48$	0.008
	Y	14.38 (3.19)		
<i>Shannon Diversity Index (H)</i>	N	1.51 (0.44)	$F_{1,61} = 0.57$	0.452
	Y	1.60 (0.38)		
<i>Simpson's Diversity Index (DI)</i>	N	0.65 (0.16)	$F_{1,61} = 0.09$	0.760
	Y	0.66 (0.15)		
<i>Evenness (J)</i>	N	0.61 (0.15)	$F_{1,61} = 0.01$	0.924
	Y	0.61 (0.14)		
<i>Dominance (D₃)</i>	N	0.79 (0.12)	$F_{1,61} = 0.74$	0.393
	Y	0.76 (0.11)		

zebra mussels ($F_{1,52} = 11.32$; $p = 0.0014$), where lakes with zebra mussels present were characterized as having greater human population and road network densities in their vicinities, and more boating activity than study lakes with no zebra mussels (means presented in Table 1b).

The proportion of variation explained by the first dimension derived from principal coordinate analysis of lake geographical coordinates was 84%, while the second dimension explained 16% of the variation. The first dimension was correlated with longitude, and did not differ significantly between lakes with or without zebra mussels (t -test: $F_{1,61} = 0.11$; $p = 0.743$). The second dimension was correlated with latitude, and did significantly vary between the two lake groupings (t -test: $F_{1,61} = 10.45$; $p = 0.002$). Lakes with zebra mussels

were located further south on average (mean latitude (standard deviation): 44.74700 (0.35198)) than lakes with no zebra mussels (mean latitude (standard deviation): 45.07981 (0.38549)).

Fish biodiversity metrics

Species richness (of fish susceptible to small and large mesh gill nets) was significantly greater in lakes where zebra mussel were detected than in lakes where zebra mussels were absent. There were no detectable differences in species diversity, evenness or dominance between lakes with and without zebra mussel (Table 2). However, retrospective power analyses indicate that the ability to detect true differences in these metrics between lake types was low.

Condition and growth of game fish

Walleye

There were significant differences in both the condition and growth of walleye among study lakes with and without presence of zebra mussels. In lakes with zebra mussels, the interaction (i.e., slope) between length and weight for walleye was greater than in lakes with no zebra mussels (Table 3). That is, as walleye in lakes with zebra mussels increase in length, they put on weight at a greater rate than in lakes without this invasive species. In contrast, while the slopes did not differ between the two types of lake for the growth metric, at any given age, individual walleye in lakes with zebra mussels were consistently smaller (i.e., smaller intercept) compared to individuals from lakes without zebra mussels (Table 3).

Smallmouth bass

Smallmouth bass condition and growth significantly varied among waterbodies with and without zebra mussels (Table 3). Similarly to walleye, the interaction (i.e., slope) between length and weight for smallmouth bass was greater in lakes with zebra mussel than in lakes with no zebra mussels (Table 3), indicating that bass are in better condition as larger individuals in lakes where zebra mussel are present. However, growth rates of smallmouth bass were greater (i.e., greater slope of length vs. age regression line) in study lakes where zebra mussel were not detected.

Lake trout

There was no significant difference in the condition of lake trout in waterbodies with or without zebra mussel (Table 3). However, there was a significant difference in lake trout growth, with the interaction (i.e., slope) between age and length being greater (and the intercept smaller) in lakes without the invasive species. That is, while they enter the population at smaller sizes, lake trout exhibit faster growth rates, achieving larger sizes at older ages in uninvaded lakes (Table 3).

Northern pike

There was no significant difference in the condition of northern pike in the study lakes with or without zebra mussels (Table 3). However, there was a significant difference in the growth rates of northern pike, as measured using length at

age, between the two groups of lakes. As with lake trout, the interaction (i.e., slope) between age and length was greater (and the intercept smaller) in lakes without zebra mussel meaning that individuals enter the population at smaller sizes, but grow faster and achieve larger sizes at ages than in lakes with zebra mussel (Table 3).

Relative abundance and depth selectivity of game fish

Relative abundance of walleye and lake trout significantly varied in the study lakes with and without zebra mussel (Table 4). While the relative abundance of walleye was significantly greater in lakes without zebra mussel, the relative abundance of lake trout was significantly greater in lakes with zebra mussel. There was no significant difference in the mean CUE of either smallmouth bass or northern pike among lakes with and without zebra mussel (Table 4). We found depth selectivity did not differ in of any of the four select species among lakes with or without zebra mussels (Table 5).

Predicting zebra mussel presence/absence based on large-bodied fish assemblages

Discriminant function analysis demonstrated that lakes could be classified as supporting zebra mussel or not with 81% accuracy (i.e., 51 of 63 lakes classified correctly) based on species composition and relative abundance sampled in the large mesh nets (Table 6). This confirms that presence/absence of zebra mussel within a waterbody could be predicted if previously unconfirmed based upon community index netting alone.

Discussion

Benefiting from a comprehensive and multivariate dataset collected following standardized protocols through the BsM program for a large number of lakes randomly distributed across the Southern Ontario landscape, this study represents one of the first to empirically examine the potential consequences of zebra mussel invasions to fisheries in inland lakes. By focusing on lakes within a geographically confined region that were largely similar with respect to lake morphometry, but which differed with respect to presence or absence of zebra mussels, we were able to examine potential correlations between this well-known aquatic invasive species and the biodiversity of fish assemblages, and the size and abundance of important game fish species in these systems.

