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Lake Erie Trophic Status Collaborative Study

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INTRODUCTION

Lake Erie is in a stage of transition, reflecting human and environmental influences simultaneously acting on a poorly understood system. For several decades, the ecosystem has been a focus of both directed and fundamental research. As the shallowest and most heavily populated of the Great Lakes, it has been the first to reflect the consequences of both stress and of remediation efforts. Consequently, Lake Erie is a sentinel of the changes to be expected in other large, mesotrophic systems (Munawar *et al.* 1999a).

During the 1960s, Lake Erie experienced significant cultural eutrophication resulting in huge algal blooms, low oxygen waters, and fish kills (Snodgrass 1987). Eutrophication of the western and central basins driven by years of unregulated inputs of nutrients stimulated efforts to understand the dynamics of Lake Erie's trophic structure, and resulted in the implementation of a phosphorus reduction program (Burns 1985).

Research on Lake Erie played a major role in the limiting nutrient debate and in identifying phosphorus control as the best means of controlling eutrophication. Phosphorus was being released from wastewater treatment plants, as well as non-point sources such as agricultural runoff (DePinto *et al.* 1986). Study of these problems led to the recognition of the relationship between nutrients and water quality and the development of an ecosystem approach (Burns 1985). Target levels for phosphorus loading were determined by binational collaborative programs, which generated models of ecosystem structure and function (reviewed in State of Lake Erie collection of papers in the *Journal of Great Lakes Research*) (Vollenweider 1987). The Great Lakes Water Quality Agreement (GLWQA) (Burns and Ross 1972, 1972 U.S./Canada Water Quality Agreement, International Joint Commission 1978) set target P loads for each lake or major embayment, and the International Joint Commission (IJC) recommended programs that would achieve those loads.

Twenty years later this process was heralded as one of humankind's greatest environmental success stories and since then it has been copied and implemented in numerous other locations throughout the world. Regular ship-board monitoring of dissolved oxygen concentrations in the hypolimnion of Lake Erie by the United States Environmental Protection Agency Great Lakes National Program Office (GLNPO) and by the National Water Research Institute (NWRI) of Environment Canada was established to monitor the status of the lake and determine if the water quality was meeting the terms of the Great Lakes Water Quality Agreement. Phosphorus concentrations declined steadily beginning in the late 1970s from over 25,000 Tonnes/y to their present levels of 8,000–12,000 Tonnes/y (Dolan and McGunagle 2001, 2006). Chlorophyll concentrations dropped markedly in 1990, coincident with widespread establishment of dreissenid mussels. Phytoplankton standing stock declined by approximately 20% from historical levels but biomass became and remained significantly below that predicted from empirical chlorophyll-phosphorus relationships (Millard *et al.* 1999, Nicholls *et al.* 1999). Furthermore, size structure and composition of the phytoplankton community has changed, possibly in response to dreissenid grazing pressure (Munawar *et al.* 1999b). At the same time, both greater transparency and rising incident UV radiation levels have increased the depth of the euphotic zone (Smith *et al.* 2006). Increased transparency should facilitate primary production, but intense UV incident radiation can inhibit primary production by up to 38% (Hiriart *et al.* 2002), and can stimulate photolysis of polychlorinated aromatic hydrocarbons (PAHs) and related organic compounds into increasingly phytotoxic byproducts (Marwood *et al.* 1999, 2000). Concentrations of essential trace metals can also potentially limit primary production (Twiss *et al.* 2000, McKay *et al.* 2001). These changes in phosphorus and trace metal limitation, potential grazing pressure by dreissenids and zooplankton, UV effects and their interaction with photolytic chemicals on phytoplankton dynamics may all have contributed to the observed changes in chlorophyll *a* concentrations through the 1990s.

