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Distribution and community-level effects of the Chinese mystery snail (*Bellamya chinensis*) in northern Wisconsin lakes

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Abstract Managing invasive species requires information about their distributions and potential effects, but community-level impacts of invasive animals remain poorly understood. The Chinese mystery snail (*Bellamya chinensis*) is a large invasive gastropod that achieves high densities in waters across North America, yet little is known about its ecological significance in invaded systems. We surveyed 44 lakes to describe the patterns and determinants of *B. chinensis* distributions in northern Wisconsin, USA, and to assess the likelihood of effects on native snail communities in the invaded systems. *B. chinensis* was widespread among surveyed lakes (21 of 42 lakes with snails) and its occurrence was correlated with indicators of lake productivity and anthropogenic dispersal vectors (boat landings, distance to population centers, shoreline housing density). Some native snail species tended not to occur at sites where *B. chinensis* was abundant; among these was *Lymnaea stagnalis*, which suffered reduced survival in the presence of *B. chinensis* in a recently published mesocosm study. However, there was no difference in overall snail assemblage structure at either the site or lake level as a function of *B. chinensis* presence or abundance. Lake occurrences of many snail species have apparently been lost over time, but a comparison to a 1930s survey showed that there was no increased likelihood of species loss in lakes invaded by *B. chinensis* (or by the invasive crayfish *Orconectes rusticus*). Although *B. chinensis* is widespread and sometimes abundant in northern Wisconsin lakes, it does not appear to have strong systematic impacts on native snail assemblages.

Keywords Gastropoda · Viviparidae · Biogeography · *Cipangopaludina* · *Bellamya japonica*

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Introduction

The ecological impacts of an invasive species are a function of its range, abundance, and per-capita effects, and may be manifested at levels of biological

organization ranging from the genome to the ecosystem (Parker et al. 1999). For researchers and managers interested in conserving species diversity, understanding impacts at the community level is particularly important. An emerging consensus suggests that the risk of an invasive species causing ecological change depends on the degree of functional similarity between that species and the native species pool; distinctiveness of the invader enhances its impact on native species (Ricciardi and Atkinson 2004), and competitors rarely cause extinctions, whereas predators are more likely to do so (Davis 2003; Sax et al. 2007). However, there remains a high level of taxonomic and geographic bias in the study of invasive species (Pysek et al. 2008), and relatively few studies have quantified the community-level consequences of invasive animals (Parker et al. 1999).

Freshwater gastropod assemblages provide a useful and important model system for studying the community-level effects of invasive competitors. Field studies of gastropods show patterns consistent with interspecific competition, and experimental manipulations have demonstrated the importance of interspecific resource competition and other negative interactions within this group (Brown 1982; Hershey 1990; Adam and Lewis 1992; Turner et al. 2007; see review in Dillon 2000). Furthermore, freshwater gastropods are of significant conservation importance because they are both highly diverse and highly threatened (Lydeard et al. 2004; Strayer 2006; Lysne et al. 2008). Concurrently, many gastropods have become invasive; for instance, the United States Geological Survey's Nonindigenous Aquatic Species database lists ∼40 invasive gastropod species in the United States (http://nas.er.usgs.gov). Yet while some invasive gastropods are known to have large effects on invaded ecosystems (e.g., Hall et al. 2003; Carlsson et al. 2004) or on particular native species (e.g., Pointier and McCullough 1989), their community-level effects on potential competitors within the snail assemblage remain relatively unexplored.

The Chinese mystery snail (*Bellamya* [=*Cipangopaludina*] *chinensis* (Reeve 1863)) is a viviparid gastropod native to Asia. It is very large, reaching a shell length of ∼65 mm and dry tissue mass of ∼1 g (Jokinen 1982; Solomon unpubl. data). Its first reported occurrence in North America was in a food market in San Francisco in the early 1890s (Wood

1892). Since that time, it has spread across much of the United States and parts of southern Canada, with occurrences in at least 27 states plus Quebec (Jokinen 1982, http://nas.er.usgs.gov). Limited published literature, anecdotal accounts, and our own observations suggest that it can reach extremely high densities in systems where it occurs. Due to its wide distribution and high densities, some authors have speculated that it might have significant impacts in invaded systems (Bury et al. 2007), and experimental studies indicate it can negatively affect native gastropods (Johnson et al. 2009). However, very little is known about the distribution of *B. chinensis* within invaded regions, and no study has attempted to quantify its impacts in invaded ecosystems.

In this study, we surveyed snail assemblages in 44 lakes in a region known to be invaded by *B. chinensis*. We sought to describe the patterns and determinants of *B. chinensis* distributions, and to assess whether invasions of *B. chinensis* have altered the composition of native snail assemblages. Because impacts of invasive species may be localized or widespread, and may occur rapidly or gradually, we considered multiple spatial and temporal scales in our analysis. We tested for impacts of *B. chinensis* on native snails at both the lake and site (within lake) scale, and combined our own data with historical survey data from the 1930s to test whether contemporary assemblage structure or long-term changes in assemblages were related to the occurrence or abundance of *B. chinensis*.

Methods

Study system

We surveyed snail assemblages in lakes of the Northern Highlands Lake District (NHLD), Wisconsin, USA. There are >7,500 lakes in this region, which vary widely with regard to morphology, chemistry, human use, and other factors (Kratz et al. 1997; Hanson et al. 2007). These lakes are an important cultural and economic resource, and invasive species are a primary management concern.

Recent reports indicate that *B. chinensis* is widely distributed across Wisconsin and Minnesota (Jass 2004; Bury et al. 2007; Johnson et al. 2009), and anecdotal accounts and our own observations indicate that it has been present in some lakes in the NHLD

since at least 2003. However, the date of first occurrence of *B. chinensis* in the NHLD can be given only generally based on current knowledge, as some time between 1940 and 2000. The earliest records of the species in the Great Lakes and Upper Mississippi region are from the late 1930s and 1940s (Mills et al. 1993; Bury et al. 2007), and the earliest Wisconsin record is from the 1950s (Teskey 1954).

The taxonomy of introduced *Bellamya* in North America is somewhat uncertain. Some authors have recognized two species (*B. chinensis* and *B. japonica*), whereas others have argued that the two forms are simply variants of *B. chinensis*. For many years, taxonomists placed the species in the genus *Cipangopaludina*. We follow Smith (2000), who provided a complete synonymy and the most recent taxonomic revision, affirming the two-species concept and placing the species in the genus *Bellamya*.

Field sampling

During the summer of 2006 we collected snails at 4–6 sites in each of 44 focal lakes. Survey lakes ranged in surface area from 14 to 1,400 ha (median = 130 ha), and were selected to span broad gradients of landscape position, water chemistry, human use, and other characteristics, and to maximize overlap with lakes where Morrison (1932) has previously described snail assemblages. For each lake, site locations were chosen randomly within each compass quadrant of the shoreline, using Geographic Information System (GIS) software (ArcGIS 9.2; ESRI, Redlands, California). At each site we placed a 20 m transect line on the lake bottom along the 1 m depth contour. At 2 m intervals along the transect, two snorkelers collected all the snails from within $0.25 \, m^2$ quadrats (10 quadrats per site). They then searched the vicinity of the transect haphazardly for 5 minutes to reduce the likelihood that *B. chinensis* presence at a site escaped detection. Sampling ceased after the fourth site if at least 25 quadrats with non-zero snail abundances had been sampled; otherwise, sampling continued at alternate sites until that threshold was reached or 6 sites had been sampled. At some sites the entire 20-m transect fell in thick macrophyte beds, precluding effective snorkel surveys. In these cases we sampled snails by vigorously sweeping a D-net (500 µm mesh) through the macrophytes in two $1 \, m^2$ areas. Collected snails were preserved in 80% ethanol. Identifications

were made according to Burch (1989), following the revision of Hubendick (1951) for the Lymnaeidae, Hubendick (1955) for the Planorbidae, and Wethington and Lydeard (2007) for the Physidae. All samples are being curated into the Illinois Natural History Survey Mollusk Collection.

