

Benthification of Freshwater Lakes *Exotic Mussels Turning Ecosystems Upside Down*

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ABSTRACT

Many north-temperate lakes are experiencing a shift in energy production from the open pelagic to the benthic region. This process termed “benthification” is occurring across lakes due to increased water clarity. Benthification alters habitats within aquatic ecosystems by augmenting benthic production and escalating the flow of energy and materials between the pelagic and benthic subsystems. Two anthropogenically driven factors, reduced phosphorus inputs and filter feeding by nonindigenous species (i.e., zebra and quagga mussels, *Dreissena polymorpha* and *Dreissena rostriformis bugensis*, respectively), can both enhance water clarity. However, long-term data from seven lakes in North America and Europe indicate that *dreissenids* are driving benthification more than

nutrient reductions. Therefore, ecosystem engineering by these two nonindigenous species is changing the fundamental, physical nature of an entire category of ecosystems.

INTRODUCTION

North-temperate freshwater systems throughout North America and Europe have experienced a number of anthropogenic drivers during the twentieth century. These systems have experienced: (1) excessive phosphorus loading or eutrophication that can promote nuisance levels of phytoplankton and consequently limit water clarity and reduce bottom dissolved oxygen levels (Smith 2003); (2) a subsequent reduction in phosphorus levels via nutrient abatement programs that has been termed oligotrophication (e.g., Sommer et al.

1993, Ludsin et al. 2001); and (3) an accelerated rate of non-indigenous species introductions (e.g., Mills et al. 1994).

Two of these anthropogenically-driven factors, planned reductions in phosphorus inputs and the unplanned introduction and spread of two efficient, invasive filter-feeders, zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena rostriformis bugensis*), are frequently independently cited as the cause of recent increased clarity in north-temperate lakes. Increased water clarity is a potentially important alteration of physical structure that may have implications for a variety of ecosystem-level processes. However, defining the relative importance of *Dreissena* filter feeding and decreased nutrient inputs in promoting water clarity in lakes is complicated by the historical and temporal overlap in these two ecosystem drivers. Nonetheless, understanding which of these two factors, one planned and the other unplanned, is most responsible for returning lakes to a clearer state is crucial to lake and land management practices and to our understanding of ecological processes in aquatic ecosystems.

Indeed, many north-temperate lakes currently have greater water clarity now than during the peak period of eutrophication. Negative consequences of eutrophication have spurred international policies to curb nutrient inputs and thereby ameliorate problems such as nuisance algal blooms. For example, in North America, reductions of nutrient loads in the Great Lakes began after the United States and Canada passed legislation during the early 1970s (e.g., the 1972 Clean Water Act and the Great Lakes Water Quality Agreement) that set target levels for phosphorus inputs. Further, research into the mechanisms underlying eutrophication and possible solutions contributed to the development of important concepts about ecosystem structure and function (Vollenweider 1968, Likens 1972, Shapiro and Wright 1984, Carpenter et al. 1985, McQueen et al. 1986). Phosphorus frequently limits phytoplankton growth in freshwater (Schindler 1977) and is usually implicated as the cause of eutrophication in lakes and rivers. Positive relationships between total phosphorus (TP) and standing crops of phytoplankton have been well documented (e.g., Dillon and Rigler 1974). Therefore, reductions in phosphorus loads via abatement programs likely resulted in lower standing stocks of phytoplankton. However, load reductions and declines in phosphorus levels occurred during the same time period as the introduction of a large number of nonindigenous species (Mills et al. 1994, Holeck et al. 2004), which also affected food web structure and hence productivity (Carpenter et al. 1985, McQueen et al. 1986). Consequently, defining the relative importance of these two potential factors in driving ecosystem-level change is a real challenge.

Dreissenid mussels were introduced into the Great Lakes in 1986 (Carlton 2008) and have since spread to large areas across North America. Dreissenids are also widespread in

Europe outside of their native Pontocaspian region. These mussels have been associated with reduced phytoplankton standing stocks and increased water clarity (e.g., Fahnenstiel et al. 1995a,b, Binelli et al. 1997, Higgins 2013). However, their spread coincided with the time period when nutrient loads were decreasing and similar changes in phytoplankton and water clarity were expected. Further, there is likely an interaction between TP and *Dreissena* effects because in addition to reducing phytoplankton standing stocks as measured by chlorophyll *a*, dreissenids modify the relationship between chlorophyll and TP so that chlorophyll levels are lower than would be expected for a given level of phosphorus (Higgins et al. 2011). It is unlikely that there will be an experimental answer to the question of the relative importance of these two anthropogenic drivers of ecosystem change as no intentional, whole-lake-scale studies on *Dreissena* introduction have been conducted. Consequently, the question remains: which of these two anthropogenic drivers of ecosystem change (reductions in phosphorus vs. dreissenid filter feeding) have had a greater impact on water clarity in north-temperate lakes?

