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Do Dreissenid Mussels Affect Lake Erie Ecosystem Stability Processes?

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ABSTRACT.—Ecosystem stability processes such as constancy, resilience and persistence are important, but often neglected, topics of invasive species research. Here we consider how invasive dreissenid mussels affect ecosystem stability processes in Lake Erie through both consumptive and excretory processes using the stability landscape heuristic (Gunderson, 2000). Consumption of phytoplankton by dreissenid mussels adds complexity to the system and potentially slows energy transfer from lower to higher trophic levels decreasing system constancy and lowering system resiliency. Excreting soluble waste products at low nitrogen to phosphorus ratios exacerbates these impacts on stability processes because low nutrient ratios favor growth of cyanobacterial blooms, less preferred food of zooplankton, further decreasing the transfer of energy from lower to higher trophic levels. We also provide evidence for recent changes in Lake Erie's stability landscape including a return towards eutrophy.

INTRODUCTION

Ecosystem stability processes characterize the ways in which natural systems respond to perturbations or disturbances over various levels of organization (producers, consumers, detritivores), spatial scales (millimeter, meter, kilometer) and temporal scales (seconds, days, decades). Following the well-constructed definition of Grimm and Wissel (1997), ecosystem stability processes include the main properties of constancy, resilience and persistence along with the related properties of resistance, elasticity and the domain of attraction. Constancy refers to a system's ability to remain unchanged when compared to a reference state; resilience, the system's ability to return to a reference state; persistence refers to remaining an identifiable entity through ecological time; resistance, remaining unchanged in the face of disturbances; elasticity, the time taken to return to a reference state after a disturbance; and the domain of attraction refers to the various states from which a system will return to a reference state after a disturbance (Grimm and Wissel, 1997). Studying and understanding ecosystem stability has a long history in ecology (Rosenzweig, 1971; Holling, 1973) and is extremely important in the face of ecosystem change due to stressors imposed by human population growth and expansion into pristine systems, in sustainability of ecosystems (Choi and Patten, 2001) and in ecological risk assessment (Belovsky, 2002).

Invasion of exotic species due to human activities is an ever-important stressor on already imperiled ecosystems. Most studies of invasive species impacts focus upon individual-, population- or community-level interactions of invasives with endemic organisms and neglect the ability of invasive species to affect ecosystem stability processes (Ehrenfeld and Scott, 2001; Simon and Townsend, 2003). Several studies, however, have investigated how invasives affect ecosystem stability processes. For example, Evans *et al.* (2001) and Windham and Ehrenfeld (2003) found that invasive plants (*Bromus tectorum*, an annual grass species,

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and *Phragmites australis*, a reed species, respectively) altered the soil nitrogen dynamics in invaded fields possibly decreasing the systems' constancy. Furthermore, Sharp and Whittaker (2003) implicate the introduction of cattle and the subsequent heavy grazing of Australian grassland in the replacement of grasses by woody shrubs. Woody shrub dominance caused by cattle grazing decreases the fire-susceptibility of the ecosystem thereby further promoting woody shrub dominance making the altered system more constant and less resilient (in reference to the non-cattle dominated, grassland system).