We also tested the effectiveness of a rapid assessment protocol for detecting the presence of *B. chinensis*. Two observers snorkeled around the vicinity of the boat launch (if present) for up to 5 min each, or until *B. chinensis* was found. We conducted this rapid assessment at 27 of the focal survey lakes, as well as at 8 additional lakes where we did not conduct full quadrat surveys.

Statistical analyses

The raw data from our sampling consisted of abundances (counts) for each species in each quadrat. For most analyses we aggregated these data, as either the summed abundance at the site level or the mean density at the lake level. Unless otherwise noted, all statistical analyses were conducted in the R statistical package (R Development Core Team 2008); the "vegan" package was used for multivariate analyses (Oksanen et al. 2008).

We assessed the adequacy of our sampling design in two ways. First, we used linear regression to test for a relationship between sampling effort and lake-level species richness. Sampling effort varied from a minimum of 8 quadrats per lake (in lakes where all sites occurred in dense macrophytes, and only net sweep samples were taken) to a maximum of 60 quadrats per lake (in lakes where snails were rare or absent, and 10 quadrats were sampled at each of 6 non-vegetated sites). Second, we developed species-effort curves by rarefaction. Within each lake, we constructed 500 bootstrap samples of the quadrat-level data at each possible level of sampling intensity (from 1 quadrat up to the number actually sampled in that lake). We plotted the mean bootstrapped species richness against sampling effort for each lake.

We described the probability of *B. chinensis* occurrence in a lake using multiple logistic regression (a generalized linear model with a logit link function). We considered eight predictors describing lakes in terms of their physical and chemical characteristics (area, conductivity, and Secchi depth), potential anthropogenic dispersal vectors (shoreline housing

density, distance to population center, and accessibility to boats), and the presence of other invasive species that might interact with *B. chinensis* (rusty crayfish *Orconectes rusticus* and banded mystery snail *Viviparus georgianus*). Sources and methods for these data are described in the Appendix (Table A1—Electronic Supplementary Material). Continuous predictor variables were log-transformed when necessary to normalize distributions, and all continuous predictors were transformed to Z-scores. We used all-subsets regression based on Akaike's Information Criterion to identify the best subsets of predictors, assessed the significance of each term in the selected model using likelihood ratio tests, and described the predictive power of the model by quantifying the area under the receiver operating characteristic curve (ROC AUC) of sensitivity versus 1-specificity (Agresti 2002).

We also considered whether within-lake distributions of *B. chinensis* were related to the relative proximity of boat launches. For all lakes where *B. chinensis* was present, we calculated the shoreline distance between each survey site and the nearest boat launch using a Geographic Information System (GIS). To allow comparisons between lakes of different sizes that may have been invaded at different times, we relativized all of the site-to-launch distances for each lake by dividing by the maximum site-to-launch distance for that lake. Thus all the distances for all lakes ranged between 0 and 1. We then used logistic regression to test the hypothesis that the likelihood of *B. chinensis* presence at a site was higher for sites close to boat launches. We excluded from this analysis one lake where *B. chinensis* was present at every site.

Potential effects of *B. chinensis* on the native snail assemblage were examined using multivariate analyses. First, we used non-metric multidimensional scaling (NMDS) to reduce the dimensionality of the community data and display how dominant gradients of variation in species composition were related to environmental variables and to the presence and abundance of *B. chinensis*. NMDS is an ordination method that preserves the ranked-ordered distances between sample points in ordination space by minimizing a measure of disagreement (referred to as stress) between the compositional dissimilarities and the distance between points in the ordination diagram (Kruskal 1964). In the context of our study, we were particularly interested in separating the effects on assemblage structure due to *B. chinensis* from those

due to environmental variables and other invasive species. In our study lakes, conductivity is a primary environmental determinant of snail assemblage structure (see Results), and the rusty crayfish (*Orconectes rusticus*) and the banded mystery snail (*Viviparus georgianus*) are invasive species that might also influence snail assemblages. We therefore tested for an effect of *B. chinensis* on assemblage structure while controlling for conductivity and the presence of *O. rusticus* and *V. georgianus*. This analysis was conducted using permutation MANOVA (perMANOVA; (Anderson 2001), which allows for ANOVA-style partitioning of variance among predictors when the response is a multivariate community distance matrix. Both NMDS and perMANOVA consider the ranked dissimilarities in assemblage structure among locations, which we calculated using Sørensen's (Bray-Curtis) distance metric. Prior to the analyses, species abundance data were $\log(x + 1)$ transformed and relativized by species maxima. NMDS ordinations were conducted in the PC-ORD software package (McCune and Mefford 1999), and perMANOVA tests were performed using the "adonis" function in R. We also inspected plots of the abundance of each species versus the abundance of *B. chinensis* for evidence that higher *B. chinensis* abundances were associated with lower abundances of native species.

We quantified changes in lake-level snail assemblages from 1930 (prior to invasion by *B. chinensis*) to the present and considered whether these changes were related to invasion by *B. chinensis*. Historical snail assemblage data were available for 30 of our survey lakes (Morrison 1932). To make those data comparable with our own, two differences in methods and objectives had to be reconciled. First, advances in freshwater gastropod systematics over the last 75 years dictated a substantial simplification of Morrison's taxonomy. Second, Morrison's paper focused on compiling a list of the localities where species where known to occur, rather than describing the snail assemblages in lakes. The omission of a lake from his list of localities for a species could therefore represent merely a lack of data, rather than a true absence of that species in that lake. To account for this we classified snail occurrences (species-lake combinations) recorded by Morrison as either retained (still present in our survey of that lake) or lost (absent from our survey of that lake), and ignored occurrences in our own data that were not recorded by Morrison. We

used logistic regression to test whether the likelihood that occurrences were lost was predicted by the current-day presence of *B. chinensis*. In this analysis we controlled for other factors that might influence the likelihood that an occurrence was lost, including the presence of the invasive snail predator *O. rusticus*; the presence of the invasive snail *V. georgianus*; and contemporary shoreline housing density, an indicator of the extent of human alteration of littoral zones, which is the primary anthropogenic impact on these lakes (Carpenter et al. 2007). The Morrison data and the species synonomy that we used are available in Tables A2 and A3 (Electronic Supplementary Material).

Results

Sampling efficiency and snail community composition

We collected and identified 17,516 snails representing 21 species (Table A4—Electronic Supplementary Material). Our sampling strategy effectively represented the species membership of the snail assemblages. There was no evidence that we found more species when effort was higher; in fact, there was a negative relationship between species richness and the number of quadrats sampled ($F_{1,42} = 25.4$, $P < 0.0001$, $R^2 = 0.38$), suggesting that the adaptive sampling strategy was effective in concentrating the greatest effort in lakes where snails were most difficult to find. Rarefaction analysis demonstrated that sampling effort was sufficient to find most or all of the species present in the habitats that we surveyed. For every lake, species-effort curves reached an asymptote at or near the species richness that we observed in our samples, often at a sampling intensity less than the number of quadrats that we actually surveyed in the lake (Fig. A1—Electronic Supplementary Material).

