Report to the
Great Lakes Science Advisory Board

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

Based on Conclusions and
Recommendations from
Food Web II Workshop

Held at
Canada Centre for Inland Waters
on February 25-27, 1987

International Joint Commission
Great Lakes Regional Office
March 1988

DISCLAIMER

The views expressed in this report are those of the Workshop Steering Committee and not necessarily those of the Great Lakes Science Advisory Board.

ACKNOWLEDGEMENTS

The efforts of all workshop participants are appreciated and their contributions recognized. In addition, the enthusiasm and support of the Workshop Steering Committee (J. F. Kitchell, D. Scavia, S. B. Brandt, D. M. Whittle, T. B. Reynoldson, C. J. Edwards and J. H. Hartig) are hereby acknowledged. L. B. Crowder and J. M. Haynes provided further review and constructive criticism of the report.

"Far below, Lake Ontario takes in what

Lake Erie sends her."

Gordon Lightfoot
Wreck of the Edmond Fitzgerald

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EXECUTIVE SUMMARY

In December 1985, the Science Advisory Board (SAB) of the International Joint Commission (IJC) hosted the Food Web I Workshop, which focused on our understanding of the relationship between recent water quality changes in Lake Michigan and changes in biological community structure. It was the consensus of the workshop participants that abatement of nutrients (bottom-up control) reduced winter-time phosphorus levels in Lake Michigan and that this phenomenon lowered the amount of spring phytoplankton and chlorophyll. In addition, predation (top-down control) initiated a cascade effect in which reduced alewife abundance resulted in an increase in large zooplankton. Increased zooplankton abundance resulted in higher rates of grazing on phytoplankton, which in turn led to increased summer water clarity.

Subsequent to the Food Web I Workshop, the SAB hosted the Food Web II Workshop on February 25-27, 1987; it focused on food web dynamics in Lake Ontario. Lake Ontario was chosen because rates of fish stocking and phosphorus reduction are parallel with those in Lake Michigan. In general, the consensus of Food Web II was that the abatement of nutrients (bottom-up control) has significantly reduced phosphorus concentration in Lake Ontario, resulting in some minor changes in phytoplankton, e.g. a decrease in blue-green algal abundance and a possible shift in size structure to smaller algae. At the time of the workshop, predation effects by salmonines were only modestly apparent in Lake Ontario. However, some workshop participants noted that the system appears to be on the verge of responding to predation effects (top-down control) and noted that there is a need to continue monitoring the lake's response as a high priority activity.

The overall recommendation from the Food Web II Workshop was that policy coordination between water quality and fisheries agencies, e.g. management, monitoring and research is a requisite. Such interagency coordination offers substantial opportunity for continued water quality improvement and is therefore highly desirable. In addition, three specific recommendations were made:

- The IJC established task forces to develop and assess implementation of water quality surveillance plans for each of the lakes, and the Great Lakes Fishery Commission (GLFC) established lake committees to assess the state of fish stocks and aquatic habitat. Food Web II participants pointed out the need to strengthen existing communications between the IJC and the GLFC, to adopt the "ecosystem approach," and to take advantage of the potential additive effects of phosphorus management and fishery management strategies. It was also pointed out that, as evidenced in Lake Michigan, the management of salmonid densities can facilitate the restoration and rehabilitation of some native biological communities, e.g. fish. Ecological restoration and rehabilitation are common goals of the IJC and the GLFC. Because of the significance of food web interactions in the Great Lakes, it is recommended that water quality and fisheries agencies coordinate monitoring activities, standardize reporting techniques, and establish and maintain compatible long-term data sets to evaluate the effects of each program, i.e. water quality and fisheries both separately and together.

- Considerable economic development recently has occurred along the Great Lakes shoreline as a result of improved water quality resulting from initiatives of the IJC under the auspices of the 1978 Great Lakes Water Quality Agreement and increased sport fishing opportunities resulting from initiatives of the GLFC under the auspices of the Strategic Great Lakes Fishery Management Plan, and other factors. Both the IJC and the GLFC are obligated to protect these resources, which are vital to sustaining local economies. Based on what was learned at both the Food Web I and II Workshops, it was concluded that IJC and GLFC could benefit from a better understanding of food web interactions. It is, therefore, recommended that controlled, meso-scale, whole-system experiments should be performed to quantify rates of food web interactions, i.e. growth and predation. Such empirical data from controlled, meso-scale, whole-system experiments are essential to our understanding and management of the Great Lakes ecosystem.

- Alewife are a major portion of the salmonine diet and are known to contain relatively high levels of toxic substances. If the diet of salmonines were to change, at least in part, from alewife to other forage fishes which contained lower levels of toxic substances, this situation might reduce biomagnification of toxic substances in the salmonids. It is, therefore, recommended that the Great Lakes scientific community needs to promote initiatives which quantify the impact of changes in food web dynamics on changes in toxic substances levels in Great Lakes sport and commercial fishes.

As a footnote, workshop participants suggested that one novel way to implement the above recommendations would be to undertake a joint IJC/GLFC initiative to determine how food web dynamics affect the goals of the IJC's phosphorus management strategy and GLFC's fishery management strategy. Other initiatives could be pursued with financial support from the National Science Foundation and/or the National Science and Engineering Research Council.

INTRODUCTION

In the past ten years, phosphorus and fishery management strategies have evoked dramatic effects in the Great Lakes. As a result of increasing concern about cultural eutrophication of the Great Lakes in the late 1960s, the 1972 Great Lakes Water Quality Agreement (GLWQA) adopted a phosphorus management strategy to control nuisance algal problems in the lower lakes and maintain the oligotrophic state of the upper lakes. Since 1972, phosphorus loadings to the Great Lakes have decreased substantially (Table 1) as a direct result of this phosphorus management strategy. There has been a corresponding change in biological parameters, particularly in Saginaw Bay and the lower Great Lakes (Table 2). Simultaneously, the fishery interests implemented a sea lamprey (Petromyzon marinus) control program and a massive program of stocking pacific salmonids and native trout. Over the past ten years, salmon stocking of the Great Lakes has increased substantially (Table 3), resulting in a sport fishery worth $2 billion per annum (Talhelm 1987).

The fundamental question for management agencies is: "Are the phosphorus management and fishery management strategies compatible?" The trophic cascade (Carpenter et al. 1985) that can develop through predator stocking may alter pelagic communities and can be manifest in water quality indicators. Lake Michigan's history offers credence to that prospect (Scavia et al. 1986; Kitchell and Carpenter 1987).

To answer the above question one must first understand the relationships between implemented management strategies and ecosystem changes, e.g. water quality. To help identify the effects of phosphorus abatement, i.e. bottom-up control, and salmonid stocking, i.e. top-down control via predation, on Lake Michigan, the Science Advisory Board of the International Joint Commission hosted the Food Web I Workshop in December 1985; it focused on our understanding of the relationship between recent changes observed in water quality and biological community structure. It was the consensus of the Food Web I Workshop that phosphorus abatement or bottom-up control decreased winter and spring phosphorus concentrations in Lake Michigan, which resulted in a reduction in spring phytoplankton and chlorophyll concentrations (see Appendix I; Kitchell et al. 1987). In addition, predation or top-down control initiated a cascading effect: it reduced alewife abundance, which resulted in an increase in large Daphnia abundance (Table 4). Higher Daphnia abundance increased grazing on phytoplankton, which caused an increase in summer water clarity (Scavia et al. 1986, Scavia and Fahnenstiel 1987).

As a follow-up to the Food Web I Workshop, the SAB hosted the Food Web II Workshop in February 1987; it focused on food web dynamics in Lake Ontario. Lake Ontario was chosen because its phosphorus and salmon stocking trends were following phosphorus and salmon stocking trends in Lake Michigan. As such, Lake Ontario could be the next Great Lake to manifest the effects of top-down and bottom-up controls. The Food Web II Workshop included presentations on the available long-term water quality and biological community data sets from Lake Ontario, how empirical data can be interpreted and used to manage Lake Ontario, top-down and bottom-up group deliberations on questions related to trends and possible causes, and a collective discussion and debate on top-down and bottom-up findings to develop conclusions and recommendations. Appendix II presents abstracts of presentations given at the Food Web II Workshop; Appendix III, a list of top-down and bottom-up group participants and Appendix IV, participant addresses.

TABLE 1. MUNICIPAL TOTAL PHOSPHORUS LOADINGS (tonnes/year) TO THE GREAT LAKES, 1972–1985 (IJC 1987).

YEAR	LAKE SUPERIOR	LAKE MICHIGAN	LAKE HURON	LAKE ERIE	LAKE ONTARIO
1972	–	–	–	15,260	9,860
1975	286	2,325	624	6,951	4,220
1976	293	2,336	578	5,840	3,082
1977	262	1,660	557	6,406	3,089
1978	239	1,314	495	5,478	2,728
1979	207	1,224	444	4,234	2,898
1980	203	1,047	427	3,500	2,512
1981	170	934	475	2,874	2,208
1982	179	885	416	2,449	2,115
1983	151	960	401	2,614	1,903
1984	144	894	441	2,767	1,894
1985	150	894	462	2,449	1,710

TABLE 2. EVIDENCE OF RECENT IMPROVEMENTS IN WATER QUALITY PROBLEMS ASSOCIATED WITH EUTROPHICATION OF SAGINAW BAY, LAKE HURON AND LAKES ERIE AND ONTARIO (Hartig and Gannon 1986).

	EVIDENCE OF IMPROVEMENTS IN WATER QUALITY PROBLEMS ASSOCIATED WITH EUTROPHICATION
Saginaw Bay, Lake Huron	Decrease in spring and fall chlorophyll a concentration between 1974 and 1980.
	Reduction in taste and odor problems in municipal water supplies between 1974 and 1980.
	Decreases in zooplankton species indicative of eutrophy and increases in certain species indicative of oligotrophy between 1974 and 1980.
Lake Erie	Reductions in blue-green algal biomass between the mid-1960s and late-1970s.
	Reduction in total phytoplankton biomass and a shift in phytoplankton composition toward more oligotrophic species between 1970 and 1980.
	Reductions in the amount of algae windrowed on bathing beaches between the mid-1960s and late-1970s.
	A decreasing chlorophyll trend in the central and eastern basins between 1968 and 1980.
	Oxygen depletion rates in the central basin appear to have decreased in recent years (1980-1984) and are less variable.
Lake Ontario	Between the late 1960s and the late 1970s there has been a shift in phytoplankton community structure and composition toward more species indicative of mesotrophic and oligotrophic conditions.

TABLE 3. ANNUAL PLANTINGS (in thousands) OF COHO AND CHINOOK SALMON IN THE GREAT LAKES, 1966–1984 (GREAT LAKES FISHERY COMMISSION).

YEAR	LAKE SUPERIOR	LAKE MICHIGAN	LAKE HURON	LAKE ERIE	LAKE ONTARIO	TOTAL
1966	192	660	–	–	–	852
1967	500	2,534	–	–	–	3,034
1968	432	1,888	676	111	40	3,147
1969	706	3,998	917	236	309	6,166
1970	799	5,447	1,214	675	580	8,715
1971	869	5,068	1,869	678	520	9,004
1972	769	4,782	764	369	969	7,653
1973	644	5,251	1,067	996	1,208	9,166
1974	1,052	6,809	1,276	1,599	1,843	12,579
1975	528	6,785	1,282	1,788	1,958	12,341
1976	893	6,580	1,521	2,872	936	12,802
1977	881	6,064	1,149	3,904	352	12,350
1978	618	8,050	1,502	2,869	674	13,713
1979	701	9,028	2,407	1,538	999	14,673
1980	1,079	9,049	2,253	2,515	1,283	16,179
1981	589	7,198	1,658	1,530	1,843	12,818
1982	1,549	8,493	2,454	2,443	2,557	17,496
1983	1,223	8,903	3,121	2,436	3,547	19,230
1984	1,007	10,664	3,617	1,815	5,415	22,518
						213,716

TABLE 4. A COMPARISON OF TRENDS IN TOP-DOWN AND BOTTOM-UP INDICATORS OF CHANGE IN LAKES MICHIGAN AND ONTARIO.

	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 1976-1977 and 1983-1984).
Zooplankton	_Daphnia_ _pulicaria_, a relatively large cladoceran, was first observed in autumn 1978 and became the dominant species in the summer of 1983.	Limited data available. A comparison of zooplankton community structure and abundance from 1981-1985 with that of earlier studies (1967-1972) found no detectable change in the range of abundances or community composition between the two periods.
Phytoplankton	Historical studies suggest changes in species composition. However, no dramatic change in 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 middle 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 $\mu g \cdot \ell^{-1}$ in 1976 to approximately 4 $\mu g \cdot \ell^{-1}$ in 1985.	Spring, mid-lake total phosphorus concentration has decreased from a maximum of 30.6 $\mu g \cdot \ell^{-1}$ in 1973 to 10.7 $\mu g \cdot \ell^{-1}$ in 1985.
Phosphorus Loading	A decrease in municipal total phosphorus loading from 2,325 $t \cdot yr^{-1}$ in 1975 to 894 $t \cdot yr^{-1}$ in 1985.	A decrease in municipal total phosphorus loading from 9,860 $t \cdot yr^{-1}$ in 1972 to 1,710 $t \cdot yr^{-1}$ in 1985.

The purpose of this report is to present a summary of the conclusions from the Food Web II Workshop and the recommendations on research, monitoring and future management.

SUMMARY REPORT FROM THE "BOTTOM-UP" SYNTHESIS GROUP

Evaluation of trends in Lake Ontario's lower food web proved to be difficult because, unlike Lake Michigan (see Food Web I Summary in Appendix I), there have not been dramatic changes in recent years. The bottom-up group focused on the period 1975–1986 and came to the following conclusions:

- Total phosphorus loads have decreased considerably and are approaching the target set by the Great Lakes Water Quality Agreement (GLWQA).

- Winter/spring total phosphorus decreased slowly from the 1971 high of ca. 25 $\mu g \cdot \ell^{-1}$ and then more dramatically after 1977; the current concentration is near 14 $\mu g \cdot \ell^{-1}$. During the same time period summer epilimnetic total phosphorus decreased from ca. 17 to 15 $\mu g \cdot \ell^{-1}$. Nitrate concentrations continue to increase, as is the case for the other Great Lakes (see Stevens; Appendix II). In Lake Ontario, increasing nitrate plus nitrite and decreasing phosphorus concentrations have resulted in winter/spring total nitrogen/total phosphorus ratios increasing from about 16 in 1977 to over 32 in 1982. These ratios continue to increase annually.

- Summer epilimnetic chlorophyll concentrations have not changed over the period of analysis, although some evidence exists to suggest 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.

- Comparison of zooplankton abundance between the 1970s and 1980s was difficult due to differences in methodology and reporting. One analysis suggests no change, another suggests an increase in abundance since the 1970s. There have been few changes observed during the 1980s, based on the internally consistent analysis of BIOINDEX stations.

- Alewife abundance has varied considerably year-to-year since their dramatic increase after the major 1976–77 die-off; however, no clear trend in their abundance is obvious after 1980.

Phytoplankton Limitation

A summary of the apparent changes over this time period suggests a rather stable period, with only subtle changes in algal species composition. This condition has occurred during the more obvious decreases in total phosphorus (TP) and increase in total nitrogen (TN) concentrations (see Stevens; Appendix II). The magnitude of these small changes is inconsistent with expected phytoplankton biomass decrease associated with decreases in TP. The lack of correlation between TP and chlorophyll changes seems linked to Lake Ontario's transparency and the 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 of nitrogen-limited to phosphorus-limited lakes, it is likely that until about 1982-1983, Lake Ontario's summer phytoplankton were potentially limited by nitrogen. Only after those years would further decreases in TP result in decreased phytoplankton biomass or chlorophyll. Total phosphorus decreases after 1983 have been slight compared to the 1977–1982 period. Thus, chlorophyll changes should continue to be small.

It appears that light penetration into Lake Ontario may also play a significant role in the apparent lack of correlation between TP decreases and phytoplankton changes. During summer, the 1% light penetration reaches 9–10 m, which is 1–2 m less than the mixing depth. In comparison, Lake Michigan mixing depth is near 10 m, but the 1% light penetration reaches 27–33 m. During much of the year, Lake Ontario phytoplankton may be limited by the availability of light.

The arguments thus far are consistent with a "bottom-up" control scenario for Lake Ontario phytoplankton, with light and nutrients (nitrogen during the 1970s and early 1980s and phosphorus thereafter) determining their summer epilimnetic phytoplankton abundance.

Phytoplankton–Zooplankton Uncoupling

There 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 algae are perhaps not the direct nutrition of the zooplankton. A second line of reasoning derives from a 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 zooplankton, Bosmina spp.

It was suggested that the still relatively high phosphorus concentrations allow the large algal forms to persist, leading to a mismatch of zooplankton food supply. "Top–down" influence may also be important if alewife grazing structures the zooplankton size spectrum toward small species. An alternative hypothesis is that size-selective 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. Without more information concerning the relative rates of algal and zooplankton production and loss rates, it is difficult to sort the major forces of "top–down" and "bottom-up" at the phytoplankton–zooplankton interface.