Greater light (PAR) reaching shallow water zones can stimulate epilithic and epipelic primary production (Lowe and Pillsbury 1995, Heath *et al.* 2006, Lowe and Stewart 2006) as well as promote expansion of vascular macrophyte beds in soft substrates and wetlands (Lougheed and Chow-Fraser 2006). Yet, budgets of carbon transfer to primary and secondary consumers indicated that autotrophic production was insufficient to support the existing biomass of zooplankton and zoobenthos (Sprules *et al.* 2000). This implied that other carbon sources were potentially contributing to either microbial processes (Munawar *et al.* 1999b, Heath *et al.* 2006) or directly to zoobenthic (Roditi *et al.* 2000) or zooplankton production (Johannsson *et al.* 2000, Sprules *et al.* 2000). Zoobenthic composition, abundance, and distribution had become dramatically altered by 2000. Dreissenids were thought to be abundant enough to regulate phytoplankton production, but they were becoming increasingly subject to predation by invading benthivores (especially round gobies; Weimer and Keppner 2000, Johnson *et al.* 2006). Dreissenid encroachment onto soft substrates (Haltuch *et al.* 2000, Berkman *et al.* 2000) may ultimately be limited by bioturbation caused by burrowing mayflies, whose populations rapidly expanded through the center of the western basin during the mid 1990s (Schloesser *et al.* 2000). Other dreissenid effects include facilitation of some macrobenthic crustaceans (*Gammarus*, *Echinogammarus*, crayfish (Stewart *et al.* 1998) and eventual extirpation of others (*Diporeia;* Dermott and Kerek 1997). These changes were suspected to potentially influence the community structure of both benthivorous and planktivorous fish populations (Ryan *et al.* 2006).

Other paradoxical observations also were made during the period 1995–2001. Water quality monitoring by both the US EPA (Rockwell and Warren 2003) and Environment Canada (Charlton and Milne 2004) revealed that although total phosphorus (TP) loadings declined or held constant for the interval 1989–1995 relative to the 1980s, central basin and eastern basin TP and soluble reactive phosphorus (SRP) concentrations appeared to rise for the period 1995–2001. Both researchers reported that concentrations of chlorophyll *a* remained very low despite apparent increases in phosphorus concentrations. Hecky *et al.* (2004) reported increases in the incidence of *Cladophora* accumulations along Canadian shorelines of central and eastern Lake Erie. Heath *et al.* (2006) showed that carbon fixation via the microbial loop may be an important complement to primary production, perhaps partly explaining the apparent paradox that secondary (benthic) production in Lake Erie seemed to be exceeding the lake's net primary production (Sprules *et al.* 2000).

Equally disturbing were reports that Lake Erie bottom waters had gone anoxic sooner in the late summer months, and the areal extent of the anoxia had increased relative to previous years (Rockwell and Warren 2003). The traditional eutrophication model predicts that a decrease in phosphorus loading will result in a decrease in phosphorus concentration reducing algal production that should result in less hypolimnion oxygen depletion. This was observed in the central basin of Lake Erie during the 1970–1990 time period. Decreasing loadings of phosphorus during the 1970s to the 1990s were accompanied by decreases in phosphorus concentrations in the water column, decreases in the chlorophyll (algal) concentrations, and slight reductions in the hypolimnetic oxygen depletion rate. However, since then these systems appeared to be disconnected. Phosphorus loadings have remained at or below the target loadings of 11,000 tonnes/y except during wet years characterized by marked flood pulses. Total phosphorus concentrations have increased to levels as high as in the 1970s, while chlorophyll concentrations in Lake Erie's eastern basin have dropped to the lowest values observed (Rockwell and Warren 2003). Central basin hypolimnetic oxygen depletion rates appear to have increased. In addition, the extent of harmful and nuisance algal blooms (*Microcystis; Cladophora*) has increased.

This situation appeared to be unique to Lake Erie. Barbiero *et al.* (2006) used multivariate analysis to summarize relationships among and temporal trends in nutrients among the five Great Lakes for the period 1990–2000. They found strong associations and tight clustering of the patterns of nutrient concentrations through time for all of the Great Lakes except Lake Erie. In particular, in Lake Erie concentrations of TP changed completely independently of concentrations of nutrients (including silica) that are tightly coupled with phosphorus in the other lakes. Rockwell (cited in Dolan and McGunagle 2001) noted that the Schelske and Stoermer (1971) empirical model relating silica and phosphorus dynamics had not been holding for Lake Erie. For the period 1998–2001, the total quantity of phosphorus leaving Lake Erie via the Niagara River markedly exceeded the quantity entering through loadings (Charlton and Milne 2004).

In 2001, it was evident that i) the biomass of phytoplankton, measured as chlorophyll *a*, in the central and eastern basins appeared to be at historically low levels, despite the fact that ii) concentrations of TP seemed to have been increasing over the previous 5 years, even though loadings of TP to Lake Erie had not risen, iii) that oxygen demand in the central basin had not changed through the 1990s, and iv) that hypolimnial oxygen depletion continued to occur in the central basin. Such patterns are inconsistent with the predictions and dynamics of models of internal lake function that were developed or adapted to provide guidance on management of Lake Erie's nutrient budget (e.g., Vollenweider 1976, Schelske and Stoermer 1971, Charlton 1980, Di Toro and Connolly 1980).

