

Potential Oxygen Demand of Sediments from Lake Erie

Don W. Schloesser^{1,*}, Richard G. Stickel¹, and Thomas B. Bridgeman²

¹U.S. Geological Survey
Great Lakes Science Center
1451 Green Road
Ann Arbor, Michigan 48105

²Lake Erie Center
University of Toledo
6200 Bay Shore Road
Toledo, Ohio 436184

ABSTRACT. *Dreissenid mussels (Dreissena polymorpha and D. bugensis) biodeposit large quantities of filtered materials (i.e., feces and pseudofeces) directly on bottom substrates. These biodeposits have the potential to increase oxygen demand in sediments and overlying waters and thus contribute to hypolimnetic anoxia in Lake Erie. We hypothesized that higher potential oxygen demand of sediments would occur in areas near shore than in offshore hypolimnetic waters as a result of biodeposits carried by currents from littoral water where mussels, available foods, and biodeposits may be most abundant. To address this hypothesis, we measured potential oxygen demand (mg O₂/L/120 h incubation) at six sites near shore and six sites offshore monthly June to September 2002 and August 2003. In addition, we compared, in post priori hypothesis, seven sites with and five sites without dreissenid mussels. Contrary to our hypotheses, potential oxygen demand was not significantly higher in bottles containing nearshore sediments than offshore sediments. Similarly, potential oxygen demand was not significantly higher at sites with dreissenid mussels than at sites without mussels. Data are consistent with pre-dreissenid studies which show oxygen demand and percent ash-free dry weights of sediments were higher offshore than near shore and ash-free dry weight of sediments decreased June to September. Therefore, the present study provides no evidence that dreissenid mussels have contributed directly—via biodeposition—to increased anoxia observed in Lake Erie in the mid to late 1990s.*

INDEX WORDS: Oxygen, sediments, dreissenid mussels, near shore, offshore, Lake Erie, biodeposits.

INTRODUCTION

In the mid 1990s, phosphorus concentrations and hypolimnetic anoxia increased in the central basin of Lake Erie but algal production remained at historically low levels (Dolan 1993, Nichols *et al.* 2001, Rockwell *et al.* 2002, Rockwell and Warren 2003). These observations created a “trophic paradox” for eutrophication models developed in the late 1960s and early 1970s for many waters in the Great Lakes and possibly throughout North America (National Academy of Sciences 1969, Vollenweider 1974, Vollenweider *et al.* 1974, McGuckin 2000). Eutrophication models predicted that reductions in phosphorus loadings would create a cas-

cade effect that would reduce phosphorus concentrations in water, reduce algal production, reduce decomposition of settled algae in profundal-offshore areas, and reduce anoxia in hypolimnetic waters. In Lake Erie, model expectations of decreased hypolimnetic anoxia were obtained between the late 1970s, when pollution-abatement programs were initiated, and the early 1990s, a decade after target-phosphorus loadings were reached (Makarewicz and Bertram 1991, Sweeney 1993). However, low phosphorus loadings since the early 1980s coincided with, paradoxically, increased phosphorus concentrations, decreased algal production, and increased anoxia in central Lake Erie in the mid and late 1990s.

The following hypotheses were proposed to explain the paradox observed in Lake Erie (DePinto

*Corresponding author. E-mail: dschloesser@usgs.gov

2002; personal communications, workshop participants, Lake Erie Trophic Transfer Study, University of Windsor, Ontario): (1) increased phosphorus loadings that were undocumented; (2) reduced hypolimnion volume attributed to low water levels and/or increased heat penetration caused by increased water clarity (this would increase anoxia due to the reduced volume of oxygen in the hypolimnion); (3) reduced oxygen diffusion between epilimnetic and hypolimnetic waters due to meteorologic conditions (this would increase anoxia due to less movement of oxygen from the epilimnion into the hypolimnion); (4) increased oxygen demand due to dreissenid mussels (zebra [*Dreissena polymorpha*] and quagga [*D. bugensis*] mussels) (through respiration when live and through decomposition when dead); and (5) increased oxygen consumption by sediments as dreissenid mussels contribute organic materials to the microbial pool (mussels concentrate and increase the speed at which organic materials are removed from the water and deposit these materials on substrates in the form of feces and pseudofeces).

Hypotheses that include dreissenid mussels to account for the Lake Erie "trophic paradox" are plausible because the magnitude of ecological changes that mussels caused in littoral waters of Europe, North America, the Great Lakes, and especially Lake Erie has been great (Nalepa and Schloesser 1993, Dermott and Kerec 1997, Karatayev *et al.* 1997, Berkman *et al.* 1998, Johannsson *et al.* 2000). For example, dreissenid mussels are believed to be one of the two most influential factors that impacted the trophic status of Lake Erie during the past 200 years (Nalepa and Schloesser 1993, Stoermer *et al.* 1996). One mechanism by which dreissenid mussels impact trophic status is through filtration of particulate material from water and subsequent deposition of resulting materials as feces and pseudofeces in the form of lightly compacted biodeposits on substrates where they enter the benthic-detrital pool (MacIsaac *et al.* 1992, Nichols and Hopkins 1993, Botts *et al.* 1996, Stewart *et al.* 1998, Makarewicz *et al.* 1999, Nichols 2001, Pires and Van Donk 2002).

Biodeposits from dreissenid mussels could impact profundal oxygen concentration by increasing organic materials in sediments and subsequent decomposition. These processes may have contributed to the increased hypolimnetic-oxygen depletion observed in Lake Erie. Biodeposits could originate from mussel populations found on substrates in hypolimnetic areas but densities of mussels on profun-

dal sediments are relatively low (ca. 6,000/m²) and it is likely that the majority of mussel-derived biodeposits in Lake Erie would originate in littoral waters where densities of mussels are high (e.g., 30,000–700,000/m²) (Griffiths *et al.* 1991, Dermott and Munawar 1993, Nalepa and Schloesser 1993, Stanczykowska and Lewandowski 1993). Thus, transport of dreissenid biodeposits from littoral to nearby areas by currents could have substantial impacts on the organic content of substrates in nearshore hypolimnetic waters. For example, in shallow western Lake Erie, it has been estimated that dreissenid mussels significantly reduced phytoplankton abundance by consuming 5 million metric tonnes of phytoplankton per year and ejecting 1.4 million metric tonnes of this material per year onto surrounding sediments (ca. 28%) as feces and pseudofeces (Madenjian 1995, Makarewicz *et al.* 1999).

