

## Appendix S1

Strayer, D.L., Adamovich, B.V., Adrian, R., Aldridge, D.C., Balogh, C., Burlakova, L.E., Fried-Petersen, H., G.-Tóth, L., Hetherington, A.L., Jones, T.S., Karatayev, A.Y., Madill, J.B., Makarevich, O.A., Marsden, J.E., Martel, A.L., Minchin, D., Nalepa, T.F., Noordhuis, R., Robinson, T.J., Rudstam, L.G., Schwalb, A.N., Smith, D.R., Steinman, A.D., and J.M. Jeschke. 2019. Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis*): a cross-system analysis. *Ecosphere*.

### *Approaches to data analysis*

Analyzing boom-bust dynamics is more complicated than it first appears, especially in small, noisy data sets for which there is no *a priori* or independent evidence as to the timing of the bust (i.e., whether the crash comes 5 years, 15 years, or 50 years after the invader appears, if at all). The most obvious approach, to look for declines from a peak (either visually or with some metric such as [current population size]/[highest observed population size] is badly biased, and can greatly overestimate the frequency and severity of population decline in cases where the population fluctuates a lot from year to year or is estimated with large sampling errors (as shown by the simulations reported by Strayer et al. 2017). All of these problems (unknown timing of population crash, if any, fluctuating populations, large sampling errors) apply to many biological invaders, and especially to *Dreissena*, so simple visual comparisons and metrics are unreliable indicators of boom-bust dynamics. At the other end of the spectrum of analytical possibilities, there are good methods to identify “busts”, derived from economics and other disciplines (some reviewed by Strayer et al. 2017), but they require much longer runs of data (sometimes thousands of data points) than we have for *Dreissena*, and so are not useful for our analysis.

Given these constraints, and the characteristics of our data (small number of time-points, large errors that are not normally distributed, different number of time-points and different size errors among studies), we applied multiple methods to try to detect general temporal patterns in the data.

First, we did do a simple visual inspection of the data. Despite the caveat noted above, if most or all of the data sets followed similar trajectories, it might be apparent on visual inspection. We looked at both the raw data, and at splines fit through the data (in an attempt to smooth out noise), and did not see any general patterns. It is certainly possible to pick out patterns (e.g., booms and busts, long-term declines) that apply to some of the sites, but it is equally possible to pick out other sites that follow different or contradictory patterns. Therefore, it would be hard to argue that a visual inspection of the data presented in Appendix S2: Figs. S1-S7 supports a conclusion that *Dreissena* populations generally follow a particular kind of time-course (other than rapid increase following introduction, and frequent decline of zebra mussels after quaggas appear).

Second, we tried to follow Strayer et al.'s (2017) recommendation to fit an expected time-course to the data, then look for deviations from that time-course that would indicate a bust or long-term decline. It seems reasonable to expect from first principles that the population density of an invader should follow a logistic growth curve, and that a bust or long-term decline would be indicated by the statistical significance of an additional "decline" term in the model (step or ramp), or by a pattern of residuals from the simple logistic model that increased over time, either gradually or abruptly. However, we were not successful in fitting logistic growth models to the data generally (too many parameters to be fitted from too few and noisy data), so had to abandon this approach. We also considered using piecewise linear regression to fit the

data, with a rising limb fitted to the initial period of population growth, but our data sets included only 0-2 data points in this rising limb, which would not allow us to fit a two-piece regression to the data.

Third, we applied a simple method based on changes between successive sampling times that allowed us to combine data from different sites and different variables. We began by calculating the proportional change in the value of a variable from one sampling time to the next sampling time as  $V_{t+1}/V_t$ . 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. We repeated this calculation for all  $n$  sites or variables that had data for that time period, resulting in a vector of  $n$   $\log_{10}$ -transformed changes. Finally, we took the median of this vector as a measure of the typical change in a *Dreissena* population over that time period. 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.

The advantages to this approach are: (i) it is relatively simple and transparent; (ii) it is independent of the unit of measurement, because it is based on changes calculated within data sets, regardless of the units in which data are expressed (wet mass, dry mass, with or without shells, etc.); (iii) it allows use of all data (adult densities, biomass, veliger densities, recruitment) in a single analysis, hopefully increasing the power of the analysis over what would be possible using any single variable; (iv) it does not assume any particular pattern of temporal change (e.g., linear, sigmoidal), but merely describes the actual pattern displayed by the data. In the resulting plot (Fig. 1 in the main paper), periods of general (synchronous) change across many sites appear simply as median values well higher (population increase) or lower (population decrease) than 0.

Figure 1 includes just comparisons between successive sample times (e.g., year 3 to year 4), but this analysis can be extended to include all pairs of sample times (e.g., year 3 to year 12). By considering all pairs of sampling times, whether successive or not, we can improve our ability to detect change that is not closely synchronous among sites (for example, if zebra mussel populations typically decline somewhere between years 5 and 15, but the exact timing differs among sites). The results of this more complicated analysis are triangular contour plots (Fig. 2 in the main paper) that contain a lot of information but which may not be intuitive to interpret. As an aid to interpretation of these contour plots, the top two panels of Fig. 2 show the idealized plots that would be expected for general, synchronous decline and general, asynchronous decline. Figure 2 has the advantage of being able to detect general changes in population sizes over time, whether they are synchronous across different study sites or not. Strictly speaking, the simpler Fig. 1 isn't needed, because all of the information that it contains is also contained in Fig. 2 (specifically, the graphs shown in Fig. 1 are the lower diagonal edges of the corresponding panels of Fig. 2), but it may help readers understand Fig. 2. Both Figs. 1 and 2 were able to clearly show some patterns (rapid increases in both zebra and quagga mussel populations in the first 2 years after detection, declines in zebra mussel populations after quagga mussels arrive), and hint at others (increases in total *Dreissena* populations after quagga mussels arrive – Fig. 2f), but did not show evidence of long-term declines in either zebra mussel populations in the absence of quagga mussels, or in total *Dreissena* populations.

