Ecosystems (2023) 26: 1224–1237
https://doi.org/10.1007/s10021-023-00828-2

ECOSYSTEMS

Time Scales of Ecosystem Impacts and Recovery Under Individual and Serial Invasions

Vadim A. Karatayev,[1]* Lars G. Rudstam,[2] Alexander Y. Karatayev,[3] Lyubov E. Burlakova,[3] Boris V. Adamovich,[4] Hanna A. Zhukava,[4] Kristen T. Holeck,[2] Amy L. Hetherington,[2] James R. Jackson,[2] Csilla Balogh,[5] Zoltán Serfőző,[5] Christopher W. Hotaling,[2] Tatyana V. Zhukova,[4] Tamara M. Mikheyeva,[4] Raisa Z. Kovalevskaya,[4] Oleg A. Makarevich,[4] and Darya V. Kruk[4]

[1]Kansas Biological Survey, University of Kansas, Lawrence, Kansas, USA; [2]Department of Natural Resources and Environment, Cornell University, Ithaca, New York, USA; [3]Great Lakes Center, SUNY Buffalo State, Buffalo, New York, USA; [4]Faculty of Biology, Belarusian State University, Minsk, Belarus; [5]Balaton Limnological Research Institute, Eötvös Lóránd Research Network, Tihany, Hungary

ABSTRACT

The impacts of species invasions can subside over time as ecosystems 'adapt' and invaders decline or increase over time as additional species invade. The character and timescales of invasion impacts provide important insights into ecosystem dynamics and management. Yet long-term studies of invasion impacts remain rare and often confound invasive species impacts with coincident environmental change. One way to address this challenge is to ask: what ecological changes over time since invasion are recapitulated in ecosystems that span a range of conditions, are located in different regions, and were invaded in different decades? We synthesize many-decade time series across seven ecosystems to resolve shared changes in seven key ecosystem features following invasion by zebra mussels and subsequent invasion by quagga mussels. These two congeners are among the most widespread invasive species that re-engineer and increasingly co-invade freshwater ecosystems. Seven polymictic shallow lakes with long-term data sets reveal remarkably similar trends, with the strongest ecosystem impacts occurring within 5–10 years of zebra mussel invasion. Surprisingly, plankton communities then exhibited a partial, significant recovery. This recovery was absent, and impacts of initial invasion amplified, in four lakes where quagga mussels outcompeted zebra mussels and more completely depleted phytoplankton. Thus, we show that the ecosystem impacts of invasive species can subside over time but amplify with serial introductions of competing, even closely similar, taxa.

Key words: ecosystem dynamics; species introduction; invasive species; transient dynamics; long-term monitoring; zebra mussels; quagga mussels.

Received 19 October 2022; accepted 30 January 2023;

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s10021-023-00828-2.

Author contributions: VAK led data analysis and writing, with extensive input from AYK, LGR, LEB, BVA, and HAZ. KTH, ALH, JRJ, CB, and ZS also contributed to editing the manuscript. All authors participated in collecting primary data and preliminary analyses.

**Corresponding author; e-mail:* vkaratayev@ucdavis.edu

HIGHLIGHTS

- We quantify ecosystem effects of dreissenid invasions across many lakes
- Impacts of invasive species over time can decline after an initial peak
- Serial, successful invasions by a similar species amplifies ecosystem impacts

INTRODUCTION

Introductions of keystone or ecosystem engineering species can profoundly transform multiple ecosystem features (reviewed in Hui and Richardson 2017). For example, cattle can overgraze grasslands (Noy-Meir 1975) and wolf re-introduction can transform grasslands into forests (Ripple and Beschta 2011). In lakes, ecosystem engineers include two of the most aggressive invaders in temperate lakes, the zebra mussel (*Dreissena polymorpha,* Pallas 1771) and the quagga mussel (*Dreissena rostriformis bugensis,* Andrusov 1897). Zebra mussel invasions have been shown to transform lakes from turbid to clear water phases (Karatayev and others 2002; Ibelings and others 2007; Mayer and others 2014) and quagga mussels appear to have additional impacts, at least in deep lakes (Vanderploeg and others 2010; Barbiero and others 2018; Li and others 2021). Less is known about the ultimate long-term impacts of these species on lake ecosystems and the time scales involved. This is important for evaluating management options as mitigating invasion impacts can require costly or risky management interventions (for example, biological control, Simberloff and Stiling 1996). This raises two key questions: how strong are the ultimate impacts of widespread species introductions and how quickly do they affect different ecosystem features?

The response of ecosystems to a species introduction can be complex and difficult to predict. As invaders increase to a steady-state biomass, we may expect their impacts to increase monotonically to a maximum that is then maintained over time. Alternatively, initial impacts of introductions can subside as species traits or ecosystem structure adapt (reviewed in Strayer and others 2006); these changes could vary widely depending on environment or makeup of resident species (Alpert and others 2000; Strayer and others 2006; Martin and others 2017). Population abundance and impacts of invasive species often exhibit an invasion cycle where after initial high abundance, invader populations decline (Simberloff and Gibbons 2004; Karatayev and others 2015; Strayer and others 2017) due to changes in community structure, density-dependent changes in the abundance of the invader or evolutionary and behavioral adaptations (learning, eco-evo dynamics) by resident species to the new invader. This may also be true for ecosystem features known to be affected by dreissenid mussels, including chlorophyll, water clarity, total phosphorus, phytoplankton, zooplankton, zoobenthos, and macrophytes (Karatayev and others 2002, 2021; Higgins and Vander Zanden 2010; Rudstam and Gandino 2020).

A simple time course of acute invasion impacts followed by ecosystem recovery may be complicated, however, if multiple species are introduced in series (for example, invasion meltdown, Simberloff and Von Holle 1999). Interactions among invaders have been studied extensively for plants (Kuebbing and Nuñez 2015), aquatic animals (Johnson and others 2009), and terrestrial animals (Jackson 2015). These studies show that the ecological impact of an additional invader is hard to predict, and can be neutral, synergistic or antagonistic. In general, invasion biology anticipates small impacts of invaders when they are functionally similar to species already present in an ecosystem (Ricciardi and Atkinson 2004; Strayer and others 2006; Ricciardi and others 2013). Alternatively, competition theory (Tilman 1985) suggests greater impacts from a second invader that outcompetes an initial invader by utilizing ecosystem resources more efficiently and completely (reviewed in Russell and others 2014). Therefore, even for functionally similar species, the predicted impacts of serial invasions range from minimal ecosystem change to an amplification of initial invader's impacts and prevention of ecosystem recovery.

Zebra mussels and quagga mussels exemplify widespread invaders that increasingly co-occur in waterbodies. Both species have high reproductive and dispersal potential, often comprise a large portion of animal biomass in invaded ecosystems (Mills and others 1996; Pollux and others 2010; Benson 2014; Karatayev and others 2015, Karatayev and Burlakova 2022), and represent two of the most aggressive freshwater invaders (Karatayev and others 2002, 2015). Zebra mussels exhibit faster landscape-level spread than quagga mussels, which often invade waterbodies that already have established zebra mussel populations (Karatayev and others 2011, 2015; Strayer and others 2019). As highly efficient suspension feeders, both dreissenid species are powerful ecosystem engineers that restructure energy flows from pelagic to benthic habitats and create complex substrates (Karatayev and others ; Gutiérrez and others 2003; Zhu and others 2006; Sousa and others 2009; Higgins and Vander Zanden 2010; Karatayev and Burlakova 2022). Despite this, the magnitude, pace, and interaction of impacts caused by these introduced species remain obscure because long-term ecosystem studies are rare and typically analyzed separately for each system, which confounds invasion impacts with many coincident environmental changes.