Expected Trends

The work group assessed the directions it expects Lake Ontario to take under nutrient and grazing control. If phytoplankton appear phosphorus-limited as hypothesized, then further reductions in winter/spring TP will 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 total phytoplankton concentration changes accompanied by more subtle species shifts. The shifts will likely be toward smaller species and perhaps a larger representation of diatoms in summer as the Si:P ratio increases. As TP continues to decrease, primary production may also decrease, with consequent reductions in grazer biomass (zooplankton and benthos). Those changes, however, will again be slight and perhaps not detectable with current methodologies.

Overall, trends tied to "bottom-up" effects of TP reductions will be slow, small and subtle.

Should "top-down" influences be manifest in a dramatic decrease in alewives abundance and should no major planktivore quickly increase in abundance to replace alewife, then we may expect certain abrupt changes similar to those observed in Lake Michigan. There may be shifts to large body size zooplankton within the extant assemblage, followed by species shifts to larger organisms as intraspecific plasticity reaches limits. This movement to larger body size could signal a reduction in algal biomass. While this phenomenon was also predicted in the "bottom-up" scenario, 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 will be accompanied by release from its benthivory as well, and an increase in vulnerable benthic prey could be expected.

Lake Ontario = Lake Michigan + X YEARS ????

There was some concern expressed that the Lake Michigan "experience" may not be a harbinger for Lake Ontario. Several aspects of Lake Ontario's ecology and limnology are different from those of Lake Michigan. The differences may be substantial enough to result in different responses of the Lake Ontario ecosystem to similar stimuli. Some of the notable differences include:

- Lake Ontario has a much smaller silica reserve in winter, which likely limits its diatom production more severely than that of 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.

- During summer stratification, Lake Ontario's primary production is limited to the epilimnion, whereas a substantial portion of Lake Michigan's summer production is below the thermocline.

- 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 pressure be released, is not known.

- Lake Ontario's zooplankton community is currently 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 to dominance.

- From the paleolimnological record, it appears that Lake Michigan's long-term algal succession never progressed beyond conditions found in the early 1900s in Lake Ontario. Thus, entirely different sets of potential responses are possible in Lake Ontario.

Research 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 efforts can be identified which specifically address the issues of "top-down" versus "bottom-up" controls. Data addressing some of these issues may already exist and, if so, they should be made available. A partial list of some strategic research areas follows:

- Establish nutrient, i.e. P, Ni or Si, and/or light limitation of Lake Ontario phytoplankton.

- Evaluate 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. These dynamics may be critical in the evaluation of N–, P– and light–limitation.

- Determine algal growth and loss rates. 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.

- Based on the importance of the level of zooplankton secondary production, a full evaluation of "top–down" versus "bottom–up" influences on Lake Ontario's food web will be required. Empirical information will allow comparison of zooplankton production and predation loss rates.

- Lake Ontario's food web energy transfers appear to rely on heterotrophic pathways and the dynamics of detrital carbon. Further studies should focus on the role of detritus, heterotrophic bacteria and the microbial food web in passing carbon to the traditional food web should be evaluated.

Monitoring, Surveillance and Management Strategies

It was considered that monitoring the seasonal progression of phytoplankton and zooplankton species composition was critical. Particular attention should be placed on evaluating changes in organism sizes. These changes will be early indicators of ecosystem structure shifts that may result from predation effects. The seasonal trends of nutrients are also an important factor to evaluate. Of particular concern are the seasonal depletion of silica and nitrogen, as these may be sensitive indicators of reduced P–load effects.

The consensus was that management at both the top and bottom of the ecosystem should hold the line at current strategies. Because the phytoplankton currently appear to be under P limitation, the slow decrease in phosphorus concentration as the lake continues to respond to current load reductions should result in some reduction in algal biomass. It is critical to note that removal of P–load restrictions could result in conditions far worse than those in the early 1970s because the lake plankton may not revert to nitrogen limitation. This condition occurs because, while TP concentrations have decreased, nitrate concentrations have dramatically increased. Even with a return to the TP concentrations of the 1970s, the TN:TP ratio could remain in the P–limited region.

Estimates of stress imposed on the forage base suggest that current levels of predation by stocked species may already be sufficient to evoke a dramatic response in alewife abundance biomass should a severe winter cause catastrophic mortality. Maintaining current stocking rates for the next few years will enable an evaluation of this hypothesis under stable predation conditions.

SUMMMARY REPORT FROM "TOP-DOWN" SNYTHESIS GROUP

Recent Directions in Fishery Management Strategies in Lake Ontario

The goals of both Canadian and United States agencies responsible for fishery resource management on Lake Ontario are to protect, enhance and restore fish stocks and their environment. Priority is given to those management strategies which promote the long-term stability of harvest and balance in the fish community. Three objectives were formulated to meet those goals:

- Rehabilitate populations of extirpated native species, emphasizing lake trout and Atlantic salmon but including deepwater ciscoes and sculpin and the enhancement of walleye
- Provide total annual fish yields of 2.5 kg • ha^{-1}, with emphasis on harvest of coldwater salmonines and
- Maintain other stocks as self-sustaining populations at optimal recruitment levels

Common strategies for these objectives include large-scale stocking of salmonines. Stocking programs for lake trout and Atlantic salmon are designed to produce spawning stocks of a suitable size and age composition, whereas Pacific salmon, brown trout and rainbow trout stocked in United States waters are for put-grow-and-take recreational fisheries. A major objective of both Canadian and United States agencies is that these introductions remain at levels that will provide optimum use of the forage community (primarily alewife, rainbow smelt and slimy sculpin) on a sustained yield basis.

Prudent management of the forage community is an important component in realizing all three fishery objectives. Forage stocks are controlled by regulating stocking and harvest rates of salmonines. This process involves establishing stocking rates that will effectively convert planktivore biomass to useable piscivores, but at the same time providing an adequate margin of safety to promote stability of forage/salmonine production. Controlling alewife and smelt populations is also a strategy for enhancing populations of fish that appear to be limited by competition from these forage species, e.g. yellow perch and lake herring. Finally,comprehensive monitoring of the forage community (including young-of-the-year and yearling alewife) is crucial to effective, responsible management of forage stocks, since it provides the necessary feedback for managers to regulate piscivore abundance. These assessments currently include estimates of annual changes in relative abundance, recruitment, size composition and condition for forage species, and condition and survival rate of piscivores. Greater emphasis must be placed on the assessment of juvenile alewife. Given the two to four year lag between stocking and peak predation rates, a management protocol must be developed that offers rapid response to changing forage populations. Otherwise, we are left with a trial and error approach to management (Kitchell and Crowder, 1986).

Recent Changes in the Lake Ontario Food Web

Data were insufficient to show linkages in phosphorus concentration and fish production in Lake Ontario, although it was the general consensus of the top-down group that recent reductions in phosphorus loading and open-lake phosphorus concentration have not yet limited fish production. Similarly, although salmonine stocking in Lake Ontario has increased to the point where the total number stocked per unit area or per unit volume are ca. 50% higher than in Lake Michigan, it was generally agreed that significant predation effects (top–down control) were not yet broadly demonstrated. However, two observations in Lake Ontario 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, 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. Workshop participants noted that we may be on the verge of seeing predation effects. Given that salmonine consumption levels in the lake as a whole have not yet peaked, alewives are generally in poor condition, and the occurence of severe winter conditions, and hence alewife mortality, has not coincided with peak salmonine predation rates.

Alewife is an important species in the Lake Ontario food web in that it forms the primary prey of all species of adult salmonines, is an efficient size–selective zooplanktivore that has the ability to dramatically alter zooplankton abundance and community structure, and has been shown to affect recovery of native species, e.g. predation on yellow perch larvae. Yet the key factors which control alewife abundance (recruitment variabilities, salmonine predation, overwinter mortality) are not yet understood. Alewife relative abundance has not declined in Lake Ontario during recent years, but comparisons of alewife densities in Lake Ontario with other Great Lakes or with salmonine consumption rates on an absolute basis cannot be validly made.

Some recent reductions in the density of slimy sculpins and in the condition of adult chinook salmon were observed, but longer time series and larger spatial coverage are needed. Long–term data sets on key factors such as zooplankton size spectra were not available for Lake Ontario nor was the natural variability of abundances of key populations understood.

Long–Term Surveillance and Monitoring Requirements

Long–term monitoring of system level indicators of change is needed to assess the relative impact of predation effects on other controls such as climate and nutrient inputs. Fisheries production and stocking, nutrient and phytoplankton concentrations, and contaminant cycling are clearly interrelated through food web interactions. It was strongly considered that close coordination and standardization of methodology between management, monitoring and research agencies is esssential to take full advantage of the potential additive effects of phosphorus management and fishery management strategies.

It was strongly recommended to continue, expand and coordinate ongoing surveillance and monitoring programs. These programs provide data on annual stocking rates of salmonines, lake trout growth and mortality, annual assessment of relative abundance of forage fishes (alewife, smelt, sculpin) mainly from the United States portion of the lake, an open lake BIOINDEX zooplankton/phytoplankton community assessment program and commercial catch statistics. Particular attention needs to be paid to:

- Lakewide shifts in biological size spectra
- Rate measures of fish growth and mortality
- Systemwide environmental (climatic) monitoring of the lake and
- Standardization and calibration of methodology associated with sampling, data analysis and reporting format

Information presented during the workshop suggested that reducing predation on a lower trophic level releases the subsequent trophic level so that it can attain the carrying capacity based upon its food resource. This process results in alternating high and low abundances between successive trophic levels. The effect of changing predation pressures is to modify the amplitude of these oscillations and size structure within trophic levels. Both the change in amplitude and the shifts in the size of particles within a trophic level are indicators of a change in the food web relationships of the system.

Expected changes within the size spectrum due to 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 of zooplankton. Expected shifts in species abundances would be 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 the abundance of non-prey fishes such as lake herring, yellow perch and white perch. Shifts in fish growth rates and/or condition would be expected as prey abundances change. Finally, interpretation of any changes in biological community structure must be made in the context of current environmental conditions. Systematic measures of within-lake conditions, e.g. thermocline depths and mean lake temperatures, need to be developed and incorporated into routine sampling programs.

A simplified strategy should be developed to characterize particle size characteristics of the food web structure on a lakewide basis and to be integrated with biochemical indicators of community stress:

- By selecting indicator components of the size spectrum in piscivores, planktivores and zooplankton assemblages
- By defining spatial sampling densities required to characterize lakewide conditions
- By selecting time periods and temporal frequencies required to reflect significant trends in the data sets and
- By developing a method to select a standard array of community health indicators based upon analysis of naturally occurring organic compounds such as lipids and hormones. Most of this work could be done within the context of ongoing monitoring and surveillance programs

Currently, the Canadian Department of Fisheries and Oceans perform a BIOINDEX monitoring program at two offshore stations (one in the eastern basin and one in mid-lake) in Lake Ontario. The program is carried out from the end of March to the end of October and includes: weekly monitoring of nutrients, phytoplankton and zooplankton species composition; monthly monitoring of Mysid abundance; and spring and fall assessment of benthos. The top-down group thought that these offshore data generated by the BIOINDEX program are essential to our understanding of food web dynamics in Lake Ontario. This program should also be closely coordinated with the fish sampling program and should incorporate measures of zooplankton size spectra and consider instituting a "Daphnia watch". One of the most sensitive (and easily measurable) indicators of the intensity of planktivory is zooplankton size structure. Post-hoc analysis of the Lake Michigan data suggested that a shift in zooplankton size began in the mid-1970s. In particular, shifts in species composition of Daphnia were important. Daphnia pulicaria first appeared in zooplankton samples in 1979 or 1980 and became the summer dominant in 1983. Because filtering capacity increases rapidly with body size in Daphnia, even minor changes in the species composition of Daphnia can have large effects on total filtering capacity and thus, water clarity. The top-down group proposed that Lake Ontario zooplankton sampling focus on zooplankton size structure as an early indicator of shifts in total planktivory.

In particular, if Daphnia pulicaria appears, it would be likely that alewife have dramatically declined. No other indicator of system change in Lake Michigan was as sensitive as Daphnia size, though a number of other indicators should be useful. The Lake Ontario system may differ, however, because of the presence of zooplanktivores other than alewife, such as the exotic predator Bythotrephes sp., which may assume the role of small fishes as a predator on Daphnia. Recent, dramatic increases in Bythotrephes abundance in Lakes Huron and Michigan suggest the potential for a complex set of predator/prey interactions.

The top-down group also recommended the continuation of measures of relative abundance, size and condition of forage fishes, but expanded to lakewide coverage. They also suggested that more consideration be given to the links between inshore (warmwater) and offshore (coolwater) communities and the implications of spring vs. fall sampling. Long-term monitoring of salmonine diets was further suggested. Although measures of the relative abundances of forage fishes are useful for monitoring long-term changes, estimates of lakewide absolute biomass and production of the important forage fishes are essential to determine more precisely the ultimate upper limits of salmonine production potential. (See research recommendation 2 for Quantitative Biomass and Production Measures on p. 14.)

Finally, the calibration and standardization of surveillance and monitoring methodologies among the Great Lakes is critical for multi-lake comparisons and the ultimate interpretation of causality. For example, the top-down group was unable to make comparisons between Lake Michigan and Lake Ontario forage abundances because of seasonal differences in forage assessment programs. Also, since it seems unrealistic to plan indefinitely long observational series involving all trophic components for all such communities, it was suggested that the appropriate approach is to limit the number of comprehensive time series, and supplement with homologous comparisons of various Great Lakes systems simultaneously observed at different states. Comparability depends on substantially improved attention to the calibration and standardization of sample collection and data handling methods within and among lakes. Given that the U.S. Fish and Wildlife Service has accepted both the charge and resources for forage assessment in U.S. waters and that the Great Lakes Fishery Commission can provide for intergovernmental coordination, these agencies should take an aggressive, leadership role in developing calibration, standardization and timely reporting of forage assessment programs. If the federal fisheries agency is unable to perform this vital responsibility, then the state and provincial agencies must do so. Understanding forage dynamics (alewife, in particular) is the key to understanding food web effects in the Great Lakes. IJC and GLFC must coordinate, convey and implement this charge to the fisheries agencies.

Research Recommendations

- Indicators of Food Web Dynamics

  Research is needed to identify appropriate biological indicators of community change in large aquatic systems. The two Food Web Workshops have reflected the new understanding of the general integrity of Great Lakes systems, and no matter how poorly the dynamic processes are understood, the impacts of cultural stresses can and should be measured in terms of changes in system structure. In practical terms, the interests of water quality and fishery managers have been converging for a long time. There is strong scientific agreement on the requirement for a common "currency" of standard measurements to express density and size spectra changes between and within trophic levels. More importantly, we need to advance toward measures which are realistically calibrated, each in relation to the other.

This movement includes the appropriate concern for spatial and temporal scales that range from nutrient uptake kinetics to lake trout generation time.

Once key indicators, e.g. fish and zooplankton, are identified, there is a need to establish and maintain long-term data sets and analyze them with appropriate statistics on appropriate scales, e.g. size spectra, growth rates, condition factors. It was clear from the Lake Michigan experience that shifts in zooplankton size/species composition are much more sensitive indicators of change than zooplankton abundance or salmon condition. Priority should be given to incorporating zooplankton size/species composition in monitoring programs.

- Quantitative Biomass and Production Measures

Research is needed to quantify the absolute biomass and production of dominant forage organisms and their spatial and temporal dynamics (this research must be done in relation to available habitat). Current bioenergetic models are capable of calculating the consumption potential of stocked salmonines, but this information is relevant only in the perspective of the absolute biomass and production of target prey species. A more complete picture of spatial and temporal dynamics of total forage production can provide an improved basis for comparing the present status of Lake Ontario to other systems, such as Lake Michigan, where striking changes in fish communities have occurred. Major shifts in the species composition of the forage base might mean large changes in the carrying capacity of the system, but the relative production potential of the various species is poorly known. New technologies, e.g. hydroacoustics, should be useful in answering these questions. Young-of-the-year fishes have been poorly quantified, yet they can make important contributions to the total annual production and predation of zooplankton. Older age classes of pelagic forage fishes are reasonably well quantified on the United States side of the lake but less studied on the Canadian side, yet highly valued salmonines ignore jurisdictional boundaries in their seasonal movements. Productive nearshore and embayment areas also must be surveyed with respect to habitat, potential production and current biomass.

- Food Web Dynamics

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) at the Great Lakes Fishery Commission suggested an intensive lakeswide 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 multi-species fisheries. Equally important, it contributed substantial methodological advances, which can now be applied elsewhere. The BOTE recommendation was accepted in principle by the Council of Lake Committees and cleared to begin an examination of its feasibility. The top-down group supported this feasibility study and recommended that agencies and universities support this effort for the Great Lakes.

As with many Great Lakes issues, the principles employed in our understanding derive from whole system experimental studies conducted in small, inland lakes.Certain embayments and lagoon systems of the Great Lakes contain many of the species common to the adjacent large lakes. Where possible, the top-down group encouraged the development of meso-scale, whole-system experiments designed to evaluate responses of the Great Lakes communities to manipulations of food web interactions.