Whereas invasions have been present in the Laurentian Great Lakes region since settlement by Europeans, the rate of invasion by exotic species has increased in recent decades (Mills *et al.*, 1993), with many recent invasions attributable to ballast water discharge. Carlton and Geller (1993) equate the invasion of exotic species into natural systems through ballast water discharge as "ecological roulette" where species that could never have crossed ocean barriers are easily translocated through ballast water. The invasion in the Great Lakes with arguably the greatest impact on lake ecosystem function and subsequent research has been that of the dreissenid mussels: the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*D. bugensis*; collectively referred to hereafter as dreissenids). Both species were introduced through ballast water discharge (Hebert *et al.*, 1989; May and Marsden, 1992) and quickly spread throughout Lake Erie (Mills *et al.*, 1999). Initially, most research focused on the impact of dreissenids on phytoplankton populations due to their high filtration capacity (MacIsaac *et al.*, 1992; Bunt *et al.*, 1993; Nicholls and Hopkins, 1993), while later in the invasion, the role of dreissenids in Lake Erie's phosphorus and nitrogen budgets through nutrient excretion has been studied (Mellina *et al.*, 1995; Arnott and Vanni, 1996; Conroy *et al.*, 2004a). Dreissenid mussels may also affect the environment by increasing benthic habitat complexity facilitating macroinvertebrate community colonization and growth (Gonzalez and Downing, 1999) and enhancing substrate roughness due to the structural complexity of mussel beds that increases mixing in the benthic boundary layer (Commito and Rusignuolo, 2000). The goal of our study is to conceptually evaluate the role of dreissenids on the main ecosystem stability processes of constancy and resilience in light of the two contrasting mechanisms of filtration and nutrient excretion. We will not consider system persistence because it is unlikely that dreissenids can affect this stability process due to the time required to modify Lake Erie to the extent needed to make it no longer an identifiable entity. The additional dreissenid effects due to increased habitat complexity and substrate roughness may affect the system constancy and resilience, but we believe that filter feeding and nutrient excretion have a more direct impact and are therefore more important to consider.

Analysis will examine how both roles of dreissenids as filter-feeding benthic invertebrates and internal nutrient recyclers change the "stability landscape" (Fig. 1; sensu Gunderson, 2000) in Lake Erie. The stability landscape has been used to qualitatively demonstrate the current state of an ecosystem, possible stable states, domains of attraction around stable states and the tendency of the system to remain at a particular stable state (Scheffer *et al.*, 1993; Gunderson, 2000). We will first propose and provide evidence for a stability landscape for Lake Erie based upon nutrient loading. We will then describe how dreissenids potentially affect Lake Erie's stability landscape by changing system constancy and resilience (Grimm and Wissel, 1997) through modification of the width of basins of attraction and/or the height and slope of peaks between stable points. Next, we will discuss how nonlinearities in biological, physical and chemical processes generated by dreissenids makes their ultimate impact on Lake Erie ecosystem stability processes more difficult the ascertain. Finally, we will discuss other confounding factors that impede discernment of the actual effects of dreissenid mussels on Lake Erie and suggest avenues for further research to help elucidate the role dreissenids play in affecting Lake Erie ecosystem stability processes.

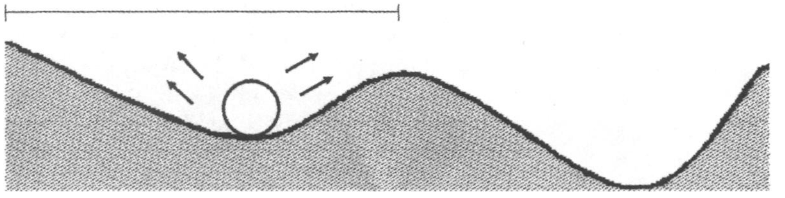

FIG. 1.—Generalized stability landscape (after Gunderson, 2000). The ball shows the ecosystem's current state along the landscape. Low points in the valleys represent stable points in the landscape (in this case there are two) and the arrows show the directions in which disturbances could deflect the system. The valleys around each stable point represent the domain of attraction (for the left stable point this is indicated by the bracketed line). If a disturbance moves the ecosystem to a different state in the same domain of attraction, it will eventually return to the same stable point. The peak in the center of the stability landscape indicates the barrier to moving from one domain of attraction and stable point to another. Ecosystem resilience is related to the height and steepness of these peaks between stable states

LAKE ERIE ECOSYSTEM STABILITY

Lake Erie is the oldest, shallowest, warmest and most productive of the Laurentian Great Lakes (Bolsenga and Herdendorf, 1993). It covers an area of approximately 25,000 km^2, is bordered by five states and one province and its watershed includes the major cities of Detroit, Cleveland, Buffalo and Toledo (Fig. 2). Lake Erie is 388 km long and is divided into three basins separated by two ridges that run between Point Pelee and Lorain, Ohio, and Long Point and Erie, Pennsylvania (Bolsenga and Herdendorf, 1993). The western basin is the shallowest with a mean depth of 7 m and receives most of its nutrient input from the Maumee River (Richards and Baker, 2002). The central basin is somewhat deeper with a mean depth of 18 m. However, due to flat bottom morphometry, it has a tendency to develop a hypoxic or anoxic hypolimnion during the summer (Charlton, 1980). The eastern basin has a mean depth of 24 m with much of the basin deeper than the central basin's average depth making this basin less susceptible to hypoxia.