Here, we assemble high-resolution data sets spanning seven key ecosystem features, five decades, and seven lakes in four regions (New York State USA, Belarus, Hungary, and The Netherlands) invaded by dreissenid mussels. We analyze changes shared among lakes across time since invasion to robustly attribute ecosystem changes to the effects of dreissenid introduction rather than system-specific environmental changes and to reduce uncertainty from intermittent gaps in data. We begin with the question: how quickly does a zebra mussel impact manifest in each ecosystem feature? Next, we test the null expectation that invasion impacts increase monotonically to a maximum level *versus* the alternative hypothesis that impacts decline after an initial peak due to complex invasion dynamics or when native communities adapt to the invader. Then, in systems experiencing a subsequent invasion by quagga mussels, we evaluate whether serial invasions of a closely related competing species magnify the impacts of the initial invader.

Materials and Methods

We study long-term trends collected in seven polymictic lakes located in North America (New York, USA), and Europe (Belarus, the Netherlands, Hungary (Table 1). To our knowledge, these shallow freshwater ecosystems have the longest time series of zebra mussel impacts (20–37 years) on both benthic and plankton communities, with an additional 6–15 years of baseline pre-invasion data in each system. These datasets are also among the longest time series on dreissenid population dynamics available anywhere (Strayer and others 2019). We analyze standardized changes in four communities (phytoplankton (both as chlorophyll and biomass), zooplankton, zoobenthos, macrophytes) and abiotic variables (Secchi depth, phosphorus) as a function of time since the initial invasion by zebra mussels and the subsequent (serial) invasion by quagga mussels. These variables are resolved at an annual time scale, but depending on the lake, we note that some variables were not sampled each year (see Appendix S1, Burlakova and others 2023). All lakes have a long-term dreissenid presence, but span a wide range of mean mussel biomass (100–800 g/m^2), lake morphometry (1.8–9 m mean depth), and area (15–200 km^2).

Data Collection

For all lakes we collected authors' unpublished data as well as available information from peer-reviewed papers, unpublished reports and archive materials on water transparency (Secchi depth, m), total phosphorus concentration (µg/L), chlorophyll *a* concentration (mg/L), macrophyte coverage (%), wet phytoplankton biomass (g/m^3), wet zooplankton biomass (g/m^3), wet benthic biomass excluding molluscs (g/m^2), and *Dreissena* spp. wet biomass (tissue and shells, g/m^2). We provide detailed methods of data collection in these systems in Appendix S1. We note that for Oneida Lake zoobenthos, we use standardized density as a proxy for standardized biomass, which was not recorded. Additionally, in Lake Balaton zebra mussels invaded 75 years before quaggas and 69 years before monitoring began; therefore, we include data from this system in analyzing the effects of serial invasions (as detailed below) but not in the effect of initial zebra mussel invasion. Information on the time course of chlorophyll, water clarity, macrophytes, and total phosphorus from lakes Eem and Veluwe was retrieved from Noordhuis and others (2015).

Modeling Framework

Throughout, we resolved the impact of each species introduction on each ecosystem variable x using a generalized additive model (GAM) framework. We first standardized observations in each lake i and year t into z-scores as $x^z_{i,t} = (x_{i,t} - \overline{x_i})/s_{x,i}$. To account for both direct effects of invader biomass/activity and delayed ecosystem responses, we then modeled invasion effects on standardized variable time series x^z across all lakes as a smooth function of time using mgcv (Wood 2017) in R 3.5.2. Specifically, to account for multiple invasions, we fitted two-dimensional splines to (1) years since zebra mussel invasion and (2) the proportion of dreissenid abundance comprised by zebra mussels and assumed (and verified in preliminary analyses) a normal error distribution. Importantly, having invader species composition as an explicit, second dimension of the fitted splines allowed our model to account for both species differences in per-bio-

Table 1. Physical Characteristics of Lake Lukomskoe (Lyakhnovich and others 1988), the Narochanskie Lakes (Burlakova and others 2006), Oneida Lake (Hetherington and others 2019), Lake Balaton (Balogh and others 2008, 2018), and Lakes Veluwe and Eem (Noordhuis and others 2015) with the Dates of *Dreissena* spp. first Records (*D. polymorpha*, ZM, and *D. r. bugensis*, QM)

Lake	Coordinates	Surface area, km^2	Maximum depth, m	Average depth, m	ZM invasion	QM invasion	ZM biomass (g/m^2); filtration capacity	QM biomass (g/m^2); filtration capacity	Figure (analysis) data used in
Lukomskoe	54° 40′ N, 29° 5′ E	36.7	11.5	6.7	1972	None	262; 4% (1970–1990)		1, 2
Naroch	54° 51′ N, 26° 45′ E	79.6	24.8	9.0	1989	None	114; 1.2% (1993–2016)		1, 2
Myastro	54° 51′ N, 26° 53′ E	13.1	11.3	5.4	1984	None	409; 7% (1993–2017)		1
Oneida	43°10′ N, 75°52′ W	207.0	16.8	6.8	1991	2005	804; 11% (1992–2006)	1178; 17% (2007–2018)	1, 2, 3, 4
Balaton (eastern basin)	46° 57′ N, 18° 3′ E	218	12.2	3.7	1930s	2008	293; 8% (2001–2005)	1310; 34% (2008–2017)	2, 3
Veluwe	52° 24′ N, 5° 45′ E	31.3	5.0	1.8	1995	2009	NA; 40% (2000–2010)	NA; 77% (2013)	1, 3
Eem	52° 17′ N, 5° 20′ E	15.2	4.0	2.1	1995	2009	NA; 66% (2000–2008)	NA; 429% (2011, 2013)	1, 3

Mussel filtration capacity denotes percent of lake volume filtered per day at 20 °C (assuming filtering rate of 40 ml h^{-1} g^{-1} *mussel wet biomass, Karatayev and Burlakova 1995) filtration in Veluwe and Eem from Noordhuis and others (2015) and year(s) corresponding to the estimate. NA, data not available. The last column indicates the figure (and corresponding analysis) in which data from each lake was used (1: initial, zebra mussel invasion impacts; 3: serial, quagga mussel invasion impacts; 2: mussel biomass dynamics; 4: mechanisms of serial invasion impacts).*

mass ecosystem impacts as well as a cross-species interaction in impacts (for example, pronounced changes in years when the proportion of zebra mussels is between 0 and 1).

Quagga mussels quickly become dominant in all studied lakes they invade (Heiler and others 2013; Strayer and others 2019) and follow a similar trajectory of rapidly replacing zebra mussels in all lakes invaded by both species (Heiler and others 2013; Rudstam and Gandino 2020). Therefore, we assumed that detailed mussel data available for Oneida Lake (Hetherington and others 2019) was representative of dreissenid species in the two Dutch Lakes. This was supported by more intermittent data on zebra and quagga mussel densities in these lakes (Noordhuis and others 2015). Given the short periods when both species are abundant, we note that the potential for synergistic zebra and quagga mussel impacts may be limited. Quagga mussel invasions happened 15 years after initial zebra mussel invasion in all lakes with serial invasions except in Lake Balaton. Therefore, we omitted Lake Balaton data preceding the quagga mussel invasion from the spline model fits and, to standardize time effects, designated years 2008–2021 in this lake as years since invasion t = 15–28.

Given our focus on resolving general invasion impacts, we minimized lake-specific effects for each ecosystem variable x by using a Bayesian Information Criterion to select the maximum basis dimension k_x of the fitted spline (rejecting increases in k_x with $\Delta\mathrm{BIC} < 2$). For each variable x, we additionally fit separate lake-by-lake splines using the basis dimension k_x (omitting lakes with < 6 observations of x). We then calculated the total residual sum of squares across lake-specific splines $t\mathrm{RSS}_{\mathrm{lake}}$, the residual sum of squares in the cumulative spline fitted to data from all lakes $\mathrm{RSS}_{\mathrm{cuml}}$, and $C = t\mathrm{RSS}_{\mathrm{lake}}/\mathrm{RSS}_{\mathrm{cuml}}$, an estimate of how well the cumulative spline captures lake-specific trends.