Table 3. Summary of ANCOVA models for differences in derived condition (weight at length) and growth (length at age) metrics for walleye, smallmouth bass, lake trout and northern pike between lakes with (Y) and without (N) zebra mussels. Significant differences ($p < 0.05$) in slopes and/or intercepts of the regression lines are bold.

Fish species	Fish metric		Zebra Mussel	Value	F statistic df	p value
Walleye (<i>Sander vitreus</i> , Mitchill, 1818)	Condition	Slope	N	3.19	$F_{1,703} = 3.92$	0.048
			Y	3.26		
	Intercept	N	5.56	$F_{1,703} = 3.84$	0.051	
		Y	-5.73			
	Growth	Slope	N	3.57	$F_{1,710} = 0.03$	0.861
			Y	3.61		
Intercept	N	13.20	$F_{1,711} = 22.40$	< 0.001		
	Y	12.55				
Smallmouth Bass (<i>Micropterus dolomieu</i> , Lacepede, 1802)	Condition	Slope	N	3.32	$F_{1,791} = 6.03$	0.014
			Y	3.49		
	Intercept	N	-	$F_{1,791} = 10.15$	0.002	
		Y	35.87 - 39.62			
	Growth	Slope	N	0.54	$F_{1,791} = 6.12$	0.014
			Y	0.50		
Intercept	N	2.11	$F_{1,791} = 14.79$	< 0.001		
	Y	2.15				
Lake Trout (<i>Salvelinus namaycush</i> , Walbaum, 1792)	Condition	Slope	N	3.24	$F_{1,198} = 1.25$	0.265
			Y	3.30		
	Intercept	N	-5.71	$F_{1,199} = 2.60$	0.108	
		Y	-5.87			
	Growth	Slope	N	0.52	$F_{1,201} = 5.43$	0.021
			Y	0.40		
Intercept	N	2.16	$F_{1,201} = 7.44$	0.007		
	Y	2.28				
Northern Pike (<i>Esox lucius</i> , Linnaeus, 1758)	Condition	Slope	N	3.04	$F_{1,324} = 0.00$	0.989
			Y	3.04		
	Intercept	N	-5.35	$F_{1,325} = 0.66$	0.417	
		Y	-5.35			
	Growth	Slope	N	0.41	$F_{1,328} = 12.60$	< 0.001
			Y	0.28		
Intercept	N	2.52	$F_{1,328} = 8.72$	0.003		
	Y	2.59				

Table 4. Catch per unit effort (CUE) of target game fish species in large mesh nets from lakes with (Y) and without (N) zebra mussels, and results of negative binomial generalized linear model to test for differences between lake types. Significant differences ($p < 0.05$) in bold.

Fish species	Zebra Mussel	Mean CUE (SE)	Z	p value	df
Walleye (<i>Sander vitreus</i>)	N	2.41 (0.34)	-4.04	<0.001	689
	Y	1.26 (0.12)			
Smallmouth Bass (<i>Micropterus dolomieu</i>)	N	1.66 (0.22)	-0.07	0.948	870
	Y	1.65 (0.15)			
Lake Trout (<i>Salvelinus namaycush</i>)	N	0.48 (0.10)	2.23	0.025	282
	Y	0.82 (0.11)			
Northern Pike (<i>Esox Lucius</i>)	N	0.93 (0.13)	0.50	0.617	527
	Y	1.02 (0.09)			

Table 5. Test statistics of negative binomial generalized linear model to assess differences in the depth selectivity of target game fish species in large mesh nets from lakes with and without zebra mussels present. Significant differences ($p < 0.05$) in bold.

Fish species	Z	p value	df
Walleye	-0.15	0.880	667
Smallmouth Bass	1.77	0.077	849
Lake Trout	-1.35	0.176	260
Northern Pike	-0.13	0.893	497

Table 6. Classification rates of discriminant function analysis on fish assemblage composition in each lake based on catch counts and identity of fish species caught in large mesh gill nets. Accuracy included in parentheses.

Actual	Classified	
	Present	Absent
Present	40(85.1%)	7(14.9%)
Absent	5(31.3%)	11(68.8%)

Key findings of this study suggest that the condition, growth, and relative abundance of some of the most highly valued game fish varied among waterbodies with and without zebra mussels, and that the species composition (i.e., identity and relative abundance) of assemblages of large-bodied, active fishes within a lake can indicate zebra mussel presence/absence with a high degree of certainty.

Fish biodiversity metrics

The relationship between invasive species and the diversity, richness and evenness of a recipient community is complex, and can be either correlational or causal (Didham et al. 2005). On the one hand, there are numerous examples within the invasion biology literature documenting reductions in biodiversity and changes in community structure as a result of invasive species introductions (Vitousek et al. 1996; Wilcove et al. 1998; Ricciardi 2004). On the other hand, it is often held that communities with high species richness and diversity are more stable and resilient to disturbances and invasions than species poor communities (reviewed in Stachowicz et al. 1999; Fridley et al. 2007).