These observations may represent situations that have naturally occurred at times prior to that for which intensive monitoring data are available. Alternatively, they may reflect consequences of novel environmental and biological pressures modifying energy and nutrient flow through the ecosystem. We have termed this apparent change in the system the "Lake Erie Trophic Paradox" and it indicates that there is a need to better understand the current nutrient cycling and food web dynamics in Lake Erie.

Lake Erie has a history of collaborative research, fostered by its large size, location on the boundary of adjacent countries, and socioeconomic importance. Previous initiatives, such as the Lake Erie Ecological Modeling Initiative (International Joint Commission 1997), the Great Lakes Modeling Summit (Council of Great Lakes Research Managers 2000), and the Lake Erie Millennium Network recommended further investigation of three phenomena. First, the increased size and/or increased persistence of the central basin hypolimnion, possibly accompanied by increased rates of sediment oxygen demand or a change in the ratio of autotrophic to heterotrophic carbon fixation. Second, the reduced benthic and/or planktonic primary production caused by high grazing pressure and/or nutrient limitation and/or trace metal limitation and/or UV or contaminant-induced inhibition of photosynthesis. And third, the increased net rates of organic carbon accumulation in hypolimnetic areas. This collection of research papers was designed to begin to address these issues by coordinating the activities of a diverse group of active researchers to collect the field data, modeling, and hypothesis testing required to resolve ecosystem-level problems.

OVERVIEW OF CONTRIBUTIONS

Reported here is a collection of papers that stem from a binational, multi-institutional, multi-investigator, EPA-funded project that supported the collection of field data in Lake Erie during 2002 and 2003. These projects included the assembly and interpretation of existing (post-dreissenid) field data and the collection of new data that would be useful in formulating a better understanding of carbon and nutrient cycling, food web dynamics, and oxygen depletion in the central basin hypolimnion. The papers are focused in six broad topical areas: 1) introductory paper (this paper), 2) interpretation of historical data sets (three papers), 3) measurements of primary and secondary production and phosphorus cycling (10 papers), 4) studies of benthic processes (five papers), 5) evaluation of patterns of oxygen demand and depletion (four papers) and 6) management implications (one paper). These papers are organized in this special collection in the order shown in Table 1. Highlights of each of the papers are summarized below.

Historical Data Sets

Three papers in this issue examine the recent and historical monitoring data to determine trends in water quality. Burns *et al.* and Rockwell *et al.* present some of the key data that triggered this collaborative study. Rockwell *et al.* report on changes in spring turbidity, spring and summer total phosphorus concentrations, and dissolved reactive silica. They describe three trends in these parameters—declines during the 1980s following implementation of controls on total phosphorus loadings, increases in the western and central basins between

TABLE 1. Summary listing of the papers in this collection.

INTRODUCTORY PAPER
Lake Erie Trophic Status Collaborative Study.
Gerald Matisoff and Jan H. Ciborowski

HISTORICAL DATA SETS
Lake Erie Total Phosphorus Loading Analysis and Update: 1996–2002
David M. Dolan and Kevin P. McGunagle

Lake Erie's Indicators Monitoring Program 1983 to 2002
David C. Rockwell, Glenn J. Warren, Paul E. Bertram, Douglas K. Salisbury, and Noel M. Burns

Trends in temperature, Secchi depth and dissolved oxygen depletion rates in the central basin of Lake Erie 1983 to 2002.
Noel M. Burns, David C. Rockwell, Paul E. Bertram, and Jan H. Ciborowski

PRIMARY AND SECONDARY PRODUCTION AND PHOSPHORUS CYCLING
Planktonic primary production in the offshore waters of dreissenid-infested Lake Erie in 1997
Ralph E.H. Smith, Veronique P. Hiriart-Baer, Scott N. Higgins, Stephanie J. Guilford, and Murray N. Charlton

Annual variability of phytoplankton primary production in the western basin of Lake Erie (2002–2003)
David Porta, Mark A.J. Fitzpatrick and G. Douglas Haffner

Phytoplankton nutrient status in Lake Erie in 1997
Stephanie J. Guildford, Robert E. Hecky, Ralph E.H. Smith, William D. Taylor, Murray N. Charlton, Lisa Barlow-Busch, and Rebecca L. North

Temporal trends in Lake Erie plankton biomass: roles of external phosphorus loading and dreissenid mussels
Joseph D. Conroy, Douglas D. Kane, David M. Dolan, William J. Edwards, Murray N. Charlton, and David A. Culver