In this chapter, we present evidence that supports the theory that *Dreissena*, and not phosphorus reductions, is the more important driver of the observed improvements in water clarity. Further, we argue that changes in water clarity have triggered a suite of connected changes that increase the importance of benthic processes. We term this process “benthification” and propose that it is occurring over a broad geographic range and is having a strong influence on the structure and function of lake ecosystems.

BENTHIFICATION

Benthification is a point process of ecosystem engineering (Jones et al. 1994) wherein increased water clarity (a physical alteration) triggers a predictable suite of modifications to ecosystem structure (e.g., species composition, spatial distribution of primary producers and consumers) and function (e.g., primary production, benthic–pelagic flux) (Figure 36.1). Further, water clarity can affect human aesthetic perception of a lake, with higher water clarity generally being thought of as more desirable. In a turbid, eutrophic lake, large abundances of phytoplankton act much like a forest over-story, limiting light to primary producers in deeper habitats. Increased water clarity affects a lake in a manner similar to cutting down trees in a forest and results in a restructuring of the spatial distribution of primary production, organic material, and energy flow. The spatial extent of potential benthic primary production (algae and macrophytes) will increase because more light reaches a greater proportion of the bottom. In addition to affecting primary producers, increased light penetration will allow visually-feeding

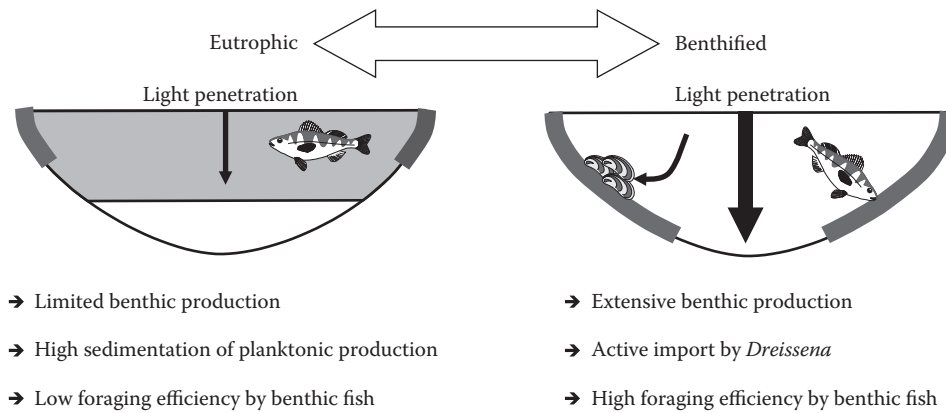


Figure 36.1 Depiction of changes associated with the process of “benthification.” An increase in water clarity allows for greater rates and spatial extent of benthic primary production. Transport of material from pelagic to benthic zones changes from passive sedimentation to active importation to areas colonized by *Dreissena*. Transfer of energy and material from the benthic to pelagic zone increases because bottom-foraging fish become more efficient.

fish to forage more efficiently on benthic invertebrates, thereby augmenting the rate of material flux from benthic to pelagic zones. Unlike trophic cascades, in which changes are transmitted to subsequent trophic levels indirectly by a series of linked interactions between organisms, the physical–biotic coupled changes associated with benthification affect organisms directly and simultaneously at multiple trophic levels. As a result, these changes will have intense and rapid system-wide effects.

The degradation of benthic energy pathways (Vadeboncoeur et al. 2003) is a negative consequence of eutrophication that historically has received little attention from limnologists. Phytoplankton blooms, which are promoted in eutrophic waters, shade benthic (bottom associated) primary producers. Benthic primary production is an important, though seldom-measured, component of total ecosystem productivity (Vadeboncoeur et al. 2002), and fish may rely heavily on this energy (Vander Zanden and Vadeboncoeur 2002). Therefore, the consequence of excessive pelagic productivity can be a loss of benthic production and the dwindling of this potentially important energy pathway in aquatic food webs. Consequently, insight into the mechanisms behind the reestablishment of benthic energy fixation and flux is critical to an understanding of total ecosystem function.