Considering both scenarios, we expected to see lower species richness, diversity, and evenness in fish assemblages in invaded lakes (i.e., if zebra mussels result in biodiversity losses in these systems), and greater indices of diversity and

evenness in un-invaded lakes (i.e., if highly diverse communities are more resilient against invasions). Interestingly, we detected greater species richness (i.e., total number of fish species caught in large and small-mesh gillnets) in lakes with zebra mussels present. A number of factors are correlated with fish species richness in freshwater lakes including lake size and habitat complexity (Matuszek and Beggs 1988), connectivity with other waterbodies (Meeuwig et al. 2008), latitude (Stevens 1989), and pH—especially for lakes with $\text{pH} < 6.0$ (Matuszek and Beggs 2011). Although none of the study lakes had pH values less than 6.9, lakes with zebra mussels present had higher pH values than lakes without (Table 1). Furthermore, there were latitudinal differences between lakes with and without zebra mussels, with invaded lakes being located further south, on average, than uninvaded lakes. Thus, it is possible that differences in lake chemistry characteristics and/or latitudinal effects have contributed to the observed differences in species richness.

Contrary to our expectations, we did not detect any significant differences in the diversity, evenness or dominance of fish assemblages between lakes with and without zebra mussels it may be that we were unable to detect a true effect of zebra mussel on fish assemblage biodiversity owing to several limitations of the study, including the fact that zebra mussel abundance and time since introduction were not quantified here. Because potential effects of an invasive species on native fish assemblages would likely be related to the establishment phase and abundance of the invader, this information may be required to better elucidate effects on fish assemblages. Consequently, within-lake comparisons of fish assemblage biodiversity metrics before and after invasion, or between lakes that differ with respect to time since invasion may be a more appropriate means of detecting effects. However, fish assemblage surveys conducted before and after zebra mussel invasion in the Huron River revealed that there were no significant changes in either fish species richness or diversity (Birkett 2011). As one possible explanation for this finding, it has been suggested that invasions in aquatic ecosystems may be less mediated by the composition or diversity of the recipient community than they are by dispersal opportunities and favourable abiotic conditions (Vitousek et al. 1997). That is, highly diverse communities, or low diversity communities may be equally vulnerable to invasion in aquatic ecosystems.

Although we did not detect changes in species diversity, evenness or dominance between invaded and un-invaded lakes, perhaps the most intriguing finding of this study was that lakes with and without zebra mussels could be categorized based on the structure of assemblages in the catch. Based on the identity and abundance of the fish species caught in large mesh index nets, we were able to predict the presence or absence of zebra mussels within these waterbodies with a high level of certainty. This indicates that there is an effect of zebra mussels on the structure of large-bodied fish assemblages in the study lakes, even though this was not apparent using conventional diversity indices. Interestingly, while no change in fish species richness or diversity was found in the Huron River after zebra mussel invasion, several significant changes in fish community composition were detected (Birkett 2011). Therefore, in order to detect changes in community structure, in certain cases it may be necessary to examine the identity or functional guild of fish species within the community.

Discriminant function models such as the one derived here to classify lakes as having zebra mussels present or absent based on the catch in large mesh index nets could be used to identify their presence in similar waterbodies where its status is otherwise unknown. Depending on the time required since introduction for zebra mussels to affect changes to fish assemblages, such models may or may not be useful for early detection. It would be a valuable exercise to test the model's ability to predict zebra mussel presence/absence in other lakes where standardized index netting and zooplankton hauls have been conducted, in addition to lakes where zebra mussel presence/absence was unknown but confirmed with field studies.

Condition and growth of game fish

Condition and growth of both walleye and smallmouth bass significantly varied among lakes with and without zebra mussel. Furthermore, although we found differences in growth of both lake trout and northern pike, we did not detect any difference in the condition of either of the latter two game fish species between lakes with and without zebra mussels.

For both walleye and smallmouth bass, the interaction (i.e., slope) between weight (condition) and length was significantly greater, and the intercept smaller for individuals deriving from lakes with zebra mussels present than for

individuals caught in lakes without zebra mussels. That is, individual fish gain weight at faster rates as they increase in length in lakes with zebra mussels. Thus, for both species, fish entering the population have reduced weights, and smaller individuals have lower body condition in lakes with zebra mussels than without. However, the opposite is true of larger individuals in the populations, which are heavier and in better condition in lakes with zebra mussels present than in lakes where they are absent. This type of trend in fish condition data is suggestive of possible resource limitations for different size categories between populations (Pope and Kruse 2007). There was no effect of zebra mussel presence/absence on the condition of either lake trout or northern pike.

While there may be other influencing factors, the results of these analyses could suggest that zebra mussels may have a negative relationship on the feeding ecology of larval or young of the year walleye and smallmouth bass. For both species, larval and age-0 life stages feed primarily on zooplankton (Scott and Crossman 1973; Bozek et al. 2011). Because zebra mussels have been documented to cause significant reductions in zooplankton in lakes where they have become established (Higgins and Vander Zanden 2010), it is possible that reduced early life stage condition or growth of these species could be the result of food limitation caused by zebra mussels. In addition, dense beds of zebra mussels can also reduce the foraging success of fish for soft-sediment zoobenthos (Beekey et al. 2004), which could further limit prey availability for fingerling walleye that feed on these organisms during critical growth stages (Kerr and Grant 2000). The finding that larger individuals displayed improved condition in lakes with zebra mussels relative to smaller individuals may reflect ontogenetic diet shifts that occur in both species after the first year. That is, larger juvenile and adult smallmouth bass prey primarily on crayfish (Bevelhimer 1996) while juvenile and adult walleye are mostly piscivorous (Frey et al. 2003). Consequently, larger individuals of both species would escape any potential food limitation effects of zebra mussels on condition or growth.

