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Evidence for the Restoration of the Lake Erie Ecosystem

Water quality, oxygen levels, and pelagic function appear to be improving

Joseph C. Makarewicz and Paul Bertram

Of the five Great Lakes, Lake Erie has been most seriously affected by eutrophication (Figure 1). It is the best-publicized example of eutrophication and of severe deterioration of water quality through pollution (Burns 1985, Mortimer 1987). The effects of pollution, which some scientists have considered irreversible (Hartmen 1972), included extensive floating algal blooms, disappearance of certain benthic organisms, and oxygen depletion in the deep bottom waters of the lake (Boyce et al. 1987).

A binational commission, the International Joint Commission (IJC), was formed to investigate problems of specific boundary waters and to make recommendations to the governments of Canada and the United States. Extensive loadings of phosphorus in the 1950s and 1960s were identified as the principal cause of eutrophication in the Great Lakes (IJC 1986). To mitigate the problem, the two governments have invested a total of more than 7.5 billion dollars since 1972 to improve municipal waste facilities and bring major municipal discharges into compliance with a 1.0 mg/L phosphorus limitation on effluent. As a result of the phosphorus abatement program, annual phosphorus loadings from US and Canadian municipal dischargers were reduced by 84%—from 15,260 tons in 1972 to 2449 tons in 1985 (IJC 1987). During this time, the reduction in phosphorus entering Lake Erie from another major source, the Detroit River, which itself received municipal discharges, declined 68%—from 12,000 tons to 3796 tons (Fraser 1987, IJC 1987). As a result of these decreased phosphorus loadings and those associated with other tributaries, ambient offshore phosphorus concentrations have steadily decreased (Figure 2d; DePinto et al. 1986).

The data suggest cautious optimism on the phosphorus-reduction program

A second management practice implemented in Lake Erie during the 1970s involved the fishery resources. During the last century, dramatic changes in the composition of the Lake Erie fish community have occurred, including the decline of some of the most desirable and economically valuable species due to overexploitation and habitat deterioration (Hartman 1972, Leach and Nepszy 1976). The walleye (*Stizostedion vitreum vitreum*) fishery is a case in point. By 1960, the commercial fishery had collapsed, and walleye fishing was formally prohibited in US waters in 1972. During the mid-1970s, when the phosphorus abatement program was implemented, walleye abundance began to increase, and a dramatic recovery in the walleye stocks of Lake Erie was evident by the early 1980s (Figure 2a,b; Kutkuhn 1976, ODNR 1985). In addition, annual stocking of another group of top-level predators, salmonines, to Lake Erie was begun by the Lake Erie states; New York State alone stocked 1 million fish annually.

Regulation of trophic-level biomass and species composition of an aquatic ecosystem may be influenced by nutrients in the water (bottom-up control) or by top-level predators such as walleye and salmonines (top-down control; McQueen et al. 1989). The phosphorus-abatement program and the restoration of top-level predators in Lake Erie represent a unique opportunity to examine top-down and bottom-up influences on the water quality of Lake Erie.

Ambient phosphorus levels in the open waters have decreased, but whether trends in biological responses parallel the trends in water chemistry has been a matter of intense debate and modeling (Mortimer 1987). What predator-induced effects have occurred at lower trophic levels with the resurgence of a top-level predator? Could bottom-up and top-down regulation of trophic level biomass be occurring simultaneously? Finally, after millions of dollars invested in remedial

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programs, has the functioning of the pelagic ecosystem been restored and has the quality of Lake Erie's water improved?

To assess the current status of the Lake Erie ecosystem and the interaction of top-down and bottom-up controls, samples for water chemistry, phytoplankton, and zooplankton were collected from several offshore sites in Lake Erie (Figure 1) during 24 cruises in the spring, summer, and autumn from 1983 to 1985.

The lake

Lake Erie is 92 km wide at its widest point, 388 km long, and has a surface area of approximately 25,690 km^2. It is the shallowest, southernmost, and warmest of the Great Lakes and is the twelfth largest lake in the world. Discharges from Lake Superior, Lake Michigan, and Lake Huron drain into Lake Erie through the Detroit River. The annual average flow of the Detroit River represents approximately 95% of the total inflow to Lake Erie (Hartman 1972). Lake Erie drains into Lake Ontario through the Niagara River.