Phytoplankton dynamics and hypoxia in Lake Erie: a hypothesis concerning benthic-pelagic coupling in the central basin
Hunter J. Carrick, Jessica B. Moon, and Barrett F. Gaylord

Relationship between labile dissolved organic carbon (LDOC), bacterioplankton cell phosphorus quota, and bacterial phosphate uptake rate in lakes
Xueqing Gao and Robert T. Heath

Ratios of community respiration to photosynthesis and rates of primary production in Lake Erie via oxygen isotope techniques
Nathaniel E. Ostrom, Mary E. Russ, Amanda Field, Leah Piwinski, Michael R. Twiss, and Hunter J. Carrick

Phytoplankton distribution in Lake Erie as assessed by a new *in situ* spectrofluorometric technique
Anas Ghadouani and Ralph E.H. Smith

Field investigations of trace metal effects on Lake Erie phytoplankton productivity
Michael R. Twiss, Sandra P. Gouvêa, Richard A. Bourbonniere, R. Michael L. McKay, and Steven. W. Wilhelm

Determination of bioavailable Fe in Lake Erie using a luminescent cyanobacterial bioreporter
David Porta, George S. Bullerjahn, Michael R. Twiss, Steven W. Wilhelm, Leo Poorvin and R. Michael L. McKay

BENTHIC PROCESSES
Initial measurements of benthic photosynthesis and respiration in Lake Erie
John-Mark Davies and Robert E. Hecky

Sediment suspension by burrowing mayfly bioturbation (*Hexagenia* spp., Ephemeroptera: Ephemeridae)
André M. Bachteram, Kerry A. Mazurek and Jan J.H. Ciborowski

(Continued)

TABLE 1. Continued.

BENTHIC PROCESSES (Continued)
The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002 Matthew W.R. Patterson, David R. Barton and Jan J.H. Ciborowski
A potential new energy pathway in central Lake Erie: the round goby connection Timothy B. Johnson, David B. Bunnell and Carey T. Knight
Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002-2004 David R. Barton, Reagan A. Johnson, Linda Campbell, Jennifer Petruniak, and Matthew W.R. Patterson
OXYGEN
Hypolimnetic oxygen depletion dynamics in the central basin of Lake Erie William J. Edwards, Joseph D. Conroy and David A. Culver
Potential oxygen demand of sediments from Lake Erie Donald W. Schloesser, Richard G. Stickel, and Tom Bridgeman
Oxygen concentration and demand in Lake Erie sediments Gerald Matisoff and Thomas M. Neeson
Middle Holocene hydrologic change in Lake Erie Rebecca A. Clotts, Constance E. McCambridge, Enriqueta Barrera, John P. Coakley, Donald F. Palmer, and Beverly Z. Saylor
MANAGEMENT IMPLICATIONS
Modeling as a tool for nutrient management in Lake Erie Luis F. León, Jorg Imberger, Ralph E.H. Smith, David C.L. Lam, and William M. Schertzer

1990 and 1997 (corresponding to a period when abundances of dressenids were high in these basins), and a decline between 1998 and 2001. However, spring 2002 turbidity and total phosphorus concentrations were among the highest measured during the 20-y surveillance period. Burns *et al.* evaluate data from the same monitoring data sets and report a gradual rise in seasonally adjusted water temperature, a gradual decline in total phosphorus concentrations, and no consistent change in trophic state index. These patterns do not appear to be caused by changes in total phosphorus loadings. Year-to-year summer turbidity may reflect whether phytoplankton density maxima are eplimnetic or metalimnetic, as is discussed by Carrick *et al.* Hypolimnetic volume oxygen demand (HVOD) has also been highly variable, but has exhibited a gradual decline through the 1980s and a gradual rise through the 1990s. Thickness of the hypolimnion has been a key determinant among years.

Dolan and McGunagle show that phosphorus loadings to Lake Erie have decreased since the late 1960s. They reached a minimum around 1992, and have varied above and below the target level of 11,000 Tonnes/y since then. Annual variations appear to be related to annual variations in tributary flows. They also calculate that about 2/3 of the loading is now from tributaries.

