Solomon Christopher (Orcid ID: 0000-0002-2850-4257)
Strayer David (Orcid ID: 0000-0002-6767-4486)

# Long-term research reveals multiple relationships between the abundance and impacts of a non-native species

David L. Strayer[1,2]

Christopher T. Solomon[1]

Stuart E.G. Findlay[1]

Emma J. Rosi[1]

[1]Cary Institute of Ecosystem Studies, P.O. Box AB, Millbrook, NY 12545;

strayerd@caryinstitute.org, solomonc@caryinstitute.org, findlays@caryinstitute.org,

rosie@caryinstitute.org

[2]Graham Sustainability Institute, University of Michigan, Ann Arbor, MI 48104

Corresponding author: David L. Strayer, strayerd@caryinstitute.org, 845-677-3581

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## Abstract

Non-native species are among the most important drivers of the structure and function of modern ecosystems. The ecological impacts of a non-native species ought to depend on the size and characteristics of its population, but the exact nature of this population-impacts relationship is rarely defined. Both the mathematical form of this relationship (e.g., linear, exponential, threshold) and the attributes of the invading population (e.g., density, biomass, body size) that most efficiently describe its impacts could vary greatly across invaders, ecosystems, and ecological variables. Knowing the shape of this relationship could improve management and help to infer mechanisms of interaction between the invader and ecosystem. We used a long-term data set on the invasion of the Hudson River ecosystem by two species of *Dreissena* (the zebra mussel, *D. polymorpha*, and the quagga mussel, *D. rostriformis*) to explore the shape of the population-impacts relationship for selected ecological variables, including seston, phytoplankton, and several taxa of zooplankton. Most population-impacts relationships appeared to follow a negative exponential form, but we also found apparent thresholds and scatter plots for some variables. Including information on the traits of *Dreissena* (body size and filtration rate) often substantially improved models of impacts. We found only slight evidence that the resistance of the Hudson River ecosystem to the *Dreissena* invasion might be increasing over time. Our results suggest important refinements to widely used conceptual models of invasive species impact, and indicate that defining the population-effects relationship will be essential in understanding and managing the impacts of non-native species.

## Introduction

Non-native species are one of the most important drivers of the structure and function of modern ecosystems, affecting everything from population genetics to biogeochemical cycles (e.g., Strayer 2010; Lockwood et al. 2013). The most common way to assess the impacts of a species invasion has been to compare the ecosystem before and after invasion; i.e., to treat the invading population as a binary variable (either present or absent). However, there may be substantial variability in impacts after the invasion as a result in changes in the size or traits of the invader's population.

Parker et al. (1999) proposed to incorporate this variation by describing the impact of a non-native species as:

Impact ($I$) = abundance ($A$) x range ($R$) x per capita effect ($E$)

Although appealing, this equation has several possible shortcomings. For instance, impacts may not be a linear function of abundance (Fig. 1). And although abundance is most obviously interpreted as population density, some other measure of the abundance of the invader (e.g., biomass, % cover) may more effectively describe its impacts. If the per capita effect term is to be understood as something other than a catch-all to be interpreted *post hoc* after observing impacts, then we must consider the possibility of changing per capita effects as a result of changes in traits of the invader or resistance of the ecosystem. Parker et al. did recognize some of these complications in their original paper, but subsequent authors have not always considered these nuances, and the Parker et al. equation often is quoted uncritically.

Why does the form of the relationship between the invader's population and the impacts on the ecosystem matter? In addition to any interest this relationship may have for academic invasion ecologists, the details of this relationship are of the highest importance to management (e.g., Yokomizo et al. 2009). Consider the simple question of whether it would be worthwhile to spend a certain amount of money to cut the invader's population by 50%. As Fig. 1 shows, a 50% reduction in an invader's population could reasonably be expected to have an effect of anywhere between 0 and 100%, or be completely unpredictable, depending on the form of this relationship. Without knowing something about the form of the relationship between the invader's population and ecosystem structure and function, it is difficult to evaluate proposed management actions (Yokomizo et al. 2009). Additionally, knowing the shape of the population-impacts relationship may reveal fundamental information about the mechanisms by which the invader influences other species or processes in the ecosystem.