Lake Erie and its watershed have undergone substantial modification due to the influence of European settlers, a process that continues with increased population growth and demand for lake services such as potable water, recreation activities such as fishing and sunbathing and commercial fishing. In the last century, the most conspicuous forcer of Lake Erie ecosystem change was due to the input of excessive amounts of phosphorus from non-point (mainly agriculture) and point (mainly water treatment plants) sources as the watershed's population increased from the early 1900s to maximum levels in the 1960s and 1970s (Sly, 1976). With excessive phosphorus input, evidence for cultural eutrophication in the form of excessive algal biomass and growth, harmful algal blooms and hypolimnetic hypoxia/anoxia were present throughout the lake (Beeton, 2002). Holling (1973) argued that the degradation of closed homogenous systems such as the Great Lakes indicated that these systems were constant, but not resilient. That is, the systems remained relatively unchanged in reference to their state before disturbance by humans in the watershed (constant), but once disturbed, the systems were unable to maintain their function as compared to before the disturbance (low resilience). For example, Holling (1973) uses the invariant commercial fishery of the Great Lakes to illustrate constancy and resiliency. This fishery exhibited low year-to-year variability before being fished by humans (high constancy) and was dramatically reduced with the extirpation of several species with heavy fishing (low resiliency; Beeton, 2002). After passage and implementation of the Great Lakes Water Quality Agreement of 1978, phosphorus input decreased to target levels (11,000 tonnes per

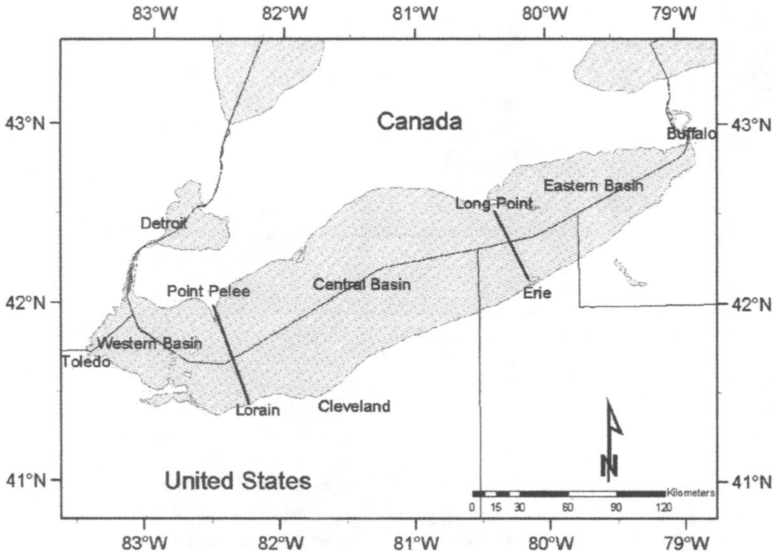

FIG. 2.—Lake Erie. Bolded lines delineate the boundaries between basins

annum) set in the Agreement (Dolan, 1993), phytoplankton biomass and cyanobacterial blooms decreased by the mid-1980s (Makarewicz, 1993a), zooplankton biomass decreased over the same time period (Makarewicz, 1993b) and oxygen depletion rates in the central basin decreased (Bertram, 1993). All of these changes indicate that Lake Erie was shifting from the cultural eutrophic state toward a less eutrophic (or possibly mesotrophic) state.