Existing assessments of the impact of zebra mussel invasions on the condition, growth, and diet of age-0 individuals of other game species have yielded inconsistent findings. Trometer and Busch (1999) reported no changes in the growth of age-0 yellow perch (*Perca flavescens* (Mitchill, 1814)), walleye, or freshwater drum

(*Aplodinotus grunniens* (Rafinesque, 1819)) after zebra mussel invasion in Lake Erie. However, mean weight, length, condition, and growth rates of age-0 rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) in the Muskegon River were all found to decrease, coincident with a significant change in diet, after zebra mussel invasion (Guiliano 2011). Although differences in the growth and condition of walleye and smallmouth bass were observed here, the results of this study cannot confirm zebra mussel presence/absence as the causative mechanism driving these differences. However, given the correlations between zebra mussel presence and fish condition noted here, the potential influence of zebra mussels on the feeding ecology of early life stages of game fish is certainly an area warranting further study.

For important game species, factors influencing individual growth rates could have significant implications for recreational fisheries, since there is greater value to fish that achieve bigger sizes as adults. In addition, there may also be implications for population growth metrics, since increased growth rates and larger sizes of reproductive individuals are critical determinants of fecundity and ultimately population growth rate (reviewed in Wootton 1998 and Jenkins et al. 1999). ANCOVA models for walleye revealed that while the slopes of the growth (length at age) lines were similar for lakes with and without zebra mussel, the intercept was significant smaller in lakes with zebra mussel. This indicates that individuals in zebra mussel lakes are consistently smaller across all age classes than in lakes with no zebra mussels. For smallmouth bass, lake trout, and northern pike there was a significant effect of zebra mussel presence on the slope of the growth curve. In the case of all three species, individuals displayed faster growth rates in lakes without zebra mussels than those in lakes with zebra mussels.

Although significant correlations with zebra mussel presence and game fish growth were noted, these findings cannot confirm whether zebra mussel invasions in the study lakes are the cause of observed reductions in growth rates. Clearly, even though lakes were broadly comparable with respect to morphometry and lake access metrics, they differed with respect to several water chemistry parameters as well as in their spatial location (i.e., latitude). These and other potential underlying differences between the lakes (including the presence of other invasive species) could be driving variation in growth rates among these populations.

Relative abundance

Invasive species are often feared to have detrimental impacts on native species of economic importance, yet this may not always be the case for all species in invaded systems. Here, we found that the presence of zebra mussels had no correlation with the relative abundance of smallmouth bass or northern pike based on CUE in large-mesh gillnets. Conversely, lake trout were found in greater abundance and walleye in lower abundance in lakes with zebra mussels present than in lakes without.

Given the fact that zebra mussel fouling of spawning shoals has been shown to reduce lake trout spawning success where they co-exist in the Great Lakes (Marsden and Chotkowski 2001), we might have predicted lower lake trout abundance in lakes where zebra mussels have colonized. Although our study results demonstrate the opposite, differences in the character and biological communities of lake trout lakes may have confounding effects on the results of the abundance analyses for this species, and renders interpretation of these results difficult. For example, being a coldwater fish, lake trout generally inhabit deeper, oligotrophic lakes that support different fish communities (Kerr and Grant 2000) than the lakes typically inhabited by the other three species of game fish assessed in this study. It is possible that the abundance of lake trout is not correlated at all to the presence of zebra mussels and that there are other factors contributing to the greater abundance in these lakes.

Within the province of Ontario, walleye the most sought after game fish species, supporting the most economically valuable recreational fishery in the province (Fisheries and Oceans Canada 2005; Ontario Ministry of Natural Resources 2005). As a result, our detection of a significant negative relationship of zebra mussel presence with the relative abundance of this species in inland lakes in Southern Ontario is perhaps the most critical finding of the study. However, it was not necessarily surprising, as walleye CUE in Lake St. Clair declined by nearly 50% following the establishment of zebra mussels (Ontario Ministry of Natural Resources 1995; cited in MacIssac 1996), with similar declines documented in eastern Lake Ontario (Hoyle et al. 2008).

Previous studies have found no significant impacts of zebra mussel infestation of spawning shoals on the spawning success of walleye (Leach 1993; Fitzsimons et al. 1995) which suggests that

they do not affect walleye abundance via impacts on spawning habitat quality or quantity. Furthermore, while lake trout were in greater abundance in lakes with zebra mussels, there has yet to be consistent evidence of significant competitive interactions between this species and walleye (Kerr and Grant 2000). Although potential competitive or predatory interactions between other fish species and walleye in the study lakes cannot be entirely ruled out as a factor contributing to differences in walleye abundance between lakes, our finding of lower walleye abundance in lakes with zebra mussels could also be attributed to possible direct and indirect food limitation mediated by the invasive species.

