

Whole-lake effects of invasive crayfish (*Orconectes* spp.) and the potential for restoration

Sadie K. Rosenthal, Samantha S. Stevens, and David M. Lodge

Abstract: Effects of invasive species are often extrapolated to whole systems based on small-scale, short-term, and (or) single-system studies. For example, previous laboratory studies and in-lake cage experiments suggest that invasive crayfish *Orconectes rusticus* and *O. propinquus* reduce macrophyte and snail abundance in north temperate lakes, and snapshot lake surveys provide supporting evidence. Still, these impacts have not been demonstrated in multiple whole lakes over time. Thus, in summer of 2003, we resurveyed benthic invertebrates and macrophytes in lakes originally surveyed by the Michigan Department of Natural Resources in the late 1930s. Our multilake survey supports the macrophyte results from small-scale and comparative studies: macrophyte species richness and abundance declined significantly in invaded lakes relative to uninvaded lakes. We next conducted a laboratory seed-bank study to examine the potential for macrophyte restoration in a lake occupied by rusty crayfish for at least 15 years. Only two macrophyte species (*Najas flexilis* and *Chara* spp.) germinated from sediments from the invaded lake compared with eight species from reference sediments. This suggests that invaded lakes may have depauperate seed banks and that restoration of invaded macrophyte communities may require manual planting, even if crayfish could be removed.

Résumé : Les effets des espèces envahissantes sont souvent extrapolés à systèmes entiers à partir d'études à petite échelle, à court terme ou sur un seul système. Par exemple, des études antérieures en laboratoire et des expériences en lac dans des cages laissent croire que les écrevisses envahissantes *Orconectes rusticus* et *O. propinquus* réduisent l'abondance des macrophytes et des gastéropodes dans les lacs tempérés nordiques; des inventaires instantanés de lacs fournissent des données qui appuient ces résultats. Néanmoins, ces impacts n'ont pas été démontrés dans un grand nombre de lacs entiers sur une longue période. C'est pourquoi, à l'été 2003, nous avons inventorié de nouveau les invertebrés benthiques et les macrophytes dans des lacs inventoriés à l'origine par le ministère des ressources naturelles du Michigan à la fin des années 1930. Notre inventaire de nombreux lacs confirme les résultats obtenus sur les macrophytes dans les études à petite échelle et les études comparatives : la richesse spécifique et l'abondance des macrophytes ont diminué de façon significative dans les lacs envahis par les écrevisses par comparaison aux lacs non envahis. Nous avons ensuite mené une étude en laboratoire de banques de graines pour déterminer le potentiel de restauration des macrophytes dans un lac occupé par l'écrevisse rousse depuis au moins 15 ans. Seules deux espèces de macrophytes, *Najas flexilis* et *Chara* spp., ont germé dans les sédiments recueillis dans le lac envahi, alors que huit espèces ont germé dans les sédiments témoins. Cela indique que les lacs envahis peuvent avoir des banques de graines appauvries et que, même si les écrevisses pouvaient être retirées, la restauration des communautés de macrophytes envahies par les écrevisses pourrait exiger des plantations manuelles.

[Traduit par la Rédaction]

Introduction

Invasive species have tremendous economic and ecological impacts. They are estimated to cost the US at least \$137 billion annually (Pimentel et al. 2000), are a threat to imperiled species (Wilcove et al. 1998), and are the leading cause of biodiversity loss in lakes (Sala et al. 2000). Nevertheless, the impact of invasive species is often anecdotal and poorly quantified because pre-invasion data are lacking.

Given the potential for irreversible harm, it is unethical to experimentally introduce potentially invasive species into natural systems. Therefore, species are studied most often

with laboratory experiments or with small-scale field experiments within an already invaded system. Unfortunately, such experiments often lack realism (Diamond 1986), and small-scale phenomena may not scale easily to a whole system (Lodge et al. 1998). One-time, multilake correlative studies incorporate more realism than do small-scale studies, but because correlation does not imply causation, we cannot confidently attribute observed ecological changes to invasive species. Short of a planned experiment, the most realistic type of study is a natural trajectory experiment in which multiple systems are studied before and after a disturbance (Diamond 1986). Often lacking, however, are both pre-

Received 3 June 2005. Accepted 22 December 2005. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 2 May 2006.
J18724

S.K. Rosenthal,¹ S.S. Stevens, and D.M. Lodge. Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA.

¹Corresponding author (e-mail: srosenth@alumni.nd.edu).

invasion baseline data against which to measure change, and reference lakes to account for other potential drivers. In this study we have such data and are afforded a rare opportunity to test the effects of invasive crayfish in whole lakes over time.

The spread and impacts of crayfish have been studied in lakes of the US Upper Midwest since the 1970s (Capelli and Magnuson 1983). In the Northern Highland Lake District of Wisconsin and the upper peninsula of Michigan specifically, the focus has been on one native and two nonindigenous species. Virile crayfish (*Orconectes virilis*) are native throughout the region, northern crayfish (*O. propinquus*) are nonindigenous to some areas, and rusty crayfish (*O. rusticus*) are nonindigenous throughout (Creaser 1931, 1932). All three crayfish species are omnivores, feeding as shredders, collectors, scrapers, and predators (Lorman and Magnuson 1978), and studies suggest that invasive crayfish have strong trophic interactions in the littoral zones of lakes and reduce the abundance of macroinvertebrates, macrophytes, and periphyton (Lodge et al. 1994; Hill and Lodge 1995).

Rusty crayfish generally extirpate both congeners (Olsen et al. 1991), whereas northern crayfish either replace or coexist with virile crayfish (Lodge et al. 1986; Olsen et al. 1991). Of the other littoral invertebrates, snails are the best studied. Rusty crayfish reduced snail populations in a field experiment (Lodge et al. 1994) and were negatively associated with snail densities in a multilake correlative study (Lodge et al. 1998). Introduced crayfish affect macrophyte communities through consumption and nonconsumptive damage, reducing macrophyte biomass, shoot density, and species richness in field experiments (Lodge and Lorman 1987; Lodge et al. 1994). The reduction of macrophyte surface area may yield a net periphyton loss, even as periphyton-grazing snails decline (Lodge et al. 1994). Finally, the loss of macrophyte habitat, combined with egg predation by crayfish (Dorn and Mittelbach 2004), may lead to negative effects on fish populations.