Based upon concurrence of the chemical and biological changes with changing nutrient input, we propose that Lake Erie has at least two stable points with associated domains of attraction in addition to a barrier between them restricting easy movement from state to state (Fig. 3). Importantly, this proposed stability landscape does not imply a direct linear relationship between external load and trophic state of Lake Erie. Rather, the relationship is modified by physical processes such as the amount of rainfall in the watershed, heating of the lake, wind strength, storm frequency along with other chemical and biological processes that affect how algae use nutrients entering from the drainage basin. Furthermore, the proposed landscape illustrates that Lake Erie has some capacity to mediate disturbances such as extra nutrient load due to inherent system resiliency (Charlton *et al.*, 1993). Consequently, the height and slope of the peak separating the meso- and eutrophic states is dependent on physical, chemical and biological processes and the innate connections between components of Lake Erie.

The stability landscape allows inference about Lake Erie's ecosystem stability processes of constancy and resilience as defined by Grimm and Wissel (1997). Lake Erie was a relatively constant system before disturbance by increasing human population density in the watershed. Most likely, the lake initially maintained a mesotrophic status that was only interrupted by glaciation events that covered the lake and after glacier melting when the lake was shallower and extremely productive (Sly, 1976). Lake Erie does not show great resilience, but as discussed earlier, it is able to absorb some disturbance before shifting to an alternate stable state. Lake Erie has remained an identifiable system for 12,000 y since the last glacial retreat (Bolsenga and Herdendorf, 1993) and will most likely continue to

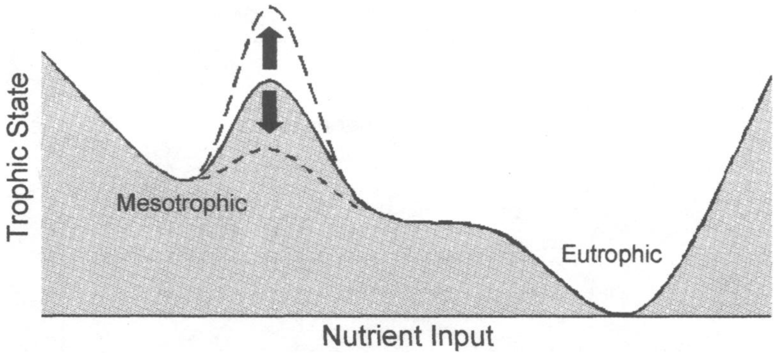

FIG. 3.—Stability landscape for Lake Erie along with potential changes after dreissenid mussel invasion. The "pristine" mesotrophic stable state to the left represents the pre-European settlement state of the lake. Excess nutrient addition due to increased agriculture and waste production by increasing population moved the state of Lake Erie over the peak separating the mesotrophic stable state from the eutrophic state. Likewise, reduced nutrient addition with removal of phosphates from detergents, further wastewater treatment and conservation tilling practices moved the state of Lake Erie back toward the "pristine" mesotrophic state with lower plankton biomasses, decreased frequency of cyanobacterial blooms and slower hypolimnetic oxygen depletion rates. A decrease in constancy and resilience in the landscape due to dreissenid mussels is depicted with the lower peak (short dash) whereas the higher peak (long dash) depicts an increase in constancy and resilience. Arrows indicate deviations from the reference landscape without dreissenid mussels

maintain its persistence. Now that a stability landscape for Lake Erie is established, we turn to a discussion of how dreissenid mussels modify this landscape.

