Diversity and Distributions, (Diversity Distrib.) (2007) **13**, 155–165

BIODIVERSITY RESEARCH

Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis

Jessica M. Ward and Anthony Ricciardi*

Redpath Museum and Department of Biology, McGill University, Montreal, Quebec, Canada

*Correspondence, Anthony Ricciardi, Redpath Museum, 859 Sherbrooke Street West, Montreal, Quebec H3A 2K6, Canada.
Tel.: 514-398-4086 ext. 4089; Fax: 514-398-3185;
E-mail: tony.ricciardi@mcgill.ca

ABSTRACT

Dreissenid mussels (the zebra mussel *Dreissena polymorpha* and the quagga mussel *Dreissena bugensis*) have invaded lakes and rivers throughout North America and Europe, where they have been linked to dramatic changes in benthic invertebrate community diversity and abundance. Through a meta-analysis of published data from 47 sites, we developed statistical models of *Dreissena* impact on benthic macroinvertebrates across a broad range of habitats and environmental conditions. The introduction of *Dreissena* was generally associated with increased benthic macroinvertebrate density and taxonomic richness, and with decreased community evenness (of taxa excluding *Dreissena*). However, the strength of these effects varied with sediment particle size across sites. The effects of *Dreissena* differed among taxonomic and functional groups of macroinvertebrates, with positive effects on the densities of scrapers and predators, particularly leeches (Hirudinea), flatworms (Turbellaria), and mayflies (Ephemeroptera). Gastropod densities increased in the presence of *Dreissena*, but large-bodied snail taxa tended to decline. *Dreissena* was associated with declines in the densities sphaeriid clams and other large filter-feeding taxa, as well as burrowing amphipods (*Diporeia* spp.), but had strong positive effects on gammarid amphipods. These patterns are robust to variation in the methodology of primary studies. The effects of *Dreissena* are remarkably concordant with those of ecologically similar species, suggesting universality in the interactions between introduced byssally attached mussels and other macroinvertebrates.

Keywords

Biodiversity, biological invasions, ecosystem engineer, exotic species, facilitation, freshwater ecosystems, statistical models, zebra mussel, zoobenthos.

INTRODUCTION

A central goal of invasion biology is the development of models to predict the ecological impacts of introduced species (Parker *et al*., 1999; Ruiz *et al*., 1999). A major challenge to prediction is context dependence, because impacts of the same species may vary across different communities (Ricciardi, 2003; Ross *et al*., 2003; Ricciardi & Atkinson, 2004). By integrating results from multiple studies, synthetic statistical approaches such as meta-analysis offer powerful tools for detecting predictable patterns; indeed, recent syntheses have discovered new patterns explaining variation in invasion success and impact (e.g. Levine *et al*., 2004; Ricciardi & Atkinson, 2004; Parker *et al*., 2006; Ricciardi & Ward, 2006). Despite its promising potential, meta-analysis has only just begun to be applied to study invasions (Levine *et al*., 2004; Agrawal *et al*., 2005; Parker *et al*., 2006), and has been used primarily to address questions about species establishment rather than the ecological consequences of invasion (but see McCarthy *et al*., 2006).

Among the introduced species that cause major ecological impacts are bivalves, whose activities can alter resource availability and ecosystem functioning (Crooks & Khim, 1999; Gutiérrez *et al*., 2003). Dreissenid mussels [the zebra mussel *Dreissena polymorpha* Pallas and the quagga mussel *Dreissena bugensis* (Andrusov)] have invaded lakes and rivers throughout North America and Europe, where they are the only molluscs that attach to hard substrates. These invasions have been linked to dramatic changes in benthic invertebrate diversity and abundance (Karatayev *et al*., 1997; Vanderploeg *et al*., 2002; Ricciardi, 2003). Their effects are largely positive, but vary in magnitude across studies (Ricciardi, 2003), and may vary spatially even within a single lake (Mayer *et al*., 2002) or river (Ricciardi *et al*., 1997). Negative effects on individual species are relatively rare, but usually involve large gastropods and filter-feeding taxa (Wisenden &

DOI: 10.1111/j.1472-4642.2007.00336.x
www.blackwellpublishing.com/ddi

Bailey, 1995; Ricciardi *et al*., 1997; Haynes *et al*., 2005). Although increases in species richness have been observed at multiple sites (Ricciardi, 2003), changes in diversity indices vary in significance across studies (e.g. Horvath *et al*., 1999; Nalepa *et al*., 2003). A burgeoning literature on the community-level effects of *Dreissena* provides an opportunity for quantitative synthesis, allowing us to broadly test hypotheses and explore the generality of community responses. The objectives of this study are to develop statistical models of the impacts of *Dreissena* invasions on benthic macroinvertebrate communities, and to identify predictable patterns across a broad range of habitats and environmental conditions. We treat both species as a single taxon, because they have similar attributes and commonly occur together in mixed colonies (Jones & Ricciardi, 2005). Given that benthic macroinvertebrates are valuable indicators of water quality (Washington, 1984; Gabriels *et al*., 2005), a predictive understanding of the impact of *Dreissena* is necessary so that observed changes to invaded communities are not erroneously attributed to watershed management (e.g. nutrient abatement) or other environmental stressors.

Mussels, like other ecosystem engineers (Jones *et al*., 1994, 1997), often have large community-level effects resulting from their ability to modulate the availability of resources to other species by building and modifying habitats. These impacts may be predictable. Engineer species that increase the structural complexity of benthic habitats tend to cause increases in the abundance and species richness of benthos (Crooks, 2002). Byssally attached mussels create spatially complex patches that can support diverse assemblages of associated organisms (Suchanek, 1986; Seed, 1996). These patches provide gastropods and other benthic herbivores with added grazing area and spatial refugia from predators (Griffiths *et al*., 1992; Ricciardi *et al*., 1997). However, in marine systems, mussel shells limit the size of interstitial spaces — and thus the size of colonizing organisms (Jacobi, 1987; Griffiths *et al*., 1992). Mussels also affect nutrient availability via biodeposition of faeces and pseudofeces (Izvekova & Lvova-Katchanova, 1972; Sephton *et al*., 1980), increasing microhabitat complexity on rocky substrata through biodeposition and sediment focusing in pits (Yager *et al*., 1993). Their effects on resident species should vary depending on whether the resources they provide are limiting in the local environment. Hence, we derived the following predictions:

1 The effects of *Dreissena* on macroinvertebrate abundance and taxonomic richness are positively correlated with *Dreissena* density.

2 *Dreissena* colonization increases densities of gastropods, but limits their mean body size and displaces large-bodied taxa.

3 The effects of *Dreissena* vary across functional feeding groups, with strong positive effects on scrapers and deposit-feeding taxa and strong negative effects on filter-feeding taxa.

4 The effects of *Dreissena* vary with the characteristics of the underlying sediments. Effects on burrowing and epilithic taxa are positively and negatively correlated, respectively, with sediment particle size.

Because predictive models of *Dreissena*'s impact on native mussels have already been developed (Ricciardi *et al*., 1995; Ricciardi, 2003), we have restricted our study to its effects on non-mussel taxa.

METHODS

We searched the literature for studies that compared benthic macroinvertebrate communities in the presence and absence of *Dreissena* and reported effects on total non-dreissenid macroinvertebrate abundance or diversity. Here, the term 'effect size' is used to describe a measure of the direction and magnitude of *Dreissena*'s effect. Relevant studies were located by searching Aquatic Sciences and Fisheries Abstracts (ASFA, 1971 to June 2006), Ecology Abstracts (1982 to June 2006), and Science Citation Index Expanded (SCI-Expanded, 1900 to June 2006). Search terms included all possible combinations of (1) zebra mussel*, *Dreissena*, dreissenid, (2) communit*, benth*, macroinvertebrate*, and (3) abundance, diversity, richness, impact*. Additional studies were located by examining the reference lists of primary studies and narrative reviews, and by forward reference tracking in SCI-Expanded.

