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Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis*): a cross-system analysis

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Abstract. Dreissenid mussels (including the zebra mussel *Dreissena polymorpha* and the quagga mussel *D. rostriformis*) are among the world's most notorious invasive species, with large and widespread ecological and economic effects. However, their long-term population dynamics are poorly known, even though these dynamics are critical to determining impacts and effective management. We gathered and analyzed 67 long-term (>10 yr) data sets on dreissenid populations from lakes and rivers across Europe and North America. We addressed five questions: (1) How do *Dreissena* populations change through time? (2) Specifically, do *Dreissena* populations decline substantially after an initial outbreak phase? (3) Do different measures of population performance (biomass or density of settled animals, veliger density, recruitment of young) follow the same patterns through time? (4) How do the numbers or biomass of zebra mussels or of both species combined change after the quagga mussel arrives? (5) How does body size change over time? We also considered whether current data on long-term dynamics of *Dreissena* populations are adequate for

science and management. Individual *Dreissena* populations showed a wide range of temporal dynamics, but we could detect only two general patterns that applied across many populations: (1) Populations of both species increased rapidly in the first 1–2 yr after appearance, and (2) quagga mussels appeared later than zebra mussels and usually quickly caused large declines in zebra mussel populations. We found little evidence that combined *Dreissena* populations declined over the long term. Different measures of population performance were not congruent; the temporal dynamics of one life stage or population attribute cannot generally be accurately inferred from the dynamics of another. We found no consistent patterns in the long-term dynamics of body size. The long-term dynamics of *Dreissena* populations probably are driven by the ecological characteristics (e.g., predation, nutrient inputs, water temperature) and their temporal changes at individual sites rather than following a generalized time course that applies across many sites. Existing long-term data sets on dreissenid populations, although clearly valuable, are inadequate to meet research and management needs. Data sets could be improved by standardizing sampling designs and methods, routinely collecting more variables, and increasing support.

Key words: biological invasions; *Dreissena;* invasive species; long-term studies; population performance.

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Introduction

The long-term dynamics of biological invasions are important in determining their ecological and economic effects and therefore their best management. As the abundance and traits of an invader change through time, its impacts may change (e.g., Parker et al. 1999, Higgins and Vander Zanden 2010, Strayer et al. 2019). We know that populations of invaders may exhibit a wide range of dynamics, including lags, explosive growth, sudden crashes (even to extirpation), and long-term declines or increases, but these dynamics are generally not well understood, either empirically or theoretically (e.g., Crooks 2005, Strayer et al. 2006, Aagaard and Lockwood 2016, Strayer et al. 2017).

Freshwater mussels of the genus *Dreissena* are among the most problematic of invaders, having spread widely and rapidly across Europe and North America from their native ranges in the Ponto-Caspian region. They often form dense populations and cause large changes to ecosystems through both food web and ecosystem engineering effects (e.g., Higgins and Vander Zanden 2010, Nalepa and Schloesser 2014). In addition, they cause substantial direct economic damages by fouling water intakes and other infrastructure (e.g., Connelly et al. 2007, Nakano and Strayer 2014). As a result of these large ecological and economic effects, *Dreissena* species present serious management challenges and are often included on lists of the world's worst invaders (e.g., Lowe et al. 2004).

Evaluating the long-term behavior of *Dreissena* populations is important to understanding their impacts and managing them wisely. Several papers have discussed how *Dreissena* populations might behave over the long term (e.g., Stańczykowska 1977, Burlakova et al. 2006, Strayer and Malcom 2006, Karatayev et al. 2015). In particular, after an initial period of rapid population growth, *Dreissena* populations often are said to decline over the long term, thereby easing ecological and economic impacts. However, these ideas have not been rigorously tested using long-term data from multiple ecosystems.

The long-term interactions between species of *Dreissena* also are inadequately understood. Two species of *Dreissena* have been widely dispersed by human activities: the zebra mussel (*D. polymorpha*) and the quagga mussel (*D. rostriformis*, also known as *D. bugensis* or *D. rostriformis bugensis*, Stepien et al. 2014). Zebra mussels usually arrive first in a body of water, and then usually are displaced quickly by quagga mussels when they subsequently arrive (e.g., Karatayev et al. 2011, 2015, Heiler et al. 2013, Hetherington et al.

2019). Specifically, Heiler et al. (2013) calculated that the percentage of quagga mussels in the dreissenid community at 13 sites in western Europe increased by 26%/yr until they essentially displaced zebra mussels. However, the two species coexist at some locations (e.g., Zhulidov et al. 2010, Karatayev et al. 2014, Strayer and Malcom 2014). The frequency, speed, and conditions under which quagga mussels displace zebra mussels are still incompletely known, as are the consequences of this displacement for the ecosystem.

Analyses of many individual *Dreissena* populations have been published, which describe dynamics at one or a few locations, and discuss the factors thought to be responsible for those dynamics (e.g., Stańczykowska and Lewandowski 1993, Karatayev and Burlakova 1995, Burlakova et al. 2006, Strayer and Malcom 2006, Balogh et al. 2008, 2018, Nalepa et al. 2010, Karatayev et al. 2014, Marsden et al. 2014, Martel and Madill 2018, Hetherington et al. 2019), but there have been no attempts at a global analysis. Here, we analyze multiple long-term data sets on *Dreissena* populations to try to answer the following questions.

How do Dreissena populations change through time? Do all populations follow a single or a small number of trajectories, or are the dynamics of each population idiosyncratic? Earlier work has suggested that some *Dreissena* populations are relatively stable, whereas others decline, increase, cycle, or fluctuate irregularly over time (e.g., Ramcharan et al. 1992, Stańczykowska and Lewandowski 1993, Aldridge et al. 2004, Burlakova et al. 2006, Strayer and Malcom 2006).

A particularly important variant of the first question is: *Do Dreissena populations decline substantially over time?* There is a persistent idea that populations of biological invaders tend to decline steeply after an initial boom period (e.g., Simberloff and Gibbons 2004, Strayer et al. 2017). Such boom–bust dynamics would be of obvious importance to management; if the severe impacts during the boom period could be tolerated or mitigated, then perhaps little or no management would be required after the population crashed. Boom-bust dynamics have been reported for specific *Dreissena* populations (e.g., Stańczykowska 1977, Burla and Ribi 1998, Petrie and Knapton 1999), but not analyzed quantitatively for a large number of populations.

Do different measures of population performance (post-larval biomass or density, veliger density, recruitment of young-of-year) follow the same or different patterns through time? Most monitoring programs measure only one attribute or life stage of *Dreissena* populations (see *Characteristics of the data sets*). Can the dynamics of other population attributes be inferred accurately from those of any single measured attribute? If so, then one could sample the attribute that can be measured with the greatest precision, least cost, or greatest convenience with the confidence that other attributes follow a similar temporal dynamic.

How do the numbers or biomass of zebra mussels or combined Dreissena species respond after the quagga mussel arrives at a site? As noted above, quagga mussels usually invade later than and displace zebra mussels, but exceptions occur. How frequently and how quickly do quagga mussels replace zebra mussels? Can we identify the environmental conditions that allow long-term coexistence? The replacement or augmentation of zebra mussels by quagga mussels may have important ecological consequences if the two species have different impacts (Baldwin et al. 2002, Burlakova et al. 2014, Karatayev et al. 2015), or if the arrival of the quagga mussel greatly changes the total numbers or biomass of dreissenids in the ecosystem, as it did in Lake Michigan (Nalepa et al. 2010, Madenjian et al. 2015), where total dreissenid biomass and impacts increased greatly when quagga mussels appeared. It is unclear how frequently such an increase occurs. These questions are especially important because quagga mussels are still spreading and displacing zebra mussels across wide areas of North America and Europe (Karatayev et al. 2015, Balogh et al. 2018).

How does body size of Dreissena change through time? Several interacting factors (increased predation from native or non-native predators; changing food resources, disturbance regimes, or water temperatures; or any other changes to growth rates or survivorship schedules) might change over time and affect body sizes of dreissenids (e.g., Carlsson et al. 2011, White et al. 2015). Because body size affects the biomass of dreissenid populations, as well as some of their per capita effects on other parts of the ecosystem (e.g., MacIsaac et al. 1995, Pace et al. 2010, Strayer et al. 2019), changes in body sizes could

have important consequences for communities and ecosystems.

