Rehabilitation of Lake Ontario: the Role of Nutrient Reduction and Food Web Dynamics

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The Laurentian Great Lakes have a complex history of changes due to eutrophication, invasion of exotic species, and fisheries and phosphorus management practices. Remedial actions have reduced nutrient loadings and enhanced the role of food web interactions in improving water quality. Workshops sponsored through the United States – Canada International Joint Commission have addressed the relative importance of nutrient abatement and/or food web manipulation in affecting water quality trends. Both controls have combined to enhance water clarity in Lake Michigan. Lake Ontario has already exhibited the effects of nutrient controls and may be on the verge of manifesting food web controls. Research and monitoring recommendations to elucidate the effects of nutrient and food web controls include the following: (1) water quality and fisheries agencies must coordinate monitoring activities, standardize techniques, and establish and maintain long-term data sets to evaluate the effects of water quality and fisheries programs separately and together; (2) controlled, mesoscale, whole-system experiments should be performed to quantify rates (e.g. growth, predation, etc.) of food web interactions; and (3) the scientific community should promote research which quantifies the impact of changes in food web dynamics on changes in toxic substance levels in Great Lakes fishes.

Au cours de leur histoire, les Grands Lacs Laurentiens ont été transformés par l'eutrophisation, l'invasion d'espèces exotiques et par la manière dont les phosphates et les pêches ont été gérés. Des mesures correctives ont permis de réduire l'accumulation de nutriments et mis en valeur le rôle des interactions trophiques dans l'amélioration de la qualité de l'eau. Des ateliers parrainés par la Commission mixte internationale États-Unis – Canada ont traité de l'importance de réduire la quantité de nutriments dans ces eaux ou d'agir sur le réseau alimentaire pour les assainir. Ces deux types d'action ont permis de rendre plus pur les eaux du lac Michigan. Les effets des mesures de réduction des nutriments se sont déjà faits sentir dans le lac Ontario et on s'apprête à y agir sur le réseau alimentaire. Voici certaines recommandations en matière de recherche et de surveillance visant à améliorer notre connaissance des effets des mesures de contrôle des nutriments et du réseau alimentaire : 1) les organismes responsables de la qualité des eaux et des pêches doivent coordonner leurs activités de surveillance, normaliser leurs méthodes et établir et maintenir des ensembles de données à long terme leur permettant d'évaluer séparément ou ensemble les effets de la qualité de l'eau et des programmes portant sur les pêches; 2) des expériences contrôlées à échelle moyenne et de type holistique devraient être menées de façon à quantifier les taux (de croissance, de prédation, etc.) des interactions ayant lieu dans le réseau alimentaire et 3) la communauté scientifique doit promouvoir les recherches visant à quantifier l'impact des modifications de la dynamique du réseau alimentaire sur les concentrations des substances toxiques présentes dans les poissons des Grands Lacs.

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In the past 10 yr, two management strategies have evoked dramatic effects in the Great Lakes: phosphorus management and fishery management. The 1972 Great Lakes Water Quality Agreement adopted a phosphorus management strategy to control nuisance algal problems in the lower lakes and maintain the oligotrophic state of the upper lakes. Phosphorus loadings to the Great Lakes have decreased substantially (e.g. approximately a 13 000 tonne (t) decrease to Lake Erie since 1972) and resulted in dramatic improvements, particularly in Saginaw Bay and the lower Great Lakes (Hartig and Gannon 1986). Simultaneously, the fishery interests (Great Lakes Fishery Commission or GLFC) implemented a strategy to control the parasitic sea lamprey (*Petromyzon marinus*) which provided an opportunity to stock Pacific salmon and native trout. Over the past 10 yr, salmon stocking in the Great Lakes has increased substantially (e.g. over 15 million salmon and trout stocked in Lake Michigan in 1984), resulting in a sport fishery worth an estimated \$2–4 billion per annum (Talhelm 1987). Fundamental management questions include the following: are phosphorus management and fishery management strategies compatible? Will nutrient reductions limit fish production? Can predator stocking, through trophic cascading effects (Carpenter et al. 1985), alter planktonic communities and, ultimately, water quality indicators?

To address these questions requires an understanding of the linkages between management strategies and ecosystem changes. To help identify the effects of phosphorus abatement (i.e. nutrient control) and salmonine stocking (i.e. food web control via predation) on Lake Michigan, the Science Advisory Board of the International Joint Commission (IJC) hosted the 1985 Food Web I Workshop which focused on an evaluation of the relationship between recent improvements in water quality and the current changes in biological community structure. Lake Michigan historical data documented the decrease in alewife (*Alosa pseudoharengus*) abundance that coincided with increased stocking of piscivores and increases in abundance of native species such as bloaters (*Coregonus hoyi*) and yellow perch (*Perca flavescans*) (Kitchell and Crowder 1986). Large-sized *Daphnia* also increased in abundance during summer. Concomitantly, total phosphorus loadings and in-lake concentrations decreased, while water clarity increased substantially (Scavia et al. 1986).