Given the expected large negative effects stemming from crayfish invasions, the prospect of reversing these effects should be addressed to prioritize management efforts (Parker et al. 1999). Because macrophytes have major impacts on physical, chemical, and biological properties in lakes (Carpenter and Lodge 1986), they are a natural focus in testing the potential for recovery should rusty crayfish numbers decrease. Studies in other contexts suggest that a viable seed bank may provide the necessary rescue to reestablish a degraded plant community (McFarland and Rogers 1998; de Winton et al. 2000). However, if sustained herbivory results in seed-bank depletion, macrophyte communities may not recover even when herbivore populations are reduced or eliminated. This has never been tested with respect to crayfish invasions.

The thought that invasive crayfish cause dramatic shifts in macrophyte and macroinvertebrate communities in whole

lakes has previously been inferred from correlative studies (Lodge et al. 1998; Wilson 2002), small-scale laboratory experiments (Olsen et al. 1991), short-term, in situ caging experiments (Lodge and Lorman 1987; Lodge et al. 1994), and single-lake studies (Wilson et al. 2004). Here we use a natural trajectory experiment to examine whether impacts of invasive crayfish predicted from small-scale experiments manifest at the whole-lake scale. For lakes in the upper peninsula of Michigan, we compare changes in the macrophyte and invertebrate communities between the 1930s and 2003 in invaded lakes and in uninvaded reference lakes. We then use a laboratory seed-bank study to test the potential for macrophyte recovery following crayfish removal. The results of this seed-bank experiment have implications for any restoration efforts.

Materials and methods

Multilake surveys

General

In the 1930s, biologists with the Michigan Department of Natural Resources (MI DNR) Institute for Fisheries Research (IFR) conducted comprehensive lake surveys in the upper peninsula of Michigan with the objective of better managing fish populations (McMurry et al. 1933; Eschmeyer 1936). Recognizing the importance of habitat and prey items to fish, they sampled macrophytes and benthic macroinvertebrates in a number of lakes, and we use these data as a baseline against which to compare ecological change between lakes invaded by crayfish and uninvaded reference lakes.

In 2003, we resampled macrophytes (in seven lakes) and macroinvertebrates (in nine lakes) (Table 1 and supplementary data²), using methods identical with those used in the 1930s, as best as we could determine from the available historical documentation (Eschmeyer and Hazzard 1936³; Miller 1936; Hazzard and Brown 1938³). Because we were interested in the effects of invasive crayfish on lake biota, we selected only lakes for which we found no obvious evidence (from the IFR records or from current long-term homeowners) of other contributing factors. For example, we excluded lakes that had been dammed at the outflow post-1930s because the resulting change in the water level may have had an effect on littoral communities. In 2003, we conducted surveys from late June through late August to approximate the dates surveyed in the 1930s and sampled at the same locations within lakes, as determined from IFR site descriptions and detailed maps of the sampling stations.

Crayfish

Crayfish were not specifically targeted in the 1930s sampling by the IFR or subsequently by the MI DNR. However, their occurrence was noted in the context of potential prey items for fish. In the records of the IFR and MI DNR, cray-

²Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5027. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

³Dates of undated historical documents were approximated from dated documents referring back to these methods and from the authors' tenures at the IFR (Tina Tincher, Librarian, MI DNR, Fisheries Division, Institute for Fisheries Research, 212 Museums Annex Building, 1109 North University Avenue, Ann Arbor, MI 48109, USA, personal communication).

Table 1. Crayfish data.

Lake	Past crayfish (species)	No. crayfish·trap ⁻¹ (species) in 2003	Lakes sampled for		
			Benthos	Snails	Macrophytes
Beatons	1991 (Y)	0.3 (P)	×		×
Crooked	1938 (Y)	0.1 (R, P)	×	×	×
Gogebic	1940s (Y)	2.1 (P, V)	×	×	
Smoky	1989 (R)	0.0 ^a (R)	×		
Sucker	1938 (Y)	1.0 (V)	×	×	×
Winslow	1938 (Y)	0.9 (P, I ^b)	×		×
Hagerman	1938 (Y)	25.1 (P, V^b)	×		×
Ottawa	1938 (Y); 1987 (R)	30.7 (R)	×	×	×
Thousand Island	1938 (Y); 1995 (R)	8.5 (R)	×	×	×

Note: Lakes with high abundances of crayfish (in 2003) are in bold type. All lakes were originally sampled for other benthos in 1937 (Beatons) or 1938 (all other lakes), but for some lakes, information on crayfish is available only for later years. Crayfish species abbreviations: R, rusty (*Orconectes rusticus*); P, northern (*O. propinquus*); V, virile (*O. virilis*); I, immune (*O. immunis*); Y, crayfish unidentified.

^aRusty crayfish found by hand.

^bIn Winslow, only one of 17 crayfish trapped were immune crayfish; in Hagerman, only two of the 499 crayfish were virile crayfish.

fish were not identified to species, with the exception of rusty crayfish, which have been distinguished from other species since about 1987 (Bill Ziegler, Fisheries Management Biologist, MI DNR, Northern Lake Michigan Management Unit, 1420 US 2 West, Crystal Falls, MI 49920, USA, personal communication). However, in other pre-1931 surveys specifically targeting crayfishes, the only species of *Orconectes* found in the counties (Gogebic and Iron) of our study was the virile crayfish (*O. virilis*) (Creaser 1931), which we thus refer to as the native crayfish. The northern crayfish (*O. propinquus*) was found in Michigan's Upper Peninsula, but only in counties bordering the Great Lakes (Creaser 1931). Northern crayfish were thus either absent or rare in our counties until post-1931. The exact timing of their invasion is unknown, but by the 1970s, they occurred in many lakes of northern Wisconsin outside their original Great Lakes watershed distribution (Capelli and Magnuson 1983). Rusty crayfish, which are native to Indiana, Kentucky, and Ohio, were first noted in northern Wisconsin in the 1970s (Capelli and Magnuson 1983), where they have been used by anglers as bait.

In 2003, we determined crayfish composition of each lake by trapping with standard methods (Capelli and Magnuson 1983; Lodge et al. 1986) in August, an intermolt period during which adult males are active. Approximately 20 Gee minnow traps (Memphis Net and Twine, Memphis, Tennessee) with enlarged openings (~5 cm diameter) were baited with 120 ± 10 g beef liver and distributed roughly evenly around the perimeter of each lake. Traps were set in the afternoon at a depth of 1.5 ± 0.5 m and collected the following day. We recorded species, sex, and form for all crayfish caught.