- Toxic Cycling

  Research is needed to determine the impact and implications (biological, social and economic) of changes in food web dynamics and top-down control on toxic substances cycling and contaminant bioaccumulation in fishes. Alewife are notoriously inefficient in food conversion and therefore are expected to pass a large amount of food through their system and accumulate a commensurate amount of contaminants. Alewife are also high in lipid content. A shift in salmonine diet toward other endemic species, such as yellow perch and bloater, as predator-prey ratios change and top-down control effects take place, may result in changes in fish contaminant levels. These relationships need to be elucidated to enhance a forward looking evaluation of the effects of diet change on bioaccumulation. Through appropriate choices of fishery management tools, it may be possible to effect reductions in human consumer exposure to toxic contaminants.

- Expatriated Species

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

Conclusions

The top-down group considered that if the Lake Ontario system is pushed hard enough from the top, i.e. heavy salmonine stocking, it will eventually respond, but the group could not determine:

- What levels of predation would be necessary for a system level response to occur?
- How far the system could be driven?
- How dependent top-down control is on other factors such as climate and phosphorus loading?
- What are the time lags involved?
- What are the most sensitive indicators of systemwide change?

Most of the top-down group's 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, are confounded by co-occurring perturbations, and that Lake Michigan and Lake Ontario species complements and sampling methodologies differ.

In the future, management agencies will have to recognize that fish management strategies also affect non-fishery components of the Lake Ontario ecosystem. For example, food web effects of alewife on the zooplankton community can have a major impact on algal biomass, such that it obscures the expected response from phosphorus reduction. Monitoring and research will need to encompass more sensitive indicators of food web induced changes in community structure, e.g. zooplankton size/species composition. Close interagency coordination between water quality and fisheries agencies responsible for management, surveillance and monitoring, and research is requisite to continue water quality improvement and to sustain or enhance the value of fisheries resources.

SYNTHESIS AND CONCLUSIONS

There is an obvious need for an appreciation of the many complex interactions 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 food web effects. For example, the intense stocking of piscivores can reduce planktivore biomass. Reduced planktivore biomass can cause an increase in zooplankton biomass, which can in turn reduce phytoplankton biomass. This is the cascade effect that was described for Lake Michigan (Carpenter et al. 1985, Kitchell et al. 1987). Another possible scenario might be that intense fishing or predation, e.g. lamprey predation on lake trout would allow planktivore biomass to increase, causing a decrease in zooplankton biomass which could cause an increase in phytoplankton abundance. It is also important to realize that the system can be controlled from the bottom up. For example, elevated phosphorus loadings can increase in-lake phosphorus concentrations, which can increase phytoplankton biomass (Figure 2). However, increased phytoplankton biomass does not necessarily increase zooplankton biomass because of short algal life spans. In some aquatic systems, increased phytoplankton biomass may have a direct impact on piscivores through lowered dissolved oxygen concentrations and loss of spawning habitat. These scenarios are but a few 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 the management of the Great Lakes ecosystem.

While separation into bottom-up and top-down synthesis groups in the Food Web II Workshop may seem contradictory to an ecosystem perspective, a synthesis effort was developed from this perspective for three reasons:

- Some investigators disagreed with regard to the analysis and interpretation of extant data. The workshop steering committee hoped that a synthesis effort would help build consensus and identify directions for research to resolve disagreements as well as identify emerging issues.

- It was intended to establish a comparative and duplicated effort toward the synthesis of a whole-system approach, but from each of the perspectives represented by alternative views of food web interactions.

- It was apparent that food web issues require the coordination of International Joint Commission and Great Lakes Fisheries Commission activities. The dual view derived from the synthesis groups would best identify ways to enhance that coordination.

As evidenced in the report of the bottom-up synthesis group, substantial disagreement remains with regard to the relative and absolute changes in nutrient limitation to phytoplankton growth, the role of grazing by zooplankton in regulating algal communities, and the relative importance of predation by fishes as a determinant of zooplankton species composition. Nevertheless, it was apparent that phosphorus load reductions have reduced in-lake total phosphorus concentrations (Table 4).

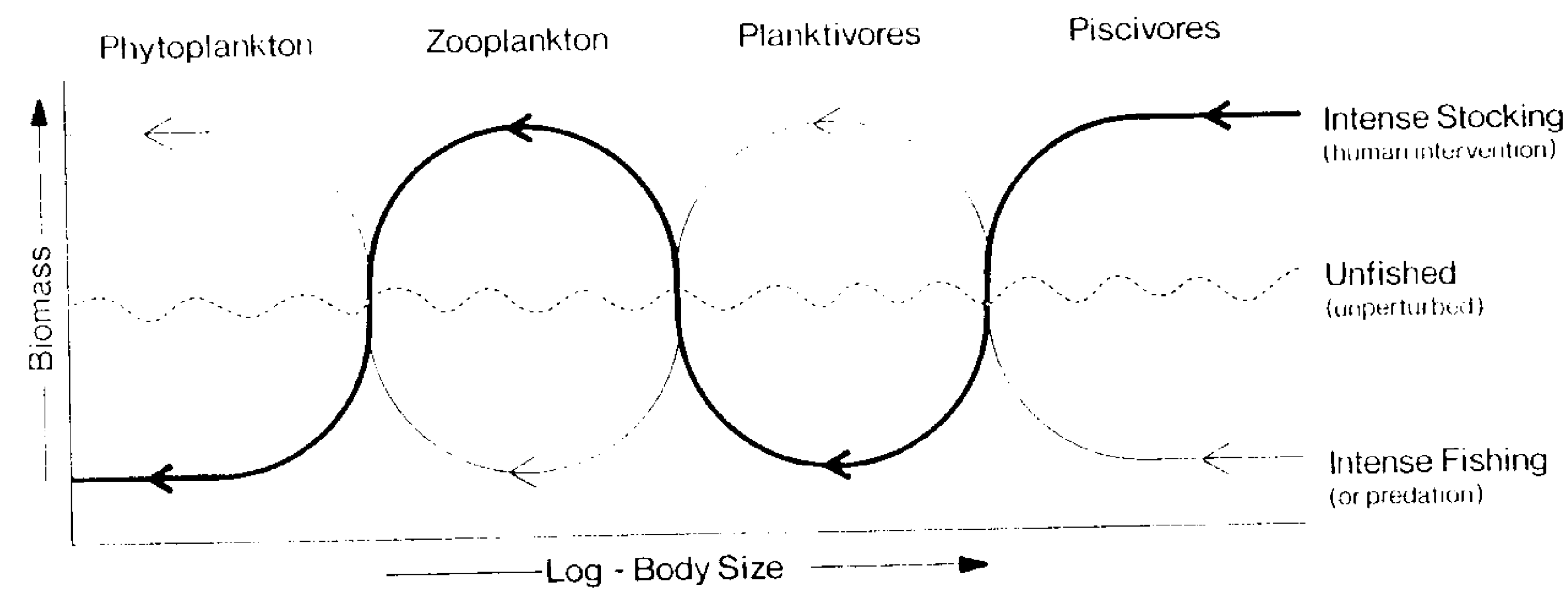

Figure 1. A generalized model of a simple phytoplankton:zooplankton:planktivore:piscivore system and some possible outcomes due to interrelationships (adapted from Christie et al. 1987).

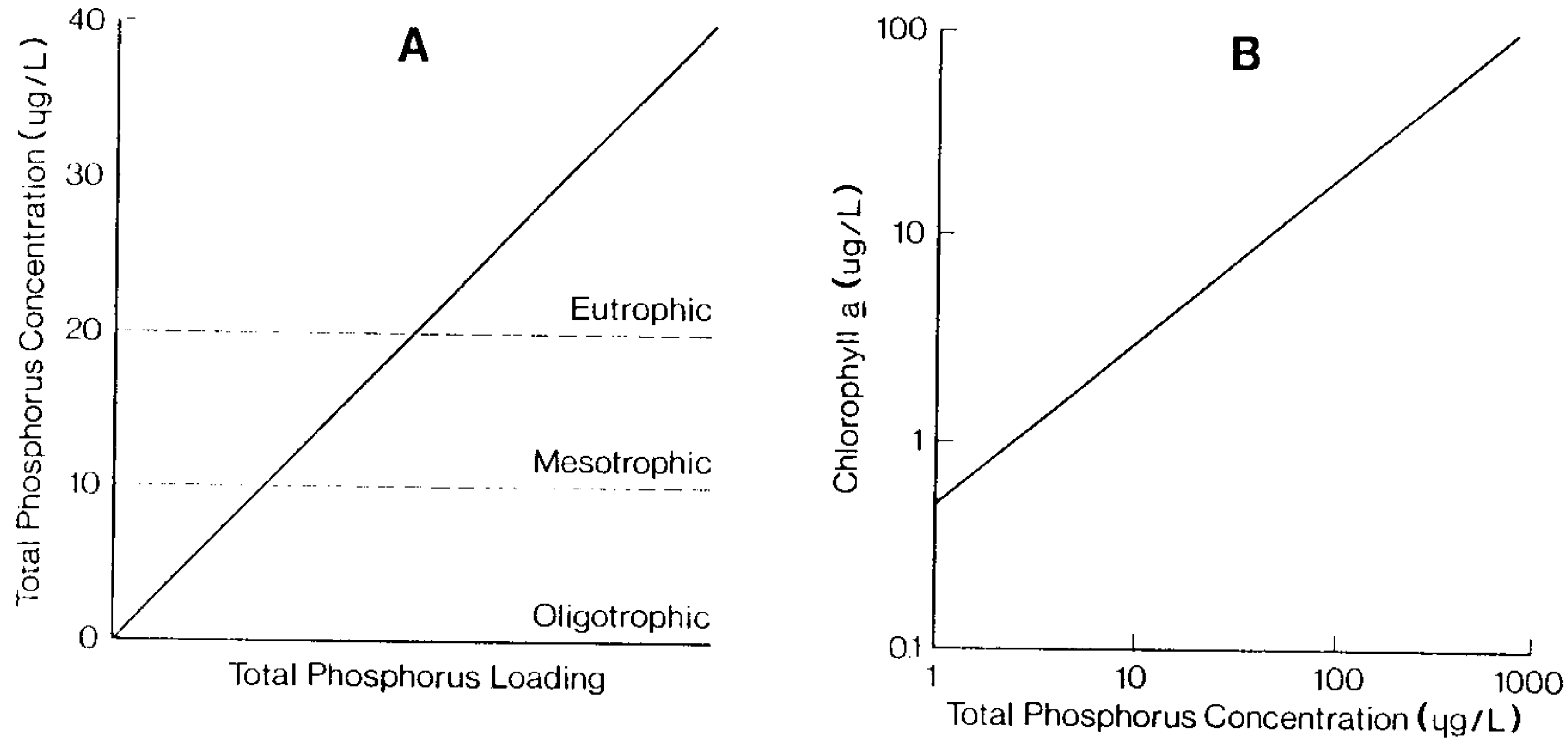

Figure 2(A). A General depiction of the relationship between phosphorus loading and concentration in lakes.
Figure 2(B). The relationship between total phosphorus concentration and chlorophyll a concentration in North American lakes (adapted from Vollenweider 1979).

Rapidly increasing nitrogen/phosphorus ratios may soon produce major changes in phytoplankton species composition and biomass.

Among Lake Ontario's offshore zooplankton, there has been little evidence of change over the past decade, suggesting that size-selective predation by zooplanktivorous fishes (primarily alewife) and/or invertebrate predators are the major causes of apparent uncoupling, i.e. components behave relatively independently, between herbivores and the phytoplankton-nutrient interactions (Table 4). Growth rates and the condition factor of alewives appear strongly density-dependent. Zooplankton abundance, size and species composition change (but only modestly) in response to density-independent effects, e.g. over-winter mortalities, on alewife populations.

High growth rates and alewife-dominated diets of salmon and trout suggest little evidence of forage limitation. Recent evidence of declining slimy sculpin stocks may indicate that piscivory is a significant cause of mortality among certain prey species populations and that those effects are largely due to the intensive stocking of lake trout. Intensive Pacific salmon stocking is relatively recent (Table 2). Predation effects on alewife stocks may not be apparent until the latter part 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, stocking rates are and have been such that if predation effects are to occur, they should be manifest within the next few years.

The harbingers of food web effects in Lake Ontario should resemble those observed in Lake Michigan. Large Daphnia populations are the key component of a suite of changes that should derive if and as alewife stocks are reduced by piscivores. Lake Erie continues to "seed" Lake Ontario in ways that suggest little lag in the response capability of the plankton community if and as the current constraints are altered. Priority should be given to monitoring zooplankton size/species composition as key indicators of change. The potential role of burgeoning Bythotrephes populations is unknown.

Water quality improvements will continue as phosphorus load reduction continues. Food web effects can be additive so that both the basic nutrient supply (bottom-up) and the internal cycling of epilimnetic nutrients due to food web interactions (top-down) combine to enhance the manifestations of improved water quality.

In general, the consensus of the Food Web II workshop was that abatement of nutrients (bottom-up control) has significantly reduced phosphorus concentration in Lake Ontario, resulting in some minor changes in phytoplankton composition, e.g. a decrease in blue-green algal abundance and a possible shift in size structure to smaller algae (see Table 4). In addition, there has been a continuous increase in salmonine stocking of Lake Ontario. At the time of the workshop, predation effects were not quantifiable in Lake Ontario. However, some workshop participants noted that we may be on the verge of seeing predation effects (top-down control) and noted that the need to continue to monitor this system response should be a high priority.

Many specific research suggestions emerged from the group discussions. It was a consensus from the Food Web II Workshop that to elucidate and understand the effects of bottom-up (phosphorus abatement) and top-down controls (predation) in Lake Ontario, water quality and fisheries agencies must: standardize and calibrate existing monitoring techniques and therefore establish and maintain compatible, long-term, limnological data sets; cooperate on research, e.g. controlled, meso-scale, whole-system experiments, designed to quantify the rates, e.g. growth and predation, of food web interactions with emphasis on an interdisciplinary approach that explicitly accounts for time and spatial scale effects; and promote initiatives which quantify the impact of changes in food web dynamics on the reduction of toxic substances levels in Great Lakes fishes.

Support for these recommendations was given by the IJC in its Third Biennial Report (1986). In that report the IJC recommended that the Parties and jurisdictions, i.e. states and provinces, implement their respective portions of the Great Lakes International Surveillance Plan, which were established to coordinate monitoring and surveillance activities deemed crucial to IJC responsibilities under the 1978 Great Lakes Water Quality Agreement. Further, the IJC recognized the role of research in assessing the consequences of human activities in the Great Lakes Basin Ecosystem and recommended that the Parties and jurisdictions consider the development of appropriate experiments in mid-scale ecosystems, e.g. limnocorrals, ponds and bays, to test the potential application of promising ideas, e.g. the relative influence of top-down and bottom-up controls on water clarity.

As mentioned in the introduction, a fundamental question for management agencies is: "Are the Great Lakes phosphorus management and fishery management strategies compatible?" The phosphorus management strategy has been quite successful at reducing phosphorus loadings to the Great Lakes (Table 1) while the fishery management strategy has been able to increase salmonine populations via stocking (Table 3), creating a high economic return from sport fisheries. These two 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 salmonid sport fishery (alewife provide much of the diet of salmonids). Alewife predation can also control zooplankton and phytoplankton size spectra and species composition and can depress native forage stocks through competition and other ecological interactions. By decreasing phosphorus loads and increasing salmonid predation pressure, the current management strategies may be imposing simultaneous negative feedback pressures on alewife. Another important factor may be the impact of a severe winter, which may periodically overwhelm density dependent controls. An important question is how much stocking and phosphorus control is too much? The answer to this question depends on the relative priorities of management goals, i.e. maximizing fish production, maximizing economic returns, maximizing water clarity and restoring native species.

Coordination among agencies is now more important than ever. The IJC and GLFC have many goals in common but some may be in conflict as a result of fisheries management practices which can affect food web interactions that are expressed in both water quality and contaminant concentrations.

The lessons of Lake Michigan's history and the opportunities of Lake Ontario's future offer unique potential for the closest link between basic research and applied scientific management. We should seize this opportunity, nurture and test it. If we are wrong, we have lost little, for the gains are the same for basic science. If we are right, then we will have gained the basic understanding and enjoyed the success of its application. Given the lags of planning and funding, we urge the IJC to act promptly in implementing a response to this remarkable opportunity.

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APPENDIX I

SUMMARY OF FOOD WEB I WORKSHOP

FOOD WEB REGULATION OF WATER QUALITY IN LAKE MICHIGAN

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Submitted for publication to the
Journal of Great Lakes Research
May 1986

ABSTRACT

During the past 20 years, Lake Michigan has experienced a substantial reduction in nutrient inputs, major changes in the biological community and reconfiguration 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 the consensus of participants in an IJC-sponsored workshop on Food Web Interactions convened in Ann Arbor, 4–6 December 1985. The results of 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.