Are the data being collected on the long-term dynamics of Dreissena populations adequate for science and management? It would be useful to know whether data are being collected in enough bodies of water to reveal general patterns or distinguish among different kinds of patterns in different kinds of ecosystems. We would also like to assess whether the data are of sufficient quality (length of record, frequency of sampling, spatial coverage, consistency of methods, precision of estimates, etc.) to confidently answer key questions about *Dreissena* populations. If current data are insufficient, how can we improve monitoring programs so that adequate data will be available in the future?

Methods

Locating and selecting data sets

We attempted to include all available long-term, quantitative data on *Dreissena* populations. We began by searching the Web of Science and Google Scholar for published studies of *Dreissena* populations and posting a call for information on the Unio listserve. From this initial set of studies, we searched for additional data (including unpublished data) by scanning bibliographies and contacting authors and researchers known to us to be studying *Dreissena*.

We included all data sets that spanned at least 10 yr, during which the population was sampled in at least 3 yr using the same or a comparable method, and that quantitatively measured some aspect of density or biomass of a *Dreissena* population. We included data on all life stages, including numbers or biomass of settled animals (i.e., post-larvae) on native substrata (which for convenience we here call "adult" density and biomass, respectively, although some of these animals are not sexually mature), numbers of planktonic veligers, or numbers of newly settled animals, usually on artificial substrata (which we call "recruitment," as these data record animals settled since substrata were deployed). These data sets included samples taken using a number of different sampling designs, collection methods, and measurement units (the data shown in our figures, along with a data file that provides details about study sites and data sets, are freely available at https://doi.org/10.5061/dryad.m3t6764). In addition to the sources listed in the 5th paragraph of the Introduction, primary data sources included bij de Vaate (1991), Martel (1995), Timm et al. (1996), Martel et al. (2001), Marti et al. (2004), Watkins et al. (2007), Wilhelm and Adrian (2007), Steinman et al. (2008), Noordhuis et al. (2010), Birkett et al. (2015), Rudstam (2016), Rudstam and Gandino (2016), and VTDEC (2016). Generally, "site" refers to an individual body of water (e.g., lake or river), but in a few cases (Lakes Champlain and Erie, Rideau River) in which the body of water was large, heterogeneous, and easily divisible into distinct zones, we split it into multiple, more homogeneous sites.

Details of analyses

Our statistical and graphical analyses were matched to the unique properties of the data sets (see Appendix S1 for more details on our statistical analyses). Data sets often were small (only 3–10 yr with data over the 10+ yr period), and sites frequently were sampled at irregular time intervals rather than every year. The resulting data typically were far from normally distributed and had very large variances, so techniques such as parametric time-series analysis were not appropriate. Data were collected using different methods, sampling designs, and times of collection, so they were often not directly comparable across studies. In addition, measurement units often differed across studies (e.g., densities were areally weighted or not, veliger densities were volumetric or areal, and biomass data were wet or dry mass, with or without shell, and so on). Consequently, many of our analyses were ad hoc or exploratory.

How do Dreissena populations change through time?

We used time (in years) since the first detection of *Dreissena* in a body of water as the independent variable in our graphs and analyses of temporal dynamics. This allowed us to compare the temporal dynamics of *Dreissena* populations that were invaded at different times, from the early 19th century to the early 21st century. It was unclear what date to use for the time of first detection for Onondaga Lake, New York, USA. Both species of *Dreissena* were first detected in or

near this lake in 1992 (Mills et al. 1993), but the lake was too badly polluted to allow for large populations to develop until 1998 or 1999 (Spada et al. 2002). We used 1992 as the year of first detection but recognize that 1998 or 1999 could be regarded as the year at which substantial population growth began, so that the points plotted for Onondaga Lake in Fig. 5 and Appendix S2: Figs. S3, S5, and S10 could reasonably be shifted by 6 or 7 yr. However, we do not believe that this decision substantially affects any of our general conclusions about *Dreissena* dynamics (see Appendix S2: Fig. S8 for an example showing how shifting the date of initial detection for Onondaga Lake affected the results).

Generally, before undertaking parametric statistical analyses, we transformed the data by taking the fourth root. We chose the fourth-root transformation because it is widely used for overdispersed benthic invertebrate data (e.g., Downing 1979), and because a Box–Cox transformation of a sample of ten of our data sets produced a mean value for λ of 0.21 (which is very close to the value of $\lambda = 0.25$ that would indicate that a fourth-root transformation would be optimal), showing that a fourth-root transformation was appropriate for our data.

We modeled time-trends of fourth-root-transformed data with both linear fixed- and mixed-effects models including a first-order autoregressive term, fit by REML (restricted maximum likelihood) using the lme function in the nlme package in R (R Foundation for Statistical Computing 2018). Separate models were run for density of adult zebra mussels, density of both *Dreissena* species combined, biomass of adult zebra mussels, biomass of both species combined, density of veligers, and recruitment of young-of-year. For each variable, we ran two kinds of models, producing 12 models in total. The first set of models fit individual time-trends at each site as fixed effects but allowed for an autoregressive correlation structure in the model errors:

$$\sqrt[4]{Y_{ij}} = \beta_{0i} + \beta_{1i}\text{year} + \beta_{2i}Q \times \text{year} + \varepsilon_{ij}$$

The second set of models fit a population-averaged (averaged across all study sites) time-trend that allowed random fluctuations in the intercepts and slopes for each of the sites:

$$\sqrt[4]{Y_{ij}} = \beta_0 + \beta_1\text{year} + \beta_2 Q \times \text{year} + \delta_{0i} + \delta_{1i}\text{year} + \delta_{2i}Q \times \text{year} + \varepsilon_{ij}$$

In these equations, Y is the dependent variable (e.g., biomass, density in the ith site in the jth year since *Dreissena* appeared), β_{0i}, β_{1i}, and β_{2i} denote the fixed-effect intercepts and slopes, respectively, for the ith site, β_0, β_1, and β_2 are the overall (population-averaged) intercept and slopes across all sites, respectively, δ_{0i}, δ_{1i}, and δ_{2i} denote the random intercepts and slopes at each site, respectively, ε is the error term, year is the number of years since the first appearance of *Dreissena* at the site, and Q is an indicator variable noting whether quagga mussels have appeared at the site. Because samples of veligers and new recruits did not distinguish between the two species of *Dreissena*, models for these variables did not include quagga effects. The fixed-effects approach assumes that each site has an independent population with its own individual dynamics, whereas the mixed-effects model treats the individual sites as part of a collection of sites that are drawn from a population of sites where mussels occur, and which have some common characteristics as well as individual characteristics. As we will see below, the two modeling approaches yielded similar results. These models included only sites for which five or more time points were available. We excluded data from the initial outbreak phase of population growth to focus on subsequent population growth, decline, or stability. Figs. 1, 2 suggested that the initial phase of rapid population growth was typically over by 2 yr after first detection of *Dreissena*, so we ran these models after excluding data from years 0 and 1 after first detection of *Dreissena*.