Many changes associated with *Dreissena* have been documented in individual systems (Vanderploeg et al. 2002), but there has been little recognition that changes in primary producers, invertebrates, and fish are linked, and such changes constitute a major shift in the function of lake ecosystems across a broad geographic range. In the Great Lakes, direct importation of organic material to the benthic region by the filtration activities of *Dreissena* supports the idea that phosphorus is being redirected to benthic areas by *Dreissena*, as detailed in the “nearshore shunt” hypothesis proposed by Hecky et al. (2004). Benthic primary producers have increased in response to *Dreissena*

introduction (Lowe and Pillsbury 1995, Skubinna et al. 1995, Zhu et al. 2006, Cecala et al. 2008, Auer et al. 2010). Also, *Dreissena* beds create a heterogeneous benthic habitat that has had a positive impact on most benthic invertebrates by entrapping dreissenid biodeposits that serve as a food resource and by offering protection from potential predators (e.g., Botts et al. 1996, Ricciardi et al. 1997, Stewart et al. 1998). Benthic invertebrates considered to be grazers have benefited from increased benthic production (Mayer et al. 2002). *Dreissena* provide attachment substrate for invertebrates that require hard substrate (Mayer et al. 2002) as well as for benthic algae such as *Cladophora* (Hecky et al. 2004). Benthic prey consumption by fish has increased after *Dreissena* establishment (Mayer et al. 2000). A review of *Dreissena* effects in Europe (Karatayev et al. 2002) concluded that the role of the benthic community increased dramatically after dreissenid introduction and that the benthic community becomes capable of controlling processes and dynamics in the entire ecosystem. Nevertheless, these changes have generally been interpreted as individual interactions, and there has been little synthetic understanding of the direct linkage of physical changes (ecosystem engineering) to trophic processes and ecosystem function.

The overall effect of benthification, stemming partly from enhanced water clarity and partly from enhanced deposition of organic material, is an increase in benthic primary production and an increase in benthic feeding by fishes. Subsequently, there is an increased flux of organic material associated with the lake’s bottom that permeates the off web. Because benthification directly affects organisms, ranging from primary producers to top carnivores, it may in fact initiate both bottom-up and top-down cascading interactions that thus far have been viewed only as trophic cascades without an appreciation for the physically driven mechanism behind the interactions.

EPIDEMIC OF BENTHIC STABLE STATES

The existence of alternative pelagic (phytoplankton) and benthic (algae and macrophytes) stable states has been described for small, shallow lakes (Scheffer et al. 1993) and also suggested for large, shallow lakes such as Lake Erie (Kay and Regier 1999). The concept of benthification builds on the theory of alternate stable states, which suggests that over a range of nutrient levels across systems, an extrinsic disturbance may be required to switch a system from a turbid to clear state. We suggest that dreissenids are indeed providing such a disturbance across a geographically extensive range and are therefore causing an “epidemic” of newly stable benthic states in north-temperate lakes. Further, we suggest that the initial change in water clarity triggers a suite of responses in which multiple trophic levels, not just primary producers, are directly impacted, and therefore the effects may be more pervasive than simple cascading interactions. Lastly, this ecosystem engineering provides a dramatic example of whole-system alteration by a nonindigenous species.

LONG-TERM DATA

To quantify the relative roles of *Dreissena* introduction and nutrient reduction in causing increased water clarity and associated ecosystem change (i.e., benthification), we selected north-temperate lakes in both North America and Europe that had long-term data (>15 years) that spanned both pre- and post-*Dreissena* and pre- and post-phosphorus reductions. We also surveyed available literature to determine the magnitude of water clarity increase that is associated with *Dreissena*. We selected seven water bodies that represented a range of trajectories in phosphorus

concentration prior to *Dreissena* introduction, as shown by the relationships of TP to year (Table 36.1). Water bodies that were experiencing significant declines in TP prior to *Dreissena* introduction were Bay of Quinte (two sites, Lake Ontario, Canada), western Lake Erie (United States), and Lake Naroch (Belarus), whereas a marginal decrease was occurring in Oneida Lake (United States). In contrast, TP in Lake Erken (Sweden) was increasing prior to *Dreissena* introduction, and TP in Lakes Myastro and Batorino (Belarus) showed no statistically detectable trend with time. Regardless of the trend prior to *Dreissena* introduction, each water body showed a lower TP level in the post-*Dreissena* period, and the average TP among all the water bodies was significantly lower after *Dreissena* introduction (paired t-test $P < 0.0001$). The only water body for which the decline in TP may have been temporally connected with *Dreissena* introduction was Lake Erken where an increasing trend in TP reversed around the time of *Dreissena* introduction.

SEPARATING THE RELATIVE IMPORTANCE OF DECLINES IN TOTAL PHOSPHORUS AND DREISSENA

To determine the relative importance of changes in TP levels and *Dreissena* introduction in affecting water clarity, we used an analysis of covariance (ANCOVA) model in which average annual water clarity data (indexed by Secchi depth transparency) from each water body were the response variable. We considered *Dreissena* introduction to occur the first year that populations were reported to be established. *Dreissena* were included as a categorical independent variable and annual TP served as a covariate. All data were \log_{10} transformed to stabilize variance for statistical analyses.