In the present study, we address possible impacts of dreissenids on sediments to explain the paradox of increased phosphorus, less abundant algae, and increased anoxia in Lake Erie. We hypothesized that dreissenid mussel populations found in littoral waters would increase organic material found in depositional areas along the perimeter of the lake (i.e., near shore) where stratification occurs relative to offshore sediments and that these deposits would increase oxygen demand of sediments, thereby contributing to the increased area of hypolimnetic anoxia. We developed our study design around the sampling schedule of the Research Vessel *Lake Guardian* in 2002 and 2003 and two basic questions; can potential oxygen demand be used to measure impacts of dreissenids (1) based on proximity to shore, where impacts would most be expected, and (2) based on *post priori* knowledge of the presence and absence of mussel populations? In addition, we evaluated whether potential oxygen demand of sediments can be used to differentiate between sites and measure metabolism of sediments in Lake Erie.

METHODS

We determined potential oxygen demand and ash-free dry weight (AFDW, ca. organic content) of surface sediments at 12 sites located throughout Lake Erie June to September 2002 and August 2003 (Fig. 1). A total of ten replicate samples were obtained at each of three sites (ER 43, ER 78, and ER 15) 17–19 June and 18–20 July 2002, six samples at each of these three sites and nine additional sites (6L, Sandusky, Port Alma, Cleveland, ER 30,

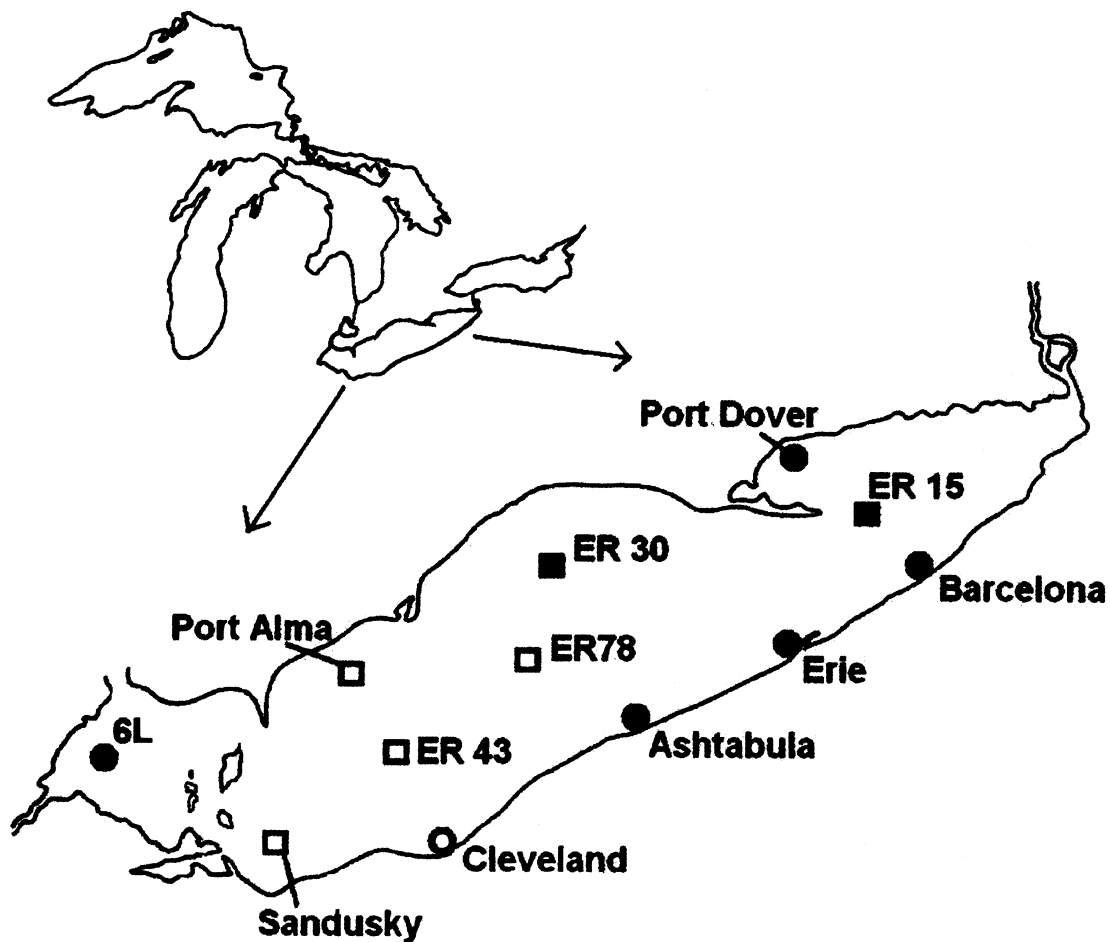


FIG. 1. Site locations where sediments were collected for potential oxygen demand studies of Lake Erie in 2002 and 2003. Circles = nearshore sites, squares = offshore sites, solid = sites with observed dreissenid mussels, and open = sites without observed dreissenid mussels.

Ashtabula, Erie, Port Dover, and Barcelona) 7–21 August 2002 and 14–18 September 2002, and 16 samples at each of four sites (6L, ER 43, ER 78, and ER 15) 14–18 August 2003 (Table 1).

A total of six nearshore and six offshore sites were sampled to address our first geographically derived hypothesis (Fig. 1). In addition, seven sites with and five sites without dreissenid mussels were sampled to address our second hypothesis (Fig. 1, Table 1). Pre-selected nearshore sites were located in 7 m of water where sediments are typically hard and composed of sand, gravel, and rocks (Bedford and Abdelrhman 1987, Marvin *et al.* 2002). These pre-selected nearshore sites correspond to sites simultaneously sampled for other Lake Erie trophic studies (this volume). Unfortunately, most near-

shore, pre-selected sites occurred in extensive beach ridges formed approximately 6,000 years ago and much of this area has remained free of depositional sediments due to strong currents and wave energy (Bolsenga and Herdendorf 1993). As a result, several nearshore site locations were moved to deeper water to obtain depositional sediments because biodeposits of mussels are unlikely to accumulate in high current areas dominated by sand, gravel, and rock substrates (Kemp and Thomas 1976, Thomas *et al.* 1976, Hargrave 1972, Belanger 1979). Two nearshore sites along the north shore were moved south (Ports Alma [moved 15 km] and Dover [10 km]) and three sites along the south shore were moved north (Cleveland [2 km], Ashtabula [4 km], and Barcelona [3 km]) to obtain

TABLE 1. Number of replicate samples obtained for potential oxygen demand and ash-free dry weight determinations of sediments from Lake Erie 2002 and 2003. Category designation; O = offshore, N = near shore, A = dreissenids absent, and P = dreissenids present.