Zebra Mussel Ecosystem Impacts

In estimating zebra mussel impacts, we omitted observations under conditions of quagga dominance, such that the splines reflect trends in six lakes before year 15 and three lakes thereafter. In addition, only 20 years of post-invasion data from Lake Lukomskoe was used in model fitting as subsequent hypoxia depleted zebra mussel biomass.

We approximated the timing and direction of zebra mussel effects based on the slope of fitted splines calculated using the package 'tsgam,' where negative (positive) slopes indicate a decrease (increase) in the ecosystem variable. We conservatively determined changes as significant when (1) the confidence intervals of the slope at year t exclude zero and (2) the same change detection (that is, positive or negative slope) is maintained for at least 4 consecutive years since zebra mussel invasion. For year 'zero' (before zebra mussel invasion), we averaged data for Lake Lukomskoe for 1960–1970, Naroch 1978–1989, Myastro 1978–1987, Oneida Lake 1985–1989, and for lakes Veluwe and Eem 1985–1994.

Effects of Serial *Dreissena* Invasions

Four of our studied systems experienced an invasion by quagga mussels after the initial zebra mussel invasion (lakes Oneida, Balaton, Eem, and Veluwe). Due to the limited time span of quagga mussel invasion, we resolved the impacts of this second invasion on each ecosystem variable by comparing the performance of our full models (that is, 2d splines across time and invader species composition) and a null model of time only (that is, 1d spline), with quagga mussel effects being significant for $\Delta\mathrm{BIC} > 4$. We visualized quagga mussel effects by comparing the mean and 95% confidence intervals of each effect for (a) a lake invaded by zebra mussels only *versus* (b) a lake invaded first by zebra mussels at $t = 1$ and then by quagga mussels at $t = 15$ (to represent the time of quagga mussel arrival since the zebra mussel (re)invasion in lakes Eem, Veluwe, and Oneida).

Although quagga mussel introduction amplified the impacts of initial zebra mussel invasion in all lakes, we can additionally quantify the magnitude of differences in zebra and quagga mussel effects. For this, we measured the effects of each species' biomass on ecosystem features in Oneida Lake, where biomass data are available annually for both species (Hetherington and others 2019). Unlike zebra mussels, substantial quagga mussel filtering activity and growth occurs in early spring and late fall (Baldwin and others 2002). At the annual time scale of our data, we therefore explore the potential for quagga mussels to have a different per-biomass ecosystem impacts than zebra mussels. In this quantitative comparison only, we therefore included data from March–November and limited analyses to ecosystem features sampled over this entire period (Secchi depth, chlorophyll, total phosphorus, and phytoplankton) and included observations during 1987–1989 when both dreissenid species were absent from the lake. To measure impacts, we used linear regressions of each ecosystem variable as a function of zebra mussel biomass plus quagga mussel biomass: $\widehat{x^z_{i,t}} = \alpha_0 + \alpha_{ZM}B_{ZM,t} + \alpha_{QM}B_{QM,t} + \varepsilon_{i,t}, \varepsilon \sim N(0,\sigma)$. We then (1) evaluated the significance of each species' impact (that is, regression slope) and (2) compared the similarity of species' impacts using linear hypothesis tests in the package 'car.' Finally, to better visualize how differences in species effects arise, we compared the seasonal pattern of chlorophyll and Secchi depth in Oneida Lake in years with zebra mussel dominant and years with quagga mussel dominant.

RESULTS AND DISCUSSION

Lake Ecosystem Impacts Manifest Quickly

Across six ecosystems and every feature examined, we find strong ecosystem changes that peak within 5 to 10 years of the initial zebra mussel invasion (Figure 1). In lakes with the longest time series of dreissenid population dynamics, zebra mussel biomass increased to a steady level within 3 years (Naroch, Oneida), although a partial decline followed this initial increase in Lake Lukomskoe (Figure 2). Our best-fit splines of each ecosystem variable *versus* time since invasion fitted to cumulative data from all lakes aptly summarize trends within each lake (mean consistency $C = 0.57$; *see* Methods). These trends identify significant declines in total phosphorus, chlorophyll *a*, phytoplankton biomass, and zooplankton biomass accompanied by increases in Secchi depth, zoobenthos, and macrophyte coverage.

These changes characterize a shift from a turbid to a clear water phase ('benthification') and a net transfer of resources from the plankton community to the benthos by mussel filter feeding (reviewed in Karatayev and others 1997, 2002; Mayer and others 2002; Zhu and others 2006; Higgins and Vander Zanden 2010). Mussels directly reduced chlorophyll ($R^2 = 0.73$, $C = 0.58$) and phytoplankton ($R^2 = 0.42$, $C = 0.77$), in turn reducing zooplankton ($R^2 = 0.34$, $C = 0.62$). Mussels have a positive but less consistent, indirect impact on zoobenthos and facilitate macrophyte coverage by deepening the photic zone. In one lake, we did not detect a decline or recovery in zooplankton after zebra mussel invasion (Oneida Lake, see Figure S1 for lake-specific trends). Zooplankton dynamics in this period were highly variable due to multiple factors, including fish predation; in Oneida Lake, age-0 fish are known to affect zooplankton biomass (Mills and Forney 1988) and relatively low age-0 yellow perch abundance occurred after the zebra mussel invasion (Rudstam and others 2016). Lower zebra mussel impacts on zooplankton in Oneida Lake may also have been influenced by the deepened photic zone, which in this lake increased phytoplankton turnover and compensated for reduced phytoplankton biomass, producing little change in total phytoplankton primary production (Idrisi and others 2001; see Idrisi and others 2016 for an overview of phytoplankton community changes in Oneida Lake).

Rooted in high-resolution, ecosystem-level monitoring studies, these results support findings across aquatic and terrestrial systems. Bradley and others (2019) found that invaders have disproportionally strong impacts on species they consume (here, phytoplankton) at lower levels of invader abundance early in an invasion. In line with this, Strayer and others (2006) highlight the importance of considering both the short-term, 'acute' impacts of invaders as well as long-term, 'chronic' invasion outcomes.

Ecosystems Partially Recover from Invasion

Following initial invasion impacts, plankton communities did not stabilize and instead partially recovered in three ecosystems invaded only by zebra mussels (Figure 1). Lakes Lukomskoe, Naroch, and Myastro exhibited significant, synchronized recoveries toward pre-invasion levels of phytoplankton biomass (~ 50%, $C = 0.77$), zooplankton biomass (~ 30%, $C = 0.62$), and Secchi depth (~ 15%). Secchi depth recovery was weaker because this feature was less synchronized across lakes ($C = 0.43$; see *Results robustness* below).

Two broad possible drivers can underlie these partial plankton community recoveries: (a) reduced grazing capacity of the mussel population and (b) increased phytoplankton resistance to grazing. A decline in mussel biomass or filtering activity could arise through intraspecific processes, for example as competition reduces mussel populations (Karatayev and others 2021) or as populations become dominated by large adults with lower mass-specific filtration rates. Mussel biomass could also decline as species interactions or stochastic events increase mortality. These include anoxia (Karatayev and others 2018), native predators learning to feed on mussels (Molloy and others 1997; Watzin and others 2008), or the arrival of new predators (Naddafi and Rudstam 2014). However, the declines in mussel impacts we observe happened synchronously across lakes and are not consistent with stochastic events such as new invaders or anoxic