There are many ways by which invasion ecologists might test and refine alternative models of invasion impacts, including direct experimentation, modeling, cross-system comparisons, and long-term studies (cf. Carpenter 1998; Vander Zanden et al. 2017). Here, we use long-term data from the Hudson River ecosystem to compare alternative models of how the invasion of *Dreissena* spp. (the zebra mussel, *D. polymorpha*, and the quagga mussel, *D. rostriformis*) affected the Hudson River ecosystem.

Specifically, we compare the effectiveness of several kinds of models to describe the impact of *Dreissena*. First, we compare models based solely on the presence or absence of the invader with models that include some measure of its abundance. Although it seems obvious that models including some measure of abundance would outperform presence-absence models, presence-absence (=before/after invasion designs) are very common in invasion ecology, either because abundance data are lacking or because such simple models are convenient and effective (e.g., Strayer et al. 2008). If the abundance of the invader varies over a sufficiently wide range, either over time or across sites, such presence-absence models will be inadequate to describe these impacts.

Second, we compared models using a linear function of abundance (as suggested by the Parker et al. formulation) with a specific non-linear model (a negative exponential function). Although linear models are simple and widely used, they are likely to be inappropriate for many kinds of interactions between invaders and the ecosystems they invade (Yokomizo et al. 2009; Thiele et al. 2010; Vander Zanden et al. 2017). For instance, the impacts of suspension-feeders like *Dreissena* are more likely to follow a negative exponential form than be linear with *Dreissena* density (e.g., Caraco et al. 2006; Higgins and Vander Zanden 2010).

Third, we compared models that included some information on the traits of the invader with models based solely on abundance. Individuals within an invading species often vary in traits such as body size, gape width, chemical content, and so on, in ways that affect their roles within an ecosystem. Body size of Hudson River *Dreissena* has varied considerably from year to year (Strayer and Malcom 2014), which could have two important consequences. To begin with, filtration rate is a nonlinear function of body size (Kryger and Riisgard 1988), so a population of large animals filters more water than a population of small animals of the same population density. In addition, there is some evidence that large *Dreissena* can capture a different mix of particles than small *Dreissena*, and specifically are more effective at capturing zooplankton (MacIsaac et al. 1995). Therefore, we compared models based on population density with those that were based on filtration rates, and those that included only filtration rates of the largest animals.

Fourth, we searched for evidence that the Hudson ecosystem has developed resistance to the *Dreissena* invasion over time, so that per capita *Dreissena* impacts have declined. There is a persistent idea in invasion ecology that ecosystems might become more resistant to an invader over time as species already in the ecosystem develop morphological or behavioral defenses against the invader, incorporate the invader into their diets, and so on (e.g., Carlsson et al. 2009; Strayer 2012; Iacarella et al. 2015; Langkilde et al. 2017), or as new enemies of the invader arrive in the ecosystem.

Finally, we close by using the results of these comparisons to extend Parker et al.'s framework for describing the impacts of non-native species.

## The study area

The study area is the freshwater tidal section of the Hudson River in eastern New York, extending from RKM 99-247 (i.e., river kilometers from the mouth of the river at The Battery in New York City). This part of the Hudson averages 900 m wide and 8 m deep, and is well mixed by strong tidal currents, which prevent stratification. Mean annual discharge is ~500 $m^3$/sec, depending on location along the river, but tidal flows usually are much larger than net freshwater flows downriver. Mean water residence time during the growing season in the years of our study was 3-17 weeks. The river bottom is predominately sand or mud, although ~7% of the area is rocky; these rocky areas support most of the *Dreissena* population. The water is turbid (Secchi transparency ~1-2 m, chiefly a result of suspended silt), moderately hard (pH ~ 8, Ca ~ 20-25 mg/L) and rich in nutrients (TP ~ 80 µg/L, $NO_3$-N ~ 400 µg/L). Allochthonous inputs dominate the organic carbon budget, although autochthonous production by phytoplankton and rooted plants can be important locally or to parts of the food web (Caraco et al, 2010; Cole and Solomon, 2012). Bacterial production greatly exceeds phytoplankton production (Findlay 2006). Dominant species include diatoms and cyanobacteria in the phytoplankton; rotifers, cyclopoids, and *Bosmina* in the zooplankton; bivalves and oligochaetes in the zoobenthos; and young-of-the-year of *Alosa* and *Morone* in the fish. Further information about the freshwater tidal Hudson is available in Levinton and Waldman (2006).