Table 36.1 Regression Parameters for the Relationship between TP (\log_{10} Transformed) and Year for Seven Water Bodies Prior to *Dreissena* Introduction. Effect Considered Significant at $P < 0.05$. Five of Seven Sites Showed a Significant Decreasing Trend with Time, Whereas One System Showed a Significant Increasing Trend with Time. N, Number of Years Prior to *Dreissena* Introduction. (Data Sources: Bay of Quinte [S. Millard]; Oneida Lake [E. L. Mills and L. G. Rudstam]; Lake Erken [P. Eklöv]; Lakes Batorino, Myastro, Naroch, Belarus [L. E. Burlakova, A. Karatayev, A. P. Ostapenya, T. V. Zhukova]; Western Lake Erie [Ohio Department of Natural Resources and the U.S. Environmental Protection Agency])

Lake	N	Slope	R ²	P-Value
Batorino, Belarus	9	-0.01	0.05	0.6450
Erie, United States	17	-0.03	0.31	0.0208
Erken, Sweden	8	0.06	0.96	0.0001
Myastro, Belarus	9	-0.01	0.07	0.5572
Naroch, Belarus	15	-0.03	0.65	0.0003
Oneida, United States	17	-0.01	0.23	0.0532
Bay of Quinte B (Lake Ontario, Canada)	22	-0.02	0.74	0.0001
Bay of Quinte N (Lake Ontario, Canada)	16	-0.02	0.81	0.0001

In no case was there a significant interaction between the *Dreissena* and TP effect, consequently this term was dropped from each model.

We found that average annual Secchi depth transparency increased in all water bodies after *Dreissena* introduction (untransformed mean increase = 0.94 m). The ANCOVAs for each system showed that six of eight *Dreissena* effects were statistically significant, whereas two locations (one Bay of Quinte site and Lake Batorino) showed a statistically significant, positive within-site relationship between TP and annual Secchi depth (Table 36.2). These results indicate that, in a given system, the introduction of *Dreissena* had a greater effect on water clarity than TP declines.

To contrast changes in water clarity across systems, we tested for an increase in water clarity between the pre- and post-*Dreissena* periods using a t-test, paired by site. Water clarity was significantly higher in the post-*Dreissena* period (paired t-test, one tailed, P = 0.0003); moreover, all sites showed some increase (Figure 36.2). In contrast, the relationship between percent change (decrease) in TP and the percent change (increase) in Secchi depth between the pre- and post-*Dreissena* periods was not significant (Figure 36.3; regression, R² = 0.05, P = 0.58). This trend confirms that lakes that had large declines in TP did not necessarily experience large increases in clarity and further supports the importance of a prolific grazer, *Dreissena*, in influencing increased water clarity.

Table 36.2 Results of ANCOVA Examining Effects of *Dreissena* Introduction and TP on Water Clarity (Secchi Depth Transparency). *Dreissena* Is a Categorical Effect and TP Is a Covariate. Sums of Squares for *Dreissena* and TP Effects Are Type III (Not Dependent on Model Order). Data Sources Are Given in Table 36.1. Effect Considered Significant at P < 0.05

Lake	Source	DF	SS	F	P
Bay of Quinte, Lake Ontario (station B), Ontario, Canada	Model	2	0.106	18.96	0.000
	Error	27			
	<i>Dreissena</i>	1	0.040	14.42	0.001
	TP	1	0.016	5.83	0.023
Bay of Quinte, Lake Ontario (station N), Ontario, Canada	Model	2	0.324	24.94	0.000
	Error	21	0.098		
	<i>Dreissena</i>	1	0.098	20.91	0.000
	TP	1	0.007	1.60	0.220
Batorino, Belarus	Model	2	0.101	22.67	0.000
	Error	21			
	<i>Dreissena</i>	1	0.005	2.16	0.157
	TP	1	0.025	11.32	0.003
Erie, United States and Canada	Model	2	0.382	34.69	0.000
	Error	25			
	<i>Dreissena</i>	1	0.320	58.10	0.000
	TP	1	0.000	0.01	0.913
Erken, Sweden	Model	2	0.034	6.87	0.006
	Error	19	0.046		
	<i>Dreissena</i>		0.022	8.897	0.008
	TP		0.000	0.005	0.818
Myastro, Belarus	Model	2	0.261	15.46	0.000
	Error	21	0.017		
	<i>Dreissena</i>	1	0.048	2.83	0.107
	TP	1	0.047	2.76	0.112
Naroch, Belarus	Model	2	0.018	0.88	0.000
	Error	21	0.003		
	<i>Dreissena</i>	1	0.119	44.67	0.000
	TP	1	0.004	1.34	0.260
Oneida, NY	Model	2	0.089	10.18	0.001
	Error	24	0.105		
	<i>Dreissena</i>	1	0.045	10.20	0.004
	TP	1	0.000	0.00	0.970