INTRODUCTION

Recent increases in summer water clarity in Lake Michigan suggest a complex interaction derived from two 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 the 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 the 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, 4-6 December 1985. A more extensive review of the workshop and research recommendations is presented in Evans and Kitchell (MS). We hope that this brief summary can convey a sense of the magnitude of changes occurring in Lake Michigan and the spectrum of forces effecting those changes.

HIGHLIGHTS OF THE CONTRIBUTIONS

Lakewide stock assessment data presented by LaRue Wells (U.S. Fish and Wildlife Service) document the recent, substantial changes in the abundance of fishes in Lake Michigan (Wells 1985). David Jude (Univ. 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 its 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. Increasing predation by salmon, trout and charr is the most parsimonious reason for alewife decline (Stewart et al., 1981).

Hansen (1986) analyzed size distributions of salmonines taken in Wisconsin's sport fisheries since 1969. Although there is evidence of a 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.

Based on extensive surveys of benthos conducted throughout the southern basin of Lake Michigan during the 1960s, Tom Nalepa (NOAA, Great Lakes Env. Res. Lab) designed and conducted a similar program during 1980 as a basis for assessment of changes over the past two decades (Nalepa MS). The 1980 abundance of major benthic species was generally several-fold 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. Larry Crowder (North Carolina State Univ.) 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., MS).

As summarized by Marlene Evans (Univ. Michigan), large zooplankton began to reappear in increasing abundance as the alewife declined in the early 1980s. In particular, the increase of large Daphnia species in offshore waters during the 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 easterly regions. The sustained high abundance of large Daphnia in offshore waters during the summer months remains remarkable in that the recovery of native zooplanktivorous fishes and has not yet had an apparent effect on this typically preferred prey.

Donald Scavia (NOAA, Great Lakes Env. Res. Lab.), 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 John Lehman (Univ. 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 the 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 decades (Barry Lesht, Argonne National Lab.) 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 or more in the past several years (Scavia et al., 1986).

Historical and paleolimnological studies also revealed major shifts in community composition and food web interactions. Art Brooks' (Univ. Wisconsin–Milw.) analysis of phytoplankton community changes determined at the Milwaukee water intake suggest long-term trends in phytoplankton composition that reflect both the changing relative concentrations of nutrients and the effects of altered food web interactions (Brooks et al., 1984). Gene Stoermer (Univ. Michigan) presented results from the 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. Kitchell's (Univ. Wisconsin) review of the 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, 1986). 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. Nevertheless, the species interactions that persisted before alewife invaded are likely developing to some unknown extent in the current plankton community.

DISCUSSION

Controls of Water Quality: A Consensus

Discussion during the presentations and working group sessions evoked a consensus view of the hierarchy and interactions of factors currently controlling water quality in Lake Michigan. The major components are summarized in Figure 1. Spring phytoplankton densities are regulated by a combination of vernal mixing, nutrient loading, and relative nutrient concentrations. Summer phytoplankton densities and composition are controlled by nutrient cycling and grazing by zooplankton. Size-selective predation determines the abundance and size of the zooplankton. Recent reductions 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 large zooplankton. 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 and extend to intense herbivory (Carpenter et al., 1985). 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 the 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 the summer months makes improved water quality most apparent to the public. Recreational use of the lake is most intense during those times when increased water clarity is most obvious. Indicators of nearshore water quality may exhibit the effects of local nutrient sources but the average condition of surface waters will continue to improve as food web effects in offshore waters persist.

Management for the Future

The potential for the enhancement of food web controls over water quality remains poorly known. The current biological community is dominated by interactions among exotic species. Most of the stocked salmonines and the alewife were not native species in the early history of Lake Michigan. The largest cladoceran species (Daphnia pulicaria) which was abundant in the 1983-85 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 Fisheries Commission, plans are now being developed for 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.

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 the public value of Lake Michigan: water clarity during the summer months and fishing are better than ever before in history.

There remain susbstantial 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 been and will continue to be effective in Lake Michigan. Management that regulates food web effects has enhanced 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.

Acknowledgments

First and foremost, we thank the workshop participants. Their contributions and creativity are the basis for this report. We apologize for any misrepresentations developed in this distillate. Second, we thank the IJC for its financial and logistic support to this effort. In particular, we wish to acknowledge those IJC staff members whose aid and enthusiasm were most beneficial: John Hartig, Trefor Reynoldson, Rich Thomas and John Gannon. Much of the planning and report preparation was performed while J.F. Kitchell was on leave from the University of Wisconsin-Madison and in Ann Arbor under joint sponsorship by the NOAA Great Lakes Environmental Research Laboratory and the Great Lakes Fishery Commission.

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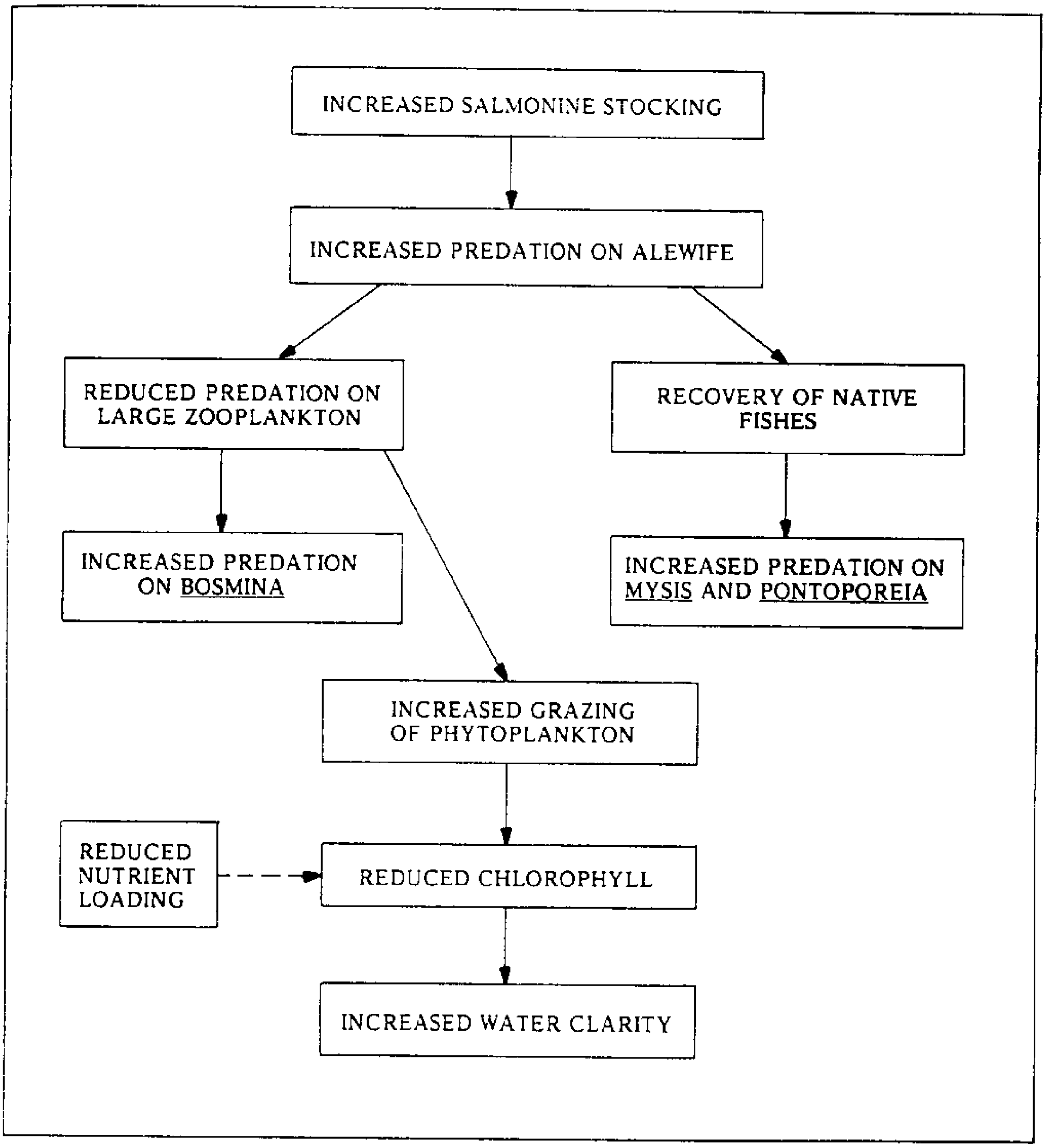


FIGURE 1: Flow diagram of cause-effect interactions expressed during summer conditions in Lake Michigan. Boxes denote direct management actions.

APPENDIX II

ABSTRACTS OF PAPERS PRESENTED AT FOOD WEB II WORKSHOP

WEDNESDAY, FEBRUARY 25, 1987

SEMINAR ROOM, SECOND FLOOR, CORRIDOR:

11:00 a.m. – 12:00 p.m.		*REGISTRATION*

SEMINAR ROOM, SECOND FLOOR:

1:00 p.m.	INTRODUCTION	*J. Vallentyne*
1:10 p.m.	FOOD WEB SUMMARY	*J. Kitchell*
	PRESENTATIONS:	
1:30 p.m.	The Effects of Vertebrate Zooplanktivory on Ecosystem Structure: The Lake Michigan Experience	*D. Scavia*
2:00 p.m.	Response of Lake Ontario to Reductions in Phosphorus Load: 1967–1982	*R. Stevens*
2:30 p.m.	Phytoplankton Community Structural Changes and Their Response to Nutrients and Contaminants	*M. Munawar* *I. Munawar* *L. McCarthy*
2:50 p.m.	Lake Ontario North-Shore Phytoplankton and Nutrient Trends (municipal water intake monitoring)	*K. Nicholls*
3:10 p.m.	Trends in Lake Ontario Open Water Zooplankton	*O. Johansson*
3:30 p.m.	Inshore and Offshore Abundance of Zooplankton, including *Mysis relicta*, Lake Ontario	*J. Makarewicz*
3:50 p.m.	Lake Ontario Benthos: Multiple Roles in Food Web Dynamics	*W. Flint* *P. Sly*
4:20 p.m.	Changes in Forage Fish Populations of Southern Lake Ontario, 1977–86	*B. O'Gorman*
4:40 p.m.	Recent Changes in the Food Web of Eastern Lake Ontario	*J. Christie* *P. Sly*
5:00 p.m.	Salmonine Predator-Prey Dynamics in Lake Ontario	*S. Brandt*
5:20 p.m.		*WRAP-UP*
6:00 p.m. – 8:00 p.m.	*– RECEPTION –* *"THE POACHERS", 436 Pearl Street*	

THURSDAY, FEBRUARY 26, 1987

SEMINAR ROOM, SECOND FLOOR:

9:00 a.m.	Phosphorus Management Strategy for Lake Ontario: What, Why, How Implemented, and Effectiveness	*J. DePinto*
9:30 a.m.	Fish Management Strategy: What, Why, How Implemented, and Effectiveness	*E. Gage*
9:45 a.m.	Theory of Food Web Interactions in Lakes	*S. Carpenter* *J. Kitchell*
10:15 a.m.	A Perspective on Great Lakes Fish Community Rehabilitation	*J. Christie*
10:30 a.m.	Interpretation of Size Spectra in Lakes	*U. Borgmann*
11:00 a.m.	Competition Among Stakeholders on Lake Ontario	*K. Minns*
11:30 a.m.	Developing an Ecosystem Model for Lake Ontario Fisheries	*J. Haynes*
11:45 a.m.	Charge to Groups	*J. Kitchell*
12:00 p.m. – 1:00 p.m.	*– LUNCH –* *C.C.I.W. Cafeteria, on own*	
1:00 p.m.	MEET TO ANSWER QUESTIONS: "Top–Down" Group "Bottom–Up" Group	 *Main Board Room, Room L218* *O S S Board Room, Room R257*
5:00 p.m.		*ADJOURN*
5:00 p.m. – 7:00 p.m.	*– DINNER, on own –*	
7:00 p.m. – 10:00 p.m.	*– EVENING MEETING –* *VENTURE INN, 2020 Lakeshore Road*	

FRIDAY, FEBRUARY 27, 1987

SEMINAR ROOM, SECOND FLOOR:

	PRESENTATIONS:	
9:00 a.m.	"Top-Down" Group	*S. Brandt*
9:45 a.m.	"Bottom-Up" Group	*D. Scavia*
10:30 a.m.	DISCUSSION AND DEBATE	
12:00 p.m.	SUMMARY	
12:15 p.m.		*ADJOURN*
12:15 p.m. - 1:15 p.m.	*- LUNCH -* *C.C.I.W. Cafeteria, on own*	
1:15 p.m.	PLANNING FUTURE FOOD WEB INITIATIVES AND OUTLINE FOR FOOD WEB II REPORT	*(Optional)Steering Committee & Interested Persons*

AUTHOR: Donald Scavia

TITLE: THE EFFECTS OF VERTEBRATE ZOOPLANKTIVORY ON ECOSYSTEM STRUCTURE: THE LAKE MICHIGAN EXPERIENCE

ABSTRACT:

Trends in Lake Michigan water quality over 1975–84 appear to reflect reduced nutrient loadings as indicated by gradual declines in spring total phosphorus (TP) and summer epilimnetic chlorophyll a (Chl a). Deviations from these trends during 1977 and 1983–84 were apparently caused by abiotic and biotic factors, respectively. Prolonged ice cover during 1977 decreased sediment resuspension, resulting in lower TP, reduced CHl a levels, and increased water clarity. A similar dramatic result occurred in 1983 and to a lesser extent in 1984, but via a different mechanism. Burgeoning populations of stocked salmonids reduced populations of the planktivorous alewife (Alosa pseudoharengus), which allowed large Daphnia to flourish. Because the Daphnia are more voracious and more non-selective grazers than the formerly dominant calanoid copepods, they reduced seston concentrations, causing dramatic increases in Secchi disk transparency. These exceptions to the gradual changes demonstrate the far-reaching consequences that unusual weather conditions and fish management practices may have on water quality indicators.

In addition to summer zooplankton changes observed while total P load, P concentration, and abundance of the dominant zooplanktivore, alewife decreased, the substantial summer contribution by filamentous blue-green algae has been replaced by phytoflagellate dominance. Alternative hypotheses of nutrient loading and species interactions as determinants of both zooplankton and phytoplankton summer epilimnetic species composition are developed. We explore these hypotheses with a food web model, calibrated to measured ecosystem components and processes, that simulates gradients of both P loads and predation–competition interactions. We conclude that the summer plankton community is controlled largely by predation effects.

AUTHOR: Robert J. Stevens

TITLE: RESPONSE OF LAKE ONTARIO TO REDUCTIONS IN PHOSPHORUS LOAD: 1967–1982

ABSTRACT:

Total phosphorus (TP) loading to Lake Ontario has declined from 14,600 $t.yr^{-1}$ in 1969 to 8,900 $t.yr^{-1}$ in 1982. Mid-lake spring TP has responded rapidly to these reductions, decreasing at the rate of 1.09 $\mu g.L^{-1}$, from a maximum of 30.6 $\mu g.L^{-1}$ in 1973 to 12.8 $\mu g.L^{-1}$ in 1982. Spring soluble reactive phosphorus (SRP) exhibited a proportionally larger decrease than TP, such that 1982 SRP was 33% of 1973 levels, compared to 42% for TP. A multiple regression equation indicated an 80% response time of spring TP within two years, and a 90% response time within four years. Spring nitrate plus nitrite has increased since 1969 at the rate of 9.5 $\mu g.L^{-1}.yr^{-1}$, causing N:P ratios to increase from 10 to 32. Mean summer epilimnetic TP declined at the rate of only 0.3 $\mu g.L^{-1}.yr^{-1}$ from 1977 to 1982 so that mean summer TP levels now exceed spring TP by 1–2 $\mu g.L^{-1}$. This occurrence suggests that loading to the lake during the stratified period has not shown a similar decline and may be responsible for the lack of a trend in algal biomass indicators during this period.