In order to limit problems of non-independence (Gurevitch & Hedges, 1999), we used only one effect size estimate per study site in each analysis. We considered multiple study sites from a single publication to be independent if the authors reported results separately for each site or group of sampling stations (i.e. we used the authors' definition of independence). When multiple publications reported *Dreissena* effects for the same site, we included a single effect size estimate for that site, according to the following protocol. When authors compared macroinvertebrate communities both experimentally and observationally (inside and outside mussel beds, or before and after invasion) at the same site, we included the experimental data preferentially. When multiple *Dreissena* density treatments were reported in an experiment, we used the density treatment that most closely resembled ambient *Dreissena* density at the site. For studies where *Dreissena* treatments were crossed with other treatments (e.g. predators), we used the *Dreissena* and control treatments that most resembled conditions in the single factor experiments. When data from multiple sampling dates were available for a given site, we used the final sampling date. Because *Dreissena*'s effects on macroinvertebrates are driven largely by the characteristics of clustered mussels (e.g. interstitial habitat; Botts *et al*., 1996; Ricciardi *et al*., 1997), we excluded sites where the mean *Dreissena* density was less than 100 m^{-2}, as clusters are rare at such densities (J.M. Ward & A. Ricciardi, pers. obs.). We also excluded pre- and post-invasion comparisons that were separated by more than 20 years. Our search identified a total of 47 study sites that met all our predefined inclusion criteria. To investigate patterns of context dependence, we also recorded information about several study site characteristics chosen a *priori* (Table 1). These were variables hypothesized to explain variation in *Dreissena* impacts across sites, as well as methodological variables that could potentially bias or confound our results. Sediment particle size was calculated by taking the weighted average phi ($-\log_2$ particle diameter, in mm) of the sediments sampled, or by using the diameter of a sphere with surface area equal to that of experimental substrates.

Table 1 Univariate regression models of *Dreissena* effect on macroinvertebrate numerical density vs. study site characteristics and methodological variables recorded for each site[1]

Factor	*n*	Slope (β)	*P*	*r*
Dreissena density (No. m^{-2})*	31	0.524	0.106	0.30
Depth (m)*	34	−1.196	**< 0.001**	−0.66
Phi	28	−0.083	**0.012**	−0.47
Flow environment†	36	0.259	0.649	0.08
Time since invasion (years)*	26	−0.831	0.151	−0.29
Continent‡	36	0.755	0.214	0.21
Type of comparison 1§	36	0.584	0.339	0.16
Type of comparison 2¶	36	−0.812	0.056	−0.32
Sampling date (days)	30	−0.014	**0.019**	−0.43
Sieve aperture size (mm)	34	0.100	0.605	0.09
Multisite data**	34	−0.780	0.236	−0.21

[1] Significant *P* values are in bold.

*Factor was $\log_{10}$-transformed.

†Coded as lentic (0) or lotic (1).

‡Site was located in North America (0) or Europe (1).

§Comparison between communities was experimental (0), spatial (1), or temporal (0).

¶Comparison between communities was experimental (0), spatial (0), or temporal (1).

**Effect size calculated with single site (0) or multisite (1) data.

Negative phi values denote coarse (hard) substrates, while positive phi values denote increasingly fine sediments.

We examined the responses of benthic macroinvertebrate communities to *Dreissena* using standard meta-analytical techniques (Cooper & Hedges, 1994; Osenberg *et al.*, 1999; Gurevitch *et al.*, 2001). The community response variables used in these analyses were measures of non-*Dreissena* macroinvertebrate abundance and diversity. We also explored patterns of response among different macroinvertebrate groups, measured as changes in the numerical density of individual taxa. For each response variable, the effect size in our meta-analysis was the $\log_e$ response ratio ($\ln(X_{+D}/X_{-D})$), calculated using measures of that response variable in the presence (X_{+D}) and absence (X_{-D}) of a dense *Dreissena* colony. Thus, a positive ratio indicates that macroinvertebrate density or diversity increased in the presence of *Dreissena*. This metric was chosen for several reasons. Unlike other commonly used metrics, it does not confound differences in variance between studies with differences in the size of effect (Osenberg *et al.*, 1997), nor does it depend on the magnitude of the average value of the response variable in a study (Englund *et al.*, 1999). It also meets the assumptions of parametric analyses and has a clear biological interpretation as the ($\log_e$-transformed) proportionate change in a response variable associated with *Dreissena* invasion (Hedges *et al.*, 1999). The use of the $\log_e$ response ratio assumes that experimental durations are sufficiently long for equilibrium conditions to be reached (Hedges *et al.*, 1999). This assumption was supported by available experimental time-series data (Slepnev *et al.*, 1994) and by some authors' use of pilot studies to determine the appropriate experimental duration (Stewart *et al.*, 1998).

We did not weigh the effect size values by the inverse of their sampling variance because of incomplete reporting in primary studies. Many studies did not report sampling variances and sample sizes for the response variables measured, rendering the corresponding weights incalculable. Exclusion of these studies would greatly reduce the sample size of our data set and could possibly introduce biases into our analyses (Englund *et al.*, 1999). Instead, following the advice of Gurevitch & Hedges (1999) for synthesis of poorly reported data, we used unweighted standard parametric statistical tests. We caution that our estimated *P*-values may be less precise and that our tests less powerful as compared to weighted analyses (Gurevitch & Hedges, 1999). Nonetheless, by including a greater number of sites we have reduced the probabilities of both type I and type II errors in our meta-analysis (Lajeunesse & Forbes, 2003).

Community-level effects of *Dreissena* were measured as changes in non-*Dreissena* macroinvertebrate numerical density (number per m^{-2}), biomass density (g m^{-2}), taxonomic richness (number of taxa), taxonomic density (number of taxa per sample), Simpson's diversity index, and Simpson's evenness index. We attempted to avoid the 'apples and oranges' problem (Gurevitch *et al.*, 2001) by only combining effects measured in the same units in any given analysis (e.g. we did not combine numerical and biomass densities). We compiled diversity and evenness indices for studies that either reported them directly or contained sufficient information to allow their calculation. Simpson's diversity was calculated as $D = 1/\Sigma(p_i)^2$, where p_i was the proportion of individuals accounted for by the i^{th} taxon, and evenness was calculated as $E_D = D/D_{max}$, where D_{max} was the number of taxa (excluding *Dreissena*). For each community response variable, we calculated the mean effect size across all study sites and its 95% confidence interval.

To assess the most important factors explaining variation in the response of benthic macroinvertebrate communities to *Dreissena*, we created a backward stepwise multiple regression model for the most widely reported community response variable: numerical density (Lipsey & Wilson, 2001). Because incomplete reporting of study site characteristics resulted in missing data in our data matrix, we used univariate regression to pre-select variables for inclusion in the multiple regression, including only those variables significant in univariate tests ($P < 0.05$). Prior to regression analyses, *Dreissena* density, depth, and time since invasion were $\log_{10}$-transformed, and categorical variables were dummy coded as follows: flow environment was lentic (0) or lotic (1), the site was located in North America (0) or Europe (1), and the effect size was calculated using single site (0) or multisite (1) data. We created two dummy variables in order to tests whether effects varied among experimental (0,0), spatial (1,0), and temporal (0,1) comparisons of macroinvertebrate communities. Here we infer significant relationships only for those variables retained by the backward stepwise multiple regression using a significance level of 0.05 for variable entry and retention. Furthermore, we determined whether the factors retained by the stepwise regression explained variation in the response of macroinvertebrate taxonomic richness (the second most commonly reported community response variable), using least squares regression analyses.