Of ecological importance is the natural geological division of Lake Erie into three basins—western, central, and eastern (Figure 1). Because of the shallow depth of the western basin (average depth 7.4 m) and its proximity to large urban centers such as Detroit and Toledo, this basin is highly vulnerable to change caused by human activities. Unlike the smaller western basin (13% of the total lake surface area), the large central basin (63% of the surface area, maximal depth of 29 m), and the deep eastern basin (maximal depth of 64 m and an average depth of 24.4 m) thermally stratify each summer (Hartman 1972).

Phytoplankton

The phosphorus-reduction plan was implemented specifically to reduce the nutrient that most controlled the growth of phytoplankton and thereby reduce the level of algal biomass below that of a nuisance condition. Consequently, a successful program would be reflected by decreased phytoplankton biomass and chlorophyll *a* levels in the water. Since the implementation of the phosphorus-abatement program, two limited historical comparisons of phytoplankton biomass in Lake Erie have been reported. The first observed that a decline (42%) in nearshore phytoplankton biomass of the western basin occurred between 1967 and 1975 (Nichols et al. 1977). Because of concerns over phytoplankton preservation, identification, and enumeration techniques, this conclusion has been questioned (Gladish and Munawar 1980). The second study (Munawar and Munawar 1980) compared offshore sites from 1970 to 1979 and observed decreases in phytoplankton biomass of 40% in the western basin and 22% in the central basin.

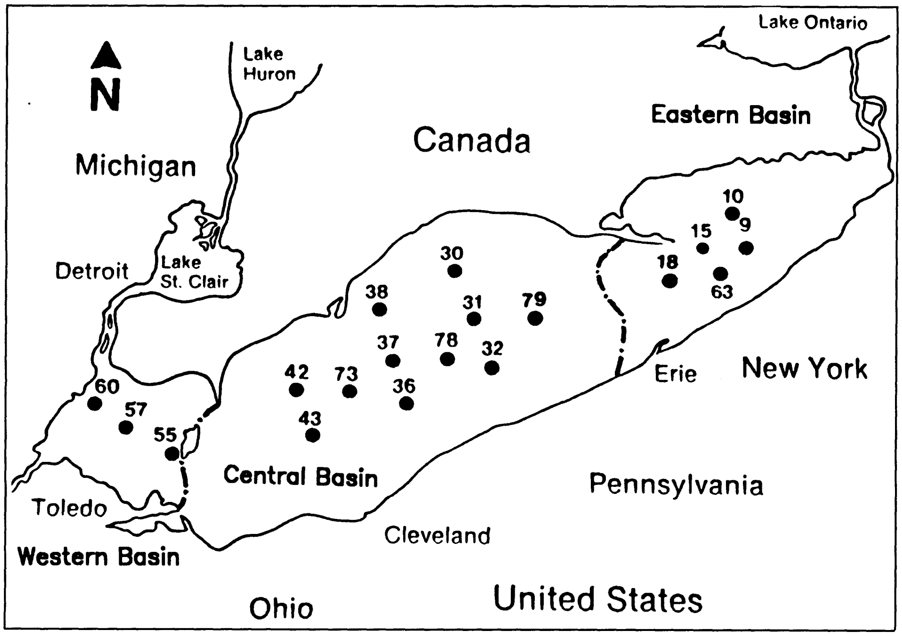

Figure 1. Composite of Lake Erie sampling stations, 1983–1985. Not all stations were sampled in all years. Seven sampling cruises were made in 1983, 11 in 1984, and 6 in 1985.

A few phytoplankton investigations have intensively sampled all three lake basins (Makarewicz 1988, Munawar and Munawar 1976, Rathke 1984). In these studies, a trend of decreasing phytoplankton biomass is evident in all three basins from 1970 to the mid-1980s (Figure 2f). The mean basin-weighted biomass for the 1983 to 1985 period was 1.18 g/m^3; a 65% reduction in algal biomass in offshore waters from the 1970 average of 3.4 g/m^3 (Munawar and Munwar 1976). This reduction in biomass was evident for all seasons of the year (Figure 3) and for all three basins (Figure 2e,f), including the historically highly productive western basin (Munawar and Burns 1976).

Classification schemes of lake trophic status, based on the maximal algal biomass and the average biomass observed (Vollenweider 1968), suggest shifts in trophic state from eutrophic to mesotrophic conditions in the western basin and from mesoeutrophic to oligotrophic in the eastern basin from 1970 to 1983–1985 (Makarewicz and Bertram 1991, Munawar and Munawar 1982). Dramatic reductions in maximal biomass of several common species have also occurred between 1970 (Munawar and Munawar 1976) and 1983–1985 (Makarewicz and Bertram 1991). For example, the nuisance blue-green algae *Aphanizomenon flos-aquae* decreased 89% from 2.0 g/m^3 in 1970 to an average of 0.22 g/m^3 for the 1983–1985 period. *Stephanodiscus binderanus*, a eutrophic indicator species, decreased in biomass by 85% in the western basin, and *Fragilaria capucina*, another eutrophic indicator, decreased by 94%. These reductions are consistent with expectations of programs to reduce phosphorus loadings to the lake and bottom-up control of trophic-level biomass.