Not only could the presence of zebra mussels limit the availability of zooplankton prey available to larval walleye as discussed above, but there is evidence to suggest that they may limit prey availability for other life stages of this species as well. Colonies of zebra mussels increase the structural complexity of benthic habitats in freshwater systems where they have been introduced (Beekey et al. 2004) which can provide refugia from predation for various benthic invertebrates (Cobb and Watzin 2002) including many soft-sediment zoobenthos (e.g., Ephemeroptera and Diptera; Beekey et al. 2004). The latter are particularly important dietary components of fingerling and juvenile walleye (Scott and Crossman 1973; Ritchie and Colby 1988; Kerr and Grant 2000). As a result, the presence of zebra mussels could adversely affect the foraging success of walleye during these critical growth periods, just as it has been shown to do for other common benthic foraging life stages or species of fish (Beekey et al. 2004).

While we have proposed several food-limitation mechanisms by which the zebra mussel could reduce the relative abundance of this species, the presence of zebra mussel cannot be confirmed as the cause of observed decreases in walleye abundance. For example, it may be the case that lakes with zebra mussels present also experience greater fishing pressure targeted at walleye. Our analyses did reveal a difference in human access metrics between lakes with and without zebra mussel, with zebra mussel lakes having greater population density and more road networks in their vicinities than lakes without zebra mussels. However, while these factors may certainly influence the likelihood of zebra mussel presence within a lake, they are not necessarily indicative of angler effort. Unfortunately, the relationships between angling activities in lakes, invasive species

presence/ absence, and the abundance of preferred game species are closely interrelated, making it difficult to establish causal and correlated factors in observed changes in abundance or fish community structure.

Depth selectivity

Based on the analysis of catch data from the depth-stratified BsM netting design, there was no evidence of an effect of zebra mussel presence on the depth selectivity of smallmouth bass, lake trout, northern pike and walleye. We might have expected to see changes in the depth selectivity of walleye since this species prefers moderate to low light conditions (Lester et al. 2004), and there have been demonstrated effects of zebra mussels on water clarity (Zhu et al. 2006). Thus, we would have predicted that if zebra mussels increased water clarity, walleye in lakes with this species would have to move to deeper waters to find optimal optical habitat. For example, since the zebra mussel invasion in Lake St. Clair, walleye are now primarily found in the shipping channel, which is the deepest and most turbid part of the lake (MacIsaac 1996). However, we did not see any associated changes in water clarity with the presence of zebra mussels as measured by Secchi depth (Table 1), implying that there may have been no physical drivers to induce a change in walleye depth selectivity.

Conclusion

Invasive species are now a widespread and significant component of many freshwater ecosystems, and several of these have the propensity to cause changes to food webs, community structure and ecosystem function in receiving systems (Ricciardi and MacIsaac 2000). Among these species is the zebra mussel, whose adverse effects in systems where it has invaded are well-documented, particularly within the Great Lakes. Here we examined the effect of zebra mussels on the biodiversity, growth, condition and abundance of active, large-bodied fish species to assess whether this well-known invader is causing similarly significant changes in inland freshwater lakes in Ontario.

Our study indicates that while the establishment of species such as the zebra mussel may be associated with adverse effects on the growth, condition and abundance of certain fish species, they may also directly or indirectly benefit, or have no effect on other fish species. By

disproportionately or differentially affecting fish species or life stages, the presence of zebra mussels could thereby affect the structure or biodiversity of fish assemblages. Although we did not detect any changes in fish assemblage structure as indicated by generic metrics of species diversity, evenness, or dominance we did discover that the lakes in our study can be categorized as having zebra mussels present or absent with a relatively high degree of certainty based on the identity and respective relative abundance of individual species of large-bodied fish within a lake community, corroborating the prediction that zebra mussels can affect fish assemblage structure.

While correlations between zebra mussel presence and the identity, abundance, growth, and condition of certain fish species were found, the results of this study indicate that the potential consequences of this invasive species to fisheries in inland lakes may be less dramatic than those reported within the Great Lakes. However, efforts to better elucidate the potential causal role that zebra mussel invasions could be playing in the structuring of large-bodied fish communities within inland lakes are warranted. To this end, it is hoped that the inclusion of a temporal component in further analyses of these lakes will enhance our understanding of the potential consequences of this invasive species outside the context of the Great Lakes.

Acknowledgements

We would like to thank Mike Rawson for his help querying the Southern Region Broad Scale Fish Community Monitoring (BsM) Program database. We thank Mike Rawson and Jeff Brinsmead, as well as two anonymous referees for their reviews and constructive criticism on previous versions of this manuscript. We could not have completed this study without having had access to the vast and comprehensive amount of data collected during the BsM program, funded by and implemented through the Science and Information Resources Division of the Ontario Ministry of Natural Resources. Funding for this project was provided by the Science and Information Resources Division of the Ontario Ministry of Natural Resources, and the Invasive Species Centre.