FIGURE CAPTIONS

Figure 1. Mid-lake zone of Lake Ontario selected for trend analysis

Figure 2. Annual total phosphorus load (mta x 10^3) and spring total phosphorus concentrations ($\mu g \cdot \ell^{-1}$) for the period 1967-1982

Figure 3. Changes in log-transformed spring soluble reactive phosphorus ($\mu g \cdot \ell^{-1}$) in response to changes in log-transformed total phosphorus ($\mu g \cdot \ell^{-1}$) 1969-1982

Figure 4. Mean summer epilimnetic total phosphorus for the years 1969, 1972 and 1976-1982

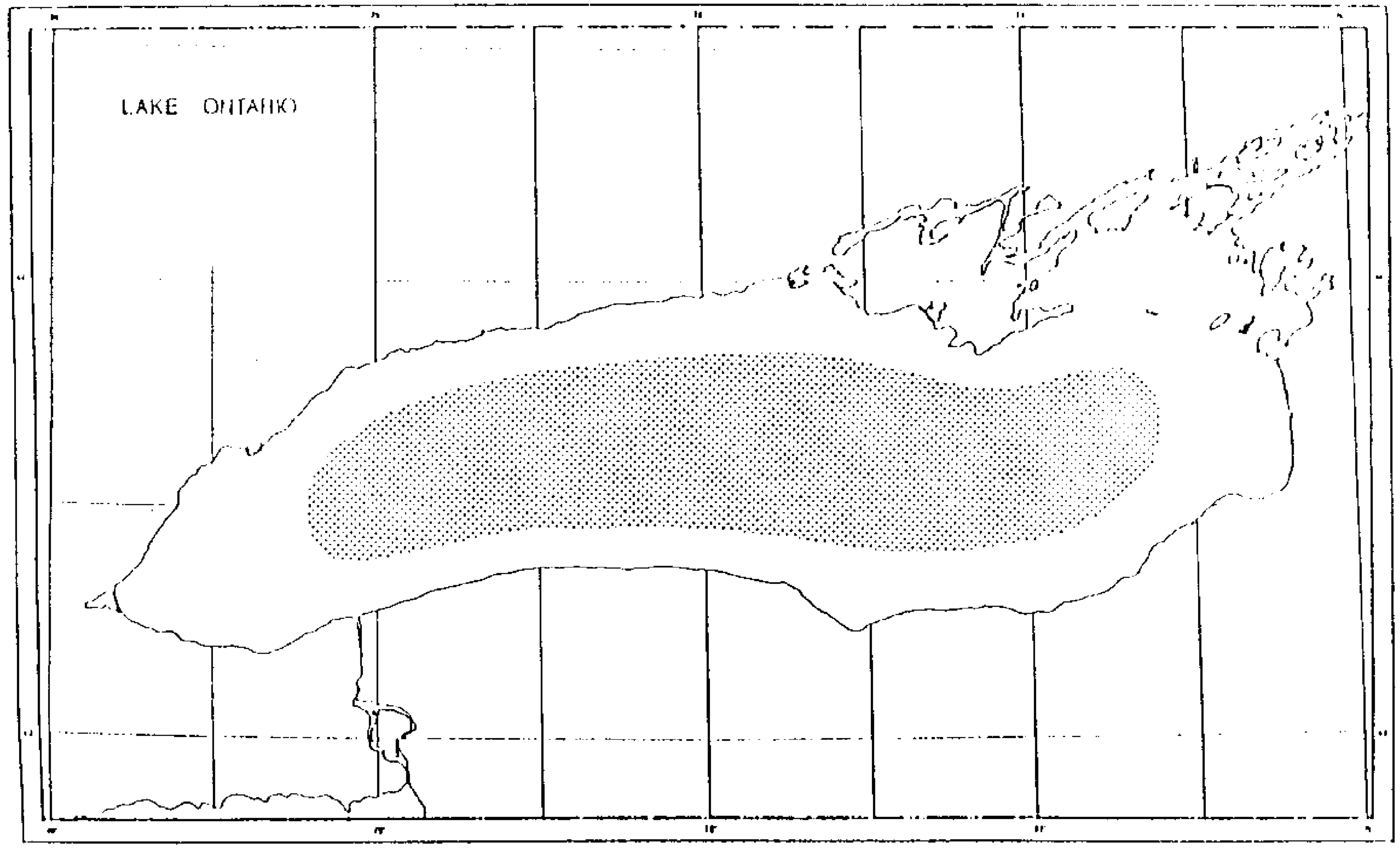
Figure 5. Trend in spring nitrate + nitrite ($\mu g \cdot \ell^{-1}$) from 1969 to 1982 and dissolved organic nitrogen ($\mu g \cdot \ell^{-1}$) from 1972 to 1982. Dashed line denotes the 95% confidence interval of the regression line

Figure 6. Change in spring N:P ratio (N calculated as nitrate + nitrite + ammonia, P calculated as total phosphorus) from 1969 to 1982

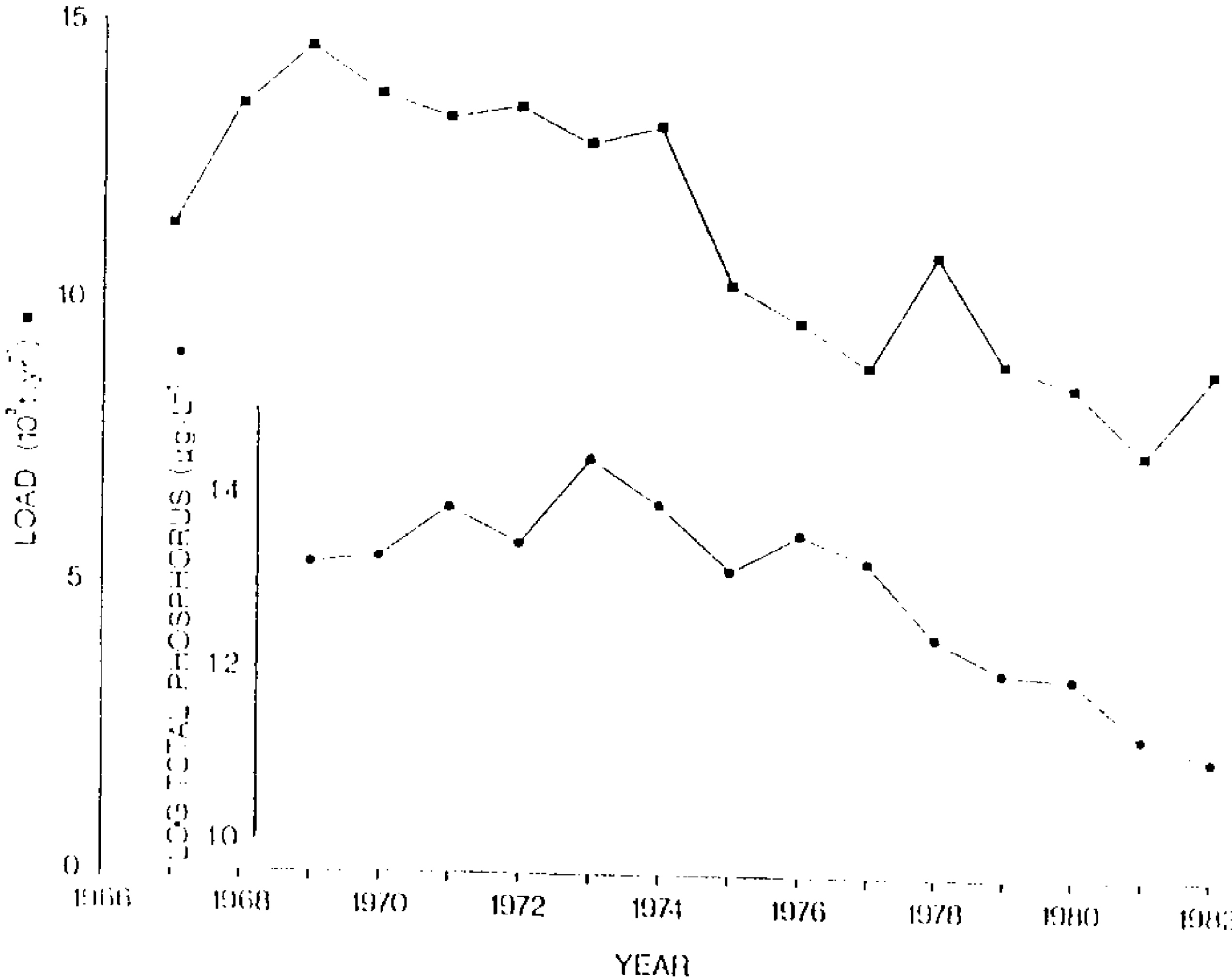
Figure 7. Seasonal distribution of particulate organic carbon, particulate organic nitrogen and chlorophyll a -corrected ($\mu g \cdot \ell^{-1}$) combined for the years 1974 to 1982

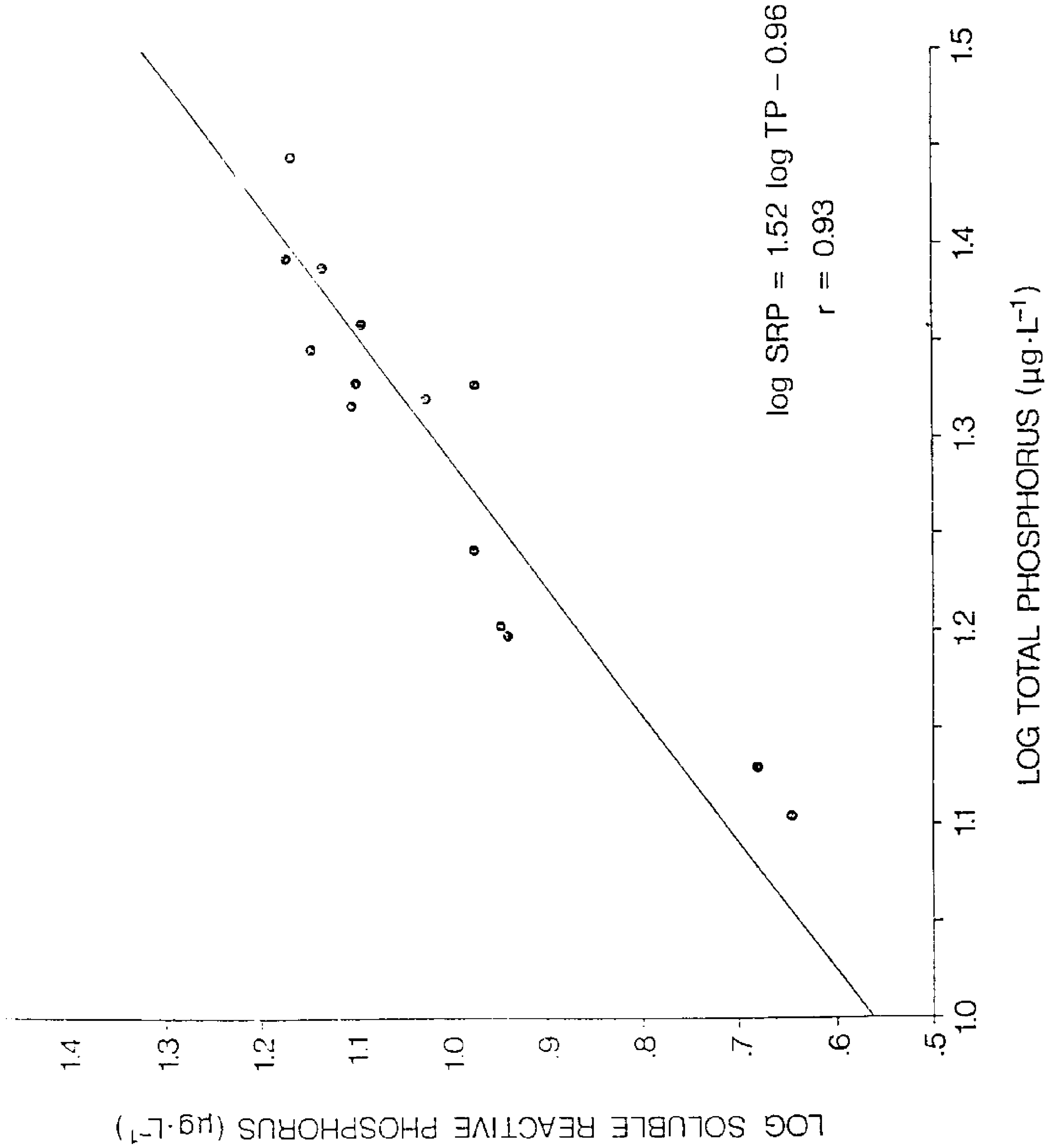
Figure 8. Comparison of Vollenweider's (1976) predicted spring total phosphorus concentrations for Lake Ontario with observed concentrations ($\mu g \cdot \ell^{-1}$)

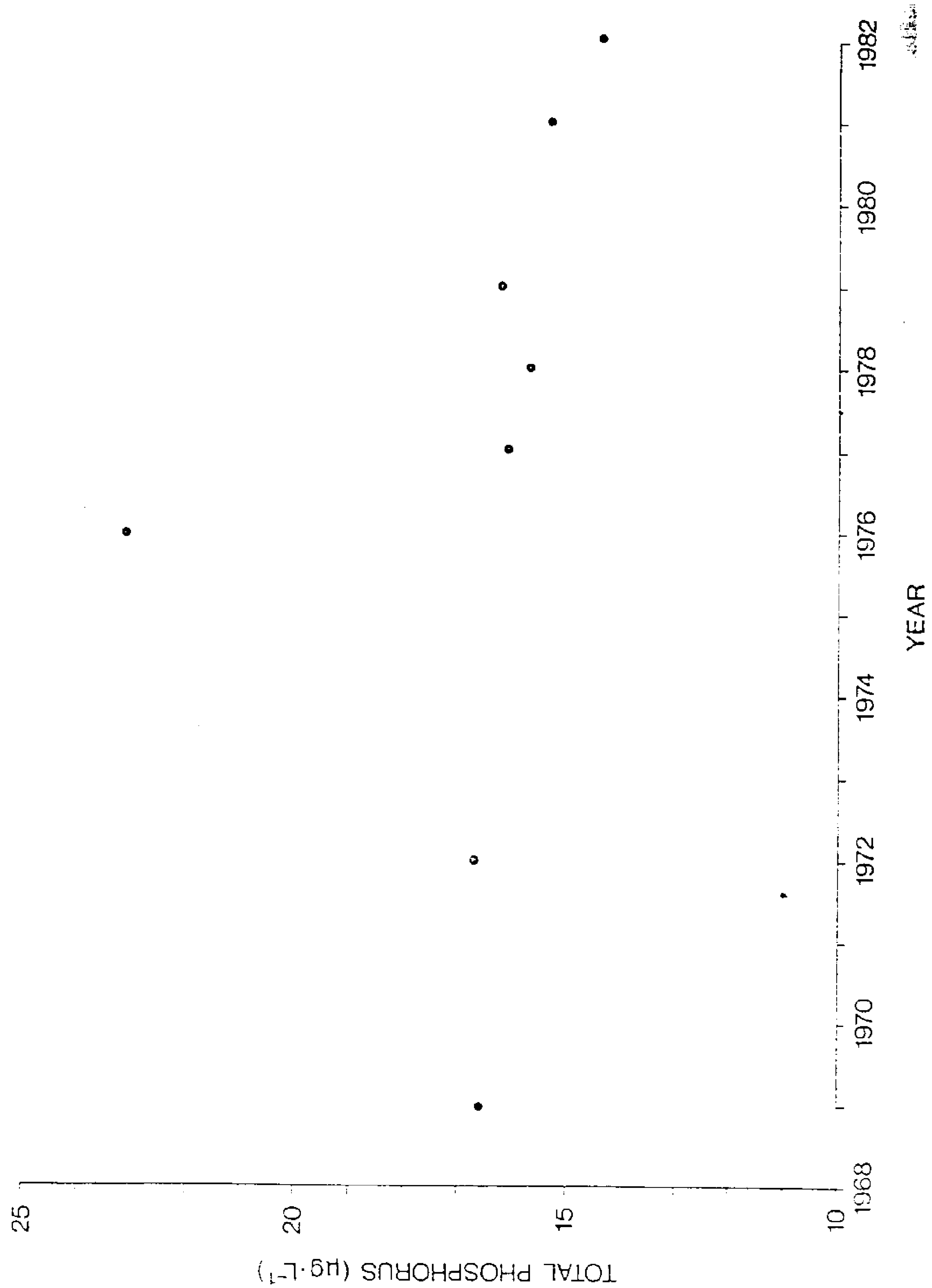
Region of Lake Ontario Selected for Trend Analysis