Other phytoplankton species have recently exhibited variable abundances. *Asterionella formosa*, prevalent in Lake Erie before 1950 (Gladish and Munawar 1980, Munawar and Munawar 1980, Verduin 1964), had the highest diatom biomass and second-largest abundance in the entire lake during the spring of 1984. The April 1984 average was 226 cells/ml with a maximal abundance of 942 cells/ml in the western end of the central basin. This level is comparable to the maximal density in March of 1938 (966 cells/ml), with a mean of 553 cells/ml (Hohn 1969). Similar high abundances of *A. formosa* were not observed in 1985, however. *Melosira islandica*, a mesotrophic indicator species, has historically not been a common species in Lake Erie, but in 1984 it was the fourth most prevalent diatom (4.1% of the total biomass).

In general, the number of dominant (more than 5% of the biomass for a sampling date) eutrophic diatom species has decreased in the western basin from 1970 (Munawar and Munawar 1980) to 1985 (Makarewicz 1988, Makarewicz and Bertram 1991), whereas the number of dominant mesotrophic algal species increased from one in 1970 to four in 1985; that is, the ratio of the number of species indicative of eutrophic conditions to those indicative of mesotrophic conditions has declined. The pelagic ecosystem has become less eutrophic.

Zooplankton

In addition to phytoplankton, species composition and abundance of Crustacea and Rotifera are believed to reflect the trophic status of a lake (Gannon and Stemberger 1978). Within the Crustacea, the suborder Calanoida is primarily made up of filter-feeding organisms more common in oligotrophic conditions, the suborder Cyclopoida is made up of non–filter-feeders, and the suborder Cladocera is made up of filter feeders more common in eutrophic waters.

The ratio of biomass of calanoid copepods to biomass of cyclopoid copepods plus cladocerans, the zooplankton ratio, remained lower for the 1983–1985 period (mean = 0.21) in the western basin than for the central basin (mean = 0.41) and the eastern basin (mean = 0.47), reflecting the eutrophic status of that basin compared with the other basins. The zooplankton ratio should increase for waters of decreasing eutrophy. Comparable zooplankton data from an earlier date in the 1960s or 1970s is not available for comparison with the 1983–1985 data. However, during 1983–1985, the zooplankton ratio did increase each year for the central basin (0.31 to 0.35 to 0.49). No discernible trend was evident between 1983 and 1985 in the western and eastern basins.

Historically, during July and August, Copepoda abundance increased in the western basin from 1939 to the late 1950s, and Cladocera abundance increased until at least 1967 (Figure 4). By 1983–1985, Cladocera and Copepoda abundances had returned to abundance levels comparable with those of the 1940s. The observed decrease in Crustacea abundance is consistent with the expectations of long-term nutrient or bottom-up control of trophic abundance.

Some recent changes in the composition of the zooplankton community, however, cannot be attributed solely to nutrient control. *Daphnia pulicaria*, a large herbivorous Cladocera, was first observed in Lake Erie in 1983, and it was the dominant zooplankter in 1984 (mean = 492/m^3, 14.8% of the total biomass) but not in 1985 (mean = 44/m^3). In October of 1985, *Bythotrephes cederstroemi*, a large (more than 10-millimeter-diameter) predaceous Cladocera, was first observed (mean = 4.5/m^3, maximum = 72/m^3) in Lake Erie. Because it can effectively crop down *Daphnia* populations (Lehman 1988), *B. cederstroemi* may have contributed to the reduced abundance of *D. pulicaria* observed in 1985. The appearance and dominance of large-bodied cladocerans (more than 2-millimeter diameter) in the zooplankton community suggest a relaxation of size selective planktivory or a top-down induced community effect (Brooks and Dodson 1965, Carpenter et al. 1985, Wells 1970).

