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REPORT

REGULATION OF WATER QUALITY IN LAKE MICHIGAN: REPORT OF THE FOOD WEB WORKSHOP

James F. Kitchell
Center for Limnology
University of Wisconsin
Madison, Wisconsin 53706

Marlene S. Evans
Great Lakes Research Division
The University of Michigan
Ann Arbor, Michigan 48109

Donald Scavia
National Oceanic and Atmospheric Administration
Great Lakes Environmental Research Laboratory
Ann Arbor, Michigan 48105

Larry B. Crowder
Department of Zoology
North Carolina State University
Raleigh, North Carolina 26795

ABSTRACT. During the past 20 years, Lake Michigan has experienced substantial reduction in nutrient inputs, major changes in the biological community, and re-configuration of the pelagic food web. Alewife, the previously dominant zooplanktivore, has decreased to 10-20% of its former abundance, a new assemblage of zooplankton has become dominant, and summer water clarity has increased nearly three-fold in that time. This report summarizes an International Joint Commission (IJC)-sponsored Workshop on Food Web Interactions convened in Ann Arbor during 4-6 December 1985. In general, physical-chemical conditions are the major regulators of water quality during spring and fall periods. Food web effects are most manifest in offshore waters during the period of summer stratification. Discussion during the workshop led to insights regarding the causes of recent changes, their association with nutrient controls and/or food web interactions, and the likely dimensions for future effects.

ADDITIONAL INDEX WORDS: Phosphorus, nutrients, fish, zooplankton, predation.

INTRODUCTION

Recent increases in summer water clarity in Lake Michigan suggest a complex interaction derived from two very different management practices. As a result of the international water quality agreements (Slater and Bangay 1980) and subsequent management actions, a general reduction in nutrient loading has been effected over the past decade and should be expressed in water quality improvements. Similarly, international fisheries agreements (Anon. 1984) have resulted in major changes in the fish communities of Lake Michigan (Wells 1985, Jude and Tesar 1985, Kitchell and Crowder 1986). Development of sea lamprey control programs and increased stocking of salmon and trout now form the basis for an immensely successful, high-value sport fishery (Talhelm *et al.* 1979, Talhelm 1985). The effects of enhanced predator populations cascade through food webs and can be expressed in a miscellany of water quality variables (Carpenter *et al.* 1985). Thus, observed water quality changes can be associated with nutrient abatement and/or food web effects.

Scavia *et al.* (1986) and Lesht and Rockwell (1985) provide evidence that the general reduction in phosphorus loading over the past decade is reflected in surface water chemistry. An important departure from the general trend became most apparent during the summers of 1983-85 as evidenced by substantial increases in water clarity. Although other limnological variables show less apparent effects, the increase in water clarity is readily perceived by the public and, therefore, of interest to both the basic and applied scientific institutions. Recent observations with regard to composition of the biological community and food web interactions also demonstrate most extreme changes during the summers of 1983-85 (Scavia *et al.* 1986). For example, the exotic alewife declined to abundances lower than any observed for more than two decades and many native fish species exhibited increases of equivalent magnitude (Wells 1985).

This report summarizes the results of a workshop organized through the Ecological Considerations Committee under the aegis of the Science Advisory Board of the International Joint Commission. The general goal of the workshop was to bring together researchers currently involved with the various components of the interactions between nutrient control and food web control of water quality. This meeting sought to increase our collective understanding of the cause-and-effect relationships underlying the recent changes in Lake Michigan. In addition, we invited representatives of research groups and agencies that might profit from our discussions as they developed plans for work on other Great Lakes. The workshop was held in Ann Arbor, Michigan, during 4-6 December 1985. This brief summary is designed to convey a sense of the magnitude of changes occurring in Lake Michigan and the spectrum of forces effecting those changes.

HIGHLIGHTS OF THE CONTRIBUTIONS

Lake-wide stock assessment data presented by L. Wells (U.S. Fish and Wildlife Service) document the recent, substantial changes in abundance of fishes in Lake Michigan (Wells 1985). D. Jude (University of Michigan) presented evidence from nearshore monitoring in southeastern regions of the lake that suggests changes similar to those for the whole lake but preceding them by several years (Jude and Tesar 1985). The alewife (*Alosa pseudoharengus*) population increase during the early 1960s had profound effects on Lake Michigan's zooplankton (Wells 1970). Alewife remained the dominant zooplanktivore for nearly two decades but has declined since the middle 1970s to 10-20% of former abundance. Populations of native fishes such as the deepwater cisco (*Coregonus hoyi*), deepwater sculpin (*Myoxocephalus thompsoni*), and yellow perch (*Perca falvescens*) have dramatically increased in the past few years. As presented by D. Stewart (University of Wisconsin), increasing predation by salmon, trout, and charr is the most parsimonious reason for alewife decline (Steward *et al.* 1981).