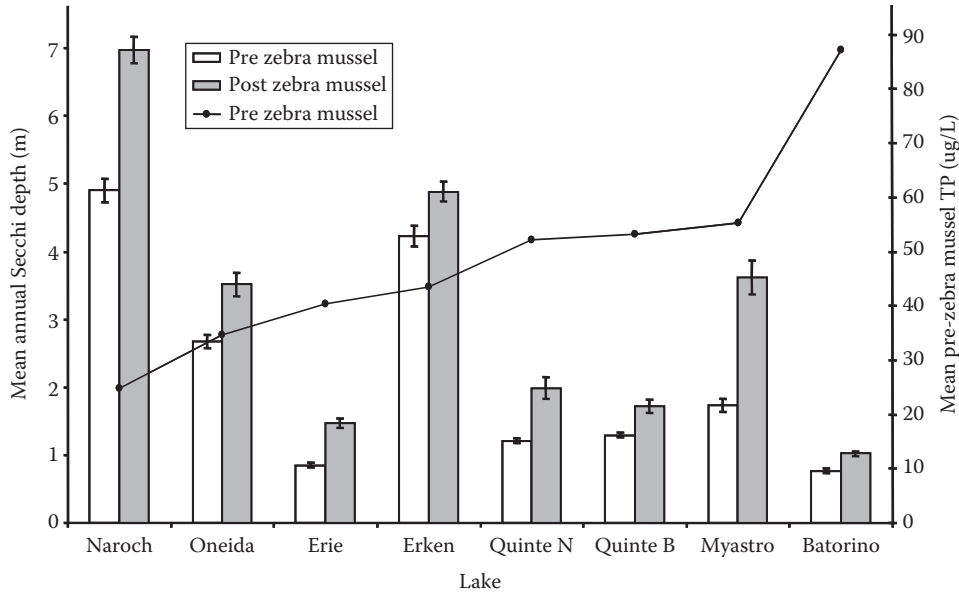


Figure 36.2 Mean (± 1 SE) annual Secchi depth transparency (m) in various water bodies in the period before (pre-; open bar) and after (post-; solid bar) establishment of *Dreissena*. Also given is the mean TP (solid line) concentration ($\mu\text{g/L}$) in each of the water bodies in the period before *Dreissena* establishment. Lakes are arranged in order of increasing TP in the pre-*Dreissena* period.

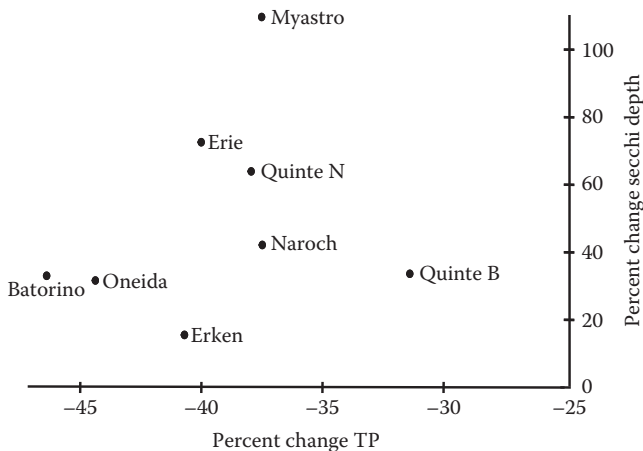


Figure 36.3 Relationship between percent change in TP and Secchi depth transparency (m) in the period before (pre-) and after (post-) establishment of *Dreissena* in various water bodies. The relationship was not statistically significant (regression, $P = 0.58$).