The zebra mussel, *Dreissena polymorpha*, appeared in the Hudson in 1991, and quickly developed a large population; by the end of 1992, the biomass of zebra mussels exceeded the biomass of all other heterotrophs in the ecosystem (Strayer et al. 1996). We observed large and pervasive effects of zebra mussels throughout the Hudson River ecosystem, including on water chemistry and clarity (Caraco et al. 1997, 2000), bacterioplankton (Findlay et al. 1998), phytoplankton (Caraco et al. 1997, 2006), zooplankton (Pace et al., 2010), zoobenthos (Strayer et al. 2011; Strayer and Malcom 2014), and fish (Strayer et al. 2014b). Zebra mussels have caused similarly large and wide-ranging impacts in many other freshwater ecosystems (reviewed by Higgins and Vander Zanden 2010). A second species of *Dreissena*, the quagga mussel (*D. rostriformis*, formerly called *D. bugensis*) appeared in the Hudson in 2008, although it still constitutes <10% of the combined *Dreissena* population in the river (Strayer and Malcom 2014, and unpublished). In this paper, we combine the two species as *Dreissena* spp.

## Methods

We analyzed the responses of suspended particulate inorganic matter, phytoplankton biomass, tintinnid ciliates (henceforth, “ciliates”), rotifers, nauplii, cladocerans, and copepods to different densities of *Dreissena*, as expressed by the presence, population density, aggregate filtration rate, and filtration rate of the largest animals (shell length >20 mm) of *Dreissena*. We chose particulate inorganic matter as a variable that we expected to be unaffected by *Dreissena*. These mussels do take up particulate inorganic matter, but it is egested in feces and pseudofeces and rapidly resuspended into the water column by strong tidal mixing in the Hudson (Roditi et al. 1997). Thus, we expected to see no effect of *Dreissena* on this variable. In contrast, we expected that *Dreissena* would cause the other, biotic, variables to decline, either because of direct ingestion by *Dreissena* (phytoplankton, ciliates, rotifers, and nauplii) or because of indirect effects transmitted through the food web (cladocerans and copepods). Furthermore, we expected that the body size of *Dreissena* would matter more to larger, more motile particles than smaller, less motile particles, in the sequence copepods~cladocerans>nauplii~rotifers>ciliates>phytoplankton.

Field and laboratory methods were described in detail by Findlay et al. (1991), Strayer et al. (1996), Caraco et al. (1997), and Pace et al. (1998). Briefly, water chemistry and plankton were sampled during 1987-2016 every two weeks during the ice-free season near Kingston (RKM 151). Water samples for analysis of seston and chlorophyll were taken from 0.5 m below the water's surface using a peristaltic pump. Triplicate samples for seston were filtered onto pre-combusted Whatman 934-AH filters which were dried at 70ºC for at least 12 hours before being weighed, then combusted at 450 ºC for four hours and reweighed to estimate both organic and inorganic particulate matter. Triplicate samples for chlorophyll analysis were filtered onto Whatman GFF filters which were frozen until a basic methanol extraction was performed and analyzed using a Turner Designs fluorometer. Microzooplankton were sampled by filtering water collected using the peristaltic pump through a 35 µm mesh in the field, and macrozooplankton were sampled by filtering water collected using a calibrated open-diaphragm bilge pump through a 73 µm mesh in the field. Animals in these samples were narcotized using carbonated water and preserved in a buffered 4% formaldehyde solution (60 g/L of sucrose plus 8.4 g/L of $NaHCO_3$) to yield a final formaldehyde concentration of 2%, then counted in the laboratory under an inverted microscope (microzooplankton) or a dissecting microscope (macrozooplankton). Data used here are growing season means (1 May-30 Sept).

The density, body size distribution, and filtration rate of the *Dreissena* population were estimated from samples deployed in a stratified random design throughout the freshwater tidal Hudson. Seven hard-bottom sites were sampled by divers in June (no June samples were taken in 1993, 1994, 1995, or 2000) and August and 44 soft-bottom sites were sampled by standard (23 by 23 cm) PONAR grab in June-July, then sieved in the field. Rocks collected by divers and sieve residues from PONAR samples were sorted in the laboratory, and representative subsamples of animals were measured (shell length using calipers and shell-free dry mass after animals were dried for at least 24 hours at 60ºC). We estimated filtration rates using the regression of Kryger and Riisgard (1988), which is based on the body mass of individual mussels, and combined the data from the different sampling times into a single growing-season mean. The range of *Dreissena* in the Hudson has not changed substantially since 1992 (Strayer et al. 1996 and unpublished), so we do not include range in our models (including it would simply introduce a scaling constant to the models and not affect any of our conclusions). More than 75% of the *Dreissena* population lives in RKM 151-213 (Strayer and Malcom 2006), immediately upriver from the Kingston station where plankton samples were taken.