Finally, we used a less formal, more inclusive method to look at temporal change in *Dreissena* populations that uses all of the data from all of the sites to detect time-trends. We started by calculating the change in the value of a variable from one sampling time to any subsequent sampling time as Y_{j+1}/Y_j. For example, if zebra mussel density at site i was 1000 in year 3 and 1500 in year 4, we calculated a change of 1.5. We then took the $\log_{10}$ of this number (0.176). We then calculated change at all n sites that had data for that time interval, resulting in a vector of n $\log_{10}$-transformed changes. Then, we took the median

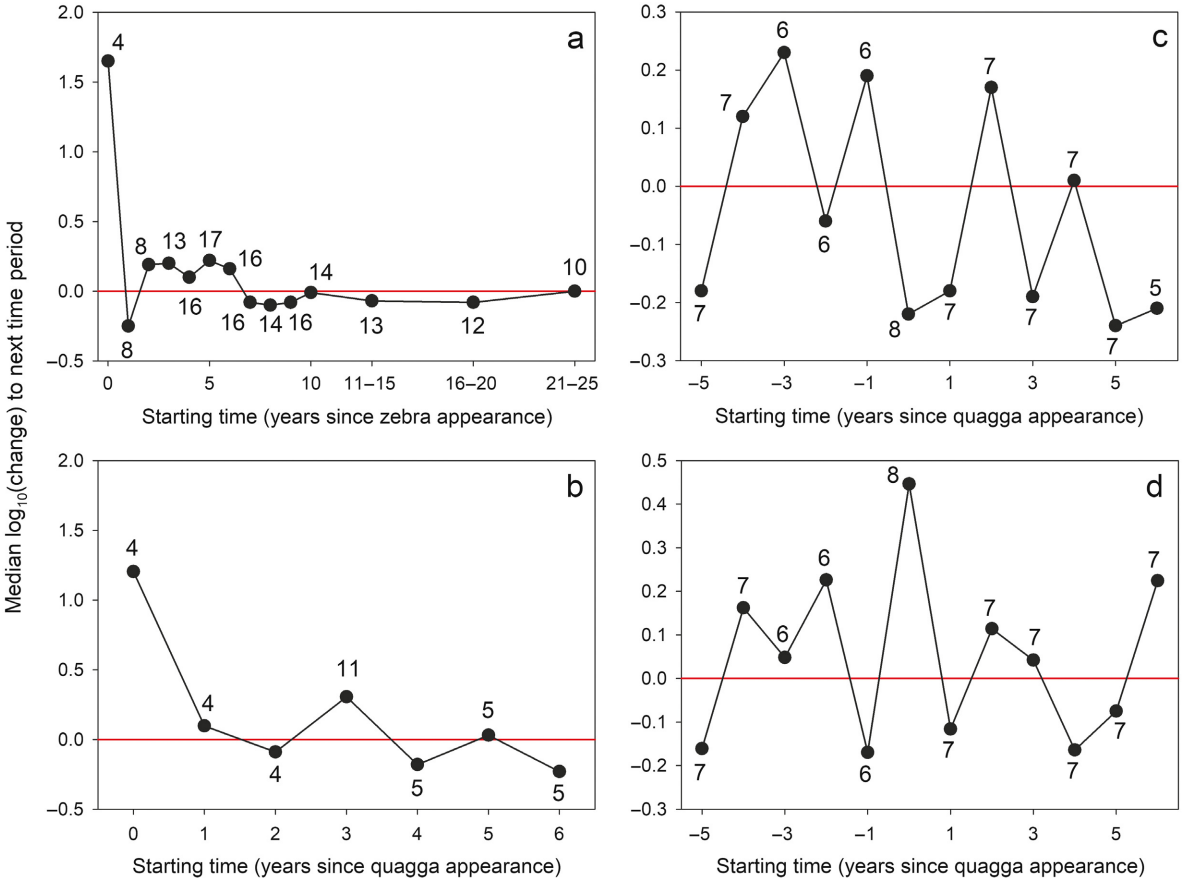

Fig. 1. Temporal change in *Dreissena* populations, summarized over all sites and all variables. The y-axes show the median $\log_{10}$ change in all variables (density of settled animals, biomass of settled animals, density of veligers, or recruitment of settlers) between adjacent time periods. For instance, if the value on the *y*-axis is 1, then the median *Dreissena* population increased by a factor of 10 during that time interval. The number of data points for each time interval is shown next to each plotted point. Panel (a) temporal change in zebra mussel populations at sites when quagga mussels were absent; (b) temporal change in quagga mussel populations; (c) temporal change in zebra mussel populations after quagga mussels arrived; (d) temporal change in combined *Dreissena* populations after quagga mussels arrived. Time intervals are annual except as shown in panel (a). Note the differences in axis scales among plots.

of this vector as a measure of the typical change in a *Dreissena* population over that time interval. Our intent in taking logs and using medians (rather than means) was to provide a robust estimate of change in a highly heterogeneous and non-normal data set. We conducted this analysis both for adjacent time periods (e.g., years 3 and 4, years 6 and 7, and so on) and for all pairs of time periods (e.g., years 3 and 7, years 4 and 9, and so on) for which we had adequate data.

The advantages to this approach are (1) it is relatively simple and transparent; (2) it is independent of the unit of measurement, because it is based on relative changes calculated within data sets, regardless of the units in which data are expressed (wet mass, dry mass, with or without shells, etc.); (3) it allows use of all data (adult densities, adult biomass, veliger densities, recruitment) in a single analysis, hopefully increasing the power of the analysis over what would be possible using any single variable; and (4) it can detect any pattern of population change, whether linear or not, and whether synchronous across sites or not.

Congruence of different measures of population performance

To assess the degree of agreement in temporal dynamics of different population attributes, we visually compared plots of multiple variables measured at the same sites. We also calculated Pearson's correlation between annual means of all pairs of variables from the same sites.

Effects of the arrival of the quagga mussel

To assess the effect of the arrival of the quagga mussel on zebra mussels, or on total *Dreissena* populations, we began by visually examining the time courses of zebra mussel populations at sites subsequently invaded by quagga mussels. For a statistical test, we removed data from years 0 and 1 after zebra mussels were first detected, and years 0 and 1 after quagga mussels were first detected, assuming that populations were still growing rapidly in these periods (consistent with the models described above; cf. Figs. 1, 2). Then, we calculated the ratio of the mean size of the zebra mussel or total dreissenid population after the quagga invasion to before the quagga invasion and used a Wilcoxon ranked sum test to test for statistical significance. We also used the informal method described above, under *How do Dreissena populations change through time?* to summarize changes that followed the appearance of quagga mussels, pooled across all data sets and all variables.

Temporal changes in body size

We expressed body size as the mean mass of an individual animal (usually the only data available). The units in which body mass is expressed varied widely across studies (some wet mass, some dry mass, some ash-free dry mass; some including the shell and some excluding it). We did not try to bring all of these data into a single unit of body mass because we were interested primarily in dynamics within a site rather than comparing across sites, and because wet:dry mass ratios and shell:body ratios can vary substantially across sites, seasons, and investigators (e.g., Nalepa et al. 1993, Costa et al. 2008). Also, different studies collected animals at different times of the year, so any differences across sites could simply be seasonal differences. For the analysis that combined data from multiple sites, we first standardized data by dividing the annual mean by the overall mean for the site, resulting in a unitless measure that was independent of the original measurement units.

Sampling error and adequacy of data sets

Because the various studies used so many different sampling designs (see https://doi.org/10.5061/dryad.m3t6764 for details) and many studies did not report error terms or original data, we cannot provide a uniform, comprehensive assessment of sampling error. Instead, we selected for analysis a few data sets for which we have primary data, and which span a range of habitats, life stages, replication, and between-sample variation.

We calculated 90% confidence limits around annual means of density or biomass of settled animals (adults), following fourth-root transformation of the data (see *How do Dreissena populations change through time?*). For sites with explicitly stratified sampling designs (Hudson River, Oneida Lake), we used the formulas in Thompson (1992), with Satterthwaite's equation for estimating the approximate number of degrees of freedom.

Results

Characteristics of the data sets

We found 67 long-term data sets on *Dreissena* populations from 50 different study sites (Table 1), excluding the data on body mass that we discuss below. These data sets covered both North America and Europe, although none was in the native (pre-1800) range of the genus. Data sets were available from 11 bodies of water that were invaded by quagga mussels following invasion by zebra mussels; none of our study sites were invaded first or only by quagga mussels. Even though *Dreissena* is widespread in rivers and reservoirs as well as lakes, almost all of the long-term data are from lakes, which prevents us from statistically comparing population dynamics in running and standing waters. Data are predominately numbers or biomass of settled animals, but data on multiple variables were collected at several sites. The mean length of the record was 23 yr, with the longest record (from Lake Mikołajskie, Poland) spanning 56 yr. Twenty of the data sets include samples from every year; the remaining 47 have gaps or represent populations that were sampled less