Benthos sampling

We used maps made during the 1930s to relocate the 4–11 clearly marked benthos sampling stations for each of the nine lakes in which we resurveyed benthic communities. As in the 1930s, we took two standard 15.2 cm Ekman grabs at each station, for a combined sampling area of 464.5 cm². The sediments collected were sieved (850 µm mesh, previously No. 20) (Miller 1936) in the field, and organisms were

immediately identified to the same taxonomic levels used in the 1930s (usually class or order).

Benthos analysis

To provide an index of lake-wide changes in total abundance of benthic invertebrates, we first calculated a metric of change at each station:

$$\text{Station metric} = \log \left(\frac{2003 \text{ abundance} + 1}{1930s \text{ abundance} + 1} \right)$$

We then averaged this metric across all stations to calculate our lake-wide metric. We compared changes in macroinvertebrate abundance from the 1930s to 2003 between invaded and uninvaded lakes with *t* tests (SYSTAT 10.2; Systat Software Inc. 2002). Because we expected that crayfish would have strongest negative effects on littoral benthos, we did separate analyses for littoral (1–10 stations sampled in each lake) and profundal (1–5 stations per lake) benthos. Littoral stations were defined as either being shallower than maximum rooting depth for submergent macrophytes based on each lake's Secchi depth (Skogerboe et al. 2003) or containing snails. We expected no change in abundance for profundal macroinvertebrates but performed the analysis as a reference for littoral changes. We performed a separate analysis for snail abundance (one-tailed *t* test), because evidence from smaller-scale experiments suggests that snails are strongly reduced by crayfish (Lodge et al. 1994). We limited the snail analysis to littoral stations where snails were present in either sampling year. We did not analyze invertebrate species richness because of the coarse taxonomic classifications used in the 1930s.

Macrophyte sampling

The 1930s records indicate that submergent macrophytes were sampled visually at two scales. First, detailed observations for species presence and abundance were taken at 2–7 sampling stations in each lake, which were clearly indicated on lake maps. For the sampling stations, notes on species' aerial cover and depth indicated that vegetation was sampled from a broad area that differed among stations. We examined historical notes before sampling to best determine that

area for each station. Second, the general presence of macrophytes was noted at the lake-wide scale.

For the detailed station surveys, we visually inspected sampling stations in seven lakes from a flat-bottomed boat, drifting slowly across the sampling area along 1–2 m depth contours. Most lakes were clear and we could easily identify species from above the water. Where we could not, we pulled plants to the surface with a modified rake (a 1.4 m tall rake with a 42 cm × 42 cm square of 12.7 mm mesh hardware cloth secured to the handle at the base). A photograph taken of early surveys (Hubbs and Eschmeyer 1938, their fig. 8) shows such a device, and Cooper (1974, p. 142) stated that scientists “dredge[d] for bottom food and weeds” in earlier surveys.

We identified submergent macrophytes to the taxonomic level assigned in the 1930s, which was generally species (Crow and Hellquist 2000). We assessed each species' abundance according to the 1938 classifications of sparse (S), medium (M), and dense (D). In 1937, five categories were used: I (rare), II (sparse), III (common), IV (abundant), and V (dense). To include in our analysis lakes that were sampled in different years, we converted the five 1937 categories (Beatons Lake) to the three 1938 categories (all other lakes) as follows: we designated I (1937) and II (1937) as sparse (1938), III (1937) as medium (1938), and IV (1937) and V (1937) as dense (1938). Sparse, medium, and dense were undefined in the section on lake sampling in the methods reported by Hazzard and Brown (1938)³. However, in the section on stream methods, a species was classified as sparse if seldom observed, medium if covering about half of the rocks or in patches and here and there, and dense if noticeable on practically every rock or if margining the stream. We followed these generalizations in our lakes: sparse if seldom observed, moderate if here and there, and dense if it was noticeable over most of the sampling station.

For the lake-wide surveys, markings on the lake maps indicated where submergent vegetation was historically present, in addition to the detailed sampling stations. We traveled the shoreline in these areas and classified the bottom as either firm (sand or gravel) or soft (muck), as we also did for each macrophyte sampling station. We then computed the proportion of the historically vegetated area with firm or soft bottom substrate. We did this because recent work has shown that crayfish are more abundant on firm than soft substrates (Kershner and Lodge 1995), and we therefore expected that the crayfish impact would be greater on firm than soft substrates.

Macrophyte analysis

To provide an index of change in species richness of submergent macrophytes for each station, we summed the number of taxa at each station and calculated a metric of change between years, as we did with invertebrate abundance above:

$$\text{Station metric of change} = \log \left(\frac{2003 \text{ species richness} + 1}{1930s \text{ species richness} + 1} \right)$$

We calculated the mean metric of change for firm and soft substrates separately and multiplied these by the proportion of shoreline historically occupied by submergent macrophytes

in that substrate. We then summed across substrates to provide a lake-wide index of change for the area of the lake that was historically occupied by submergent macrophytes:

$$\begin{aligned} \text{lake metric} = & [(\text{proportion of lake in firm}) \\ & \times (\text{mean change on firm substrate})] \\ & + [(\text{proportion of lake in soft}) \\ & \times (\text{mean change on soft substrate})] \end{aligned}$$

Predicting that invaded lakes would have a more negative change than uninvaded lakes, we then compared this metric between invaded and uninvaded lakes with a one-tailed *t* test.

To provide an index of macrophyte abundance (regardless of species richness), we assigned each species at a station an index of abundance: 1 to sparse, 2 to medium, and 3 to dense. We summed the index of abundance across all submergent macrophyte species in a station for 1930s and 2003 data separately. We then did the same type of analysis as with species richness to calculate a metric of change (described above) for each lake. Recognizing that the assignment of 1, 2, and 3 is arbitrary, we examined the sensitivity of results to our classifications by repeating the analysis with postsampling estimations of average aerial cover for each category. On average, we estimated that macrophytes categorized as sparse covered 7% of the sampling station's surface area, medium 30%, and dense 53%.