We fit generalized linear models to describe the relationships between the response variables and several measures of the abundance or potential impact of the *Dreissena* population. We considered both linear models (using an identity link function) and exponential models (using a log link function) of *Dreissena* effects on the response variables. (We did not attempt to fit any other mathematical functions because our understanding of suspension-feeding suggested to us that a negative exponential was the most promising non-linear functional form.) For both types of models we assumed that observations were Gamma distributed, given that the response variables were all bounded by zero with relatively high variances. We included the freshwater flow of the Hudson as a covariate in all models, and also fit null models including only this covariate, because previous work suggests that freshwater flow is an important predictor of plankton and seston in the Hudson (e.g., Strayer et al. 2008). We considered using mean water temperature as an additional covariate, but it was correlated with flow ($r$=-0.40, $p$=0.03, log-log), and including it often created convergence problems in the fitting algorithm. The models were fit using the glm() function in R (R Core Team 2017). We used likelihood profiles to determine 95% confidence intervals for the parameters of each model using the confint() function, calculated Nagelkerke's pseudo-$R^2$ for each model using the pR2() function in the pscl package (Jackman 2017), and compared models using the small-sample Akaike Information Criterion ($\mathrm{AIC_c}$).

To test whether the resistance of the Hudson ecosystem to *Dreissena* might be changing over time, we plotted the residuals of our best model against year, and tested whether the linear regression slope was significantly greater than 0 (i.e., a 1-tailed test). If the ecosystem has been getting more resistant to *Dreissena*, these residuals should rise through time.

## Results

The population size of *Dreissena*, as well as all of the response variables, varied greatly from year to year over the course of our study (Fig. 2). The results of the statistical models are summarized in Fig. 3, with full details in Supplementary Table S1. As expected, the null model (freshwater flow only), which did not include any *Dreissena*-related variable, was a satisfactory model (i.e., lowest $\mathrm{AIC_c}$ and high $R^2$) only for particulate inorganic matter. Concentrations of suspended inorganic matter were positively correlated with freshwater flow and not much affected by *Dreissena*; adding *Dreissena*-related variables to models for suspended inorganic matter slightly increased $AIC_c$ over the null model ($\Delta AIC_c = 0.6$ to 2.7). In contrast, effects of freshwater flow on biotic variables almost always were negative, though rarely significantly different from zero at $p$=0.05. Our further description of the modelling results for the biotic variables, which were affected by *Dreissena*, is organized around the five questions presented in the Introduction.

### *Presence-absence vs. abundance models*

Models based on the presence or absence of *Dreissena* usually were outperformed by models that included some measure of the size or traits of the *Dreissena* population. The striking exception was for phytoplankton, for which the presence-absence model had substantially the lowest $AIC_c$. Plots of phytoplankton biomass vs. *Dreissena* density or filtration rates (Fig. 4) showed a steep, consistent decline between pre-invasion years with growing season means of 17-29 µg chl-a/L and post-invasion years with growing season means of 4-11 chl-a/L, but relatively little interpretable variation in the post-invasion years.

Presence-absence models for particulate inorganic matter and cladocerans were also slightly better than models based on measures of *Dreissena* population size or traits. However, none of these was very good: as just noted, PIM was best predicted by freshwater flow alone, and cladoceran densities were not well predicted by either freshwater flow or any of the *Dreissena*-related variables that we used (Fig. 3, Supplementary Table S1).

### *Linear vs. nonlinear models*

Attempting to fit linear models to the bounded positive and clearly non-linear data (Fig. 4) led to convergence problems in fitting models. Furthermore, linear models assume constant variance and allow for negative values of the response variable, but the response variables often had non-constant variance and of course must always be positive. Fitting linear models to the data led to negative and nonsensical predicted values of response variable at high *Dreissena* densities. Therefore, we abandoned further attempts to fit linear models to the data, and rejected linear functions of *Dreissena* abundance as an appropriate description of impacts.