Fourth, we ran the fixed and mixed-effects models that fit linear trends to the data from each site (reported in Table 2 of the paper). These are simple, robust models that ought to pick up pervasive patterns of decline, if they exist. Because they are constrained to see only linear patterns, we removed data from the initial phase of rapid population growth before applying

these models. Figures 1 and 2 in the main paper suggest that the initial rapid population growth is usually over within 2 years of the first appearance of *Dreissena*, so we removed data from years 0-1 after the initial appearance of *Dreissena* before running these models. This analysis should have been able to detect pervasive patterns of decline after year 2.

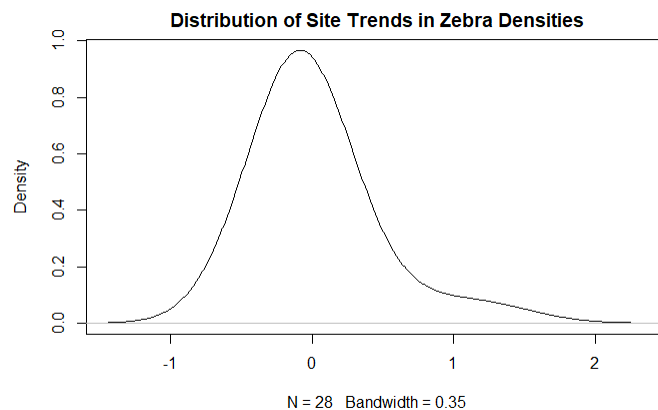
Finally, we recognized that the different kinds of study sites might show different dynamics. We tried grouping the study sites by two criteria that have been suggested to affect population dynamics (e.g., Stańczykowska 1977, Ramcharan et al. 1992, Stańczykowska and Lewandowski 1993): productivity (eutrophic, mesotrophic, oligotrophic) and surface area (we divided the sites into three groups of approximately equal size), to see whether different groups of sites showed different temporal patterns of population change. Data on these site attributes are given in <https://doi.org/10.5061/dryad.m3t6764>. We could not detect any patterns at all in either long-term population trends or interannual variability, so did not report these results.

## *Details on fixed- and mixed-effects models*

### Densities of adult *Dreissena*

We ran separate fits for densities of adult zebra mussels at each site and accounted for the arrival of quaggas at Balaton, Hudson, Oneida, and Onondaga (the only sites with at least 2 years of adult density data before the arrival of quaggas). When fitting each site separately, all sites had negative trends in *Dreissena* adult densities except for Balaton ( $p=0.57$ ), Globokie ( $p=0.71$ ), Lukomskoe ( $p=0.85$ ), Mille Lacs ( $p < 0.0001$ ), Narocho ( $p=0.38$ ), and Onondaga ( $p=0.52$ ). Of the negative trends, Erie East ( $p=0.0002$ ), Mikolajskie ( $p=0.04$ ), Ontario ( $p=0.01$ ), Rynskie ( $p=0.0067$ ), and Talty ( $p=0.0022$ ) were statistically significant at the 0.05 level. Balaton ( $p=0.23$ ), Oneida ( $p=0.26$ ), and Onondaga ( $p=0.44$ ) all showed slight downturns in zebra adult densities after the arrival of quaggas whereas Hudson ( $p=0.66$ ) showed a slight increase in zebra adult densities after the arrival of quaggas.

In this analysis, the correlation of observations on the same sites over time was accounted for through generalized least squares. The empirical distribution of the estimated site-specific slopes is given below:

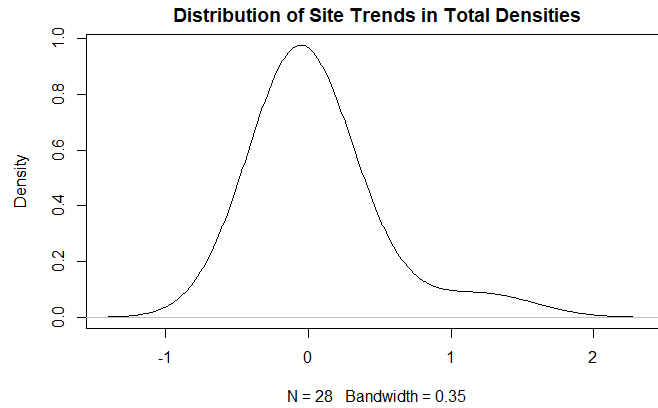


The median value of the site-specific slopes for trend in zebra adult densities is -0.04 before the arrival of quaggas, suggesting a slight negative trend over time. A Wilcoxon test of the estimated

site-specific slopes in zebra adult densities shows that the overall trend over time is marginally significant ( $p=0.05$ ). The median value of the site-specific slopes for trend in zebra adult densities is -0.39 after the arrival of quaggas, suggesting a negative trend over time. A one-sample Wilcoxon test of the estimated site-specific slopes in zebra adult densities after the arrival of quaggas, however, shows that the overall trend over time is not statistically significant ( $p=0.12$ ).

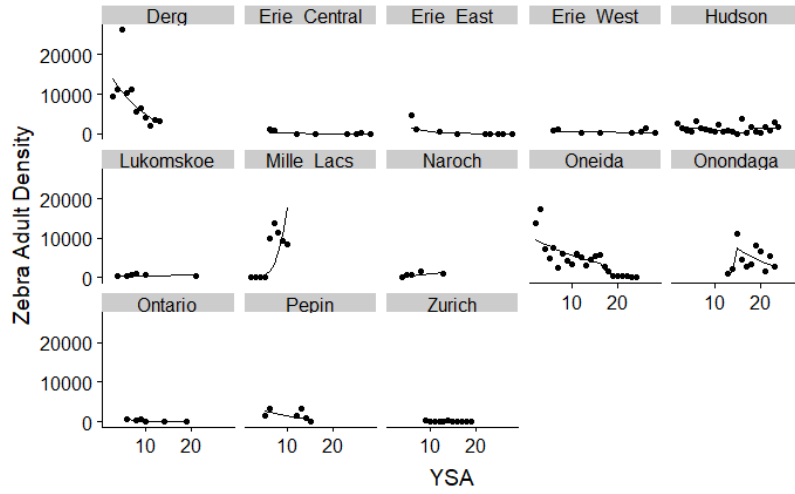
We also analyzed the 4<sup>th</sup> root of adult densities of combined *Dreissena* populations, using separate fits for each site and adjusting for arrival of quaggas at Balaton, Hudson, Oneida, and Onondaga (the only sites with at least 2 years of adult density data before the arrival of quaggas). When fitting each site separately, all sites had negative trends in *Dreissena* adult densities except for Balaton ( $p=0.55$ ), Erie West ( $p=0.28$ ), Globokie ( $p=0.70$ ), Lukomskoe ( $p=0.85$ ), Mille Lacs ( $p < 0.0001$ ), Naroch ( $p=0.37$ ), Onondaga ( $p=0.45$ ), and Ontario ( $p=0.28$ ). Of the negative trends, Erie East ( $p=0.046$ ), Mikolajskie ( $p=0.034$ ), Rynskie ( $p=0.0051$ ), and Talty ( $p=0.0016$ ) were statistically significant at the 0.05 level. Balaton ( $p=0.45$ ), Oneida ( $p=0.89$ ), and Onondaga ( $p=0.38$ ) all showed slight downturns in total adult densities after the arrival of quaggas while Hudson ( $p=0.59$ ) showed a slight increase in total adult densities after the arrival of quaggas.