The Food Web I Workshop concluded that nutrient abatement probably had reduced open-lake phosphorus levels in Lake Michigan in winter which, in turn, reduced the amount of spring phytoplankton and spring chlorophyll (Kitchell et al. 1988). Salmon predation likely initiated a cascade effect in which reduced alewife abundance caused an increase in abundance of large-sized *Daphnia* in open waters. The higher rates of grazing by these *Daphnia* on phytoplankton led to increased summer water clarity. For further information on the Food Web I Workshop, see Kitchell et al. (1988). A more extensive history of food web changes in Lake Michigan is presented in Scavia et al. (1986), Kitchell and Carpenter (1987), and Scavia and Fahnenstiel (1987).

Subsequent to the Food Web I Workshop, the IJC hosted the 1987 Food Web II Workshop which focused on food web dynamics in Lake Ontario. Lake Ontario was chosen because its phosphorus and salmon stocking trends were following those in Lake Michigan, and Lake Ontario would probably be the next Great Lake to manifest the effects of food web control. The purpose of this paper is to present a summary of the conclusions and recommendations from the Food Web II Workshop.

Food Web II Workshop

Approximately 40 scientists with expertise on Lakes Ontario and Michigan took part in the Food Web II Workshop. The workshop began with a series of presentations on long-term empirical data sets from Lake Ontario followed by presentations on how such information could be interpreted and used to manage large lakes using a whole-system approach. Two groups (i.e. nutrient controls and food web controls) were formed to answer specific questions related to trends and possible causes. The groups then came together to discuss and debate their findings and reach consensus on conclusions and recommendations. Presented below are the major conclusions on limnological changes in Lake Ontario, a comparison of the recent changes in the physicochemical and biological characteristics of Lakes Ontario and Michigan, and the consensus recommendations from workshop participants. More detailed information on the Food Web II Workshop and the abstracts and data presented at the workshop can be found in IJC (1987a).

Limnological Changes in Lake Ontario

Evaluation of trends in Lake Ontario's food web proved to be difficult because in certain areas the data were limited and in others there have not been dramatic changes in recent years. Based on the review of the available data from 1970 to 1985 (IJC 1987a), the following conclusions were drawn:

(1) Total phosphorus loads have decreased by 80% since 1972 and are approaching the target set by the Great Lakes Water Quality Agreement.

(2) Winter–spring total phosphorus (P) decreased slowly from the 1971 high of approximately 25 $\mu g \cdot L^{-1}$ and then more dramatically after 1977; the current concentration is near 14 $\mu g \cdot L^{-1}$. During the same time period, summer epilimnetic total P decreased only from approximately 17 to 15 $\mu g \cdot L^{-1}$. Nitrate concentrations continue to increase, as is the case in most of the other Great Lakes (IJC 1987b). In Lake Ontario, increasing nitrogen (N) and decreasing P concentrations have resulted in winter–spring total nitrogen/total phosphorus (TN/TP) ratios that increased from about 16 in 1977 to over 32 in 1982. N/P ratios continue to increase annually.

(3) Summer epilimnetic chlorophyll concentrations have not changed over the period of analysis, although some evidence exists to suggest that algal biomass has decreased. There also appear to be recent shifts in algal species composition, including the disappearance of potentially N-fixing blue-greens and an increase in the relative proportion of small species.

(4) No major changes in water clarity (e.g. Secchi disc transparency) have been observed in recent years.

(5) A comparison of zooplankton community structure and abundance from 1981 to 1985 with that of earlier studies (1967–72) found no detectable change in the range of abundances or community composition between the two periods. This is consistent with Taylor et al. (1987) who found no marked change in zooplankton during the 1970s. Few changes were observed during the 1980s, based on the internally consistent analysis of BIOINDEX stations (a Lake Ontario long-term biological monitoring program established by the Department of Fisheries and Oceans (Canada)).

(6) Lake Ontario zooplankton size structure and species composition seem strongly regulated by heavy alewife predation.

(7) Alewife abundance has varied considerably year-to-year, since it increased after the major 1976–77 die-off; however, no clear trend in abundance is obvious after 1980 (O'Gorman et al. 1987). In recent years, alewives have generally been in poor condition.

(8) Slimy sculpin (*Cottus cognatus*) and, perhaps, rainbow smelt (*Osmerus mordax*) populations in the Kingston basin have declined as lake trout (*Salvelinus namaycush*) stocking has increased there (Christie et al. 1987a).

(9) Coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) stocking in Lake Ontario increased from 40 000 in 1968 to 5 415 000 in 1984.