Primary and Secondary Production and Phosphorus Cycling

The heart of the field effort was focused on developing a better understanding of the nature of primary and secondary production and how they may have changed in response to widespread establishment of dreissenid mussels. Five papers address phytoplankton distributions in the lake, two papers present new techniques for phytoplankton measurement and the measurement of production rates, one paper examines the role of bacterioplankton, and two papers look at the role of micronutrients on production rates. Smith *et al.* examined the 1997 phosphorus and chlorophyll *a* concentrations throughout Lake Erie. They report that average areal primary production varied little between basins and that the lake remained highly efficient at translating TP into primary production. In a complementary paper, Guildford *et al.* examined indicators of phytoplankton nutritional status to determine whether the observed decrease in TP concentrations resulted in a strongly P deficient phytoplankton community. They found that in 1997 the phytoplankton community was not strongly nutrient deficient. Porta, Fitzpatrick and Haffner examined primary production rates for the western basin in 2002 and 2003. They report that changes in carbon fixation are regulated by variability in available underwater light caused by wind events and that overall, rates are not much different than they had been in the 1980s. Conroy *et al.* report that in individual basins and lake-wide, both phytoplankton and zooplankton biomasses in 1996–2002 increased compared to previously published values, although concentrations of chlorophyll *a* remained low. In addition, they report that neither plankton biomass nor chlorophyll *a* concentrations correlate to external phosphorus loading estimates, a finding consistent with that of Rockwell *et al.* Ghadouani and Smith apply a new spectrofluorometric technique to estimate phytoplankton biomass from pigment fluorescence. They found substantial vertical and temporal variation of biomass and taxonomic composition over scales of meters and hours that conventional sampling would not resolve. They found evidence of reduced biomass in shallow water areas whose substrates were dominated by dreissenids. Incubations of water labeled with ^{18}O were used by Ostrom *et al.* to determine the ratio of respiration to primary production (R:P). The wide range of the R:P ratios, the fraction O_2 saturation and the $\Delta^{18}O$-O_2 values were all indicative of a eutrophic system. In addition, Ostrom *et al.* calculate that 61% of hypolimnion O_2 respiration occurs within sediments and 39% occurs within the water column.

A few papers address other productivity issues. Carrick *et al.* measured late spring metalimnetic and summer benthic algal assemblages in the central basin. These assemblages had biomass (estimated from chlorophyll *a* concentrations) comparable to that in the upper water column. Their estimates of P:R ratios corresponded in time and magnitude to those of Ostrom *et al.* Carrick *et al.* identify this assemblage as meroplanktonic—an algal assemblage that spends different portions of its life history associated with both the pelagic and benthic environments. Gao and Heath cultured natural assemblages of bacterioplankton and found that as labile dissolved organic carbon concentration increased, bacterioplankton growth rate and biovolume increased, but cell P content and velocity of phosphate uptake decreased.

Two papers examine the relationships between trace metals and productivity. Twiss *et al.* report that trace metals are not as important as phosphorus in controlling phytoplankton productivity, but that trace metal enrichment can occasionally have a stimulatory effect, particularly on the picoplankton size class. Porta *et al.* use a cyanobacterial bioreporter to assess the role of iron bioavailability as a constraint on primary production. They found that although there was a seasonal depletion in bioavailable iron, in most cases there was sufficient iron for growth.

Benthic Processes

Five papers examine the benthic community. Davies and Hecky report the first *in situ* measurements of benthic photosynthesis and respiration in Lake Erie. They found that the highest rates of gross photosynthesis were on rocky substrates populated with both *Cladophora* and dreissenid mussels, and the lowest rates were found on soft sediments. Bachteram *et al.* conducted laboratory experiments on the rates of sediment suspension induced by burrowing mayfly larvae. They conclude that bioturbation by *Hexagenia* larvae in western Lake Erie contributes a small fraction of the basin-wide annual sediment load but that it can be locally great enough to theoretically inhibit dreissenid filter feeding. Patterson *et al.* conducted a lake-wide benthic survey of Lake Erie during 2002 and found that *Dreissena bugensis* is the dominant dreissenid in Lake Erie and that dreissenid densities decreased in the western and central basins but markedly increased in the eastern basin from 1998–2002. On a lake-wide basis shell-free tissue dry mass has doubled during that time. They observed a strongly bimodal size distribution, and an increase in the average size of mature mussels, possibly because of size-selective predation by round gobies. The densities and diets of round gobies in eastern Lake Erie were found by Barton *et al.* to have a potential impact on the abundances of other macrobenthos. They found that smaller round gobies eat primarily chironomids and amphipods and that consumption of dreissenid mussels increases as gobies grew larger. The benthic-pelagic coupling by round gobies was also studied by Johnson, Bunnell, and Knight. They used a bioenergetic model to estimate the type and amount of prey eaten, the biomass accumulation rate for the round goby population, and a partitioning of the food energy derived from dreissenids and from zooplankton and non-dreissenid benthic prey. They report that piscivorous fish show an increased reliance on round gobies as prey that has modified the food web to bring new energy into the pelagic food web. They estimate that round gobies feeding on dreissenid mussels contribute significantly greater quantities of biomass to higher trophic levels of the food web than would occur in their absence.