In this analysis, the correlation of observations on the same sites over time was accounted for through generalized least squares. The empirical distribution of the estimated site-specific slopes is given below:

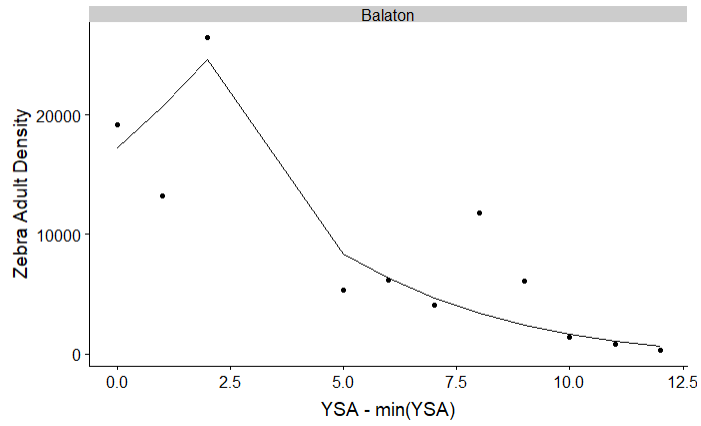
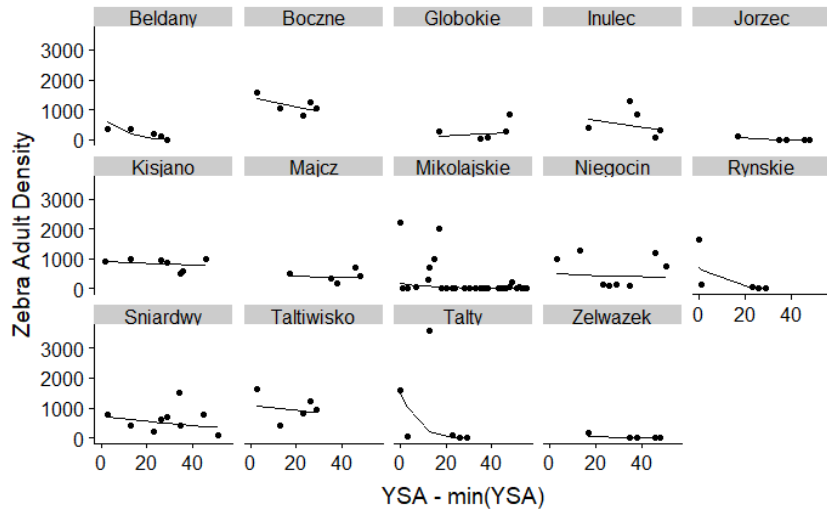


The site-specific slopes for trends in total adult densities have a slightly skewed right distribution in trends. The median value of the site-specific slopes in total adult densities before the arrival of quaggas was -0.023, suggesting a slight negative trend over time. A Wilcoxon signed-rank test on the median of the estimated site-specific slopes in total adult densities before the arrival of quaggas reveals that the overall trend over time is not statistically significant at the 0.05 level ( $p=0.24$ ). The median value of the site-specific slopes after the arrival of quaggas was -0.18, suggesting a negative trend over time after the arrival of quaggas. A Wilcoxon signed-rank test on the median of the estimated site-specific slopes is not statistically significant at the 0.05 level ( $p=0.25$ ).