References

- Aldridge DC, Elliott P, Moggridge DG (2004) The recent and rapid spread of the zebra mussel (*Dreissena polymorpha*). *Biological Conservation* 119: 253–261, <http://dx.doi.org/10.1016/j.biocon.2003.11.008>
- Ackerman JD, Sim B, Nichols SJ, Claudi R (1994) A review of the early life history of zebra mussels (*Dreissena polymorpha*): Comparisons with marine bivalves. *Canadian Journal of Zoology* 72: 1169–1179, <http://dx.doi.org/10.1139/z94-157>
- Beekey MA, McCabe DJ, Marsden JE (2004) Zebra mussels affect benthic predator foraging success and habitat choice on soft sediments. *Oecologia* 141: 164–170, <http://dx.doi.org/10.1007/s00442-004-1632-1>
- Bevelhimer MS (1996) Relative importance of temperature, food, and physical structure to habitat choice by smallmouth bass in laboratory experiments. *Transactions of the American Fisheries Society* 125: 274–283
- Birkett KM (2011) An analysis of spatial and temporal changes in fish and benthic macroinvertebrate communities associated with zebra mussel (*Dreissena polymorpha*) abundance in the Huron River, southeastern Michigan. MSc Thesis, University of Michigan, Ann Arbor, Michigan, USA, 52 pp
- Bonar SA, Hubert WA, Willis DW (eds) (2009) Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland, USA, 335 pp
- Bozek MA, Baccante DA, Lester NP (2011) Walleye and sauger life history. In: Barton BA (ed), *Biology, Management and Culture of Walleye and Sauger*. American Fisheries Society, Bethesda, Maryland, USA, pp 233–301
- Case TJ (1990) Invasion resistance arises in strongly interacting species - rich model competition communities. *Proceedings of the National Academy of Sciences of the USA* 87: 9610–9614, <http://dx.doi.org/10.1073/pnas.87.24.9610>
- Claudi R, Mackie GL (1993) Practical manual for zebra mussel monitoring and control. Lewis Publishers, CRC Press. Boca Raton, Florida, USA, 240 pp
- Claudi R, Graves A, Taraborelli AC, Prescott RJ, Mastitsky SE (2012) Impact of pH on survival and settlement of dreissenid mussels. *Aquatic Invasions* 7: 21–28, <http://dx.doi.org/10.3391/ai.2012.7.1.003>
- Cobb SE, Watzin MC (2002) Zebra mussel colonies and yellow perch foraging: Spatial complexity, refuges, and resource enhancement. *Journal of Great Lakes Research* 28: 256–263, [http://dx.doi.org/10.1016/S0380-1330\(02\)70581-9](http://dx.doi.org/10.1016/S0380-1330(02)70581-9)
- Coblenz BE (1990) Exotic organisms: A dilemma for conservation biology. *Conservation Biology* 4: 261–265, <http://dx.doi.org/10.1111/j.1523-1739.1990.tb00287.x>
- Didham RK, Tylianakis JM, Hutchinson MA, Ewers RM, Gemmel NJ (2005) Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution* 20: 470–474, <http://dx.doi.org/10.1016/j.tree.2005.07.006>
- Dodge DP, Tilt JC, MacRitchie I, Goodchild GA, Waldriff DG (1982) Aquatic Habitat Inventory Surveys. Ontario Ministry of Natural Resources, Queen's Printer for Ontario, 248 pp
- Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (eds) (1989) *Biological Invasions: A Global Perspective*. John Wiley & Sons, Chichester, UK, 525 pp
- Dudgeon D, Arthington AH, Gessner MO, Kawabata Z, Knowler D, Lévêque C, Naiman RJ, Prieur-Richard A-H, Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews of the Cambridge Philosophical Society* 81: 163–182, <http://dx.doi.org/10.1017/S1464793105006950>
- Elton CS (1958) *The Ecology of Invasions by Animals and Plants*. John Wiley, New York, New York, USA, 181 pp, <http://dx.doi.org/10.1007/978-1-4899-7214-9>
- Fisheries and Oceans Canada (2005) Survey of Recreational Fishing in Canada. <http://www.dfo-mpo.gc.ca/stats/rec/can/2005/section4-eng.htm> (Accessed 13 March 2012)
- Fitzsimons JD, Leach JH, Nepszy SJ, Cairns VW (1995) Impacts of zebra mussel on walleye (*Stizostedion vitreum*) reproduction in western Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 578–586, <http://dx.doi.org/10.1139/f95-058>