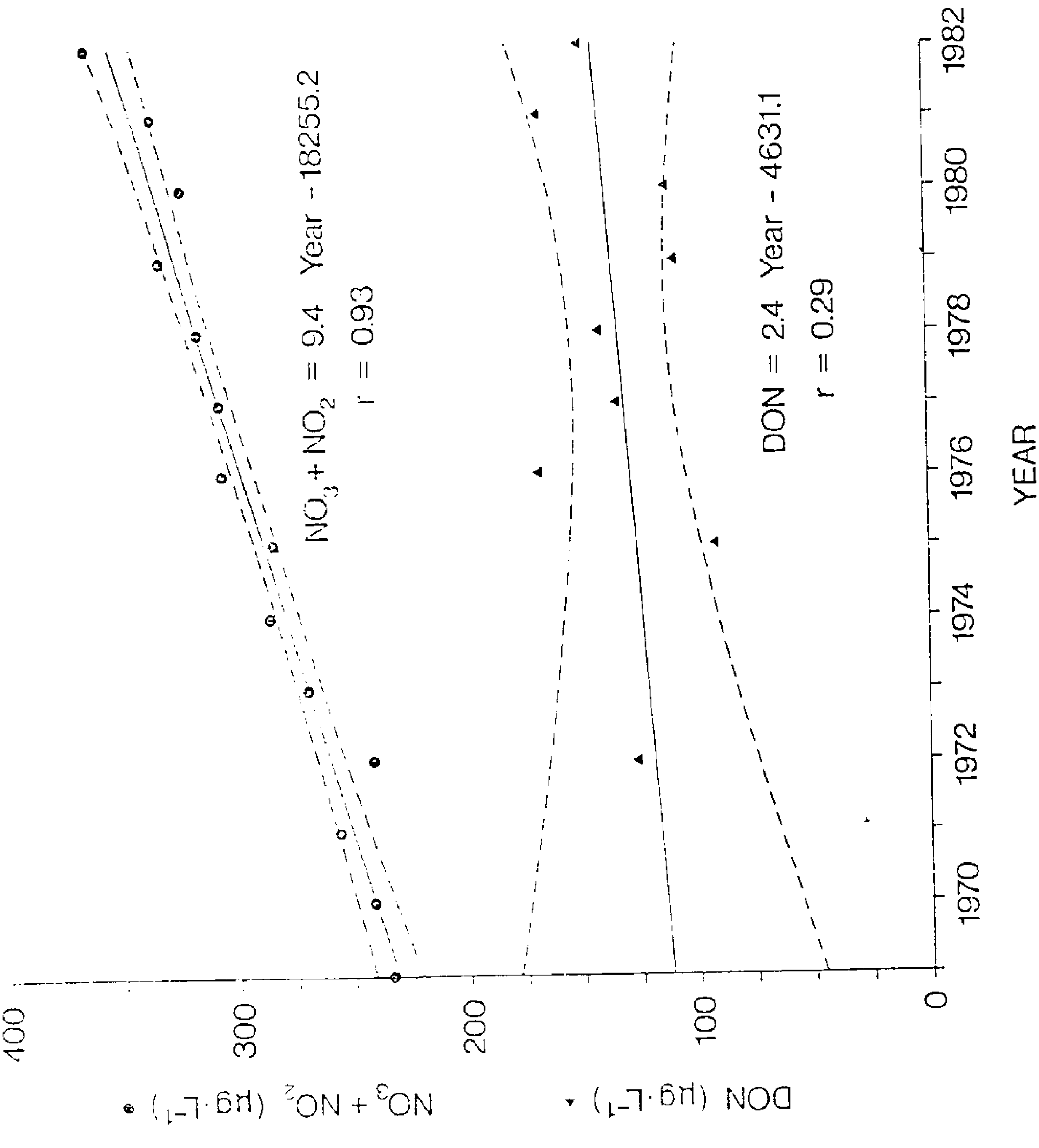


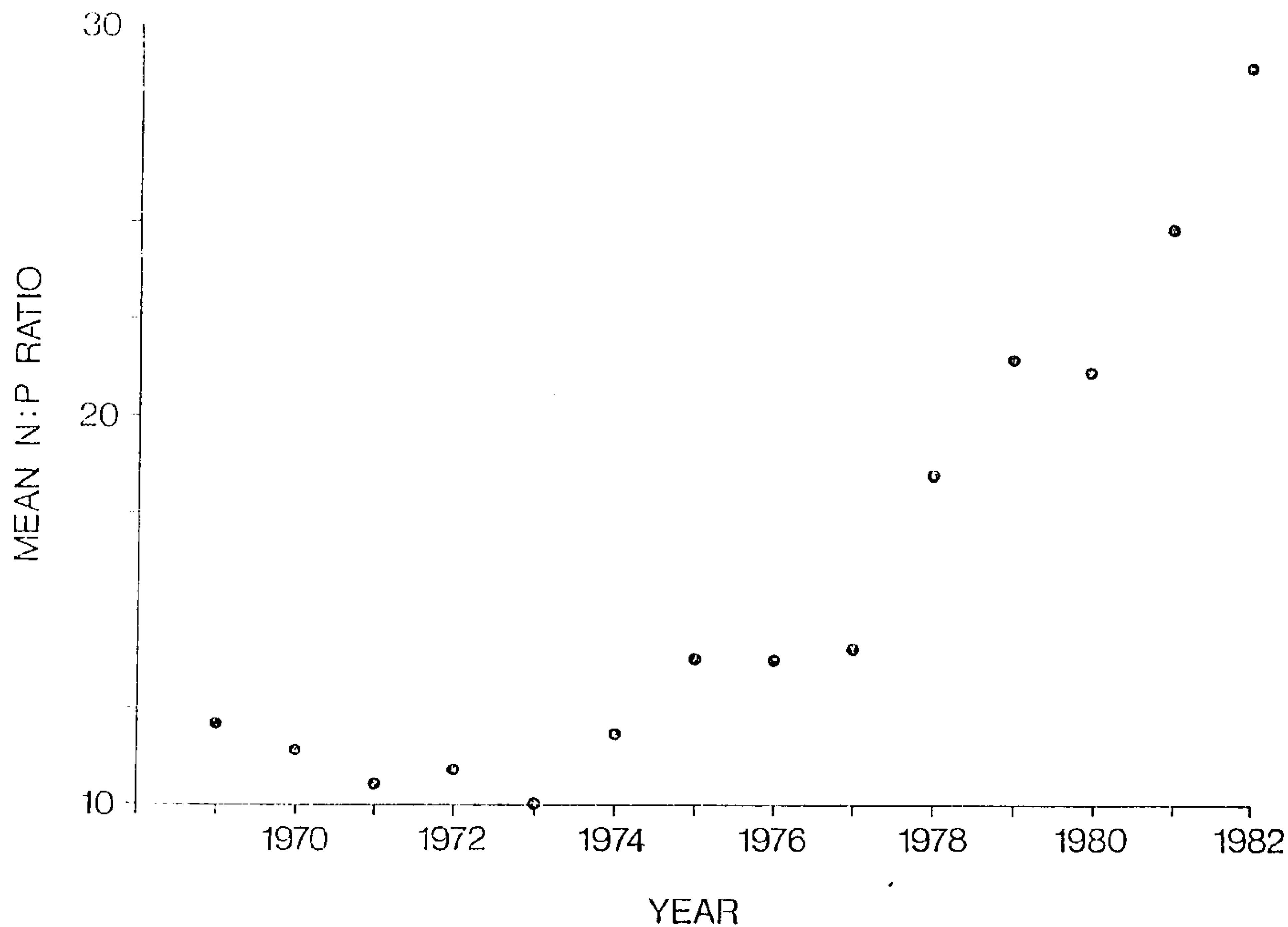
Annual Total Phosphorus Load and Spring Total Phosphorus Concentration 1967-1982

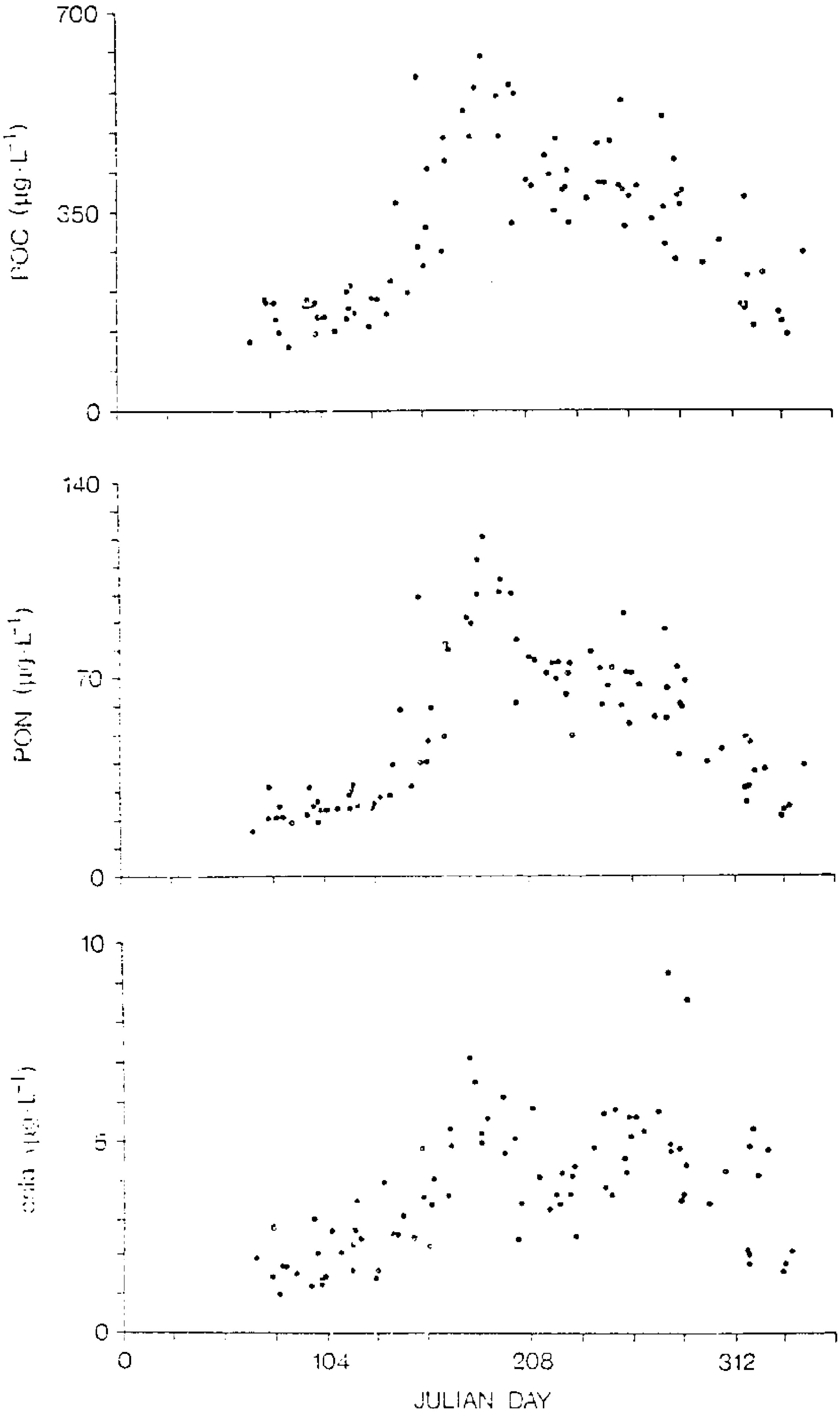


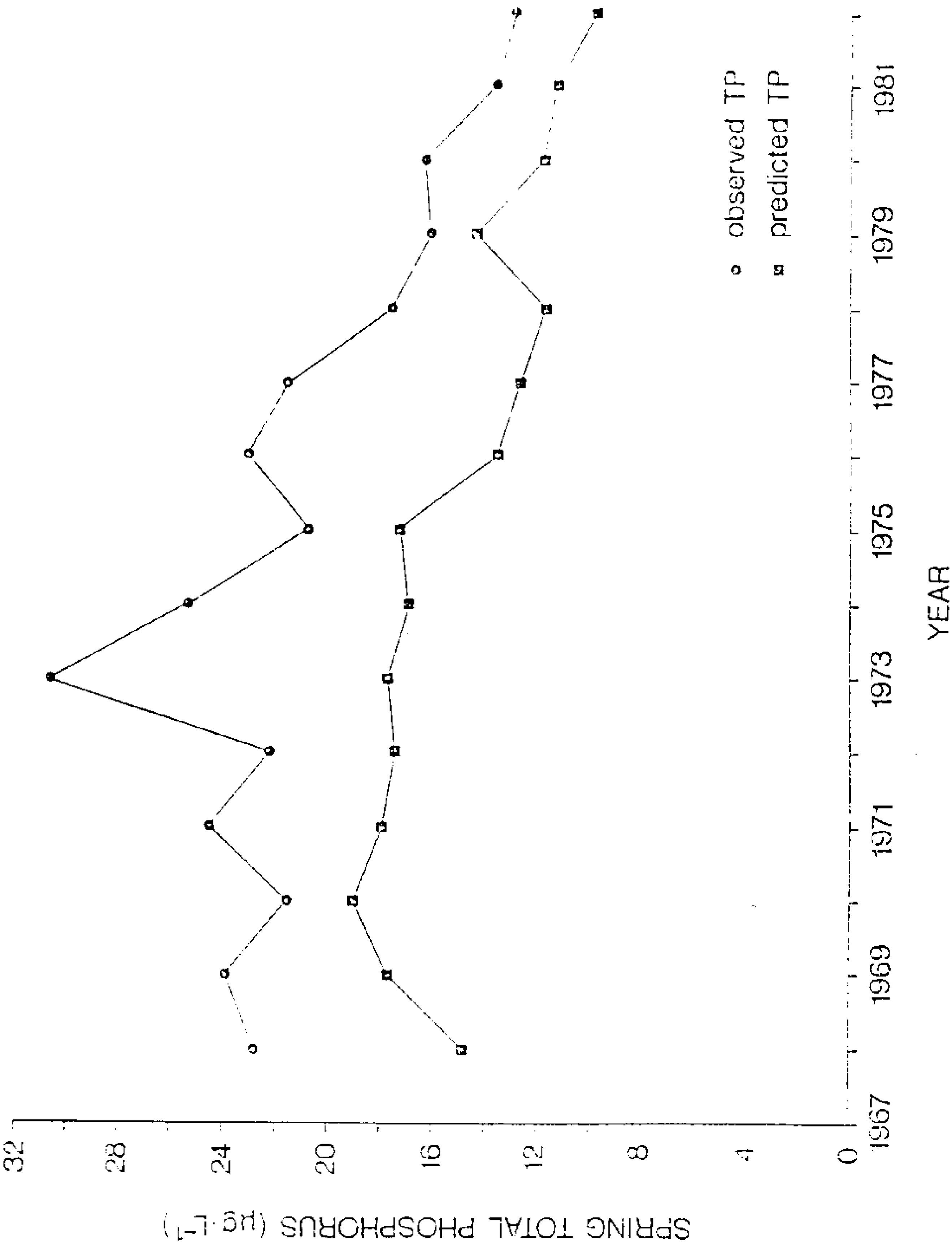

log SRP = 1.52 log TP – 0.96
r = 0.93
LOG TOTAL PHOSPHORUS (µg·L⁻¹)
LOG SOLUBLE REACTIVE PHOSPHORUS (µg·L⁻¹)
1.0
1.1
1.2
1.3
1.4
1.5
.5
.6
.7
.8
.9
1.0
1.1
1.2
1.3
1.4


TOTAL PHOSPHORUS (μg·L⁻¹)
25
20
15
10
YEAR
1968
1970
1972
1974
1976
1978
1980
1982


$NO_3 + NO_2$ = 9.4 Year - 18255.2
r = 0.93
DON = 2.4 Year - 4631.1
r = 0.29
YEAR
1970
1972
1974
1976
1978
1980
1982
0
100
200
300
400
$NO_3 + NO_2$ ($\mu g \cdot L^{-1}$) DON ($\mu g \cdot L^{-1}$)


30
20
10
MEAN N:P RATIO
1970
1972
1974
1976
1978
1980
1982
YEAR


700
350
0
POC (μg·L⁻¹)
140
70
0
PON (μg·L⁻¹)
10
5
0
chla (μg·L⁻¹)
0
104
208
312
JULIAN DAY



SPRING TOTAL PHOSPHORUS (µg·L⁻¹)
0
4
8
12
16
20
24
28
32
YEAR
1967
1969
1971
1973
1975
1977
1979
1981
observed TP
predicted TP

AUTHORS: Mohi Munawar, Iftekhar Munawar, and Linda McCarthy

TITLE: **PHYTOPLANKTON COMMUNITY STRUCTURAL CHANGES AND THEIR RESPONSE TO NUTRIENTS AND CONTAMINANTS**

ABSTRACT:

Phytoplankton analyses in the North American Great Lakes have been carried out since the end of the last century. However, most of the data are not comparable due to the diversity of microscopic techniques and data-processing procedures. Consequently, very little information is available concerning the long-term changes in biomass and its species composition as a result of changing water quality conditions. The standarization of phycological methodology by the Canadian Department of Fisheries and Oceans since 1969 has resulted in a massive phycological and ecological data base essential for exploring the food web dynamics. Long-term community structural changes have been analyzed. Furthermore, the study includes the evaluation of biomass, group and species composition, size spectrum, and size-fractionated primary productivity. These data were supplemented with experimental work on the ecology of ultraplankton-picoplankton. Lake Ontario is presented here as a case study. Its phytoplankton community exhibited changes in its biomass and species composition, consisting of both eutrophic and oligotrophic assemblages. The water quality of the mid-lake station appeared to have improved by 1983. This was confirmed by a higher abundance of ultraplankton and u-algae and high chlorophyll/biomass and P/B quotients. Algal Fractionation Bioassays carried out recently indicated that Lake Ontario ultraplankton and picoplankton which comprise the major food resource for zooplankton were found to be sensitive to metals and metal/nutrient combinations. These results indicate the vulnerability of its food web to nutrient and contaminant pollution, a condition which might have long-term implications for the Lake Ontario ecosystem.