Species abundances were approximately log-normally distributed, with a few very abundant species and many rare species. For instance, the two most numerically-dominant species (*Amnicola limosa* and *Marstonia lustrica*) comprised 66% of total abundance. Lake-level species richness ranged from 0 (Camp Lake and Crystal Lake) to 14 (Allequash Lake and Tomahawk Lake). The best model describing species richness, selected by AIC using all-subsets

regression, included Secchi depth and conductivity but not log(area), *B. chinensis* presence, *O. rusticus* presence maximum depth, or an indicator for whether only vegetated sites were sampled in the lake (richness = $-0.75 \times$ Secchi + $0.05 \times$ conductivity + 6.0; $P < 0.0001$, $R^2 = 0.45$).
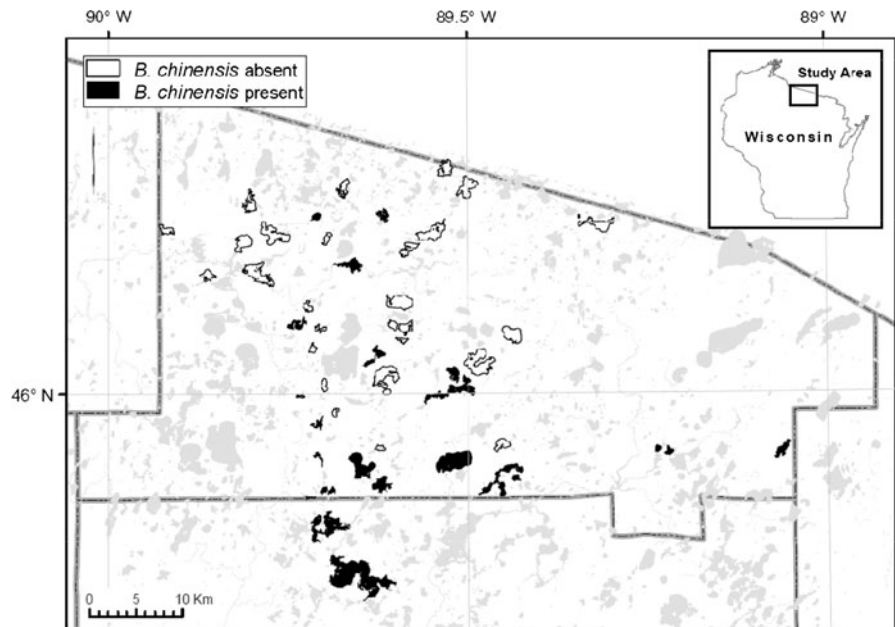
Distribution of *B. chinensis* within and among lakes

B. chinensis was widely distributed across the study region (Fig. 1). Of the 42 focal lakes in which snails were present, we observed *B. chinensis* in quadrat samples in 15 lakes, and during haphazard searching near quadrats in an additional 6 lakes. We also observed *B. chinensis* in 2 of the 8 lakes where only the rapid assessment protocol was conducted. The rapid assessment protocol was fairly effective, identifying *B. chinensis* presences at 9 of 12 lakes where it was used in conjunction with regular quadrat sampling and where *B. chinensis* was detected by either method.

There was a strong geographic pattern in *B. chinensis* occurrences, with the likelihood that a lake was invaded much higher in the south than in the north of the study region (Fig. 1). Invaded lakes in our survey occurred in the Chippewa River and Wisconsin River portions of the Mississippi River drainage basin and not in the Lake Superior basin. However, we have observed *B. chinensis* in lakes in the Superior basin that were not among the 3 lakes in that basin that we surveyed here (Johnson et al. 2009). The best model (AIC = 59.9) describing *B. chinensis* presence indicated that it was more likely to occur in lakes that were closer to a population center, or that had higher shoreline housing density or lower water clarity (Table 1). This model had good predictive power (area under the receiver operating characteristic curve = 0.83), illustrating a correct classification rate of 78 % (based on a decision threshold of 0.5). Good alternative models either added a positive conductivity term to those listed above (AIC = 60.1) or selected the conductivity term in place of the Secchi depth term (AIC = 61.0).

When present, *B. chinensis* was patchily distributed within lakes. In all but one of the fifteen lakes where we detected *B. chinensis* in quadrat sampling, it occurred in between 2% and 56% of quadrats (mean 15% ± 16% SD), and mean densities ranged

Fig. 1 Map of the Northern
Highlands Lake District,
showing lakes where the
Chinese mystery snail
Bellamya chinensis was
present (lakes filled in
black) and absent (lakes
outlined in *black*). Lakes in
grey were not surveyed

between 0.16 and 4.00 individuals m^{-2} (mean 0.81 ± 1.04 SD). Otter Lake was a clear exception to this pattern; in this lake, *B. chinensis* was present at all four surveyed sites, and in 15 of 16 (94%) of quadrats. The mean density of *B. chinensis* in Otter Lake was 38 individuals m^{-2}. Multiplying these densities by an estimate of the mean biomass of *B. chinensis* (mean ± SD of dry tissue mass excluding shell was 0.27 ± 0.15 g for a random sample of 30 *B. chinensis* collected from Allequash Lake in 2004; Solomon unpubl. data) yields biomass estimates of 10.33 g dry mass m^{-2} in Otter Lake and 0.04–1.08 g dry mass m^{-2} in the other lakes.

Within invaded lakes, the probability that *B. chinensis* occurred at a given site was higher for sites closer to boat launches (logistic regression, $\chi_1^2 = 6.1$, $P = 0.01$; Fig. 2a). There was also weak evidence that *B. chinensis* was more likely to occur in lakes with improved public boat launches than in lakes where public access was absent or limited to carry-in boats (Pearson's $\chi^2 = 2.8$, $P = 0.09$; Fig. 2b).

Effects of *B. chinensis* on native snail assemblages

High site-level densities of *B. chinensis* were associated with low densities of some native species (Fig. 3). Specifically, *Lyogyrus granum*, the *Valvata* species, the *Lymnaea* species, *Physa acuta*, and *Helisoma trivolvis* tended not to occur at sites where *B. chinensis* abundance was greater than between 0 and 2 individuals m^{-2}. The three species of *Lymnaea* together occurred at 19 sites where *B. chinensis* was absent, but at only 3 sites where *B. chinensis* was present. In contrast, there was no evidence for a negative relationship between the site-level abundance of *B. chinensis* and that of its closest relatives in these lakes, the viviparids *Campeloma decisum* and *Viviparus georgianus*.
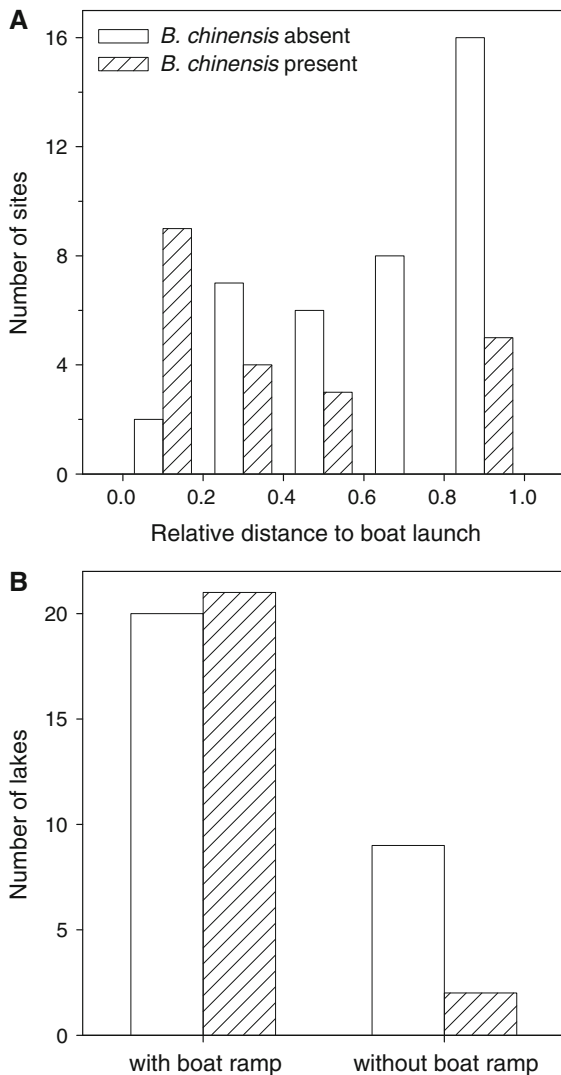
Table 1 Multiple logistic regression model describing the probability of *B. chinensis* occurrence in a lake