DREISSENID IMPACTS ON LAKE ERIE ECOSYSTEM STABILITY PROCESSES

Before the dreissenid mussel invasion, the shallow and nearshore benthic zones were dominated by amphipods, chironomids, annelids and ephemeropterans with some unionid clams (Barton and Hynes, 1978). None of these taxa are capable of removing large amounts of algae from the water column either because they feed on alternate food sources or because they were not present at high densities. With dreissenid mussels present at densities up to hundreds of thousands per square meter (Leach, 1993) they represent a new connection in the Lake Erie foodweb. Dreissenid mussel ability to consume phytoplankton is dependent on physical transport of food from the pelagic to benthic zone (Noonburg *et al.*, 2003), but recent studies including physical water mixing suggest that dreissenids may remove up to 25% of the algal standing crop in one day (Edwards *et al.*, 2004); a significant amount. Similar to their impact on phytoplankton consumption, dreissenids are a new benthic source of nutrients because particles they consume are digested and waste materials are excreted back into the water column where they are available for uptake by growing algae and bacteria. Of particular importance are excreted phosphate-phosphorus and ammonia-nitrogen because they are often the nutrients most limiting algal growth in freshwater ecosystems (Reynolds, 1984). Furthermore, low nitrogen to phosphorus ratios favor cyanobacteria growth both because some cyanobacteria are capable of fixing molecular nitrogen and because cyanobacteria cell quotas for these nutrients are high (Reynolds, 1984). Several studies have measured the ammonia and phosphate in dreissenid excreta (Arnott and Vanni, 1996; James *et al.*, 1997, 2001; Conroy *et al.*, 2004a) and found that these mussels excrete significant amounts of both nutrients. For example, Conroy *et al.* (2004a) calculated that with dreissenid mussels present, ammonia-nitrogen potentially turns over 300% faster, whereas phosphate-phosphorus turns over 25% faster than without dreissenid mussels. Phytoplankton's ability to obtain excreted nutrients is mediated by physical mixing properties and the above calculations did not take this into account, but clearly dreissenids play a new and important role in the nutrient budgets of Lake Erie, especially in well-mixed areas.

To determine the impact of dreissenid mussels on Lake Erie stability processes, we will start with the stability landscape of Figure 3 and consider how the consumptive and excretory processes of dreissenids affect this landscape. As a novel benthic consumer of phytoplankton in Lake Erie, the system becomes more connected with a significant coupling between the pelagic and benthic zones (Ackerman *et al.*, 2001). May (1974) found that model ecosystems with more connections were less likely to be stable (constant) than those with fewer when system parameters were assigned randomly. A less stable system would tend to have narrower domains of attraction or a flatter valley representing the stable state in the stability landscape. Carpenter *et al.* (1992), in a simulation study using data from a large-scale field experiment, found that longer food chains were less resilient supporting the work of Pimm and Lawton (1977). Carpenter *et al.* (1992) focused on food chains that were lengthened by adding carnivores and measured resilience as the inverse of the time taken to return to a steady state (DeAngelis *et al.*, 1989a). Whereas adding an herbivore such as dreissenids is not equivalent to adding a top carnivore such as largemouth bass (Carpenter *et al.*, 1992), energy cycling in both the dreissenid-modified and largemouth bass-modified systems takes longer because the energy now needs to go through more components to completely cycle, indicating lower resilience. In the stability landscape, lower resilience is indicated by lowering the barrier between multiple domains of attraction and stable states or by decreasing the slope of the peaks between valleys (Fig. 3, short-dashed line). Additionally, as consumers, dreissenids could remove significant energy resources from the ecosystem, shifting the current state from the eutrophic state toward the mesotrophic state (*i.e.,* moving from right to left in Fig. 3) based on the abundance of phytoplankton. Considering dreissenids as phytoplankton consumers, therefore, the stability landscape should have a narrower and/or flatter domain of attraction, a decrease in the slope and height of the peak between meso- and eutrophic states and the current state should move toward the meso- from the eutrophic state.

As discussed above, dreissenids significantly alter the dynamics of the most limiting nutrients in the Lake Erie ecosystem (Conroy *et al.*, 2004a). In the study of Carpenter *et al.* (1992), resilience was also found to be directly proportional to the turnover rate of the nutrient that limited growth (Carpenter *et al.*, 1992), supporting earlier theoretical studies (DeAngelis *et al.*, 1989a). Ecosystem resilience would increase with dreissenids, therefore, due to increased nutrient turnover rates. Increased resilience would tend to decrease the time taken to return to a reference state and would increase the slope of peaks between domains of attraction and different stable states (Fig. 3, long-dashed line). Increased turnover rates may also stabilize or destabilize system dynamics depending on the particulars of the system being studied. Increased turnover rates either support sufficient primary producers to support the herbivore community or support an overabundance of primary producers, releasing herbivores from resource limitation, allowing them to subsequently overwhelm the primary producers (DeAngelis *et al.*, 1989b). A subsequent collapse of the herbivores due to overgrazing could possibly cause a system collapse by decreasing higher trophic level production. Increased stability would tend to increase the height of the peak in the stability landscape (Fig. 3, long-dashed line), whereas decreased stability would have the opposite effect (Fig. 3, short-dashed line). Dreissenid soluble excreta are also of low nitrogen to phosphorus ratio potentially favoring cyanobacterial growth and blooms (Smith, 1983; Smith and Bennett, 1999). Whereas some authors argue that inedible algal taxa such as cyanobacteria may stabilize foodwebs by not allowing herbivorous zooplankton to over-graze their food resources (Persson *et al.*, 2001), cyanobacteria do not provide adequate food resources for zooplankton (Arnold, 1971), thereby limiting the energy transferred to higher trophic levels, increasing the turnover time and decreasing the resilience of the system (Fig. 3, short-dashed line). Consequently, ascertaining the role of the dreissenid nutrient excretion in altering the Lake Erie ecosystem stability landscape is complicated.