We tested whether the magnitude of *Dreissena* effects on macroinvertebrates varied across taxonomic and functional groups, using the subset of studies reporting numerical density data for individual taxa in the presence and absence of *Dreissena*. For each major taxonomic group, we calculated within-site effects by summing across taxa before calculating the mean effect across sites ($n > 5$). When the taxonomic resolution of primary studies permitted, we assigned each taxon to a functional feeding group, and identified infauna and epifauna, according to Merritt & Cummins (1984), Klemm (1985), Pennak (1989), Peckarsky *et al.* (1990), and Thorp & Covich (1991), and using the following definitions. For the purpose of our study, 'filter-feeder' refers to organisms carrying out all forms of suspension feeding. Infauna were organisms that spend the majority of their aquatic life cycle within soft sediments, while epifauna were organisms whose normal habit is occupying stable, solid surfaces including rocky substrates and submerged vegetation (e.g. epilithic and epiphytic taxa, respectively). For each of these functional groups, we conducted least squares regressions on the factors previously identified as most important in determining the response of total macroinvertebrate numerical density to *Dreissena*.

Finally, we tested the effect of *Dreissena* colonization on gastropod density and body size using the subset of studies that reported data for gastropod numerical densities (number per m^{-2}) to at least the family level. We calculated *Dreissena* effects on each gastropod family for a given site and determined the shell size for each family by averaging the maximum shell dimensions from all species having a distribution that includes the Great Lakes — St. Lawrence region, using data from Clarke (1981). We tested the relationship with gastropod shell size using least squares regression. All analyses were carried out using SAS release 8.02 (SAS institute, Cary, NC, USA). See Appendix SI in Supplementary Material for data sources used in this meta-analysis.

RESULTS

Macroinvertebrate communities responded positively to the presence of *Dreissena* in terms of their total non-dreissenid numerical density, biomass density, taxonomic richness, and taxa density, when data from all study sites were considered collectively (Fig. 1). In each of these variables, the mean response increased by a factor of 1.5–2.7. By contrast, Simpson's diversity was 1.2-fold lower in the presence of *Dreissena* (although this change was not significant), and Simpson's evenness declined by a mean factor of 1.3 in the presence of *Dreissena*.

Variation in effects on numerical density and taxonomic richness

The change in the numerical density of macroinvertebrates varied significantly with substrate particle size, but not with *Dreissena* density (Fig. 2). Macroinvertebrate numerical density tended to increase with increasing *Dreissena* density, but this trend was not significant (Fig. 2a). In univariate analyses, depth, sediment particle size, and sampling date were significantly related to effects of *Dreissena* on macroinvertebrate numerical density (Table 1). However, substrate particle size (phi) was the only variable retained by the backwards stepwise multiple regression. The magnitude of positive effects of *Dreissena* on the numerical density of macroinvertebrates declined with decreasing substrate particle size (i.e. increasing phi) (Fig. 2b). The magnitude of taxonomic richness response varied significantly with both substrate particle size and *Dreissena* density. *Dreissena* had larger positive effects on taxonomic richness with increasing *Dreissena* density (Fig. 2c) and in areas of fine sediment (Fig. 2d).

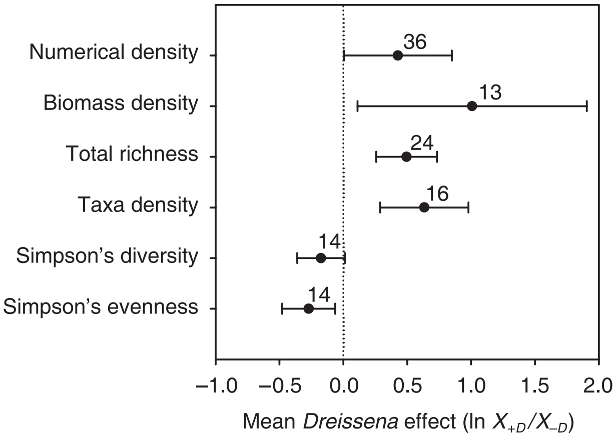

Figure 1 Mean response of benthic macroinvertebrate communities to *Dreissena*. All abundance and diversity calculations exclude *Dreissena*. Error bars are 95% confidence intervals. Numbers are sample sizes (number of study sites).

Variation in effects on taxonomic and functional groups

The average magnitude of *Dreissena* effects on the numerical density of macroinvertebrates varied across major taxonomic groups (Fig. 3). Overall, the presence of *Dreissena* was associated with significant increases in the density of leeches (Hirudinea), flatworms (Turbellaria), and gastropods and mayflies (Ephemeroptera). Isopod crustaceans also tended to be more abundant in the presence of *Dreissena*, although this effect was not significant. In general, *Dreissena* effects on the density of amphipods, dipteran flies, oligochaetes, caddisflies (Trichoptera), ostracods, and nematodes were not significantly different from zero, although the latter two groups may be severely underestimated by sieve aperture sizes of 0.5 mm and greater, as are commonly used. The density of sphaeriid clams was generally lower in the presence of *Dreissena*. Epifaunal taxa were more abundant in the presence of *Dreissena*, increasing by a mean factor of 2.5 (ln $X_{+D}/X_{-D} = 0.92$, $n = 154$), while the change in density of infaunal taxa was negative, decreasing by a mean factor of 1.4 (ln $X_{+D}/X_{-D} = -0.33$, $n = 140$). The overall response to *Dreissena* also differed between functional feeding guilds, with scrapers being the most positively affected in terms of numerical density (ln $X_{+D}/X_{-D} = 0.98$, $n = 57$), followed by predators (ln $X_{+D}/X_{-D} = 0.63$, $n = 53$), increasing by mean factors of 2.7 and 1.9, respectively. Deposit-feeding