	Estimate	SE	$P(\chi^2)$
(Intercept)	−0.26	0.35	
Secchi depth	−0.84	0.40	0.02
Distance to Minocqua	−0.71	0.37	0.04
Log (buildings km^{-1})	1.00	0.40	0.005

Variables were selected by AIC using an all-subsets procedure. Estimate, point estimate for coefficient; SE, standard error of estimate; $P(\chi^2)$, probability of statistical significance associated with a likelihood ratio test of the hypothesis that the coefficient = 0

Note: Candidate variables included those in the selected model above, as well as log (lake area), conductivity, presence of a public boat ramp, presence of rusty crayfish, and presence of the invasive snail *Viviparus georgianus*. All continuous predictors were Z-transformed

Fig. 2 Relationship between *Bellamya chinensis* occurrence and public boat launches. **a** The probability of *B. chinensis* occurrence at sites within lakes where it occurred was highest for sites close to a boat launch ($P = 0.01$). Sites were binned according to their relative distance to the nearest boat launch (see text). Data are from 14 lakes where *B. chinensis* was detected in quadrat sampling (excludes one lake where *B. chinensis* was found at all sites). **b** *B. chinensis* was more likely to occur in lakes with improved public boat launches than in lakes without launches or where access was limited to carry-in boats only ($P = 0.09$)

Despite the negative association between the site-level abundances of *B. chinensis* and some native snail species, there was no evidence that *B. chinensis* affected overall snail assemblage structure at the level of either sites or lakes (Fig. 4). Total native species richness was, if anything, higher at sites where

B. chinensis was present (mean = 6.0, $n = 20$) than at sites where only native species were present (mean = 4.8, $n = 123$; $t_{23} = 1.7$, $P = 0.1$). Assemblage structure at the lake level was correlated with environmental variables, particularly Secchi depth and conductivity (Fig. 4b). Results from the perMANOVA analysis confirmed the patterns suggested by the NMDS ordinations; even after controlling for conductivity and for the presence of *O. rusticus* and *V. georgianus*, there was no effect of the presence of *B. chinensis* on lake-level snail assemblages (Table 2).

Similarly, while there were significant changes in snail assemblages between the historical surveys and our own, there was no apparent effect of *B. chinensis* invasion on these changes. Many of the snail occurrences (species-lake combinations) that were present in the historical data were "lost" (that is, were not detected by our surveys; see Fig. 5, where most points fall below the 1:1 line). The likelihood that an historical occurrence was lost varied among species and families (Table 3; Fig. 5a). Species that were rare in the historical data (particularly lymnaeids, ancylids, and valvatids) often were not detected in any of the lakes that they historically occupied (Fig. 5a), although two of these (*Valvata sincera* and *Promenetus exacuous*) were detected in lakes that they had not been recorded in historically. The likelihood that an historical occurrence was lost did not vary as a function of present-day shoreline housing density, of main effects of the presence of *B. chinensis*, *O. rusticus*, or *V. georgianus*, or of interaction terms of those main effects with species (Table 3; Fig. 5b).

Discussion

Distribution of *B. chinensis*

The results of our regional survey and the findings of Bury et al. (2007) for Minnesota demonstrate that *B. chinensis* occurs frequently within invaded regions, besides being widely distributed across the United States (Jokinen 1982, http://nas.er.usgs.gov). In the Northern Highlands Lake District of Wisconsin, *B. chinensis* occurred in 50% of the 42 lakes in which we detected any snails with our full sampling protocol, making it among the most frequently occurring species in our study. Furthermore, the
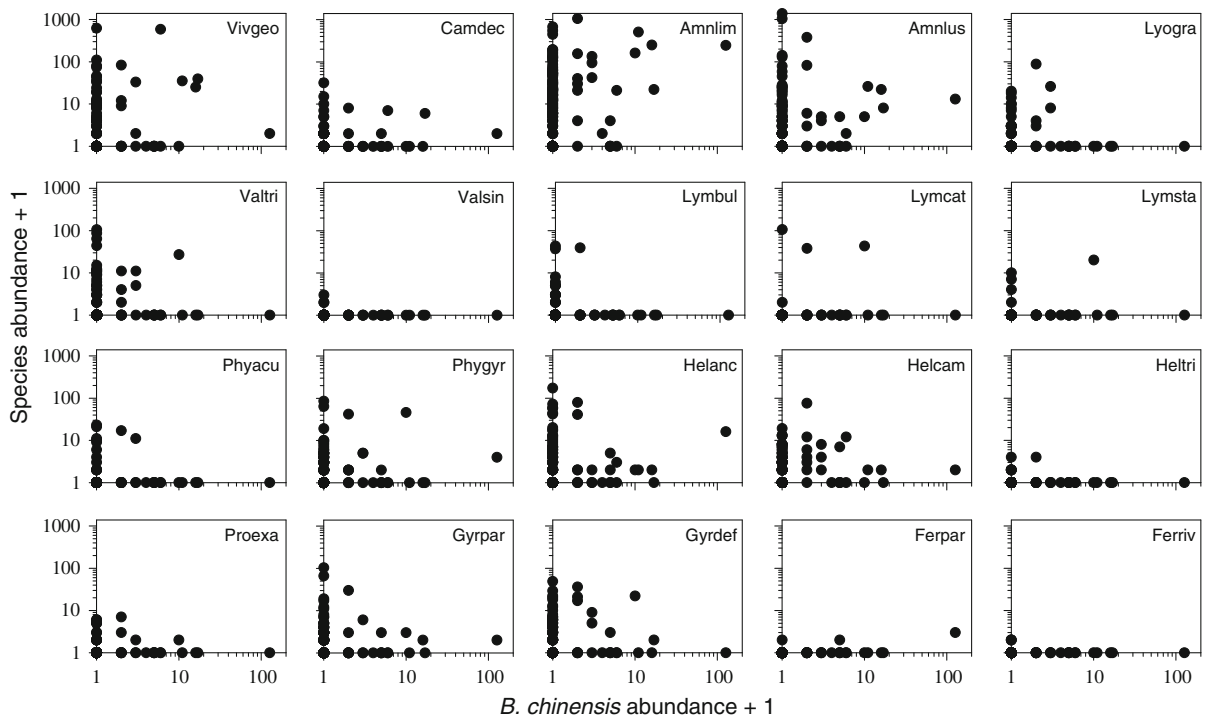
Fig. 3 Abundance of each native snail species (*vertical axis*) and *B. chinensis* (*horizontal axis*) at 197 sites in 42 lakes. Note log scale on axes. For each panel, the species plotted on the *y*-axis is indicated in the *top right corner*. Species are *Amnicola limosa* (Amnlim), *Marstonia lustrica* (Marlus), *Lyogyrus granum* (Lyogra), *Valvata sincera* (Valsin), *Valvata tricarinata* (Valtri), *Bellamya chinensis* (Belchi), *Campeloma decisum* (Camdec), *Viviparus georgianus* (Vivgeo), *Ferrissia parallela* (Ferpar), *Ferissia rivularis* (Ferriv), *Lymnaea bulimoides* (Lymbul), *Lymnaea catascopium* (Lymcat), *Lymnaea stagnalis* (Lymsta), *Physa acuta* (Phyacu), *Physa gyrina* (Phygyr), *Gyraulus deflectus* (Gyrdef), *Gyraulus parvus* (Gyrpar), *Helisoma anceps* (Helanc), *Helisoma campanulata* (Helcam), *Helisoma trivolvis* (Heltri), and *Promenetus exacuous* (Proexa)