Site	Category designation	2002				2003
		June	July	August	September	August
Sandusky	O, A			6	6	
ER 43	O, A	10	10	6	6	16
Port Alma	O, A			6	6	
ER 78	O, A	10	10	6	6	16
ER 30	O, P			6	6	
ER 15	O, P	10	10	6	6	16
6L	N, P			6	6	16
Cleveland	N, A			6	6	
Ashtabula	N, P			6	6	
Erie	N, P			6	6	
Barcelona	N, P			6	6	
Port Dover	N, P			6	6	

soft-mud substrates. In addition, an offshore site (ER 30) was substituted for one site (Port Stanley located 30 km north of ER 30) because no depositional sediments were found between these two sites. Three (Port Alma, ER 30, and Port Dover) of the six relocated nearshore sites were moved far enough to change their geographic (nearshore versus offshore) designation. Two additional sites (6L in the western basin and Erie in the central basin) were sampled in the present study to increase the number of sites sampled near shore. Four sites (ERs 43, 78, 30, and 15) correspond to long-term, water-quality monitoring sites (USEPA, Great Lakes Program Office, Chicago, Illinois). Site designation based on the absence and presence of dreissenid mussels was based on *post prior* observations of mussel occurrence.

Sediments were obtained with a box-corer (i.e., similar to an Ekman; 35 × 38 cm; n = 2/site). The box-corer obtained an undisturbed sample of substrate and overlying water. Overlying water was partially drained and individual plexiglass tubes (47 mm diameter) were placed in the box-corer and inserted into substrates. Tubes were sealed, removed, and taken to a laboratory, where the remaining water was removed. One small "plug" of surface sediment was removed from each large plexiglass tube by insertion of a smaller tube (9 mm diameter by 1.5 cm deep, 1/tube) into sediments, sealed, removed with intact sediments, and sediments were individually placed in 300 mL bottles containing well water. Each plug contained approximately 0.95

cm³ of sediment. Well water, obtained from a source routinely used for fish culture (Great Lakes Science Center, Ann Arbor, Michigan) provided a uniform medium to reduce variability of oxygen demand caused by water at individual sites throughout the lake. In August 2003, formalin (2% final solution) was added to 8 of 16 replicate bottles at each of four sites to determine chemical oxygen demand in the absence of biological metabolism (Dale 1978, Hargrave 1972). Dissolved oxygen (mg/L) within each bottle was periodically determined (ca. 24 h periods) until approximately 160 h at ambient incubation temperatures of 20–22°C. Oxygen was measured with an electric oxygen meter (YSI 5000) equipped with an electric paddle-stirrer (YSI 5010). The meter was routinely calibrated (ca. every 15–20 measurements) by air-saturation and comparison to measurements with another oxygen meter (YSI 95). Plugs of sediment were obtained for dry (105°C > 24 hours), ash (525°C > 24 h), and ash-free dry (dry minus ash-free) weights to determine organic and inorganic fractions of sediments.

Oxygen demand of sediments was determined for 120 h incubation by weighted regression models fit to oxygen depletion curves for individual bottles. Cumulative potential oxygen demand of sediment was then defined as the amount of oxygen lost from 0 to 120 h in mg O₂/L. This approach was used in order to compare oxygen demand among samples measured at different time intervals. Sites were categorized according to location (offshore and near shore) and dreissenid mussels (absent and present).

TABLE 2. Mean potential oxygen demand (mg O₂/L after 120 h incubation) and percent ash-free dry weight of sediments from Lake Erie August and September 2002. O = offshore, N = near shore, A = dreissenids absent, and P = dreissenids present.

Site	Potential oxygen demand (mg O ₂ /L)			Percent ash-free dry weight		
	August	September	Mean	August	September	Mean
Sandusky (O, A)	5.59	5.61	5.60	9.40	7.40	8.40
ER 43 (O, A)	6.22	6.69	6.46	9.60	7.70	8.65
Port Alma (O, A)	5.75	5.84	5.80	9.60	8.60	9.10
ER 78 (O, A)	3.88	4.40	4.14	7.90	6.00	6.95
ER 30 (O, P)	5.81	5.15	5.48	5.70	4.40	5.05
ER 15 (O, P)	6.40	6.93	6.67	8.50	5.40	6.95
6L (N, P)	4.47	5.08	4.78	8.10	6.30	7.20
Cleveland (N, A)	5.65	6.49	6.07	7.60	5.50	6.55
Ashtabula (N, P)	7.42	6.52	6.97	7.70	6.20	6.95
Erie (N, P)	4.74	5.53	5.14	5.00	3.00	4.00
Barcelona (N, P)	5.65	5.95	5.80	4.80	3.80	4.30
Port Dover (N, P)	4.59	4.30	4.45	5.30	2.90	4.10
Mean						
Total	5.51	5.71	5.61	7.43	5.60	6.52
Location						
Offshore	5.61	5.77	5.69	8.46	6.58	7.52
Near shore	5.42	5.65	5.53	6.41	4.61	5.52
Dreissenids						
Absent	5.42	5.81	5.97	8.82	7.04	7.93
Present	5.58	5.64	4.83	6.44	4.57	5.51

The greatest number of locations was sampled in August and September 2002, therefore these two months were chosen to test differences (ANOVA) in potential oxygen demand and percent ash-free dry weight of sediments in comparable categories. Biological oxygen demand was determined by subtraction of total oxygen demand and chemical demand (as determined in the absence of biological activity; see above). Areal oxygen demand was determined from extrapolation of the surface area of the 9 mm diameter sediment plug (63.6 mm²) placed in each bottle.

Potential oxygen demand as measured in the present study is a surrogate for sediment oxygen demand which occurs *in situ* in undisturbed lake sediments. Potential oxygen demand occurs under uniform conditions of sediment resuspension, temperature, and available nutrients present in sediments at time of sampling. Chemical oxygen demand occurs in the absence of biological activity as induced by metabolic sterilization.

RESULTS

No significant differences in mean potential oxygen demand of sediments were found between sites located offshore and near shore ($p = 0.356$) and between sites where dreissenid mussels were absent and present ($p = 0.631$) (Table 2). However, mean oxygen demand in both August and September was slightly higher offshore (5.61 and 5.77 mg/L, respectively) than near shore (5.42 and 5.65 mg/L). In addition, percent ash-free dry weights were significantly higher (ANOVA, $p < 0.05$) at offshore than nearshore sites and at sites where dreissenid mussels were absent than present.