*Population density of Dreissena vs. trait-based approaches*

Models using the estimated total filtration rate of the *Dreissena* population outperformed models using population density, except in the case of macrozooplankton (copepods and cladocerans), for which no model performed very well. The gap between density-based models and filtration-based models was especially large for rotifers ($\Delta AIC_c$ ~9). Models using filtration rate of only the largest *Dreissena* were better than models using total population filtration rate for rotifers, nauplii, and copepods, but substantially worse than models using total population filtration rate for phytoplankton and ciliates. There was little difference ($\Delta AIC_c < 0.5$) among models based on density, total filtration rate, or filtration rates of large *Dreissena* for cladocerans, for which no models performed well.

*Development of ecosystem resistance to Dreissena*

There is just a hint in the pattern of residuals that ecosystem resistance to the effects of *Dreissena* may be increasing over time (Fig. 5). Residuals from the best models for phytoplankton, nauplii, and copepods all had positive slopes against time, although these slopes were only marginally significant (1-tailed *p*-values are 0.04, 0.09, and 0.02, respectively). No variables showed a pattern of declining residuals (suggesting declining ecosystem resistance) over time.

## Discussion

### *Model agreement with predictions*

The results of the model comparisons were mostly consistent with our predictions. As predicted, concentrations of suspended inorganic particles were not strongly related to the *Dreissena* population, regardless of the variable that we used to describe it. For the biotic variables that we expected to be affected by *Dreissena*, population density of *Dreissena* was usually better than presence as a predictor of impacts. Including some trait information (total filtration rate) usually further improved the models, and focusing only on the filtration by large *Dreissena* improved models for large particles (zooplankton) but not for smaller particles (phytoplankton and ciliates). This is consistent with the idea that only large-bodied *Dreissena* can ingest small zooplankton such as rotifers (MacIsaac et al. 1995), whereas *Dreissena* of all sizes can ingest small particles such as phytoplankton and ciliates.

We found only a slight indication that ecosystem resistance to the *Dreissena* invasion may be rising in the Hudson, in the form of rising residuals through time (Fig. 5). Although the idea of increasing ecosystem resistance to invaders is pervasive in invasion ecology, it has not yet well tested empirically (Strayer 2012; Iacarella et al. 2015). More evidence like Fig. 5 is needed to resolve this question.

*Model failures*

However, we also found two important deviations from our expectations. First, impacts on phytoplankton were not related to any measure of *Dreissena* population size, but were well predicted by simply considering the presence of *Dreissena*. Phytoplankton biomass declined steeply when *Dreissena* appeared in the Hudson, but interannual variation in post-invasion years was small and unrelated to any measure of the *Dreissena* population that we considered. It is possible that the Hudson's phytoplankton are extremely sensitive to grazing because their growth rates are so slow as a result of severe light limitation (Cole et al. 1992; Caraco et al. 1997). Because *Dreissena* did not reduce concentrations of suspended inorganic matter (Supplementary Table S1), water clarity rose only modestly after the *Dreissena* invasion (Caraco et al. 1997; Strayer et al. 1999, 2014a), so phytoplankton would have been severely light limited even after *Dreissena* arrived. If this explanation is correct, the presence-absence effect that we detected could actually be an extremely steep negative exponential function that reaches its asymptote at a very low level of grazing. The fact that the asymptote is not zero suggests that a fraction of the phytoplankton is either not captured by *Dreissena*, or is returned to the water column undigested as pseudofeces and feces disintegrate. This explanation is consistent with previous work on the Hudson showing that *Dreissena* biodeposits (feces and pseudofeces) contain substantial amounts of live algae (Roditi et al. 1997; Bastviken et al. 1998) that could be resuspended in the turbulent

Hudson. Alternatively, the relationship between grazing and phytoplankton biomass could be a threshold function with the threshold at low grazing rates. The data (Fig. 4) are consistent with all three of these interpretations and currently insufficient to distinguish among them.