(10) Significant piscivore effects (predator control) are not broadly demonstrated in Lake Ontario. Some recent reductions in slimy sculpin density and the condition of adult chinook salmon have been observed, but longer time series and larger spatial coverage are needed. Recently, food web – nutrient interactions have been identified as an important factor in water quality improvements in Lake Ontario's Bay of Quinte (Minns et al. 1987).

(11) Recent reductions in phosphorus loading and open-lake phosphorus concentration do not appear to be limiting fish production.

The phytoplankton trend data suggest a rather stable period, with only subtle changes in algal species composition. This has occurred during the more obvious decreases in TP and increase in TN concentrations (see IJC 1987b). The lack of correlation between TP and chlorophyll (Stevens and Neilson 1987) changes seem linked to Lake Ontario's light climate and TN/TP ratio. Model analyses of Lake Ontario during the early 1970s indicated that the lake became nitrogen limited by summer's end (Thomann et al. 1975; Scavia 1979, 1980). Because winter–spring TN/TP has only recently crossed the threshold of 29 set by a cross-sectional analysis of several lakes (Smith 1983) for transition from nitrogen-limited to phosphorus-limited lakes, it is likely that until about 1982–83, Lake Ontario's summer phytoplankton potentially were limited by nitrogen. Only after those years would further decreases in TP result in decreased phytoplankton biomass or chlorophyll. TP decreases after 1983 have been slight compared with the 1977–82 period. Thus, chlorophyll changes should continue to be small.

It appears that the subsurface light climate in Lake Ontario may also play a significant role in the apparent lack of correlation between TP decreases and phytoplankton changes. Summer penetration depth of 1% of surface light reaches only 9–10 m, which is 1–2 m short of the mixing depth. Therefore, Lake Ontario phytoplankton may also be limited by the availability of light during much of the year.

There also appears to be an uncoupling (i.e. components behave relatively independently) of phytoplankton and zooplankton in the open waters of Lake Ontario. This notion comes from two sources. The first is based on correlations between the abundance of edible algae (defined by size of extant cells) and measures of zooplankton production (e.g. egg ratios) Except for a few daphnid species, this correlation is very low, indicating that this size range of algae is perhaps not the direct nutrition of all zooplankton. A second line of reasoning derives from comparison of algal size spectra in relation to the preferred food sizes of the dominant zooplankton. While a shift to smaller phytoplankton sizes has been noted in recent years, the dominant forms until then have been relatively large compared with the preferred size for the dominant small zooplankton, *Bosmina* spp.

It was suggested that the still relatively high phosphorus concentrations allow the large algal forms to persist, leading to a size mismatch of zooplankton and their food supply. Food web influence may also be important if size-selective predation by alewife structures the zooplankton size spectrum toward small species. An alternative hypothesis is that predation by alewife forced size structure toward these smaller *Bosmina*, and their removal of smaller algal cells resulted in the shift toward more grazing-resistant, larger algal cells. Among Lake Ontario's offshore zooplankton, little evidence of change over the past decade suggests that size-selective predation by zooplanktivorous fishes (primarily alewife) and/or invertebrate predators is the major cause of apparent uncoupling between herbivores and the phytoplankton–nutrient interactions. However, without more information concerning the relative rates of algal and zooplankton production and loss in Lake Ontario, it is difficult to establish causality of food web and nutrient controls at the phytoplankton–zooplankton interface.

Alewife is a critically important species in the Lake Ontario food web. It forms the primary prey of all species of adult salmonines (Brandt 1986), is an efficient size-selective zooplanktivore that has the ability to dramatically alter zooplankton abundance and community structure, and has been shown to impact recovery of native species (e.g. predation on yellow perch larvae; Brandt et al. 1987). Yet the key factors which apparently control alewife abundance (recruitment variabilities, predation, overwinter mortality) are not understood. Alewife relative abundance has not declined steadily in Lake Ontario during recent years. Although salmon stocking in Lake Ontario has increased to the point where total number stocked per unit area or per unit volume is much higher than in the other Great Lakes, significant predation effects are not yet broadly demonstrated.

What directions might Lake Ontario take under nutrient and grazing control? If phytoplankton are phosphorus limited, then further reductions in winter–spring TP should result in lower summer epilimnetic phytoplankton biomass or chlorophyll concentrations; however, as TP reductions will likely be small as phosphorus target loads are approached, a more reasonable expectation is one of small changes in phytoplankton density accompanied by subtle species shifts. Shifts will likely be toward smaller species and perhaps a larger percentage of diatoms in summer as the silicon/phosphorus (Si/P) ratio increases. As TP continues to decrease, primary production may also decrease, with consequential reductions in grazer biomass (zooplankton and benthos); however, those changes will again be slight and perhaps undetectable with current methods. Overall, trends tied to effects of TP reductions will probably be slow, small, and subtle.