Potential oxygen demand and ash-free dry weight of sediments exhibited consistent differences between sites June to September 2002 (Fig. 2). Relative ranks of these variables (i.e., first, second, and third in order of decreasing value) were: ER 15, ER 43, and ER 78 for potential oxygen demand and ER 43, ER 15, and ER 78 for ash-free dry weight, except in September when ash-free dry weight was higher at ER 78 than ER 15. No consistent seasonal

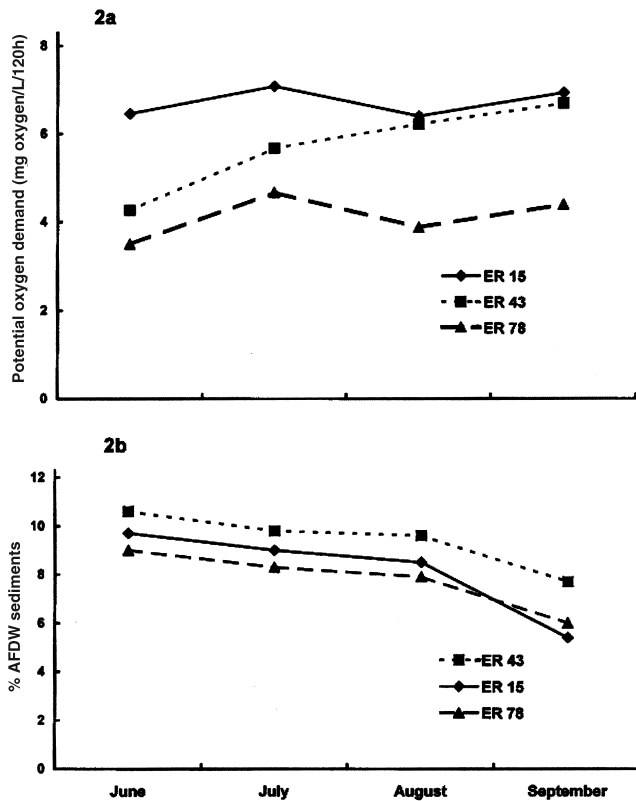


FIG. 2. Mean potential oxygen demand (2a) and percent ash-free dry weight (AFDW) (2b) of sediments from Lake Erie, June to September 2002.

trend was observed in oxygen demand at sites ER 15 and 78, whereas significant increases (ANOVA, $p < 0.05$) occurred at ER 43 between June and September. Ash-free dry weight exhibited significant seasonal downward trends at each site June to September ($p < 0.05$).

In general, biological and chemical oxygen demand did not occur at the same rate and were not the same at each site within each of the three basins of Lake Erie (Fig. 3). Biological demand occurred at a slower rate than chemical demand. After 40 h incubation, mean percent oxygen demand of biological and chemical components was 34 and 66%, respectively; after 80 h mean proportions were 58 and 42%, respectively; and, at 155 h incubation mean percent demand was 55 and 45%, respectively. Biological demand in the central basin accounted for a higher proportion (ERs 43 and 78 = 67 and 62%, respectively) of potential oxygen demand than in the western (6L = 47% biological) and eastern (ER 15 = 45% biological) basins.

Potential oxygen demand of surficial sediments in Lake Erie is about one order of magnitude greater than total sediment oxygen demand measured using chambers placed directly over sediments in the lake (Table 3). In general, potential demand remained relatively stable at two of three sites (ER 15 and ER 78) and increased at one site (ER 43) June to September, and increased at 9 of 12 sites between August and September, whereas total sediment oxygen demand measured *in situ* was greatest in June and decreased August–September (Tables 2, 3, and Fig. 2).

DISCUSSION

Results of the present study do not support the hypothesis that potential oxygen demand and ash-free dry weight of sediments was higher near shore, in closer proximity to high densities of dreissenids, than offshore, where dreissenid densities are relatively low. In addition, *post prior* comparisons of an additional hypothesis indicate no differences occurred where dreissenids were present and where they were absent. The rationale underlying these hypotheses is that filtering of suspended materials by dreissenid mussels would increase biodeposits to sediments and these biodeposits would increase oxygen demand and ash-free dry weight of sediments relative to contrasting categories.

Causes for unsupported hypotheses in the present study are not known, but several probable explanations exist. First, biodeposits from dreissenid mussels may not accumulate in nearshore waters where mussels are most abundant. Biodeposits from mussels may be light enough to be carried by currents directly into offshore-profundal areas. In addition, sediment resuspension that occurs throughout Lake Erie may incrementally carry dreissenid biodeposits to offshore areas thereby preventing them from accumulating near shore (Charlton and Lean 1987). However, it has been shown that biodeposits, especially pseudofeces, are concentrated in mucus pellets and may accumulate within a few meters of dreissenid colonies relative to areas without dreissenid mussels (Hamburger *et al.* 1990, Ten Winkel and Davids 1982, Stanczykowska and Lewandowski 1993, Botts *et al.* 1996).

Second, there may not be a net increase in the amount of organic material reaching sediments as a result of biodeposition by mussels. For example, in a small reach of the Seneca River, total oxygen demand of benthos and sediments was about the same before and after dreissenid colonization (Canale and