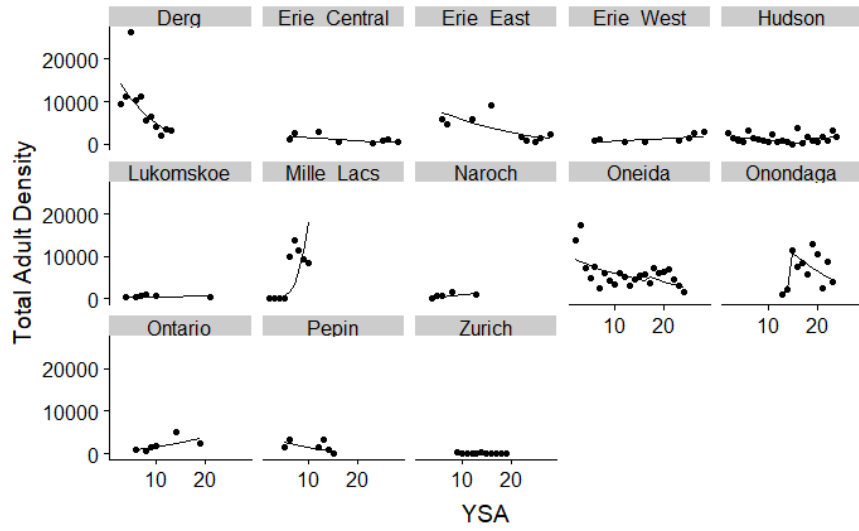




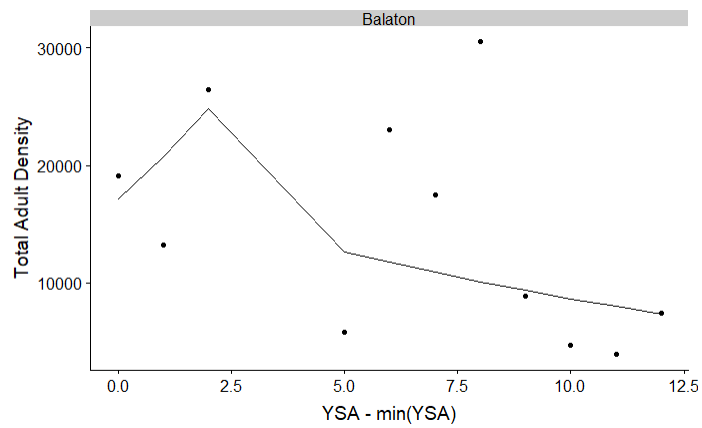
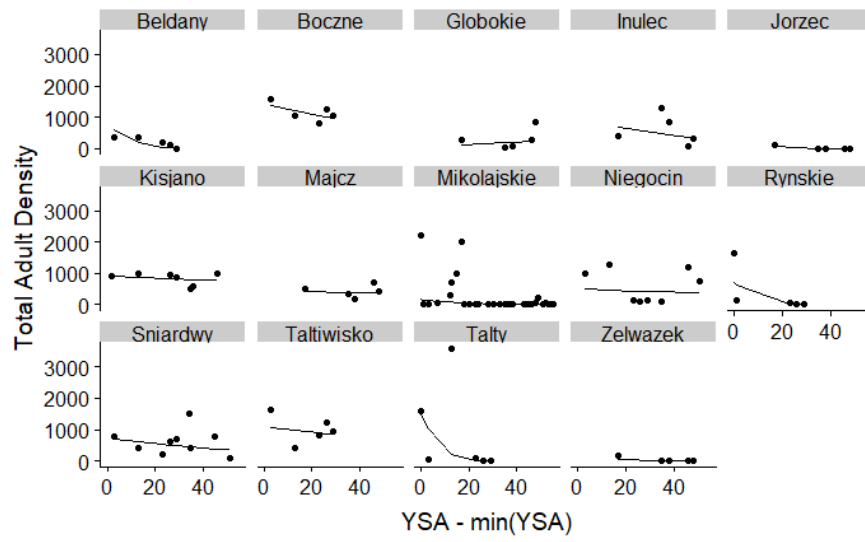
*Site-specific trends in zebra adult density for those sites having data near the onset of the arrival of Dreissena (within 28 years)*



*Site-specific trends in zebra adult densities for those sites having data long after the onset of the arrival of Dreissena (i.e. after 28 years)*



*Site-specific trends in total adult density for those sites having data near the onset of the arrival of Dreissena (within 28 years)*



*Site-specific trends in total adult densities for those sites having data long after the onset of the arrival of Dreissena (i.e. after 28 years).*

Instead of fitting separate trends for each site, we can treat the sites as a collection of locations that ‘belong together’ and estimate an overall trend across sites as well as site-specific means but allowing shrinkage to have an effect. Shrinkage implies that zebra and total adult densities over time should behave somewhat similarly and as such, we should consider the site-specific trends over time as coming from a probability distribution – when we do this, the means are adjusted toward the overall mean trend (by overall, the grand mean). See the baseball analogy of Efron and Morris (1977). Here the model is as follows:

$$\sqrt[4]{Zebra\_AdultDense_{ij}} = \beta_0 + \beta_1 YSA + \beta_2 Quag + \beta_3 Quag * YSA + \delta_{0i} + \delta_{1i} YSA + \varepsilon_{ij}$$

In the above,  $\sqrt[4]{Zebra\_AdultDense_{ij}}$  denotes the 4<sup>th</sup> root of the observed zebra adult density (or similarly, total *Dreissena* density) at the *i*<sup>th</sup> site in the *j*<sup>th</sup> year. The  $\beta_0$  term denotes the predicted mean total zebra adult density (or total adult density), across all sites, in the initial year that *Dreissena* appeared in the system. This does not have practical meaning here because many sites did not have data collected in the year in which *Dreissena* appeared. The  $\beta_1$  terms denotes the average per-annum change in the 4<sup>th</sup> root of zebra adult density (or total adult density) across all sites (i.e. grand mean trend). The  $\beta_2$  term allows for a mean difference in zebra adult density (or total adult density) before and after the arrival of quaggas. The  $\beta_3$  term allows for a mean difference in the per-annum change before the arrival of quaggas vs. after their arrival. The random effect  $\delta_{0i}$  (subscript goes from 1 to the total number of sites) allows for the fact that sites will differ from one another in terms of the zebra adult density (or total adult density) in the initial year that they enter the population – some sites have particular ecological conditions that are more conducive to higher zebra adult density (or total *Dreissena* adult density) when they

first arrive than other sites which are less conducive (e.g., sites may differ in pH, water temperature, biota, etc.). The random effect  $\delta_{1i}$  (subscript goes from 1 to the total number of sites) allows for the fact that sites will differ from one another in terms of the per-annum changes in zebra adult density (or total *Dreissena* adult density) – weather changes will be different from site to site across years, some systems will respond differently over time as adult density changes, etc.

The common overall trend model for adult densities of zebra mussels did not converge. Interestingly, the overall grand per-annum trend in total adult density is estimated to be -0.022 before the arrival of quaggas ( $p=0.0001$ ). The magnitude of this trend is similar in size to the median grand trend when we took the median per-annum trend across the 28 sites in the first analysis (median = -0.023). In the first analysis, when conducting the Wilcoxon test, we did not account for the fact that there was more information on some sites and less information on others – this analysis accounts for the differing amounts of information per site. The overall grand per-annum trend in total adult density is estimated to be -0.031 ( $p=0.67$ ) after the arrival of quaggas. The magnitude of this trend is less than the estimated median of the site-specific slopes of total adult densities over time (-0.18) but neither value was statistically significant at the 0.05 level. Site-specific plots when analyzing the data with a common trend are similar in appearance to the site-specific analyses.