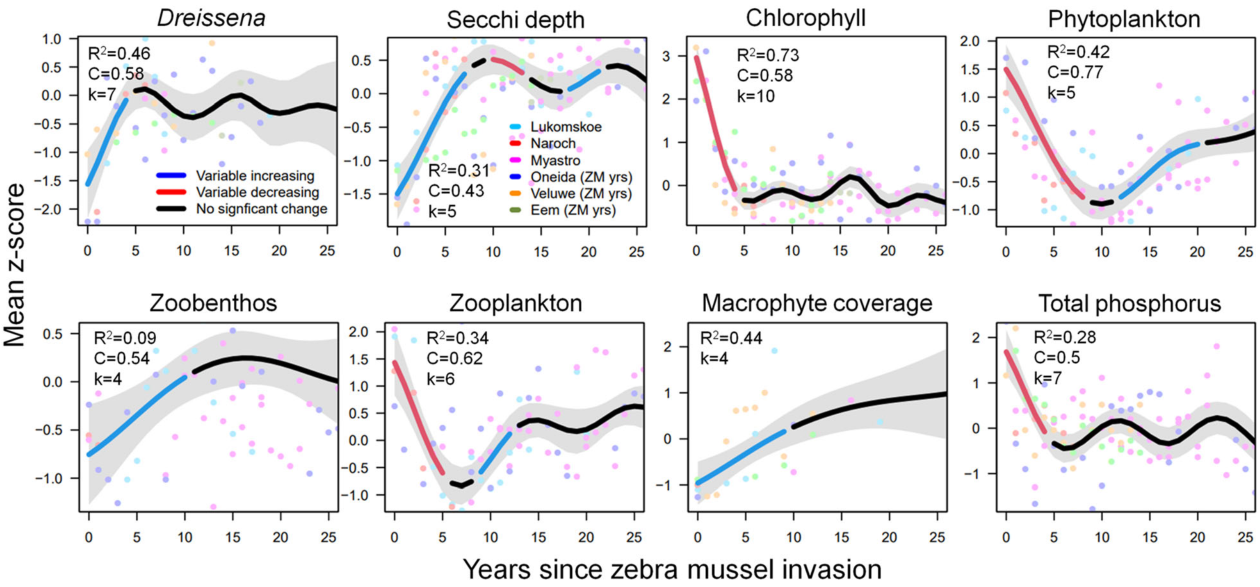

Figure 1. Zebra mussel invasion corresponds to significant long-term changes in ecosystem variables across six polymictic lakes in Europe and North America. Lines denote mean z-score changes in variables predicted by best-fit splines across years since invasion (x-axes) across all lakes and years with zebra mussels only (that is, lakes and years without, or preceding, quagga mussel invasion). For each variable, line colors denote significant increases in blue, significant decreases in red, no significant change in black, and gray areas denote 95% confidence intervals of the mean. For each variable, R^2 denotes the proportion of total variance explained by fitted models, k_x denotes the basis dimension (maximum smoothness) of fitted splines, and C denotes the consistency of lake-specific trends (Figure S1) with the cumulative trend plotted (see Methods).

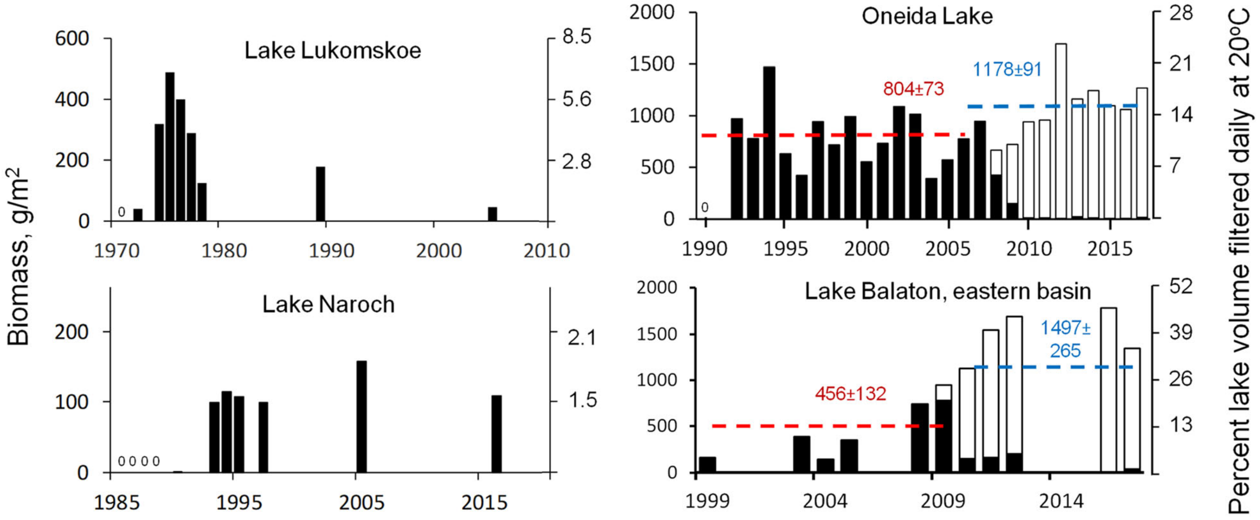

Figure 2. Long-term dynamics of wet biomass of zebra mussels (black bars) and quagga mussels (white bars) in lakes Lukomskoe, Naroch, Balaton, and Oneida Lake. Horizontal dashed lines for lakes Oneida and Balaton denote mean mussel biomass ± standard error for periods of zebra mussel dominance (red line) and quagga mussel dominance (blue line). Secondary axes denote the percent of lake volume filtered daily, estimated from biomass, mean depth, and assuming a filtering rate of 40 ml h^{-1} g^{-1} mussel wet biomass (Karatayev and Burlakova 1995). Unless denoted by zeroes, no data were collected in years with bars absent.

conditions. Demographic processes within the invading population and functional or numerical responses by native molluscivores may happen across systems (Karatayev and Burlakova 2022) on similar time scales, and we therefore suggest demography or predator responses as a more likely driver of observed recoveries.

An alternative mechanism for the partial plankton community recoveries is increased resistance of phytoplankton to grazing. This can arise with a change in traits or community structure. For example, phytoplankton communities can change to species that avoid bottom filter feeders by regulating their buoyancy or are too large to be consumed by mussels, such as some cyanobacteria (Vanderploeg and others 2001; Raikow and others 2004; Fahnenstiel and others 2010; Fishman and others 2010). New studies and data are needed to test this hypothesis, which may additionally explain why phytoplankton biomass increased while chlorophyll *a* concentration remained stable in each of the three lakes not invaded by quagga mussels (Figure 1, S1). This result implies that the phytoplankton community changed toward species with less chlorophyll per unit biomass, perhaps an adaptation to higher light levels (Reynolds 2006; Scofield and others 2020).

Consistent with a broader meta-analysis by Strayer and others (2019), we did not detect a decline in zebra mussel biomass over 5–15 years since invasion, during which impacts on an array of ecosystem features declined (Figure 1). It is of course possible that declines in mussel biomass are not being detected due to gaps in population time series, or because populations peak and decline at different times in different lakes (that is, no net decline when averaging across lakes). In addition, mussel density may decline while biomass remains high if remaining mussels grow larger over time. This could lead to lower mussel impacts as various rates (including filtering and excretion) per unit biomass will likely be lower for large mussels than small mussels (Walz 1978). On the other hand, if there is no true decline in mussel biomass, the declines in mussel impacts that we observe here might signal the role of community adaptation to an ecological regime of high filter feeding.

In other systems, it is known that ecosystem structure and community composition can shift toward a higher abundance of animals consuming the introduced species or shift toward taxa resistant to the introduced species' impacts. Therefore, the impacts of introduced species commonly change over time due to evolution, shifts in species composition, or abiotic changes in the environment (reviewed in Strayer and others 2006; Hui and Richardson 2017). For example, invasive garlic mustard evolved reduced allelochemical concentration, while several native species evolved increased tolerance of garlic mustard allelochemicals (reviewed in Hui and Richardson 2017). Similarly, introduction of domestic ungulates leads to a dominance of grazing- and trampling-resistant grasses or woody vegetation (Cox 2004). In most instances, such changes in species impacts can only be resolved by long-term studies (Strayer and others 2006; Hui and Richardson 2017). Such studies are essential to provide a temporal context for species introductions and insights into the common mechanisms by which ecosystems respond to invasions.