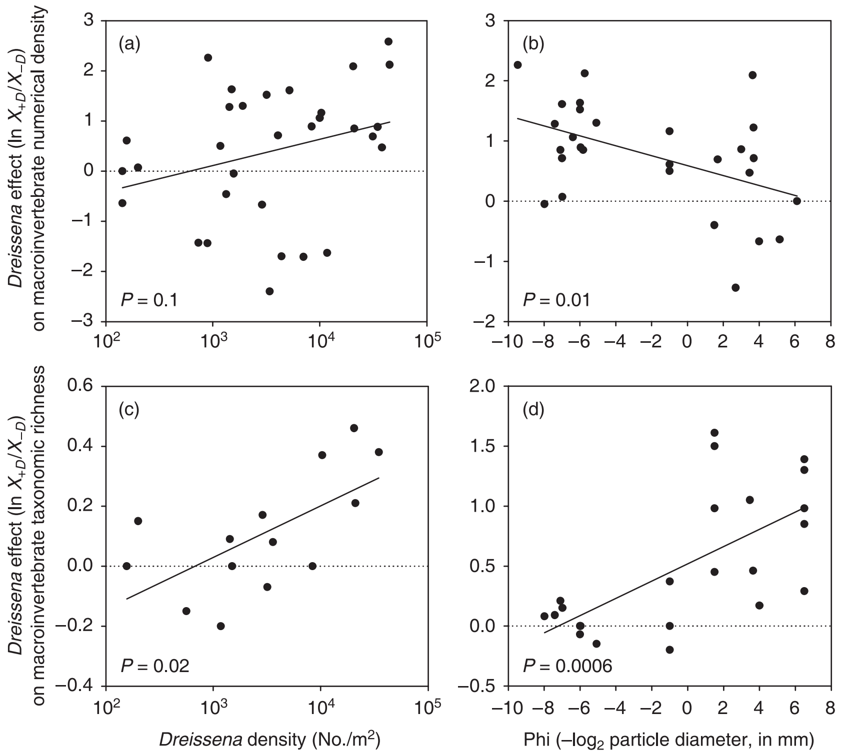

Figure 2 Top panels: Relationship between community-level effects of *Dreissena* on the numerical density of benthic macroinvertebrates (excluding *Dreissena*) and (a) *Dreissena* density ($r = 0.30$, $n = 31$, $P = 0.1$), or (b) decreasing substrate particle size (increasing phi values) of the site where macroinvertebrates were sampled ($r = –0.47$, $n = 28$, $P = 0.01$). Bottom panels: Relationship between community-level effects of *Dreissena* on the taxonomic richness of benthic macroinvertebrates (excluding *Dreissena*) and (c) *Dreissena* density ($r = 0.63$, $n = 14$, $P = 0.02$), or (d) decreasing substrate particle size ($r = 0.66$, $n = 23$, $P = 0.0006$). Lines were generated by least-squares regression.

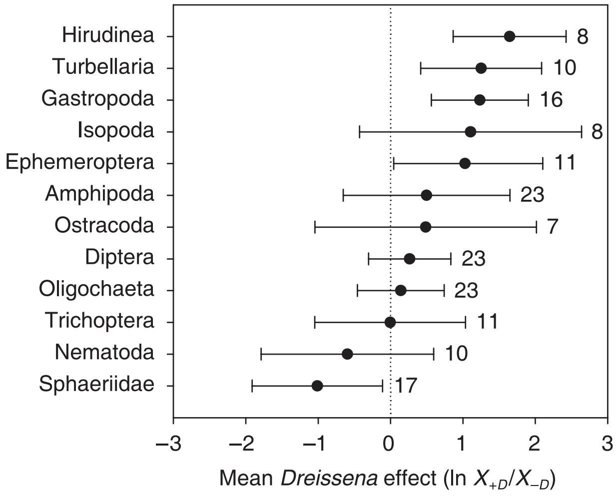

Figure 3 Mean effects of *Dreissena* on the numerical density of major groups of benthic macroinvertebrates (excluding *Dreissena*). Error bars are 95% confidence intervals. Numbers are sample sizes (study sites).

(ln $X_{+D}/X_{-D} = 0.12$, $n = 161$) and filter-feeding taxa were, on average, not significantly affected by Dreissena (ln $X_{+D}/X_{-D} = –0.52$, $n = 36$).

Variation in the magnitude of *Dreissena* effects on macroinvertebrate numerical density across a substrate particle size gradient differed among functional groups of macroinvertebrate taxa. The magnitude of *Dreissena* effects on epifaunal and infaunal macroinvertebrates was related to substrate particle size (Fig. 4). Positive effects on epifauna declined with decreasing substrate particle size (Fig. 4a), while effects on the numerical density of infaunal (burrowing) taxa tended to be positive on hard substrates and negative on fine sediments (Fig. 4b). *Dreissena* effects on the numerical density of deposit feeders (Fig. 5a) and predators (Fig. 5c) were also negatively correlated with decreasing substrate particle size. Effects on filter feeders tended to decrease with decreasing substrate particle size, although this trend was not significant (Fig. 5b). The change in the numerical density of scrapers (primarily gastropods) was not related to substrate particle size, although there were few effect estimates for this group on soft substrates (Fig. 5d). As predicted, the positive effects of *Dreissena* on the numerical density of gastropods decreased with increasing gastropod shell size (Fig. 6). However, this result was due to strong negative effects on pleurocerid snails and the relationship was no longer significant when the effects on this family were removed ($n = 36$, $P = 0.19$).

DISCUSSION

Predictable patterns of *Dreissena* impact

The magnitude of *Dreissena* impacts on the density and richness of benthic macroinvertebrate communities were positively and negatively correlated, respectively, with sediment particle size (i.e. decreasing phi). The relationship between sediment particle size and the effect of *Dreissena* on total numerical density reflects changes in the abundances of multiple functional groups, including deposit-feeding, predatory, and filter-feeding taxa. These effects were not significantly related to *Dreissena* density, even though the latter varies positively with sediment particle

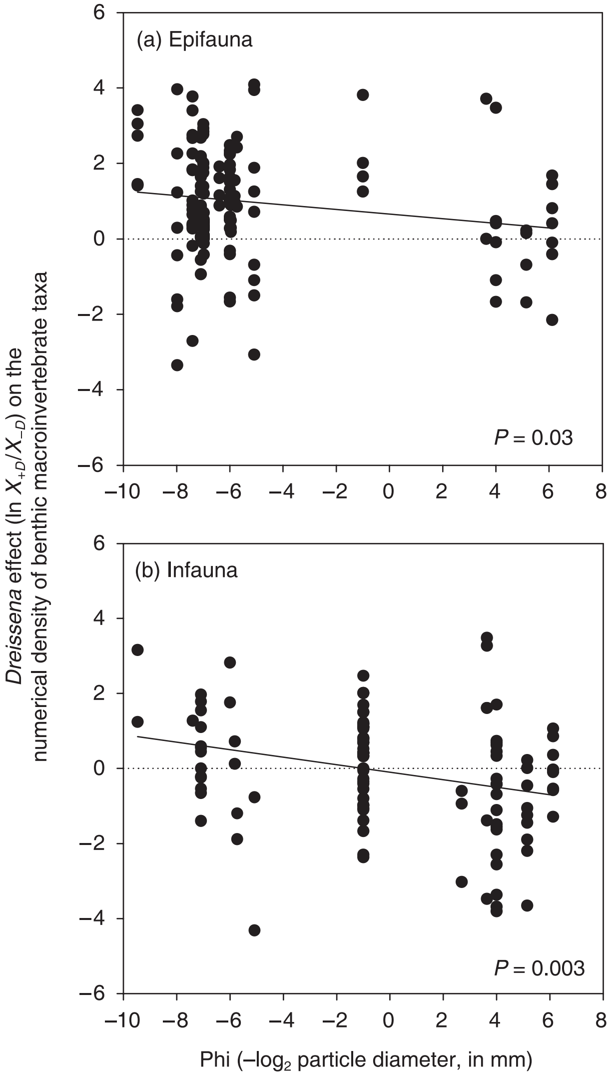

Figure 4 Relationship between taxon-level effects of *Dreissena* on the numerical density of (a) epifaunal macroinvertebrates ($r = -0.18$, $P = 0.03$, $n = 145$) or (b) infaunal macroinvertebrates ($r = -0.29$, $P = 0.003$, $n = 110$) and decreasing substrate particle size (increasing phi values) of the site where macroinvertebrates were sampled. Lines were generated by least-squares regression.

size (Jones & Ricciardi, 2005). *Dreissena* effects on the taxonomic richness of macroinvertebrates showed the opposite pattern across a sediment particle size gradient, with effects being greatest on fine sediments. This result is driven by differences in the occurrence of epifaunal and infaunal taxa among sediment environments. *Dreissena*-associated communities on soft sediments frequently include organisms more typical of rocky substrata, such as gammarid amphipod and isopod crustaceans, hydroids, flatworms, leeches, and snails (e.g. Karatayev *et al*., 1997; Bially & MacIsaac, 2000; Beekey *et al*., 2004; Reed *et al*., 2004). Similarly, in marine sedimentary environments, epifauna normally unable to occupy soft sediments are restricted in their occurrence to the mussel bed (Dittmann, 1990; Robinson & Griffiths, 2002). But this is not true for infauna taxa richness in *Dreissena* colonies on rocky substrates. Sedimentary microhabitats within mussel beds on hard substrates develop via passive and active deposition (Jacobi, 1987; Yager *et al*., 1993), which will vary spatially and temporally among mussel colonies and sites. Furthermore, while highly mobile epifauna may quickly colonize mussel patches on soft sediments (Mörtl & Rothhaupt, 2003), many infaunal species are less mobile (Merritt & Cummins, 1984). These factors may limit the ability of infauna to colonize and persist in *Dreissena* colonies on rocky substrates.