Fish

There is evidence supporting a change in planktivory in Lake Erie. A cause-

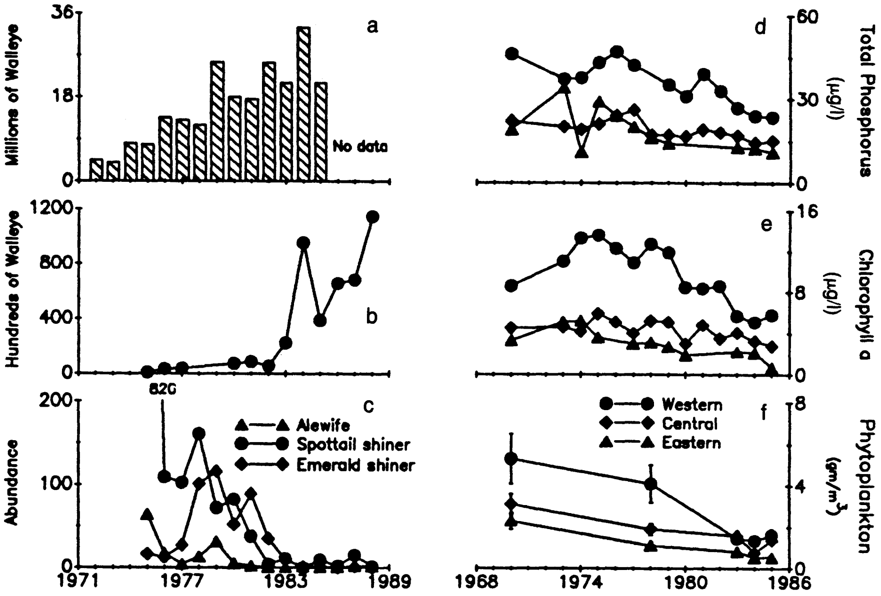

Figure 2. a. Projected abundance of fishable walleye (age 2 years and older) in western Lake Erie (Ohio waters; ODNR 1985). **b.** Sport angler harvest of walleye from the central basin (districts II and III) of Lake Erie (ODNR 1985). **c.** Time trend of autumn emerald and spottail shiner abundance (age 1 year and older) in the central basin and of alewife (young of the year) from the western basin (ODNR 1985). Values represent the geometric mean of catch per trawling hour. **d.** Time trend of annual cruise average of total phosphorus since 1970 (Depinto 1986, Rockwell et al. 1989). **e.** Chlorophyll *a* (Rockwell et al. 1989, Rathke 1984). **f.** Phytoplankton (Munawar and Munawar 1980, 1976, Rathke 1984). Values in Figure 2f represent the mean ±1 SE. In some instances, the standard error limits are obliterated by the symbol. Mean annual standard error (MSE) from 1983 to 1985 in the western basin is ±0.471. MSE for 1978 and for 1983–1985 are 0.280 (central) and 0.119 (eastern).

and-effect relationship is suggested by the large increase in the abundance of piscivorous walleye and the equally impressive decrease in the abundance of the planktivorous alewife (*Alosa pseudoharengus*), spottail shiner (*Notropis hudsonius*), and emerald shiner (*Notropis atherinoides*) in the western (Figure 2a–c) and central basins (ODNR 1987). These planktivorous fish species comprise the primary diet of walleye (Knight et al. 1984) and salmonines in Lake Erie, although other factors, such as changes in climate, turbidity, toxic chemicals, and the commercial bait industry, may have influenced the decline in planktivore abundance.

Figure 3. Seasonal fluctuation of weighted mean phytoplankton biomass in 1970 (Munawar and Munawar 1976), 1983, 1984, and 1985. Values are corrected by using the weighting factors of 15.6%, 59.6%, and 24.6% for the western, central, and eastern basins (Munawar and Munawar 1976). The mean seasonal standard errors were 0.217 (1983), 0.295 (1984), and 0.235 (1985). One-liter composite phytoplankton samples were obtained by compositing equal aliquots from samples collected at depths of 1, 5, 10, and 20m as allowed by depth with an 8-liter PVC Niskin bottle mounted on a General Oceanics Rossette sampler with a Guildline electrobathythermograph. Phytoplankton samples were immediately preserved with 10 mL of Lugol's solution, and formaldehyde was added on arrival in the laboratory. The settling chamber procedure (Utermöhl 1958) was used to identify (except for diatoms) and enumerate phytoplankton at a magnification of 500×. A second identification and enumeration of diatoms at 1250× was performed after the organic portion was oxidized with 30% H_2O_2 and HNO_3. The cleaned diatom concentrate was air dried on a #1 cover slip and mounted on a slide (75 × 25 mm) with HYRAX™ mounting medium. A maximum of ten specimens of each species from each sample were measured, where possible (length, width, and depth), for the cell volume calculation. The 1970 study of Munawar and Munawar (1976) used similar enumeration procedures and sampling locations as the 1983 to 1985 study; that is, the top 20 m of the offshore region of all three basins was sampled and the settling chamber procedure was used to enumerate phytoplankton.