Serial Invasions Amplify Ecosystem Impacts

After the initial zebra mussel invasion, lakes Oneida, Balaton, Eem, and Veluwe experienced an invasion by quagga mussels, which quickly displaced zebra mussels to low densities (~ 5 years in lakes Oneida and Balaton, Balogh and others 2018, Hetherington and others 2019). We find that this serial invasion amplified the ecosystem impacts of the preceding zebra mussels (Figure 3). In all four lakes, quagga mussels increased total dreissenid biomass (and hence total filtering capacity, Table 1) and further depleted chlorophyll *a* concentrations. In Oneida Lake, this serial invasion prevented the recovery of phytoplankton biomass observed in lakes experiencing a single invasion and also reduced zooplankton biomass. Given that increases in mussel biomass and declines in chlorophyll *a* were similarly strong in all lakes with quagga mussel invasion (Figure S1), we anticipate that similar phytoplankton and zooplankton biomass occurred in lakes Balaton, Eem, and Veluwe.

Serial *Dreissena* invasions amplify ecosystem impacts because quagga mussels utilize resources more completely than zebra mussels across space and time. Quagga mussels utilize a wider array of habitat types because they colonize rocky shallows as well as colder, soft-sediment habitats in deep areas of lakes (reviewed in Karatayev and others 2015, 2021). This allows the species to achieve higher total biomass, as evident in the North American Laurentian Great Lakes where serial quagga mussel invasion increased total dreissenid biomass tenfold (Karatayev and others 2021). In addition to higher total mussel biomass, in Oneida Lake our results indicate that quagga mussels also utilize resources more completely across seasons by actively filter feeding during cold periods. Compared to years of zebra mussel dominance (1993–2007), quagga mussel dominance in 2009–2017 corresponded to significantly greater water clarity and lower chlorophyll concentrations during early spring and late fall but not in warmer months (Figure 4). This confirms findings in lakes Michigan and Huron, where the spring diatom blooms disappeared only after quagga mussel invasion (Vanderploeg and others 2002; Nalepa 2010; Karatayev and others 2015; Barbiero and others 2018). These patterns likely arise from higher physiological activity of quagga mussels compared to zebra mussels at colder temperatures (Baldwin and others 2002; Stoeckmann 2003) and explain the higher per-biomass impact of the species on phytoplankton (Figure 4).

Taken together, our results suggest that in displacing zebra mussels, quagga mussels achieve higher total biomass (Figure 2; see Nordhuis and others (2015) for the two Dutch lakes) as well as higher per unit biomass impacts (Figure 4), and therefore deplete phytoplankton more completely. Classical resource competition theory predicts this to be a general phenomenon when the serially introduced species are superior competitors: a species establishes and outcompetes a preceding invader because it can deplete resources more completely (that is, persist at a lower R*, Tilman 1985). Thus, competitive displacement by functionally similar invasive species (often from the same genus) is known as 'over-invasion' and has been documented for wasps (Matthews 2000), mosquitoes (Braks and others 2004), foxes (Bailey 1993), nectar-thieving ants (Lach 2005), and amphipods (van Riel and others 2009); reviewed in (Russell and others 2014). Our results demonstrate that even for closely related species, subtle differences in physiology and environmental preferences drive large ecosystem-level impacts of serial invasions. Data available in Rudstam(2021).

Results Robustness

Initial and serial invasion impacts found here are remarkably consistent across the shallow, polymictic lakes studied here even though these ecosystems span an eightfold range in long-term *Dreissena* biomass, 14-fold range in lake area, and fourfold range in mean lake depth. The different regions and dates of initial invasion (1972–1995) also mean that any undetected changes in the abiotic environment could only skew our qualita-

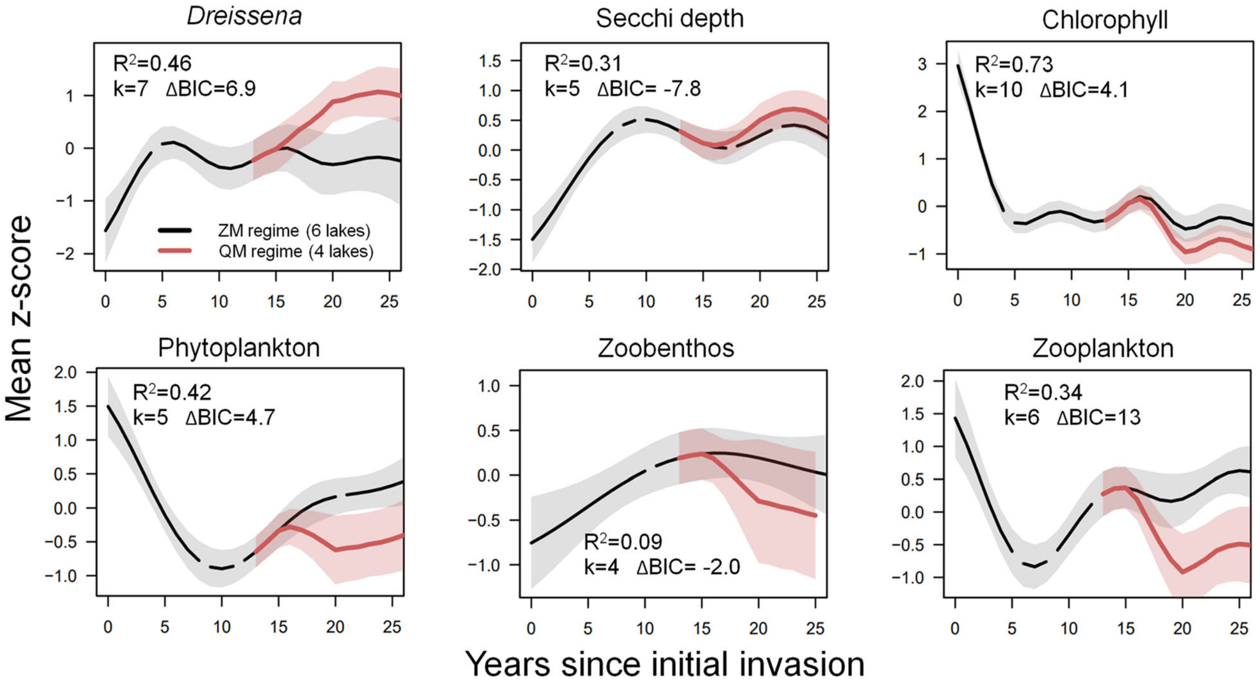

Figure 3. Secondary invasion by quagga mussels leads to significant changes in several ecosystem variables across four polymictic lakes. Lines denote mean z-score changes in variables predicted by best-fit splines with only zebra mussels (black lines, reproduced from trend lines of zebra mussel impacts in Figure 1) and with the added invasion of quagga mussels at year 15 (red lines, lakes Eem, Veluwe, Balaton, and Oneida). Following data in Oneida Lake, the proportion of zebra mussels in models with quagga mussels was decreased to about 0% by year 20. Shaded areas denote 95% confidence intervals of each mean. R^2 denotes the proportion of total variance explained by fitted models and k denotes the maximum basis dimension (decreasing smoothness) of fitted splines. Note that data on zoobenthos, phytoplankton, and zooplankton with quagga mussels are available only for Oneida Lake. Averages are from May through October.