We tested whether *Dreissena* effects on macroinvertebrate numerical density were correlated with site characteristics that were either not significant in univariate analyses or not retained by the multiple regression model. Primary studies have contrasted the effects of *Dreissena* among shallow and deep sites (Strayer *et al*., 1998; Nalepa *et al*., 2003). While sampling depth was highly significant in a univariate regression, it was not retained by the multiple regression. Depth is correlated with sediment particle size and, while depth by itself explained a greater amount of variation, particle size explained additional variation independent of this correlation. This pattern describes variation in the local-scale effects of *Dreissena* in dense mussel beds, whereas negative effects at deepwater sites have generally been measured outside of dense *Dreissena* beds and are attributable to the distal effects of *Dreissena* filtration via the transfer of energy from pelagic to benthic food webs (Strayer *et al*., 1998; Ricciardi, 2003). Time since invasion may be an important factor moderating an invader's impacts within sites (Strayer *et al*., 2006), but this variable did not explain variation in *Dreissena* effects on macroinvertebrate density. We also found no difference in community response between study sites located in North America and in Europe, although the latter group was limited in size ($n = 6$). Dreissenid mussels are alien to both regions (apart from south-eastern Europe within the Black Sea basin) and so may similarly affect communities with which they do not share an evolutionary history. Finally, impact magnitude did not differ between lentic and lotic sites, perhaps because of spatial heterogeneity within large systems (e.g. fluvial lakes in the St. Lawrence River).

Macroinvertebrate abundance has been correlated with *Dreissena* density within sites (e.g. Horvath *et al*., 1999; Kuhns & Berg, 1999; Strayer & Smith, 2000; Mayer *et al*., 2002), but this relationship did not emerge across sites in our meta-analysis. Variation in site-specific environmental conditions (e.g. species richness, productivity, resource limitation) may modify the effect of *Dreissena* density. Alternatively, biomass or size frequency distribution may be more important in determining impact magnitude, the latter being a more accurate predictor for a mussel population's filtering capacity and pseudofeces production rate (Young *et al*., 1996). Thus, differences in the population structure of *Dreissena* across sites might render mussel population densities incomparable. Limited reporting of *Dreissena* biomass and population size structure prevented us from investigating this further. It is also difficult to compare correlations involving numerical density and taxonomic richness (Fig. 2a,c), because of differences in sample size and in the range of effect sizes. However, our results suggest that increases in taxonomic richness

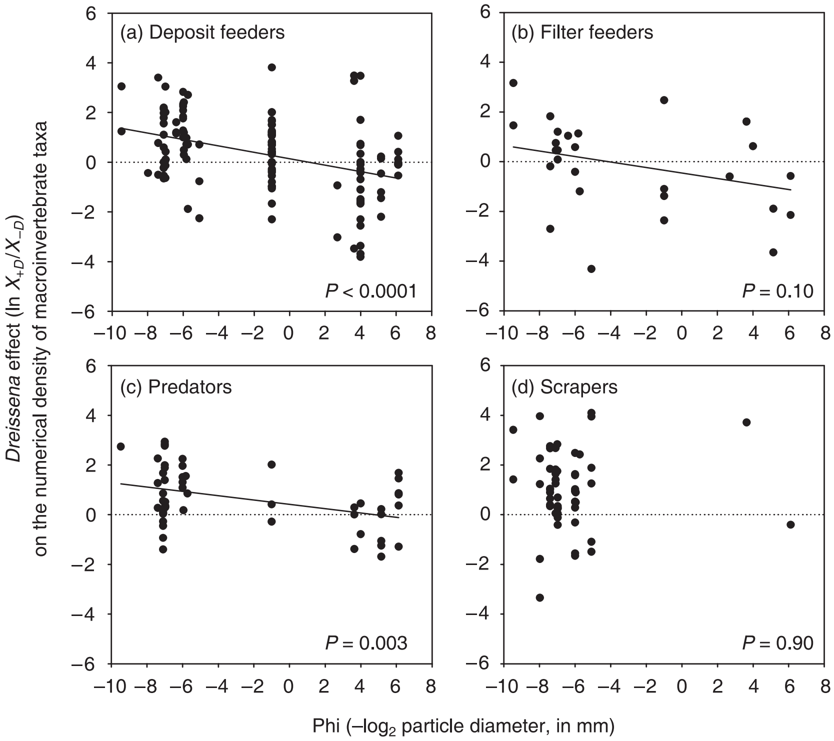

Figure 5 Relationship between taxon-level effects of *Dreissena* on the numerical density of (a) deposit-feeding ($r = –0.40$, $P < 0.0001$, $n = 129$) (b) filter-feeding ($r = –0.32$, $P = 0.10$, $n = 28$) (c) predatory ($r = –0.41$, $P = 0.003$, $n = 51$) or (d) scraping macroinvertebrates ($P = 0.90$, $n = 56$) and decreasing substrate particle size (increasing phi values) of the site where macroinvertebrates were sampled. Lines were generated by least-squares regression.

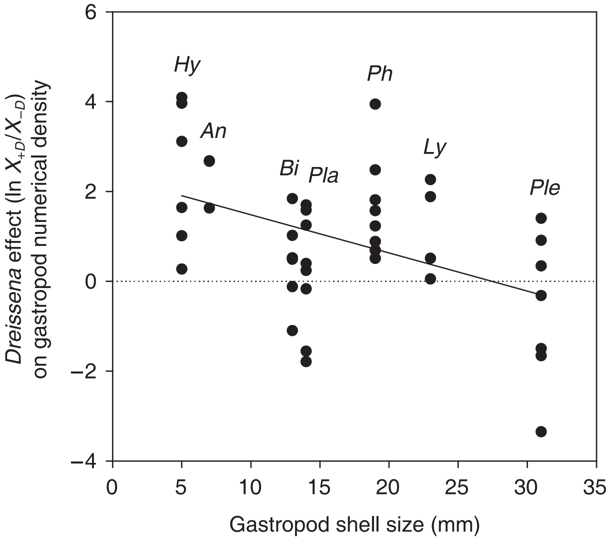

Figure 6 Relationship between *Dreissena* effect on the numerical density of gastropod taxa and the average shell size across gastropod species within a family. The line was generated by least-squares regression ($r = –0.45$, $P = 0.003$, $n = 43$). *Hy*, Hydrobiidae; *An*, Ancylidae; *Bi*, Bithyniidae; *Pla*, Planorbidae; *Ph*, Physidae; *Ly*, Lymnaeidae; *Ple*, Pleuroceridae.

for a given *Dreissena* density may be more predictable across sites than increases in the numerical density of macroinvertebrates.