Emerald and spottail shiners and alewife feed heavily on microcrustaceans, some midge larvae, and algae (Dymond 1926, McCann 1959, Scott and Crossman 1973, Smith and Kramer 1964). For example, the diet of emerald shiners in Lake Erie during the winter of 1940 included *Diaptomus*, *Daphnia*, *Cyclops*, and *Bosmina* (Gray 1942). The succession and competitive success of zooplankton may be regulated by planktivorous fish causing a distinct shift favoring survival of small species that are not readily captured in the gill raker of the fish (e.g., Brooks and Dodson 1965).

Thus a substantial decline in the planktivorous fish base of Lake Erie, that is, a release from size-selective predation pressure, appears to have led to the dominance of the large-bodied *D. pulicaria* by 1984. The decline in planktivorous fish may have contributed to the establishment of *B. cederstroemi* by 1985. This observation is consistent with numerous experimental and field studies of the size-selective predation hypothesis (McQueen et al. 1989).

Trophic interactions

In an aquatic ecosystem dominated by large and efficient herbivores, such as *D. pulicaria* and *Daphnia galeata mentodae*, a grazing effect on phytoplankton would be expected. Each year in the annual succession of the zooplankton, the plankton community of Lake Erie changes from one dominated by rotifers and copepods in the spring to rotifers, copepods, and cladocerans, including large *Daphnia* species, in the summer. In Lake Erie in 1985, phytoplankton biomass during the summer was inversely correlated with crustacean size (r = -0.81), *Daphnia* biomass (r = -0.63), and *Calanoida* biomass (r = -0.67; Figure 5).

However, biomass of filamentous algae (mostly blue-greens) was positively correlated with *Daphnia* (r = 0.98) and *Calanoida* biomass (r = 0.92); i.e., biomass of potentially inedible filamentous algae increased to 17% of the total algal biomass during the summer compared to less than 1.5% in the spring and autumn (Figure 5). Similarly, the dominance of the large *Asterionella formosa* in 1984 and its decline in 1985 may be related to the presence and dominance of *D. pulicaria* in 1984, and its decrease in importance within the ecosystem in 1985 (Bergquist et al. 1985). Biomass of large unicells, such as *Pediastrum*, and colonial algae either did not change or decreased. Not all changes were attributable to top-down control, however. The decrease in *A. flos-aquae* in Lake Erie is more

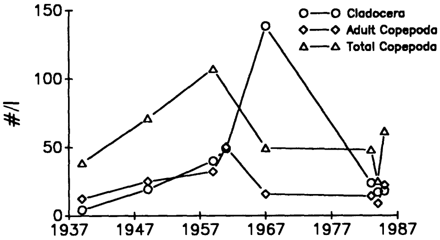

Figure 4. July and August abundance of Cladocera and Copepoda in the western basin of Lake Erie (Britt et al. 1973, Chandler 1940, Davis 1969, Hubschmann 1960). Total Copepoda refers to adults plus the naupliar stage. The number of adults and total Copepoda in 1939 and 1959 follow Bradshaw's calculations (Bradshaw 1964). Vertical tows for zooplankton were taken from 20 m to the surface with a Wildco Model 30-E28 conical net at each station (62-μm mesh net; D:L ratio = 1:3; 0.5-meter diameter mouth). If the depth of the station was less than 20 m, the tow was taken from 2 m above the bottom to the surface. Filtration volume and towing efficiency were determined with a Kahl flow meter mounted in the center of the net. After collection, the net contents were quantitatively transferred to 500-milliliter sample bottles, narcotized with club soda, and preserved with 5% formalin. For each cruise, the length of at least 20 specimens of each rotifer species was measured in each lake. Width and depth were also measured on one date for each lake to develop length-width and length-depth ratios for use in calculating species volume (Bottrell et al. 1976). Average (n = 20) length of crustaceans was determined for each station of each cruise. The dry weights of Crustacea were calculated using length-weight relationships (Downing and Rigler 1984). Identifications and counts of all plankton were done by Norman A. Andreson and his staff at the Bionetics Corporation, Chicago.

Table 1. Simple correlation (r) of phytoplankton abundance with total phosphorus concentrations and zooplankton abundance within individual cruises in Lake Erie, 1985. NO, not observed.