If there is a dramatic decrease in alewife abundance due to food web influences or high winter mortality, and other major planktivores do not replace alewife, then we may expect certain abrupt changes similar to those observed in Lake Michigan. There may be shifts to large zooplankton body size within the extant assemblage, followed by species shifts to larger organisms as intraspecific plasticity reaches limits. Larger body size and greater per capita grazing rates could evoke a reduction in algal biomass. While decreases in algal biomass could also follow nutrient reduction, mean algal cell size would likely shift to larger, less edible species under grazer control rather than to smaller species expected under nutrient control. Release from alewife planktivory should be accompanied by released benthivory and a possible increase in vulnerable benthic prey.

Intensive salmon stocking is relatively recent. Predator effects on alewife stocks may not be apparent until the end of this decade, and then perhaps only as a depensatory (constant amount per predator) agent acting in conjunction with density-independent mortality (Kitchell and Crowder 1986). In any event, salmon stocking rates are and have been such that if predation effects are to occur, they should be manifest within the next few years.

Expected shifts in community structure caused by salmonine predation would be a reduction in the size and abundance of zooplanktivores which form the main prey of salmonines and a corresponding increase in the size spectra upon which these zooplanktivores feed. One might expect a decrease in the abundance of target zooplanktivores, an increase in the abundance of large species of zooplankton such as *Daphnia* spp., and an increase in abundance of nonprey fishes such as lake herring (*Coregonus artedii*), yellow perch, and white perch (*Morone americana*). Shifts in fish growth rates and condition would be expected as prey abundances change. Future effects of predaceous *Bythotrephes* sp., a recent invader, cannot be predicted, although preliminary evidence suggests that *Bythotrephes* sp. can quickly dominate the dynamics of zooplankton populations, but its influence may subside equally rapidly (Lehman 1988). A new exotic, the zebra mussel (*Dreissena polymorpha*), has recently appeared in Lake Ontario. Its dramatic effects on water clarity in western Lake Erie suggest that water quality changes in Lake Ontario may include effects from a complexity of grazing activities (J. H. Leach, Ontario Ministry of Natural Resources, pers. comm.).

Lake Ontario – Lake Michigan Comparison

Most of the workshop participants' expectations for Lake Ontario were derived from observed changes in Lake Michigan, but it was well recognized that the Lake Michigan data are largely corollary in nature and are confounded by cooccurring perturbations and that Lake Michigan and Lake Ontario species complements and sampling methods differ. In Lake Michigan, phosphorus abatement probably reduced winter open-lake phosphorus levels which, in turn, reduced the amount of spring phytoplankton and spring chlorophyll (Kitchell et al. 1988). Salmon predation likely initiated a cascade effect in which reduced alewife abundance caused an increase in abundance of large-sized *Daphnia* in open waters. Higher grazing rates by these *Daphnia* on phytoplankton led to increased summer water clarity.

However, these food web effects observed in Lake Michigan have not been broadly manifest in Lake Ontario (Table 1). Several aspects of Lake Ontario's ecology and limnology are different from those of Lake Michigan. These may be substantial enough to result in different responses of the Lake Ontario ecosystem to similar stimuli (Table 2). Some of the notable differences include the following:

(1) Lake Ontario has a much smaller silica reserve in winter, which likely limits spring diatom production there more severely than in Lake Michigan. The dominance of spring net diatom production in Lake Michigan may be an important precursor for subsequent grazer control in the summer epilimnion.

(2) During summer stratification, Lake Ontario's primary production is limited to the epilimnion (mixing depth 11–12 m; 1% light at 9–10 m) whereas a substantial portion of Lake Michigan's summer production is below the thermocline (mixing depth 10 m; 1% light at 27–33 m).

(3) Lake Ontario's zooplankton community has a sizeable population of invertebrate grazers (e.g. *Cyclops*, *Diacyclops*) that were not important in Lake Michigan, and their influence on the zooplankton community, should vertebrate predation be released, is not known.

(4) Lake Ontario zooplankton is presently dominated by *Bosmina*, a small cladoceran, rather than by the calanoid copepod *Diaptomus* spp. that dominated Lake Michigan's summer population before the rise of *Daphnia*.

(5) Based on paleolimnology, it appears that Lake Michigan long-term algal succession never progressed beyond conditions found in the early 1900s in Lake Ontario. Thus, entirely different Lake Ontario responses are possible.

TABLE 1. Comparison of Lake Michigan's and Lake Ontario's recent trends in indicators of change.