Seed-bank experiment

Study sites

We began monitoring Lake Ottawa (223 ha, 27 m maximum depth), one of the study lakes above, in summer 2001. We caught an average of 36 male rusty crayfish-trap⁻¹ in late July 2001 and observed that little of the vegetation noted on the 1930s map was still present. To test the potential for natural vegetation restoration if management efforts could reduce crayfish abundance, we tested the seed banks of two 1938 macrophyte sampling stations. Bay 1, the northernmost bay of Lake Ottawa, was dominated by light-colored muck over sand. Bay 2, the lake's southwestern bay, consisted of dark muck. We used Tenderfoot Lake (179 ha, 10 m maximum depth), at the mouth of Tenderfoot Creek, as a reference site. This site had abundant vegetation on muck substrate, with species overlapping those historically present in Lake Ottawa (Table 2).

Sample collection

On 16 August 2001, we took five sets of sediment cores at each of the two bays in Lake Ottawa and in Tenderfoot Lake to test for germination. A cylindrical metal-edged corer with an area of 0.018 m² was pushed into the sediments to a depth of 10 cm. A metal plate was slid underneath to collect the sediments (Lodge et al. 1998). Each set consisted of four cores taken at least 10 m apart at a given site at a water depth of 1 m.

Experiment and analysis

Sediment samples were placed in dark, cold storage (4 °C) at the University of Notre Dame (Notre Dame, Indiana) for 20 weeks to simulate winter conditions needed by some species to break seed dormancy (Baskin and Baskin 1998). Sediments from each sample (a layer approximately 4 cm deep) were then laid over a 5 cm layer of sand

Table 2. Macrophyte species present in the lakes and those that germinated in the seed-bank experiment.

Macrophytes	Lake Ottawa			Tenderfoot	
	1938	2001–2003	Seed bank	2001	Seed bank
Submergent species					
<i>Ceratophyllum demersum</i>	×			×	
<i>Chara</i> sp.	×		×	×	×
<i>Elodea canadensis</i>		1 stem		×	
<i>Megalodonta beckii</i>				×	
<i>Myriophyllum</i> sp.	×			×	
<i>Najas flexilis</i>	×		×	×	×
<i>Potamogeton amplifolius</i>	×	×		×	
<i>P. epihydrus</i>		×			
<i>P. gramineus</i>				×	
<i>P. illinoensis</i>	×				×
<i>P. natans</i>	×				
<i>P. pusillus</i>	×			×	
<i>P. richardsonii</i>	×	2 plants		×	
<i>P. robbinsii</i>				×	×
<i>P. spirillus</i>				×	×
<i>P. zosteriformis</i>	×			×	×
<i>Stuckenia pectinata</i>	×				
<i>Vallisneria americana</i>				×	
<i>Zosterella dubia</i>	×			×	×
Floating species					
<i>Nuphar variegata</i>	×	×		×	×
<i>Nymphaea odorata</i>	×			×	
<i>Polygonum amphibium</i>	×	×			

Note: Species both historically present in Lake Ottawa and that germinated from either lake in the experiment are in bold type. 1938 data are from Institute for Fisheries Research (IFR) lake files. For current species presence, we snorkeled extensively in Lake Ottawa during the summers of 2001–2003 and surveyed Tenderfoot in the summer of 2001 from a boat.

(QUIKRETE® Play Sand, Atlanta, Georgia) in individual greenhouse tanks (0.457 m × 0.406 m) and covered with 12 cm of water. We put a single aquarium bubbler in each tank for aeration. The greenhouse was kept at about 20 °C (Haag (1983) germinated some of the same species at 19 °C), and 1000 watt, coated, metal halide lamps (400–700 nm spectrum bulbs) provided 14 h of daylight (0600–2000), supplementing natural light. A randomized block design was used to account for slight variability of light intensity resulting from light placement. In addition to the five replicates from each site, we set up one tank with 5 cm of sand to confirm the absence of macrophyte seeds in the sand. Thus a total of 16 tanks constituted the experiment, which ran from 28 January to 15 April 2002.

At the conclusion of the experiment, all germinated macrophytes were identified and counted. We used a randomized blocks analysis of variance with Tukey's multiple contrasts to test whether species richness, total number of macrophyte shoots, and total number of macrophyte shoots (excluding *Chara* spp.) differed between treatments.

Results

Lake surveys

Crayfish

Between the 1930s and 2003, three lakes were invaded such that the invader had attained high abundance by 2003:

Lake Ottawa and Thousand Island Lake by rusty crayfish and Hagerman Lake by northern crayfish (Table 1). Rusty crayfish were first noted in Lake Ottawa in 1987 at which point they made up about 20% of the crayfish community (records in IFR lake files). By 1997, they were clearly the dominant species, comprising an estimated 75% of the crayfish community (records in IFR lake files). Since 2001, they have made up 100% of the crayfish trapped. In Thousand Island Lake, rusty crayfish were detected in 1995 (Perry and Lodge, unpublished data), but not quantified. Five additional lakes (Beatons, Crooked, Gogebic, Smoky, Winslow) have been invaded by rusty or northern crayfish, but the abundance of the invader is still very low (0–2 crayfish-trap⁻¹) (Table 1); thus for analysis these five lakes were included with the uninvaded lakes. Sucker Lake has only native virile crayfish.

Macroinvertebrates and macrophytes

In comparing invaded ($n = 3$) and uninvaded ($n = 6$) lakes, no significant difference existed in the changes of either littoral ($p = 0.388$; Fig. 1a) or profundal ($p = 0.108$; Fig. 1c) invertebrate abundance. The difference in the change of snail abundance was apparently large but not significant ($p = 0.075$, invaded $n = 2$, uninvaded $n = 3$; Fig. 1b). Low sample numbers limited the power of these analyses. Species richness of macrophytes in historically vegetated areas declined in invaded lakes ($n = 3$) as compared with uninvaded lakes ($n = 4$) ($p = 0.007$; Fig. 2a). Likewise, macrophyte abun-

dance declined in invaded lakes as compared with uninvaded lakes, regardless of which categorical scale we used (with density categories of 1, 2, and 3, $p = 0.006$ (Fig. 2b), and with density categories of 7, 30, and 53, $p = 0.017$ (not shown)).