While *Dreissena* colonization generally increases the taxonomic richness of benthic macroinvertebrates, the dominance structure of the community is changed even when the most obvious dominant, *Dreissena*, is excluded from evenness calculations. A tendency towards declining Simpson's diversity even with increased richness, combined with a significant overall decline in Simpson's evenness index in the presence of *Dreissena*, indicates that some taxa are much more positively affected by *Dreissena* than others. *Dreissena* colonization has preceded dramatic increases in the densities of gammarid amphipods and predatory macroinvertebrates (Ricciardi, 2003). In particular, leeches, flatworms, and snails are more abundant in the presence of *Dreissena*, whereas sphaeriid clams are typically reduced in density. The response of scrapers and predatory taxa was also typically positive, the latter likely reflecting increased prey availability in the form of *Dreissena* and associated invertebrates. Some taxa, such as caddisfly larvae (Trichoptera), had a mixture of positive and negative responses to *Dreissena*. This partly reflects the facilitation of small filter-feeding caddisflies (e.g. *Brachycentrus*) that can exploit filtration currents generated by the mussels, in contrast with the competitive exclusion of large net-spinning caddisflies from *Dreissena*-colonized substrates (Ricciardi *et al*., 1997). Similarly, the overall non-significant effect of *Dreissena* on amphipods was driven by a balance of large positive effects on epibenthic gammarid amphipods and large negative effects on burrowing amphipods (*Diporeia* spp.). *Diporeia* differs from gammarids in its ability to feed on *Dreissena* fecal deposits and may be out-competed by *Dreissena* for particulate food (reviewed by Lozano *et al*., 2001).

The decline of large snails on substrates colonized by *Dreissena* has been reported by several authors (e.g. Dusoge, 1966; Wisenden & Bailey, 1995; Ricciardi *et al*., 1997) and is concordant with observations of the competitive exclusion of large grazers from marine mussel beds (e.g. Griffiths *et al*., 1992; Lohse, 1993; Tokeshi & Romero, 1995). Our study found limited support for the hypothesized exclusion of families of large-bodied gastropods. We classified gastropod families on the basis of the maximum shell size obtained but were unable to account for variation in size among individuals. With the exception of pleurocerid snails, these families may be too small relative to the size of *Dreissena* to be competitively excluded and may persist on secondary substrata provided by mussel shells. In fact, some evidence suggests that gastropods grow more quickly on *Dreissena* colonized substrates (Greenwood *et al*., 2001). Furthermore, mussel beds may serve as gastropod nursery grounds, harbouring juveniles of taxa in which the large adults are found only on bare rock (cf. Tokeshi & Romero, 1995); marine mussels may thereby competitively exclude large limpets but enhance recruitment of juveniles (Griffiths *et al*., 1992). Differences in the size-at-maturity of gastropods may also modify the outcome of their interactions with *Dreissena*, as observed for marine mussels (Branch & Steffani, 2004). In addition to these effects, *Dreissena* may have an indirect positive effect on gastropods and other scrapers by stimulating benthic algal growth through enhanced water clarity (Vanderploeg *et al*., 2002).

Caveats

Several notes of caution are required due to the nature of our analysis and limitations of the available data. First, meta-analyses of variation in effect sizes are inherently correlational; explanatory variables were generally not controlled or manipulated across studies. Nonetheless, we take a first step in explaining large-scale variation in *Dreissena* impacts and provide a means for making quantitative predictions. Second, the available literature contained a limited number of experimental manipulations, so we included observational data that likely have additional sources of variation; increases or declines in macroinvertebrates may have been caused by concomitant factors, such as changes in water quality. In addition, responses measured over different time-scales may be differentially influenced by indirect or feedback effects of *Dreissena* (e.g. through changes in benthophagous fish populations or algal species composition).

However, some strong patterns emerge despite this heterogeneity. Ideally, we would have divided the available data and used a subset to test our models, but limited availability of data made this unfeasible. Third, relatively few of the sites were located in Europe so our results may be biased towards describing North American macroinvertebrate communities. Fourth, while we made efforts to reduce problems associated with non-independence, our data set was too limited to allow a rigorous assessment of such effects. Finally, our meta-analysis could not calculate effect sizes with zero values, and we are aware of no satisfactory method to deal with this problem, therefore we omitted these values.

Comparisons with other introduced mussel species

Facilitation of benthic organisms may be a general effect of introduced habitat engineers that create physical structures or increase habitat complexity (Crooks & Khim, 1999; Crooks, 2002; Rodriguez, 2006). Overall, this appears to be an accurate description of the effects of introduced byssally attached mussels. Significant increases in the abundance or taxonomic richness of benthic macroinvertebrates have been reported for several introduced mussel species, including *Mytilus galloprovincialis* (Lamarck) on sand (Griffiths *et al*., 1992; Robinson & Griffiths, 2002; Branch & Steffani, 2004), *Musculista senhousia* (Benson) on soft sediments (Crooks, 1998; Crooks & Khim, 1999; Mistri, 2002), and *Limnoperna fortunei* (Dunker) on rocky substrates (Darrigran *et al*., 1998). However, declines in the abundance and richness of macroinvertebrates in the presence of introduced *M. senhousia* have also been reported (Creese *et al*., 1997). The modulation of facilitative interactions between habitat engineers and benthic macroinvertebrates by environmental gradients may help to explain some of this variation (Cummings *et al*., 2001; Norkko *et al*., 2006).

Similar types of organisms may respond in comparable ways to the presence of introduced mussels. Like the effects of *Dreissena* on sphaeriid clams, infaunal filter-feeding bivalves tend to be negatively affected by mats of *M. senhousia* (Creese, 1997; Mistri, 2002). Soft sediments underlying introduced mussel beds may become inhospitable for burrowing taxa through smothering and/or anoxia (Creese, 1997; Robinson & Griffiths, 2002). Also paralleling the effects of *Dreissena*, invasions by *My. galloprovincialis* have promoted the replacement of naturally occurring sandbank communities with species more typical of rocky shores (Robinson & Griffiths, 2002). Increased densities of surface-feeding taxa, including amphipods and small gastropods, have been noted among beds of introduced *M. senhousia* (Crooks, 1998; Crooks & Khim, 1999; Mistri, 2002) and *My. galloprovincialis* on soft sediments (Robinson & Griffiths, 2002). Predatory macroinvertebrates were also more abundant inside introduced mussel mats (Crooks & Khim, 1999). Consistent with effects of *Dreissena* on hard substrates, densities of both epifaunal and infaunal taxa were higher in beds of introduced *L. fortunei* compared to bare rock (Darrigran *et al*., 1998).

Facilitative effects of introduced engineer species are predicted to vary such that the size of the effect is dependent on whether the resource provided by the engineer is limiting (Crooks, 2002; Rodriguez, 2006). In the case of *Dreissena*, several mechanisms of its effect on benthic macroinvertebrates may vary in importance across sites. First, the importance of habitat provision for epifaunal and infaunal taxa is expected to vary with the local availability of suitable rocky and sedimentary habitats. Our examination of variation in the effects of *Dreissena* on the numerical densities of macroinvertebrate taxa across a range of substrate particle sizes supported this prediction for infaunal taxa, but not for epifaunal taxa. Conversely, changes in taxonomic richness appear to show the opposite pattern, with large positive effects on epifaunal taxa richness on fine sediments and smaller effects on infaunal taxa richness on hard substrates; however, low taxonomic resolution in primary studies prevented us from explicitly comparing changes in epifaunal and infaunal taxa richness. Depositional environments may represent suboptimal conditions for epilithic taxa (e.g. through interference with feeding; Stewart *et al*., 1999), thereby preventing them from attaining high densities. Second, the importance of nutrient enrichment through mussel biodeposition should vary with the degree of nutrient limitation in the habitat. We found that positive effects of *Dreissena* on deposit-feeding taxa increased with sediment particle size, although the same pattern was observed for other feeding groups. This pattern is consistent with a decreasing role of biodeposition as the organic matter content of sediments increases, also noted for the suspension-feeding pinnid bivalve *Atrina zelandica* (Gray) (Hewitt *et al*., 2002). Finally, the importance of spatial refugia from biotic and abiotic stresses is expected to vary along environmental stress gradients (not examined here). Alternatively, the size of facilitative effects may be determined, or at least constrained, by local species pools.