	Lake Michigan	Lake Ontario
Salmonids	Annual stocking of coho and chinook salmon has increased from 660 000 in 1966 to 10 664 000 in 1984	Annual stocking of coho and chinook salmon has increased from 40 000 in 1968 to 5 415 000 in 1984
Planktivores	Alewife (the dominant zooplanktivore) abundance decreased by 80–90% between the mid-1970s and the early 1980s	The size of the alewife population fluctuated widely between 1977 and 1986 because of two weather-related die-offs (die-offs in winters of 1976–77 and 1983–84)
Zooplankton	*Daphnia pulicaria*, a relatively large cladoceran, was first observed in autumn 1978 and became the summer dominant in 1983	Limited data available. A comparison of zooplankton community structure and abundance from 1981 to 1985 with that of earlier studies (1967–72) found no detectable change in the range of abundances or community composition between the two periods
Phytoplankton	Historical studies suggest changes in species composition. Spring chlorophyll *a* concentrations decreased slightly between 1976 and 1984. No dramatic change in summer chlorophyll *a* concentration between 1976 and 1984	Between the late 1960s and early 1980s there has been a change in species composition toward more species indicative of mesotrophic and oligotrophic conditions and an increase in abundance of small species
Water transparency	Summer Secchi disc depths increased from 4–5 m in mid-1960s to 15 m or greater in the early 1980s	No apparent trend between the late 1960s and early 1980s
Phosphorus concentration	A slight decrease in mean annual total phosphorus concentration from approximately 7 $\mu g \cdot L^{-1}$ in 1976 to approximately 4 $\mu g \cdot L^{-1}$ in 1985	Spring, midlake total phosphorus concentration has decreased from a maximum of 30.6 $\mu g \cdot L^{-1}$ in 1973 to 10.7 $\mu g \cdot L^{-1}$ in 1985
Phosphorus loading	A decrease in municipal total phosphorus loading from 2325 $t \cdot yr^{-1}$ in 1975 to 894 $t \cdot yr^{-1}$ in 1985	A decrease in municipal total phosphorus loading from 9860 $t \cdot yr^{-1}$ in 1972 to 1710 $t \cdot yr^{-1}$ in 1985

TABLE 2. Municipal total phosphorus loadings ($t \cdot yr^{-1}$) and annual stocking (thousands) of coho and chinook salmon in Lakes Michigan and Ontario. Phosphorus data were obtained from IJC (1987b) and salmon stocking data were obtained from M. Dakota (Great Lakes Fishery Commission, Ann Arbor, MI, pers. comm.).

	Phosphorus loadings		Salmon stocking	
Year	Michigan	Ontario	Michigan	Ontario
1966	—	—	660	—
1967	—	—	2534	—
1968	—	—	1888	40
1969	—	—	3998	309
1970	—	—	5447	580
1971	—	—	5068	520
1972	—	9860	4782	969
1973	—	—	5251	1208
1974	—	—	6809	1843
1975	2325	4220	6785	1958
1976	2336	3082	6580	936
1977	1660	3089	6064	352
1978	1314	2728	8050	674
1979	1224	2898	9028	999
1980	1047	2512	9049	1283
1981	934	2208	7198	1843
1982	885	2115	8493	2557
1983	960	1903	8903	3547
1984	894	1894	10664	5415
1985	894	1710	9137	4293

Despite such differences, workshop participants felt that harbingers of Lake Ontario food web effects should resemble those observed in Lake Michigan. Two classes of evidence parallel the sequence of events in Lake Michigan. First, Lake Ontario zooplankton size structure and species composition seem strongly regulated by heavy alewife predation. Second, slimy sculpin and, perhaps, rainbow smelt populations in the Kingston basin have declined as lake trout stocking has increased there. A similar decline of slimy sculpin, presumably due to predation by stocked lake trout, occurred in Lake Michigan prior to the major decline of alewife. Given that salmonine consumption levels in the lake as a whole have not yet peaked, we may be on the verge of seeing predation effects. Alewives are generally in poor condition and winters have not yet been severe during times of high salmonine predation rates. Large *Daphnia* populations (e.g. *D. pulicaria*) are the key component of a suite of changes that should result if and as alewife stocks are reduced by piscivores.

Research and Monitoring Needs

While it is clear that more and better information concerning the processes and mechanisms controlling Lake Ontario's ecosystem is needed, certain strategic research and monitoring efforts can be identified which specifically address the issues of interactions and synergisms of food web and nutrient controls. A list of some strategic research and monitoring needs follows:

(1) Seasonal progression of phytoplankton should be monitored and nutrient and light limitation established.

(2) The causes of the relatively slow decrease (on annual scales) of summer epilimnion TP concentrations and the increase (on seasonal scales) of those concentrations over spring values should be evaluated. These dynamics may be critical in the evaluation of nitrogen, phosphorus, and light limitation of phytoplankton growth.