- Frey AP, Bozek MA, Edwards CJ, Newman SP (2003) Diet overlap and predation between smallmouth bass and walleye in a north temperate lake. *Journal of Freshwater Ecology* 18: 43–54, <http://dx.doi.org/10.1080/02705060.2003.9663950>
- Fridley JD, Stachowicz JJ, Naemm S, Sax DF, Seabloom EW, Smith MD, Stohlgren TJ, Tilman D, Von Holle B (2007) The invasion paradox: Reconciling pattern and process in species invasions. *Ecology* 88: 3–17, [http://dx.doi.org/10.1890/0012-9658\(2007\)88\[3:TIPRPA\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2)
- Great Lakes Aquatic Nonindigenous Species Information System (2011) NOAA Great Lakes Environmental Research Laboratory. Ann Arbor, Michigan, USA
- Greenway JC Jr. (1967) Extinct and Vanishing Birds of the World. Dover, New York, New York, USA, 520 pp
- Griffiths RW, Schloesser DW, Leach JH, Kovalak WP (1991) Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1381–1388, <http://dx.doi.org/10.1139/f91-165>
- Guiliano A (2011) Effects of zebra mussel invasion on juvenile steelhead distribution, diet, growth, and condition in the Muskegon River, Michigan. MSc Thesis, University of Michigan, Ann Arbor, Michigan, USA, 34 pp
- Higgins SN, Vander Zanden MJ (2010) What a difference a species makes: A meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs* 80: 179–196, <http://dx.doi.org/10.1890/09-1249.1>
- Hosler DM (2011) Early detection of dreissenid species: Zebra/Quagga mussels in water systems. *Aquatic Invasions* 6: 217–222, <http://dx.doi.org/10.3391/ai.2011.6.2.10>
- Hoyle JA, Bowlby JN, Morrison BJ (2008) Lake whitefish and walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. *Aquatic Ecosystem Health and Management* 11: 403–411, <http://dx.doi.org/10.1080/14634980802530392>
- Ingram RG, Girard RE, Clark BJ, Paterson AM, Reid RE, Findeis JG (2006) Dorset Environmental Science Centre, Lake Sampling Methods. Ontario Ministry of the Environment Data Report. ISBN 1-4249-2049-3 21 pp + 8 appendices
- Jenkins TM Jr., Diehl S, Kratz KW, Cooper SD (1999) Effects of population density on individual growth of brown trout in streams. *Ecology* 80: 941–956, [http://dx.doi.org/10.1890/0012-9658\(1999\)080\[0941:EOPDOI\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(1999)080[0941:EOPDOI]2.0.CO;2)
- Johnson LE, Padilla DK (1996) Geographic spread of exotic species: ecological lessons and opportunities from the invasion of the zebra mussel *Dreissena polymorpha*. *Biological Conservation* 78: 23–33, [http://dx.doi.org/10.1016/0066-3207\(96\)00015-8](http://dx.doi.org/10.1016/0066-3207(96)00015-8)
- Kerr SJ, Grant RE (2000) Ecological Impacts of Fish Introductions: Evaluating the Risk. Fish and Wildlife Branch, Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada, 473 pp
- Leach JH (1993) Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. In: Nalepa TF, Schloesser DW (eds), Zebra mussels. Biology, impacts, and control. Lewis Publishers, Boca Raton, Florida, USA, pp 381–397
- Lester N, Dextrase AJ, Kushneriuk RS, Rawson MR, Ryan PA (2004) Light and temperature: Key factors affecting walleye abundance and production. *Transactions of the American Fisheries Society* 133:588–605, <http://dx.doi.org/10.1577/T02-111.1>
- Litvak MK, Mandrak NE (1999) Baitfish trade as a vector of aquatic introductions. In: Claudi R, Leach JH (eds), Nonindigenous Freshwater Organisms: Vectors, Biology, and Impacts. Lewis Publishers, Boca Raton, Florida, USA, pp 163–180
- MacIsaac HJ (1996) Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoology* 36: 287–299
- Marsden JE, Chotkowski MA (2001) Lake trout spawning on artificial reefs fouled by zebra mussels: Fatal attraction? *Journal of Great Lakes Research* 27: 33–43, [http://dx.doi.org/10.1016/S0380-1330\(01\)70621-1](http://dx.doi.org/10.1016/S0380-1330(01)70621-1)
- Matuszek E, Beggs L (1988) Fish species richness in relation to lake area, pH, and other abiotic factors in Ontario lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1931–1941, <http://dx.doi.org/10.1139/f88-225>
- McNickle GG, Rennie MD, Sprules WG (2006) Changes in benthic invertebrate communities of South Bay, Lake Huron following invasion by zebra mussels (*Dreissena polymorpha*), and potential effects on lake whitefish (*Coregonus clupeaformis*) diet and growth. *Journal of Great Lakes Research* 32: 180–193, [http://dx.doi.org/10.3394/0380-1330\(2006\)32\[180:CIBICO\]2.0.CO;2](http://dx.doi.org/10.3394/0380-1330(2006)32[180:CIBICO]2.0.CO;2)
- Meeuwig MH, Guy CS, Fredenberg WA (2008) Influence of landscape characteristics on fish species richness among lakes of Glacier Mountain National Park, Montana. *Intermountain Journal of Sciences* 14: 1–16
- Mills EL, Leach JH, Carlton JT, Secor CL (1993) Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19: 1–54, [http://dx.doi.org/10.1016/S0380-1330\(93\)71197-1](http://dx.doi.org/10.1016/S0380-1330(93)71197-1)
- Ontario Ministry of Natural Resources (2005) Walleye State of the Resource Report for Southern Region. Peterborough, Ontario, Canada, 6 pp
- Pace ML, Findlay SEG, Fischer D (1998) Effects of an invasive bivalve on the zooplankton community of the Hudson River. *Freshwater Biology* 39: 103–116, <http://dx.doi.org/10.1046/j.1365-2427.1998.00266.x>
- Pimentel D, McNair S, Janecka J, Wightman J, Sommonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment* 84: 1–20, [http://dx.doi.org/10.1016/S0167-8809\(00\)00178-X](http://dx.doi.org/10.1016/S0167-8809(00)00178-X)
- Pope KL, Kruse CG (2007) Condition. In: Guy CS, Brown ML (eds), Analysis and Interpretation of Freshwater Fisheries Data. American Fisheries Society, Bethesda, Maryland, USA, pp 423–472
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK, 556 pp
- Ramakrishnan PS, Vitousek PM (1989) Ecosystem-level processes and consequences of biological invasions. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (eds), Biological Invasions. A Global Perspective. John Wiley & Sons, Chichester, UK, pp 281–328
- Reaser JK, Meyerson LA, Cronk Q, De Poorter M, Eldrege LG, Green E, Kairo M, Latasi P, Mack RN, Mauremootoo J, O'DOWD D, Orapa W, Sastroutomo S, Saunders A, Shine C, Thrainsson S, Vaiuti L (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation* 34: 98–111, <http://dx.doi.org/10.1017/S0376892907003815>
- Rennie MD, Sprules WG, Johnson TB (2009) Factors affecting growth and condition of lake whitefish (*Coregonus clupeaformis*). *Canadian Journal of Fisheries and Aquatic Sciences* 66: 2096–2108, <http://dx.doi.org/10.1139/F09-139>
- Ricciardi A (2004) Assessing species invasions as a cause of extinction. *Trends in Ecology & Evolution* 19: 619, <http://dx.doi.org/10.1016/j.tree.2004.09.021>
- Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology & Evolution* 15: 62–65, [http://dx.doi.org/10.1016/S0169-5347\(99\)01745-0](http://dx.doi.org/10.1016/S0169-5347(99)01745-0)