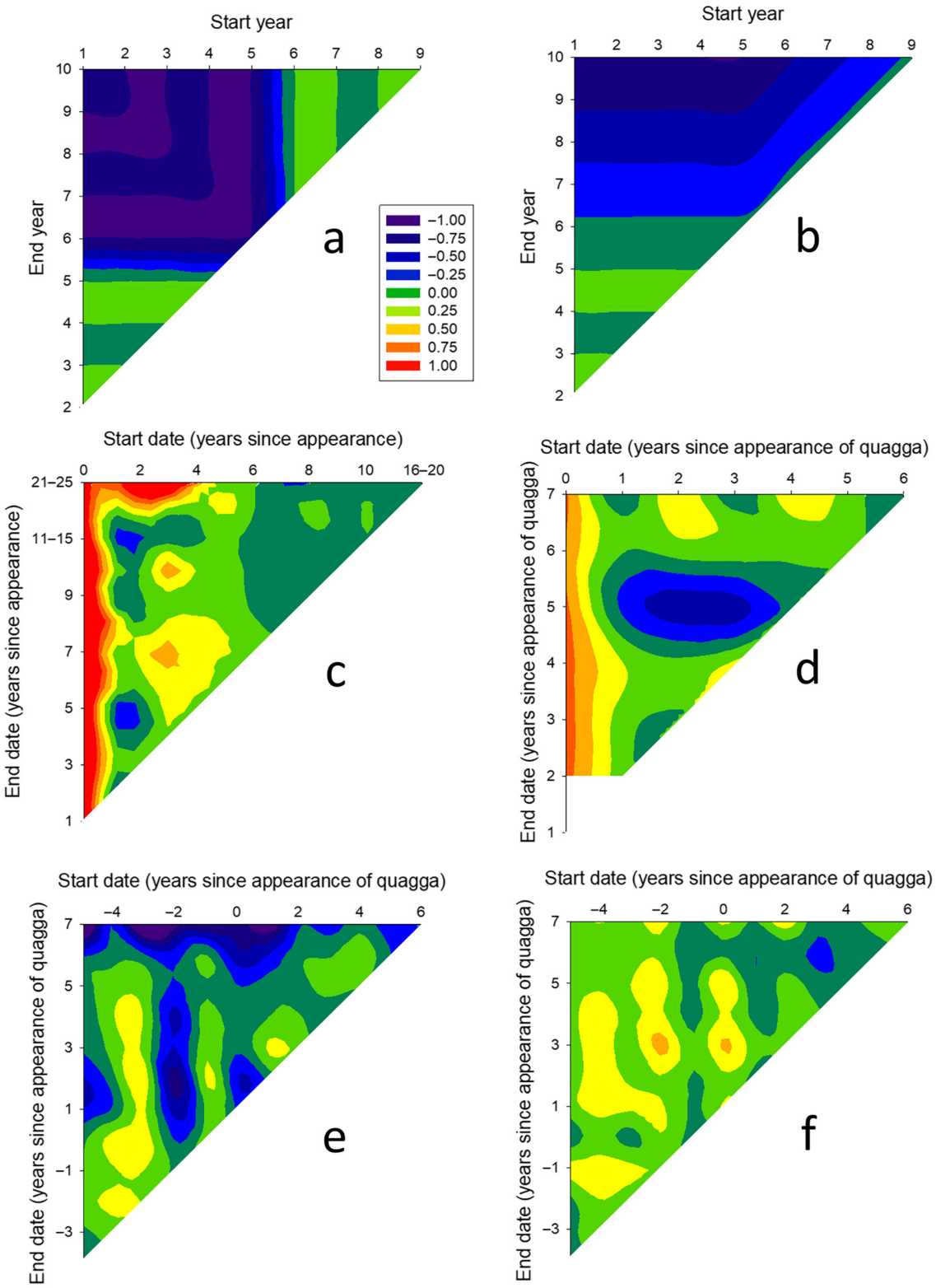

Fig. 2. Idealized and actual results for temporal changes in *Dreissena* populations, calculated for all pairs of

(Fig. 2. *Continued)*

sampling times at a site. Red shows time intervals during which populations were growing; blue shows periods over which populations declined. The numerical scale is the same as in Fig. 1 (the median $\log_{10}$ change between sampling times, so that a value of 1 indicates an increase of 10-fold, 0.3 shows an increase of twofold, 0 shows no change, −0.3 shows a decrease of threefold, and −1 shows a decrease of 10-fold, and so on). Panel (a) is idealized contour diagram for a species that declines synchronously across all sites, with a population decline of 90% between years 5 and 6; (b) idealized contour diagram for a species that declines asynchronously across all sites, with a population decline of 90% between years 5–6 and years 9–10 at different sites; (c) temporal changes in zebra mussel populations when quagga mussels were absent (covering only years 0–25 of the invasion period, for which data are available for multiple sites) (average number of data points for each time interval = 10.9); (d) temporal changes in quagga mussel populations (average number of data points for each time interval = 4.8); (e) temporal change in zebra mussel populations associated with the arrival of quagga mussels (average number of data points for each time interval = 6.6); (f) temporal changes in total *Dreissena* populations associated with the arrival of quagga mussels (average number of data points for each time interval = 6.0).

frequently than annually. The time span covered by the different data sets ranges widely: Some began with the initial appearance of *Dreissena*, whereas some began more than a century later (e.g., Appendix S2: Figs. S1–S7). Year-to-year variation was high for all variables (coefficient of variation of untransformed data typically ~1), with biomass data showing slightly less variation than the other variables (Appendix S3: Table S1).

Long-term population trajectories

Inspection of the time courses (Appendix S2: Figs. S1–S7) shows a wide range of temporal dynamics. No general pattern (or a small number of typical patterns) is obvious from these graphs. The analysis that summarized population changes between adjacent time periods (Fig. 1a) showed that zebra mussel populations at sites without quagga mussels grew rapidly in the first year after detection and tended to continue to grow a little in years 1–7 (dynamics in the presence of quagga mussels are discussed below in *Effects of the quagga mussel invasion*). The analysis based on all pairs of time periods confirmed this pattern (as shown by the red and orange strip along the left side of Fig. 2c). Neither analysis showed any hint of population decline out to year 30. Beyond year 30, data are available for only a few sites, so we cannot test for general trends after that time.

The results of the fixed-effects and mixed-effects models (Table 2) suggested that density (but not biomass) of adult zebra mussels tended to decline over time, in cases in which time-trends were statistically significant (most trends at individual sites were not statistically significant). In contrast, adult biomass of combined *Dreissena* populations, as well as combined

Table 1. Summary of sampling sites and long-term data sets about *Dreissena* populations.

Attribute	Distribution of values
Location of sites	Europe (31), North America (19)
Habitat type of sites	Lake (41), Great Lake (5), river (3), reservoir (1)
Species present at study site	Zebra mussel only (39), both species (11)
Type of data collected	Density of settled animals (35), biomass of settled animals (16), recruitment of settlers (5), density of veligers (11)
Length of record of data sets (years)	Mean = 23.0, median = 21, range = 10†–56
Proportion of years that were sampled	Mean = 0.54, median = 0.33, range = 0.1–1
Spatial coverage of sampling	Single sampling point (5), multiple sampling points (40), system-wide coverage (22)

Notes: There are more data sets than sites, because multiple variables (e.g., adult density plus veliger density) were sampled at some sites. More details are available at https://doi.org/10.5061/dryad.m3t6764.

† We included a single data set (veligers in Mille Lacs, Minnesota, USA) that spanned only 8 yr, because a longer run of data on adults was available for this site.

Table 2. Summary of results of fixed- and mixed-effects models of temporal changes in *Dreissena* populations.