strong south-to-north pattern in occurrences and the link between occurrences and boat launches suggest that this species has not yet reached all of the lakes in the NHLD in which it could potentially persist. While our focal lakes were selected with some bias towards lakes where previous studies had observed snails, they were otherwise broadly representative of lakes in the region. It may therefore be reasonable to expect that 50% or more of the accessible lakes in this region are or could be invaded by *B. chinensis*. In comparison, maximum potential distributions of many aquatic invasive species seem to be near or below half of the lakes in a region. For instance, 41% of 179 Minnesota lakes were estimated to be susceptible to invasion by spiny water flea *Bythotrephes longimanus* (Branstrator et al. 2006), 55% of 8,110 Ontario lakes and 11% of 5164 Wisconsin lakes were estimated to be susceptible to invasion by rainbow smelt *Osmerus mordax* (Mercado-Silva et al. 2006), and

9.9% of 3908 Wisconsin lakes are deemed environmentally suitable for rusty crayfish *Orconectes rusticus* (Olden, unpubl. data). In regions where it occurs, *B. chinensis* may be among the most ubiquitous of invasive aquatic animals.

An important research need for managing any invasive species is to identify which systems are susceptible to invasion. Our analyses indicated that the likelihood of *B. chinensis* occurrence was influenced both by intrinsic properties of lakes (Secchi depth and conductivity) and by human activities (distance to population center, shoreline housing density, and boat launches). Apparent relationships between environmental characteristics and the occurrence of *B. chinensis* should be interpreted with caution given the suggestion above that this species has not yet saturated the landscape in the NHLD (Peterson 2003). With that caution in mind, we discuss below what general properties of lakes
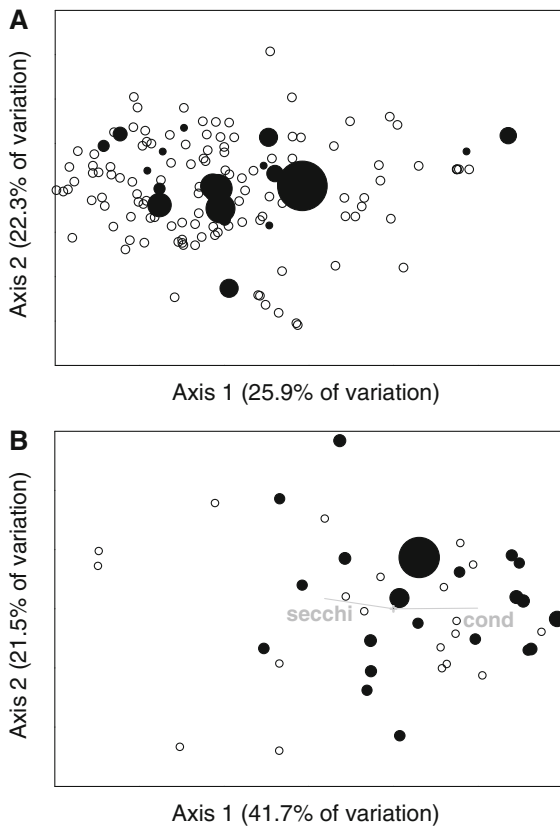
Fig. 4 Non-metric multidimensional scaling (*NMDS*) of snail assemblage data, showing the two axes (of three total) that explained the most variation in assemblage structure in each ordination. **a** Points represent assemblage structure at the site level (143 sites in 42 lakes) for sites where *B. chinensis* was absent (*empty circles*) or present (*filed circles*; diameter of circle proportional to log(abundance) of *B. chinensis* at the site). Final stress = 0.20. **b** Points represent assemblage structure at the lake level (42 lakes). Symbols as in (**a**). Radiating lines indicate the direction and strength of correlations between ordination axis and environmental variables that explained >10% of the variation along any axis (*secchi*, Secchi depth, and *cond*, conductivity). Ordination has been rotated to maximize the correlation between conductivity and Axis 1. Final stress = 0.14

Table 2 perMANOVA tests of hypothesized factors influencing snail assemblage structure, using lake-level data

	df	SS	*F*	*P*
Conductivity	1	0.91	3.06	<0.001
O. rusticus	1	0.36	1.21	0.24
V. georgianus	1	0.22	0.75	0.76
B. chinensis	1	0.29	0.97	0.47
Residual	37	10.96		

Interaction terms are excluded for simplicity; none were significant (all $P > 0.4$). *df*, degrees of freedom; SS, sums of squares; *F*, pseudo-*F* statistic for the perMANOVA test; *P*, probability of statistical significance (based on 1,000 permutations of the data) associated with a test of the hypothesis that there is no effect of a predictor. Terms for species are presence-absence of three invasive species: *Orconectes rusticus* (rusty crayfish), *Viviparus georgianus* (banded mystery snail), and *Bellamya chinensis* (Chinese mystery snail)

ecosystems may increase their susceptibility to *B. chinensis* invasion.

The relationships between *B. chinensis* occurrence and lake conductivity and Secchi depth may indicate an affinity for more productive systems, and/or minimum Ca requirements for shell growth. Both Secchi depth and conductivity are correlated with lake productivity, and more productive systems may allow greater snail species richness (and greater likelihood of *B. chinensis* occurrence) because of

greater food availability (Dillon 2000). Conductivity is also strongly correlated with Ca concentration in these lakes (e.g., Johnson et al. 2008). Calcium requirements for *B. chinensis* are likely to be high due to its large shell, and Ca limitation has been suggested to be a primary determinant of occurrence for other invasive mollusks (e.g., Whittier et al. 2008). A survey of >200 Connecticut water bodies found *B. chinensis* only in those with Ca concentrations >5 mg l^{-1}, even though 75% of the waters surveyed had Ca concentrations lower than that threshold (Jokinen 1982). We found *B. chinensis* in some systems that likely had Ca concentrations <5 mg l^{-1} (based on the relationship between conductivity and Ca in 50 NHLD lakes; data not shown), but nonetheless the positive relationship between conductivity and the likelihood of *B.chinensis* occurrence could indicate a Ca limitation effect. It is also important to note that conductivity is correlated with many important properties of lakes in this region (Kratz et al. 1997), and so its relationship with *B. chinensis* occurrence could be masking the effects of other factors. For instance, lakes with high conductivity may also be those most frequently visited by boaters, since they tend to be large and support recreational fishing opportunities (Reed-Andersen et al. 2000).