Seed-bank experiment

The number of macrophyte species that germinated was greater in sediments from the reference lake than in those from either site in Lake Ottawa ($p < 0.001$; Fig. 3a). Only *Najas flexilis* (hereafter referred to as *Najas*) and the macroalga *Chara* spp. (hereafter referred to as *Chara*) germinated from the Lake Ottawa sediments, whereas eight macrophyte species, including *Najas* and *Chara*, grew from the Tenderfoot Lake reference sediments (Table 2). More shoots germinated from the organic-rich sediments of Bay 2 than from the sandier sediments of Bay 1 or the reference sediments ($p = 0.002$; Fig. 3b). This trend was driven by high numbers of 5 cm tall sprouts of *Chara* in the sediments from Lake Ottawa's Bay 2. When *Chara* was excluded from the analysis, Tenderfoot Lake had a greater number of shoots than either site in Lake Ottawa ($p < 0.001$; Fig. 3c). No effects of treatment block were detected.

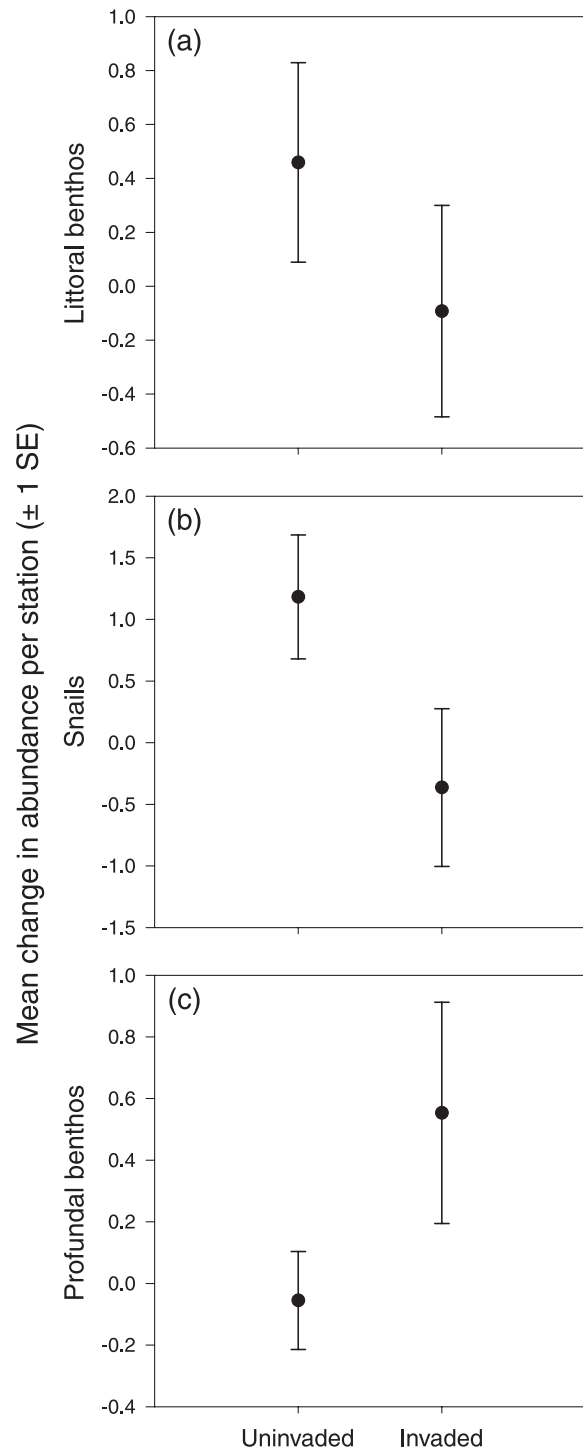
Discussion

Detailed historical sampling records in multiple lakes allowed us to examine long-term, whole-lake effects of invasive crayfish. As predicted from small-scale experiments, macrophyte species richness and abundance declined in invaded lakes relative to uninvaded lakes. For at least Lake Ottawa (the lake in which the timetable of invasion is clearest), these changes were quick (<15 years) relative to the 65-year duration of this study. The removal of macrophytes is expected to have many indirect effects not examined in this study. We expect lower periphyton biomass as a result of reduced colonizable surface area (Lodge et al. 1994) and fewer juvenile fish because of loss of habitat.

Effects on littoral benthos, though not statistically significant, were in the direction predicted from smaller-scale studies. We expected littoral invertebrate populations, especially snails, in invaded lakes to be low in abundance and diversity (Lodge et al. 1994, 1998). Our nonsignificant results (in the expected direction) may relate to both sampling bias and low power. When we sampled among macrophytes, the Ekman grab rarely retained vegetation, which is a primary habitat for snails (Brown and Lodge 1993); therefore the grabs likely underestimated snail abundance in vegetated habitats. Because vegetation occurred primarily in uninvaded lakes, the grabs likely underestimated snail abundance in uninvaded lakes relative to invaded lakes. Combined with the low power of our comparisons (limited by the small number of study lakes), these considerations suggest that our test of the impact of invasion on snails was conservative. Attributing biological significance to the apparent decline in snails after invasion is supported by the apparent opposite trend in profundal benthos, which occur at depths where crayfish predation is not important.

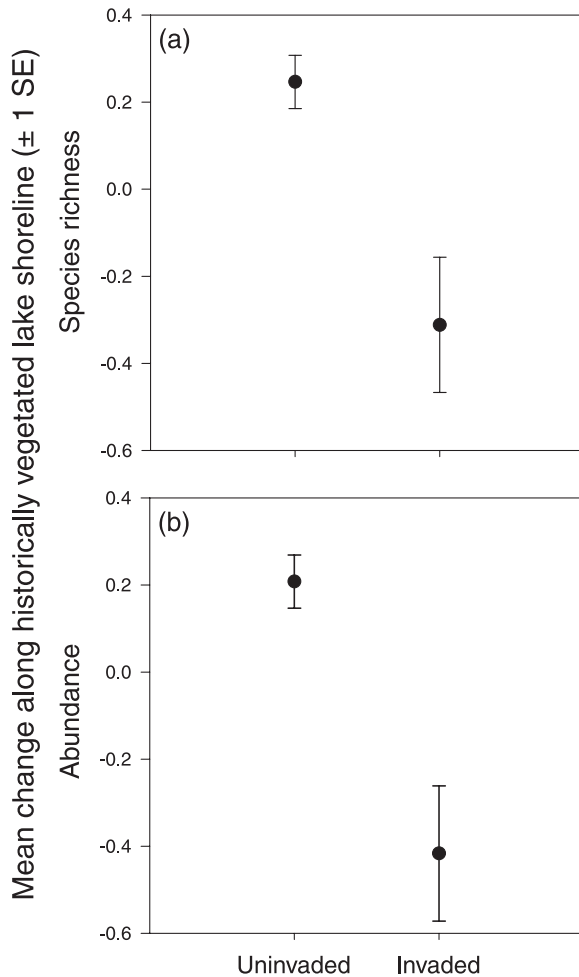
If uninvaded lakes were absolutely stable over time and our sampling methods in 2003 were exactly identical with those of the 1930s, the mean index of change for both