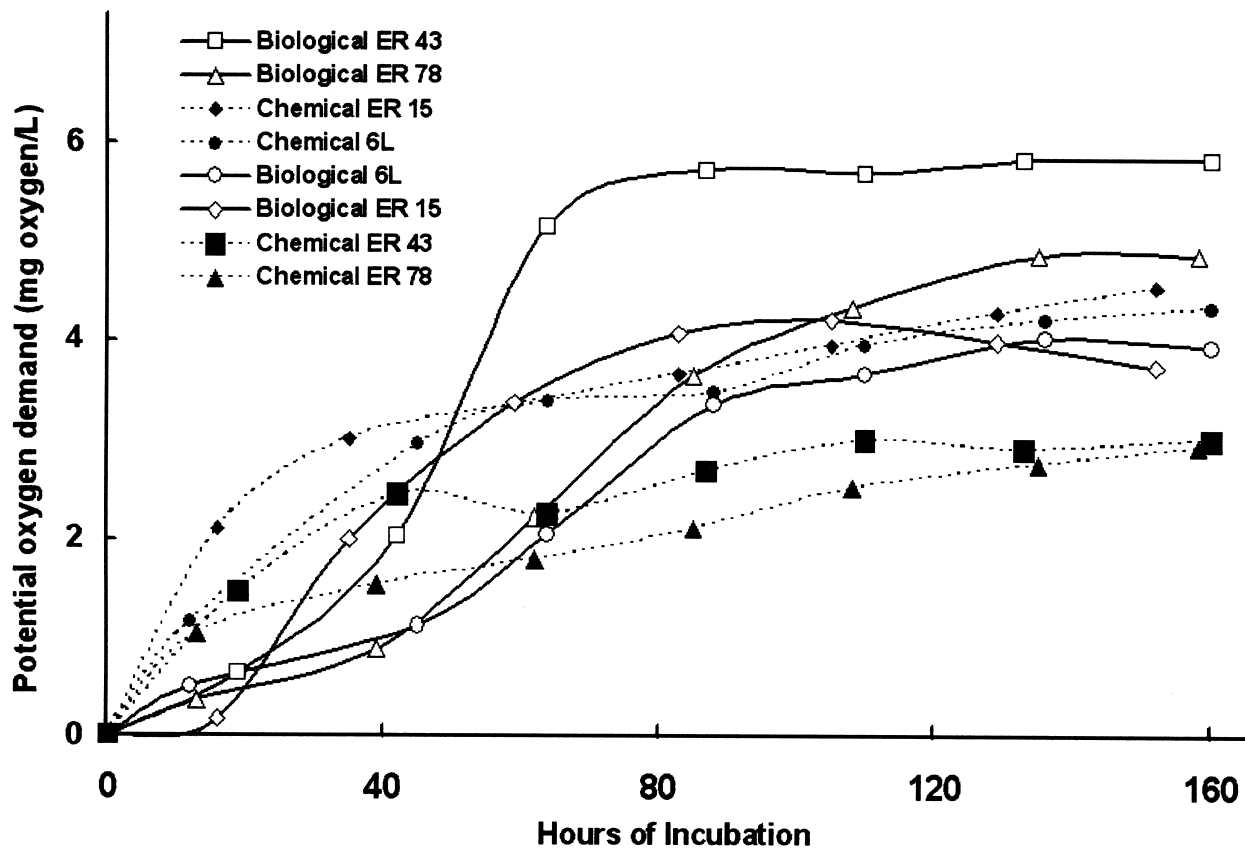


FIG. 3. Biological and chemical potential oxygen demand of sediments from the western (site 6L), central (ERs 43 and 78), and eastern (ER 15) basins of Lake Erie, August 2003.

Chapra 2002). However, oxygen demand of macrobenthos (primarily dreissenid mussels) in the river was seven times higher after mussel colonization than before colonization suggesting that mussels were more efficient at utilizing carbon through respiration than sediments were through decomposition (Canale and Chapra 2002). In addition, Rakesh *et al.* (2001) determined that oxygen demand caused by dreissenid respiration in the river could be one order of magnitude higher than sediment oxygen demand. Therefore, respiration by dreissenid mussels could actually reduce oxygen demand of sediments by utilizing organic materials above sediments that would otherwise accumulate in sediments.

Third, sites were categorized by presence and absence of mussels only. Relative densities of dreissenids in these hypotheses-derived categories were not considered. If biodeposits accumulate in sediments in proportion to mussel densities, then areas with high densities of mussels would be expected to

have higher oxygen demand and ash-free dry weight of sediments. In addition, if mussels were not detected due to low sampling effort ($n = 2$ box cores/site/visit) then comparisons based on dreissenid categories would be negated. For example, mussels were not observed at ERs 43 and 78 but potential oxygen demand and ash-free dry weight were 25–50% higher at ER 43 than ER 78. If mussels occurred at ER 43 then our measures of oxygen demand would be in line with the hypothesis of presence and absence of dreissenids. At present, there are no data on the lake-wide distribution and densities of mussels to correlate with hypotheses-derived categories. However, observed presence and absence of dreissenid mussels in box-core samples correspond closely with the presence and absence of mussels throughout the lake in 1992 (Dermott and Munawar 1993). Mussels were absent in the western third of the central basin in 1992 and this is the same area where mussels were absent in 2002–2003 (Fig. 1). This area corresponds to the

TABLE 3. Mean-areal oxygen demand of sediments from Lake Erie. *T* = triangle and *D* = dome shaped chambers.

Source	Oxygen demand (g O ₂ /m ² /d)					
	June	July	August	September	Mean	
Potential oxygen demand						
Present study 2002						
Sandusky			5.28	5.29	5.29	
ER 43	4.27	5.67	5.86	6.31	5.53	
Port Alma			5.43	5.51	5.47	
ER 78	3.50	4.67	3.66	4.15	4.00	
ER 30			5.48	4.86	5.17	
ER 15	6.46	7.08	6.03	6.54	6.53	
6L			4.22	4.80	4.51	
Cleveland			5.33	6.12	5.73	
Ashtabula			7.00	6.16	6.58	
Erie			4.47	5.22	4.85	
Barcelona			5.33	5.61	5.47	
Port Dover			4.32	4.06	4.19	
Mean	4.74	5.81	5.20	5.39	5.28	
Total oxygen demand						
Snodgrass and Fay 1987	(T)	1.25–1.49	0.76–1.19	0.66–0.68	0.60–0.71	0.86
	(D)	0.44–0.49	0.21–0.33	0.03–0.45	0.00–0.20	0.32
Davis <i>et al.</i> 1987	(T)	1.45	0.93	0.48	0.87	0.93
Snodgrass 1987	(D)	0.50	0.26	0.62		0.2–0.3

area where anoxia has been most prevalent in Lake Erie for decades.