M. Hansen (Wisconsin DNR) analyzed size distributions of salmonines taken in Wisconsin's sport fisheries since 1969 (Hansen 1986). Although there is evidence of recent reduction in the mean size and condition of "trophy" chinook salmon (*Oncorhynchus tshawytscha*), the several-fold reduction in estimated alewife abundance—the major prey species—has not been generally reflected in predator growth and condition indices recorded through 1984. This unexpected result remains unexplained.

Extensive surveys of benthos were conducted throughout the southern basin of Lake Michigan during the 1960s. T. Nalepa (NOAA, Great Lakes Environmental Research Laboratory) designed and conducted a similar program during 1980 as a basis for assessment of changes over the past two decades (Nalepa 1987). The 1980 abundance of major benthic species was generally severalfold that observed during the 1960s. Benthic invertebrate populations increased in ways that can be directly associated with the general decline in alewife observed after peak abundance occurred in the mid-1960s. L. B. Crowder (North Carolina State University) summarized recent work conducted at southern basin stations near Grand Haven, Michigan. Deepwater cisco is now much more abundant than alewife in that region of the lake and is likely responsible for local declines in the abundance of their primary benthic prey (*Mysis relicta* and *Pontoporeia affinis*) observed over the period of 1977-85 (Crowder *et al.* 1987).

As summarized by M. Evans (University of Michigan), large zooplankton began to reappear in increasing abundance as the alewife decline developed in the early 1980s. In particular, the increase of large *Daphnia* species in offshore waters during summers of 1983-85 is regarded as substantial evidence of changing food web interactions. Gradual changes in the nearshore zooplankton also reflect the reduction in predation by declining alewife followed more recently by increased predation on larger zooplankton as nearshore native fish populations recovered (Evans and Jude 1986). Discussion confirmed the general impression that recent fish and zooplankton community changes have and are occurring as gradients seen first in the nearshore, southeastern regions of the lake then proceeding over time to the offshore and more northerly and westerly regions. The sustained high abundance of large *Daphnia* in offshore waters during summer months remains remarkable in that the recovery of native zooplanktivorous fishes has not yet had apparent effect on this typically preferred prey.

D. Scavia (NOAA, Great Lakes Environmental Research Laboratory), demonstrated that reduced concentrations of chlorophyll and increased transparency are directly associated with the seasonal increase of large cladocerans. Based on the experimental studies conducted by J. Lehman (University of Michigan) in collaboration with Scavia's cruise series, total water column grazing rates have increased several-fold as *Daphnia* spp. have come to dominance in summers since 1983. Intensified grazing of the epilimnetic phytoplankton is the apparent cause of remarkably increased water transparency most apparent during the latter months of recent summers (Scavia *et al.* 1986).

A review of water quality data collected over the last two decades (B. Lesht, Argonne National Laboratory) reveals that the most general indicator of water quality—Secchi depth—has changed nearly three-fold since alewife were most abundant. In the middle 1960s, summer Secchi depths recorded before whitings began were generally 4–5 meters (Lesht and Rockwell 1985). Summer Secchi depths were regularly 15 meters or more in recent years (Scavia *et al.* 1986).

Historical and paleolimnological studies also revealed major shifts in community composition and food web interactions. A. S. Brooks' (University of Wisconsin—Milwaukee) analysis of phytoplankton community changes determined at the Milwaukee water intake suggest long-term trends in phytoplankton composition that reflect interannual differences due to seasonal, weather effects and a main trend due to altered food web interactions (Brooks *et al.* 1984). E. F. Stoermer (University of Michigan) presented results from analysis of sediment cores which suggest that changes in diatom species composition may have begun before food web effects were apparent (Stoermer *et al.* 1985). It is likely, therefore, that changes in relative nutrient availability (nutrient ratios for N, P, and/or Si) have played a major role in the historic diatom community. J. F. Kitchell's (University of Wisconsin) review of analysis of zooplankton fossils and plant pigments in cores also reflects the major changes in food web interactions coincident with the invasion and explosive increase of alewife during the 1960s (Kitchell and Carpenter 1987). Changes in the abundance and morphology of *Bosmina* fossils reflect the relative abundance of large, predaceous copepods which were substantially reduced during the period of abundant alewife. At the same time, small herbivorous copepods increased and the concentration of grazing-related chlorophyll degradation products increased in sediment samples. The most recent decline in alewife abundance and dramatic changes in the plankton community observed since 1980 are not yet represented in the sediment record.