Fig. 1. Mean index of change (± 1 standard error (SE)) in (a) littoral benthos, (b) snails, and (c) profundal benthos per station (profundal and littoral benthos: uninvaded, $n = 6$; invaded, $n = 3$; snails: uninvaded, $n = 3$; invaded, $n = 2$).



macrophytes and invertebrates would have been zero. That our indices differed from zero may result from natural changes in the lake biota, although previous long-term studies of macrophytes in this northern highland lakes region suggest that without obvious drivers, changes in macrophyte composition are minor (Carpenter and Titus 1984; Lodge et al. 1989; Nichols 2001). Equally likely is that they are an in-

Fig. 2. Mean index of change (± 1 standard error (SE)) in macrophyte species (a) richness and (b) abundance of the lake shoreline historically occupied by submergent macrophytes (uninvaded, $n = 4$; invaded, $n = 3$).

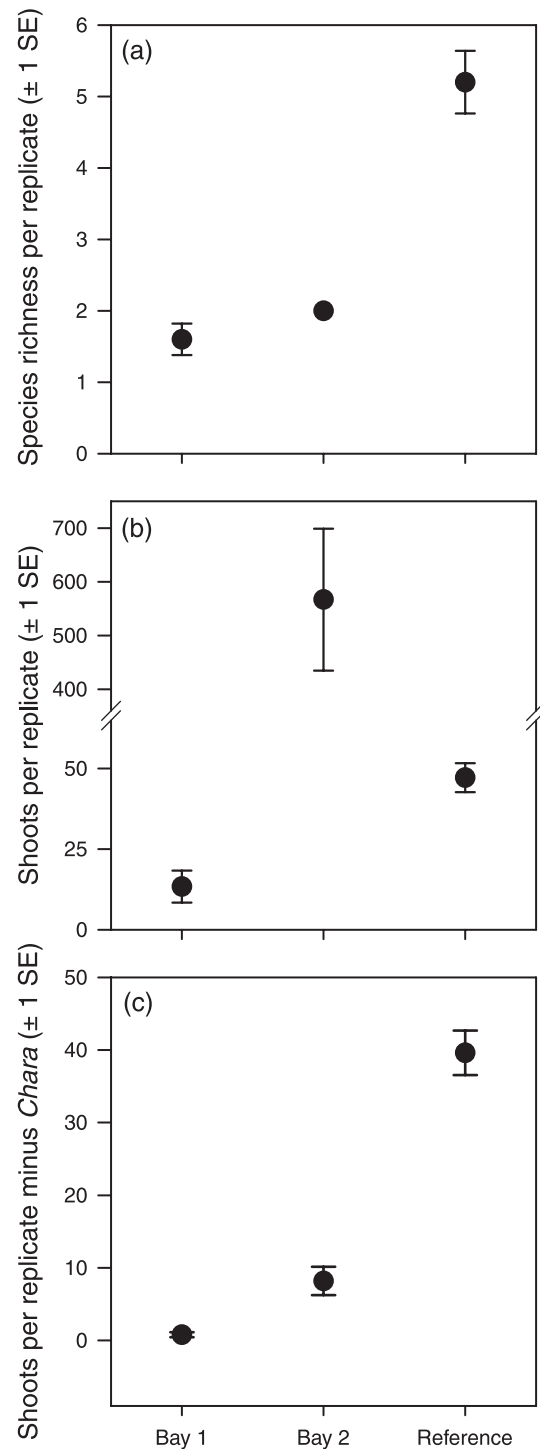


dication of different sampling efforts as opposed to large, lake-wide changes. This is especially true for macrophytes for which the details of the original sampling methods were less clear than for invertebrates. We consistently encountered more macrophyte species than were found by the 1930s biologists. The records indicate that the 1930s field crew spent about 3 days at each lake, and we suspect that they did not give sampling stations the same attention we did, because they had many additional duties including mapping the lake, testing water chemistry, and sampling fish.

This is the first study to suggest that northern crayfish, in addition to rusty crayfish, can cause community changes at the whole-lake scale. This is not particularly surprising, given the high abundance that northern crayfish achieve. However, other lakes in which this might have been observed have subsequently been invaded by rusty crayfish (Olsen et al. 1991), possibly masking the effects of northern crayfish.

Several lakes contained nonindigenous crayfish but are not "invaded" in the sense of high abundances of the introduced species. This may be a function of time, and repeated sampling of these lakes in the future might reveal an ongoing invasion. This seems most likely, given that it has hap-

Fig. 3. Seed-bank experiment: mean (± 1 standard error (SE)) species richness, shoots, and shoots excluding *Chara* per replicate ($n = 5$). Bay 1 and Bay 2 sediments are from invaded Lake Ottawa. Reference sediments are from uninvaded Tenderfoot Lake.



pened in every other lake that we have observed to have a low abundance of the rusty crayfish (Olsen et al. 1991). On the other hand, it is possible that some lakes may simply not provide conditions or resources suitable for high population levels of crayfish and that such lakes would not experience

community changes. Although we can relate certain lake attributes to whether crayfish will become established in a lake (Capelli and Magnuson 1983; Lodge and Hill 1994), we cannot yet predict in which lakes crayfish will become invasive, as defined by reaching population densities that cause large ecological effects.

Crayfish density may be related to amounts of preferred, shelter-providing substrate or to predation by fish, neither of which was examined in this study. Predators not only impact crayfish directly by consuming them, but also indirectly by causing them to be less active (Collins et al. 1983; Hill and Lodge 1995). Determining the degree to which shelter, predators, and other factors influence whether a community is likely to be invaded will help managers predict, and potentially prevent, future negative community shifts. This information could also help facilitate shifts to a lake's original status. In this respect, further understanding of the separate steps of invasion (Kolar and Lodge 2001) will be important for management. The ability to separately predict the lakes in which crayfish are likely to be introduced, establish, and achieve high densities would allow managers to focus their prevention and control efforts to specific waters.