In summary, although macroinvertebrate response is highly correlated with *Dreissena* density at a given site, or across sites within a given region, these correlations do not necessarily hold true for all *Dreissena* invasions. However, increased benthic macroinvertebrate density and taxonomic richness, and decreased community evenness, are effects generally associated with the introduction of *Dreissena*. The strength of these effects is context-dependent, as they vary systematically with sediment particle size. Nevertheless, these patterns are robust to heterogeneity in the methodology of primary studies. Interestingly, the effects of *Dreissena* are generally consistent with those of ecologically similar taxa, suggesting universality in the interactions between introduced byssally attached mussels and other macroinvertebrates.

REFERENCES

Agrawal, A.A., Kotanen, P.M., Mitchell, C.E., Power, A.G., Godsoe, W. & Klironomos, J. (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology*, **86**, 2979–2989.

Beekey, M.A., McCabe, D.J. & Marsden, J.E. (2004) Zebra mussel colonization of soft sediments facilitates invertebrate communities. *Freshwater Biology*, **49**, 535–545.

Bially, A. & MacIsaac, H.J. (2000) Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshwater Biology*, **43**, 85–97.

Botts, P.S., Patterson, B.A. & Schloesser, D.W. (1996) Zebra mussel effects on benthic invertebrates: physical or biotic? *Journal of the North American Benthological Society*, **15**, 179–184.

Branch, G.M. & Steffani, C.N. (2004) Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *Journal of Experimental Marine Biology and Ecology*, **300**, 189–215.

Clarke, A.H. (1981) *Les Mollusques d'eau douce du Canada*. Musée National des Sciences Naturelles, Musées Nationaux du Canada, Ottawa, Canada.

Cooper, H.M. & Hedges, L.V. (1994) *The handbook of research synthesis*. Russell Sage Foundation, New York.

Creese, R., Hooker, S., De Luca, S. & Wharton, Y. (1997) Ecological and environmental impact of *Musculista senhousia* (Mollusca: Bivalvia: Mytilidae) in Tamaki Estuary, Aukland, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **31**, 225–236.

Crooks, J.A. (1998) Habitat alteration and community-level effects of an exotic mussel, *Musculista senhousia*. *Marine Ecology Progress Series*, **162**, 137–152.

Crooks, J.A. (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, **97**, 153–166.

Crooks, J.A. & Khim, H.S. (1999) Architectural vs. biological effects of a habitat-altering, exotic mussel, *Musculista senhousia*. *Journal of Experimental Marine Biology and Ecology*, **240**, 53–75.

Cummings, V.J., Thrush, S.F., Hewitt, J.E. & Funnell, G.A. (2001) Variable effects of a large suspension-feeding bivalve on infauna: experimenting in a complex system. *Marine Ecology Progress Series*, **209**, 159–175.

Darrigran, G., Martin, S.M., Gullo, B. & Armendariz, L. (1998) Macroinvertebrates associated with *Limnoperna fortunei* (Dunker, 1857) (Bivalvia, Mytilidae) in Río de la Plata, Argentina. *Hydrobiologia*, **367**, 223–230.

Dittmann, S. (1990) Mussel beds — amensalism or amelioration for intertidal fauna? *Helgoland Marine Research*, **44**, 335–352.

Dusoge, K. (1966) Composition and interrelations between macrofauna living on stones in the littoral of Mikolajskie Lake. *Ekologia Polska Seria A*, **14**, 755–762.

Englund, G., Sarnelle, O. & Cooper, S.D. (1999) The importance of data-selection criteria: meta-analysis of stream predation experiments. *Ecology*, **80**, 1132–1141.

Gabriels, W., Goethals, P.L.M. & De Pauw, N. (2005) Implications of taxonomic modifications and alien species on biological water quality assessment as exemplified by the Belgian Biotic Index method. *Hydrobiologia*, **542**, 137–150.

Greenwood, K.S., Thorp, J.H., Summers, R.B. & Guelda, D.L. (2001) Effects of an exotic bivalve mollusc on benthic invertebrates and food quality in the Ohio River. *Hydrobiologia*, **462**, 169–172.

Griffiths, C.L., Hockey, P.A.R., van Erkom Schurink, C. & Le Roux, P.J. (1992) Marine invasive aliens on South African shores: implications for community structure and trophic functioning. *South African Journal of Marine Science*, **12**, 713–722.

Gurevitch, J. & Hedges, L.V. (1999) Statistical issues in ecological meta-analyses. *Ecology*, **80**, 1142–1149.

Gurevitch, J., Curtis, P.S. & Jones, M.H. (2001) Meta-analysis in ecology. *Advances in Ecological Research*, **32**, 199–247.

Gutiérrez, J.L., Jones, C.G., Strayer, D.L. & Iribarne, O.O. (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos*, **101**, 79–90.

Haynes, J.M., Tisch, N.A., Mayer, C.M. & Rhyne, R.S. (2005) Benthic macroinvertebrate communities in southwestern Lake Ontario following invasion of *Dreissena* and *Echinogammarus*: 1983–2000. *Journal of the North American Benthological Society*, **24**, 148–167.

Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.

Hewitt, J.E., Thrush, S.F., Legendre, P., Cummings, V.J. & Norkko, A. (2002) Integrating heterogeneity across spatial scales: interactions between *Atrina zelandica* and benthic macrofauna. *Marine Ecology Progress Series*, **239**, 115–128.

Horvath, T.G., Martin, K.M. & Lamberti, G.A. (1999) Effect of zebra mussels, *Dreissena polymorpha*, on macroinvertebrates in a lake-outlet stream. *American Midland Naturalist*, **142**, 340–347.

Izvekova, E.I. & Lvova-Katchanova, A.A. (1972) Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae. *Polish Archives of Hydrobiology*, **19**, 203–210.

Jacobi, C.M. (1987) The invertebrate fauna associated with intertidal beds of the brown mussel *Perna perna* (L.) from Santos, Brazil. *Studies on Neotropical Fauna and Environment*, **22**, 57–72.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946–1957.

Jones, L.A. & Ricciardi, A. (2005) Influence of physicochemical factors on the distribution and biomass of invasive mussels in the St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 1953–1962.

Karatayev, A.Y., Burlakova, L.E. & Padilla, D.K. (1997) The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in Eastern Europe. *Journal of Shellfish Research*, **16**, 187–203.

Klemm, D.J. (1985) *A guide to the freshwater Annelida (Ploychaeta, Naidid and Tubificid Oligochaeta, and Hirudinea) of North America*. Kendall/Hunt Publishing Co, Dubuque, Iowa.

Kuhns, L.A. & Berg, M.B. (1999) Benthic invertebrate community responses to round goby (*Neogobius melanostomus*) and zebra mussel (*Dreissena polymorpha*) invasion in southern Lake Michigan. *Journal of Great Lakes Research*, **25**, 910–917.