Fourth, impacts of dreissenids on potential oxygen demand and ash-free dry weight of sediments may not be detectable compared to other processes that determine oxygen demand and anoxia in Lake Erie. For example, the most likely factor that would mask measurement of dreissenid impacts on sediments is the pelagic-derived organic material produced in the trophogenic zone which settles and, when combined with a relatively small hypolimnion, results in hypolimnetic anoxia in the western-third of the central basin of Lake Erie (Burns and Ross 1972; Burns 1976a, b; Charlton and Lean 1987). In the late 1970s, before the invasion of dreissenid mussels, as much as 80% of the hypolimnetic oxygen demand in the central basin was attributed to phytoplankton produced in the epilimnion (Davis *et al.* 1981). This resulted in higher sediment oxygen demand (including macrobenthos) and ash-free dry weight of sediments offshore than near shore (Davis *et al.* 1981, Charlton and Lean 1987). This corresponds to the geo-

graphic pattern of potential oxygen demand and ash-free dry weight found in the present study. In addition, the temporal pattern of decreasing ash-free dry weights between spring and fall observed in the present study is similar to those before dreissenids colonized Lake Erie (Davis *et al.* 1981). However, in 1978 the greatest total sediment oxygen demand occurred in the western basin near site 6L, whereas the present study found relatively low potential oxygen demand in western basin sediments. Davis *et al.* (1981), using *in situ* chambers, attributed high oxygen demand in the western basin to the abundance of macrobenthos. Macrobenthos, including dreissenid mussels, were not included in the present study but it has been shown that oxygen use by dreissenid respiration can exceed sediment oxygen demand by an order of magnitude and be substantial enough to impact oxygen balances in freshwater systems (Effler and Siegried 1994, Rakesh *et al.* 2001, Canale and Chapra 2002). In the late 1990s, it is unlikely that respiration by dreissenids contributed substantially to anoxia in the western third of the central basin of Lake Erie

because this area has been periodically anoxic for many decades (perhaps centuries) and seasonal colonization by mussels has not been observed (Burns 1976b, Delorme 1982, Charlton 1987, Mortimer 1987). Therefore, the absence of mussels in this area is more likely a result of anoxia caused by other ecological processes in the lake.

The last possibility for unconfirmed hypotheses is that the increase in sediment oxygen demand caused by dreissenid mussels is not detectable using methods in the present study. A small increase in dreissenid oxygen demand offshore may not easily be detected with the present study design, especially if both offshore and nearshore areas exhibited increases due to dreissenid biodeposits. Methodology to detect differences would even have to be sensitive enough to separate atmospheric factors which, based on eutrophication models of the late 1960s and early 1970s, could account for hypolimnetic oxygen changes observed in the 1990s (Charlton In press). Testing for relatively small and uniform increases caused by dreissenids may require use of identical methodology and determination of a total oxygen budget of the hypolimnion before and after mussel colonization.

Use of potential oxygen demand as measured in the present study is an efficient way to compare scale and relative importance of metabolic activities of sediments from different sites and basins in Lake Erie. Consistent differences between individual sites and differing proportions of biological and chemical oxygen demand between basins (Fig. 3) indicate the usefulness of measuring sediment metabolism. However, the present study indicates that one or more unknown limiting factors occasionally occurred during incubation of bottles. The potential list of limiting factors could be substantial. For example, Davis *et al.* (1981) measured 23 variables (e.g., depth, temperature, oxygen, benthos, percent sediment size, phosphorus, bacteria, and light) within large plexiglass chambers incubated *in situ* to measure sediment oxygen demand and determined that 14 variables significantly affected oxygen demand. In the present study, two likely limiting factors include percent organic content of sediments and oxygen concentration. Organic content of sediments is often positively correlated with oxygen demand, especially in sediments with low organic contents (< 10%) (Davis *et al.* 1981). The present study included sediments with low organic contents; however no relationship was found between oxygen demand and organic content of sediments in the lake or sediments left in bottles after

incubation. Therefore, oxygen limitation is the most likely limiting factor in the present study because concentrations in bottles were often reduced to < 2.5 mg/L (43% of bottles) and occasionally reduced to < 0.5 mg/L (3%) after 120 h of incubation. In general, metabolism of aerobic bacteria decreases substantially below about 2 mg/L and ceases below about 0.5 mg/L as aerobic bacteria die and anaerobic bacteria thrive (Zobell 1943, Berg *et al.* 1962, Berg and Jonasson 1965). About 17% of oxygen concentrations below 2.5 mg/L occurred in bottles from ER 15 and Ashtabula, whereas the remaining 26% occurred in bottles containing sediments from the other 10 sites.

Explanations for higher biological and chemical demand in the central basin and relatively fast rates of chemical oxygen demand are not known. In addition, it is not known whether it is higher biological activity that contributed to central basin anoxia observed in the 1990s. However, the rate of oxygen demand by biological and chemical components is unusual in that chemical demand exceeded biological demand in the first 40 h of incubation. In general, biological demand occurs first when oxygen concentrations are relatively high (> 2 mg/L) and chemical demand usually proceeds with an inverse relation to oxygen concentrations (Walker and Snodgrass 1986, Davis *et al.* 1981).

At present, there are two basic methods to measure oxygen metabolism of sediments—*in vitro* and *in situ*. Three *in vitro* studies were performed during the Lake Erie trophic studies program; potential oxygen demand in the present study, measurement of oxygen changes in overlying water of sediment cores, and measurement of oxygen profiles in sediment cores (Matisoff and Neeson 2003, Matisoff *et al.* 2005). All three methods allow measurement of oxygen metabolism of sediments during cruise-interval sampling. *In situ* methods, which were not used in the subject studies, include sediment-contact chambers and sediment-containing bottles (e.g., Davis *et al.* 1987, Snodgrass and Fay 1987). Placement of chambers over undisturbed substrates may include water circulation and/or water replacement devices and bottle techniques may include *in situ* incubation and *in vitro* laboratory temperature and current simulation to mimic ambient conditions. Placement of *in situ* chambers has shown that oxygen metabolism of sediments before dreissenid colonization accounted for 59% (range 30–81%, n = 4) of the total-hypolimnetic oxygen demand in Lake Erie (Davis *et al.* 1981, 1987).

Potential oxygen demand undoubtedly overesti-

mates actual demand of the microbial and chemical components of sediments in the hypolimnion compared to *in situ* chamber techniques because sediments are resuspended in bottles when oxygen is periodically determined. Therefore, the value of the potential oxygen demand technique is the ease in which the same method can be used to make geographic and temporal comparisons. In addition, resuspension of sediments in hypolimnetic waters of Lake Erie occurs at a much greater rate than previously thought (Charlton and Lean 1987), so use of suspended sediments in incubation studies may lead to a greater understanding of oxygen deficits in Lake Erie, especially if impacts of sediment resuspension can be related to current driving variables. One of our conclusions is similar to that of Davis *et al.* (1981, 1987) who suggested that some measure of sediment-oxygen metabolism be incorporated into trophic-status monitoring in the Great Lakes. Adequate measurement of sediment oxygen demand seems even more important since benthic dreissenids have invaded, colonized, and potentially impacted oxygen concentrations in hypolimnetic waters that are used to measure progress of water-pollution abatement programs in Lake Erie and the other Great Lakes.