Macrophyte restoration

Results from the seed-bank study indicate that if crayfish densities are reduced, depauperate seed banks may prevent lakes from returning to their previous, vegetated status. Laboratory seed-bank studies may not always be indicative of what emerges in the field (Brown 1998; Lundholm and Simser 1999). However, eight different macrophyte species germinated from the reference sediments, indicating that our experiment provided adequate germination and growing conditions for a number of species. Because they grew in the reference sediments and were previously found in Lake Ottawa, at least three submergent species (*Potamogeton illinoensis*, *P. zosteriformis*, and *Zosterella dubia*) in addition to *Najas* and *Chara* should have germinated from the Ottawa sediments if they were present. We cannot discount the possibility that propagules of these and other species are rare and that a larger volume of sediments may have yielded additional species. However, in contrast to detection from above the water by the 1930s biologists, we found no above-ground evidence of these species in 3 years of intensive snorkeling, suggesting that propagule abundance is lower than in the past.

Only *Najas* and *Chara* germinated from Lake Ottawa's sediments. These species have likely persisted because *Najas* germinates from seed annually (Voss 1972) and the macroalgae *Chara* reproduces from spores. Many other submergent macrophytes, on the other hand, rely on clonal reproduction, overwinter as turions, tubers, rhizomes, or standing plants, and rarely set seed (Sculthorpe 1967). The absence of aboveground *Chara* and *Najas* in Lake Ottawa is probably due to continuous herbivory by crayfish. In a lake enclosure-exclosure experiment, *Najas* occurred in exclosures but did not grow in the crayfish exclosures (Lodge et al. 1994), and in a stream experiment, Perry et al. (2000) found that macroalgae (*Chara* and *Nitella*) were completely removed from crayfish exclosures but remained in exclosures.

Potamogeton amplifolius was present in Lake Ottawa but did not germinate in the experiment. We think it is unlikely that this is an effect of laboratory conditions because we germinated species within the same genus and of the same general growth form (e.g., *P. illinoensis*). More likely is that *P. amplifolius* propagules are rare. Since 2001, we have not seen *P. amplifolius* flower or set seed in Lake Ottawa, and if it set seed in the past, the general sparseness of the species makes sampling seeds difficult.

The apparently limited reversibility of the impacts of invasion is not unexpected, because long lag times and (or) strong hysteresis occur in other systems in which community-wide changes are the result of a stressor. For example, reducing eutrophication in lakes does not always lead to macrophyte recovery, because turbidity and low light penetration maintain unfavorable conditions for macrophyte germination (Scheffer et al. 1993). Because of sustained crayfish herbivory for about 15 years, any restoration of many of the macrophyte species that inhabited Lake Ottawa in the 1930s would likely require manual planting, even if crayfish abundance could be reduced dramatically. Despite the small volume of sediments in our germination experiment, it seems unlikely that propagules of all 12 submergent species are sufficiently abundant in the lake for unaided restoration to occur in Lake Ottawa. Conclusions for other lakes would depend on lake-specific factors, including differences in invasion histories and macrophyte communities. Even in Lake Ottawa, an alternative strategy would be to remove crayfish and then observe which species of macrophytes reappear before any replanting effort.

Acknowledgments

Comments by Reuben Keller, Gary Lamberti, Gary Belovsky, and two anonymous reviewers have greatly improved this manuscript. We thank Tim Kreps, Brett Peters, Jody Murray, Jay Frentress, Justin Allen, Angela Bobeldyk, and Tim Davidson for field and laboratory assistance. We also thank the Michigan Department of Natural Resources (MI DNR) Institute for Fisheries Research (IFR) staff, especially Jim Breck, Ellen Grove, and Tina Tincher, for assistance with the lake archives, Bill Ziegler for DNR sampling information, and the US Forest Service Ottawa National Forest (ONF) personnel, including Jerry Edde, John Pagel, Bob Evans, and Michelle Holland. This project was supported by a challenge cost-share agreement between the University of Notre Dame and the ONF and by the National Science Foundation. A sabbatical fellowship (to DML) provided time for manuscript preparation.

References

- Baskin, C.C., and Baskin, J.M. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California.
- Brown, S.C. 1998. Remnant seed banks and vegetation as predictors of restored marsh vegetation. *Can. J. Bot.* **76**: 620–629.
- Brown, K.M., and Lodge, D.M. 1993. Gastropod abundance in vegetated habitats — the importance of specifying null models. *Limnol. Oceanogr.* **38**: 217–225.