REVIEW FROM OTHER SYSTEMS

To supplement our analysis, we also searched the published literature for studies that examined water clarity in pre- and post-*Dreissena* periods, but did not necessarily present data collected over the long term. Published papers were obtained by searching the Cambridge Scientific Abstracts database for Biological Sciences and AGRICOLA, using the key words “zebra mussel, *Dreissena*, Dreissenid, water clarity, water quality, water transparency, turbidity, Secchi, and light.” We supplemented the published literature with technical reports and data from websites in order to diminish the effects

of publication bias. Secchi depth was the most frequently reported index of water clarity; therefore, studies reporting other indices, for example, turbidity (NTU) or attenuation (kPAR), were not used in this analysis. Many of the studies that reported water clarity trends did not report data on nutrient levels and therefore did not help to separate the effects of *Dreissena* from nutrient reduction. However, these studies allowed us to compare the magnitude of change observed in our long-term data sets to that seen in other systems. We found 17 published papers that reported water clarity data during in the pre- and post-*Dreissena* periods; these data were collected in 12 lakes and 1 river (Table 36.3). Different papers examined different time periods or different basins for the same lake (see Lake Erie, Saginaw Bay of Lake Huron, and Oneida Lake). Also, some papers reported trends for specific seasons, whereas some reported means over the entire growing season (Table 36.3). Overall, 33 pre- and post-*Dreissena* values were compared from the 13 water bodies. Of these, 27 showed an increase in post-*Dreissena* water clarity, 3 showed a decrease in water clarity, and 3 showed no change (Table 36.3). The mean change was calculated for each system (lake or river) for which multiple values or studies were available (Figure 36.4). For example, there were 13 measurements reported from different areas of Lake Erie, and the mean of these (0.88 m) was used to represent this system. The overall mean across systems ($n = 13$) was an increase of 1.02 m (± 0.50 SD).

Most of the pre- and post-dreissenid comparisons that did not show an increase in water clarity were in Lake Erie; four of the six instances of no increase in water clarity were in the western or central basins of this lake. The western basin of Lake Erie is a large, shallow system, and physical contributions to turbidity such as wind-driven resuspension

Table 36.3 Comparisons of Secchi Depth Transparency (Meters) in Various Water Bodies in North America and Europe in the Period before and after *Dreissena* Establishment

System	Site Location	Season	Preinvasion Secchi (m)	Post-Invasion Secchi (m)	Difference (m)	Years Compared	Reference
Hargus Lake	Littoral		1.22	2.17	+0.95	93–95	17
Hargus Lake	Pelagic		1.7	2.52	+0.82	93–95	17
Lake Bolduk	Pelagic	Summer	3.70	4.50	+1.20	72 vs. 98	10
Lake Bolshiye Shvakshty	Pelagic	Summer	2.50	3.10	+0.60	71 vs. 98	10
Lake Como			7.5	7.6	+0.10	91–92 vs. 95–96	2
Lake Erie	Central	Spring	4.39	2.84	–1.55	82–04	1
Lake Erie	Central	Summer	6.57	7.12	+0.55	82–04	1
Lake Erie	East	Spring	3.24	7.8	+4.56	82–04	1
Lake Erie	East	Summer	6.11	6.59	+0.48	82–04	1
Lake Erie	Hatchery Bay	Fall	0.99	2.39	+1.41	83–87 vs. 90–95	16
Lake Erie	Hatchery Bay	Spring	0.76	2.14	+1.38	83–87 vs. 90–95	16
Lake Erie	Hatchery Bay	Summer	1.37	3.29	+1.92	83–87 vs. 90–95	16
Lake Erie	Hatchery Bay	Winter	1.28	1.73	+0.45	83–87 vs. 90–95	16
Lake Erie	Hatchery Bay		1.23	2.37	+1.14	84–86 vs. 90–92	6
Lake Erie	West	Spring	2.21	1.31	–0.90	82–04	1
Lake Erie	West	Summer	2.21	2.20	–0.01	82–04	1
Lake Erie	West		1.5	2.74	+1.24	88–89	11
Lake Erie	West–central		3.3	4.05	+0.75	88–89	11
Lake Huron	Saginaw Bay	Spring	1.31	2.42	+1.11	74–80 vs. 91–95	15
Lake Huron	Saginaw Bay	Summer	1.07	1.71	+0.64	74–80 vs. 91–95	15
Lake Huron	Saginaw Bay		1.15	1.79	+0.64	74–80 vs. 91–93	5
Lake Huron	Saginaw Bay		1.26	2.05	+0.79	74–80 vs. 91–93	5
Lake Huron	Saginaw Bay		1.32	2.45	+1.13	74–80 vs. 91–93	5
Lake Lukomskoe	Pelagic	Summer	2.00	4.00	+2.00	65 vs. 80	12
Lake Michigan	Southwest		3.98	5.21	+1.23	81–90 vs. 91–00	8
Lake Myadel	Pelagic	Summer	3.00	4.80	+1.80	80 vs. 98	10
Lake Svir	Pelagic	Summer	1.00	1.77	+0.77	80 vs. 98	10
Lake Volchin	Pelagic	Summer	4.60	3.80	–0.80	80 vs. 98	10
Oneida Lake			3.25	3.88	+0.63	75–91 vs. 92–94	7
Oneida Lake			2.64	3.60	+0.96	88–91 vs. 92–97	9
Oneida Lake			2.56	3.60	+1.04	75–91 vs. 92–97	13
Oneida Lake			2.66	3.18	+0.52	89–91 vs. 92–93	14
Seneca River			0.75	2.1	+1.35	90–91 vs. 93	3 & 4