DISCUSSION

Controls of Water Quality

Discussion during the presentation and working group sessions evoked a general view of the hierarchy and interactions of factors currently controlling water quality in Lake Michigan. Spring phytoplankton densities are regulated by a combination of vernal mixing, nutrient loading, and relative nutrient concentrations. Community composition is regulated by competition for nutrients, sinking, and increased light penetration which interact strongly as thermal stratification develops in late spring. The conditions, mechanisms, and dynamics during this period are summarized by Scavia and Fahnenstiel (1987).

Once summer stratification is well developed, food web interactions become a major regulator of the plankton community. Summer phytoplankton densities and composition are controlled by nutrient cycling, and grazing by increasing zooplankton populations. Size-selective predation determines the abundance and size of the zooplankton. Recent reduction in the abundance of the alewife due to predation by stocked salmonines is largely responsible for the observed increase in summer water clarity effected through intense grazing by greater numbers of large zooplankton. The major components of food web interactions are summarized in

Figure 1. Although these conditions have been developing to varying degrees for several years, they have been most apparent since 1983 and will likely persist in future years given the current and intended practices of fisheries agencies that determine stocking policy.

Summer water clarity is strongly influenced by a cascade of predation effects that begin with intense piscivory, extend to intense herbivory (Carpenter *et al.* 1985), and are expressed in competition for nutrients (Scavia *et al.* 1988). In the years when alewife was the dominant zooplanktivorous fish, summer zooplankton biomass was primarily comprised of calanoid copepods which are highly selective but relatively ineffective algal grazers. During the present decade, alewife have declined in concert with the increased predation of stocked salmonines. Large cladocerans (*Daphnia* spp.) have become increasingly abundant during summer months. *Daphnia* are much less selective and highly efficient grazers. Their feeding rates can exceed the growth rates of phytoplankton, and water clarity increases as a consequence.

Although food web effects are most manifest during a relatively short period of the annual limnological cycle (Fig. 1), their strongest occurrence during summer months makes improved water quality very apparent to the public. Recreational use of the lake is most intense during those times when increased water clarity is most obvious. Nearshore water quality may exhibit effects of local nutrient sources and food web interactions but the average condition of surface waters will continue to be improved as food web effects in offshore waters develop and persist each summer.

Management for the Future

The potential for enhancement of food web controls of water quality remains poorly known. The current biological community is dominated by interactions among exotic species. Most of the stocked salmonines and the alewife are not native species in the early history of Lake Michigan. The largest cladoceran species (*Daphnia pulicaria*) which was very abundant in the 1983-84 summer zooplankton is not known from any previous work in Lake Michigan.

There is reason to be concerned about the stability of the present community and little other than speculation can be offered with regard to its future. Through the auspices of the Great Lakes Fishery Commission, plans are now being developed toward the definition of fish community goals and the coordinated management programs required to establish and sustain them. The resultant fisheries management practices may have substantial impact on water quality. Among the possible outcomes is a reversal of water quality trends in the nearshore zone; reduction of alewife populations has been accompanied by a remarkable increase in littoral fishes such as the yellow perch. Their effects on the nearshore plankton community may be the opposite of those observed in the offshore waters. More recently, the appearance and rapid increase of the exotic, predaceous cladoceran *Bythotrephes* raises the prospect that an invertebrate predator may flourish in the absence of significant populations of planktivorous fishes. *Bythotrephes* preys on other cladocerans; it may reduce *Daphnia* populations and their grazing effect on offshore water clarity during summer months (Scavia *et al.* 1988).

Clearly, recent changes observed in Lake Michigan and the cause-effect scenario developed above demonstrate the necessity for coordination and effective interaction among agencies charged with water quality considerations and those responsible for fisheries management. We now enjoy improvements in both worlds with regard to public value of Lake Michigan: offshore water clarity during summer months and fishing are better than ever observed in recent decades!