Date	*Daphnia pulicaria*	*Daphnia* spp.	Rotifera	Calanoida	Total phosphorus
4/24–26	.230	.526	.414	.837	.660
4/27–28	.179	−.028	.328	.767	.476
8/6–8	−.182	−.510	.321	−.705	.858
8/12–14	−.237	−.134	.028	−.537	.008
11/21–22	NO	−.145	.515	−.161	−.059
11/23–25	NO	−.495	.290	−.431	.589

readily attributed to decreased phosphorus concentration and the increasing nitrogen:phosphorus ratio (>30 to 1; Smith 1983) than by *Daphnia* cropping (Hawkins and Lampert 1989, Lynch 1980, Scavia et al. 1986).

The length of the average algal cell in 1985 (not including filamentous and colonial forms) was inversely related to the abundance of Crustacea and *Daphnia* (r = -0.79) and to the size of the Crustacea (Figure 5). That is, the weighted mean cell size of the edible portion of the algal community decreased during the summer when the larger Cladocera, such as *D. pulicaria* and *D. galeata mendotae*, were abundant and grazing. These results agree well with models (Carpenter and Kitchell 1984), experimentally verified (Bergquist et al. 1985), of size-structured plankton communities that predict shifts to small algae at low biomass of small grazers and shifts to larger algae as grazer size or biomass increase. However, the shifts in algal size and biomass reported here in Lake Erie are changes that occur each summer and do not necessarily represent permanent shifts in size structure of the algal community. The mechanism for the decrease in algal biomass may be similar to that for the spring "clear-water" phase described in some temperate lakes and experimentally shown to be caused by high *Daphnia* biomass (Lampert et al. 1986).

Top-down and bottom-up control of phytoplankton can be inferred from data on a short-term basis. Correlation coefficients of phytoplankton abundance versus total phosphorus and zooplankton abundance for each cruise on Lake Erie in 1984 are presented in Table 1. For each cruise, 11 stations were sampled covering the entire length of the lake over a two-day period in 1985. Interpretation of the correlations is as follows: a negative correlation between a zooplankton group and phytoplankton implies grazing pressure on phytoplankton, whereas a positive correlation between total phosphorus and phytoplankton abundance suggests an enhancement of phytoplankton abundance due to phosphorus.

All correlations (Table 1) were positive in April, suggesting that bottom-up effects were influencing the food web. A different situation was evident by August. Phytoplankton were blooming, and all zooplankton groups had increased in abundance. High negative correlations existed for *Daphnia* spp. and the Calanoida, suggesting a top-down influence on phytoplankton abundance. When *D. pulicaria* became dominant in August, a fairly high negative correlation existed between *D. pulicaria* and phytoplankton. By November, other species of *Daphnia* and Calanoida exerted some influence on phytoplankton abundance. Calanoids were also negatively correlated with phytoplankton abundance throughout the year, except April, suggesting a constant baseline effect on phytoplankton.

At least two factors appear to regulate phytoplankton abundance. In Lake Erie, phosphorus control was evident during the summer, but there were also fairly high negative correlations among phytoplankton and *D. pulicaria, Daphnia* spp., and calanoids. Similar correlations were reached with the 1984 data, with the exception of a stronger negative correlation between *D. pulicaria* and phytoplankton abundance. *D. puli-*