References are as follows: 1, Barbiero and Tuchman (2004); 2, Binelli et al. (1997); 3, Effler and Siefried (1994); 4, Effler et al. (1996); 5, Fahnenstiel et al. (1995a,b); 6, Holland (1993); 7, Horgan and Mills (1999); 8, <http://waterbase.glwj.uwm.edu>; 9, Idrisi et al. (2001); 10, Karatayev et al. (2000); 11, Leach (1993); 12, Lyakhovich et al. (1988); 13, Mayer et al. (2002); 14, Mellina et al. (1995); 15, Nalepa et al. (1999); 16, GLERL/NOAA (1996); 17, Yu and Culver (2000).

of sediment and inputs from the large Maumee River likely added to the variability of water clarity. In a sense, western Lake Erie is much like the Hudson River, where *Dreissena* have lowered standing stocks of phytoplankton (Strayer et al. 1999), but physical forces in this tidal system frequently drive turbidity and water clarity. In western Lake Erie turbidity is driven by both physical and biotic factors. In fact, under some circumstances *Dreissena* themselves may promote late season blooms of toxic algae by selectively filtering competitors (Vanderploeg et al. 2001). In Green Bay, Lake Michigan, Secchi depth transparency did not significantly increase in the post-*Dreissena* period possibly because TP was higher after *Dreissena* than before (Qualls et al. 2007). This suggested that watershed influences can

override the grazing effect of *Dreissena*. However, there appears to be an overall trend of increased water clarity in the post- *Dreissena* period for most systems despite the effects of physical disturbance, local eutrophication, and within-lake ecological interactions.

UPSIDE-DOWN ECOSYSTEMS PAST AND FUTURE

The availability of long-term data for water clarity, TP, and *Dreissena* populations for a number of lakes has allowed us to determine the relative importance of two anthropogenic drivers of habitat change. We conclude that,

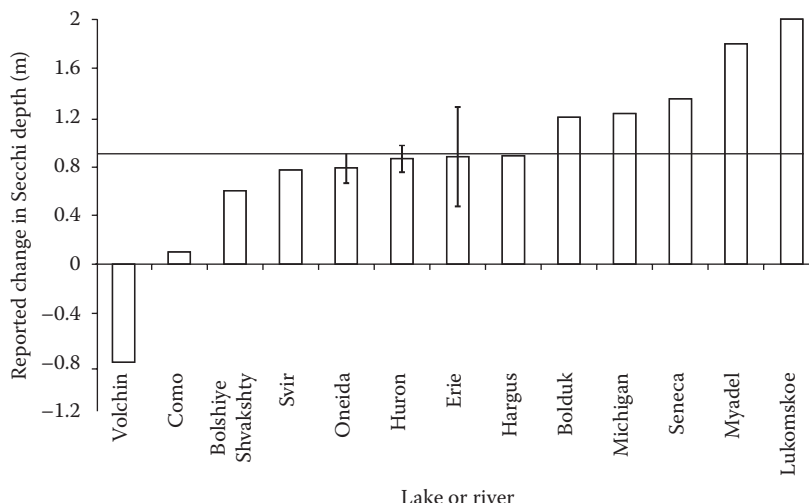


Figure 36.4 Change in mean (± 1 SE) Secchi depth transparency (m) in the period before (pre-) and after (post-) establishment of *Dreissena* in various water bodies. Data are derived from published studies that lasted <15 years. Means were calculated when more than one study was available for a given water body. Horizontal line indicates the mean change for all water bodies. See Table 36.3 for data sources.

in the water bodies examined in this study that have over 15 years of data collection, establishment of *Dreissena* rather than phosphorus abatement best explains observed increases in water clarity. In addition, data examined from other published studies with shorter-term data sets support this conclusion. The mean increase in water clarity after *Dreissena* introduction was 0.94 m (as measured by Secchi depth) for lakes with long-term data sets compared to an increase in 1.02 m for lakes with shorter data sets. The shift from a turbid to a clear-water system is not only a change between stable system states (*sensu* Scheffer et al. 1993); it is a switch between two qualitatively different types of ecosystems, as distinct from each other as forests and grasslands. Paradoxically, benthification, which we attribute primarily to the effects of *Dreissena* filter feeding, may return lakes to a state similar to their prehuman-influenced condition. Prior to anthropogenic eutrophication, many northern temperate lakes probably had water clarity similar to or greater than after *Dreissena* and nutrient abatement. Further, many of these systems likely supported a large biomass of benthic species including gastropods, unionid mussels, and fish. Indeed, benthification may favor benthic fish that were once ecologically and economically important but were in decline due to eutrophication. After *Dreissena* introduction, benthic-feeding littoral fish have shown abundance increases in the Hudson River (Strayer et al. 2004), in Lake Erie (Ludsin et al. 2001), and in many European lakes (Karatayev et al. 2002).