The second failure of our modeling is our inability to describe cladoceran densities; all of our models had low $R^2$, and none contained significant terms for either freshwater flow or *Dreissena* (Supplementary Table S1). We can suggest two causes for this poor model performance. First, cladoceran populations in the Hudson, consisting almost entirely of *Bosmina freyi*, are extraordinarily dynamic, typically blooming in June for just a few weeks at densities ~100- to 1000-fold above background (Pace and Lonsdale 2006). This high variability makes our estimates of growing season means (based on samples taken every two weeks) imprecise. Imprecision in estimating both *Bosmina* and *Dreissena* populations may degrade model performance. Second, it appears that *Bosmina* is too large for even large *Dreissena* to capture effectively (MacIsaac et al. 1991, 1995), so impacts of *Dreissena* are indirect, transmitted through the food web. Unsurprisingly, models of parts of the ecosystem that were affected directly by *Dreissena* grazing (phytoplankton, ciliates, rotifers) tended to have higher $R^2$ than models for particles too large for *Dreissena* to graze, and therefore affected only by indirect pathways (copepods, cladocerans). Populations of these latter organisms presumably are affected by factors such as predation from young-of-year fish (Limburg et al. 1997; Pace and Lonsdale 2006) as well as changes in their food supply arising from *Dreissena* grazing.

### *Functional relationships between invaders and ecosystems*

The different functional forms shown in Fig. 1 have strikingly different implications for management (cf. Yokomizo et al. 2009). As we have noted, a control program that reduces the population of the invader by 50% could nearly eliminate the impacts of the invader, have no effect on those impacts, be more than is needed to produce the desired relief from impacts (“overkill”), or have completely unpredictable effects. Such programs often require substantial time and money, and often have harmful side-effects on other species and the environment (e.g., see pp. 154-156 of Davis 2009; Rinella et al. 2009; Zarnetske et al. 2010). Management undertaken without considering the functional relationship between the invader’s population and the ecosystem thus may waste money and produce unnecessary harm to ecosystems (Yokomizo et al. 2009).

But is it practical to predict the functional relationships between invaders and ecosystems without making detailed measurements on every invader and every ecosystem that is invaded? This is an open question, but given the diversity and complexity of the relationships between invaders and ecosystems, it seems unlikely that we will be able to predict such relationships with precision. Nevertheless, it may be possible to develop useful predictions by considering the traits of the invader, the ecosystem, and the response variable being considered. The easiest cases probably will be those in which a single direct process links the invader to the ecosystem (e.g., an invading predator eating a native prey). In such cases, it may be possible to use laboratory experiments and simple models to define the functional and numerical response curves of the actors (e.g., Dick et al. 2017; Laverty et al. 2017) and predict the shape (linear, exponential, threshold) and perhaps even the parameters of the relationship between invader and ecosystem. Suspension-feeding by *Dreissena* and other bivalves might seem to be a promising example, but even here interactions between grazing, nutrients, and the development of toxic algae (e.g., Vanderploeg et al. 2001; White et al. 2011; Horst et al. 2014) complicate matters. On the other hand, if the effects of an invader on one part of an ecosystem are strongly affected by other parts of the ecosystem, as will be the case for indirect effects, the relationship between invader and ecosystem may be noisy and even unpredictable. The poor relationships we observed between *Dreissena* and crustacean zooplankton in the Hudson may be an example of this, where factors such as fish predation (Limburg et al. 1997), advection (Pace et al. 1992), the availability of alternative food resources (Maguire and Grey 2006), or indirect effects propagated through the food web may have obscured the effects of *Dreissena* on the food resources of the crustaceans. Time lags may also introduce unpredictability and hysteresis into the invader-ecosystem relationship, whether they arise from different dynamic speeds of the invading population and the response variable, or from the processes that indirectly link the invader and the response variable. Thus, predicting the shape and parameters of the relationships linking invaders and ecosystem variables may be tractable, but it is not likely to be easy.

### *Improving the Parker et al. equation*

The simple Parker et al. model failed in two ways as an adequate description of *Dreissena* impacts in the Hudson. First, impacts are clearly not a linear function of *Dreissena* abundance, whether that abundance is expressed as population density, total population filtration rate, or filtration rate of the largest animals (Fig. 4). Considering the mechanisms that link invading species to their ecosystems (see above), we suggest that nonlinearity is more likely than linearity to be the rule in invasions (see also Yokomizo et al. 2009; Thiele et al. 2010; Vander Zanden et al. 2017).