Four papers addressed oxygen concentrations in the water column or oxygen demand by the sediments. Edwards *et al.* employed a temperature gradient microprofiler to determine hypolimnetic oxygen depletion rates. They conclude that hypolimnetic oxygen depletion is most sensitive to sediment oxygen demand and hypolimnion respiration. Schloesser *et al.* measured the sediment "potential oxygen demand" and found that it was not higher in nearshore sediments than in offshore sediments, nor was it higher at sites with dreissenids than at sites without the mussels. They conclude that their study provides no evidence that dreissenids have contributed directly to increased hypolimnetic anoxia in Lake Erie. Matisoff and Neeson calculate sediment oxygen demand by modeling oxygen microelectrode profiles in sediment cores. Their results agree well with the hypolimnetic oxygen depletion rate derived from EPA monitoring cruises and suggest that modeling of oxygen profiles holds promise as an alternative technique to regular monitoring for determining hypolimnetic oxygen depletion rates. Clotts *et al.* obtained deep cores and measured sediment properties and $\Delta^{18}O$ of shell carbonates. They interpret the changes at 4200–3900 y BP as a higher lake stand resulting from an influx of surface drainage from the upper Great Lakes. This higher lake level induced a seasonal hypolimnion and set the stage for the low pH, oxygen-depleted bottom waters of today.

Management Implications

León *et al.* present hydrodynamic modeling simulations of Lake Erie using the 3D ELCOM and data from 1994 and 2001. The model was used to understand the flushing of the deep water, the internal wave weather, and residual circulation of gyres in the central and eastern basins. They argue that such models are critical to improving our understanding of patterns of nutrient transport within and among basins and the productivity consequences of these fluxes.

TRENDS AND FUTURE CONSIDERATIONS

This collection of papers represents only a small contribution toward understanding the dynamic nature of a system as complex as the coupled physical, chemical, and biological entity of Lake Erie. The combined data confirm that summer epilimnetic chlorophyll *a* concentrations in the central and western basin are indeed low, although greater than the minima observed during the 1990s. However, chlorophyll *a* concentrations may not truly reflect primary production budgets, given the increasing prevalence of benthic primary production in shallow waters and springtime metalimnetic production. The relative distribution of dreissenid mussels among basins has changed since their appearance in the early 1990s. They likely play a significant role in nutrient dynamics of shallow waters, and their production is apparently transferred to higher levels in the food web. All of these findings suggest an increasing importance of benthic processes to functioning of the Lake Erie food web.

The role of total phosphorus in regulating the food web is still unclear. Phytoplankton appear to be nutrient-limited, but there is evidence of a disconnect between total phosphorus loads and in-lake concentrations. It is still unclear whether this discrepancy reflects uncertainties in loadings estimates or changes in internal dynamics. Yet, estimates of the role of sediment oxygen demand do not seem to have changed. Insufficient data were collected to permit one to ascertain whether episodic central basin anoxia is a consequence of changing trophic dynamics. However, other research (Charlton and Milne 2004) suggests that the onset of anoxia is governed by the same processes of thickness and persistence of the hypolimnion as has been historically observed. Prevailing environmental conditions may ultimately prove to be the major determinants of the frequency and spatial extent of central basin anoxia.

While the collection of the field data and its interpretation are extremely important in helping understand the trophic changes in Lake Erie, it is not sufficient. The conditions in the lake change from 1 year to the next, so it is difficult to generalize conclusions reached during 1 year's field work to long-term lake behavior. Even 30-y data records are thought by some to be too short to allow reliable trend-estimation of physical and chemical parameters. The rapidity with which the ecosystem accommodates new biota and environmental pulses adds to the challenge of developing definitive tests of our hypotheses. Studies such as the one presented in this collection and others that will surely follow help us refine our understanding of the physical, chemical, and biological linkages in the food web and permit us to more accurately describe nutrient and energy flow in the Lake Erie trophic system. This collaborative physical, chemical, and biological ecosystem approach worked for us in the 1960s and early 1970s as we developed the Great Lakes Water Quality Agreement, so it should work for us again to solve the similar problems we currently face.

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