CURRENT STABILITY LANDSCAPE OF LAKE ERIE AND THE ROLE OF DREISSENID MUSSELS

Since the settlement of Lake Erie by Europeans, the ecosystem has undergone extensive modification due to activities in the watershed. As documented above, with increasing population in the watershed and the associated increase in nutrient-generating activities, Lake Erie shifted from a meso- to eutrophic state due to increases in phosphorus loading (Sly, 1976). When nutrient control strategies were undertaken, however, the lake started to return to a less eutrophic state with decreased phosphorus input (Dolan, 1993), decreased phytoplankton and zooplankton biomasses (Makarewicz, 1993a, b) and recurrence of mesotrophic indicator species such as the calanoid copepod *Limnocalanus macrurus* (Kane *et al.*, 2004). However, recent research indicates that since the mid-1990s, Lake Erie has started to return to more eutrophic conditions with increases in phytoplankton biomass (Fig. 4a; Conroy *et al.*, 2004b) and recurrence of wide-spread cyanobacterial blooms in the western basin and in the nearshore areas of the central and eastern basins (Figs. 4b, c; Budd *et al.*, 2001; J. D. Conroy, pers. obs.). These indications of a return to a more eutrophic condition were not accompanied by an increase in phosphorus load from the watershed, however (Conroy *et al.*, 2004b). Consequently, other factors would seem to be operational. Whereas underreporting of phosphorus point source discharge, under-calculation of phosphorus load and/or problems associated with non-reporting of phosphorus input from combined sewer overflow discharge all could potentially play a part in the return to eutrophic conditions, the role of dreissenids in changing the stability landscape of Lake Erie and facilitating a return towards the eutrophic state seems equally or more likely.

By adding a significant connection to the foodweb, dreissenids would decrease the constancy by increasing the system complexity and decrease system resiliency by slowing the energy turnover time, decreasing the breadth of the domain of attraction and decreasing the slope in the peak between the meso- and eutrophic stable states, respectively. Additionally, excreting at low nitrogen to phosphorus ratios facilitates basin-wide cyanobacterial blooms by making nitrogen more limiting, favoring algal species that can fix nitrogen or those species that have high cellular quotas for nitrogen, further decreasing the flow of energy up the trophic pyramid and slowing the turnover time with a concomitant decrease in resiliency. With a decrease in resiliency, even a small perturbation could push the system over the peak between stable states and shift the system to the eutrophic state. Once at the eutrophic state, returning to the mesotrophic state would be made more difficult due to the same processes mentioned above, namely slow turnover time due to decreased energy flow to higher trophic levels. Furthermore, because the Lake Erie ecosystem has a strong seasonal aspect (*i.e.,* complete circulation each spring and autumn), returning to the mesotrophic state is even more difficult because the system is effectively reset each year (Hastings, 2004) and any improvement in one year can be offset by deterioration in the next year. Consequently, we propose that the current state of Lake Erie is somewhere to the right of a peak between the mesotrophic and eutrophic stable states. Whereas the system is not as