There remain substantial unknowns with regard to the limits of current trends, the specific regulators of variability, and the stability of the food web system that creates them. There are strong reasons to expect similar developments in other lakes. Stocking rates are increasing in Lakes Superior, Huron, Erie, and Ontario. The states of Michigan and Wisconsin reduced their 1985 and 1986 stocking rates for Lake Michigan, yet the major impact of predation will not be expressed until fish stocked before 1985 complete their life cycle. Piscivory will peak in the period of 1987-89 (Kitchell and Crowder 1986). Restrictions on stocking policy are largely precautionary but will likely persist until a more effective understanding is developed of the current predator-prey system and a rational basis for community-level (i.e., food web) management is formulated. It is no small irony that the alewife—previously a curiosity and then a major nuisance—is now viewed as a major resource.

Water quality improvements sought through nutrient abatement have and will continue to be effective in Lake Michigan. Management that reg-

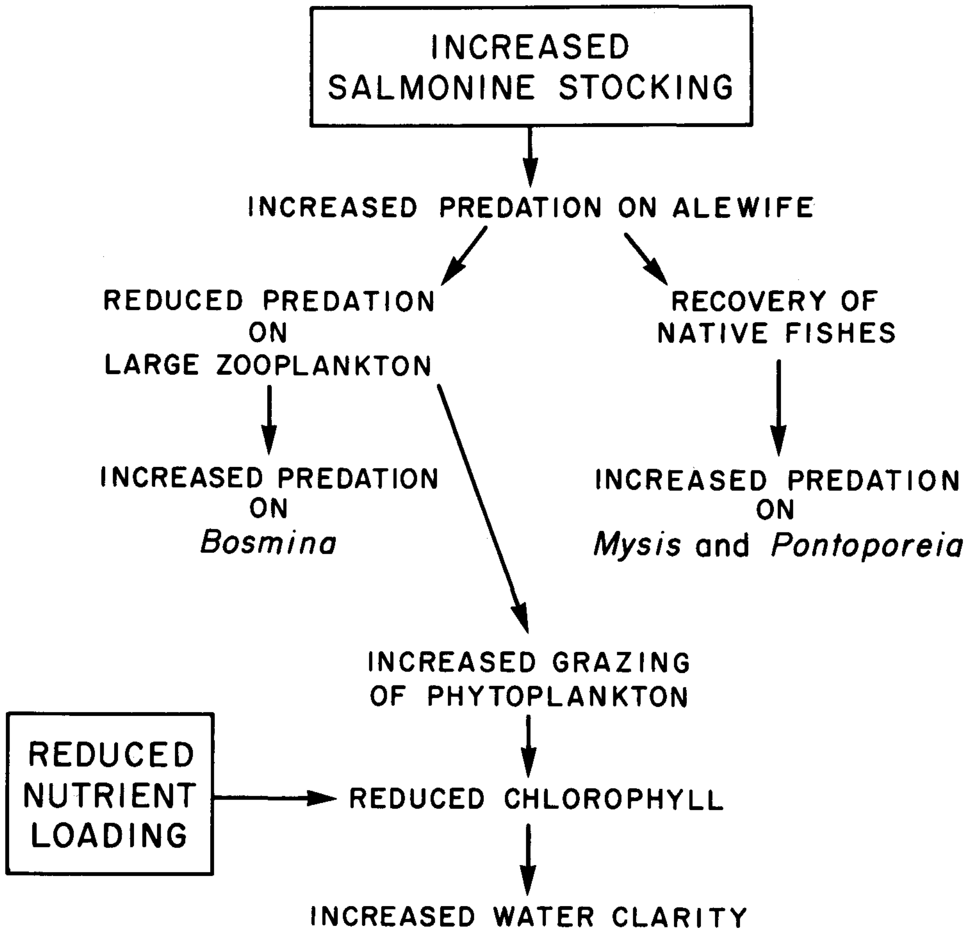

FIG. 1. Flow diagram of cause-effect interactions expressed during summer conditions in Lake Michigan. Boxes denote direct management actions.

ulates food web effects has and may continue to enhance water quality improvements. The extent and potential for a coordinated management approach that takes advantage of the synergism of nutrient abatement and food web controls has been insufficiently explored. Clearly, research and management planning could profit from a dual consideration in developing programs for future work in the Great Lakes.

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