The relationships between *B. chinensis* occurrence and distance to population center, shoreline housing density, and boat launches indicate that greater human use of a lake is associated with a higher
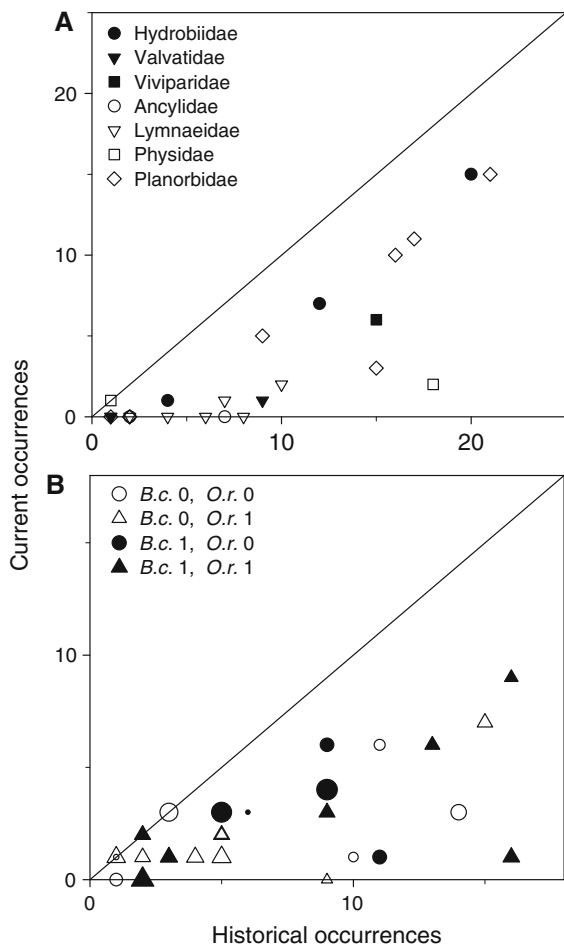
Fig. 5 Our surveys detected some but not all of the snail occurrences (species-lake combinations) recorded by Morrison (1932). **a** Number of lakes in which a species was found in our surveys plotted against number of lakes in which it historically occurred. *Symbols* are *coded* to indicate the family to which each species belongs, including both prosobranchs (*solid points*) and pulmonates (*hollow points*). **b** Number of species found in a lake in our surveys plotted against number of species historically found there. Symbols are coded according to the presence (1) or absence (0) of the invasive species *Bellamya chinensis* and *Orconectes rusticus*. Size of symbols is proportional to present-day shoreline housing density at each lake. *Solid line* indicates 1:1 relationship in each panel

Table 3 Results from a multiple logistic regression describing the likelihood that species occurrences (species-lake combinations) recorded by Morrison (1932) were lost (i.e., were not detected in our surveys)

	df	Deviance	Likelihood ratio	$P(\chi^2)$
Shoreline housing density	1	148.2	1.66	0.2
Species	24	277.2	83.73	<0.0001
O. rusticus	1	193.5	0.001	1.0
V. georgianus	1	193.5	0.013	0.9
B. chinensis	1	193.6	0.067	0.8
Species × *O. rusticus*	17	165.6	19.0	0.3
Species × *V. georgianus*	16	162.6	16.1	0.4
Species × *B. chinensis*	19	163.4	16.8	0.6

The full model was focused on identifying effects of the invasive Chinese mystery snail *Bellamya chinensis* on the likelihood of loss. We controlled for among-lake differences in human alterations to littoral zone habitat (as indicated by log-transformed shoreline housing density); for differences among native snail species; for possible effects of the invasive crayfish *Orconectes rusticus* and the invasive snail *Viviparus georgianus*; and for the possibility that the effects of the invasives on the natives varied among natives. The table gives the degrees of freedom (*df*), deviance, likelihood ratio, and probability of statistical significance (*P*) for likelihood ratio tests of the significance of each term in the model

Buchan and Padilla 1999; MacIsaac et al. 2004). *B. chinensis* individuals will attach to macrophytes that could get tangled on boat trailers, and we have observed individuals brought into boats inadvertently with sediments on anchors. The ability of *B. chinensis* to close its operculum probably makes it fairly resistant to desiccation once on a boat or trailer; that trait, and the fact that it bears live young which may be "stored" for long periods inside the adult, could facilitate invasions even when boaters do not visit new lakes on the same day. Intentional releases from aquaria and water gardens and dispersal along stream corridors could also spread *B. chinensis* to new lakes.

We are not aware of previous studies that have linked within-lake distributions of invasive species to boat launches, as our results do for *B. chinensis*. Yet this pattern may be common for animal and plant species with limited mobility, as spread around a lake may take years after establishment at an invasion point (Wilson et al. 2004). If rates of spread were available, this information would allow dates of invasion to be back-calculated in cases where species had not yet established throughout the lake. Furthermore, the

likelihood of *B. chinensis* establishment. The link between boat launches and within-lake distributions of *B. chinensis* suggests that boater movements in particular play an important role in dispersal. Boats are an important vector of spread for many aquatic invasive species, and previous studies have observed correlations between patterns of boater movement and lake-level occurrences of invasive species (e.g.,

strong link between boat launches and localized distributions of *B. chinensis* raises an interesting hypothesis. If boater movements play such an important role in determining the distribution of *B. chinensis*, it seems reasonable to expect that they could also affect the distribution of native snails. It might be interesting to ask whether entire snail assemblages in these lakes are to some extent structured by patterns of human movement across the landscape.

B. chinensis impacts on native snail assemblages?

Evidence that *B. chinensis* invasions influenced native snail assemblages varied with the spatial scale of analysis. At the whole-lake scale, neither the contemporary data nor the historical comparison showed any effects of *B. chinensis* on the presence or abundance of native snails. These results are consistent with the idea that invasive species rarely extirpate their competitors (Davis 2003; Sax et al. 2007). At the more local scale of sites, the abundance of *B. chinensis* was negatively associated with that of several native species. This pattern might result from competitive effects, but might simply reflect differences in niche requirements. Teasing apart these alternative explanations is a notoriously difficult problem in community ecology, although controlled experiments can sometimes shed light on patterns observed in the field. A recent mesocosm experiment demonstrated that *B. chinensis* at densities ~ 10 individuals m^{-2} had stronger effects on *Lymnaea stagnalis* (reduced survival) than on *Physa gyrina* (reduced growth) (Johnson et al. 2009). In our surveys, *L. stagnalis* (but not *P. gyrina*) was one of the species that did not occur at high abundance at sites where *B. chinensis* was present (Fig. 3). This qualitative agreement between experimental and observational results lends some support to the idea that *B. chinensis* has had negative effects on at least some of the species with which it is negatively associated. On the other hand, any such effects are relatively subtle, in that no *B. chinensis* effect on overall assemblage structure at the site level was detectable (Fig. 4b). On balance our results provide, at most, weak evidence that *B. chinensis* negatively impacts native snails.

Why do we not see strong evidence that *B. chinensis* invasion has negative effects on native snail popula-

tions? At least three explanations are plausible. First, it could be that insufficient time has elapsed since invasion to detect the effects of what are in fact strong competitive interactions (Strayer et al. 2006). This explanation seems fairly unlikely given that no *B. chinensis* effects were observed in the re-survey analysis. However, the temporal perspective gained from that analysis goes back only as far as the invasion of a given lake, and it is possible that some of our survey lakes were invaded relatively recently. Furthermore, the re-survey analysis can only detect *B. chinensis* effects if they result in lake-wide extirpation of a native, whereas significant impacts could occur below that threshold. Indeed, a second explanation for the lack of strong evidence for a negative impact is that the impacts are not strong, but rather are weak and localized.