While one consequence of benthification by dreissenids is a directional shift to a more prehuman-influenced state, in reality the process is complex with unexpected feedback loops. *Dreissena* strongly interacts with a variety of native and invasive species in the Great Lakes, and the overall effect promotes macrophytes and shallow-water,

benthic invertebrates (DeVanna et al. 2011). Many of the species that are expected to invade the Great Lakes and associated waters in the near future are benthic (Ricciardi and Rasmussen 1998), and many of these species are likely to have strong interactions with *Dreissena*. Thus, changes brought about by *Dreissena* are likely to facilitate continued physical and biotic modifications to lake ecosystems that contribute to uncertainties in predicting eventual outcomes of benthification.

PHYSICAL VERSUS TROPHIC CHANGE

Regardless of directional extent, benthification has strong impacts on ecosystems because habitat change connects directly to a number of trophic levels rather than being transmitted through a series of links. For example, an increase in water clarity and light penetration directly affects the photosynthetic rate of plants and algae, while the same change in light also directly alters the environment for visual predators and prey. The direct, simultaneous connection of habitat change to all trophic levels, from primary producers to top predators, distinguishes this process from both “bottom-up” and “top-down” effects (McQueen et al. 1986, Carpenter et al. 1991), which cascade through a system via a sequence of linkages. However, it is likely that benthification will go on to initiate both top-down and bottom-up trophic cascades. An increase in benthic algae production may favor grazing benthic invertebrates, which may then provide an added resource to benthic-feeding fish, thereby triggering what would be seen as a bottom-up cascade. Alternatively, higher light and lower turbidity may increase efficiency of visual foragers and initiate top-down cascades in either benthic or pelagic zones.

This is not to say that *Dreissena* does not have direct trophic interactions. Grazing on phytoplankton is an obvious trophic connection; however, it is the physical manipulation of the environment by *Dreissena* that is likely to drive the strongest change.

MACROPHYTES VERSUS BENTHIC ALGAE

Macrophytes often play a structural role in lakes and therefore also act as ecosystem engineers. Hence, *Dreissena*-mediated increases in macrophytes can be seen as a “cascading” effect of ecosystem engineering. Filtration of phytoplankton by *Dreissena* and consequent engineering of light levels have indirect ecosystem effects on many types of organisms (algae, invertebrates, and fish) that utilize macrophyte beds as habitat. A further consequence of enhanced macrophyte growth may be an alteration of the quality and distribution of detritus within a lake as macrophytes can provide a major contribution of detrital material to inshore areas (Covich et al. 1999, Schindler and Scheuerell 2002). Ironically, some bottom-dwelling consumers may decline from the benthification process. Organisms that rely on seston settling from the water column, such as the amphipod *Diporeia*, may be negatively affected if benthic input of seston in deep areas is reduced by *Dreissena* (Landrum et al. 2000, Lozano et al. 2001). Other benthic filter feeders may also be negatively affected (Strayer et al. 1998).

Emphasis on shifts between turbid and clear states in lakes has often focused on a dichotomy between phytoplankton and macrophytes, with little emphasis given to the potential importance of increased bottom-associated algae (periphyton and epiphyton). However, many invertebrates readily consume benthic algae, whereas only a small number of specialized taxa directly consume macrophytes (Newman 1991). Therefore, an increase in benthic algae is likely to have direct implications for the spatial dynamics of aquatic food webs.

CONCLUSIONS

We propose that the term benthification is the best descriptor of a process of ecosystem change involving increased water clarity and light penetration, associated primarily with *Dreissena*. This process contemporaneously acts to modify physical habitat and to redirect energy from the pelagic to the benthic habitat. As used here, the term benthification was mostly associated with lakes, but similar processes should occur in any type of ecosystem (marine, freshwater, or terrestrial) where there is a dramatic restructuring of light and energy flow due to physical habitat alteration. We suggest that recognition of the process of benthification will expand our current understanding of energy and trophic pathways leading from lower trophic levels to

fish. Insights from research on the process of benthification, along with associated physical and biological changes, may be analogous to how research on the widespread nature and magnitude of the problem of eutrophication led to many novel insights into ecosystem function.

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