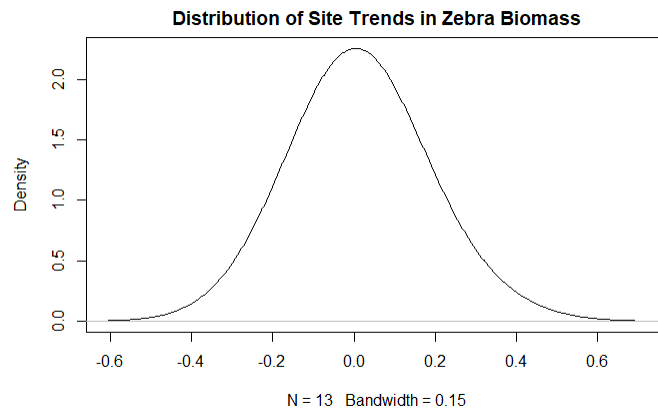
#### *Dreissena* biomass

In modeling the 4<sup>th</sup> root of zebra mussel biomass, we made separate fits for each site and adjusted for the arrival of quaggas at IJsselmeer, Oneida, Onondaga, and Hudson (these were the only sites with at least 2 years of biomass data before the arrival of quaggas). When fitting each site separately, all sites had negative trends in zebra mussel biomass except for Derg ( $p=0.30$ ),

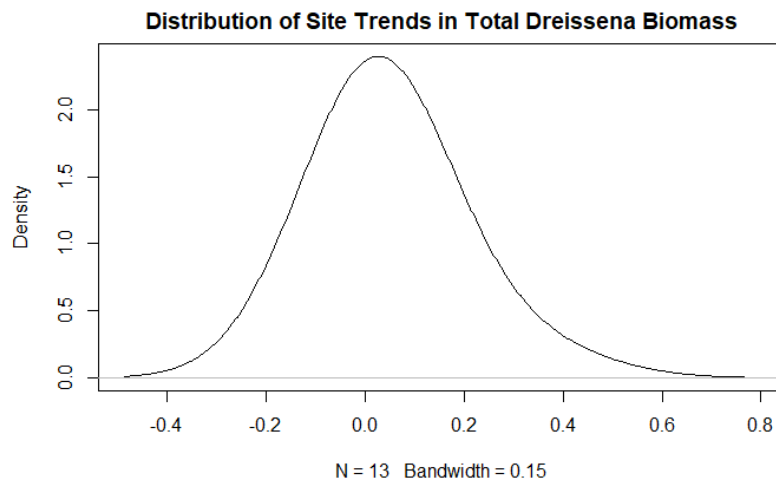
IJsselmeer ( $p=0.35$ ), Lukomskoe ( $p=0.90$ ), Naroeh ( $p=0.49$ ), Onondaga ( $p=0.74$ ), Peipsi ( $p=0.0039$ ), and Uchinskoe ( $p=0.35$ ). Of the negative trends, Erie Central ( $p=0.0003$ ) and Erie East ( $p<0.0001$ ) were statistically significant at the 0.05 level. IJsselmeer ( $p=0.82$ ), Oneida ( $p=0.075$ ), and Onondaga ( $p=0.65$ ) all showed slight downturns in zebra biomass after the arrival of quaggas whereas Hudson ( $p=0.32$ ) showed a slight increase in zebra biomass after the arrival of quaggas.

In models of the 4<sup>th</sup> root of total *Dreissena* biomass, we made separate fits for each site and adjusted for the arrival of quaggas at IJsselmeer, Oneida, Onondaga, and Hudson. When fitting each site separately, all sites had positive trends in total *Dreissena* biomass except for Erie Central ( $p=0.30$ ) and Hudson ( $p=0.41$ ). Of the sites with positive trends in total biomass, only Peipsi ( $p=0.0055$ ) demonstrated a significant trend at the 0.05 level. IJsselmeer ( $p=0.075$ ), Oneida ( $p=0.69$ ), and Hudson ( $p=0.32$ ) all showed slight increases in total *Dreissena* biomass after the arrival of quaggas whereas Onondaga ( $p=0.58$ ) showed a slight decline in total *Dreissena* biomass after the arrival of quaggas.

In this analysis, the correlation of observations on the same sites over time was accounted for through generalized least squares. The empirical distribution of the estimated site-specific slopes is given below:

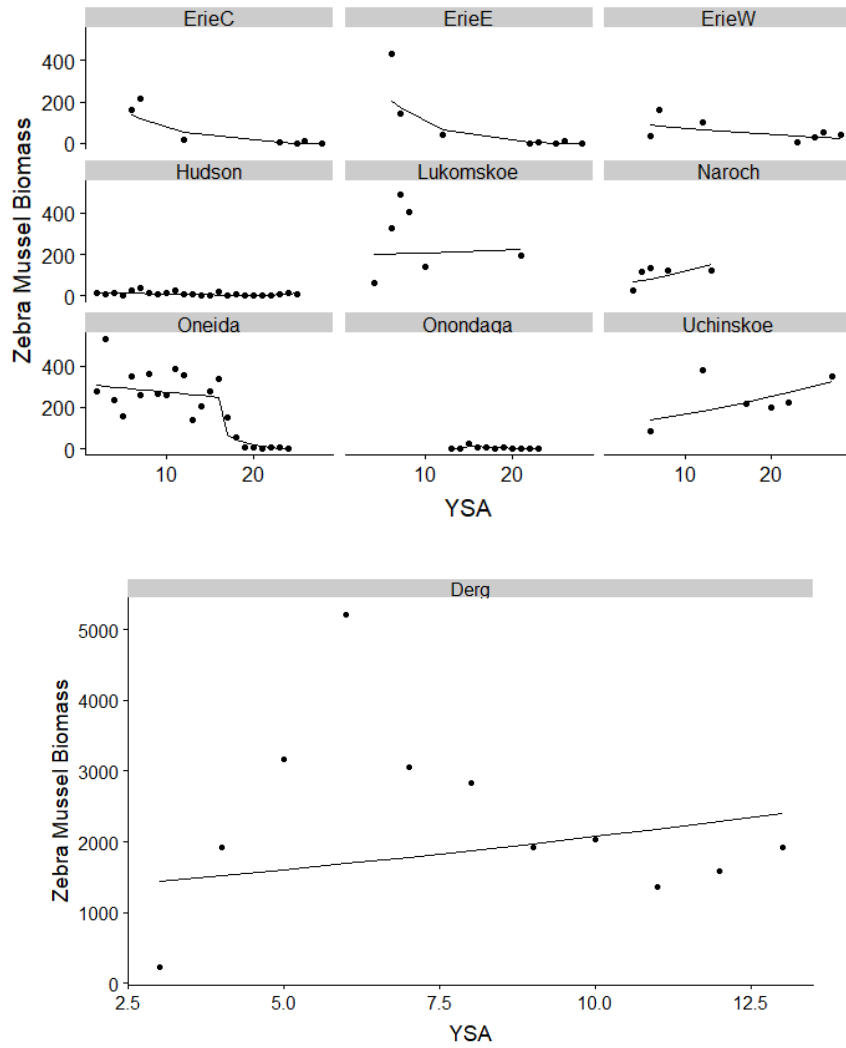


The mean value of the site-specific slopes for the trend in zebra biomass is 0.014 before the arrival of quaggas, suggesting a slight positive trend over time. A one-sample  $t$ -test of the estimated site-specific slopes in zebra biomass, however, shows that the overall trend over time is not significant ( $p=0.65$ ). The mean value of the site-specific slopes for the trend in zebra biomass is -0.067 after the arrival of quaggas, suggesting a slight negative trend over time. A one-sample  $t$ -test of the estimated site-specific slopes in zebra biomass after the arrival of quaggas, however, shows that the overall trend over time is not significant ( $p=0.47$ ).

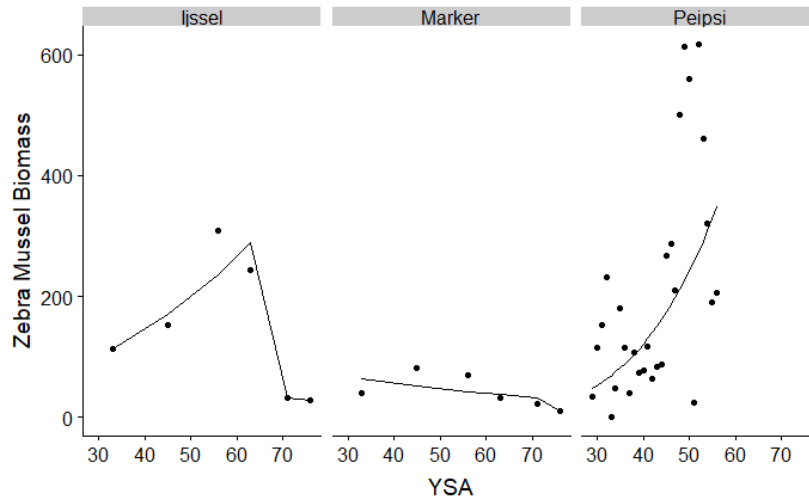


The site-specific slopes for trends in total *Dreissena* biomass have a slightly skewed-right distribution in trends. The median value of the site-specific slopes before the arrival of quaggas was 0.028, suggesting a slight positive trend over time. A Wilcoxon signed-rank test on the median of the estimated site-specific slopes in total *Dreissena* biomass before the arrival of quaggas reveals that the overall trend over time is statistically significant at the 0.05 level ( $p=0.048$ ). The median value of the site-specific slopes after the arrival of quaggas was 0.089, suggesting a positive trend over time after the arrival of quaggas. A Wilcoxon signed-rank test on the median of the estimated site-specific slopes is not statistically significant at the 0.05 level ( $p=0.38$ ).