Finally, of course, it could be that *B. chinensis* simply does not compete with native snails. This would suggest either resource partitioning among the species or that resources are not limiting. Resource partitioning seems unlikely; all of the snails collected in our survey were co-occurring at fine spatial scales, suggesting minimal potential for diet specialization given that most snails seem to consume diet items unselectively within the constraints imposed by habitat selection (Dillon 2000). Some members of the Viviparidae will filter feed from the water column, but stable isotope ratios of *B. chinensis* collected from one of our study lakes suggest heavy reliance on benthic resources and little if any reliance on pelagic resources (C. Solomon, unpubl. data). If these species are indeed generalized deposit feeders, then a quick glance at the lake bottom supports the hypothesis that resources are not limiting: in most locations in most lakes in the NHLD, an ample layer of organic detritus mixed with periphyton covers the bottom. This provides an interesting contrast with some stream ecosystems where the invasive New Zealand mud snail (*Potamopyrgus antipodarum*) reaches biomasses up to 10–30 g ash-free dry mass m^{-2} and appears to reduce production of native invertebrates by appropriating much of the available primary production (Kerans et al. 2005; Hall et al. 2006). Differences between streams and lakes in the size of organic matter pools may help to explain this apparent difference in the effects of *B. chinensis* and *P. antipodarum*.

Structure of snail assemblages

What factors do control snail assemblage structure in this region? Of those that we considered, conductivity and Secchi depth were the most important (Fig. 4b). Increased availability of food (via greater primary production), increased availability of Ca for shell growth, and increased connectivity to dispersal corridors in drainage lakes with higher conductivity are all possible explanations for these effects. A number of studies have identified similar patterns, particularly between species richness and these indicators of lake ion content and productivity (Dillon 2000). Other factors identified as important determinants of snail assemblage structure in previous studies include habitat diversity (Aho 1966; Harman 1972; Bronmark 1985), predators (Lodge et al. 1987), and dispersal (Bronmark 1985; Lewis and Magnuson 2000; Heino and Muotka 2006). We did not consider the effects of habitat diversity, but we did consider the effects of at least one important snail predator, the invasive rusty crayfish *Orconectes rusticus*.

Correlative studies, small-scale experiments, and multi-year monitoring of lakes invaded by rusty crayfish have shown that they have strong effects on the abundance of snails (e.g., Lodge et al. 1994; Lodge et al. 1998; McCarthy et al. 2006). However, we found no evidence that the presence of rusty crayfish influenced contemporary snail assemblages or the likelihood that historical species occurrences were lost from lakes (Table 3). Similarly, a recent study comparing current snail abundances in lakes with and without rusty crayfish to abundances measured in the 1930s found only weak evidence of an effect (Rosenthal et al. 2006). These apparently contradictory results may indicate that transient dynamics imply stronger impacts than are eventually manifested; alternatively, they may indicate the importance of context (e.g., lake-specific densities of rusty crayfish populations) in determining the outcome of an invasion. Either way, they illustrate the importance of a nuanced and a long-term perspective for understanding the impacts, if any, of non-native species (Strayer et al. 2006).

Many of the snail occurrences recorded by Morrison (1932) were not observed in our surveys. Regardless of whether species were rare or common in Morrison's data, they occurred in fewer lakes in our surveys than they did in the historical data (Fig. 5). This is not attributable to insufficient sampling, as rarefaction analyses demonstrated that we detected most or all of the species present in the habitats that we surveyed. However, it is possible that Morrison's data include species that rarely occur at 1 m depth, where our surveys were conducted. For instance, some of the species that were recorded by Morrison but not in our surveys, such as *Planorbula armigera* and some of the *Lymnaea*, are typical of small stagnant water bodies (Baker 1928). As one simple way to control for this potential bias, we repeated our analysis of these data after excluding species that we rarely observed in our surveys (i.e., those found in <10% of the 30 lakes in the data set). The results (not shown) were very similar to those obtained for the full data set (Table 3); that is, even when we considered only those species that we frequently detected in lakes, there were no significant effects of species invasions or shoreline development on the likelihood that species occurrences were lost from these lakes. It is possible that inconsistent identification of species (not just changes in nomenclature, which we accounted for) contributed to the apparent changes in assemblages, although it is hard to imagine how this could produce the patterns that we observed. Further research is needed, perhaps employing paleoecological techniques, to clarify the patterns and understand the drivers of the significant changes in snail assemblages that seem to have occurred in this region.

Future research

Given the widespread distribution of *B. chinensis* across the United States, the lack of information about its potential ecological impacts to date is striking. Our results suggest that *B. chinensis* at the densities that we observed has few impacts on native snail assemblages in the study lakes that we examined. However, our results also demonstrate that this species may be very widespread within some lake districts, and may occur at very high biomass in invaded lakes. In comparison to our estimate that *B. chinensis* biomass is 0.04–1.08 g dry mass m^{-2} in most of the invaded lakes we surveyed, the total biomass of benthic insects at a similar depth in nearby Crampton Lake is ~ 1.2 g dry mass m^{-2} (Babler et al. 2008). Furthermore, *B. chinensis* may occur at higher densities than we observed here. Thus this species may be a significant component of the benthic community in many lakes where it occurs.

Further study of the impacts of this species on lake biota and processes is therefore probably warranted. Experimental evidence indicates that *B. chinensis* may alter algal biomass and nutrient cycling in the benthic community (Johnson et al. 2009). The importance of benthic processes for structure and function in lake ecosystems (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002) suggest that alterations of these processes by *B. chinensis* could have far-reaching consequences for invaded lakes, which might suggest further management action targeted at this species. Alternatively, if *B. chinensis* has no appreciable effect on these processes, it might be considered to be a relatively benign invasive species, allowing management dollars to be targeted on invasive species that do have clear negative effects (Vander Zanden and Olden 2008). Distinguishing between these alternatives is an important priority for further research on this species.

References

Adam ME, Lewis JW (1992) The lack of coexistence between *Lymnaea peregra* and *Lymnaea auricularia* (Gastropoda, Pulmonata). J Molluscan Stud 58:227–231

Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken

Aho J (1966) Ecological basis of the distribution of the littoral freshwater molluscs in the vicinity of Tampere, South Finland. Ann Zool Fenn 3:287–322

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Babler AL, Solomon CT, Schilke P (2008) Depth-specific patterns of benthic secondary production in an oligotrophic lake. J North Am Benthol Soc 27:108–119

Baker FC (1928) The fresh water Mollusca of Wisconsin. State of Wisconsin, Madison

Branstrator DK, Brown ME, Shannon LJ, Thabes M, Heimgartner K (2006) Range expansion of *Bythotrephes longimanus* in North America: evaluating habitat characteristics in the spread of an exotic zooplankter. Biol Invasions 8:1367–1379

Bronmark C (1985) Fresh water snail diversity—effects of pond area, habitat heterogeneity and isolation. Oecologia 67:127–131

Brown KM (1982) Resource overlap and competition in pond snails—an experimental analysis. Ecology 63:412–422

Buchan LAJ, Padilla DK (1999) Estimating the probability of long-distance overland dispersal of invading aquatic species. Ecol Appl 9:254–265

Burch JB (1989) North American freshwater snails. Malacological Publications, Hamburg

Bury JA, Sietman BE, Karns BN (2007) Distribution of the non-native Viviparid snails, *Bellamya chinensis* and *Viviparus georgianus*, in Minnesota and the first record of *Bellamya japonica* from Wisconsin. J Freshw Ecol 22:697–703

Carlsson NOL, Bronmark C, Hansson LA (2004) Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. Ecology 85:1575–1580

Carpenter SR, Benson BJ, Biggs R, Chipman JW, Foley JA, Golding SA, Hammer RB, Hanson PC, Johnson PTJ, Kamarainen AM, Kratz TK, Lathrop RC, McMahon KD, Provencher B, Rusak JA, Solomon CT, Stanley EH, Turner MG, Vander Zanden MJ, Wu C-H, Yuan H (2007) Understanding regional change: a comparison of two lake districts. Bioscience 57:323–335

Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity? Bioscience 53:481–489

Dillon RT Jr (2000) The ecology of freshwater molluscs. Cambridge University Press, Cambridge

Hall R, Tank JL, Dybdahl MF (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. Front Ecol Environ 1:407–411

Hall RO, Dybdahl MF, VanderLoop MC (2006) Extremely high secondary production of introduced snails in rivers. Ecol Appl 16:1121–1131

Hanson PC, Carpenter SR, Cardille JA, Coe MT, Winslow LA (2007) Small lakes dominate a random sample of regional lake characteristics. Freshw Biol 52:814–822

Harman WN (1972) Benthic substrates—their effect on freshwater mollusca. Ecology 53:271–277

Heino J, Muotka T (2006) Landscape position, local environmental factors, and the structure of molluscan assemblages of lakes. Landsc Ecol 21:499–507

Hershey AE (1990) Snail populations in arctic lakes—competition mediated by predation. Oecologia 82:26–32

Hubendick B (1951) Recent Lymnaeidae. Their variation, morphology, taxonomy, nomenclature, and distribution. Kungl. Svenska Vetenskapsakademiens Handlingar 3:1–233

Hubendick B (1955) Phylogeny in the Planorbidae. Trans Zool Soc Lond 28:453–542

Jass JP (2004) Distributions of gastropods in Wisconsin. Milwaukee Public Museum Contrib Biol Geol 99:1–28

Johnson PTJ, Olden JD, Vander Zanden MJ (2008) Dam invaders: impoundments facilitate biological invasions into freshwaters. Front Ecol Environ 6:359–365

Johnson PTJ, Olden JD, Solomon CT, Vander Zanden MJ (2009) Interactions among invaders: community and ecosystem effects of multiple invasive species in an experimental aquatic system. Oecologia 159:161–170

Jokinen EH (1982) Cipangopaludina chinensis (Gastropoda: Viviparidae) in North America, review and update. Nautilus 96:89–95

Kerans BL, Dybdahl ME, Gangloff MM, Jannot JE (2005) Potamopyrgus antipodarum: distribution, density, and effects on native macroinvertebrate assemblages in the greater Yellowstone ecosystem. J North Am Benthol Soc 24:123–138

Kratz TK, Webster KE, Bowser CJ, Magnuson JJ, Benson BJ (1997) The influence of landscape position on lakes in northern Wisconsin. Freshw Biol 37:209–217

Kruskal JB (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29:1–27

Lewis DB, Magnuson JJ (2000) Landscape spatial patterns in freshwater snail assemblages across Northern Highland catchments. Freshw Biol 43:409–420

Lodge DM, Brown KM, Klosiewski SP, Stein RA, Covich AP, Leathers BK, Bronmark C (1987) Distribution of fresh water snails—spatial scale and the relative importance of physicochemical and biotic factors. Am Malacol Bull 5:73–84

Lodge DM, Kershner MW, Aloi JE, Covich AP (1994) Effects of an omnivorous crayfish (Orconectes rusticus) on a fresh water littoral food web. Ecology 75:1265–1281

Lodge DM, Stein RA, Brown KM, Covich AP, Bronmark C, Garvey JE, Klosiewski SP (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Aust J Ecol 23:53–67

Lydeard C, Cowie RH, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest TJ, Gargominy O, Herbert DG, Hershler R, Perez KE, Roth B, Seddon M, Strong EE, Thompson FG (2004) The global decline of nonmarine mollusks. Bioscience 54:321–330

Lysne SJ, Perez KE, Brown KM, Minton RL, Sides JD (2008) A review of freshwater gastropod conservation: challenges and opportunities. J North Am Benthol Soc 27:463–470

MacIsaac HJ, Borbely JVM, Muirhead JR, Graniero PA (2004) Backcasting and forecasting biological invasions of inland lakes. Ecol Appl 14:773–783

McCarthy JM, Hein CL, Olden JD, Vander Zanden MJ (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. Freshw Biol 51:224–235

McCune B, Mefford MJ (1999) PC-ORD: multivariate analysis of ecological data. MjM Software, Gleneden Beach

Mercado-Silva N, Olden JD, Maxted JT, Hrabik TR, Vander Zanden MJ (2006) Forecasting the spread of invasive rainbow smelt in the Laurentian Great Lakes region of North America. Conserv Biol 20:1740–1749

Mills EL, Leach JH, Carlton JT, Secor CL (1993) Exotic species in the Great Lakes—a history of biotic crises and anthropogenic introductions. J Great Lakes Res 19:1–54

Morrison JPE (1932) A report on the Mollusca of the northeastern Wisconsin lake district. Trans Wisconsin Acad Sci Arts Lett 27:359–396

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson G, Henry M, Stevens H, Wagner H (2008) Community ecology package (vegan). R Foundation for Statistical Computing, Vienna

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Peterson AT (2003) Predicting the geography of species' invasions via ecological niche modeling. Q Rev Biol 78:419–433

Pointier JP, McCullough F (1989) Biological control of the snail hosts of Schistosoma mansoni in the Caribbean area using Thiara spp. Acta Trop 46:147–155

Pysek P, Richardson DM, Pergl J, Jarosik V, Sixtova Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. Trends Ecol Evol 23:237–244

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reed-Andersen T, Bennett EM, Jorgensen BS, Lauster G, Lewis DB, Nowacek D, Riera JL, Sanderson BL, Stedman R (2000) Distribution of recreational boating across lakes: do landscape variables affect recreational use? Freshw Biol 43:439–448

Ricciardi A, Atkinson SK (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. Ecol Lett 7:781–784

Rosenthal SK, Stevens SS, Lodge DM (2006) Whole-lake effects of invasive crayfish (Orconectes spp.) and the potential for restoration. Can J Fish Aquat Sci 63:1276–1285

Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM, O'Connor MI, Rice WR (2007) Ecological and evolutionary insights from species invasions. Trends Ecol Evol 22:465–471

Schindler DE, Scheuerell MD (2002) Habitat coupling in lake ecosystems. Oikos 98:177–189

Smith DG (2000) Notes on the taxonomy of introduced Bellamya (Gastropoda: Viviparidae) species in northeastern North America. Nautilus 114:31–37

Strayer DL (2006) Challenges for freshwater invertebrate conservation. J North Am Benthol Soc 25:271–287

Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends Ecol Evol 21:645–651

Teskey MC (1954) The mollusks of Brown County, Wisconsin. Nautilus 68:24–28

Turner AM, Turner RR, Ray SR (2007) Competition and intraguild egg predation among freshwater snails: re-examining the mechanism of interspecific interactions. Oikos 116:1895–1903

Vadeboncoeur Y, Vander Zanden MJ, Lodge DM (2002) Putting the lake back together: reintegrating benthic pathways into lake food web models. Bioscience 152:44–54

Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. Can J Fish Aquat Sci 65:1512–1522

Wethington AR, Lydeard C (2007) A molecular phylogeny of Physidae (Gastropoda: Basommatophora) based on mitochondrial DNA sequences. J Molluscan Stud 73:241–257

Whittier TR, Ringold PL, Herlihy AT, Pierson SM (2008) A calcium-based invasion risk assessment for zebra and quagga mussels (Driessena spp). Front Ecol Environ 6: 180–184

Wilson KA, Magnuson JJ, Lodge DM, Hill AM, Kratz TK, Perry WL, Willis TV (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

Wood WM (1892) *Paludina japonica* Mart. for sale in the San Francisco Chinese markets. Nautilus 5:114–115