- Capelli, G.M., and Magnuson, J.J. 1983. Morphoedaphic and biogeographic analysis of crayfish distribution in northern Wisconsin. *J. Crustac. Biol.* **3**: 548–564.
- Carpenter, S.R., and Lodge, D.M. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquat. Bot.* **26**: 341–370.
- Carpenter, S.R., and Titus, J.E. 1984. Composition and spatial heterogeneity of submersed vegetation in a softwater lake in Wisconsin. *Vegetation*, **57**: 153–165.
- Collins, N.C., Harvey, H.H., Tierney, A.J., and Dunham, D.W. 1983. Influence of predatory fish density on trapability of crayfish in Ontario lakes. *Can. J. Fish. Aquat. Sci.* **40**: 1820–1828.
- Cooper, G.P. 1974. Michigan fisheries centennial report (1873–1973). Michigan Department of Natural Resources Fisheries Division, Lansing, Michigan. Fisheries Management Rep. No. 6.
- Creaser, E.P. 1931. The Michigan decapod crustaceans. *Pap. Mich. Acad. Sci. Arts Lett.* **13**: 257–276.
- Creaser, E.P. 1932. The decapod crustaceans of Wisconsin. *Trans. Wis. Acad. Sci. Arts Lett.* **27**: 321–338.
- Crow, G.E., and Hellquist, C.B. 2000. Aquatic and wetland plants of northeastern North America: a revised and enlarged edition of Norman C. Fasset's a manual of aquatic plants. University of Wisconsin Press, Madison, Wisconsin.
- de Winton, M.D., Clayton, J.S., and Champion, P.D. 2000. Seedling emergence from seed banks of 15 New Zealand lakes with contrasting vegetation histories. *Aquat. Bot.* **66**: 181–194.
- Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. *In* Community ecology. Edited by J. Diamond and T.J. Case. Harper and Row, New York. pp. 3–22.
- Dorn, N.J., and Mittelbach, G.G. 2004. Effects of a native crayfish (*Orconectes virilis*) on the reproductive success and nesting behavior of sunfish (*Lepomis* spp.). *Can. J. Fish. Aquat. Sci.* **61**: 2135–2143.
- Eschmeyer, R.W. 1936. Essential considerations for fish management in lakes. *In* Proceedings of the North American Wildlife Conference, Washington, D.C., 3–7 February 1936. US Government Printing Office, Washington, D.C. pp. 332–339.
- Eschmeyer, R.W., and Hazzard, A.S. 1936. [Date approximate.] Notes on survey. Archives of the MI DNR Institute for Fisheries Research, 212 Museums Annex Bldg., 1109 North University Avenue, Ann Arbor, MI 48109, USA.
- Haag, R.W. 1983. Emergence of seedlings of aquatic macrophytes from lake sediments. *Can. J. Bot.* **61**: 148–156.
- Hazzard, A.S., and Brown, C.J.D. 1938. [Date approximate.] Institute for fisheries research inventory methods. Archives of the MI DNR Institute for Fisheries Research, 212 Museums Annex Bldg., 1109 North University Avenue, Ann Arbor, MI 48109, USA.
- Hill, A.M., and Lodge, D.M. 1995. Multi-trophic-level impact of sublethal interactions between bass and omnivorous crayfish. *J. North Am. Benthol. Soc.* **14**: 306–314.
- Hubbs, C.L., and Eschmeyer, R.W. 1938. The improvement of lakes for fishing: a method of fish management. Franklin DeKleine Company, Lansing, Michigan.
- Kershner, M.W., and Lodge, D.M. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. *J. North Am. Benthol. Soc.* **14**: 414–422.
- Kolar, C.S., and Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16**: 199–204.
- Lodge, D.M., and Hill, A.M. 1994. Factors governing species composition, population size, and productivity of cool-water crayfishes. *Nord. J. Freshw. Res.* **69**: 111–136.
- Lodge, D.M., and Lorman, J.G. 1987. Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. *Can. J. Fish. Aquat. Sci.* **44**: 591–597.
- Lodge, D.M., Kratz, T.K., and Capelli, G.M. 1986. Long-term dynamics of 3 crayfish species in Trout Lake, Wisconsin. *Can. J. Fish. Aquat. Sci.* **43**: 993–998.
- Lodge, D.M., Krabbenhoft, D.P., and Striegl, R.G. 1989. A positive relationship between groundwater velocity and submersed macrophyte biomass in Sparkling Lake, Wisconsin. *Limnol. Oceanogr.* **34**: 235–239.
- Lodge, D.M., Kershner, M.W., Aloï, J.E., and Covich, A.P. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a fresh-water littoral food-web. *Ecology*, **75**: 1265–1281.
- Lodge, D.M., Stein, R.A., Brown, K.M., Covich, A.P., Bronmark, C., Garvey, J.E., and Klosiewski, S.P. 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Aust. J. Ecol.* **23**: 53–67.
- Lorman, J.G., and Magnuson, J.J. 1978. Role of crayfishes in aquatic ecosystems. *Fisheries*, **3**: 8–10.
- Lundholm, J.T., and Simser, W.L. 1999. Regeneration of submersed macrophyte populations in a disturbed Lake Ontario coastal marsh. *J. Gt. Lakes Res.* **25**: 395–400.
- McFarland, D.G., and Rogers, S.J. 1998. The aquatic macrophyte seed bank in Lake Onalaska, Wisconsin. *J. Aquat. Plant Manag.* **36**: 33–39.
- McMurry, K.C., Eschmeyer, R.W., and Davis, C.M. 1933. Objectives and methods in the lake inventory in Michigan. *Pap. Mich. Acad. Sci. Arts Lett.* **18**: 259–276.
- Miller, D.E. 1936. Michigan lake survey — a cooperative enterprise. *Trans. Am. Fish. Soc.* **66**: 128–130.
- Nichols, S.A. 2001. Long-term change in Wisconsin lake plant communities. *J. Freshw. Ecol.* **16**: 1–13.
- Olsen, T.M., Lodge, D.M., Capelli, G.M., and Houlihan, R.J. 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. *Can. J. Fish. Aquat. Sci.* **48**: 1853–1861.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., von Holle, B., Moyle, P.B., Byers, J.E., and Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, **1**: 3–19.
- Perry, W.L., Lodge, D.M., and Lamberti, G.A. 2000. Crayfish (*Orconectes rusticus*) impacts on zebra mussel (*Dreissena polymorpha*) recruitment, other macroinvertebrates and algal biomass in a lake-outlet stream. *Am. Midl. Nat.* **144**: 308–316.
- Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience*, **50**: 53–65.
- Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., and Wall, D.H. 2000. Biodiversity — global biodiversity scenarios for the year 2100. *Science (Washington, D.C.)*, **287**: 1770–1774.
- Scheffer, M., Hosper, S.H., Meijer, M.L., Moss, B., and Jeppesen, E. 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* **8**: 275–279.
- Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. St. Martin's Press, New York.
- Skogerboe, J.G., Poovey, A.G., Getsinger, K.D., and Kudray, G. 2003. Invasion of Eurasian watermilfoil in lakes of the western upper peninsula, Michigan. U.S. Army Corps of Engineers, Washington, DC. Report No. ERDC/EL TR-03-10.
- Systat Software Inc. 2002. SYSTAT 10.2 [computer program]. Systat Software Inc., Richmond, California.

- Voss, E.G. 1972. Michigan flora: a guide to the identification and occurrence of the native and naturalized seed-plants of the state. Cranbrook Institute of Science, Bloomfield Hills, Michigan.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A., and Losos, E. 1998. Quantifying threats to imperiled species in the United States. *Bioscience*, **48**: 607–615.
- Wilson, K.A. 2002. Impacts of the invasive rusty crayfish (*Orconectes rusticus*) in northern Wisconsin lakes. Ph.D. thesis, University of Wisconsin, Madison, Wisconsin, U.S.A.
- Wilson, K.A., Magnuson, J.J., Lodge, D.M., Hill, A.M., Krazt, T.K., Perry, W.L., and Willis, T.V. 2004. A long-term rusty crayfish (*Orconectes rusticus*) invasion: dispersal patterns and community change in a north temperate lake. *Can. J. Fish. Aquat. Sci.* **61**: 2255–2266.

Copyright of *Canadian Journal of Fisheries & Aquatic Sciences* is the property of NRC Research Press and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.