AUTHORS: Ken Nicholls and Gordon Hopkins

TITLE: LAKE ONTARIO NORTH SHORE PHYTOPLANKTON AND NUTRIENT TRENDS (MUNICIPAL WATER INTAKE MONITORING)

ABSTRACT:

For several years, the Ontario Ministry of the Environment has been monitoring nutrients and phytoplankton in the intakes of six municipal water treatment plants on the north shore of Lake Ontario (including one intake downstream of Lake Ontario in the St. Lawrence River). Chemical data have been collected weekly since 1976 at all locations and include total P, dissolved reactive P, inorganic N, total Kjeldahl N, silica, conductivity, chloride and chlorophyll a. The longest records of phytoplankton densities are from Brockville (St. Lawrence River) and Belleville (Bay of Quinte), where two decades of data exist for each location.

Statistically significant declines in total phosphorus concentrations were found at three of the sites and range from <1–2 μg $P.L^{-1}.yr$. Statistically significant increasing trends in nitrate were found over the 10 year period of observation, and the seasonal periodicities (within year changes) were extremely well defined. Nitrate levels were highest during late winter–early spring and declined to their annual minimum by late summer–fall. Silica has consistently been highest during late summer and lowest during the spring phytoplankton growth period, but no long term trends are evident (since 1976). Only the Belleville (Bay of Quinte) intake data have shown significant long term changes in phytoplankton. Recent data from the Bay of Quinte suggest that food chain effects may have been more influential on phytoplankton densities than phosphorus loading reductions. Spring phytoplankton biomass in Lake Ontario's outflow appears to have been controlled mainly by silica levels in late winter.

AUTHOR: Ora Johannsson

TITLE: **TRENDS IN LAKE ONTARIO OPEN WATER ZOOPLANKTON, 1967–1985**

ABSTRACT:

Two strong, contrasting management strategies have been applied to Lake Ontario during the 1970s. There has been a 40 percent reduction in phosphorus loadings to the lake and an exponential increase in salmonid stocking. A comparison of zooplankton community structure and abundance from 1981 to 1985 with that of earlier studies by Patalas 1969; Watson and Carpenter, 1974; and Czaika 1974 found no detectable change in the range of abundances or composition of the dominant community components between the two periods. Clearly neither salmonid culture nor phosphorus reduction has had a discernible impact on the zooplankton community to date.

TABLE 1. ESTIMATES OF AVERAGE ZOOPLANKTON ABUNDANCE BETWEEN JUNE AND OCTOBER FROM 1967 TO 1984, ASSUMING VARIOUS MONTHLY SAMPLING STRATEGIES IN 1981 TO 1984.

YEAR	No. $M^{-2} \times 10^3$ MEAN	S.D	95% CONFIDENCE INTERVAL
1967	3,186		
1970	1,230		
1972	1,245		
1981	1,995	±484	1,027 – 2,963
1982	2,792	±702	1,388 – 4,196
1983	1,682	±317	1,048 – 2,316
1984	1,914	±351	1,212 – 2,616

AUTHOR: Joseph Makarewicz

TITLE: INSHORE AND OFFSHORE ABUNDANCE OF ZOOPLANKTON, INCLUDING MYSIS RELICTA, IN LAKE ONTARIO

ABSTRACT:

Nearshore zooplankton abundance (475 x $10^3/m^3$) was, as expected, considerably greater than the offshore abundance (169 x $10^3/m^3$) in 1984. This was not true for Mysis relicta, which had a greater biomass at the offshore than at the nearshore station. An historical comparison of crustacean zooplankton abundance of the central portion of Lake Ontario suggests that total crustacean abundance has increased from 1967 to 1984. Bosmina longirostris, Cyclops bicuspidatus thomasi and perhaps Diaptomus sicilis plus D. oregonensis have increased in abundance while the abundance of Daphnia retrocurva and Limnocalanus macrurus appear not to have changed between 1970 and 1984. Comparatively, the abundance and species composition of the 1984 zooplankton (Rotifera + Crustacea) community in Lakes Michigan and Ontario are different.

AUTHOR: Peter Sly

TITLE: BENTHOS AS IT RELATES TO THE LAKE ONTARIO FOOD WEB AND TO MATERIAL FLOWS: PART I

ABSTRACT:

Prior to the mid-1940s, Great Lakes Fishery Commission area-weighted catch data indicate that Lake Michigan and Lake Ontario relationships for total fish, herring and chubs, whitefish, and lake trout were 1.8, 2.7, 0.7 and 4.8, respectively. However, morphoedophic index (MEI) values indicate yields/unit area should be more comparable. Differences in planktivore production are not reflected by primary production; estimates for both lakes are about $140 gC/m^2/yr$.

Amphipods are the key vector of benthic carbon and represent nearly 80% of the benthic biomass. Their densities in Lake Michigan are 2-3 times those of Lake Ontario. Since sediment organic carbon contents are similar in both lakes, it is hypothesized that organic carbon availability is less in Lake Ontario. This situation could be related to factors which influence the oxidation of surface sediments.

AUTHORS: Warren Flint and Peter Sly

TITLE: LAKE ONTARIO BENTHOS: MULTIPLE ROLES IN FOOD WEB DYNAMICS

ABSTRACT:

We hypothesize that the benthos of Lake Ontario functions in several ways to affect food webs. The importance of benthic functions is evidenced by the comparison of several system characteristics between Lakes Ontario and Michigan. Prior to 1940, Great Lakes Fishery Commission area-weighted catch data indicated that Michigan/Ontario ratios for total fish, herring and chubs, whitefish and lake trout were 1.8, 2.7, 0.7 and 4.8, respectively. Morphoedophic index (MEI) values, however, indicated yields/unit area should have been more similar. Differences in planktivore production were not reflected in primary production because estimates for both lakes ranged between 140 – 180 g C/m^2/year for phytoplankton. Amphipods were thought to be the key vector of benthic carbon and represented nearly 80% of the benthic biomass in both lakes. Densities in Lake Michigan however, are 2–3 times those of Lake Ontario. Since the sediment organic carbon content is similar in both lakes, it is suggested that organic carbon availability is less in Lake Ontario. This situation could be related to factors which influence oxidation of surface sediments.

Benthic production accounts for approximately 3 g C/m^2/year in Lake Ontario, which represents 30% of all carbon produced by the prey of predatory forage fish. Inclusion of mysid biomass increases benthic carbon production to 39% of the total. Based upon various feeding studies, the benthos provides 20% of all carbon consumed by predatory forage fish and with mysids this increases to 40%. Estimates of benthic production compared with estimates of predator feeding rates suggest that 85% of benthic carbon produced annually is consumed.

Applying Redfield's ratio to Ontario phytoplankton production indicated that 1.7 g P/m^2/year are required to support pelagic photosynthesis. Before phosphorus controls, loading was estimated to be 0.86 g P/m^2/year (1971–72). Thus, based upon data collected over a decade ago and assuming all phosphorus load goes in support of pelagic phytoplankton, only 51% of the phosphorus required to support pelagic phytoplankton production is derived from external nutrient loading. Other potential sources of phosphorus include pelagic recycling and benthic regeneration. The only data available on benthic nutrient regeneration rates in Lake Ontario indicate that 5% of the phosphorus required by phytoplankton can come from the benthos. From estimated pelagic input of carbon to the sediments, the potential for sediment phosphorus regeneration is greater than has been measured to date.

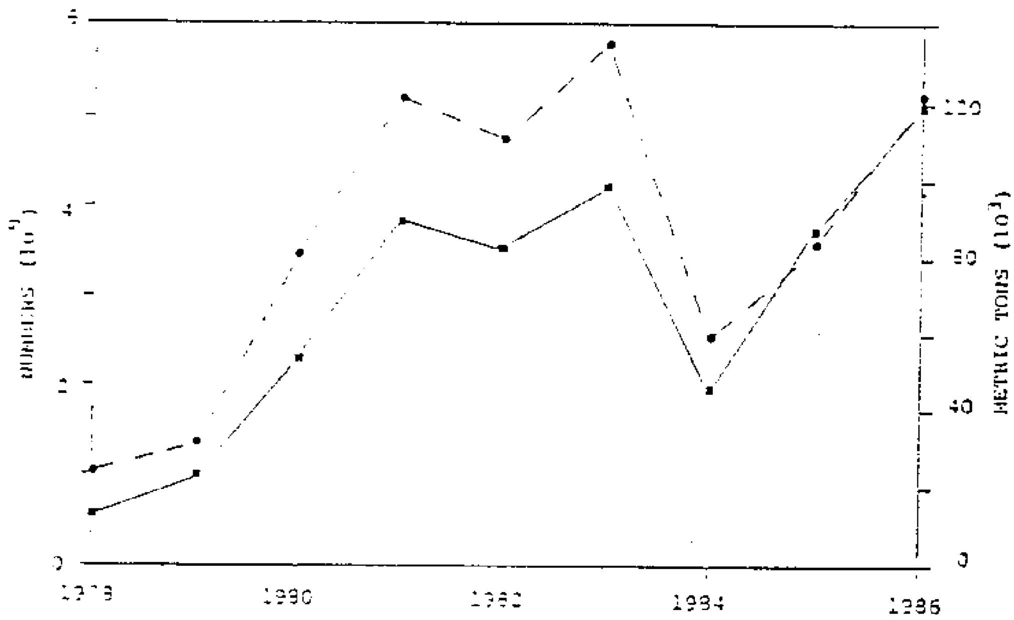
AUTHOR: Robert O'Gorman

TITLE: CHANGES IN THE FORAGE POPULATIONS OF SOUTHERN LAKE ONTARIO, 1977–86

ABSTRACT:

Alewife (Alosa pseudoharengus), rainbow smelt (Osmerus mordax) and slimy sculpin (Cottus cognatus) are major food items of salmonines in Lake Ontario. In U.S. waters, assessments of the three forage species were begun in the late 1970s by the U.S. Fish and Wildlife Service and the New York Department of Environmental Conservation.

The size of the alewife population fluctuated widely during 1977–86 because of two weather related die-offs. The stock collapsed during the winter of 1976–77

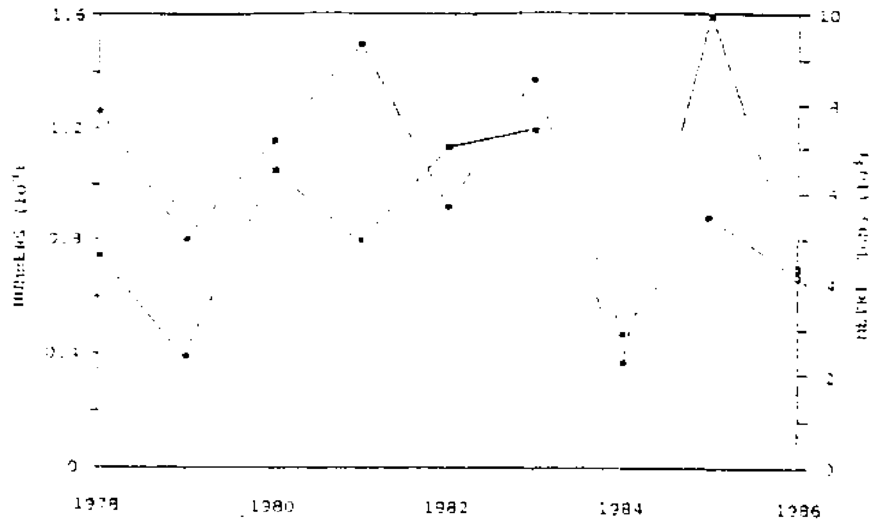


Adult alewives (≥ age II) available to bottom trawls in the U.S. waters of Lake Ontario, numbers (■) and biomass (●).

when unusually harsh weather triggered a severe die-off. The population then rose from low abundance to hyperabundance within four years (1977–81). Abundance remained high through 1983 before another, albeit smaller, die-off in the winter of 1983–84 again sharply reduced the population. Recovery from this mortality was rapid; by 1986, alewife abundance was 120% and biomass 90% of the previous high.

The abundance of yearling alewives varied 16-fold during 1978–85 and yearling survival varied 14-fold. The abundance of yearlings was dependent on the abundance of their parents in a dome-shaped spawner-progeny relation. The survival of yearlings to age II was negatively correlated with the number of adults ($r = -0.93$, $P<0.01$). The growth of young alewives declined steadily during 1978–84.

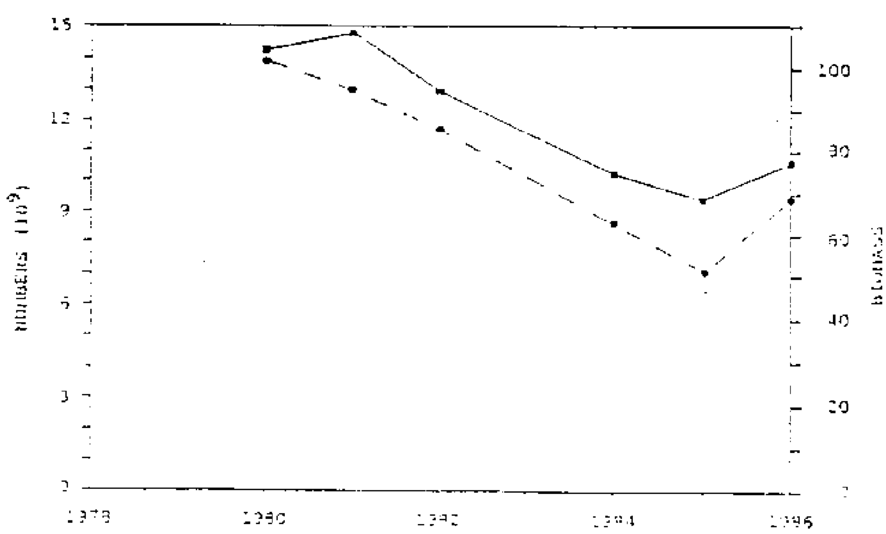
The rainbow smelt population was relatively stable during 1978–83. However, during 1984–86, smelt numbers varied widely and smelt biomass averaged 43% less



Rainbow smelt available to bottom trawls in the U.S. waters of Lake Ontario, numbers (■) and biomass (●).

than during 1978–83. All changes in the smelt population appeared to be caused, either directly or indirectly, by the larger alewife population. The survival of smelt in the third to the fifth years of life was correlated ($\underline{r}$ = +0.80, $\underline{P}$ = 0.06) with the abundance of alewives, i.e. survival was higher when alewives were abundant. The growth of the young, planktivorous smelt slowed as the alewife stock recovered from the 1976–77 die-off, presumably because alewives reduced the zooplankton [length of yearling smelt in June was significantly correlated ($\underline{r}$ = −0.81, $\underline{P}$<0.05) with alewife numbers]. Initially, reduced growth was most apparent among the youngest fish but the cumulative effects gradually reached the older age groups. Slow growth was largely responsible for the lower biomass of smelt in 1984–86. Slow growth also disrupted the mechanism regulating recruitment (predation by intermediate size smelt on young-of-year), causing smelt numbers to fluctuate widely.

The population of slimy sculpins decreased by about one-third between 1981 and 1986. The decline was probably due to predation by juvenile lake trout that have been stocked in large numbers since 1978.



Relative abundance of slimy sculpins in U.S. waters of Lake Ontario, numbers (■) and biomass (●).

AUTHORS: W. Jack Christie and Peter Sly

TITLE: RECENT CHANGES IN THE FOOD WEB OF EASTERN LAKE ONTARIO

ABSTRACT:

This study chronicles major fish species composition changes in the Kingston basin of Lake Ontario since 1960. It details the effect of the commercial fishery on the stocks of older smelt and the effects of exogenous variables on alewife. It describes the growth of lake trout and avian piscivore stocks since the mid 1970s. Slimy sculpin and smelt stocks were both affected by increased predation, and smelt are shown to have compensated. Alewife gained in importance as prey for the lake trout as the other two species diminished. The lake trout were seen to "sample" more young fish than the assessment gear. The main cause of discrepancy is the inability of fishing gear to effectively sample areas of rough or rocky bottom, and a lack of adequate sampling in the mid and upper levels of the water column. The significance of changing predator-prey relationships, limitations imposed by prey abundance, and greater species diversity of major prey stocks are discussed as they relate to fisheries management.

AUTHOR: Stephen B. Brandt

TITLE: SALMONINE PREDATOR-PREY DYNAMICS IN LAKE ONTARIO

ABSTRACT:

Lake Ontario has the highest salmonine stocking rate and the lowest diversity of cold-water prey among the Great Lakes. Numbers of salmonids stocked per annum have tripled since 1979 and overall bioenergetic requirements of these salmonids should continue to rise over the next few years even if salmonine stocking rates are held constant. For the past four years (1983-1986), adult alewife have formed the main prey of all species of adult salmonids (n=4, 550) from April through September. Subtle changes in the size breadth and species composition of the diets of adult salmonids during the last two years appear to reflect changes in prey availability as estimated by systematic bottom trawling by the U.S. Fish and Wildlife Service and the New York Department of Environmental Conservation. A reduction in the condition of adult chinook salmon during 1985 and 1986 may also indicate changes in the quantity or quality of available prey. The overall impact of salmonine predation on prey populations will depend on the bioenergetic requirements of the predators relative to prey production. Prey availability to salmonine predation is in turn largely influenced by environmental factors, prey production, interactions among prey populations and habitat preferences of predators relative to that of potential prey.