(3) Algal growth and loss rates should be determined. If a mismatch in algal size and zooplankton preferred food size exists, then grazing cannot be a major control of phytoplankton population size. Thus, growth rates must be very low or some loss mechanism other than grazing must be important.

(4) Lake Ontario's secondary production should be determined empirically to allow comparison of zooplankton production and predation loss rates.

(5) Lake Ontario's major food web energy transfers appear to rely on heterotrophic pathways and the dynamics of detrital carbon. The role of detritus, heterotrophic bacteria, and the microbial foodweb in passing carbon to the traditional food web should be evaluated.

(6) Monitoring programs must be continued, expanded, and coordinated. Particular attention needs to be paid to lakewide shifts in indicator components of biological size spectra (as these are early signs of changes in ecosystem structure that may result from predation effects, particularly *Daphnia* size/species composition), spatial sampling densities required to characterize lakewide conditions and temporal sampling frequencies to establish trends, rate measures of fish growth and mortality, relative abundance, size, and condition of forage fishes, absolute biomass and production of dominant forage fishes (new technologies such as hydroacoustics should be considered), salmonine diet, systemwide physicochemical (including climatic) monitoring of the lake (interpretation of any changes in biological community structure must be made in the context of current environmental conditions), and standardization and calibration of methods (which is critical for multilake comparisons and ultimate interpretation of causality).

(7) Lake Ontario offers an excellent opportunity to apply an adaptive management approach to salmonine stocking. Salmonine stocking rates have been and are intended to be maintained at similar levels during the 1984–90 period. If, during that time, the forage base shows no apparent response to severe weather and/or predation, then a logical next step would involve increasing stocking rates. A stepped increase of 30–50% sustained for 4–6 yr would allow reasonable evaluation of the system response. Lacking substantial evidence of a collapse of the forage base or of food web enhancements on water quality (e.g. increased water clarity), the stocking rate could be incremented again until the system responded. The enhanced value of improved water quality and the expanded fishery should yield substantial social and economic benefits. It should also be noted that concern has been raised for the lack of alternative forage species in Lake Ontario, if the alewife population was decimated.

(8) A comprehensive understanding of trophic interactions and their spatial (e.g. inshore/offshore and warmwater/coolwater) and temporal (seasonal and diet) dynamics is needed. In 1986, the Board of Technical Experts (BOTE) of the Great Lakes Fishery Commission suggested an intensive lakewide effort modeled after the 1982 "Year of the Stomach" (i.e. a survey of stomach content) in the North Sea. This multinational initiative significantly advanced understanding of the North Sea food webs and improved the scientific basis for the management of multispecies fisheries. Equally important, it contributed substantial methodological advances which can now be applied elsewhere. The Council of Lake Committees accepted the BOTE recommendation and initiated a feasibility study. Workshop participants supported this feasibility study and rec-

ommended that agencies and universities support this effort. In addition, workshop participants encouraged development of mesoscale, whole-system experiments designed to evaluate responses of the Great Lakes communities to manipulations of food web interactions.

(9) Research is needed to determine the impact and implications (biological, social, and economic) of changes in food web dynamics and food web control on toxic substances cycling and contaminant bioaccumulation in fishes. Alewives are notoriously inefficient in food conversion and therefore are expected to pass a large amount of food through their gut and accumulate a commensurate amount of contaminants. Alewife are also high in oil content. A shift in salmonine diet toward other prey species, such as yellow perch and bloater chub, as predator–prey ratios change and predator control effects take place may result in lower contaminants in fish. These relationships need to be elucidated to enhance our understanding and management of this predator–prey system.

(10) Given the Lake Michigan experience, research is needed on the feasibility of experimentally stocking expatriated species (e.g. bloater chub) into Lake Ontario to achieve International Joint Commission and Great Lakes Fishery Commission goals of restoration and rehabilitation of native biological communities in the Great Lakes.

Synthesis and Concluding Remarks

There is an obvious need for a quantitative understanding of the trophic linkages operating within the Great Lakes ecosystem. Figure 1 presents a generalized model of a simple phytoplankton–zooplankton–planktivore–piscivore system and some possible outcomes due to trophic interactions. For example, intense stocking of piscivores can reduce planktivore biomass. Reduced planktivore biomass can result in an increase in zooplankton biomass which can in turn result in a decrease in phytoplankton biomass. This is precisely the cascading effect that was observed in Lake Michigan (Carpenter et al. 1985; Scavia et al. 1986; Kitchell and Carpenter 1987; Kitchell et al. 1988). Another possible scenario might be that intense fishing or predation (e.g. lamprey predation) might allow planktivore biomass to increase. The result would be a decrease in zooplankton biomass which could result in an increase in phytoplankton abundance. Elevated phosphorus loadings obviously increase in-lake phosphorus concentrations which can increase phytoplankton biomass (Vollenweider 1979). However, increased phytoplankton biomass does not necessarily increase zooplankton biomass (because of short algal life spans). Increased phytoplankton biomass may, in fact, have a direct impact on piscivores by lowered dissolved oxygen concentrations and loss of spawning habitat. These scenarios are but a few simple examples of interrelationships among ecosystem compartments. The need for a better understanding of food web interactions and how they are affected by physicochemical factors was one of the primary reasons for undertaking the Food Web workshops. Such understanding is fundamental to management of the Great Lakes ecosystem.