- Richter BD, Braun DP, Mendelson MA, Master LL (1997) Threats to imperiled freshwater fauna. *Conservation Biology* 11:1081–1093, <http://dx.doi.org/10.1046/j.1523-1739.1997.96236.x>
- Ritchie BJ, Colby PJ (1988) Even-odd year differences in walleye year-class strength related to mayfly production. *North American Journal of Fisheries Management* 8: 210–215, [http://dx.doi.org/10.1577/1548-8675\(1988\)008<0210:EOYDIW>2.3.CO;2](http://dx.doi.org/10.1577/1548-8675(1988)008<0210:EOYDIW>2.3.CO;2)
- Sandstrom S, Rawson M, Lester N (2011) Manual of Instructions for Broad-scale Fish Community Monitoring; using North American (NA1) and Ontario Small Mesh (ON2) Gillnets. Ontario Ministry of Natural Resources, Peterborough, Ontario, Canada, 135 pp + appendices
- Schaner T (1990) Detection of zebra mussel veligers in plankton samples using sugar solution. Lake Ontario Fisheries Unit 1990 Annual Report, Chapter 6, Ontario Ministry of Natural Resources, Picton, Ontario, Canada, pp 1–3
- Scott WB, Crossman EJ (1973) Freshwater Fishes of Canada. Bulletin 184, Fisheries Research Board of Canada, Ottawa, Ontario, Canada, 966 pp
- Simberloff D (1981) Community effects of introduced species. In: Nitecki TH (ed), *Biotic Crises in Ecological and Evolutionary Time*. Academic Press, New York, New York, USA, pp 53–81
- Simberloff D (2004) A rising tide of species and literatures: A review of some recent books on biological invasions. *BioScience* 54: 247–254, [http://dx.doi.org/10.1641/0006-3568\(2004\)054\[0247:ARTOSA\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2004)054[0247:ARTOSA]2.0.CO;2)
- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions* 1: 21–32, <http://dx.doi.org/10.1023/A:1010086329619>
- Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. *Science* 286: 1577–1579, <http://dx.doi.org/10.1126/science.286.5444.1577>
- Stevens GC (1989) The latitudinal gradient in geographical range: How so many species coexist in the tropics. *American Naturalist* 133: 240–256, <http://dx.doi.org/10.1086/284913>
- Trometer ES, Busch WDN (1999) Changes in age-0 fish growth and abundance following the introduction of zebra mussels *Dreissena polymorpha* in the western basin of Lake Erie. *North American Journal of Fisheries Management* 19: 604–609, [http://dx.doi.org/10.1577/1548-8675\(1999\)019<0604:CIAFGA>2.0.CO;2](http://dx.doi.org/10.1577/1548-8675(1999)019<0604:CIAFGA>2.0.CO;2)
- Vander Zanden M, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1512–1522, <http://dx.doi.org/10.1139/F08-099>
- Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. *American Scientist* 84: 468–478
- Vitousek PM, D'Antonio CM, Loope LL, Rejma'nek M, Westbrooks R (1997) Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* 21: 1–16
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. *BioScience* 48: 607–615, <http://dx.doi.org/10.2307/1313420>
- Wootton RJ (1998) *Ecology of Teleost Fishes*. 2nd ed. Chapman and Hall, London, UK, 386 pp
- Zhu B, Fitzgerald DG, Mayer CM, Rudstam LG, Mills EL (2006) Alteration of ecosystem function by zebra mussels in Oneida Lake: Impacts on submerged macrophytes. *Ecosystems* 9: 1017–1028, <http://dx.doi.org/10.1007/s10021-005-0049-y>

Supplementary material

The following supplementary material is available for this article:

Table S1. Records of *Dreissena polymorpha* in inland, freshwater lakes in southern Ontario, Canada.

This material is available as part of online article from:

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