Variable	Site-specific time-trends (β_{1i})				Site-specific quagga effects (β_{2i})				Population-averaged time-trend (β_1)	Population-averaged quagga effect (β_2)
	–	+	NS	*P*	–	+	NS	*P*		
Adult density (*D. polymorpha* only)	5	1	22	0.05	0	0	4	0.12	NA	NA
Adult density (both *Dreissena* combined)	4	1	23	0.24	0	0	4	0.25	– ($P < 0.0001$)	NS
Adult biomass (*D. polymorpha* only)	2	1	10	0.65	0	0	4	0.47	NS	NS
Adult biomass (both *Dreissena* combined)	0	1	12	0.05	0	0	4	0.38	NA	NA
Veliger density	0	4	6	0.04	NA	NA	NA	NA	+ ($P = 0.007$)	NA
Recruitment	0	0	5	0.81	NA	NA	NA	NA	NS	NA

Notes: The columns with site-specific effects tabulate the number of individual sites with fixed-effect temporal trends (β_{1i}) or quagga effects (β_{2i}) that are significantly ($P < 0.05$) negative, significantly positive, or not significant; the *P*-value arises from a Wilcoxon signed-rank test or *t*-test testing whether the median of these fixed-effects slopes is different from 0; the population-averaged columns summarize the results of mixed-effects models that fit a single time-trend (β_1) or quagga effect (β_2) across all sites. NA = not applicable (the model does not exist or did not converge), NS = not significant at $P < 0.05$.

veliger numbers, tended to increase over time, although combined adult density tended to decline over time. The difference between trends of adult density and biomass for combined *Dreissena* populations may be a result of generally higher body mass in quagga mussels than zebra mussels (see *Temporal patterns in body mass*). There were many exceptions to these patterns (Appendix S2: Figs. S1–S7). Neither the fixed- or mixed-effects models detected any significant temporal trends in recruitment.

Coherence of different population variables

Although few of the sites had long-term data for more than one population variable, it is apparent that the long-term population trajectories of different variables can be very different. Data from the Hudson River (the only site where we have data on all four population attributes) illustrate this point clearly (Fig. 3). The data for adult biomass suggest that the Hudson's population is declining over the long term, the veliger data suggest that the population is increasing, the data on adult density suggest that the population is undergoing more or less stable cycling, and the shorter run of data on recruitment does not match any of the other variables. Considering the data from all sites that measured two or more population attributes, density and biomass of settled animals were often (but not always) well correlated, but other population attributes were weakly and insignificantly ($P > 0.05$) correlated (Fig. 4).

Effects of the quagga mussel invasion

As expected, quagga mussels largely displaced zebra mussels at most sites at which both species occur (Appendix S2: Figs. S3, S5), although the dynamic was less predictable than suggested by the Heiler et al. (2013) model (Fig. 5; Appendix S1: Fig. S8). Furthermore, substantial numbers of zebra mussels (>10% of the combined *Dreissena* population) still survived at 3 of the 11 of our sites where both species occur (Onondaga Lake, western Lake Erie, and the Hudson River) 7–25 yr after the appearance of quagga mussels (as far as the data records currently extend).

The informal analysis of all types of data also showed that zebra mussels tended to decline substantially after quagga mussels appeared, especially in the first year after quagga mussels appeared, and that this decline tended to proceed for several years (Figs. 1c, 2e). In contrast, total *Dreissena* populations tended to increase after quagga mussels appeared (Figs. 1d, 2f).

Our ability to quantify or statistically test the effects of the quagga mussel invasion on numbers or biomass of zebra mussels or total dreissenids (summarized in Tables 2 and 3) is limited by the scarcity of appropriate data. Data are available before and after the quagga invasion from only a few sites, some with only a single data point before or after the invasion. The fixed- and mixed-effects models did not detect any significant effect of the appearance of quagga mussels (Table 2). According to the analysis of

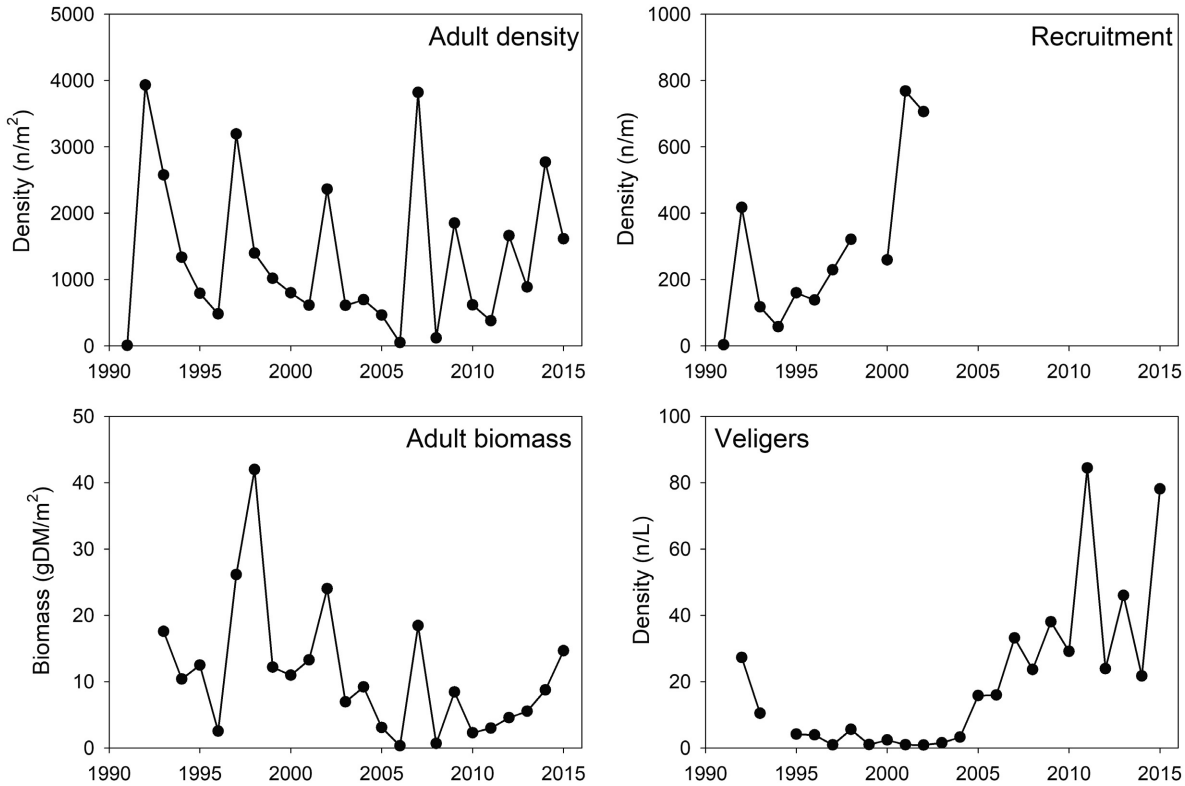

Fig. 3. Long-term dynamics of four different attributes of Hudson River *Dreissena* (both species combined, but quagga mussels were never more than 10% of the total).

Table 3, zebra mussel numbers declined significantly at two of four sites and zebra mussel biomass declined significantly at one of five sites; no other changes in numbers or biomass of zebra mussels or total dreissenids were statistically significant at any single site.

Temporal patterns in body mass

We found long-term (>10 yr) data on temporal changes in body masses from 12 sites, 5 containing only zebra mussels (Appendix S2: Fig. S9) and 7 that were subsequently invaded by quagga mussels (Appendix S2: Fig. S10). All of these data are from the first 25 yr of the *Dreissena* invasion and so represent the early stages of the invasion.

There were no apparent general trends in zebra mussel body mass through time before the quagga mussel invasion. Mean body mass increased over time at some sites, decreased at others, and fluctuated with no clear trend at others (Appendix S2: Fig. S9). When body masses were standardized to allow comparison across sites, no temporal pattern was obvious (Appendix S2: Fig. S11), and neither an ANCOVA with site and time since *Dreissena* appearance nor a simple linear regression on time since *Dreissena* appearance yielded a significant ($P = 0.05$) relationship with time since *Dreissena* appearance.