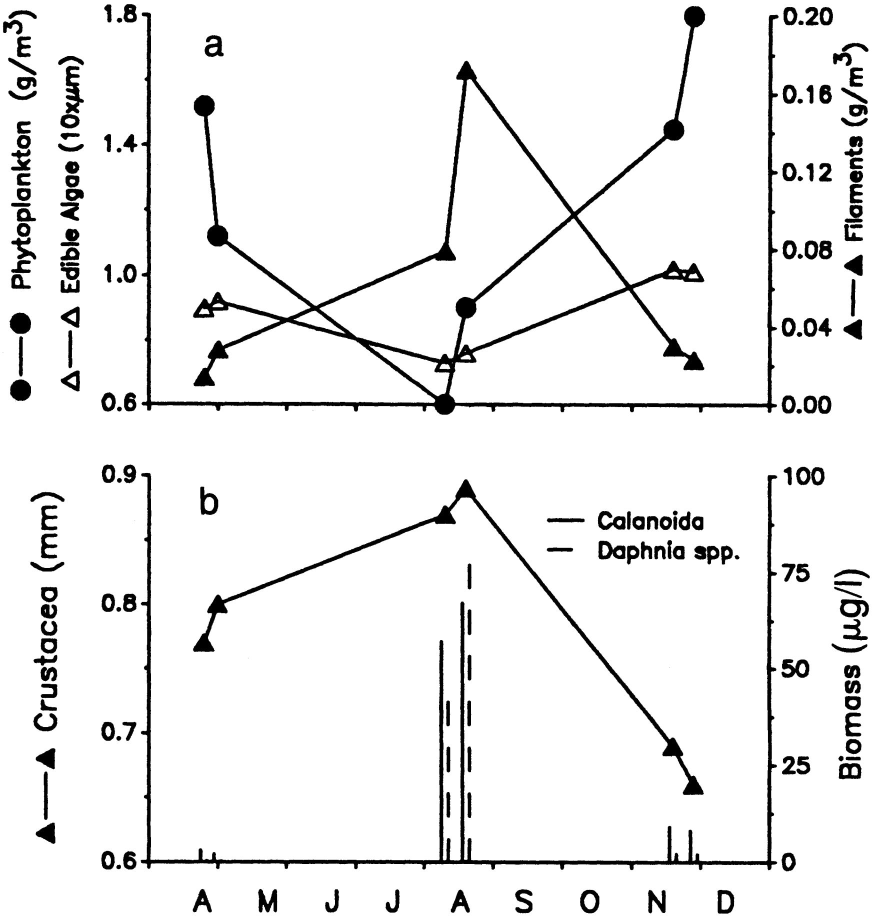

Figure 5. a. Seasonal total algal and filamentous algal biomass and mean weighted edible algal size in 1985. b. The seasonal mean crustacean size and *Daphnia* spp. and adult Calanoida abundance in 1985.

caria abundance was much greater in 1984 than in 1985. Thus top-down and bottom-up control of the trophic web of lake ecosystems exist simultaneously and either of the two mechanisms of control can vary with season. This support for the bottom-up:top-down theory of regulation of trophic biomass suggests a stronger coupling of the zooplankton-phytoplankton link in Lake Erie than might be expected for a eutrophic lake (McQueen et al. 1989).

Oxygen

Another objective of the phosphorus reduction program was restoration of year-round aerobic conditions in the bottom waters of the central basin of Lake Erie. The depletion of oxygen is caused in part by the prolific phosphorus-induced algal growth and its decay. Since 1985, estimated total annual loadings of phosphorus from all sources have been near the target load of 11,000 tons, below which an improvement in oxygen conditions was expected (Phosphorus Management Strategies Task Force 1980), but did not materialize (Rathke and McRae 1989). Typically, dissolved oxygen concentrations fall below 0.5 mg/l by late August throughout most of the central basin and remain at or below this level until autumn mixing. However, in 1987, 1988, and 1989, respectively, the mean dissolved oxygen concentrations in the central basin were 2.82, 2.04, and 4.97 mg/l in early August; 0.24, 0.50, and 3.08 mg/l in late August; and 0.36, 0.55, and 1.42 mg/l in mid-September. In 1989, dissolved oxygen was less than 1 mg/l at only 10% of the stations sampled in late August and at only 30% of the stations in mid-September before autumn mixing.

These higher ambient oxygen values of the bottom waters of the central basin in 1988 and 1989 are reflected in lower oxygen-depletion rates in 1988 (2.81 mg/l per month) and 1989 (2.69 mg/l per month; Figure 6). Values lower than 3.0 mg/l per month have been suggested as the critical point, above which produce zero oxygen values in the bottom waters (Dobson and Gilbertson 1971).

Other factors, such as meteorological conditions, biochemical processing of nonalgal sediments, and the vertical mixing of sediments by burrowing organisms, can temporarily mask the effects attributable to phosphorus reductions and increase variability in the data (DePinto et al. 1986, Rosa and Burns 1987). Given the numerous factors that affect oxygen, it is too early to make a definitive statement that oxygen conditions in the bottom waters have been restored. However, these data suggest that the persistent anoxic conditions present in the bottom waters of the central basin have improved.