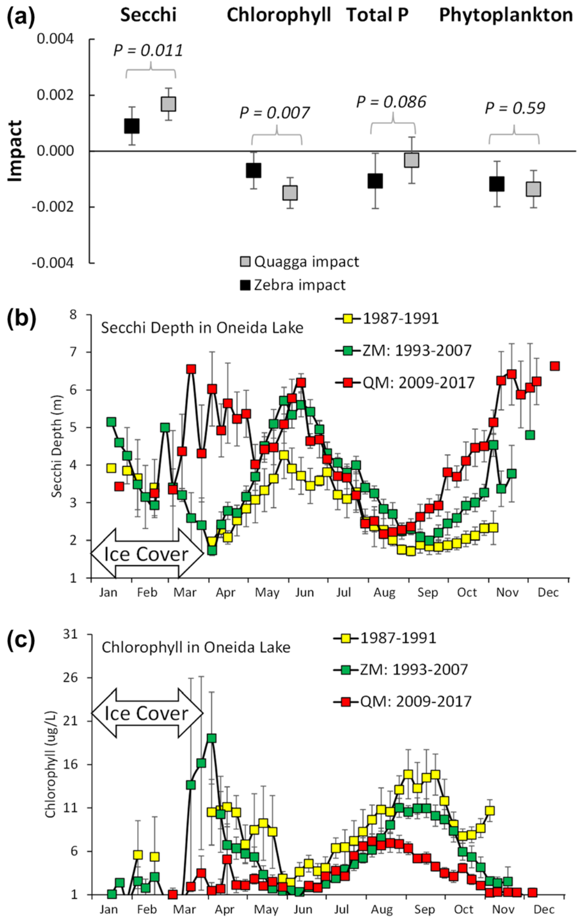

Figure 4. Compared to zebra mussels, quagga mussels in Oneida Lake have greater per-biomass impacts on water clarity and chlorophyll (a) due to filter feeding during cold months (**b**, **c**). In (**a**) points show the effect sizes of each species in general linear regression models of Secchi depth, chlorophyll *a*, total phosphorus and phytoplankton across 1987–2017 (averages from March through November) as a function of zebra mussel biomass (black) plus quagga mussel biomass (gray). *P*-values for each ecosystem feature denote the presence of significant differences in coefficients between the two species in linear hypothesis tests, and error bars denote ± 2 standard errors of each coefficient. **b**, **c** show weekly dynamics of chlorophyll *a* averaged (± 1 standard error) across years before *Dreissena* invasion (1987–1991), during zebra mussel dominance period (1993–2007), and during quagga mussel dominance period (2009–2017). Note that higher March chlorophyll levels with *versus* without zebra mussels arise from an earlier ice melt. Data available in Rudstam (2021)

tive results if they happened at similar times since invasion across all lakes, which is unlikely. However, we caution against using our results as a quantitative roadmap of dreissenid invasion impacts for two reasons.

First, trajectories in any single system may deviate from the aggregate lake trends illustrated in our analyses due to system-specific trajectories in mussel biomass and the abiotic environment mediating mussel impacts. The negative impacts of mussel filter feeding on phytoplankton might be offset by increased nutrient loading into a lake (for example, urbanization, increased fertilizer use) or, potentially, exacerbated by concurrent efforts to reduce nutrient loading. Excessive organic pollution that depletes dissolved oxygen is also known to reduce or even extirpate *Dreissena* populations, including in the central basin of Lake Erie (Karatayev and others 2018) and in Dutch lakes during the 1970s (Ibelings and others 2007; Noordhuis and others 2015). Indeed, the 1995 're-invasion' of lakes Veluwe and Eem by zebra mussels studied here occurred after large reductions in nutrient loading. Thus, the initial P declines in these lakes may be the results of both P loading reductions and the impact of mussels. Analogously, the tenfold decline in zebra mussel biomass observed in Lake Lukomskoe in 2005, 30 years after the peak in biomass (Figure 2), was most likely driven by the increase in nutrient load and oxygen depletion caused by the fish hatchery launched on the lake in 1989 (Mitrakhovich and others 2008). This dramatic decline in zebra mussel population was associated with almost complete return of Lake Lukomskoe ecosystem to pre-invasion conditions (Figure S3). Note that we only used the first 20 years of data for this lake in our analyses to avoid confounding our results with the increase in nutrient loading. Finally, quagga mussel biomass can exhibit very slow growth and reduced grazing in the profundal zones of deep lakes (Karatayev and others 2021), potentially limiting our quantitative insights to the shallow zones of the deep lakes.

Second, our approach may quantitatively underestimate the presence and degree of invasion impacts and ecosystem recovery. Clearly, factors beyond mussel grazing (for example, weather) control lake features, and lakes can differ in the precise timing of invasion impacts (increases, recoveries). Therefore, the among-lake aggregate invasion impacts estimated here become dampened as an averaging effect leads to simpler, smoother models. In the case of Secchi depth, for example, transparency peaked 5 years after invasion and then began to decline in lakes Veluwe and Oneida, but in Belarusian lakes Secchi depth continued increasing for 7–10 years after invasion (again, followed by a subsequent decline; Figure S1). We expect differences in the timing of impacts to be the norm when comparing across lake types: for example, *Dreissena* biomass grows more slowly in deeper, larger lakes (Karatayev and others 2021). Similarly, comparing trends across variables, we expect our models to correctly estimate the timing of mussel impacts, but the magnitude of invasion impacts may be under-estimated in variables with greater intrinsic levels of variability.

CONCLUSIONS

Our findings show that the effects of species introductions on many ecosystem features can manifest quickly and partially subside, except when multiple species are serially introduced into a system. This insight comes from our decades-long perspective of shared changes across multiple ecosystems. Our approach improves on traditional invasive species studies that focus on specific systems or span a shorter time period and, depending on system and timing, may only detect linearly increasing or decreasing trends.

Our results detail comprehensive ecosystem-scale impacts of *Dreissena* invasion by first zebra and then quagga mussels. As quagga mussels swiftly spread and colonize lakes already invaded by zebra mussels across Europe and North America (reviewed in Bij de Vaate and others 2014; Karatayev and others 2015), managers face both initial and serial invasions and their cascading impacts across trophic levels. In lakes Michigan and Huron, for instance, the loss of spring diatom blooms following serial *Dreissena* invasion corresponded to declining populations of salmon, lake trout, and the burrowing amphipod *Diporeia* spp. (Barbiero and others 2018) and was followed by declines in commercially valuable lake whitefish (*Coregonus clupeaformis*) that feed on amphipods (Hoyle and others 2008).

Our finding that serial invasion by functionally similar congeners amplifies invasive species impacts contrasts with predictions of reduced ecological impacts of invaders that have low functional or evolutionary distinctiveness from existing, established species (Ricciardi and Atkinson 2004; Ricciardi and others 2013). However, our observations are consistent with the increased ecosystem effect that is expected when a superior competitor invades the system (Tilman 1985). Thus, we caution that functional or taxonomic distinctiveness can be a poor predictor of invasion impacts in specific systems. This re-emphasizes that preventing invasive species' spread is the most reliable means to minimizing their landscape-level impacts.

ACKNOWLEDGEMENTS

We thank Tom Nalepa, David Strayer, and James Watkins for formative discussions of mussel population dynamics and data synthesis. Oneida Lake surveys were supported by Cornell University and New York State Department of Environmental Conservation. We are grateful to Edward Mills for initiating the mussel studies on this lake and the many Cornell technicians and students supporting sampling over decades. Narochanskie Lakes surveys were supported by Belarusian State University and partially by the Belarusian Republican Foundation for Fundamental Research. The authors thank the researchers and technicians of Belarusian State University Naroch Biological Station, and graduate student I. Selivonchik who helped to collect and produce the data presented here, as well as divers V. Katulko and A. Soldatenkov for help in *Dreissena* sampling in Narochanskie lakes in 2016–2018. Visit to Cornell BFS for Adamovich and Zhukava was funded by Cornell University Biological Field Station. Lyubov Burlakova was supported by a cooperative agreement with Cornell University under Prime Agreement Award GL00E02259-2 from the U.S. EPA''Great Lakes Long-Term Biological Monitoring Program 2017-2022'' (PI L. Rudstam, Co-PIs Burlakova and Karatayev). Lake Balaton study was financially supported by National Multidisciplinary Laboratory for Climate Change (RRF-2.3.1-21-2022-00014). Tünde Polgárdiné Klein, Henriette Szabó, Starkné Mecsnóbel Ildikó, and Éva Koltai assisted with sampling and with laboratory work.

OPEN ACCESS

REFERENCES

Alpert P, Bone E, Holzapfel C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspect Plant Ecol Evolut Syst 3:52–66.