SUMMARY

The present study of the potential oxygen demand of sediments based on proximity to shore and the presence/absence of dreissenid mussels suggests that dreissenid mussels did not have a direct impact on increased hypolimnetic anoxia in Lake Erie in 2002–2003. If our study had indicated substantial impacts in agreement with our hypotheses, it would have contributed to our understanding of increased anoxia in the central basin of Lake Erie in recent years. It is possible dreissenid mussels contribute too little oxygen demand to sediments to measure using our hypotheses and study methods. Even a small increase in oxygen demand caused by mussels may be important to hypolimnetic anoxia in Lake Erie. As is, the present study does not help explain the “trophic paradox” of decreased phosphorus loadings, increased phosphorus concentrations, decreased algal concentrations, and increased anoxia that occurred in Lake Erie in the 1990s.

However, trends in our data support historical studies that show anoxia in the central basin is caused by pelagic-rain of plankton and its subsequent decomposition. These trends include higher oxygen demand offshore than near shore, decreas-

ing ash-free dry weight of sediments June to September, higher ash-free dry weights of sediments offshore than near shore, and the absence of dreissenid mussels in the central basin where anoxia has occurred for several decades. In addition, there was a higher proportion of biological oxygen demand in the central basin than in the western and eastern basins. These observations are consistent with trophic models developed in the late 1960s and early 1970s of pelagic-derived phytoplankton that settles into the hypolimnion and causes anoxia in the western-third of the central basin of Lake Erie.

ACKNOWLEDGMENTS

We thank personnel of the Lake Guardian of the U.S. EPA, Great Lakes National Program Office, Chicago, Illinois for assistance in sample collections. This research was partially funded by the U.S. Environmental Protection Agency (Grant EPA GL-97590101), Great Lakes Program Office to G. Matisoff of Case Western Reserve University, Cleveland, Ohio. Contribution Number 1297 of the Great Lakes Science Center.

REFERENCES

- Bedford, K.W., and Abdelrhman, M. 1987. Analytical and experimental studies of the benthic boundary layer and their applicability to near-bottom transport in Lake Erie. *J. Great Lakes Res.* 13:628–648.
- Belanger, T.V. 1979. *Comparison of benthic oxygen demand techniques*. Department Environmental Science and Engineering, Florida Institute Technology, Melbourne, FL. (in Davis *et al.* 1981).
- Berg, K., and Jonasson, P.M. 1965. Oxygen consumption of profundal lake animals at low oxygen content of the water. *Hydrobiologia* 26:131–143.
- , Jonasson, P.M., and Ockelman, K.W. 1962. The respiration of some animals from the profundal zone of a lake. *Hydrobiologia* 19:1–39.
- Berkman, P.A., Haltuch, M., Garton, D., Kennedy, G., Gannon, J., Mackey, S., Fuller, J., and Liebenthal, D. 1998. Zebra mussels invade Lake Erie muds. *Nature* 393:27–28.
- Bolsenga, S.J., and Herdendorf, C.E. (eds.). 1993. *Lake Erie and Lake St. Clair Handbook*. Detroit, MI: Wayne State University Press.
- Botts, P.S., Patterson, B.A., and Schloesser, D.W. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic. *J. N. Am. Benthol. Soc.* 15:179–184.
- Burns, N.M. 1976a. Temperature, oxygen, and nutrient distribution patterns in Lake Erie, 1970. *J. Fish. Res. Board Can.* 33:485–511.
- . 1976b. Oxygen depletion in the central and east-

- ern basins of Lake Erie, 1970. *J. Fish. Res. Board Can.* 33:512–519.
- , and Ross, C. 1972. Oxygen-nutrient relationships within the central basin of Lake Erie. In *Project Hypo, Paper 6*, N.M. Burns and C. Ross, eds., pp. 85–119. Burlington, Ontario: Canada Centre for Inland Waters.
- Canale, R.P., and Chapra, S.C. 2002. Modeling zebra mussel impacts on water quality of Seneca River, New York. *J. Envir. Engrg.* 128:1158–1168.
- Charlton, M.N. 1987. Lake Erie oxygen revisited. *J. Great Lakes Res.* 13:697–708.
- . In press. *Review of thirty years of change in Lake Erie water quality*. NWRI Contribution No. 04-167. National Water Research Institute, Environment Canada, Burlington, Ontario.
- , and Lean, D.R.S. 1987. Sedimentation, resuspension, and oxygen depletion in Lake Erie (1979). *J. Great Lakes Res.* 13:709–723.
- Dale, T. 1978. Total, chemical, and biological oxygen consumption of the sediments in Lindapollene, western Norway. *Mar. Biol.* 49:333–341.
- Davis, W.S., Fay, L.A., and Herdendorf, C.E. 1981. *Lake Erie intensive study: sediment oxygen demand*. CLEAR Technical Report No. 246. The Ohio State University, Center for Lake Erie Area Research, Columbus, OH.
- , Fay, L.A., and Herdendorf, C.E. 1987. Overview of USEPA/CLEAR Lake Erie sediment oxygen demand investigations during 1978. *J. Great Lakes Res.* 13:731–737.
- Delorme, L.D. 1982. Lake Erie oxygen: the prehistoric record. *Can. J. Fish. Aquat. Sci.* 39:1021–1029.
- DePinto, J.V. 2002. *Anoxia in the central basin of Lake Erie*. Senatorial Testimony, Committee on Environment and Public Works, Cleveland, OH, August 5.
- Dermott, R., and Kerec, D. 1997. Changes to the deep-water benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. *Can. J. Fish. Aquat. Sci.* 54:922–930.
- , and Munawar, M. 1993. Invasion of Lake Erie offshore sediments by *Dreissena*, and its ecological implications. *Can. J. Fish. Aquat. Sci.* 50:2298–2304.
- Dolan, D.M. 1993. Point source loadings of phosphorus to Lake Erie: 1986–1990. *J. Great Lakes Res.* 19:212–223.
- Effler, S.W., and Siegfried, C. 1994. Zebra mussel (*Dreissena polymorpha*) populations in the Seneca River, New York: impact on oxygen resources. *Environ. Sci. Technol.* 28:2216–2221.
- Griffiths, R.W., Schloesser, D.W., Leach, J.H., and Kovalak, W.P. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Can. J. Fish. Aquat. Sci.* 48:1381–1388.
- Hamburger, K., Dall, P.C., and Jonasson, P.M. 1990. The role of *Dreissena polymorpha* (Pallas) (Mollusca) in the energy budget of Lake Esrom, Denmark. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 24:621–625.
- Hargrave, B.T. 1972. Aerobic decomposition of sediment and detritus as a function of particle surface area and organic content. *Limnol. Oceanogr.* 17(4): 583–596.
- Johannsson, O.E., Dermott, R., Graham, D., Dahl, J., Millard, E., Myles, D., and LeBlanc, J. 2000. Benthic and pelagic secondary production in Lake Erie after the invasion of *Dreissena* spp. with implications for fish production. *J. Great Lakes Res.* 26:31–54.
- Karatayev, A., Burlakova, L.E., and Padilla, D.K. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. *J. Shellfish Res.* 16(1):187–203.
- Kemp, A.L.W., and Thomas, R.L. 1976. Impact of man's activities on the chemical composition in the sediments of Lakes Ontario, Erie, and Huron. *Water, Air, Soil Pollut.* 5:469–490.
- MacIsaac, H., Sprules, W.G., Johannsson, O.E., and Leach, J. 1992. Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. *Oecologia* 92:30–39.
- Madenjian, C.P. 1995. Removal of algae by the zebra mussel (*Dreissena polymorpha*) population in western Lake Erie: a bioenergetics approach. *Can. J. Fish. Aquat. Sci.* 52:381–390.
- Makarewicz, J.C., and Bertram, P. 1991. Evidence for the restoration of the Lake Erie ecosystem. *Bioscience* 41(4):216–223.
- , Lewis, T.W., and Bertram, P. 1999. Phytoplankton composition and biomass in the offshore waters of Lake Erie: pre- and post-*Dreissena* introduction (1983–1993). *J. Great Lakes Res.* 25:135–148.
- Marvin, C.H., et al. (nine co-authors). 2002. Surficial sediment contamination in Lakes Erie and Ontario: a comparative analysis. *J. Great Lakes Res.* 28: 437–450.
- Matisoff, G., and Neeson, T. 2003. Quantifying sediment-oxygen demand in Lake Erie. In *46th Conf. Great Lakes Res. abstracts*. International Association for Great Lakes Research.
- McGucken, W. 2000. *Lake Erie Rehabilitated: Controlling Cultural Eutrophication, 1960s–1990s*. Akron, OH: The University of Akron.
- Mortimer, C.H. 1987. Fifty years of physical investigations and related limnological studies on Lake Erie, 1928–1977. *J. Great Lakes Res.* 13:407–435.
- Nalepa, T.F., and Schloesser, D.W. (eds.) 1993. *Zebra Mussels: Biology, Impacts, and Control*. Boca Raton, FL: Lewis Publishers, Inc.
- National Academy of Sciences. 1969. *Eutrophication: Causes, Consequences, Correctives*. Washington, D.C.
- Nichols, K.H. 2001. CUSUM phytoplankton and chloro-