At sites invaded by quagga mussels, there were no obvious time-trends in either quagga mussel body mass or zebra mussel body mass after quagga mussels appeared (Appendix S2: Fig. S11). Regressions of standardized body mass against time since the appearance of quagga mussels were not significant for either species ($P > 0.3$ in both cases). However, after quagga mussels arrived, interannual variation in body masses of the two species was synchronized (Appendix S2: Fig. S12). At sites where both species were present at the same time, quagga mussels were substantially larger: The median ratio of quagga mussel body mass to the body mass of co-occurring zebra mussels was 2.3 ($n = 45$, interquartile

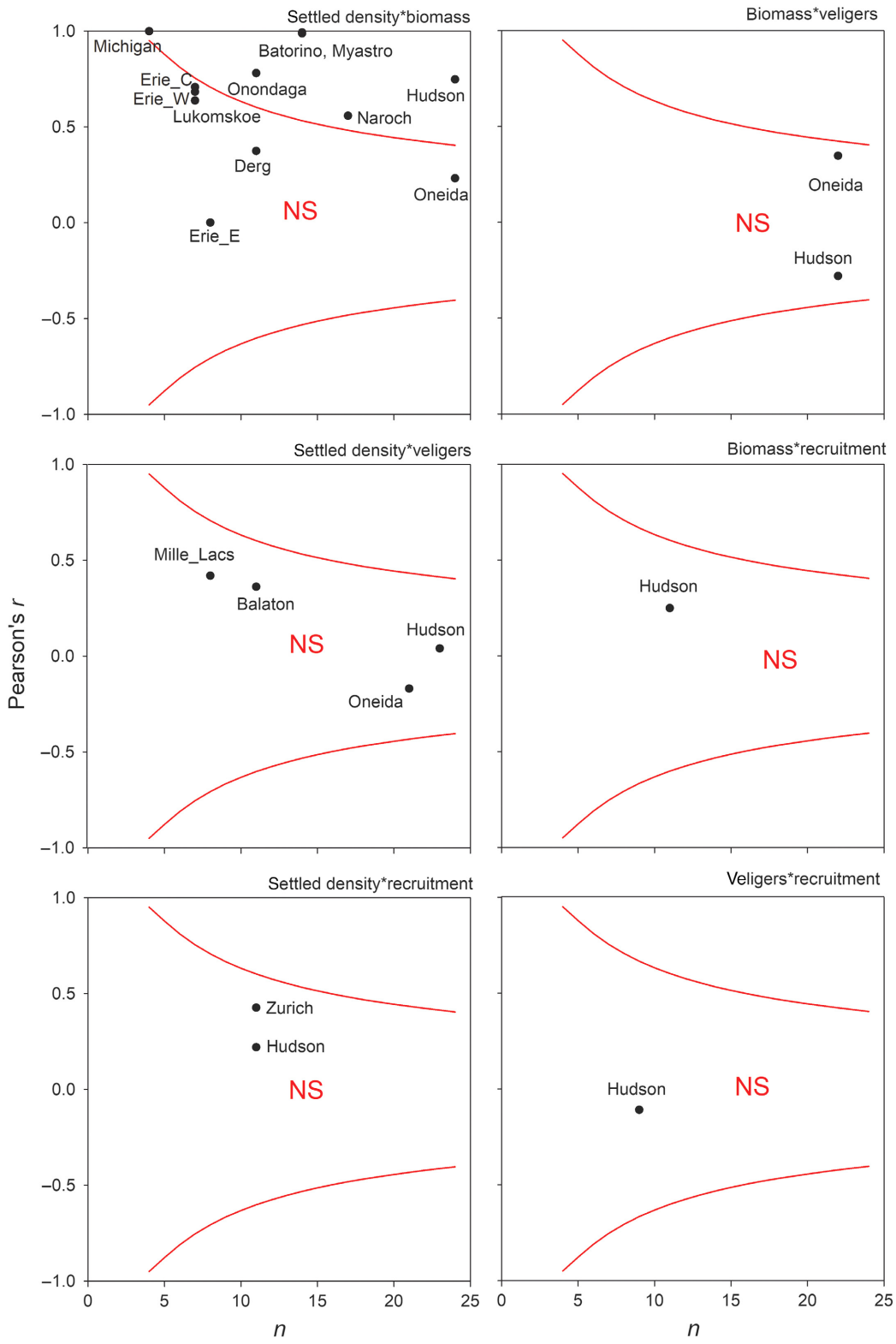

Fig. 4. Correlations between different attributes of *Dreissena* populations (both species combined), for sites

(Fig. 4. *Continued)*

where more than one attribute was measured, plotted against number of data points (n). Red lines show critical values of r for $P = 0.05$; points falling between the red lines are not significantly different from 0. Correlations involving veligers from Oneida Lake were taken from Hetherington et al. (2019).

range = 1.5–5.0). We have data on zebra mussel body mass before and after the quagga mussel invasion at only two sites (Oneida Lake and the Hudson River). At Oneida Lake, zebra mussel body mass dropped sharply with the arrival of quagga mussels (Appendix S2: Fig. S10), but there was no similar drop in the Hudson.

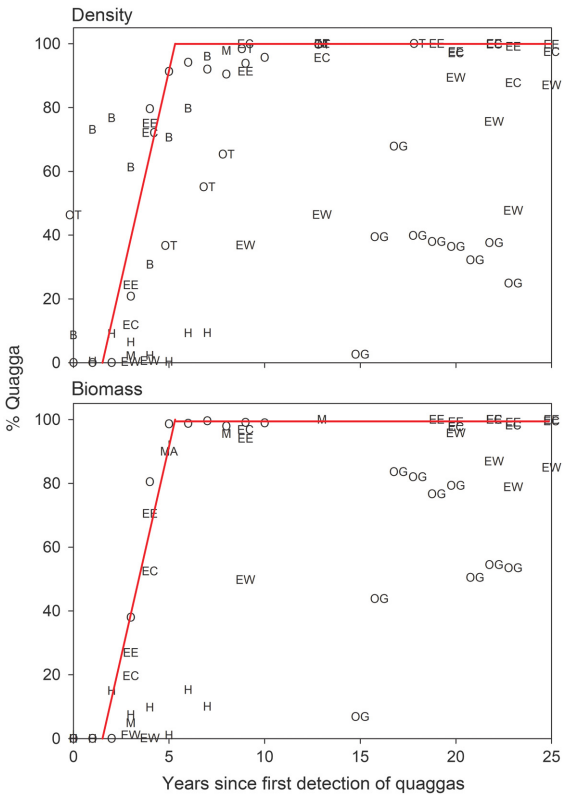

Fig. 5. Dominance of quagga mussels in the dreissenid community as a function of the time since the first quagga was detected. The red line shows the predictions of the Heiler et al. (2013) model. Abbreviations are B, Balaton; EC, Erie Central Basin; EE, Erie Eastern Basin; EW, Erie Western Basin; H, Hudson; I, Ijsselmeer; Ma, Markermeer; M, Michigan; O, Oneida; OG, Onondaga; OT, Ontario. See Appendix S2: Fig. S8 for an alternative version of this figure.

Sampling error and adequacy of data sets

Calculated confidence limits around estimates of adult density or biomass were small to moderate compared to large events in the population trajectories (e.g., outbreak dynamics in Mille Lacs or the impacts of quagga mussels in Lake Erie or Oneida Lake), but often large compared to typical interannual variation (Appendix S2: Figs. S13, S14). Unsurprisingly, confidence limits were tighter for the IJsselmeer and Markermeer, where estimates are based on a very large number of sampling locations (means of 165 and 103 sampling stations, respectively), than for other sites, where fewer stations typically were sampled (Appendix S2: Fig. S14). Many long-term data sets on *Dreissena* populations are based on sampling designs with even fewer samples than those shown in Appendix S2: Figs. S13, S14, and so presumably have wider confidence limits.

Many sampling programs for veligers are based on a single sampling station. Data from Lake Champlain, a complex basin sampled at 12 stations over the long term, show that spatial variation in veliger densities can be considerable. The time courses and densities of veliger populations in the six different parts of the lake (Appendix S2: Fig. S7) are poorly correlated (the mean r^2 between densities in the different parts of the lake is 0.16), probably because of differences in primary production, calcium, and temperature among the different parts of the lake (Marsden et al. 2014). Even within a section of the lake, population trajectories at different sampling stations (data not shown) are only moderately well correlated, with a mean r^2 of 0.4, and only two of eight within-basin correlations having r^2 >0.5.

Discussion

Our analysis demonstrates both the strengths and limitations of existing data sets on *Dreissena* populations. We were able to show that populations follow a wide range of trajectories and that these trajectories are not always similar for

Table 3. Differences in dreissenid populations before and after the quagga mussel invasion (see *Methods* for details).