Bailey EP. 1993. Introduction of foxes to Alaskan Islands - history, effects on avifauna, and eradication. Resource Publication 193. U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Baldwin BS, Mayer MS, Dayton J, Pau N, Mendilla J, Sullivan M, Moore A, Ma A, Mills EL. 2002. Comparative growth and feeding in zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for North American lakes. Can J Fish Aquat Sci 59:680–694.

Balogh C, Muskó IB, Tóth L, Nagy L. 2008. Quantitative trends of zebra mussels in Lake Balaton (Hungary) in 2003–2005 at different water levels. Hydrobiologia 613:57–69.

Balogh C, Vláčilová A, Tóth L, Serfőző Z. 2018. Dreissenid colonization during the initial invasion of the quagga mussel in the largest Central European shallow lake, Lake Balaton, Hungary. J Great Lakes Res 44:114–125.

Barbiero RP, Lesht BM, Warren GJ, Rudstam LG, Watkins JM, Reavie ED, Kovalenko KE, Karatayev AY. 2018. A comparative examination of recent changes in nutrients and lower food web structure in Lake Michigan and Lake Huron. J Great Lakes Res 44:573–589.

Benson AJ. 2014. Chronological history of zebra and quagga mussels (Dreissenidae) in North America, 1988–2010. In: Nalepa TF, Schloesser DW, Eds. Quagga and zebra mussels: biology, impacts, and control, 2nd edn. Boca Raton: CRC Press. pp 9–31.

Bij de Vaate A, van der Velde G, Leuven R, Heiler K. 2014. Spread of the quagga mussel (*Dreissena rostriformis bugensis*) in Western Europe. In: Nalepa TF, Schloesser DW, Eds. Quagga and zebra mussels: biology, impacts, and control, 2nd edn. Boca Raton: CRC Press. pp 83–92.

Bradley BA, Laginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CJB. 2019. Disentangling the abundance–impact relationship for invasive species. Proc Natl Acad Sci 116:9919–9924.

Braks MAH, Honório NA, Lounibos LP, Lourenço-De-Oliveira R, Juliano SA. 2004. Interspecific competition between two invasive species of container mosquitoes, *Aedes aegypti* and *Aedes albopictu*s (Diptera: Culicidae), in Brazil. Ann Entomol Soc Am 97:130–139.

Burlakova LE, Karatayev AY, Padilla DK. 2006. Changes in the distribution and abundance of *Dreissena polymorpha* within lakes through time. Hydrobiologia 571:133–146.

Burlakova LE, Karatayev AY, Rudstam LG, Karatayev VA, Adamovich BV, Zhukava HA, Holeck KT, Hetherington AL, Jackson JR, Balogh C, Serfőző Z, Zhukova TV, Mikheyeva TM, Kovalevskaya RZ, Makarevich OA, Kruk DV. 2023. Time scales of ecosystem impacts and recovery under individual and serial invasions. Dryad Dataset. https://doi.org/10.5061/dryad.mpg4f4qzw.

Cox GW. 2004. Alien species and evolution. Island Press.

Fahnenstiel GL, Pothoven SA, Nalepa TF, Vanderploeg HA, Klarer DM, Scavia D. 2010. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. J Great Lakes Res 36:20–29.

Fishman DB, Adlerstein SA, Vanderploeg HA, Fahnenstiel GL, Scavia D. 2010. Phytoplankton community composition of Saginaw Bay, Lake Huron, during the zebra mussel (*Dreissena polymorpha*) invasion: a multivariate analysis. J Great Lakes Res 36:9–19.

Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101:79–90.

Heiler K, de Vaate A, Ekschmitt K, von Oheimb P, Albrecht C, Wilke T. 2013. Reconstruction of the early invasion history of the quagga mussel (*Dreissena rostriformis bugensis*) in Western Europe. Aquat Invas 8:53–57.

Hetherington AL, Rudstam LG, Schneider RL, Holeck KT, Hotaling CW, Cooper JE, Jackson JR. 2019. Invader invaded: population dynamics of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) in polymictic Oneida Lake, NY, USA (1992–2013). Biol Invas 21:1529–1544.

Higgins SN, Vander Zanden MJ. 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol Monogr 80:179–196.

Hoyle JA, Bowlby JN, Morrison BJ. 2008. Lake whitefish and walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. Aquat Ecosyst Health Manag 11:403–411.

Hui C, Richardson DM. 2017. Invasion dynamics. Oxford: Oxford University Press.

Ibelings BW, Portielje R, Lammens EHRR, Noordhuis R, van den Berg MS, Joosse W, Meijer ML. 2007. Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. Ecosystems 10:4–16.

Idrisi N, Mills EL, Rudstam LG, Stewart DJ. 2001. Impact of zebra mussels, *Dreissena polymorpha*, on the pelagic lower trophic levels of Oneida Lake, New York. Can J Fish Aquat Sci 58:1430–1441.

Idrisi N, Mills EL, Rudstam LG. 2016. Long-term phytoplankton community dynamics: Oneida Lake (1975–2011). In: Rudstam LG, Mills EL, Jackson JR, Stewart DJ, Eds. Oneida Lake: long term dynamics of a managed ecosystem and its fisheries, . Bethesda: American Fisheries Society. pp 139–159.

Jackson MC. 2015. Interactions among multiple invasive animals. Ecology 96:2035–2041.

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

Karatayev AY, Burlakova LE. 1995. The role of *Dreissena* in lake ecosystems. Russ J Ecol 26:232–236.

Karatayev A, Burlakova LE, Padilla DK. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in Eastern Europe. J Shellfish Res 16:187–203.

Karatayev AY, Burlakova LE, Padilla DK. 2002. Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. In: Leppäkoski E, Olenin S, Gollasch S, Eds. Invasive aquatic species of Europe, . The Netherlands: Kluwer Academic Publishers. pp 433–447.

Karatayev AY, Burlakova LE, Mastitsky SE, Padilla DK, Mills EL. 2011. Contrasting rates of spread of two congeners, *Dreissena polymorpha* and *Dreissena rostriformis bugensis* at different spatial scales. J Shellfish Res 30:923–931.

Karatayev AY, Burlakova LE, Padilla DK. 2015. Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia 746:97–112.

Karatayev AY, Burlakova LE, Mehler K, Barbiero RP, Hinchey EK, Collingsworth PD, Kovalenko KE, Warren G. 2018. Life after *Dreissena*: The decline of exotic suspension feeder may have significant impacts on lake ecosystems. J Great Lakes Res 44:650–659.

Karatayev AY, Karatayev VA, Burlakova LE, Mehler K, Rowe MD, Elgin AK, Nalepa TF. 2021. Lake morphometry determines *Dreissena* invasion dynamics. Biol Invas 23:2489–2514.

Karatayev AY, Burlakova LE. 2022. What we know and don't know about the invasive zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis bugensis*) mussels. Hydrobiologia. https://doi.org/10.1007/s10750-022-04950-5

Kuebbing SE, Nuňez MA. 2015. Negative, neutral, and positive interactions among nonnative plants: patterns, processes and management implications. Global Change Biol 21:926–934.

Lach L. 2005. Interference and exploitation competition of three nectar-thieving invasive ant species. Insectes Sociaux 52:257–262.

Li J, Ianaie V, Huff A, Zalusky J, Ozersky T, Katsev S. 2021. Benthic invaders control the phosphorus cycle in the world's largest freshwater ecosystem. Proc Natl Acad Sci 118:e2008223118.

Lyakhnovich VP, Karatayev AY, Mitrakhovich PA, Guryanova LV, Vezhnovets GG. 1988. Productivity and prospects for utilizing the ecosystem of Lake Lukoml, thermoelectric station cooling reservoir. Soviet J Ecol 18:255–259.

Martin PA, Newton AC, Bullock JM. 2017. Impacts of invasive plants on carbon pools depend on both species' traits and local climate. Ecology 98:1026–1035.

Matthews RW, Goodisman MA, Austin AD, Bashford R. 2000. The introduced English wasp *Vespula vulgaris* (L.) (Hymenoptera: Vespidae) newly recorded invading native forests in Tasmania. Aust J Entomol 39:177–179.