AUTHOR: Joseph DePinto

TITLE: PHOSPHORUS MANAGEMENT STRATEGY FOR LAKE ONTARIO: WHAT, WHY, HOW, AND EFFECTIVENESS

ABSTRACT:

Since the late 1960's, regulation of phosphorus loading to lake ecosystems has been considered the primary method of eutrophication control. This general philosophy was adopted in the drafting of the Great Lakes Water Quality Agreement (GLWQA) of 1972. The Agreement contains a specific objective stating that phosphorus concentrations "...should be limited to the extent necessary to prevent nuisance growths of algae, weeds and slimes that are or may be injurious to any beneficial water use." While the phosphorus management strategy for the Great Lakes evolved considerably between 1972 and 1983, the measure of success in eutrophication control has remained the algal biomass levels. In addition to tracing the evolution of the phosphorus management strategy for the Great Lakes in general and for Lake Ontario in particular, this paper attempts to evaluate the success of the program in the lower Great Lakes and its effectiveness in improving Lake Ontario water quality relative to the GLWQA objectives.

There is no question that total phosphorus loads to Lake Ontario have decreased since 1972 (Fig. 1) and that the spring lakewide average total phosphorus concentration has also gone down over the same period (Fig. 2). The question of to what extent this phosphorus management accomplishment is responsible for the phytoplankton response in Lake Ontario, i.e. bottom-up control will be addressed by comparing the observed response to predictions by models that are based upon the premise of bottom-up control.

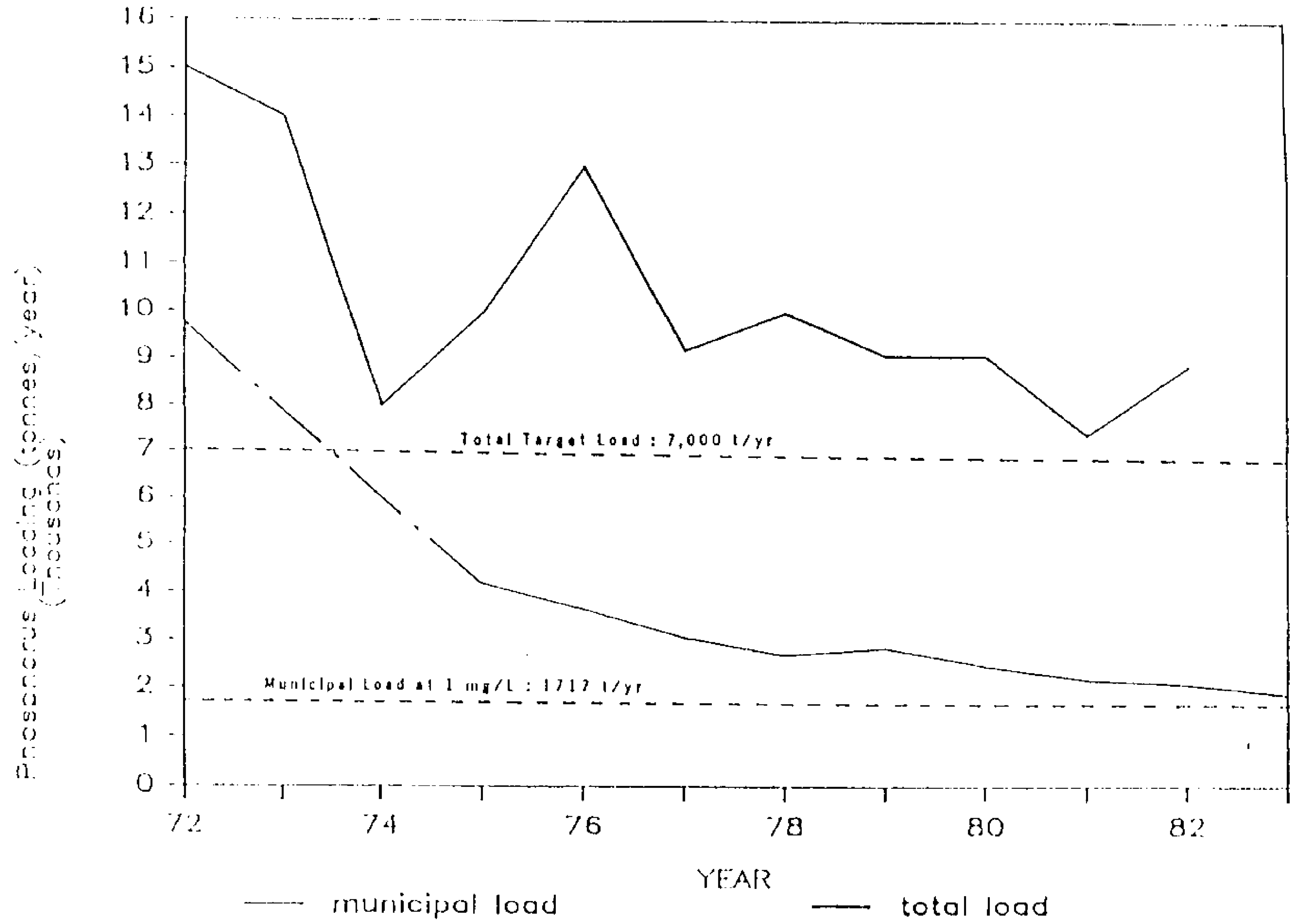


Fig. 1. Annual total phosphorus load to Lake Ontario

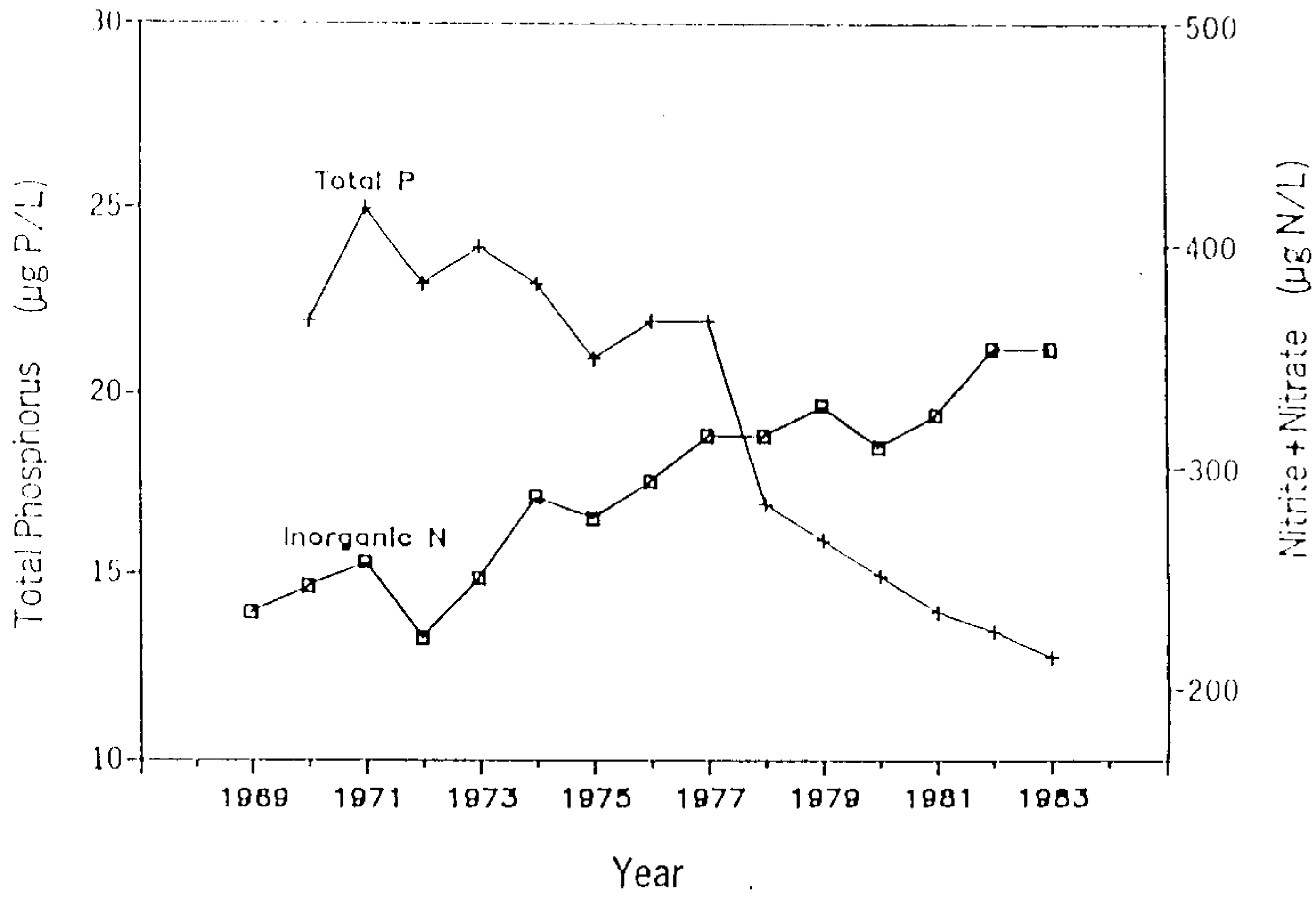


Fig. 2. Spring lakewide average TP and inorganic N in Lake Ontario

AUTHOR: Eric Gage

TITLE: FISH MANAGEMENT STRATEGY: WHAT, WHY, HOW IMPLEMENTED, AND EFFECTIVENESS

ABSTRACT:

New York and Ontario strategies are to protect and rehabilitate fish stocks and the environment for socio-economic benefits. A Joint Lake Trout Rehabilitation plan is the only "whole lake plan." New York has a draft plan; Ontario is preparing one. The New York plan sets production targets geared primarily to the angling fishery. Ontario's plan will probably include targets for both angling and commercial fisheries. The lake trout plan calls for the annual stocking of 2-1/2 million yearlings to produce, by the year 2000, a lake trout stock of 1/2 to 1 million fish, with females averaging 7.5 years. There has been some natural reproduction, but angling and commercial fishing incidental catches are causes for concern, as are losses to sea lamprey. The productivity of the lake is not known. A biomass working group, led by Dr. Jim McLean, expects to report on their findings this year. Preliminary indications are that we have probably reached, possibly slightly exceeded, the appropriate stocking levels of salmonids. The New York strategy has to date been successful in providing a major angling fishery with the resulting socio-economic benefits. The Ontario strategy has not produced as successful an angling fishery as has New York, due to lower levels of salmonid stocking. However, walleye and whitefish populations have increased greatly, and are providing major benefits to Ontario. In summary, although the final chapter is unwritten, the situation has improved during the past decade, and the outlook is promising for the future.

AUTHORS: Steven R. Carpenter and James F. Kitchell

TITLE: THEORY OF FOOD WEB INTERACTIONS IN LAKES

ABSTRACT:

Literature data and our results from a 3-year, 3-lake food web experiment indicate that fish manipulations can cause 5- to 10-fold changes in phytoplankton biomass and production. These food web effects are most evident during summer stratification and can persist for at least several years. Ecosystem responses are most pronounced when substantial changes in the plankton community structure occur. Major and persistent changes in the phytoplankton occur when large daphnids (1.0 to 2.5 mm) appear or disappear from the zooplankton following changes in fish stocks.

Models of the interaction between food web structure and nutrient load yield several surprising and instructive results. Variance in primary production (PPR) derived from meteorological sources depends only weakly on time scale, for time scales >1 year. However, variance in PPR derived from food web effects peaks at a time scale approximating the life span of the top carnivore in the food web. Therefore, spectral analysis can be used to compare top-down and bottom-up effects in long time series. However, correlations of PPR and fish time series are low and variable at time scales shorter than the fish life span, even though fish and phytoplankton are functionally related in the model. At time scales longer than the fish life span, the expected strong correlations emerge.

At intra-summer time scales, the correlation between zooplankton biomass and PPR can be nonsignificant or significant, and positive or negative, depending upon the frequency of sampling. An analysis of zooplankton vs. chlorophyll plots suggests that top-down and bottom-up effects are closely balanced. Episodes of dominance by one force or the other are brief (1-2 weeks), but differ in their persistence. Bottom-up effects, e.g. major storms and nutrient pulses damp away within a stratified season, whereas top-down effects, e.g. major changes in large daphnid biomass may persist for years.

Collectively, these observations indicate that top-down and bottom-up effects on phytoplankton are similar in magnitude and different in time scale. The strong effects of both sampling frequency and duration of the data record caution against the use of multiple regression to measure or forecast food web effects. More insight will come from an approach that explicitly accounts for time scale effects and involves: strong, large-scale manipulations; time series analysis of selected indicators of ecosystem status and/or the paleolimnological record; experimental studies of key interactions; and models.

AUTHOR: Jack Christie

TITLE: **A PERSPECTIVE ON GREAT LAKES FISH COMMUNITY REHABILITATION**

ABSTRACT:

A review of the syntheses suggests that destabilization and subsequent fish community recovery in the Great Lakes are compatible with a model in which post-glacial succession, and the structure and persistence of the fish communities were governed by piscivores. Ecosystem development is interrupted by energy surges and we infer that natural enjuvenation is associated with the characteristically high year-class strength variability observed in many species. Restoration of piscivore densities should improve ecosystem development by favouring large native species at the expense of recently dominant small exotic fishes like alewife and smelt. The effects of eutrophication and over-fishing sequentially reduced the average size and age in the fish communities. One effect of these stresses was an increase in algal densities. We suggest that re-introduction of piscivores reduces inter- and intra- specific competition among prey species in coupled systems. This improves growth rates and reduces the time spent in ontogenetic stanzas where predation is intense, thus conferring competitive advantage on larger fish such as the coregonines. This connection between size and age structure at the community level suggests a model defining community structure in terms of both attributes.

AUTHOR: Uwe Borgmann

TITLE: INTERPRETATION OF SIZE SPECTRA IN LAKES

ABSTRACT:

The biomass-size spectrum models developed so far are useful for estimating the rate of biomass or energy flow up, and the overall slope of the biomass-size spectrum. However, the predicted slope is averaged over multiple trophic levels. The models do not attempt to predict accurately the relative biomass at adjacent trophic levels or how close the system is to steady-state. Ecosystems can deviate substantially from a smooth spectrum and still be at steady-state. Furthermore, the location of the biomass peaks can also vary as predator-prey size ratios vary with the trophic status of the lake. Deviations from a smooth biomass-size spectrum do not, therefore, in themselves indicate an unstable ecosystem. Furthermore, irregularities in the biomass-size spectrum do not necessarily imply an uneven production-size spectrum. Although maximum production at all trophic levels would probably occur if the biomass-size spectrum is relatively smooth, the drop in production which accompanies the decrease in the smoothness of the biomass-size spectrum is expected to be less than proportional to the degree of irregularity in the spectrum.

AUTHOR: Charles K. Minns

TITLE: COMPETITION AMONG STAKEHOLDERS ON LAKE ONTARIO

ABSTRACT:

The paper provides a timely reminder that there is more at stake in Lake Ontario than the trophic interactions of the main lake fish assemblage. The adaptive management methodology is used to examine the complexities of managing a large lake ecosystem. The author contends that perhaps the interactions among stakeholders are more significant than those among the fish species. He argues that the social interactions need to be resolved before proceeding too far with currently perceived "correct" management actions. To date, many of the management actions appear to be at odds with the stated objectives such as (i) "using an ecosystem approach", (ii) "lake restoration", and (iii) "self-sustaining edible fish populations." Clearly management plans for any portion of the Lake Ontario ecosystem need to be developed with due attention to the overall implications.

AUTHOR: James M. Haynes

TITLE: DEVELOPING A TROPHIC WEB MODEL FOR THE LAKE ONTARIO SALMONID FISHERY

ABSTRACT:

Sponsored by the Great Lakes Research Consortium of the State University of New York, fisheries scientists from universities and management agencies will hold a two day workshop after May 1987 to discuss and create a trophic web model for the Lake Ontario salmonid fishery. To the extent possible, non-fish trophic levels will be treated as black boxes that supply relatively constant amounts of energy and materials to fishes. The group will create a qualitative trophic web model for Lake Ontario fisheries and, based on existing data, will attempt to quantify compartment sizes and community interconnections. Quantification efforts will identify gaps in knowledge that must be addressed to complete a trophic web and are intended to lead to cooperative research proposal development. In an attempt to develop a blended basic and applied fisheries research agenda that meets university and management agency needs and promotes cooperative research, the workshop will focus on three questions: What is the abundance and biomass of salmonids and their prey in Lake Ontario; What are the diets and associated forage ratios of salmonids; and What are the temporal and spatial distributions of salmonids and their prey and how do these factors affect trophic web relationships? Attendees at the IJC Food Web II workshop and others are asked to provide published and unpublished data, particularly long term data sets, that may be useful in creating and quantifying the salmonid fishery trophic web model. Useful materials would include reprints, technical reports, unpublished summarized data or references to any of these sources. Please contact Dr. Haynes immediately about relevant data you may have or of which you are aware.

APPENDIX III

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