Body of water (n_{before}, n_{after})	Pre-quagga	Post-quagga	Ratio (post/pre)	*P*
Total dreissenid density (no./m^2)				
Lake Balaton (3,6)	19,589	12,130	0.62	0.26
Hudson River (15,7)	1346	1581	1.17	0.58
Lake Michigan (1,3)	182	4309	23.7	0.50
Oneida Lake (12,9)	6813	5075	0.74	0.60
Total dreissenid biomass (various units)				
Hudson River (15,7)	14.0	7.1	0.51	0.12
IJsselmeer (4,1)	205	351	1.71	0.40
Markermeer (4,1)	56	110	1.98	0.40
Lake Michigan (1,3)	0.1438	6.5	46	0.50
Oneida Lake (12,9)	298	389	1.30	0.13
Zebra mussel density (no./m^2)				
Lake Balaton (3,6)	19,589	4070	0.21	0.02
Hudson River (15,7)	1346	1488	1.11	0.58
Lake Michigan (1,3)	182	218	1.20	1
Oneida Lake (12,9)	6813	1378	0.20	0.0003
Zebra mussel biomass (various units)				
Hudson River (15,7)	14.0	6.4	0.46	0.08
IJsselmeer (4,1)	205	28	0.14	0.40
Markermeer (4,1)	56	11	0.20	0.40
Lake Michigan (1,3)	0.14	0.22	1.57	1
Oneida Lake (12,9)	298	64	0.21	0.0005

Notes: Statistical significance is tested with a Wilcoxon ranked sum test. n = number of years of data.

different population attributes at a single site. Nevertheless, several patterns apply to many or most *Dreissena* populations. Zebra mussels typically appear first at a site (none of our study sites contradicted this pattern, although quagga mussels have sometimes arrived before zebra mussels at sites in the western United States; Stokstad 2007), whereupon their population grows rapidly. When quagga mussels later appear, this second invasion often (but not always) leads to declines in zebra mussel populations and increases in overall *Dreissena* populations. However, data are too few for us to determine what distinguishes sites where quagga mussels displace zebra mussels from sites where they coexist, or to quantify with any precision how overall *Dreissena* biomass or numbers change after quagga mussels appear. We found some evidence for long-term declines in zebra mussel populations, especially in the case of subsequent quagga mussel invasions, but mixed evidence for long-term trends in combined *Dreissena* populations. However, data are so few beyond 30 yr after invasion that it is impossible to say with any confidence what happens after that point. The overall picture is thus one in which we have valuable, but limited, insights into how *Dreissena* populations behave over the long term.

In addition, by providing the first global synthesis of long-term population dynamics of *Dreissena*, our study documents the current state of long-term data on *Dreissena* and brings together available data into one place. This should help to improve data collection and analysis in the future (see *Improving the monitoring of Dreissena populations*) and lay the groundwork for future collaborations.

Long-term population trajectories

We could detect two features that are common in long-term data on *Dreissena* populations. Most populations of both species rose steeply in the first year after they were detected, and many increased more modestly from year 1 to year 5 or so (Figs. 1, 2). In addition, after quagga mussels arrived, most populations of zebra mussels declined, while biomass of total *Dreissena* populations tended to increase (see below for a more detailed discussion).

We found only mixed evidence that *Dreissena* populations otherwise generally decline over the long term, whether zebra mussels in the absence of quagga mussels (Figs. 1, 2; Appendix S2: Figs. S1, S2, S4, S6), quagga mussels (Appendix S2: Figs. S3, S5), or the combined populations of both species (Figs. 1d, 2f, Tables 2 and 3). We caution, though, that we have few data that extend beyond 30 yr after the first appearance of *Dreissena*, so our analyses provide little general insight into what happens to populations later in the invasion.

It is apparent, though, that populations at individual sites can show dramatic dynamics, either before or after year 30, including substantial declines at some sites. Because we see so little evidence of general patterns that apply across all sites, we suggest that population dynamics are context-dependent and that explanations for population dynamics at individual sites should be sought in the ecological characteristics and their temporal changes at individual sites. For instance, changes in *Dreissena* populations at individual sites have been attributed to predation (Petrie and Knapton 1999, Carlsson et al. 2011, Naddafi et al. 2010), physical or chemical disturbance (e.g., wave action, ice scour, hypoxia; Chase and Bailey 1999, Karatayev et al. 2018), rising or extreme water temperatures (White et al. 2015), changes in nutrient inputs (Lewandowski and Stańczykowska 2014) or other aspects of water quality (Spada et al. 2002), changes in food resources, intraspecific competition within *Dreissena* populations (Strayer and Malcom 2006, Vanderploeg et al. 2009), and interspecific competition with new invaders (van der Velde et al. 1994). At this point, it would seem best to be cautious about making blanket statements about how *Dreissena* populations typically behave, or about the mechanisms that typically underlie their population dynamics.

Whatever the causes of interannual variation in dreissenid populations, such variation can be very large (i.e., often >10-fold; Appendix S2: Figs. S1–S7). Regardless of whether this variation represents long-term trends or short-term fluctuations, it must drive correspondingly large variation in ecosystem properties (water clarity, food webs, etc.), in the same way that year-to-year variation in more familiar drivers such as runoff or temperature drive ecosystem variability (e.g., Strayer et al. 2008, 2019). The ability of dreissenid invasions to contribute to or increase temporal variability in freshwater ecosystems seems not to have attracted much attention (but see Fig. 5 of Strayer et al. 2008) but is worth investigating.

Coherence of different population variables

Generally, we found little agreement among the time courses for different population metrics (Figs. 3, 4), although the density and biomass of settled animals often were well correlated (Fig. 4). In particular, veliger density is not a good predictor of subsequent recruitment into the juvenile (settled veliger) or adult population (see also Hetherington et al. 2019); that is, there is not a strong stock: recruit relationship in dreissenids. Such different dynamics for different attributes or life stages would be expected for species with multiple life stages, long lives, or plastic adult body size (e.g., trees and fishes in addition to bivalves; e.g., Elliott 1985, Oliver and Larson 1996, Woods 2000). This general lack of agreement among different population attributes means that it usually will not be possible to infer the long-term dynamics of one attribute from the observed dynamics of another attribute. Even the positive correlation, we found between density and biomass of settled animals (Fig. 4) was so weak at some sites that it would be imprudent to infer biomass dynamics from density dynamics or *vice versa*. Instead, it will be necessary to design monitoring programs to include all variables that are of interest, rather than choosing a single indicator variable on the basis of its low cost, low interannual variability, or compatibility with existing sampling programs, and then trying to extrapolate from that single variable. All of the attributes that we have included in our analysis—population density or biomass of settled animals, density of veligers, density of new settlers—will be of interest in different contexts. For instance, a plankton ecologist might be most interested in the numbers of veligers (e.g., Bowen et al. 2018), whereas an ecosystem ecologist or resource manager might be more interested in biomass of adults as an indicator of impacts. Thus, we cannot identify any single variable that is better than the others—the best variable depends on the objectives of the study—but simply note that the variable of interest must be measured rather than inferred from the dynamics of another variable.

Effects of the quagga mussel invasion

Quagga mussels rapidly displaced zebra mussels at most (8 of 11) of the sites where both species occurred, although this displacement was not as rapid and regular as suggested by Heiler et al. (2013; Fig. 5; Appendix S2: Fig. S8). Indeed, both species were still abundant at 3 of the 11 sites (western Lake Erie, Onondaga Lake, and the Hudson River) several years after quagga mussels arrived. Coexistence also has been reported at a few sites not included in our data set (e.g., some rivers and reservoirs in Russia and Ukraine; Zhulidov et al. 2010). It is too early to know whether the two species will coexist over the long term at such sites, or whether displacement of zebra mussels by quaggas at these sites is just slow. Because of the small number of study sites and the absence of quantitative information on possible drivers at these sites (see *Improving the monitoring of Dreissena populations*), we cannot determine what factors might control the speed of displacement or distinguish the sites where rapid displacement occurs from those where the species coexist. Some possibilities might include physical energy and disturbance regimes (zebra mussels attach more firmly than quagga mussels; Peyer et al. 2009), differential predation favoring zebra mussels (e.g., Naddafi and Rudstam 2014), substratum quality (quagga mussels tolerate soft substrata better than zebra mussels; Mills et al. 1996, Karatayev et al. 2015), food quality and quantity, and temperature (Zhulidov et al. 2010, Huang et al. 2016).