In general, nutrient and phytoplankton trend data are consistent with a nutrient control scenario for Lake Ontario phytoplankton, with light and nutrients (nitrogen during the 1970s and early 1980s and phosphorus thereafter) determining summer epilimnetic phytoplankton abundance. The shift to phosphorus limitation of phytoplankton growth has resulted in a decrease in blue-green algal abundance and a possible shift in size structure to smaller algae (Table 1). Rapidly increasing nitrogen/phosphorus ratios in Lake Ontario may soon evoke additional changes in phytoplankton species composition and biomass.

Salmon stocking in Lake Ontario has increased to the point where the total number stocked per unit area or unit volume is approximately 50% higher than in Lake Michigan (where food web effects have been manifest). Significant food web effects have not been broadly demonstrated in Lake Ontario. However, based on current stocking rates and some preliminary evidence (i.e. reduced slimy sculpin density, reduction in condition factor of adult chinook salmon, the decline of rainbow smelt populations in the Kingston basin), food web effects may become broadly manifest within the next few years. Monitoring the system must become a high priority, particularly tracking large *Daphnia* populations which are the key component of a suite of changes that should result if and as alewife stocks are reduced by piscivores. It was a consensus from workshop participants that to elucidate and understand the effects of nutrient controls (i.e. phosphorus abatement) and food web controls (i.e. predation) in Lake Ontario, water quality and fisheries agencies must (1) standardize monitoring techniques and establish and maintain compatible, long-term, limnological data sets, (2) cooperate on research (e.g. controlled, mesoscale, whole-system experiments) designed to quantify the rates (e.g. growth, predation, etc.) of food web interactions (emphasis must be placed on an interdisciplinary approach that explicitly accounts for time and spatial scale effects), and (3) promote initiatives which quantify the impact of changes in food web dynamics on reduction of toxic substance levels in Great Lakes fishes.

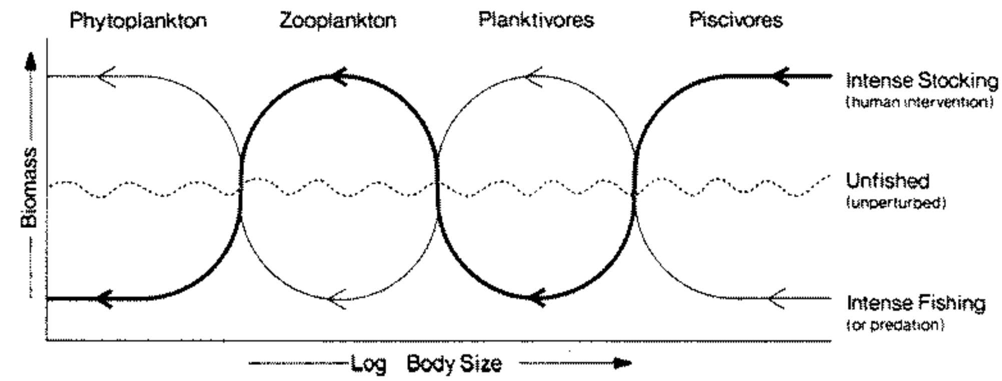

FIG. 1. Generalized model of a simple phytoplankton–zooplankton–planktivore–piscivore system and some possible outcomes due to interrelationships (adapted from Christie et al. 1987b).

As mentioned earlier, a fundamental management question is: "Are the Great Lakes phosphorus management and fishery management strategies compatible?" The phosphorus management strategy has been successful at reducing phosphorus loadings to the Great Lakes, while the fishery management strategy has been successful in establishing a high-value recreational fishery (Table 2). Water quality should continue to improve as phosphorus load reduction continues. Food web effects can be additive so that both the basic nutrient supply and the internal cycling of epilimnetic nutrients due to food web interactions can combine to enhance water clarity (Carpenter et al. 1985). However, phosphorus and fishery management strategies may in the long run promote ecosystem instability if they are not carefully coordinated. This concern arises because the alewife is now the crucial species for the support of a sustained sport fishery (alewife provide much of the diet of salmonines). Alewife can also control zooplankton and, secondarily, phytoplankton size spectra and species composition and can depress native forage stocks through competition and other ecological interactions. By decreasing phosphorus loadings and increasing salmonine predation pressure, we may be putting simultaneous negative feedback pressures on alewife. Another important factor in alewife mortality may be winter severity, which may periodically overwhelm density-dependent controls. How much stocking and phosphorus control is too much? This depends on the relative priorities of management goals (i.e. maximizing fish production, maximizing water clarity, restoring native species, etc.).