- phyll functions illustrate the apparent onset of dreissenid mussel impacts in Lake Ontario. *J. Great Lakes Res.* 27:393–401.
- , and Hopkins, G.J. 1993. Recent changes in Lake Erie (north shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. *J. Great Lakes Res.* 19:637–647.
- , Hopkins, G.J., Standke, S.J., and Nakamoto, L. 2001. Trends in total phosphorus in Canadian near-shore waters of the Laurentian Great Lakes: 1976–1999. *J. Great Lakes Res.* 27:402–422.
- Pires, L.M.D., and VanDonk, E. 2002. Comparing grazing by *Dreissena polymorpha* on phytoplankton in the presence of toxic and non-toxic cyanobacteria. *Freshwater Biol.* 47:1855–1865.
- Rakesh, K.G., Effler, S.W., and Owens, E.M. 2001. River dissolved oxygen model with zebra mussel oxygen demand (ZOD). *J. Envir. Eng.* 127(9):790–801.
- Rockwell, D.C., and Warren, G.J. 2003. Lake Erie report for the Great Lakes National Program Office's indicators monitoring program 1983–2002. In *46th Conf. Great Lakes Res. abstracts*, International Association for Great Lakes Research.
- , Warren, G.J., Barbiero, R.P., and Salisbury, D.K. 2002. *Limnology report for the Great Lakes National Program Office's indicators monitoring program*. In *45th Conf. Great Lakes Res. abstracts*, International Association for Great Lakes Research.
- Snodgrass, W.J. 1987. Analysis of models and measurements for sediment oxygen demand in Lake Erie. *J. Great Lakes Res.* 13:738–756.
- , and Fay, L.A. 1987. Values of sediment oxygen demand measured in the central basin of Lake Erie, 1979. *J. Great Lakes Res.* 13:724–730.
- Stanczykowska, A., and Lewandowski, K. 1993. Thirty years of studies of *Dreissena polymorpha* ecology in Mazurian Lakes of northeastern Poland. In *Zebra Mussels: Biology, Impacts, and Control*, T. Nalepa and D. Schloesser, eds., pp. 3–38. Boca Raton, FL: Lewis Publishers.
- Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. *J. N. Am. Benthol. Soc.* 17:81–94.
- Stoermer, E.F., Emmert, G., Julius, M.L., and Schelske, C.L. 1996. Paleolimnologic evidence of rapid change in Lake Erie's trophic status. *Can. J. Fish. Aquat. Sci.* 53:1451–1458.
- Sweeney, R.A. 1993. "Dead" sea of North America?—Lake Erie in the 1960s and '70s. *J. Great Lakes Res.* 19:198–199.
- Ten Winkel, E.H., and Davids, C. 1982. Food selection by *Dreissena polymorpha* (Mollusca: Bivalvia). *Freshwater Biol.* 12:553–558.
- Thomas, R.L., Jaquet, J.M., and Kemp, A.L.W. 1976. Surficial sediments of Lake Erie. *J. Fish. Res. Board Can.* 33:385–403.
- Vollenweider, R.A. 1974. *The Algal Bowl: Lakes and Man*. Ottawa, Canada: Department of the Environment, Fisheries and Marine Service.
- , Munawar, M., and Stadelmann, P. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. *J. Fish. Res. Board Can.* 31:739–762.
- Walker, R.R., and Snodgrass, W.J. 1986. Modeling sediment oxygen demand in Hamilton Harbour. In *Sediment Oxygen Demand: Processes, Modeling, and Measurement*. K.J. Hatcher, ed., pp. 209–234. Athens, GA: University of Georgia Press.
- Zobell, C.E. 1943. The effect of solid surfaces upon bacterial activity. *Biol. Bul.* 78:388–402.

Submitted: 27 January 2004

Accepted: 14 September 2004

Editorial handling: Gerald Matisoff