What may matter more to the ecosystem than the replacement of zebra mussels by quagga mussels is what happens to total numbers or biomass of both species after the quagga mussel arrives. (We note, however, that there are some important differences in the effects of the two *Dreissena* species on the ecosystem, so that a kilogram of quagga mussel biomass is not exactly equivalent to a kilogram of zebra mussel biomass, from the viewpoint of ecosystem impacts; Baldwin et al. 2002, Burlakova et al. 2014) It is not yet clear how much total *Dreissena* numbers or biomass change after quagga mussels arrive. At some sites (most spectacularly, Lake Michigan; Appendix S2: Figs. S3, S5; Table 3), total *Dreissena* numbers or biomass increased >20-fold after quagga mussels arrived, leading to a large increase in ecosystem impacts (Nalepa et al. 2010, 2014, Madenjian et al. 2015). At other sites, however (e.g., the Hudson River; Appendix S2: Figs. S3, S5; Table 3), quagga mussels were still a minor part of the dreissenid community several years after they arrived, and it seems unlikely that their arrival substantially changed the ecosystem.

Because quagga mussels tend to disperse between bodies of water more slowly than zebra mussels (Karatayev et al. 2011, 2015), we can expect dreissenid impacts to increase in many lakes in the future as quagga mussels eventually reach them and increase total dreissenid biomass. These increases may be especially large in lakes with extensive areas of soft sediments under oxygenated water.

Temporal patterns in body mass

We could not detect any general trend in body mass over time (Appendix S2: Fig. S11). Instead, temporal trajectories of body mass at individual sites followed a wide range of patterns (Appendix S2: Figs. S9, S10) and were presumably driven by system-specific drivers. For example, increasing predation rates in the Hudson River drove down body mass (Appendix S2: Fig. S10; Carlsson et al. 2011). Populations of *Dreissena* in Lake Naroch are small-bodied because many of them live on macrophytes, which die down periodically, killing the mussels (Burlakova et al. 2006). Frequent disturbance from ice, waves, currents, or episodic hypoxia would also be expected to keep body size small, so changes in disturbance regimes or macrophyte coverage over time should affect *Dreissena* body sizes.

The body mass of zebra mussels fell substantially when quagga mussels arrived at one of the two sites for which we have before–after data (Oneida Lake, Appendix S2: Fig. S10; see also Hetherington et al. 2019), but not the other (Hudson River). It is difficult to know the generality of these observations with so few data, except to note that quagga mussels were abundant in Oneida Lake but not in the Hudson (Appendix S2: Fig. S3), and the Hudson's small quagga mussel population may have been too small to either displace zebra mussels or affect their body mass. Finally, we note the interesting synchrony of interannual body mass dynamics between the two *Dreissena* species (Appendix S2: Fig. S12) suggesting that both may be affected by

the same environmental factors, perhaps causing synchrony in recruitment dynamics.

Sampling error and adequacy of data sets

As would be expected from a group of studies encompassing sites with a wide range of characteristics that were sampled with very different efforts and designs, the precision of estimates varied greatly across studies (Appendix S2: Figs. S13, S14). Studies of the shallow Dutch lakes IJsselmeer and Markermeer, relatively homogeneous sites that were sampled with high effort, produced relatively precise estimates of dreissenid biomass, whereas estimates from more heterogeneous sites sampled with lower effort (e.g., the Hudson River) were much less precise. Many sites were sampled with even lower effort than those shown in Appendix S2: Figs. S13, S14 and so presumably have even wider confidence limits. As a result, although we can confidently detect major changes in dreissenid populations (e.g., outbreak dynamics, changes associated with the arrival of quagga mussels; Appendix S2: Figs. S3, S5), smaller fluctuations (e.g., <3-fold changes) in observed population dynamics should be interpreted with caution. Except at very intensively sampled sites (e.g., the Dutch lakes), such smaller changes may simply arise from sampling error and not reflect true changes in population size.

Improving the monitoring of Dreissena populations

Despite the insights provided by existing data sets, one cannot help but be struck by their limitations. *Dreissena* is one of the world's worst invaders in terms of ecological and economic effects (e.g., Connelly et al. 2007, Higgins and Vander Zanden 2010), yet currently available data are not always sufficient to answer the big questions that interest scientists and managers. For instance, few of the data sets span more than 30 yr, a long time by the standard of conventional ecological studies, but possibly still in the initial period of transient dynamics (e.g., Strayer and Malcom 2018). Furthermore, many of the data sets are not continuous, but intermittent, largely because of limited funding rather than by design. The short duration and frequent gaps preclude use of powerful statistical tools such as time-series analysis, and limit inferences and predictions that can be made about long-term dynamics. Many of the data are of relatively low quality (small number of replicates, weak, nonrepresentative sampling designs), providing only approximate estimates of population sizes and trends, again largely because funding limitations have prevented the use of larger sampling campaigns. Because of differences among studies in sampling design and methods, cross-system analyses such as ours are technically difficult and cannot make full use of the data that have been collected. Finally, few monitoring programs cover more than one life stage or population attribute, which limits our understanding of demographic processes and the possible impacts of different life stages.

All of these shortcomings can be overcome. We offer the following recommendations for improving long-term monitoring of *Dreissena* populations.

Develop standard sampling designs and methods.—The design of any monitoring program must be tailored to the goals of the program, the resources available to the program, and the characteristics of the site (e.g., Strayer and Smith 2003, Lindenmayer and Likens 2010). Nevertheless, it would be helpful if designs and methods for monitoring *Dreissena* populations were more uniform across sites, facilitating cross-site comparisons. One practical step would be to update and extend the guide of Marsden (1992) to include a small number of portable, robust sampling designs and methods that could be used across all kinds of sites. This could cover different population attributes (see also *Extend monitoring programs to include a wider range of variables*) and offer different designs for different amounts of effort (and funding).

Extend monitoring programs to include a wider range of variables.—The data that we review here include only the most basic of population metrics: densities of veligers, new recruits, or settled animals, and biomass of settled animals. Other aspects of *Dreissena* populations may also change over the long term or offer insight into the causes and consequences of temporal changes in *Dreissena* populations, and so might profitably be added to long-term monitoring programs. For instance, although it is known that the genetics of *Dreissena* populations may change over the long term (e.g., Stepien et al. 2014), such genetic

changes have not often been linked to demographic changes, nor have the same programs often monitored both genetics and demography. Functionally important traits of *Dreissena*, such as morphology or physiology, may also shift over the long term (e.g., Natesan and Strayer 2016), although they are not often now included in long-term monitoring programs. Likewise, long-term data on other parts of the ecosystem (e.g., water chemistry and clarity, quantity and quality of detritus, populations of plankton, benthos, macrophytes, and fish) may help both explain observed changes in *Dreissena* populations and be explained themselves by temporal changes in *Dreissena* populations. Such parallel runs of data on *Dreissena* populations and the ecosystems they occupy have been collected for several sites, where they have been very valuable (e.g., Oneida Lake, Rudstam et al. 2016; Lake Michigan, Nalepa et al. 2010, 2014, Madenjian et al. 2015; the Hudson River, Strayer et al. 1999, 2014, 2019). Such coordinated programs could fruitfully be extended to additional sites to provide insight into both *Dreissena* demography and ecosystem dynamics.

Provide more funding and more continuity of funding for programs to monitor Dreissena populations over the long term.—Most of the data included in our analysis were collected using modest funding from a series of short-term grants, or no external funding at all. It is very obvious that inadequate funding (both amount and continuity of funding) has contributed to paucity of long-term studies, gaps in most data records, and a prevalence of bare bones monitoring programs that have an undesirably small number of sampling sites and replicates, and usually cover only one population attribute. Better funding would allow *Dreissena* ecologists to design monitoring programs that better meet the goals of the ecologists and the needs of resource managers (e.g., to track the dynamics of a major driver of freshwater ecosystems, to build and test models of *Dreissena* populations and their impacts, and understand and manage their effects). Until we adequately fund programs to monitor populations of *Dreissena* (as well as other important non-native species; J. Pergl et al., *unpublished manuscript*), we will struggle to understand their dynamics, their effects on freshwater ecosystems, and the best ways by which to manage those effects.

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Data Availability

Data used in all figures in this paper, as well as data describing the study sites, sampling designs, and sampling methods, are available at https://doi.org/10.5061/dryad.m3t6764.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2701/full