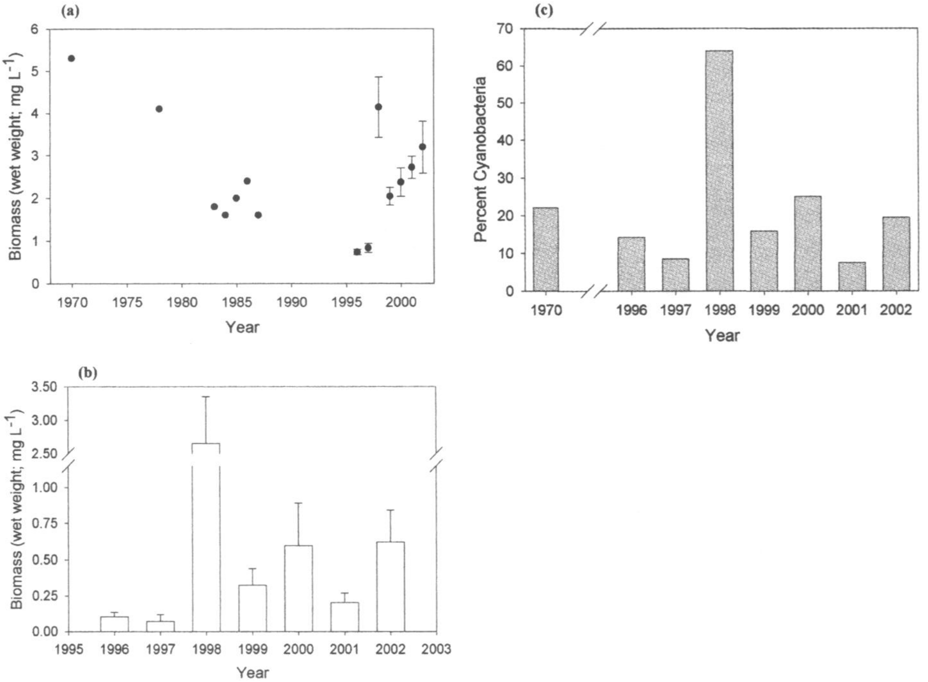

FIG. 4.—Recent changes in the western basin Lake Erie phytoplankton community. Total phytoplankton biomass **(a)** shows a decline from high biomasses from 1970 through the mid-1980s with a subsequent increase from the mid-1990s through 2002. Data for 1970 come from Munawar and Munawar (1976), those from 1978 are from DeVault and Rockwell (1986), those from 1983–1987 are from Makarewicz (1993a) and those from 1996–2002 are from Conroy *et al.* (2004b). Average cyanobacteria biomass **(b)** and percent cyanobacteria **(c)** demonstrate the recent declines in western basin water quality and recurrence of algal blooms. Data from 1970 are from Munawar and Munawar (1976) and those from 1996–2002 are from Conroy *et al.* (2004b). Note that the 1970 percent cyanobacteria data are just from summer whilst 1996–2002 data are from April–October samples (*see* Conroy *et al.*, 2004 for details). Error bars of one standard error of the mean are shown when they were available

degraded as it was in the late 1960s and early 1970s, it certainly is of lower quality than it was in the mid-1980s. The extent to which dreissenid mussels are responsible for this shift back toward eutrophy is not completely known, but the analysis presented here supports a likely role for dreissenids in modifying the stability landscape of the Lake Erie ecosystem. Further, decreases in resilience and destabilization of the ecosystem due to dreissenids are consistent with recent observations of increased phytoplankton biomass and recurrence of cyanobacterial blooms.

COMPLICATIONS AND CONCLUSIONS

Predicting and understanding the response of large ecosystems to stressors due to invasive species is a difficult task (Sakai *et al.*, 2001). Determining the impact of dreissenids on Lake Erie ecosystem stability processes is not any different. Some of the complicating factors in prediction include the size of the Lake Erie system (Fig. 2), the uncontrolled nature of the "experiment" of dreissenid invasion and the unavailability of a comparative system for

TABLE 1.—Operative timescales of several important biological, physical and chemical processes in Lake Erie. The timescale for remineralization is shown as unknown because no quantitative measures have been made of this process in situ. Dreissenids are feeding on a daily (or faster) timescale and therefore this timescale seems likely for remineralization