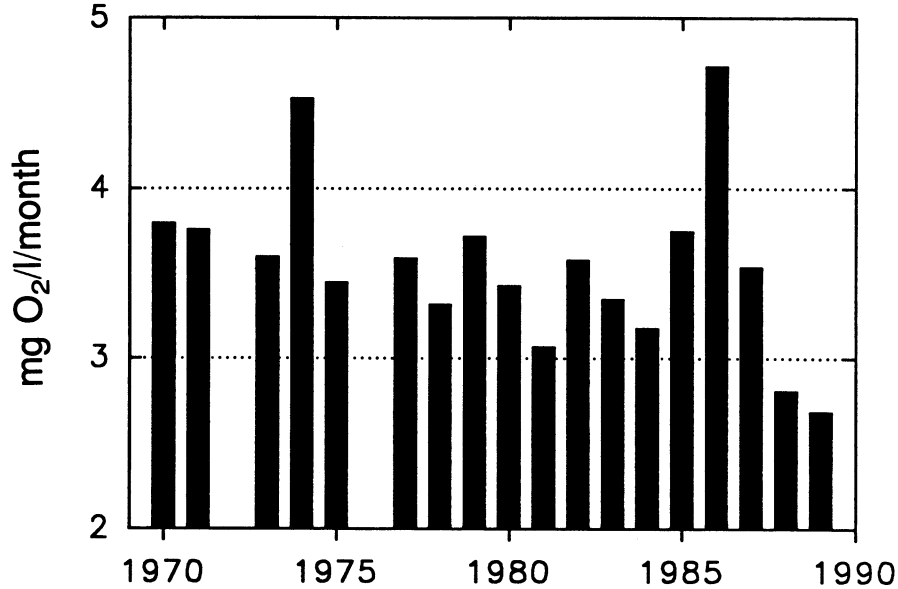

Figure 6. Average rates of oxygen depletion during thermal stratification in the central basin of Lake Erie since 1970. Values for 1970 to 1980 are taken from Rosa and Burns (1987). Oxygen depletion rates were adjusted for effects of vertical mixing, temperature, hypolimnion thickness, and season (Rosa and Burns 1987).

Conclusions

The restoration of Lake Erie to its historical assemblage of fauna and flora and its former water chemistry is not likely. For example, there is the probable extinction of the blue pike (*Stizostedion vitreum glaucum*; Werner 1980), a major commercial fishery in the first half of this century (Hartman 1972). Its genetic stock cannot be replaced.

Exotic species, such as the spiny water flea (*B. cederstroemi*), the Pacific salmon (*Oncorhynchus* spp.) and most recently the zebra mussel (*Dreissena polymorpha*) have been introduced, either accidentally or as a management practice. The spiny water flea and the zebra mussel are not easily removed from the lake, and their effects on the pelagic ecosystem are not known or are just being realized. The high abundance of the zebra mussel (as high as 70,000 per m^2) and its ability to filter relatively large quantities of water of its phytoplankton are suggested as the cause of increased water clarity in the western basin in 1989 (O'Neil and MacNeil 1990, Roberts 1990, Snyder 1989).

Major changes in ecosystem function are possible as the nearshore and offshore waters change from a pelagic foodweb to a benthic/pelagic foodweb (Roberts 1990). Similarly, conservative ion concentration (potassium, sodium, and calcium) has increased over the past 75 years as the result of surface runoff from urban, suburban, and agricultural watersheds (Beeton 1969). A reversal of these changes in water chemistry seems unlikely.

Yet there have been some dramatic successes. The phosphorus-reduction program was implemented specifically to reduce the nutrient controlling the growth of phytoplankton (IJC 1987). Up through 1985, we have observed reductions to open-lake concentrations of total phosphorus, chlorophyll a, phytoplankton abundance and biomass, nuisance species abundance and biomass, and crustacean biomass in each of the basins of Lake Erie. These changes are consistent with expectations of long-term control by nutrients.

Simultaneously, the recovery of the walleye fishery and the introduction of a new salmonine fishery have had a cascading effect on trophic structure. As top-level predators increased in abundance, forage-fish abundance decreased, perhaps contributing to the establishment of the large predaceous *B. cederstroemi* by 1985 and allowing the larger *D. pulicaria* to dominate the zooplankton community in 1984. Grazing pressure from Calanoida and *Daphnia* spp. appears to have caused a further decrease in algal abundance, an increase in filamentous algae during the summer, and a decrease in mean cell size of nonfilamentous algae. Both top-down and bottom-up control of trophic biomass appear to be working simultaneously to improve water quality in Lake Erie.

Two management practices introduced in the 1970s, one to restore the walleye and salmonine fishery and the other to improve water quality by reducing phosphorus loadings, have resulted in a general improvement in overall water quality and a restoration of function in the pelagic ecosystem of Lake Erie. There are also indications that the persistent anoxic conditions present in the bottom waters of the central basin have improved. These oxygen data are encouraging, being within the upper range of concentrations reported since 1970 (Herdendorf 1983) and suggesting cautious optimism on the ultimate objective of the phosphorus reduction program: to restore oxic conditions to the bottom waters of the central basin during summer stratification (IJC 1987).

Acknowledgments

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