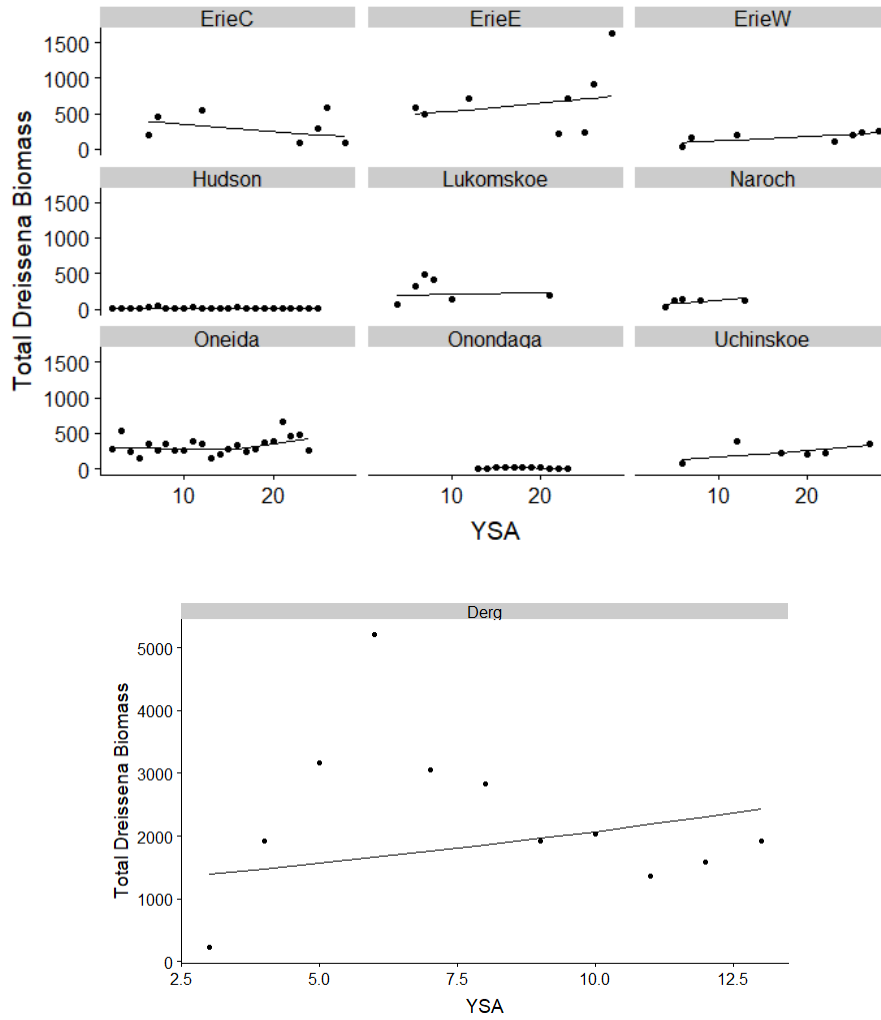




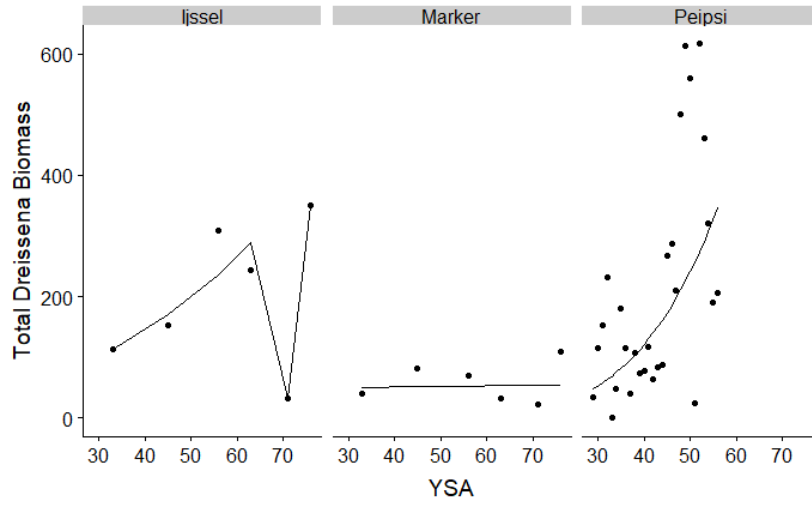
*Site-specific trends in zebra mussel biomass for sites having data near the onset of the arrival of Dreissena (within 28 years)*



*Site-specific trends in zebra mussel biomass for sites having data long after the onset of the arrival of Dreissena (i.e. more than 28 years)*

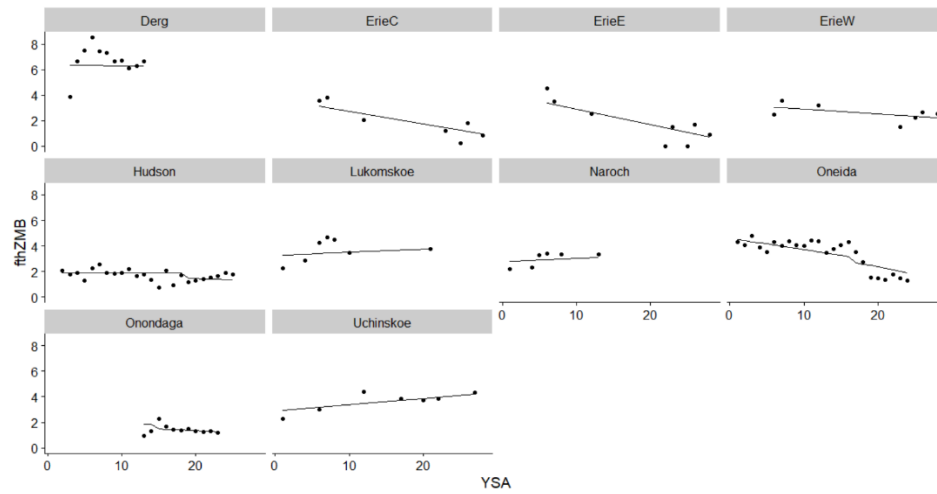


*Site-specific trends in total Dreissena biomass for sites having data near the onset of the arrival of Dreissena (within 28 years)*

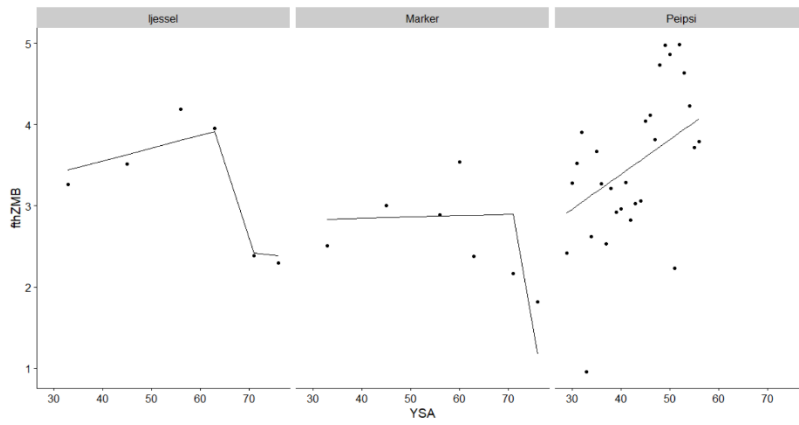


*Site-specific trends in total Dreissena biomass for sites having data long after the onset of the arrival of Dreissena (i.e. more than 28 years)*

We also ran a pooled analysis of the 4<sup>th</sup> root of zebra mussel biomass and total *Dreissena* biomass that allows for differences among sites as random effects (see fuller explanation of this pooled analysis above).



*Site-specific trend estimates in zebra mussel biomass from the pooled analysis for sites early in the invasion*



*Site-specific trend estimates in zebra mussel biomass from the pooled analysis, for sites sampled later in the Dreissena invasion.*

Interestingly enough, the overall grand per-annum trend in zebra mussel biomass before the arrival of quaggas is estimated here to be  $-0.0098$  ( $p=0.64$ ) whereas the overall grand per-annum trend in zebra mussel biomass after the arrival of quaggas is estimated to be  $-0.032$  ( $p=0.16$ ). In our earlier analysis where we treated each site as its own population, we had an overall average trend in zebra mussel biomass estimated to be  $0.022$  before the arrival of quaggas (i.e., a slight positive trend) and an estimated trend in zebra mussel biomass of  $-0.067$  after the arrival of quaggas. The trend estimates for both analyses are within 1 standard error of each other.