Mayer CM, Keats RA, Rudstam LG, Mills EL. 2002. Scale-dependent effects of zebra mussels on benthic invertebrates in a large eutrophic lake. J North Am Benthol Soc 21:616–633.

Mayer CM, Burlakova LE, Eklöv P, Fitzgerald D, Karatayev AY, Ludsin SA, Millard S, Mills EL, Ostapenya AP, Rudstam LG, Zhu B, Zhukova TV. 2014. The benthification of freshwater lakes: exotic mussels turning ecosystems upside down. In: Nalepa TF, Schloesser DW, Eds. Quagga and zebra mussels: biology, impacts, and control, 2nd edn. Boca Raton (FL): CRC Press. pp 575–585.

Mills EL, Forney JL. 1988. Trophic dynamics and development of freshwater food webs. In: Carpenter SR, Ed. Complex interactions in lake communities. Berlin: Springer. pp 11–29.

Mills EL, Rosenberg G, Spidle AP, Ludyanskiy M, Pligin Y, May B. 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. Am Zool 36:271–286.

Mitrakhovich PA, Samoilenko VM, Kartashevich ZK, Svirid AA, Kozlov EA, Korolev GN, Papko NA. 2008. Ecosystem of Lukoml thermoelectric station cooling reservoir. Minsk: Pravo and Economica Press.

Molloy DP, Karatayev AY, Burlakova LE, Kurandina DP, Laruelle F. 1997. Natural enemies of zebra mussels: predators, parasites, and ecological competitors. Rev Fish Sci 5:27–97.

Naddafi R, Rudstam LG. 2014. Predation on invasive zebra mussel, *Dreissena polymorpha,* by pumpkinseed sunfish, rusty crayfish, and round goby. Hydrobiologia 721:107–115.

Nalepa T. 2010. An overview of the spread, distribution, and ecological impacts of the quagga mussel, *Dreissena rostriformis bugensis,* with possible implications to the Colorado River System. In: Melis TS, Hamill JF, Bennett GE, Coggins Jr, L.G.,, Grams PE, Kennedy TA, Kubly DM, Ralston BE, Eds. Proceedings of the Colorado River Basin science and resource management symposium. Coming together, coordination of science and restoration activities for the Colorado River ecosystem. November 18–20, 2008, Scottsdale (Az): U.S. Geological Survey Scientific Investigations Report 2010–5135, pp 113–21.

Noordhuis R, van Zuidam BG, Peeters ETHM, van Geest GJ. 2015. Further improvements in water quality of the Dutch Borderlakes: two types of clear states at different nutrient levels. Aquat Ecol 50:521–539.

Noy-Meir I. 1975. Stability of grazing systems: an application of predator-prey graphs. J Ecol 63:459–481

Pollux BJA, van der Velde G, de Vaate A. 2010. A perspective on global spread of *Dreissena polymorpha*: a review on possibilities and limitations. In: van der Velde IG, Rajagopal S, de Vaate A, Eds. The zebra mussel in Europe. Leiden: Backhuys Publishers. pp 45–58.

Raikow DF, Sarnelle O, Wilson AE, Hamilton SK. 2004. Dominance of the noxious cyanobacterium *Microcystis aeruginosa* in low-nutrient lakes is associated with exotic zebra mussels. Limnol Oceanogr 49:482–487.

Reynolds CS. 2006. Ecology of phytoplankton. Cambridge University Press.

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

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL. 2013. Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83:263–282.

Ripple WJ, Beschta RL. 2011. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biol Conserv 145:205–213

Rudstam LG. 2021. Limnological data and depth profile from Oneida Lake, New York, 1975-present. Knowl Netw Biocomplex. https://doi.org/10.5063/F1FT8JH4.

Rudstam LG, Gandino CJ. 2020. Zebra or quagga mussel dominance depends on trade-offs between growth and defense-field support from Onondaga Lake, NY. Plos One 15:e0235387.

Rudstam LG, Jackson JR, VanDeValk AJ, Brooking TE, Fetzer WW, Irwin BJ, Forney JL. 2016. Walleye and yellow perch in Oneida Lake. In: Rudstam LG, Mills EL, Jackson JR, Stewart DJ, Eds. Oneida Lake: long-term dynamics of a managed ecosystem and its fishery. Bethesda (MD): American Fisheries Society. pp 319–354.

Russell JC, Sataruddin NS, Heard AD. 2014. Over-invasion by functionally equivalent invasive species. Ecology 95:2268–2276.

Scofield AE, Watkins JM, Osantowski E, Rudstam LG. 2020. Deep chlorophyll maxima across a productivity gradient: a case study in the Laurentian Great Lakes. Limnol Oceanogr 64:2460–2484.

Simberloff D, Gibbons L. 2004. Now you see them, now you don't! – population crashes of established introduced species. Biol Invas 6:161–172.

Simberloff D, Stiling P. 1996. How risky is biological control? Ecology 77:1965–1974.

Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: invasional metldown? Biol Invas 1:21–32.

Sousa R, Gutiérrez JL, Aldridge DC. 2009. Non-indigenous invasive bivalves as ecosystem engineers. Biol Invas 11:2367–2385.

Stoeckmann A. 2003. Physiological energetics of Lake Erie dreissenid mussels: a basis for the displacement of *Dreissena polymorpha* by *Dreissena bugensis*. Can J Fish Aquat Sci 60:126–134.

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

Strayer DL, D'Antonio CA, Essl F, Fowler M, Geist J, Hilt S, Jarić I, Jöhnk K, Jones CG, Lambin X, Latzka AW, Pergl J, Pyšek P, Robertson P, Schmalensee M, Stefansson RA, Wright J, Jeschke JM. 2017. Boom-bust dynamics in biological invasions: towards an improved application of the concept. Ecol Lett 20:1337–1350.

Strayer DL, Adamovich BV, Adrian R, Aldridge DC, Balogh CS, Burlakova LE, Fried-Petersen HB, Toth LG, Hetherington AL, Jones TS, Karatayev AY, Madill JB, Makarevich OA, Marsden JE, Martel AL, Minchin D, Nalepa TF, Noordhuis R, Robinson TJ, Rudstam LG, Schwalb AN, Smith DR, Steinman AD, Jeschke JM. 2019. Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis*): a cross-system analysis. Ecosphere 10:e02701.

Tilman D. 1985. The resource-ratio hypothesis of plant succession. Am Naturalist 125:827–852.

van Riel MC, van der Velde G, de bij Vaate A. 2009. Interference competition between alien invasive gammaridean species. Biol Invas 11:2119–2132.

Vanderploeg HA, Liebig JR, Carmichael WW, Agy MA, Johengen TH, Fahnenstiel GL, Nalepa TF. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can J Fish Aquat Sci 58:1208–1221.

Vanderploeg HA, Nalepa TF, Jude DJ, Mills EL, Holeck KT, Liebig JR, Grigorovich IA, Ojaveer H. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can J Fish Aquat Sci 59:1209–1228.

Vanderploeg HA, Liebig JR, Nalepa TF, Fahnenstiel GL, Pothoven SA. 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. J Great Lakes Res 36:50–59.

Walz N. 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments in and in Lake Constance. I Pattern of activity, feeding and assimilation efficiency. Archiv Für Hydrobiol Suppl 55:83–105.

Watzin MC, Joppe-Mercure K, Rowder J, Lancaster B, Bronson L. 2008. Significant fish predation on zebra mussels *Dreissena polymorpha* in Lake Champlain, U.S.A. J Fish Biol 73:1585–1599.

Wood SN. 2017. Generalized Additive models: an introduction with R, 2nd edn. Boca Raton (FL): Chapman and Hall/CRC.

Zhu B, Fitzgerald DG, Mayer CM, Rudstam LG, Mills EL. 2006. Alteration of ecosystem function by zebra mussels in Oneida Lake: impacts on submerged macrophytes. Ecosystems 9:1017–1028.