Lajeunesse, M.J. & Forbes, M.R. (2003) Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques. *Ecology Letters*, **6**, 448–454.

Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–989.

Lipsey, M.W. & Wilson, D.B. (2001) *Practical meta-analysis*. Sage Publications, Thousand Oaks, California.

Lohse, D.P. (1993) The importance of secondary substratum in a rocky intertidal community. *Journal of Experimental Marine Biology and Ecology*, **166**, 1–17.

Lozano, S.J., Scharold, J.V. & Nalepa, T.F. (2001) Recent declines in benthic macroinvertebrate densities in Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 518–529.

Mayer, C.M., Keats, R.A., Rudstam, L.G. & Mills, E.L. (2002) Scale-dependent effects of zebra mussels on benthic invertebrates in a large eutrophic lake. *Journal of the North American Benthological Society*, **21**, 616–633.

McCarthy, J.M., Hein, C.L., Olden, J.D. & Vander Zanden, M.J. (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology*, **51**, 224–235.

Merritt, R.W. & Cummins, K.W. (1984) *An introduction to the aquatic insects of North America*, 2nd edn. Kendall/Hunt Publishing Co, Dubuque, Iowa.

Mistri, M. (2002) Ecological characteristics of the invasive Asian date mussel, *Musculista senhousia*, in the Sacca di Goro (Adriatic Sea, Italy). *Estuaries*, **25**, 431–440.

Mörtl, M. & Rothhaupt, K.-O. (2003) Effects of adult *Dreissena polymorpha* on settling juveniles and associated macroinvertebrates. *International Review of Hydrobiology*, **88**, 561–569.

Nalepa, T.F., Fanslow, D.L., Lansing, M.B. & Lang, G.A. (2003) Trends in the benthic macroinvertebrate community of Saginaw Bay, Lake Huron, 1987–96: responses to phosphorus abatement and the zebra mussel, *Dreissena polymorpha*. *Journal of Great Lakes Research*, **29**, 14–33.

Norkko, A., Hewitt, J.E., Thrush, S.F. & Funnell, G.A. (2006) Conditional outcomes of facilitation by a habitat-modifying subtidal bivalve. *Ecology*, **87**, 226–234.

Osenberg, C.W., Sarnelle, O. & Cooper, S.D. (1997) Effect size in ecological experiments: the application of biological models in meta-analysis. *American Naturalist*, **150**, 798–812.

Osenberg, C.W., Sarnelle, O., Cooper, S.D. & Holt, R.D. (1999) Resolving ecological questions through meta-analysis: goals, metrics and models. *Ecology*, **80**, 1105–1117.

Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459–1461.

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. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.

Peckarsky, B.L., Fraissinet, P.R., Penton, M.A. & Conklin, D.J. Jr (1990) *Freshwater macroinvertebrates of northeastern North America*. Cornell University Press, Ithaca, New York.

Pennak, R.W. (1989) *Fresh-water invertebrates of the united states: protozoa to Mollusca*, 3rd edn. John Wiley & Sons, New York.

Reed, T., Wielgus, S.J., Barnes, A.K., Schiefelbein, J.J. & Fettes, A.L. (2004) Refugia and local controls: benthic invertebrate dynamics in lower Green Bay, Lake Michigan following zebra mussel invasion. *Journal of Great Lakes Research*, **30**, 390–396.

Ricciardi, A. (2003) Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. *Freshwater Biology*, **48**, 972–981.

Ricciardi, A. & Atkinson, S.K. (2004) Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters*, **7**, 781–784.

Ricciardi, A. & Ward, J.W. (2006) Comment on 'Opposing effects of native and exotic herbivores on plant invasions'. *Science*, **313**, 298.

Ricciardi, A., Whoriskey, F.G. & Rasmussen, J.B. (1995) Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1449–1461.

Ricciardi, A., Whoriskey, F.G. & Rasmussen, J.B. (1997) The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2596–2608.

Robinson, T.B. & Griffiths, C.L. (2002) Invasion of Langebaan Lagoon, South Africa, by *Mytilus galloprovincialis* — effects on natural communities. *African Zoology*, **37**, 151–158.

Rodriguez, L.F. (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions*, **8**, 927–939.

Ross, D.J., Johnson, C.R. & Hewitt, C.L. (2003) Variability in the impact of an introduced predator (*Asterias amurensis*: Asteroidea) on soft-sediment assemblages. *Journal of Experimental Marine Biology and Ecology*, **288**, 257–278.

Ruiz, G.M., Fofonoff, P., Hines, A.H. & Grosholz, E.D. (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnology and Oceanography*, **44**, 950–972.

Seed, R. (1996) Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biology Association of the United Kingdom*, **76**, 203–210.

Sephton, T.W., Paterson, C.G. & Fernando, C.H. (1980) Spatial interrelationships of bivalves and nonbivalve benthos in a small reservoir in New Brunswick, Canada. *Canadian Journal of Zoology*, **58**, 852–859.

Slepnev, A.Y., Protasov, A.A. & Videnina, Y.L. (1994) Development of a *Dreissena polymorpha* population under experimental conditions. *Hydrobiological Journal*, **30**, 24–30.

Stewart, T.W., Miner, J.G. & Lowe, R.L. (1998) Macroinvertebrate communities on hard substrates in Western Lake Erie: structuring effects of *Dreissena*. *Journal of Great Lakes Research*, **24**, 868–879.

Stewart, T.W., Miner, J.G. & Lowe, R.L. (1999) A field experiment to determine *Dreissena* and predator effects on zoobenthos in a nearshore, rocky habitat of western Lake Erie. *Journal of the North American Benthological Society*, **18**, 488–498.

Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, **21**, 645–651.

Strayer, D.L. & Smith, L.C. (2000) Macroinvertebrates of a rocky shore in the freshwater tidal Hudson River. *Estuaries*, **23**, 359–366.

Strayer, D.L., Smith, L.C. & Hunter, D.C. (1998) Effects of the zebra mussel (*Dreissena polymorpha*) invasion on the macrobenthos of the freshwater tidal Hudson River. *Canadian Journal of Zoology*, **76**, 419–425.

Suchanek, T.H. (1986) Mussels and their role in structuring rocky shore communities. *The ecology of rocky coasts* (ed. by P.G. Moore and R. Seed), pp. 70–96. Columbia University Press, New York.

Thorp, J.H. & Covich, A.P. (1991) *Ecology and classification of North American freshwater invertebrates*, 2nd edn. Academic Press, San Diego, California.

Tokeshi, M. & Romero, L. (1995) Filling a gap: dynamics of space occupancy on a mussel-dominated subtropical rocky shore. *Marine Ecology Progress Series*, **119**, 167–176.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A. & Ojaveer, H. (2002) Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1209–1228.

Washington, H.G. (1984) Diversity, biotic and similarity indices: a review with special relevance to aquatic ecosystems. *Water Research*, **18**, 653–694.

Wisenden, P.A. & Bailey, R.C. (1995) Development of macroinvertebrate community structure associated with zebra mussel (*Dreissena polymorpha*) colonization of artificial substrates. *Canadian Journal of Zoology*, **73**, 1438–1443.

Yager, P.L., Nowell, A.R.M. & Jumars, P.A. (1993) Enhanced deposition to pits: a local food source for benthos. *Journal of Marine Research*, **51**, 209–236.

Young, B.L., Padilla, D.K., Schneider, D.W. & Hewett, S.W. (1996) The importance of size-frequency relationships for predicting ecological impact of zebra mussel populations. *Hydrobiologia*, **332**, 151–158.

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Site locations and references.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/
j.1472-4642. 2007.00336.x
(This link will take you to the article abstract).