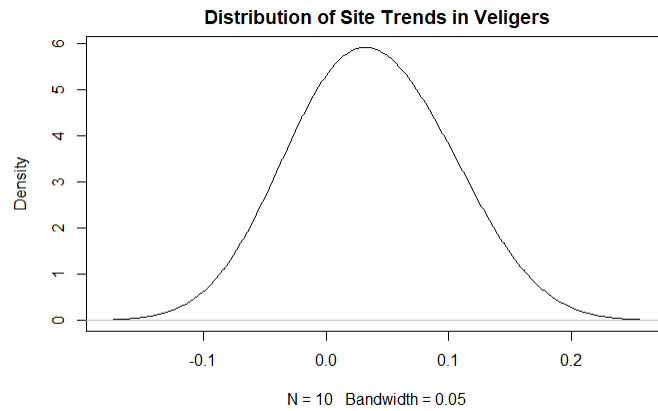
When fitting the overall grand per-annum trend in total *Dreissena* biomass and treating sites as belonging to a population of sites, the model did not converge.

#### Veliger density

When fitting separate trends for each of the sites, all sites exhibited positive trends with the exception of Balaton and Champlaine South. Champlaine\_Missiquoi ( $p= 0.00013$ ), Champlaine\_InlandSea ( $p= 0.0036$ ), Hudson ( $p=0.00025$ ), and Mueggelesee ( $p=0.0023$ ) all had statistically significant positive trends.

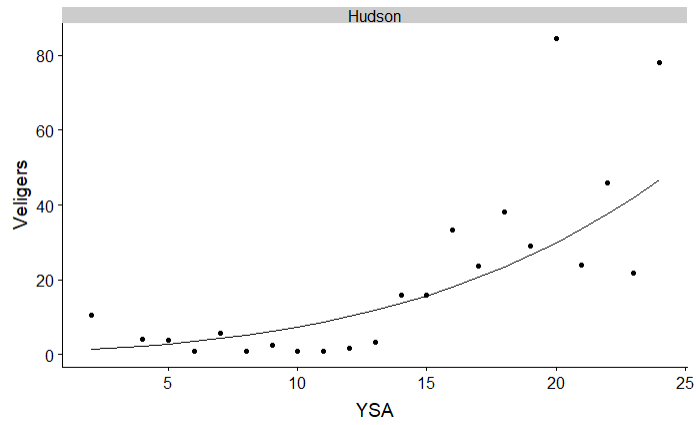
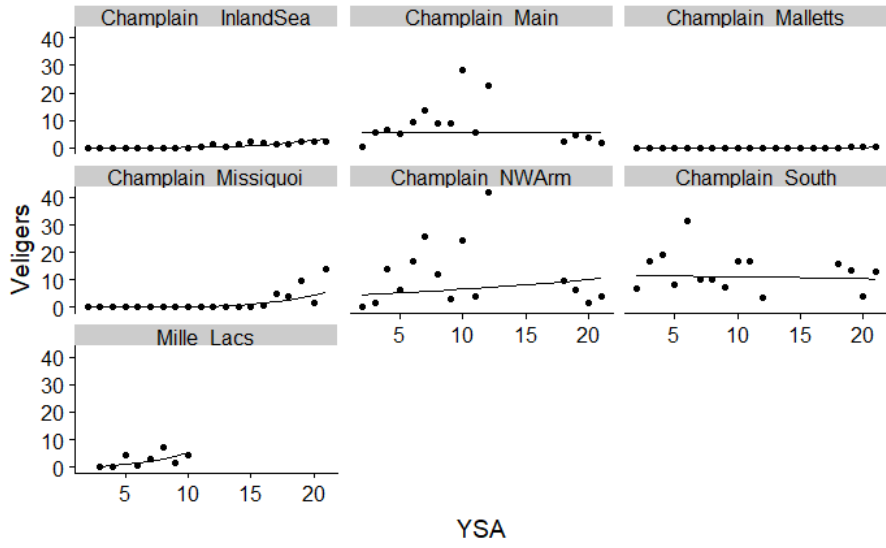
In this analysis, the correlation of observations on the same sites over time was accounted for through generalized least squares.

The empirical distribution of the estimated site-specific slopes is given below:

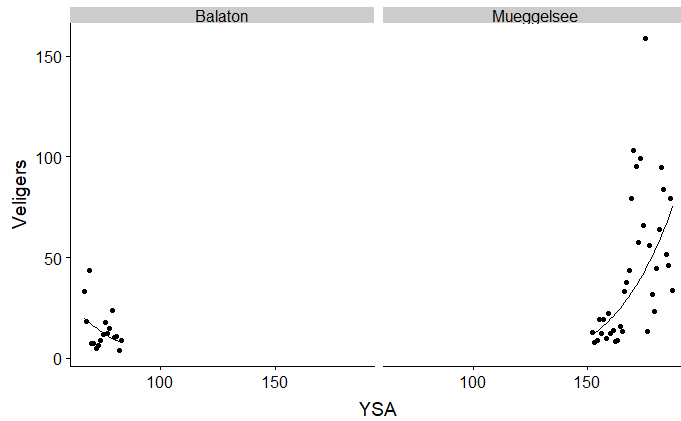


The median value of the site-specific slopes is 0.026. A Wilcoxon test of the estimated site-specific slopes in veligers shows that the overall trend over time is statistically significant ( $p=0.037$ ). All sites other than Wallensee were used in the analysis since the unit of measurement in Wallensee was different from the other sites.





*Site-specific trends for veligers at sites having data near the onset of the arrival of Dreissena.*



*Site-specific trends for veliger densities at sites having data long after arrival of Dreissena.*

Here are the results of the pooled analysis of veliger densities (after 4<sup>th</sup>-root transformation). The overall grand mean per-annum trend is estimated to be 0.028 ( $p=0.0072$ ). The magnitude of this trend is similar in size to the average per-annum trend across the sites in the earlier veliger analysis (slope = 0.026). The fits for each of the sites was nearly identical in the pooled analysis as in the site-specific analysis. The only exception was for Lake Balaton where we observed a slight positive trend in the pooled fit vs. a slight negative trend in the site-specific fit. This is due to the shrinkage to the overall mean that occurs in the pooled analysis.

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