Second, the "per capita impact" term in the Parker et al. equation is vague, and could benefit from closer examination. Rather than estimating this term by measuring range, abundance, and impact and solving the equation for per capita impact ($E = I/(A\mathrm{x}R)$), it could be fruitful to explicitly consider what contributes to the per capita impact of a non-native species, and consider how those factors might vary across time and space. In general, we might recognize that per capita impact depends on the traits of the invader and the resistance of the ecosystem (i.e., its response to a given population of an invader, with a particular density and traits). Many traits could vary over space and time and affect the impacts of an invader. In the case of *Dreissena* in the Hudson, temporal changes in body size were important in modulating impacts, probably both by affecting filtration rates and by determining what kinds of particles could be captured (Kryger and Riisgard 1988; MacIsaac et al. 1995). These changes in body size allowed partial recovery of some (e.g., rotifers) but not all (e.g., phytoplankton) parts of the ecosystem towards pre-invasion conditions. Body size or growth in *Dreissena* is affected by predation (Hamilton et al. 1994; Naddafi et al. 2010), disturbance regimes (MacIsaac 1996; Chase and Bailey 1999), and food availability (Sprung 1995; Baldwin et al. 2002), and might diminish over time as predators become more adept at eating the introduced prey, as they have in the Hudson

(Carlsson et al. 2011). Thus, differences in body size of *Dreissena* are likely to underlie differences in per capita impacts across sites and over time. The body size of many other invaders is likely to change over the course of the invasion and affect their impacts.

Traits other than body size likewise will affect per capita effects of invaders. The per capita effects of another invader in the Hudson, the aquatic plant *Trapa natans*, are determined not by individual plant size, but by the size of the plant bed: large beds have much more pronounced effects on dissolved oxygen and denitrification (Hummel and Findlay 2006). Other invader traits that might affect per capita impact include nutrient stoichiometry, chemical or morphological defenses against predation, phenology, virulence, and so on. Incorporating trait information into models of impacts of invading species will require careful attention to (and testing of) the specific mechanisms of interaction between the invader and the ecosystem.

Ultimately, the Parker et al. equation might be improved either by making it more specific or more general. We have suggested that it could be made more specific by replacing the linear form with nonlinear functions where appropriate, and by being more explicit about what “per capita effects” means, perhaps even expanding this term into two separate terms to recognize the distinct roles of invader traits and ecosystem resistance. In addition, because it is clear that all of the terms in the equation can vary over time (as they have in the Hudson), it would be useful to time-index all of the terms in the equation. Furthermore, because of the likelihood of irreversible, lagged, or hysteretic effects of invaders, this time-indexing would have to consider not only the state of the system at time $t$, but at all previous times back to $t-k$, where $k$

is the depth of the time-memory in the system. The resulting equation would thus be tailored to each invader and ecosystem being analyzed, and would become temporally dynamic.

On the other hand, it may be better to write the Parker et al. equation in a more general form, and to use it simply as an organizing framework rather than as a formal equation to be evaluated and solved. In such a case, we might replace

Impact ($I$) = abundance ($A$) x range ($R$) x per capita effect ($E$)

with

Impact ($I_t$) = f[abundance ($A_t$), range ($R_t$), per capita effect ($E_t$)]

and time-index all of the variables, as described above. Such a general formulation would allow for great flexibility, and would remind invasion ecologists, ecosystem scientists, and managers of the factors that need to be considered when analyzing the effects of an invasion.

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**Figure legends**

Fig. 1. Hypothetical examples of several kinds of possible relationships between population density of an invader and ecosystem characteristics. The points could represent either conditions at different times in a single place, or conditions in different places.

Fig. 2. Population density of *Dreissena* and growing season means for response variables at the long-term monitoring station on the Hudson River at Kingston, 1987-2016. See *Methods* for details.

Fig. 3. Akaike weights of competing models based on different measures of the *Dreissena* population for each response variable. Akaike weights indicate the relative likelihood of each model, given the data, and sum to 1 across the set of candidate models. FR(large) = riverwide filtration rate of large (shell length >20mm) *Dreissena*, FR(total) = riverwide filtration rate of all *Dreissena*, PIM = particulate inorganic matter.

Fig. 4. Plots of each response variable against *Dreissena* density, total filtration rate of the *Dreissena* population, and filtration rate of only the largest *Dreissena*. Each point represents the mean value for a year.

Fig. 5. Residuals from the best model for each dependent variable (i.e., the model having the lowest $AIC_c$) plotted against time after the *Dreissena* invasion. If the ecosystem is developing resistance to the effects of this invader, the residuals should rise through time.