Coordination among agencies is now more important than ever before. The International Joint Commission and the Great Lakes Fishery Commission have many goals in common but some may come into conflict as a result of fisheries management practices which can affect food web interactions that are expressed in both water quality and contaminant concentrations. One way of helping to ensure compatibility of phosphorus and fishery management strategies would be for the International Joint Commission and Great Lakes Fishery commission to sponsor workshops on the status of Lake Ontario every 3–5 yr to evaluate trends, review progress toward management goals, explicitly account for interrelationships between management programs, and provide opportunity for midcourse corrections.

The lessons of Lake Michigan's recent history and the opportunities of Lake Ontario's future offer unique potential for a marriage between basic research and applied scientific management. We should nurture this union and test it. If we are wrong about the role of food web dynamics in enhancing water clarity, we have lost little, for we will have gained knowledge through basic science. If we are right, then we will have gained both the basic understanding and the success of its application.

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Rehabilitation of Lake Ontario: the Role of Nutrient Reduction and Food Web Dynamics

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The Laurentian Great Lakes have a complex history of changes due to eutrophication, invasion of exotic species, and fisheries and phosphorus management practices. Remedial actions have reduced nutrient loadings and enhanced the role of food web interactions in improving water quality. Workshops sponsored through the United States – Canada International Joint Commission have addressed the relative importance of nutrient abatement and/or food web manipulation in affecting water quality trends. Both controls have combined to enhance water clarity in Lake Michigan. Lake Ontario has already exhibited the effects of nutrient controls and may be on the verge of manifesting food web controls. Research and monitoring recommendations to elucidate the effects of nutrient and food web controls include the following: (1) water quality and fisheries agencies must coordinate monitoring activities, standardize techniques, and establish and maintain long-term data sets to evaluate the effects of water quality and fisheries programs separately and together; (2) controlled, mesoscale, whole-system experiments should be performed to quantify rates (e.g. growth, predation, etc.) of food web interactions; and (3) the scientific community should promote research which quantifies the impact of changes in food web dynamics on changes in toxic substance levels in Great Lakes fishes.

Au cours de leur histoire, les Grands Lacs Laurentiens ont été transformés par l'eutrophisation, l'invasion d'espèces exotiques et par la manière dont les phosphates et les pêches ont été gérés. Des mesures correctives ont permis de réduire l'accumulation de nutriments et mis en valeur le rôle des interactions trophiques dans l'amélioration de la qualité de l'eau. Des ateliers parrainés par la Commission mixte internationale États-Unis – Canada ont traité de l'importance de réduire la quantité de nutriments dans ces eaux ou d'agir sur le réseau alimentaire pour les assainir. Ces deux types d'action ont permis de rendre plus pur les eaux du lac Michigan. Les effets des mesures de réduction des nutriments se sont déjà faits sentir dans le lac Ontario et on s'apprête à y agir sur le réseau alimentaire. Voici certaines recommandations en matière de recherche et de surveillance visant à améliorer notre connaissance des effets des mesures de contrôle des nutriments et du réseau alimentaire : 1) les organismes responsables de la qualité des eaux et des pêches doivent coordonner leurs activités de surveillance, normaliser leurs méthodes et établir et maintenir des ensembles de données à long terme leur permettant d'évaluer séparément ou ensemble les effets de la qualité de l'eau et des programmes portant sur les pêches; 2) des expériences contrôlées à échelle moyenne et de type holistique devraient être menées de façon à quantifier les taux (de croissance, de prédation, etc.) des interactions ayant lieu dans le réseau alimentaire et 3) la communauté scientifique doit promouvoir les recherches visant à quantifier l'impact des modifications de la dynamique du réseau alimentaire sur les concentrations des substances toxiques présentes dans les poissons des Grands Lacs.

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In the past 10 yr, two management strategies have evoked dramatic effects in the Great Lakes: phosphorus management and fishery management. The 1972 Great Lakes Water Quality Agreement adopted a phosphorus management strategy to control nuisance algal problems in the lower lakes and maintain the oligotrophic state of the upper lakes. Phosphorus loadings to the Great Lakes have decreased substantially (e.g. approximately a 13 000 tonne (t) decrease to Lake Erie since 1972) and resulted in dramatic improvements, particularly in Saginaw Bay and the lower Great Lakes (Hartig and Gannon 1986). Simultaneously, the fishery interests (Great Lakes Fishery Commission or GLFC) implemented a strategy to control