Biological		Physical		Chemical	
Process	Timescale	Process	Timescale	Process	Timescale
Phytoplankton Growth	Day	Stratification	Day-Season	External Load	Seasonal
Zooplankton Growth	Week	Vertical Mixing	Day-Semi-annual	Residence Time	Month-Year
Zooplankton Feeding	Day	Storms	Week	Remineralization	??
Dreissenid Feeding	Day	Seiche	Semi-daily		

replication. We may be able to learn and infer more about the Lake Erie system because of the dreissenid introduction (Sakai *et al.*, 2001), but predicting the state of the lake in the future remains difficult. Prediction and elucidating the mechanism by which dreissenids affect ecosystem stability processes is further complicated by non-linearities generated by the interactions of processes on different timescales (Harris, 1994). A list of important biological, physical and chemical processes in Lake Erie and their related timescales is shown in Table 1. From this list, it is apparent that even before the introduction of dreissenids the system was complex. After the introduction, the system became even more complex. Remineralization by dreissenids may significantly alter the cycling of nutrients in well-mixed areas of Lake Erie with implications for the rest of the system (Conroy *et al.*, 2004a). Determining the timescales of remineralization impact and how the various processes interact to generate complexities in the Lake Erie system remains an active area of research. Empirical information needed to determine the effect of dreissenids on system stability includes distribution and abundance of the two taxa throughout Lake Erie, size-frequency data and quantification of nutrient excretion rates. Theoretical information needed includes an analysis of how dreissenid mussels change system connectivity and the resultant consequences to nutrient and energy flow from this change in connectivity.

Further complicating the understanding of the impact of dreissenid mussels on Lake Erie ecosystem functioning are the many other factors involved. For example, phytoplankton abundance is the result of nutrient supply, herbivore abundance and physical processes including water movement. Pronouncing dreissenids responsible for the recurrence of cyanobacterial blooms throughout the western basin and in the nearshore areas of the central and eastern basins of Lake Erie without conducting experiments designed solely to test this hypothesis is problematic. Cyanobacteria presence is common in late summer in north temperate lakes (Sommer *et al.*, 1986) such as Lake Erie, but controls limiting nutrient input from the watershed were implemented in the late-1970s in order to decrease the frequency and duration of cyanobacteria blooms and to reduce the overall amount of phytoplankton in Lake Erie (Dolan, 1993). As these controls were implemented and nutrient (particularly phosphorus) concentrations declined toward target levels throughout the mid-1980s, phytoplankton biomass decreased (Makarewicz, 1993a). However, total phytoplankton (Fig. 4a) and cyanobacteria (Fig. 4b) biomass is now increasing without concomitant increases in phosphorus loading from the watershed (Conroy *et al.*, 2004b). This situation implies an increase in nutrient cycling from within the lake. The invasion by dreissenid mussels and their ability to remineralize particulate nutrients to useable, soluble forms provides a possible explanation.

In this study, we have attempted to qualitatively analyze how invasive dreissenid mussels affect Lake Erie ecosystem stability processes through consumptive and excretory aspects of their biology. All changes since the invasion of dreissenid mussels are not necessarily due to their invasion, however dreissenids do fundamentally change the flow of energy (and nutrients) through the ecosystem and affect the timescales of interaction by increasing the energy turnover time by adding connections between pelagic and benthic communities and by excreting at low nitrogen to phosphorus ratios, further slowing the transfer of energy through the trophic pyramid. Both changes serve to change the stability landscape of Lake Erie, modifying the constancy and resilience of the system. Through further study of dreissenid impact on benthic-pelagic coupling and the timescales of interaction between biological, physical and chemical processes in Lake Erie we can better understand the function of unperturbed ecosystems and ascertain how invasive species affect ecosystem stability processes. Furthermore, we have presented a simple conceptual model (Fig. 3) for the stability of Lake Erie that allows interpretation of the effects of other stressors (*e.g.*, increased nutrient runoff) on the system. While models such as these are merely first-order approximations, they can be useful in illustrating complex ecosystem processes.

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